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The effect of grazer size manipulation on periphyton communities*

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Summary. We examined the effect of grazer size on periphyton biomass, size structure, and species composition by removing the largest invertebrate grazers on artificial macrophytes planted in the littoral of Lake Memphremagog (Que-Vt). A series of exclosures with increasingly fine mesh prevented colonization by large invertebrates but allowed in smaller grazers. Oligochaetes, chironomids, and cladocerans effectively replaced snails so that total grazer biomass in the various treatments was not significantly different from the controls. With one exception, algal biomass, measured as chlorophyll a, did not differ significantly among the various treatments. However algal size and taxonomy were affected because the dominance of large blue-green colonies was apperantly related to the presence of large grazers. The results of the size manipulations were qualitatively similar to those induced in phytoplankton communities by size selective zooplankton grazing and are consistent with models based on general allometric equations.

If large grazers are removed from a community, the size and abundance of small grazers should increase. This in turn should promote the growth of smaller plants by increasing both grazing pressure and nutrient turnover. The pattern follows from general allometric equations (Peters 1983) and has been repeatedly demonstrated in limnetic plankton communities. Size-selective predation by fish (Hrbacek 1962; Brooks and Dodson 1965) generally results in small zooplankton and in a high biomass of small phytoplankton. Conversely, elimination of fish predation yields larger zooplankton and a lower phytoplankton biomass, often concentrated in large colonies (Shapiro et al. 1975; Anderson et al. 1978; Lynch and Shapiro 1981).

It remains unclear whether this pattern observed in plankton following size selective predation is a general one or not. The size efficiency hypothesis (Brooks and Dodson 1965; Hall et al. 1976) is based on differences in the allometry of ingestion and production of zooplankton that have as yet not been shown to be of a more general nature (Peters 1983; Calder 1984). In addition the results of plankton experiments could have been confounded by changes in nutrient status resulting from the addition or removal of fish (Nakashima and Legget 1980). If indeed the peculiarities of zooplankton biology described in the size efficiency hypothesis are responsible for the pattern noted, one would not expect that the elimination of larger herbivores in non planktonic communities would yield similar results. Conversely, if size related shifts are a general community response to changes in the size of grazers, they should also occur in non planktonic communities. We tested this by examining size related changes in periphyton communities growing on artificial plants. In such a system, invertebrate size can be readily manipulated by using exclosures fitted with screening of different mesh sizes. These exclosures prevent colonization by large grazers while allowing access by smaller grazers. The screens also allow water flow-through, maintaining a similar chemical environment in all treatments.

Specifically we tested the effect of size selective removal on taxonomic composition, size structure, and biomass of grazers and algae, by comparing the periphyton communities on artificial plants placed inside and outside the exclosures. If the general allometric model is correct, exclusion of large herbivores should lead to an increase of both small grazers and small edible algae.

Methods

All experiments were conducted in MacPherson Bay, in the mesotrophic ($TP = 14\ \mu g \cdot l^{-1}$) central basin of Lake Memphremagog (76°16″ W; 45°06″ N). Periphyton communities were grown on plastic aquarium plants ("Hygrophila", R. Hagen, Montreal), which are good mimics of the natural substrate (Cattaneo and Kalff 1979). The plants were placed inside ten nearly cubical open frames ($50 \times 50 \times 60$ cm), each consisting of 5×5 cm posts on a plywood base and fitted with a transparent Plexiglas cover. Four duplicate sets of exclosures were obtained by covering the frame walls with nylon cloth of 0.1 mm, 0.25 mm, 0.5 mm, and 2 mm mesh size, respectively. The remaining two frames remained open and served as controls. The cages were anchored to the lake bottom and adjusted so that the plywood base remained about 20 cm above the sediments and the Plexiglas cover stayed above water.

Both epiphytes and grazers were sampled every two weeks between 13 July and 13 September 1978, and epiphytes alone were collected on five additional dates. At sampling, the frame cover was lifted and two halves of a 660 ml Plexiglas box (Cattaneo 1983) were closed around the stem and two apical leaves of a plastic plant. The stem was then cut and the sample removed. Water in the boxes was carefully drained through a 100 μm mesh net and the retained material fixed with 4% neutral formalin-sucrose

