

Grazer–resource interactions in the plankton: Are all daphniids alike?

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Abstract

Daphniids have long been considered to be uniquely effective grazers in the planktonic food web of lakes, but whether all daphniid species are equivalent in this functional role is less clear. In particular, a common belief that large-bodied daphniids are more capable than smaller daphniids at controlling phytoplankton abundance has received limited testing. Using whole water column enclosures in a mesotrophic lake, we compared the ability of four common planktonic daphniids (*Ceriodaphnia reticulata*, *Daphnia ambigua*, *Daphnia mendotae*, and *Daphnia pulicaria*) to exploit a natural assemblage of phytoplankton. We established replicated monocultures of each daphniid species and allowed their populations to reach a carrying capacity determined by resources. We then compared the effects of each daphniid species on phytoplankton biomass, size structure, taxonomic composition and C:N:P stoichiometry. Populations of all four daphniids stabilized at very low birth and death rates, with larger species having a lower density but a higher biomass than smaller species. The seston C:P molar ratio was driven to equally high values (>300) in all treatments; however, daphniid effects on phytoplankton abundance and composition were quite different. The two smaller daphniids were less effective at depressing phytoplankton populations than were the two larger daphniids. This difference was associated with the persistence of a diverse assemblage of digestion-resistant green algae in the *Ceriodaphnia* and *D. ambigua* treatments but their elimination from the *D. mendotae* and *D. pulicaria* treatments. Several lines of evidence, including growth bioassays, that have used juveniles of a clone of *D. pulex-pulicaria*, suggest that body size was not an adequate explanation for these differences in daphniid species effects on phytoplankton.

Our understanding of plankton food webs is grounded on a rich literature that describes mechanisms of consumer–resource interactions, indirect effects, and nutrient recycling (Kerfoot and Sih 1987; Carpenter and Kitchell 1993; Vanni and Layne 1997). Incorporation of these mechanisms into predictive models, however, has proved difficult. A recurring problem is the significance of functional diversity within trophic levels, particularly at the level of producers and their consumers. In this regard, it is remarkable how often one

reads the words “large *Daphnia*” in literature that describes food webs with a strong coupling of grazers and producers (Vanni and Temte 1990; Mazumder 1994; Pace and Vaque 1994; Cottingham et al. 1997).

Large daphniids seem to be uniquely effective grazers of phytoplankton in freshwater lakes of the world. Whether or not this group is dominant can determine relationships among chlorophyll *a*, nutrients, phytoplankton diversity, and the magnitude of trophic cascades (Pace 1984; Leibold 1989; Mazumder 1994; Proulx et al. 1996). But what exactly are large *Daphnia*, and why do they differ in trophic role from other plankton grazers? Clearly, foraging mode explains much of their ecological dominance; daphniids are generalized foragers that consume a broader range of particles than rotifers, copepods, and some other cladocerans such as the Bosminiidae (Vanderploeg 1990). Also, filtration rate and range of particle sizes increase with body size (Knoechel and Holtby 1986; DeMott 1995). Hence, large daphniids effectively create a food chain out of what would otherwise be a web of interactions between more specialized grazers and their diverse food base.

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However, there are other generalized, filter-feeding cladocerans of equally large body size, (e.g., *Holopedium*), that do not appear to be capable of fulfilling the same functional role as large *Daphnia* (Tessier 1986). It has recently been suggested that the uniqueness of large daphniids is due to their high phosphorous content, which allows a high rate of growth and a low rate of phosphorous recycling (Sterner 1990; Carpenter et al. 1992; Elser et al. 1996). But the limited data on zooplankton stoichiometry indicates that some small daphniids (e.g., *Ceriodaphnia*) are even higher in phosphorous content than large daphniids (Hessen and Lyche 1991). In fact, although the evidence is clear that daphniids are somehow superior in the ability to exploit diverse assemblages of phytoplankton, the general significance of their size is more ambiguous. Larger size does allow capture of larger particles, but in most lakes the bulk of the phytoplankton is small (Carrick and Schelske 1997) and equally grazed by small and large daphniids (Cyr and Pace 1992). And in lakes dominated by large phytoplankton, large grazer size may prove disadvantageous via increased susceptibility to clogging interference (Gliwicz and Lampert 1990). Furthermore, some studies report strong grazer control of phytoplankton when small or medium-sized daphniids are present (Vanni 1987). And at least one study found no difference between small *Ceriodaphnia* versus large *Daphnia* assemblages in control of phytoplankton or ability to produce a trophic cascade in response to fish (Turner and Mittelbach 1992).

In the present study, we experimentally examined the relevance of daphniid body size in determining grazer-phytoplankton interactions in a mesotrophic lake. Our approach was simply to establish replicate monocultures of each of four different-sized, daphniid species in lake enclosures, allow them to reach carrying capacity, and then compare their impact on the phytoplankton assemblage. We consider effects on phytoplankton biomass, size structure, taxonomic composition, and stoichiometry. Although simple, this experimental approach has rarely been employed in plankton ecology (but see Schoenberg and Carlson 1984). Among the wealth of lake-enclosure studies, nearly all use a single, typically mixed assemblage of grazers or create different grazer treatments by manipulation of fish presence, which has confounding direct and indirect effects on the phytoplankton (Vanni and Layne 1997). Comparisons of individual species of grazers interacting with their food are mostly short-term experiments that allow very limited time for compensation in the phytoplankton assemblage (Bergquist et al. 1985; Knisely and Geller 1986). Such short-term measures may not predict longer-term interactions, given the likelihood of direct and indirect effects on nutrients (see Sarnelle 1997 for similar comments).

Methods

Study system—We isolated four species of daphniids, representing a broad range of body size, from the pelagic regions of local lakes. *Ceriodaphnia reticulata* and *Daphnia ambigua* are small forms that occur in shallow lakes having high risk of visual predation from fish (Tessier and Welser

1991). *Daphnia pulicaria* and *Daphnia mendotae* are larger forms that occur in deeper, dimictic lakes and use diel vertical migration to minimize fish predation (Leibold and Tessier 1991).

We conducted the experiment in a partial winterkill lake (Duck Lake, Kalamazoo Co., MI), because such lakes typically have low densities of large grazers. The zooplankton community is composed largely of *Bosmina* and small copepod species, in addition to numerous rotifers, but *Ceriodaphnia* and *Diaphanosoma* are also present. This composition reflects the high densities of planktivorous fish in the open water of these lakes, caused by the absence of any strongly piscivorous species (Tonn and Magnuson 1982). Consequently, the Duck Lake phytoplankton assemblage is diverse and dominated by small forms that we suspected would be relatively vulnerable to larger and effective grazers such as the daphniid species used in our treatments. Duck Lake is small (3.5 m max. depth, 11.7 ha surface area) monomictic, and mesotrophic (total phosphorus = $0.57 \mu\text{M}$, total nitrogen = $40 \mu\text{M}$). The total (water plus seston) N:P molar ratio (~ 70) suggests phosphorus is the limiting nutrient for phytoplankton in this shallow lake, but the seston C:P molar ratio in summer remains < 150 (A. J. Tessier unpubl. data), which suggests that phosphorus does not limit zooplankton (Urabe and Watanabe 1992).

