Independent and interactive effects of nutrients and grazers on benthic algal community structure

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Abstract

Algal responses to nutrients, grazing by *Helicopsyche borealis*, and concurrent grazing by *Helicopsyche* and *Baetis tricaudatus* were examined in recirculating stream chambers. Alagl communities, dominated by *Achnanthes minutissima*, *Cocconeis placentula*, and *Synedra ulna*, were primarily phosphorus-limited. Algal populations responded after only 6 days of nutrient enrichment. Initially, both the adnate diatom *Cocconeis* and erect diatom *Synedra* showed positive response to nutrient enrichment. Accumulation of algal biomass between day 3 and 6 in the P enriched treatment was resulted primarily from the growth of *Synedra*, an overstory rosette-like diatom colony. Such a shift in dominant growth from adnate to erect diatoms is a general phenomenon in periphyton succession in the absence of disturbance. Algal species showed differential responses to an increase of *Helicopsyche* densities. The accrual rate of *Achnanthes* continuously decreased with increasing grazer densities. The accrual rates of both *Cocconeis* and *Synedra* declined but reached plateaus between medium and high grazing densities. *Baetis* effectively and exclusively depressed *Synedra* and had no significant impact on *Cocconeis*. After concurrent grazing, algal communities were mainly dominated by *Cocconeis* (approximately 80% of total algal biovolume). The grazer' s mouth structures, grazing efficiencies, and mobility may account for the differential effects of concurrent grazing on algal communities.

Significant interactive effects of P and grazing by *Helicopsyche* indicated that both nutrient addition and grazing may exert significant impact on algal communities. However, grazing may have a much stronger effect on algae than nutrients. Our results indicate that enhancement of algal biomass by P was dampened by grazing activities and that P had no effect on algal biomass in the presence of grazers.

Introduction

Periphyton communities often experience concurrent grazing by multiple grazers in streams. Grazers with different feeding mechanisms may have differential grazing efficiencies (Lamberti *et al.*, 1987a) which may result in an additive effect in reducing algal standing crops if interspecific competition is not significant. Furthermore, multiple grazers can also significantly alter algal species composition because of selective grazing (Feminella & Resh, 1991; Hill & Knight, 1987).

Grazers may exert a positive impact on some periphyton populations although positive effects of grazing on algae are often subtle and difficult to be demonstrated in the field. Grazing may reduce nutrient and light limitation on adnate algae in perphyton communities by effectively removing loosely attached overstory algae (Coletti *et al.*, 1987, Hill & Knight, 1987). Some planktonic algal species can even survive passage through a grazer's digestive track and gain nutrients from the egested edible algae and grazer's metabolites during gut passage (Porter 1973, 1976). Although some benthic algae may be able to benefit similarly by gut passage, this has not been demonstrated conclu-

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sively. Grazers can also regenerate nutrients via excretion (Lehman, 1980; Lehman & Scavia, 1982). Algal mortality caused by grazing sometimes can be compensated for by fast algal growth resulting from effective utilization of nutrient regeneration from grazers (Sterner, 1986). Pringle (1985), for example, found that regeneration of nutrients from chironomids resulted in rapid growth of algae attached on chironomid retreats.

Interaction between periphyton and grazers can be confounded by contrasting impacts of grazers and differential algal responses to grazing. In this study, we examined responses of algal species to an increase of grazer densities under nutrient enriched conditions. We anticipated that periphytic algal species in streams may respond to grazing pressure in at least two ways: 1) some algal species may be resistant to grazing because of their unique morphology such as prostrate growth form with firm attachment. 2) some algae may be resiliant because of relatively high growth rates. We also examined the impact of two insects grazing concurrently on algal species composition. Finally, we assessed the relative importance of and potential interaction of nutrient enrichment and grazing on algal communities.