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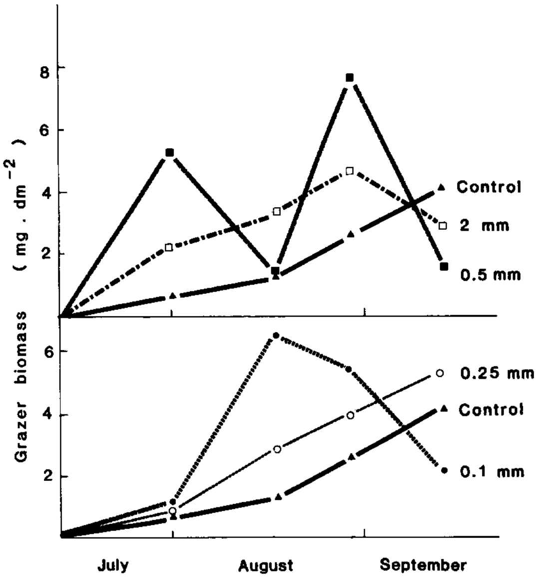

Fig. 1. The development of invertebrate biomass (as dry weight) during the experiment in the various treatments and control (illustrated in both panels). Each value is the average of two replicates

solution (Prepas 1978). The sampling minimized epiphyte dislodgement and included grazers loosely associated with the substrate, which might otherwise have been lost.

One pair of leaves (surface area = 5.2 cm^2·leaf^{-1}) was collected from three to eight randomly selected plastic plants. Three leaves were frozen for subsequent chlorophyll *a* determination and the others fixed with 4% neutral formalin-sucrose for microscopical counts of invertebrates and algae. For chlorophyll *a* determinations, plastic leaves were extracted in 96% ethanol for 24 h and the extracts read at 665 and 649 µm in a Beckman spectrophotometer (Bergman and Peters 1980). Invertebrates were examined in combined samples under a dissecting microscope at 25 × magnification. Animals in the sampling water were also counted. Oligochaetes, chironomids and snails were counted by size class. Average weights for each taxon or size class were obtained by weighing, after drying at 60° C, samples of each taxon on a Cahn electrobalance. For snails, shell-free weight was estimated as 20% of total weight. We considered only invertebrates that at least partially feed on epiphytic algae. Thus bryozooans, *Hydra* sp. and *Planaria* sp. which were sometimes present but never abundant, were not considered in the results. Algae were counted in random fields of a nannoplankton chamber of 400 × and 160 × magnification. Colonies of *Gloeotrichia pisum* and *Coleochaete* spp. were counted in a Sedgwick-Rafter chamber. Cell volumes were calculated by approximation to solids of known volume. When colonies or filaments were present, the whole volume was taken as algal size rather than the volume of the single cell.

Results

The exclosures yielded periphyton communities that differed both in size and taxonomic composition, but were similar in total biomass. Invertebrate biomass was quite variable among replicates (average difference = 40%), treatments, and dates (Fig. 1). Perhaps as a result, no treatment was significantly different either during sampling on any single date (Kruskall-Wallis $n = 10$ – Conover 1971) or over the entire experiment (Friedman test $n = 40$ – Conover 1971). Similarly, algal biomass (as chlorophyll *a*) was not significantly different between treatments, with the exception of the 0.25 mm mesh exclosure (Fig. 2) where it was significantly higher than in the other treatments (*t*-test) between August 29 and September 13.

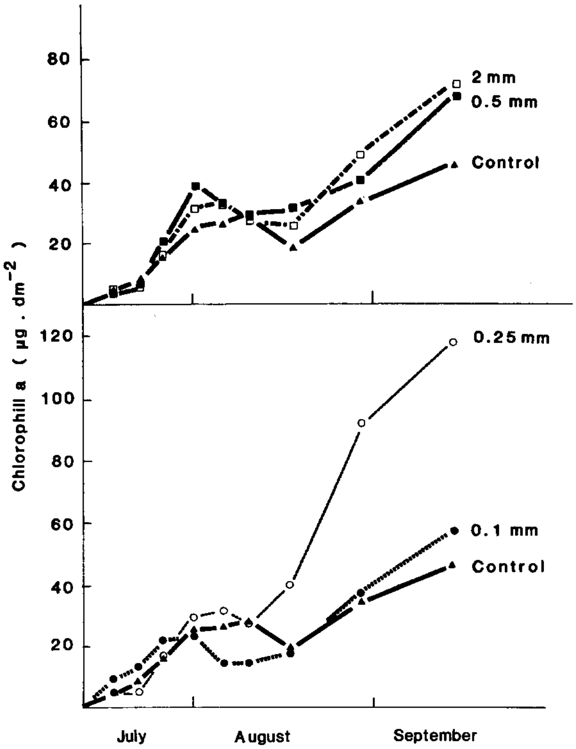

Fig. 2. The development of algal biomass (as chlorophyll a) during the experiment in the various treatments and control (illustrated in both panels). Each value is the average of six replicates (average CV = 34%)