Experiment—On 14 July 1997, we set up eight 3,000-liter clear polyethylene mesocosms (1 m^2 surface area, 3 m deep), as two spatial blocks each containing four mesocosms, sealed at the bottom and open at the lake surface. The mesocosms were filled with lake water pumped from the 1.5-m depth and screened through a $100\text{-}\mu\text{m}$ mesh. Cultures of each of four daphniid species had been raised in the laboratory in filtered lake water (see Tessier and Consolatti 1991 for general culture methods). Species cultures were separately concentrated by use of an $80\text{-}\mu\text{m}$ mesh and transported in gallon containers to the field for stocking the experimental mesocosms on 15 July. One replicate of each of the four species treatments was assigned to each mesocosm in each block. Initial stocking densities were greater for the small species and were designed to achieve similar stocking biomass. Beginning on 16 July (=day 1 of experiment), we sampled the mesocosms at 3–7-d intervals during midday. Weekly temperature profiles revealed $\leq 0.5^\circ\text{C}$ temperature variation with depth; daphniids were observed using the entire water column in all treatments.

Zooplankton were sampled by a single vertical tow from mesocosm bottom, by use of a Wisconsin bucket net ($80\text{-}\mu\text{m}$ mesh), after mixing with a Secchi disk. Each net tow filtered 22 liters, as calibrated against Schindler trap samples, out of the 3,000 liters of water in each mesocosm and, therefore, was a negligible source of mortality ($< 1\%$). The total number of daphniids in each tow was counted on each sampling date. On four dates after day 20 we also counted total eggs to determine egg ratios and estimate birth rate (water temperatures were $22 \pm 1^\circ\text{C}$ throughout the experiment, giving an egg development time of 2.25 d; Bottrell et al. 1976). After day 20, when daphniid population sizes had largely equilibrated (see Results section), we measured zooplankton biomass as ash-free dry mass of animals retained on $120 \mu\text{m}$

(*Ceriodaphnia* and *D. ambigua*) or 250 μm (*D. mendotae* and *D. pulicaria*) mesh screens. Size structure of the daphniid populations was determined by measuring total body length on 60 animals from each mesocosm (=120 animals per species treatment). We estimated daily filtration rates of the different daphniid populations from a body length–filtration rate equation (Knoechel and Holtby 1986). Size structure data was also used to calculate population biomass from body length–biomass equations in Bottrell et al. (1976), to compare with the ash-free dry mass estimates from screened samples.

Water for seston analysis was sampled from each mesocosm by a grab sample at 1.5-m depth. A 1-liter sample was fixed with acid-Lugol's solution and concentrated by settling for determination of phytoplankton composition and abundance by microscopic examination at $\times 250$ –450. We determined Chl *a* (total and $<35 \mu\text{m}$) and particulate organic matter ($<62 \mu\text{m}$ to remove grazers) by filtering samples onto glass-fiber filters (Gelman A/E). Chl *a* was extracted in 95% ethanol and measured by use of narrowband fluorometry (Welschmeyer 1994). Ash-free dry mass of the seston $<62 \mu\text{m}$ was determined after muffling at 500°C , and an empirical calibration was used to convert these values to carbon equivalents (A. J. Tessier unpubl. data). On four dates after day 20, particulate phosphorus was measured (persulfate digestion followed by molybdate reaction) on seston collected identically to that for particulate organic matter. On day 34 we also measured particulate nitrogen on seston collected identically to that for particulate organic matter and phosphorus, using a Carla-Erba C:H:N analyzer.

In several treatments, the quantity of seston remained high relative to minimum carbon demands of daphniids fed high quality algae in the lab. Hence, as an estimate of seston quality, we conducted growth rate bioassays on days 19–23 and 32–36 using a hybrid clone of *D. pulex-pulicaria*. The bioassays measure juvenile specific growth rate under standardized laboratory conditions, but with use of the natural seston collected from each mesocosm (Tessier et al. 2000). Each bioassay was started with 10 *D. pulex-pulicaria* neonates per mesocosm with an additional ~ 15 harvested to determine initial dry mass. On each day, the juveniles were changed to freshly collected water ($<80 \mu\text{m}$) from the mesocosms until age 4 d, at which point animals were harvested for dry mass measurement. We expressed specific growth as the difference between natural log of initial and final dry mass, divided by 4 d (units = $\mu\text{g} \mu\text{g}^{-1} \text{d}^{-1}$).

Statistical analysis—Our primary interest was to contrast the impact of the daphniid species on their resources during the period when grazer densities had equilibrated at carrying capacities (i.e., $r \approx 0$). A period of density equilibrium was achieved in three of the daphniid treatments (*Ceriodaphnia*, *D. mendotae*, and *D. pulicaria*) after day 20, and the fourth treatment, *D. ambigua*, exhibited a peak and moderate decline during this period (Fig. 1A). Hence, although we graphically present data from all sampling dates, we used only data collected after day 20 in statistical testing. We ran univariate, repeated-measures, analyses of variance to compare treatments. Unless otherwise noted, within-species effects (i.e., day and day \times treatment interaction) were not