Materials and methods

Artificial stream system

Artificial streams were constructed to simulate conditions in the East Branch of the Maple River at the University of Michigan Biological Station, Pellston, MI (45°45'N, 84°75'W). The Maple River originates from Douglas Lake which strongly influences the ambient nutrient concentrations. PO_4^{3-} and NO_3^- concentrations in the river prior to experiments were 3.13 ± 0.63 $\mu g\, l^{-1}$ and $10.8\pm0.24\, \mu g\, l^{-1}$ respectively, and did not vary significantly during the study period. The biota of the Maple River have been well documented (Miller *et al.*, 1987, Stevenson & Hashim, 1989; Barnese & Lowe, 1992).

All experiments were executed in cylindrical recirculating Plexiglas laboratory stream chambers (diam.: 25 cm), containing two liters of water collected from the East Branch of the Maple River and filtered twice with #20 plankton net to remove most of the seston. Each stream chamber was placed on the top of a magnetic plate and water was circulated continuously by a magnetic stir bar in the chamber. The water

was renewed every 24 hours with fresh filtered stream water. Water temperature was maintained at approximately 22 °C and the light intensity was adjusted to 120 $\mu E\, m^{-2}\, sec^{-1}$ with the photoperiod of 16L:8D to simulate the conditions in the East Branch of the Maple River.

Clay tiles (23.04 cm^2), used as artificial substrate, were colonized by algae in the East Branch of the Maple River for 4 weeks (from July 12 to August 9, 1991), and transported to the laboratory in river water. All visible invertebrates were removed under the dissecting microscope, and three randomly chosen tiles were placed in each chamber (1 chamber=1 replicate).

Experimental design

Experiment 1 — Effects of nutrient enrichment on periphyton
Three treatments, with 3 replicates of each, were used to assess the effect of nutrient enrichment on periphytic communities: (1) control (ambient nutrient level), (2) phosphate-PO$_4$ enrichment, and (3) phosphate-PO$_4$ plus nitrate-NO$_3$. A NO$_3$-N alone treatment was not included because previous experiments indicated that phosphorous was the primary nutrient limiting total algal accrual in the East Branch of Maple River (Y. Pan unpublished data). Nutrients were added with each 24-h water renewal to yield P and N levels of 25 $\mu g\, l^{-1}$ and 112 $\mu g\, l^{-1}$, approximately 8 and 6 times higher than the ambient level, respectively. The experiment was terminated and periphyton on tiles was collected after 6 days when accumulation of periphyton was so high that sloughing appeared imminent in nutrient-enrichment treatments.

Experiment 2 — Effects of grazers on periphyton
Four *Helicopsyche* densities with 3 replicates each were chosen as follows: (1) zero (no grazers), (2) low (1 grazer/tile, 435 grazers m^{-2}), (3) medium (5 grazers/tile, 2174 grazers m^{-2}) (close to the natural grazer density), and (4) high (10 grazers/tile, 4348 grazers/m^2). All treatments were P-enriched at 25 μg l^{-1} for 3 d prior to grazer introduction to offset the fact that algal density was extremely low even after 4 weeks of colonization in the East Branch of the Maple River. Water was renewed daily as in Experiment 1. Grazers in low and medium density treatments consistantly remained on the tiles. However, 2 or 3 *Helicopsyche* repeatedly moved off the tiles only after 1 d grazing in high density treatments. The individual grazers which

left the tiles were put back to the tiles whenever they were found to be off the tiles. The grazing experiment was terminated after 3 d when periphyton appeared scarce in high density treatments.

To assess the concurrent effects of two contrasting grazers on periphyton, we introduced a second grazer, the mayfly *Baetis tricaudatus*, into the stream chamber concurrently with *Helicopsyche*. We used 2 treatments with 3 replicates for each: *Helicopsyche* alone (10/tile), *Helicopsyche* (5/tile) plus *Baetis* (20/chamber). All treatments were P-enriched at 25 μg/L for 3 d prior to grazer introduction and throughout the experiment period. It was difficult to confine all of the *Baetis* to times (some *Baetis* grazed on periphyton accumulated at bottom of chamber). The concurrent grazing experiment was terminated after 3 d.