Although biomass differed little between treatments, its distribution among size classes differed greatly. The importance of large bodied grazers and algae increased with increasing mesh size while small forms declined in importance (Fig. 3). Thus, while invertebrates heavier than 1 mg represented a major portion of the biomass in the controls and in the 2 mm mesh treatment (38% and 28% of the total, respectively) they were absent from the exclosures with smaller meshes. In the controls and 2 mm mesh exclosures, the largest fraction of the algal biomass was contained in organisms larger than 10,000 µm^3, while the finest mesh treatment had the largest fraction of the algal biomass in forms smaller than 100 µm^3. Distribution was somewhat more even in frames with intermediate mesh sizes (Fig. 3). The observed pattern was most pronounced during the second half of the colonization. Both grazer size (Fig. 4) and algal size (Table 2) increased with time in the controls and large mesh treatments, whereas they changed little, and sometimes even decreased, in the exclosures with finer screens.

The differences in size distributions reflect differences in abundance and relative size of the main taxonomic groups in the various treatments. Whereas snails, mainly *Amnicola* sp., were the dominant grazers in the controls and the exclosures with the largest mesh size (2 mm), *Gammarus* sp. and the large cladoceran, *Sida cristallina*, domi-

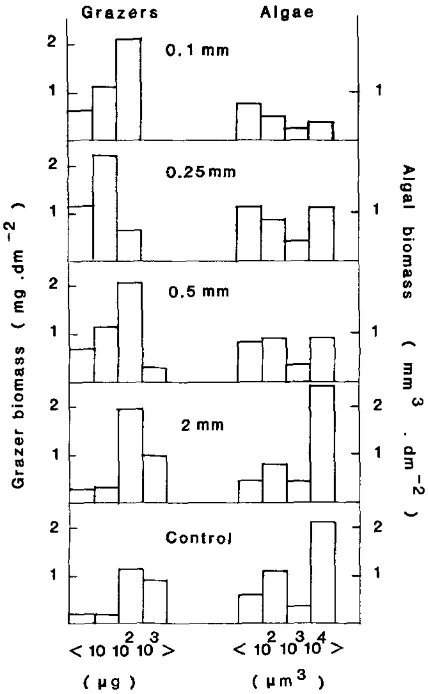

Fig. 3. The distribution of grazer (as dry weight; left panel) and algal (as biovolume; right panel) biomass in various size classes in the exclosures and controls. The data are averages over the experiment

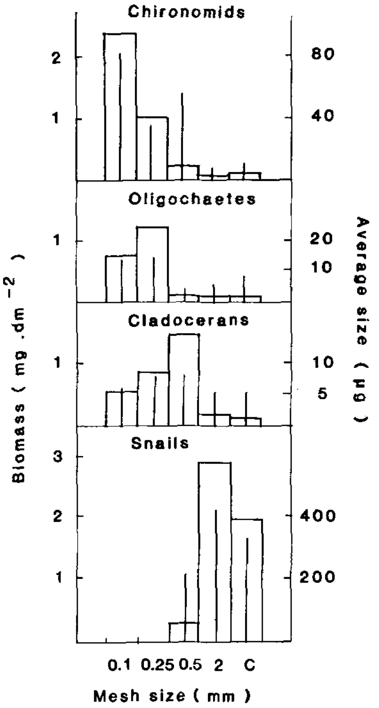

Fig. 5. Biomass (histograms) and average size (lines) of the main groups of grazers in the various treatments. The values represent the average of two replicate treatments over four sampling dates

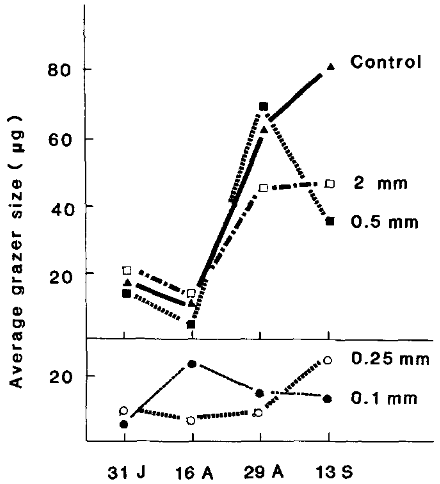

Fig. 4. Changes in average grazer size (dry weight) in the various treatments and control during colonization. The values are the average of two replicate treatments