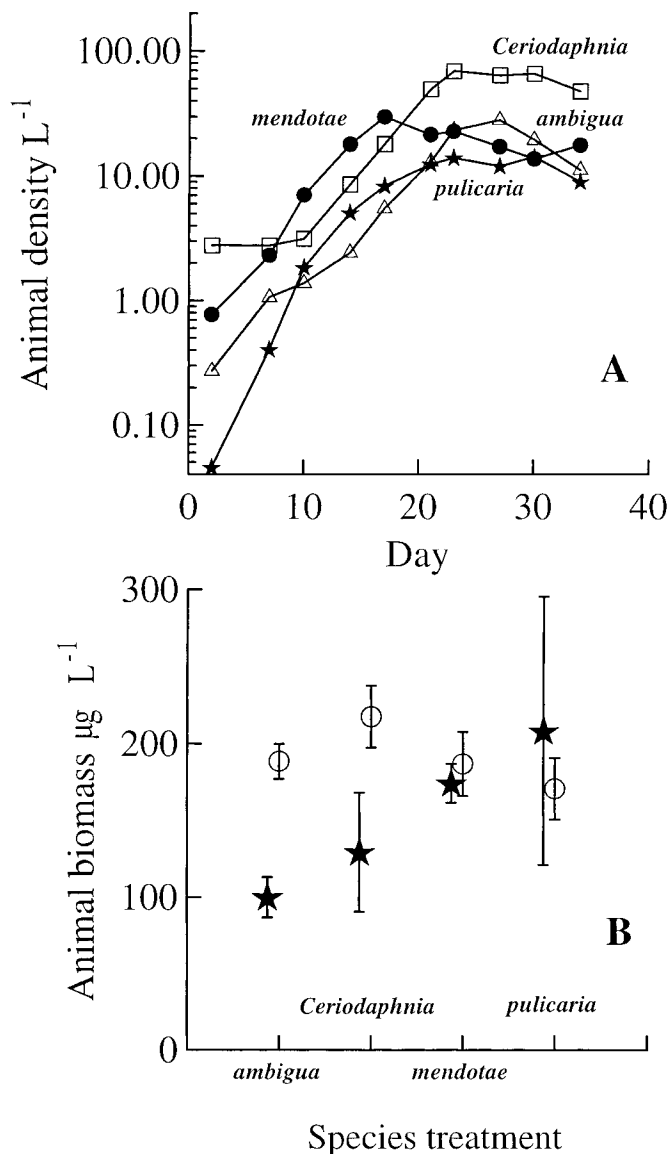


Fig. 1. (A) Daphniid abundance throughout the experiment and (B) dry mass after day 20, i.e., at grazer carrying capacities, for each daphniid treatment. Abundances reflect means of two replicate mesocosms per treatment on each date. Dry mass means \pm S.E. are based either on dry weights of screened samples (open circles, $n = 8$) or calculations from body size distribution and population density (stars, $n = 2$) of individual mesocosms measured after day 20.

significant, and so we report only between-species, treatment tests.

Because the multiple measures of seston quantity and quality were strongly correlated with one another, we used a principal components analysis (PCA) to synthesize these variables into a single measure of resource richness. We ran the PCA on the correlation matrix of particulate organic carbon, particulate phosphorus, Chl *a* $<35 \mu\text{m}$, and bioassay growth rate and used the first PCA axis in a repeated-measures analysis to contrast treatments.

Changes in the abundance of all major phytoplankton taxa were examined graphically and categorized by population

growth (r) responses to each grazer treatment (e.g., increasing, decreasing, or unchanging). Additionally, we used abundance data on the 25 most common taxa from all sampling dates to ordinate the samples to two dimension using multidimensional scaling (MDS; performed on the Euclidean distance matrix of ln-transformed abundances). Ordination axes were interpreted from correlations with each phytoplankton taxon, and sample scores were examined graphically to describe phytoplankton dynamics and treatments differences. We also used MDS scores for dates after day 20 in a repeated measures analysis to formally test for treatment differences. All statistical analyses were conducted with use of Systat version 9.

Results

Zooplankton treatments—All daphniid populations grew exponentially 1.5–2 orders of magnitude, until day 18–20 of the experiment, at which time they stabilized at densities distinct for each species (Fig. 1A). *D. ambigua* was a slight exception in that it continued to increase until day 26 and then declined toward the end of the experiment. During this period of fairly stable population densities, per capita birth rates were uniformly low for all daphniids ($b = 0.045 \text{ d}^{-1}$ with 95% confidence intervals [CI] of all 32 observations = 0.026–0.064). Because r over this period was low, death rates had to be low. Hence, populations reached carry capacities set by resources.

Densities of smaller species equilibrated at higher levels than those of larger species, but screened samples indicated that a similar dry mass of grazers was reached in all treatments ($\sim 200 \mu\text{g L}^{-1}$; Fig. 1B). Species treatments differed greatly in body length distributions so as to form a gradient in mean and maximum body lengths (Fig. 2). Biomass calculated from size structure and density was inconsistent with biomass directly measured on screened samples (Fig. 1B). Screened samples greatly overestimated biomass for the two small species (with use of a 120- μm mesh) but not the two large species (with use of a 250- μm mesh). We suspect that collection of phytoplankton on the smaller-mesh screen inflated measures of biomass of the two small species.

We combined data on body length distribution with our estimates of mean population densities during the last 18 d of the experiment (i.e., period of relative stability) to estimate a daphniid clearance rate for each enclosure (Knoechel and Holtby 1986; expressed as percentage of the total water volume filtered per day). *Ceriodaphnia* and *D. ambigua* had similar and lower filtration rates ($18.4 + 4.3 \text{ SE}$ and $20.1 + 3.2 \text{ SE}$ percentage of water volume, respectively), compared with *D. mendotae* and *D. pulicaria* ($32.6 + 2.2 \text{ SE}$ and $40.1 + 2.9 \text{ SE}$ percentage of water volume, respectively). These differences are significant ($F_{3,4} = 10.4$, $P = 0.023$) and suggest that small daphniids imposed less grazing pressure on the phytoplankton than large daphniids.

Phytoplankton quantity and quality—Chl a concentration decreased, essentially by 50%, in all enclosures during the first week of the experiment (Fig. 3). Surprisingly, it rebounded substantially during the next 2 wk as grazers reached peak densities. Total Chl a displayed an oscillatory

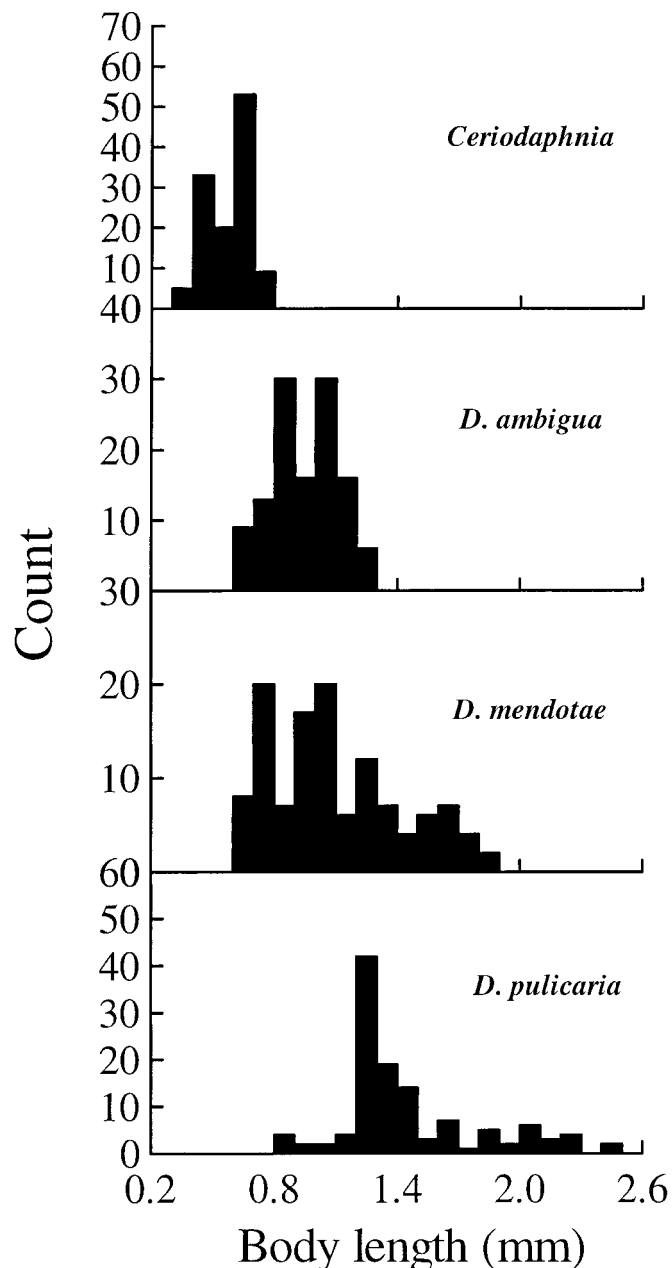


Fig. 2. Body size distribution for each daphniid treatment on day 34 of the experiment. Distributions based on 120 animals (60 from each replicate mesocosm) for each species measured from top of head to base of tail.

pattern that was striking in the *Ceriodaphnia* and *D. ambigua* treatments and was apparent but less clear in the *D. mendotae* treatment. In the *D. pulicaria* treatment, however, total Chl a was depressed to a low level by day 20 and maintained at that level throughout the end of the experiment, which resulted in significant variation among treatments ($F_{3,4} = 6.8$, $P = 0.048$).