Experiment 3 — Interactive effects of nutrient addition and grazing

A third experiment was executed to examine the relative importance of and potential interaction between *Helicopsyche* grazing and P enrichment on the periphyton communities. The experimental variables were (1) nutrient: P enriched (25 μg l^{-1} and unenriched (ambient P level), and (2) grazing: grazed (5 grazers/tile) and ungrazed (no grazers). Each treatment was replicated 3 times and periphyton was collected after 6 d.

Periphyton analysis

One tile from each chamber (1 tile/replicate) was sampled before experimental manipulations were begun to examine the homogeneity of periphytic communities among the chambers. The remaining 2 tiles in each chamber were sampled after the termination of the experiments. Periphyton was scraped from the tile surface. The algal samples were adjusted to constant volumes with distilled water and preserved with 3% gluteraldehyde.

Cell density was estimated by direct counting with a Palmer-Maloney nannoplankton counting chamber under the compound microscope at 400×. Living algal cells were counted in randomly chosen fields until 500 algal cells were counted. Cell biovolume was estimated based the geometric shapes of the taxa. Permanent diatom slides used for species identification were prepared using the acid cleaning and Hyrax mounting procedure (Patrick & Reimer, 1966).

Statistical analysis

The normality of sampling distribution and equality of variances were assessed to determine if data transformation was required to perform parametric analysis (Zar, 1984). Biovolume data were log$_{10}$(X+1) transformed. All proportional data (relative abundance) were arc-sine transformed prior to analysis. The accrual rate of algal populations (a ln cells/cm^2/day) in Experiment 2 was estimated as follows:

$$a = Ln(N_t/N_o)/T,$$

where N_t is size of populations at time T, N_o is initial size of populations, T is experimental duration.

The effects of nutrient enrichment on algal biovolume were tested by one-way analysis of variance (ANOVA) followed by the multiple comparison test (SNK) if the null hypothesis was rejected (Zar, 1984). The effects of *Helicopsyche* densities on algal accrual rates and total biovolume were assessed by one-way ANOVA with regression. This analysis allowed us to assess the significance of the linear relationship between algal accrual and grazer densities and deviation from the linear regression. If linear regression was not significant, further regression analysis was performed excluding the high density data which were believed to cause significant deviation. All reported coefficiency of regression and slopes in the results section were calculated without the high density data. The concurrent effects of 2 grazers on periphyton were assessed by a student t-test. The interactive effects of *Helicopsyche* grazing and P enrichment on periphyton were tested with a two-way ANOVA.