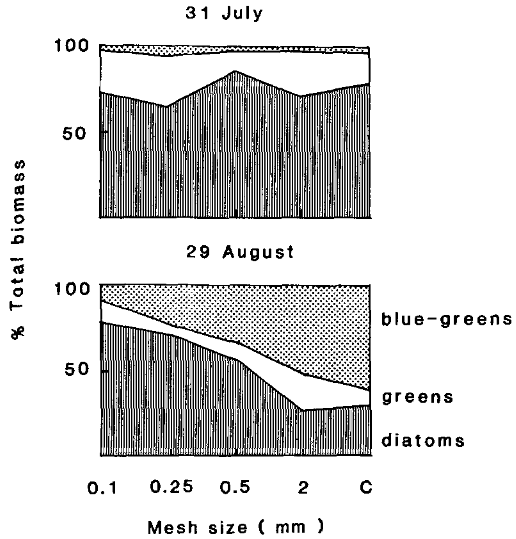

Fig. 6. Relative importance of diatoms, green, and blue-green algae expressed as percent of total algal volume in treatments and control at two dates during the experiment

nated the invertebrate biomass in exclosures with 0.5 mm mesh size. Oligochaetes, chironomids and sometimes smaller cladocerans (*Chydorus* sp. and *Bosmina* sp.) dominated treatments with still finer meshes (Fig. 5). Ostracods and cyclopoids were more abundant where snails were absent but never represented more than a small portion of the total biomass (Table 1). Interestingly, each taxonomic grouping of invertebrate had its largest average size in the same treatment where it achieved the largest biomass (Fig. 5).

In each treatment, the taxonomic composition was usually relatively constant between replicates and over time, but exceptions to this rule did occur. In the 0.5 mm treatment *Sida* dominated at some dates and *Gammarus* at others, but they were never present concurrently. The relatively large oligochaete *Stylaria* sp dominated twice in one replicate of the fine mesh treatments (in the 0.1 mm exclosure on August 29 and in the 0.25 mm exclosure on September 13) but was absent in the other set, where it was replaced by a similar biomass of chironomids. The small

Table 1. Biomass ($\mu g \cdot dm^{-2}$) of the various grazer taxonomic and size groups in the four treatments and in the control during the experiment. The values are averages of two replicates

		Mesh size (mm)				Control
		0.1	0.25	0.5	2	
31 July						
Oligochaetes	<10 μg	53	90	10	6	21
	10– 100 μg	99	322	257	67	0
Chironomids	<10 μg	213	119	2	14	30
	10– 100 μg	541	234	184	0	0
Cladocerans	<1 μg	2	1	1	0	0
	1– 10 μg	19	6	1,420	242	173
	10– 100 μg	0	35	3,375	209	0
Cyclopoids	1– 10 μg	145	24	17	15	5
Ostracods	1– 10 μg	120	131	65	57	14
Snails	<100 μg	0	0	17	160	26
	100–1,000 μg	0	0	0	319	426
	1– 10 mg	0	0	0	1,200	0
Total		1,192	962	5,348	2,289	684
16 August						
Oligochaetes	<10 μg	6	20	12	58	52
	10– 100 μg	338	295	27	305	90
Chironomids	<10 μg	84	69	10	42	8
	10– 100 μg	0	675	75	0	0
	100–1,000 μg	5,254	0	0	0	0
Cladocerans	<1 μg	20	7	8	17	6
	1– 10 μg	47	1,367	480	13	9
	10– 100 μg	452	35	452	57	135
Cyclopoids	1– 10 μg	101	4	35	19	29
Ostracods	1– 10 μg	272	335	317	187	87
Snails	<100 μg	0	0	0	40	100
	100–1,000 μg	0	0	0	2,609	735
Total		6,574	2,807	1,416	3,347	1,251
29 August						
Oligochaetes	<10 μg	24	36	32	73	8
	10– 100 μg	1,801	753	0	18	0
Chironomids	<10 μg	46	57	5	29	29
	10– 100 μg	23	172	0	0	99
	100–1,000 μg	1,979	841	0	0	0
Cladocerans	<1 μg	414	74	13	16	4
	1– 10 μg	380	1,646	9	11	9
	10– 100 μg	489	70	35	0	17
Cyclopoids	1– 10 μg	71	27	12	22	10
Ostracods	1– 10 μg	86	243	69	64	6
Amphipods	10–1,000 μg	0	0	7,577	0	0
Snails	<100 μg	0	0	0	208	0
	100–1,000 μg	74	0	0	3,310	2,454
	1– 10 μg	0	0	0	1,004	0
Total		5,387	3,919	7,752	4,755	2,636
13 September						
Oligochaetes	<10 μg	79	32	9	36	11
	10– 100 μg	529	3,247	0	109	74
Chironomids	<10 μg	147	92	17	39	47
	10– 100 μg	47	196	0	0	0
	100–1,000 μg	1,030	1,514	524	0	0
Cladocerans	<1 μg	176	4	6	1	1
	1– 10 μg	49	46	21	16	0
	10– 100 μg	87	52	0	0	0
Cyclopoids	1– 10 μg	13	15	12	21	3
Ostracods	1– 10 μg	40	24	0	5	9
Amphipods	10– 100 μg	65	0	0	0	0
Snails	<100 μg	0	0	7	0	0
	100–1,000 μg	0	0	0	1,245	652
	1– 10 mg	0	0	1,014	1,506	3,366
Total		2,262	5,222	1,610	2,978	4,163