Chl $a < 35 \mu\text{m}$ behaved quite similar to total Chl a in the *Ceriodaphnia* and *D. ambigua* treatments. In fact, even after day 20, an average of 84% (81%–87% = 95% CI) of the total Chl a passed through a 35- μm screen in these two

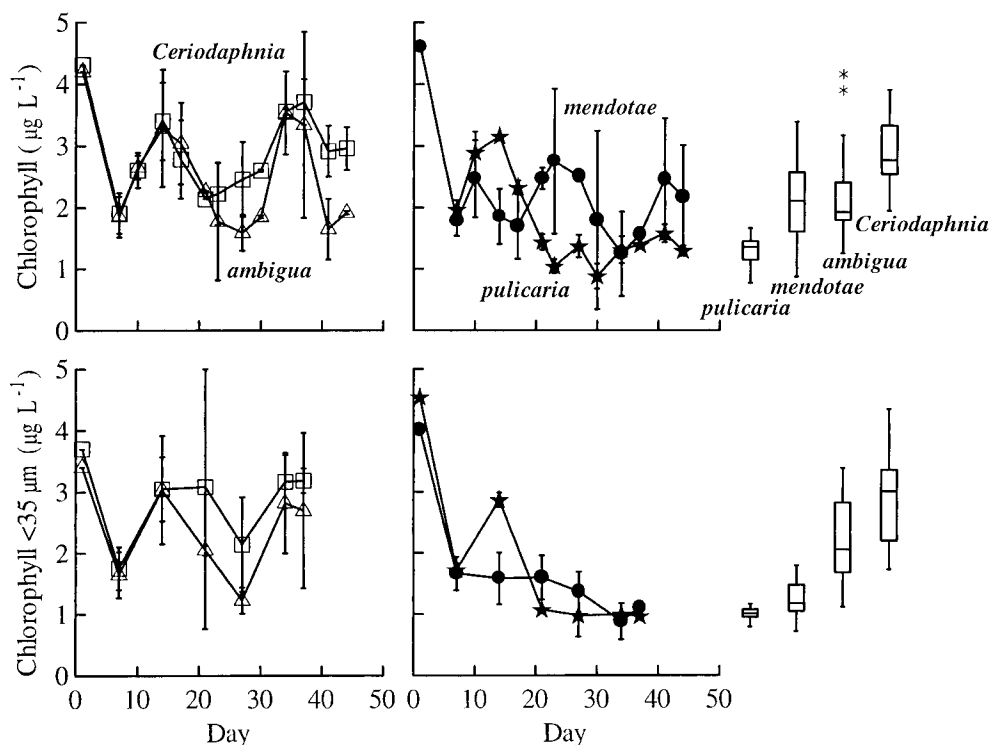


Fig. 3. Temporal dynamics of Chl *a* concentration in the small-daphniid (left) and large-daphniid (right) treatments. Top panels indicate total Chl *a* (mean \pm SE); bottom panels indicate Chl *a* $<$ 35 μm . Box plots on right show summary distributions, by daphniid treatment, for Chl *a* concentrations after day 20.

treatments. In contrast, Chl *a* $<$ 35 μm was depressed to low levels in both the *D. mendotae* and *D. pulicaria* treatments and made up only 71% (66%–75% = 95% CI) of the total Chl *a* after day 20 of the experiment. Due largely to a contrast of large versus small daphniid treatments, chlorophyll $<$ 35 μm differed significantly among treatments ($F_{3,4} = 11.1$, $P = 0.021$). Hence, although the phytoplankton assemblage remained dominated by small forms, the large daphniid species were more effective than the small daphniids at reducing these small forms.

Particulate organic carbon (POC $<$ 62 μm) reflected variation in Chl *a* ($<$ 35 μm); POC remained higher in the *Ceriodaphnia* and *D. ambigua* treatments (mean = 337 $\mu\text{g L}^{-1}$) than in the *D. pulicaria* and *D. mendotae* treatments (mean = 223 $\mu\text{g L}^{-1}$) after day 20 (Fig. 4A; $F_{3,4} = 60.0$, $P < 0.001$). Particulate phosphorus also exhibited the same significant contrast between small and large daphniid treatments (Fig. 4B; $F_{3,4} = 7.5$, $P = 0.04$). In short, all three measures of daphniid resources indicate that higher levels were maintained in the two small daphniid treatments, compared with the two large daphniid treatments. However, ratios among Chl *a*, POC, and particulate phosphorus were similar in all treatments; POC:chlorophyll averaged 137:1 (mass basis), and the ratio of particulate C:P averaged 515:1 (molar basis; Fig. 4C), without any significant variation among treatments ($F_{3,4} = 1.3$, $P = 0.38$).

Although we measured particulate nitrogen on only a single date (day 34), results indicated a significant difference among treatments ($F_{3,4} = 6.7$, $P < 0.05$), with higher values

for the smaller compared to larger daphniids (56.1 vs. 47.7 $\mu\text{g L}^{-1}$, respectively). However, these differences were small and were not reflected in variation in N:P ratios, which were 80 and 109 for the small and the large daphniid treatments, respectively ($F_{3,4} = 1.8$, $P = 0.29$).

Ratios of seston C:P $>$ 300, in the presence of POC concentrations $>$ 200 $\mu\text{g L}^{-1}$, have been interpreted as indicating phosphorus limitation of daphniid population growth (Stern and Hessen 1994; Sterner and Schultz 1998). However, our bioassay measure of resources indicated a direct relationship with the quantity of resources (Fig. 5) and no relationship with C:P ratio (Pearson correlation $r_p = 0.38$, $P = 0.14$, $n = 16$). Pearson correlations of growth rates with Chl *a* $<$ 35 μm ($r_p = 0.94$), with POC ($r_p = 0.88$) and with particulate phosphorus ($r_p = 0.77$) were all highly significant ($P < 0.001$). Given these strong correlations, we used principal components analysis to create a single estimate of resource richness from the four variables (Chl *a* $<$ 35 μm , POC, particulate phosphorus, and growth rate bioassay). The first PCA axis accounted for 87% of the total variation, correlated strongly with all four variables, and indicated higher resources in the small daphniid treatments ($F_{3,4} = 7.9$, $P = 0.037$; Fig. 6).