Results

Effects of nutrient enrichment on periphyton

Algal biovolume was not significantly different among the stream chambers before the experiment ($p>0.05$, ANOVA), however the algal community responded significantly to nutrient enrichment (Fig. 1, 2). After 3 days of enrichment, total algal biovolume in P+N treatment was approximately 3.5-fold higher than the controls ($p=0.007$ ANOVA) (Fig. 1a). Phosphorus alone did not significantly increase algal biovolume when compared with the controls ($p>0.05$, SNK). After 6 days of enrichment, total algal biovolume was approximately 3.5-fold higher in P and P+N treatments than
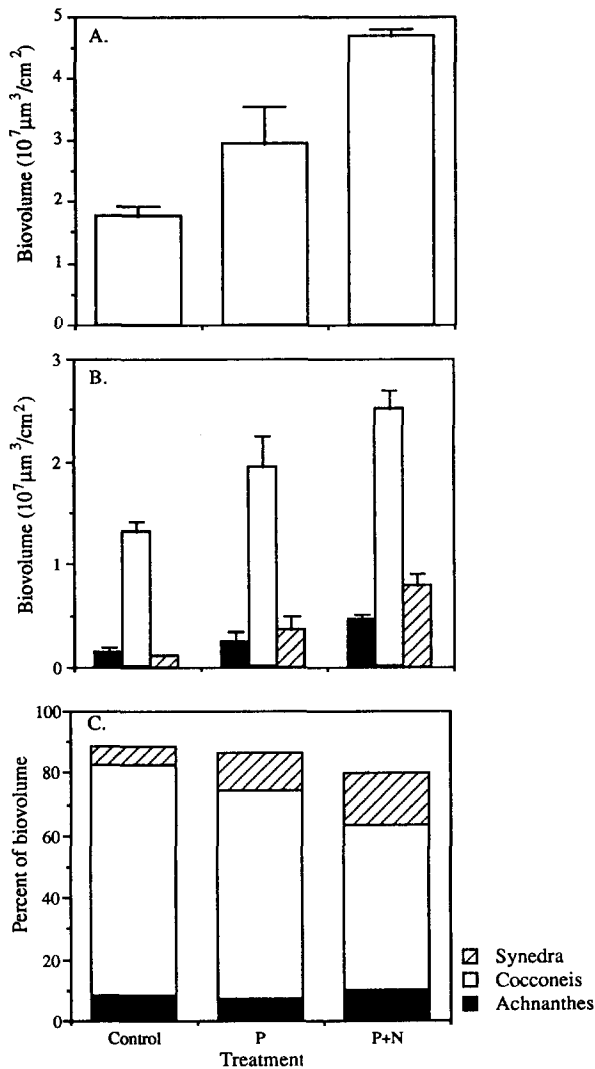
Fig. 1. Algal responses after 3 days of nutrient enrichment. (A) Mean algal biovolume (±SE) of periphytic communities. (B) Mean algal biovolume (±SE) of selected common algal taxa. (C) Relative abundance of the selected common taxa as a percentage of total algal biovolume. C: control treatment, P: phosphate-P enriched treatment, and P+N: phosphate-P plus nitrate-N enriched treatment.

Fig. 2. Algal responses after 6 days of nutrient enrichment. (A) Mean algal biovolume (±SE) of periphytic communities. (B) Mean algal biovolume (±SE) of selected common alga taxa. (C) Relative abundance of the selected common taxa as a percentage of total algal biovolume. C: control treatment, P: phosphate-P enriched treatment, and P+N: phosphate-P p nitrate-N enriched treatment.

in the controls (p=0.03, ANOVA) (Fig. 2a). There was no significant difference between the P and P&N treatments (p>0.05, SNK).

Diatoms represented an average 97.2% of the total algal biovolume. Of the 37 diatom species identified, *Achnanthes minutissima*, *Cocconeis placentula*, and *Synedra ulna* were dominant, comprising an average of 75% of the total diatom biovolume. *Cocconeis* significantly responded to P+N after 3 days of enrichment
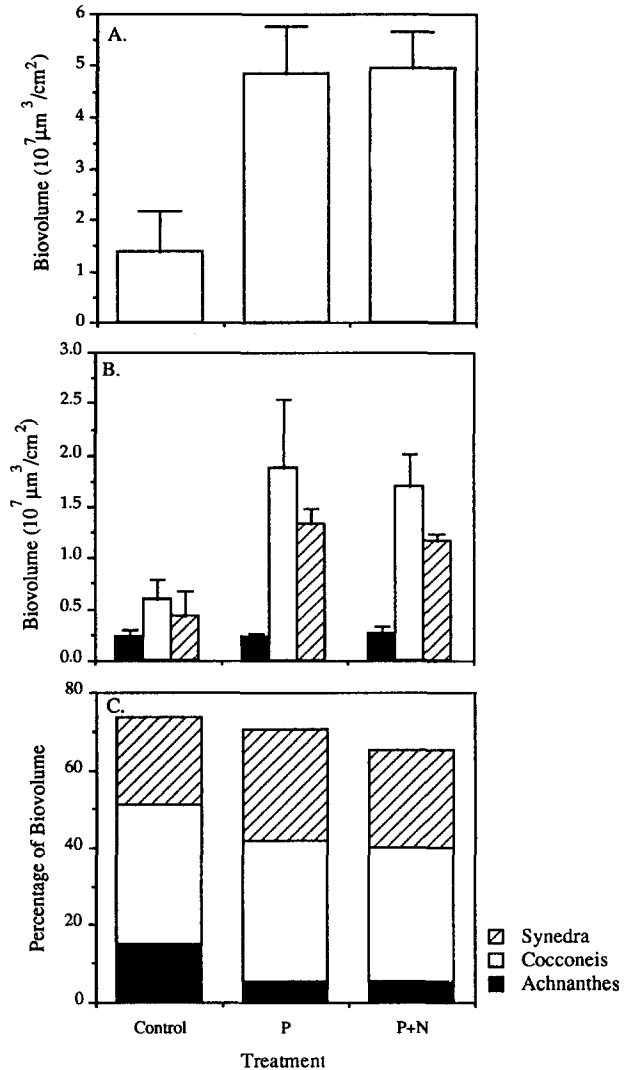
(p=0.02 ANOVA). *Synedra* responded to both P and P+N (p=0.007 ANOVA) (Fig. 1b). However, *Synedra* was the only common species that exhibited a significant positive response to P and P+N enrichment after 6 days of enrichment (p=0.02 ANOVA) (Fig. 2b). *Cocconeis* showed similar but non-significant response (p>0.05 ANOVA). *Achnanthes* showed no response to the nutrient enrichment through the entire experiment (p>0.05 ANOVA). The relative abundance of the 3