cladoceran *Chydorus* reached high biomass in one of the 0.1 mm exclosure on 29 August but was almost absent from the other, where it was replaced by a similar biomass of *Sida*.

The algal species composition was examined in samples from 31 July and 29 August (Table 2). On July 31, a taxonomically similar assemblage of diatoms clearly dominated in all treatments (Fig. 6). Nevertheless, large diatoms and filamentous forms tended to be more abundant in the fine mesh treatments than in the controls, while *Coleochaete* spp., a green alga with flat thallus, was more common in the controls. On the second date (29 August) the importance of diatoms had fallen sharply in the controls and the 2 mm mesh exclosures and *Gloeotrichia pisum*, a blue green alga with colonies of up to 2 mm in diameter, had become dominant. Diatoms continued to dominate the assemblages in the exclosures with fine mesh size (Fig. 6 and Table 2), although the forms were smaller than those observed in July.

Discussion

Minnows, which were common in the bay during the experiment (Gascon and Leggett 1977), might affect results in the open frames through grazing on the algae (Phillips 1969; Power et al. 1985) and preying on grazers (Gascon and Leggett 1977). The importance of fish grazing was indicated by the 2 mm mesh exclosures which allowed colonization by large invertebrates but excluded fish. Since algal and grazer biomass (cf. Figs. 1, 2), organismal size (Fig. 3) and taxonomic composition (Figs. 5, 6) were quite similar in the control and in the 2 mm mesh treatment, fish appear unimportant in these experiments.

Our experiments demonstrate that communities that differ greatly in size and taxonomic composition can develop in the same site at the same time under similar physicochemical conditions. The determinant of grazer taxonomy and size was their ability to enter the different exclosures, and the largest grazer able to enter normally dominated.

Table 2. Biomass (µm$^3 \cdot 10^6 \cdot$dm^{-2}) of various size and taxonomic groups of algae in the four treatments and control at two dates during the experiment. The values are averages of two replicates. The more representative algae of each group are also listed

	Mesh size (mm)				Control	Algal dominant
	0.1	0.25	0.5	2		
31 July						
Diatoms						
<100 µm^3	195	395	475	580	690	*Achanathes minutissima*
100– 1,000 µm^3	210	385	575	660	1,095	*Gomphonema intricatum*
1,000–10,000 µm^3	235	245	435	400	385	*Cymbella* sp.
10,000 µm^3	115	145	220	105	40	*Synedra ulna*
Filamentous	125	25	85	35	10	*Fragilaria* spp.
Green						
<1,000 µm^3	120	0	5	0	0	*Scenedesmus* spp.
1,000–10,000 µm^3	20	0	20	25	35	*Cosmarium* sp.
<10,000 µm^3	10	125	110	395	485	*Coleochaete* spp.
Filamentous	125	445	80	220	15	*Oedogonium* spp.
Blue Green						
<1,000 µm^3	10	10	5	0	20	*Merismopedia* sp.
1,000–10,000 µm^3	0	45	5	0	0	*Chroococcaceae* spp.
Filamentous	5	25	35	45	60	*Phormidium* sp.
Total	1,185	1,845	2,050	2,465	2,835	
Average size (µm^3)	243	194	176	163	141	
29 August						
Diatoms						
<100 µm^3	1,335	1,790	1,085	330	480	*Achanathes minutissima*
100– 1,000 µm^3	540	1,135	970	845	960	*Gomphonema intricatum*
1,000–10,000 µm^3	160	290	20	235	45	*Navicula radiosa*
<10,000 µm^3	10	80	0	85	5	*Synedra ulna*
Filamentous	0	140	5	10	30	*Fragilaria* spp.
Green						
<1,000 µm^3	0	0	5	0	10	*Scenedesmus* spp.
1,000–10,000 µm^3	50	115	80	130	30	*Closterium* sp.
<10,000 µm^3	100	125	190	295	310	*Coleochaete* spp.
Filamentous	140	115	10	730	65	*Oedogonium* spp.
Blue Green						
<1,000 µm^3	40	5	0	0	5	*Merismopedia* sp.
1,000–10,000 µm^3	5	0	0	10	25	*Chroococcaceae* spp.
<10,000 µm^3	120	1,157	1,217	3,005	3,315	*Gloeotrichia pisum*
Filamentous	25	30	5	120	5	*Phormidium* sp.
Total	2,525	4,982	3,587	5,795	5,285	
Average size (µm^3)	78	117	127	564	365	