Phytoplankton composition—More than 50 phytoplankton taxa were observed, but to simplify analysis we lumped taxa to create 25 taxa groups based on morphological or taxonomic similarity and similarity of response to the treatments. To visualize the time course of change in the phytoplankton

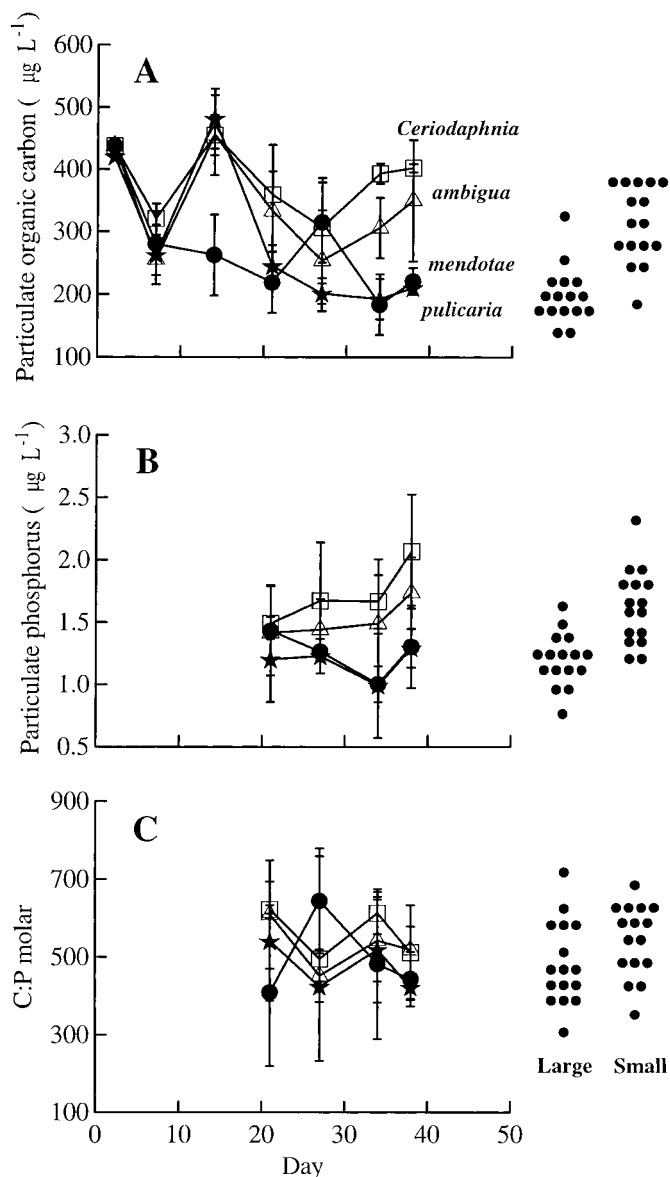


Fig. 4. (A) Seston (<62 μm) carbon and (B) phosphorus concentrations and (C) their molar ratio in each daphniid treatment (mean \pm SE). Dot plots on right provide summary distributions for days >20, grouped as either small (*Ceriodaphnia* and *D. ambigua*) or large (*D. mendotae* and *D. pulicaria*) daphniid mesocosms.

and to test for significance of differences among treatments, we first performed a multidimensional scaling of the natural log of abundances of the 25 taxa sampled on each of six different dates. An ordination in two dimensions explained 85% of the Euclidean distance matrix, and the first MDS axis captured a general succession trend that occurred in all treatments (Fig. 7). Prior to day 14, phytoplankton assemblages changed rapidly, but there was no difference among the daphniid treatments. After day 20 there was little further change in the phytoplankton assemblages in any treatments. However, between day 14 and 20 the small and large daphniid treatments diverged in phytoplankton assemblage (evident in MDS axis 2). Together, the three samplings after day

20 reveal a significant difference among the treatments, due to the contrast in MDS 2 scores of large and small daphniids ($F_{3,4} = 96.5$, $P < 0.001$; Fig. 7).

To illustrate which algal taxa responded similarly (succession shown in MDS axis 1) and which responded differently to the daphniid treatments (MDS axis 2), we plotted the natural log of abundance of each taxa versus day of experiment for each of the daphniid treatments separately. Because differences were strikingly evident in the dynamics of algal taxa in the large daphniids (*D. mendotae* and *D. pulicaria*) compared with the small daphniids (*Ceriodaphnia* and *D. ambigua*), we separately summarize the results for these two groups (Table 1).

Several phytoplankton taxa behaved similarly in all four daphniid treatments, either by great declines or increases in abundance to explain MDS axis 1. The most common alga initially present, *Peridinium pusillum*, was quickly eliminated to below detection in all enclosures. This small, single-celled dinoflagellate was likely quite susceptible to grazing by all four daphniids. Interestingly, two larger taxa, colonies of *Microcystis* and relatively large ciliates, were also eliminated quickly in all treatments, including the *Ceriodaphnia* treatment. Three other groups of algae taxa were greatly reduced in all grazer treatments: miscellaneous small flagellates (including euglenoids, chrysophytes, and chlorophytes), unicells (mostly chlorophytes and centric diatoms), and picoplankton, designated as *Synechococcus* sp. (Table 1). A different set of algal taxa increased substantially in all four daphniid treatments. The most prevalent of these were *Dinobryon* colonies, the large-celled *Ceratium hirundinella*, and two large diatoms, *Fragillaria* and *Synedra*. Finally, *Cryptomonas ovata*, *Cryptomonas* spp., and *Sphaerocystis* group were all common and small enough to be edible by the large daphniids, yet showed no decline in abundance in any daphniid treatment (or even increased slightly).

Many phytoplankton taxa showed quite different responses to small versus large daphniid treatments and explain the treatment differences evident in MDS axis 2. The general response was a reduction in abundance of several Chlorophytes in the presence of large daphniids but unchanged or even increased densities of these taxa in the presence of small daphniids (Table 1). These taxa included desmids (*Staurastrum* and *Closterium*) but were mostly members of the Chlorococcales: *Oocystis* spp., *Crucigenia* group, *Dictyosphaerium* group, and several other taxa of small gelatinous greens (e.g., *Chlamydocapsa*, *Elakatothrix*, and *Gloeocystis*). One consequence of this differential loss of taxa in the large versus small daphniid treatments is that phytoplankton diversity declined greatly in the former (Fig. 8). Richness of taxa initially increased in all treatments as grazer densities increased. But once peak daphniid densities were reached (day >20), there was a marked loss of phytoplankton taxa in the two large, but not in the two small, daphniid treatments ($F_{3,4} = 36.1$, $P = 0.002$). Only one group of algae (*Selenastrum* group, including *Scenedesmus* and *Ankistrodesmus*) was relatively more common in the large daphniid compared with the small daphniid treatments. This group initially declined in all treatments but then recovered and persisted in the large daphniid treatment.