dominant diatom species, as a percent of total biovolume, did not differ among nutrient treatments ($p>0.05$ ANOVA) (Fig. 1, 2c).

Effects of grazing on periphyton

An inverse relationship between algal biomass and *Helicopsyche* densities was observed. The total algal biovolume was reduced in a linear fashion in response to an increase of *Helicopsyche* densities from zero to medium ($r^2=0.88$, regression). However, an increase of grazer densities beyond medium densities did not yield a further significant decrease of algal biovolume (Fig. 3a). Significant deviation from linear regression indicated that the linear relationship between algal biovolume and 4 grazer densities was not significant (Table 1). The accrual rates of all 3 species responded to the increase of grazer densities in a fashion similar to total biovolume except *Achnanthes* whose accrual rate decreased continuously ($r^2=0.80$, Fig. 3b). With an increase of grazer densities from zero to medium, the rate of decrease in accrual rates was not significantly different among the three species, as indicated by their slopes (*Achnanthes*: -0.125, *Cocconeis*: -0.094, *Synedra*: -0.113). However, with high grazer densities, *Synedra* accrual slowed down to around -0.2 Ln cells cm^{-2} d^{-1}. The accrual of *Cocconeis* was about -0.5 Ln cells cm^{-2} d^{-1} (Fig. 3b).

Relative abundance of *Synedra* responded positively to increases of *Helicopsyche* densities ($p=0.04$ ANOVA), increasing from 27% of total algal biovolume in ungrazed treatments to 47% in the presence of high grazer densities (Fig. 3c). Conversely, relative abundance of *Achnanthes* showed a significant negative response to grazing ($p=0.03$ ANOVA, H<L=0, SNK). Relative abundance of *Cocconeis* was not significantly influenced by *Helicopsyche* density ($p>0.05$ ANOVA).

Concurrent effects of 2 grazers on periphyton

Total algal biovolume was significantly decreased by concurrent grazing relative to grazing by *Helicopsyche* alone ($p=0.02$ *t*-test). The accrual rate of *Synedra* was significantly decreased ($p=0.03$ *t*-test), however concurrent grazing had no significant effect on accrual rates of either *Cocconeis* or *Achnanthes* when compared to *Helicopsyche* alone. Relative abundance of *Cocconeis* increased significantly, from approximately 20% to 80% ($p=0.01$ *t*-test) with the addition of *Baetis* (Fig. 3c). Conversely, *Synedra* decreased in relative

Table 1 (A). ANOVA table. Log-transformed total biovolume is the dependent variable. The independent variable is grazer density (0, 1, 5, and 10 per tile).