Cuker (1983) similarly reported that the largest periphyton grazer dominated enclosures in an artic lake. There, the addition of snails resulted in a significant decrease in the abundance of chironomids, cladocerans, and ostracods and a slight, but insignificant, decrease in their size. Our findings also find support in the observation that oligochaetes and chironomids dominate the natural periphyton early in the season but almost disappear later when snails become dominant (Cattaneo 1983; Kairesalo 1984). The occasional dominance by different species in the replicate exclosures shows that there is an element of chance in determining the species composition and that grazer size rather than taxon determine the size structure of the periphyton.

When large grazers were excluded by the finer meshes, they were replaced by small animals that increased sufficiently in number and in size (Table 1; Fig. 5) to yield a biomass similar to that of the large grazers in the controls. Since smaller organisms generally have higher rates of turnover per unit of grazer biomass (Peters 1983), this reduction in grazer size but not in biomass, should result in a higher grazing pressure on the algae. In the present study this pressure did not lead to a reduced algal biomass but rather to a dominance by small algae, characterized by a rapid turnover rate.

It has been suggested that large algal size could provide a refuge from grazing in the presence of small invertebrates, as long as the grazing pressure on small algae is sufficiently high to release the large ones from competition (Peters 1983). This is not the case in our study. The large and probably unpalatable *Gloeotrichia pisum* appears to escape grazing by even large invertebrates and so becomes dominant in their presence (Table 2; Fig. 6), but remains rare in their absence. This alga is a late summer dominant in epiphytic communities in Lake Memphremagog (Cattaneo and Kalff 1978) and elsewhere (Young 1945; Bownick 1970), and its presence usually coincides with the dominance of snails. An analogous sequence can occur in the plankton where blooms of the large blue green colonial *Aphanizomenon* occur in the presence of large *Daphnia*, but not when smaller grazers are dominant (Lynch 1980). A probable explanation for our findings is that grazing by snails first suppresses the filamentous algae and large diatoms (31 July; Table 2), thereby lowering the competition for space and allowing the slower growing *Gloeotrichia* to become dominant. Snail grazing has often been associated with a decrease of large and filamentous algae, both in freshwater (Hunter 1980; Summer and McIntyre 1982) and marine environments (Castenholz 1961; Nicotri 1977). In the plankton, *Aphanizomenon* dominance has been attributed to *Daphnia* predation on the faster growing small algae (Lynch 1980) that would otherwise outcompete the large blue green algae for nutrients.

In the present study, exclosure mesh size determined the taxonomic and size composition of periphyton invertebrates and algae with no significant effect on their total biomass, with the exception of the 0.25 mm treatment which differed two fold from the others. Even this difference is small compared to the ten fold differences noted between treatments in the plankton (Lynch and Shapiro 1981). The general absence of a biomass effect in our study may well be the result of nutrient limitation, which ultimately determined the biomass in our exclosures. Support for this is found in the work of Benndorf et al. (1984) who reported that biomanipulation of a nutrient limited system affected the phytoplankton composition but not their biomass.

In summary when large periphytic grazers are removed 1) small grazers become dominant; 2) their size increases; 3) algae become smaller. Qualitatively these changes are remarkably similar to those that follow biomanipulation of the plankton (Shapiro et al. 1975; Lynch and Shapiro 1981; Benndorf et al. 1984). This agreement between results from periphyton and phytoplankton communities, despite major differences in species and feeding mechanisms of grazers and type of algae as well as in techniques used, strengthens the generality and applicability of allometric patterns as determinants of community structure in lakes.

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