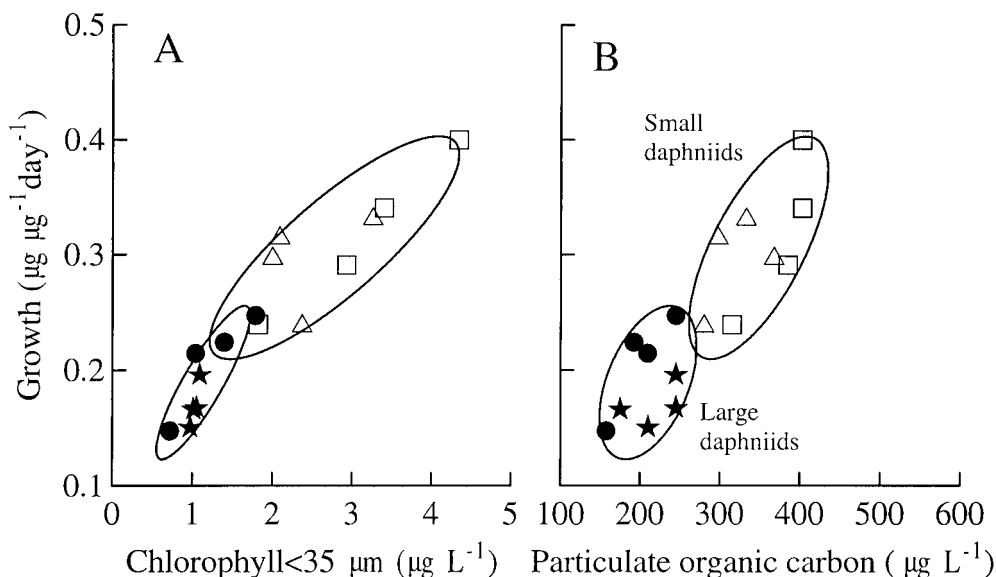


Fig. 5. Specific growth rates of juvenile (age 0–4 d) *D. pulex-pulicaria* on days 19–23 and 32–36, as a function of (A) Chl *a* <35 μm or (B) seston carbon. Daphniid treatments (source of seston) indicated as in Figs. 3 and 4; ellipses indicate bivariate SE for the *Ceriodaphnia* and *D. ambigua* (small daphniids) and the *D. mendotae* and *D. pulicaria* (large daphniids) separately.

Discussion

In answer to our title question, these results clearly illustrate that daphniids are not all alike in their role as plank-

tonic grazers. Populations of the four daphniid species differed greatly in their impact on the biomass, size structure, taxonomic composition, and richness of phytoplankton. These differences were related to grazer body size in the sense that smaller species were less effective grazers than

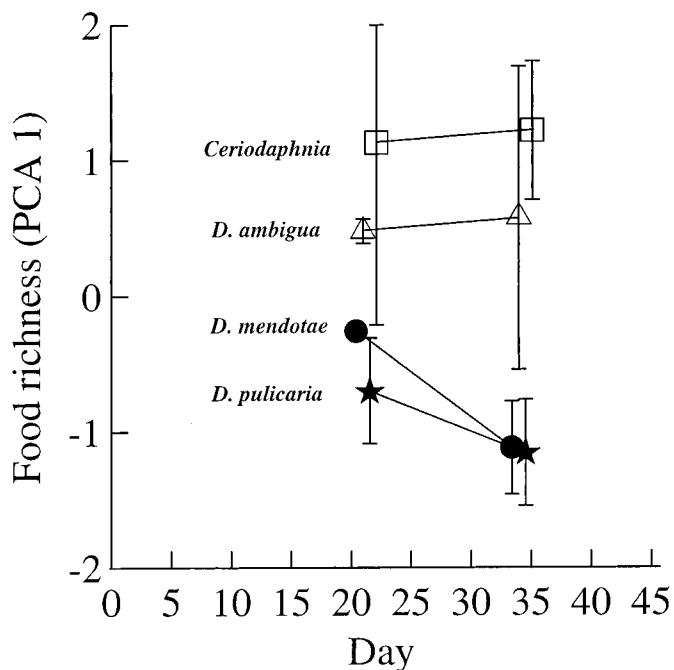


Fig. 6. Summary estimates of resource richness, expressed as the first PCA scores for each daphniid treatment on days 20 and 34 of the experiment. PCA analysis based on correlations among Chl *a* < 35 μm , seston phosphorus and carbon, and growth rate bioassays. Values, mean \pm SE of replicate mesocosms, are shifted by 1 d to avoid overlap of error bars.

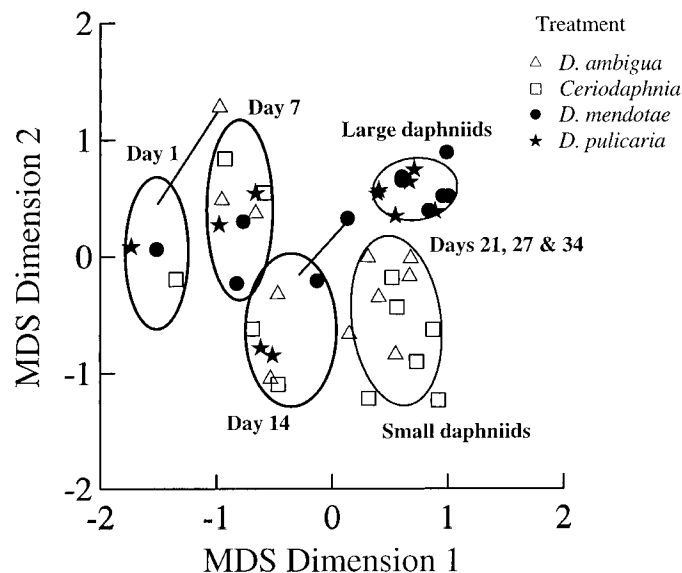


Fig. 7. Phytoplankton community dynamics in each of the mesocosms, based on a multidimensional scaling of the Euclidean distance matrix of abundances (ln transformed) for the 25 most common taxa. Ordination accounts for 85% of variance in distance matrix of all samples. Symbols indicate daphniid treatments as in Fig. 6. Ellipses for days 1–14 are drawn by eye, with outliers indicated by lines. Ellipses for days 21–34 are bivariate SE for the relatively unchanging phytoplankton communities in small and large daphniids treatments separately.

Table 1. Response of the most common phytoplankton taxa to small (*Ceriodaphnia*, *D. ambigua*) and large (*D. mendotae*, *D. pulicaria*) daphniid treatments separately. Species (sp.), congeners (spp.), or groups of taxa are placed in one of four response categories on the basis of population dynamics.