Source	DF	SS	MS	F
Among groups	3	1.258	0.419	52.375***
Linear regression	1	1.066	1.066	11.104 n.s.
Deviations from regression	2	0.192	0.096	12.000*
Within groups	8	0.065	0.008	
Total	11	1.323		

Table 1 (B). The dependent variable: accrual rate of *Achnanthes*

Source	DF	SS	MS	F
Among groups	3	1.474	0.491	15.839**
Linear regression	1	1.370	1.370	26.346*
Deviations from regression	2	0.104	0.052	1.677 n.s.
Within groups	8	0.249	0.031	
Total	11	1.723		

Table 1 (C). The dependent variable: accrual rate of *Cocconeis*

Source	DF	SS	MS	F
Among groups	3	0.564	0.188	15.667*
Linear regression	1	0.455	0.455	8.273 n.s.
Deviations from regression	2	0.109	0.055	4.583*
Within groups	8	0.097	0.012	
Total	11	0.661		

Table 1 (D). The dependent variable: accrual rate of *Synedra*

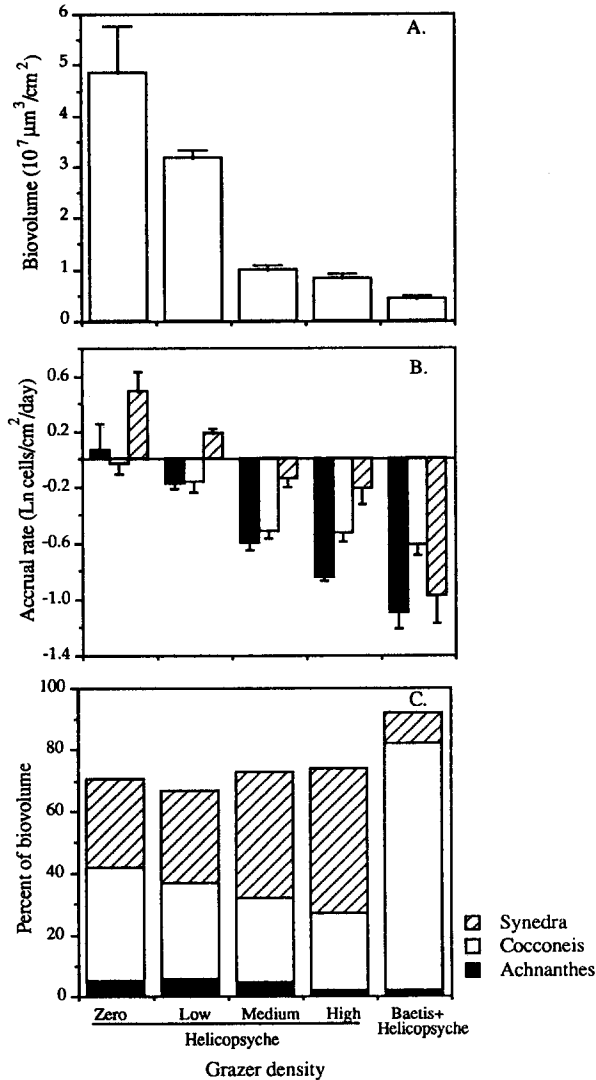| Source	DF	SS	MS	F
Among groups	3	0.928	0.309	10.655*
Linear regression	1	0.741	0.741	7.925 n.s.
Deviations from regression	2	0.187	0.094	3.224 n.s.
Within groups	8	0.234	0.029	
Total	11	1.162		

* At 95% significant level.