Phytoplankton response	Small daphniids	Large daphniids	
Increased or invaded ($r > 0$)	<i>Cryptomonas</i> sp. <i>Synedra</i> sp. <i>Dinobryon</i> spp. <i>Oocystis</i> spp. <i>Crucigenia</i> group	<i>Ceratium hirundinella</i> <i>Closterium acuminatum</i> <i>Coelastrum</i> sp. <i>Fragillaria crotonensis</i>	<i>Dinobryon</i> spp. <i>Ceratium hirundinella</i> <i>Synedra</i> sp.
Unchanged ($r \approx 0$)	<i>Gloeocystis</i> sp. <i>Elakatothrix</i> spp. <i>Peridinium willei</i> <i>Cryptomonas ovata</i>	<i>Sphaerocystis</i> group <i>Staurastrum sebaldi</i> <i>Chlorococcales</i> group <i>Dictyosphaerium</i> group	<i>Cryptomonas ovata</i> <i>Cryptomonas</i> spp. <i>Selenastrum</i> group <i>Sphaerocystis</i> group <i>Fragillaria crotonensis</i>
Declined ($r < 0$)	Unicellular flagellates Unicellular greens and diatoms <i>Synechococcus</i> group <i>Chlamydocapsa</i> sp.	<i>Selenastrum</i> group	Unicellular flagellates Unicellular greens and diatoms <i>Synechococcus</i> group <i>Staurastrum sebaldi</i> <i>Peridinium willei</i> <i>Oocystis</i> spp. <i>Closterium acuminatum</i>
Reduced to extinction ($r \ll 0$)	<i>Peridinium pusillum</i> <i>Microcystis</i> sp. Ciliata		<i>Peridinium pusillum</i> <i>Microcystis</i> sp. <i>Crucigenia</i> group <i>Gloeocystis</i> spp. <i>Coelastrum</i> sp. <i>Elakatothrix</i> spp. <i>Chlamydocapsa</i> sp. <i>Dictyosphaerium</i> group <i>Chlorococcales</i> group Ciliata

larger species. However, grazer effectiveness was not a simple function of mean body size. Moreover, differences in grazing by small and large daphniids created no substantial difference in seston C:N:P stoichiometry.

Body size distributions of the daphniid species overlapped and formed a gradient of treatments in terms of mean and maximum sizes. However, the combination of animal densities and body sizes resulted in population filtration rates that suggest a functional partitioning of grazer treatments into two groups, small (*Ceriodaphnia* and *D. ambigua*) and large (*D. mendotae* and *D. pulicaria*). The difference in fil-

tration rates between these two groups was large (~1.8 times) and provides an explanation for the two levels of treatment effects on the phytoplankton. In the presence of small daphniids, grazable seston was ~1.5 times denser than that in the presence of large daphniids, but there were no large differences between daphniid species within each size grouping. Population filtration rates, however, largely reflect population size (carry capacity) and are not in themselves a satisfactory explanation for the daphniid treatment differences.

The contrast in seston abundance between small and large daphniid treatments was a good predictor of juvenile growth rate for our standard clone of *D. pulex-pulicaria* used in the bioassays. Growth rates of these juveniles were ~1.7 times higher when fed seston from the small daphniid treatments compared with the large daphniid treatments. This result indicates that, from the perspective of the juvenile *D. pulex-pulicaria*, the higher seston levels in the small daphniid treatments represented good food.

A strong relationship between concentration of seston and a standardized measure of grazer growth may seem intuitive, but in this case it suggests an enigma. All four daphniid treatments drove the C:P ratio of the seston to similarly high values (~500 molar basis), which should indicate phosphorus limitation for all daphniids (Urabe and Watanabe 1992; Sterner and Hessen 1994). Our estimates of seston C:P fall within the range of what others have reported when daphniid grazers are allowed to exploit phytoplankton under low predation (Vanni et al. 1997; MacKay and Elser 1998b; Sterner 1998). However, our bioassay results indicate that the C:P ratio was not a good predictor of food quality. Despite having the same high C:P ratio as in the large daphniid treatments, the higher concentrations of seston C and P in the smaller daphniid treatments resulted in much higher growth rates for our bioassay clone. The prediction that seston C:P ratios higher than 300 indicate phosphorus limitation for all

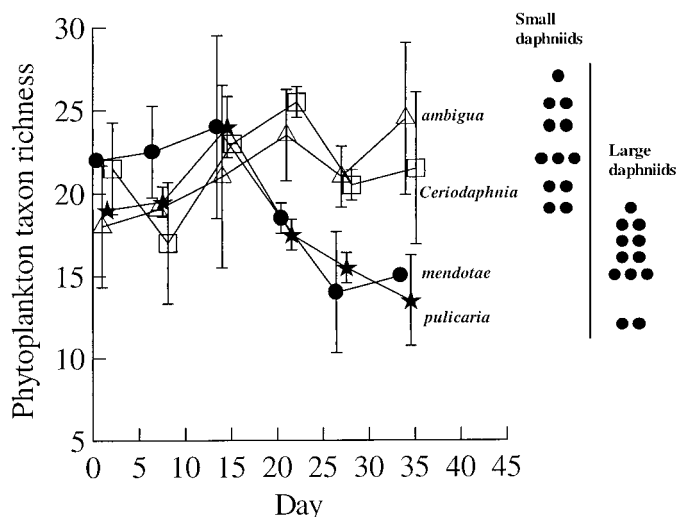


Fig. 8. Taxonomic richness of phytoplankton in the small and large daphniid treatments separately. Values, mean \pm SE of replicate mesocosms, are shifted by 1 d to avoid overlap of error bars. Dot plots on the right provide summary distributions for days >20, grouped as either small (*Ceriodaphnia* and *D. ambigua*) or large (*D. mendotae* and *D. pulicaria*) daphniid mesocosms.

Daphnia has received limited field testing, and results are mixed. MacKay and Elser (1998a) compared the juvenile growth rate of *Daphnia* fed seston from lakes with a low C:P (250) or a high C:P (750). Although *Daphnia* growth was statistically lower in the high C:P seston, the magnitude of effect was small (~15% less). Furthermore, even in the high C:P seston, the *Daphnia* grew at a rate ($>0.4 \text{ d}^{-1}$) that exceeded even the highest values we observed in our small daphniid treatments. In a review of the admittedly limited literature, Brett et al. (2000) also point out the mismatch between observed and expected reductions in *Daphnia* growth rates at elevated ratios of seston C:P.

Although seston C:P provides little explanation for the difference in bioassay growth between small and large daphniid treatments, aspects of food quality must be involved. All four daphniid species reached an apparent equilibrium with their food resources; adult fecundities and birth rates were nearly 0. Hence, the *Ceriodaphnia* and *D. ambigua* populations perceived their resources to be just as limiting as the resources perceived by the *D. mendotae* and *D. pulicaria* populations. The observations that seston was denser in the small daphniid treatments and that juvenile *D. pulex-pulicaria* (bioassay) grew much better when fed seston from the small daphniid treatments might suggest that minimum resource requirements were higher for the two small daphniid species than for the two large species. However, particulate carbon in the smaller daphniid treatments was so dense ($300\text{--}400 \mu\text{g L}^{-1}$) that individuals should have been satiated (Sterner and Schultz 1998; Kreutzer and Lampert 1999). Furthermore, $>85\%$ of the Chl *a* passed a $35\text{-}\mu\text{m}$ mesh, which suggests that it was ingestible for *D. ambigua* whose adults exceeded 1 mm in length (DeMott 1995). Hence, we conclude that higher seston concentration in the small versus large daphniid treatments is due to the smaller daphniid species becoming limited by some aspect of food quality to which the larger daphniid species were less sensitive.

That resource quality is involved does not negate the possibility that the small and large daphniids differ in minimum resource requirements. In a laboratory study, Kreutzer and Lampert (1999) estimated minimum carbon requirements for *D. pulicaria*, *D. galeata* (closely related to our *D. mendotae*), and *D. ambigua*, using a high quality alga as food. They compare their results with other literature values and conclude that *D. pulicaria* requires $\sim 20\text{--}40 \mu\text{g L}^{-1}$ C, *D. ambigua* requires $\sim 30\text{--}60 \mu\text{g L}^{-1}$ C, and *D. galeata* has intermediate food needs. These values are dramatically different than the $>200 \mu\text{g L}^{-1}$ C that we observed for equilibrium seston concentration at daphniid carrying capacity (Fig. 4A). Furthermore, the interspecific differences in minimum food values observed in lab studies ($<20 \mu\text{g L}^{-1}$ C) are much less than what we observed between small and large daphniid treatments ($>100 \mu\text{g L}^{-1}$ C). These order-of-magnitude discrepancies between field and laboratory estimates lead us to conclude that much of the seston in our enclosures was not useful or accessible as daphniid food but that our large daphniids were better at exploiting that poor resource base than were our small daphniid species.

This difference in ability to exploit the seston is not, however, easily explained by body size differences translating into differences in maximum range of particles that can be

ingested. First, a large difference in body size between *Ceriodaphnia* and *D. ambigua* resulted in only a minor difference in effect on the seston, but a smaller contrast in sizes of *D. ambigua* and *D. mendotae* resulted in a large difference in seston. Second, as was already mentioned, the bulk of the difference in seston concentration between small and large daphniid treatments involved small particles. Phytoplankton counts showed that small flagellates, unicells, and picoplankton were all more abundant in the small daphniid treatments. Finally, and most significantly, the neonate *D. pulex-pulicaria*, which grew so well in the bioassays with seston from the small daphniid treatments, were smaller (~ 0.7 mm) than even the average *D. ambigua*.

An alternative possibility is that the small daphniids became limited by phosphorus at a lower C:P ratio than the larger daphniids. There is some evidence that *Ceriodaphnia* may have an even higher requirement for phosphorus than *Daphnia* (Hessen and Lyche 1991). But this does not explain the similarity of effects by *D. ambigua* and *Ceriodaphnia*. More importantly, if seston C:P was what ultimately limited the small daphniids, why didn't the larger daphniids drive seston C:P even higher in their treatments until they were likewise limited by phosphorus?

Differences in composition of phytoplankton in the small versus large daphniid treatments suggest another explanation for the inability of small daphniids to depress resource levels. Many algal taxa exhibited defenses against grazing and these algae appear to have been more successful against *Ceriodaphnia* and *D. ambigua* than against the two larger daphniid species. A few algal taxa were obviously defended by large size (e.g., *Dinobryon* colonies and *Ceratium*), and these forms increased in all daphniid treatments. However, a large group of algae, mostly members of the Chlorococcales, exhibited thick cell walls or gelatinous sheaths, which likely afforded some degree of digestion resistance. In the presence of small daphniids, a diverse assemblage of these algae remained abundant. But these same algae were effectively grazed to very low levels in the presence of the large daphniids. Most of these algae were relatively small and should have been ingested by at least the adult *D. ambigua* among the smaller daphniids. Therefore, we speculate that *Ceriodaphnia* and *D. ambigua* were not as capable at digesting these forms, as were the two other daphniid species.

Although it is generally accepted that digestion resistance is a quantitative rather than qualitative trait of phytoplankton taxa, there is little information on whether zooplankton grazers differ in ability to overcome these defenses. Although daphniids clearly vary in their ability to grow and reproduce on the same phytoplankton (e.g., Infante and Litt 1985), there are few tests of differential assimilation ability. Vanni and Lampert (1992) observed that when fed a digestion-resistant alga (*Oocystis*), the assimilation efficiency of juveniles, but not adults, of *D. galeata* was greatly reduced (compared with a high-quality food). They speculate that differences in gut processing time or mandible development explain this difference between juveniles and adults to overcome digestion resistance. If juveniles and adults of a single daphniid species can display such variation, is it possible that gut-processing capabilities also vary among different daphniid species? We are aware of only a single study that

addresses this question. In a mesotrophic lake, DeMott (1983) documented that competitive superiority of *D. pulicaria* over *D. rosea* was associated with a better ability of *D. pulicaria* to assimilate the summer assemblage of digestion-resistant algae. It is unlikely that this difference was related to the small differences in body size of these species. In fact, our bioassay results, which showed juvenile *D. pulex-pulicaria* growing so well on seston limiting to the equally sized *D. ambigua*, suggest that size per se is not the major determinate of ability to exploit digestion resistant algae.

An inability to effectively digest much of what is ingested translates into reduced bulk assimilation efficiency. If this were true of *Ceriodaphnia* and *D. ambigua*, their populations would stabilize at higher concentrations of easily digested seston (e.g., small, unicellular flagellates) compared with populations of daphniids that have a greater ability to digest resistant algae. This is precisely what we observed. Under the assumption that variation in digestion defense among algae taxa trades off against other fitness components (e.g., growth rates; Grover 1995), higher diversity of algae would also be expected in the presence of less effective grazers. This is also what we observed. If the more easily digested algae (or bacteria) are also capable of faster growth rates, they might be higher in P content than the more defended algae (Elser et al. 2000). This would result in the assimilated fraction of ingested food having a lower C:P ratio than the bulk seston and explain the unexpected result of variable bioassay growth rates in the face of high, but unvarying, bulk seston C:P values. Finally, differential digestion ability could also explain why neonates of *D. pulex-pulicaria* were able to grow well on the same seston that was limiting to adult *D. ambigua*.

We conclude that differential digestion ability is a logical hypothesis to explain our overall results. Still, the above speculation is just that—a hypothesis in need of testing. Our experiment was not designed to resolve mechanisms of resource limitation, nor did we even measure all aspects of foraging behavior or diet quality (e.g., fatty acids or proteins) that might contribute to the differences we observed among species treatment.

In summary, the major contrast that we document was an inability of populations of *Ceriodaphnia* and *D. ambigua* to depress a diverse assemblage of digestion-resistant phytoplankton that were virtually eliminated by populations of *D. mendotae* and *D. pulicaria*. This is associated with clear differences in the abundance and size structure of phytoplankton among the daphniid treatments (i.e., more and smaller phytoplankton in the presence of the smaller daphniids). Although the importance of digestion resistance to grazer-resource interactions in the plankton has been long recognized (Porter 1975), it has received little recent attention compared with aspects of dietary components (e.g., fatty acids) and elemental (P) limitation. It is worth emphasizing that algal digestion defenses and grazer assimilation abilities are both likely to be quantitative traits. Hence, interactions with other components of food quality are potentially complex. Still, the hypothesis that the ability to overcome algal digestion varies with grazer species deserves careful attention, considering its functional significance to plankton food webs.

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