Fig. 3. Algal responses to increases of *Helicopsyche* densities and concurrent grazing by *Helicopsyche* and *Baetis*. (A) algal biovolume (mean±SE) of periphytic communities (B) Mean algal accrual rates (±SE) of selected algal taxa (C) Relative abundance of common taxa as a percentage of total algal biovolume. Zero: no grazer, Low: 1 *Helicopsyche*/tile, Medium: 5 *Helicopsyche*/tile, High: 10 *Helicopsyche*/tile, *Baetis*+ *Helicopsyche*: 5 *Helicopsyche*/tile and 20 *Baetis*/chamber. The tile area=22.03 cm².

abundance from approximately 50% to 10% (p=0.01 t-test) (Fig. 3c). Relative abundance of *Achnanthes* was not influenced by addition of a second grazer.

Interactive effects of nutrients and grazing on periphyton

A significant interactive effect of nutrient enrichment and grazing on the periphytic community was indicated by a two-way factorial analysis (Grazing effect: p=0.006, P effect: p=0.02, and interaction of grazing and P: p=0.03) (Fig. 4). In the absence of *Helicopsyche* grazing, P-enrichment elevated algal biomass nearly 4-fold relative to unenriched treatments. There was, however, no significant difference between P enriched and non-P enriched treatments in the presence of grazers.

Discussion

Algal response to nutrient enrichment

Periphytic algal biomass was primarily phosphorus limited in the East Branch of the Maple River. A stimulating effect of nutrients on algae was expected since the stream is fed by the lake water from the epilimnion of Douglas Lake, where nutrient depletion (both phosphate-P and nitrate-N) is often severe during the summer (Fairchild *et al.*, 1985).

Algal species' responses to nutrients shifted through 6-d nutrient enrichment. Such a shift may reflect an interaction between understory (adnate diatoms such as *Cocconeis* and *Achnanthes*) and overstory diatoms (erect diatoms such as *Synedra*) as the community develops, increasing the potential impact of community structural complexity on individual species growth. Paul & Duthie (1989) have shown that the growth of overstory algae become the most important component of community change while understory algal species' density remains largely unchanged as algal communities develop. Regulatory forces might vary at population level through 6-d experiment. For example, understory species may experience nutrient limitation and then light limitation due to growth of overstory species (Meulemans, 1987; Paul & Duthie, 1989). Both *Cocconeis* (understory) and *Synedra* (overstory) significantly responded to nutrients after 3-d enrichment. However, the increase of *Synedra* was much faster than *Cocconeis*. Therefore, community growth was heavily correlated with the growth of *Synedra*. The net increase ot total biovolume in the phosphate-enrichment treatment between day 3 and 6 resulted mainly from growth of *Synedra*. Fast growing *Synedra*, with rosette-like colonies, may

shade adnate diatom species. Similar community shifts resulting from overstory taxa-specific growth was also reported by Pringle & Bowers (1984).

The short-lived increase of *Cocconeis* growth in response to nutrients may indicate an inability to respond to increases in water column nutrients in a mature algal communities. *Cocconeis* was reported as the dominant diatom (70%) in a down stream site with low nitrogen in a Montana stream (Marcus, 1980). It was almost absent in an upstream site where the nitrogen level was high due to nitrogen enrichment from a hypolimetic reservoir release. Marcus suggested that this species may be able to compete for nitrogen in nitrogen limited habitat. In this study, nutrients were supplied every 24 hr in the water column. Algal species that have high uptake rates should be able to accumulate large quantities of nutrients in a short time period (Suttle & Harrison, 1988). *Synedra*, with its erect growth form and large surface area, may be able to respond to increases of nutrients in the water column better than *Cocconeis*. Pringle (1990) found that *Cocconeis* only responded to substrate nutrient enrichment but failed to respond to similar nutrient enrichment in the water.

Algal species response to an increase of grazer densities

Agal biomass, as total biovolume, decreased in an exponential negative linear fashion in response to an increase of *Helicopsyche* densities. This result is consistent with those of a previous study by Lamberi *et al.* (1987b), where algal biomass was expressed as chl a and AFDM. Algal species, however, showed differential responses to an increase of grazer densities. The decrease of accrual rates of *Cocconeis* and *Synedra* reached different plateaus. These differences may reflect different strategies in coping with intense grazing pressure. Species may be able to maintain their relatively sizable populations while being grazed by either physically resisting grazing or by quickly recovering from grazing. Differential algal strategies may be reflected by their growth form, physiognomy, and growth rates.

Cocconeis is often considered to be a grazer-resistant diatom species. This adnate diatom is commonly present and often dominant in algal communities grazed by caddisflies (Lamberti *et al.*, 1987a; Steinman *et al.* 1987), mayflies (Colletti *et al.*, 1987; Hill & Knight, 1987), or snails (Steinman *et al.*, 1987; Lowe & Hunter, 1988). This taxon can secret a tough
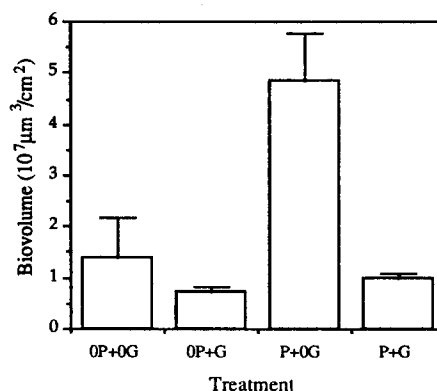

Fig. 4. Interactive effects of P and *Helicopsyche* grazing on algal biovolume (mean±SE) of periphytic communities. OP+OG: no phosphate enrichment and no grazers, OP+G: no phosphate enrichment and with grazers (5 *Helicopsyche*/tile), P+OG: phosphate enrichment and no grazers, and P+G: phosphate enrichment and with grazers (5 *Helicopsyche*/tile).

mucilage which can secure the firm attachment of the entire valve to substrate (Patrick, 1948). However, the fact that *Synedra'* s relative abundance, as total biovolume, increased in high density grazer treatments relative to ungrazed and low grazing densities seems difficult to interpret. *Synedra* is seldom regarded as grazer-resistant species. Steinman *et al.* (1987) found that response of this species to grazing by snails or caddisflies did not show a consistent pattern. We speculate the following reasons to account for the success of *Synedra*. *Synedra* had much higher accrual rate than *Cocconeis* and *Achnanthes*, even under ambient nutrient conditions. Fast growth rate may be due to its growth form. In naturally colonized communities under natural grazing pressure in the East Branch of the Maple River, *Synedra* comprised less than 10% of total algal biovolumes. *Synedra* was the main overstory species in this simply structured algal community. With an erect growth form, it may gain an advantage in both harvesting light energy and utilizing dissolved nutrients in flowing water. Steinman *et al.* (1987) found that this species was found relatively abundant in early successional stage and became less important in mature algal communities that were dominated by green filamentous algae in their laboratory streams. In another study, Steinman *et al.* (1989) reported that *Synedra* may require high light intensity. *Synedra* significantly increased its biomass in P and P+N treatments relative to the controls after 6-d of enrichment in our study.

Synedra is often distributed in rosette-like colonies (Steinman *et al.*, 1987). Its patchy distribution may

also decrease its change being grazed relative to more randomly distributed algal species in an 'overgrazed' algal community. *Helicopsyche* has been reported to be a density-dependent grazer that does not actively select any microalgal food types (Vaughn, 1986, but see Feminella & Resh, 1991). Our results showed that all 3 species were almost equally grazed in low and medium grazer densities, as indicated by similar negative regression slopes of algal accrual rates. The increase in relative abundance of *Synedra* in high grazer density treatments may result from decreased grazing efficiency caused by low algal density. Lamberti *et al.* (1987b) reported that *Helicopsyche* may experience intraspecific competition in high densities. They found that growth rates of *Helicopsyche* decreased in response to an increase in densities with high mortality due to starvation and cannibalism. In our study, food limitation in high grazer density treatments was evident, as indicated by low periphyton density and the observation that a few of the *Helicopsyche* constantly emmigrated from tiles even after being put back several times. A similar phenomenon was not observed in other treatments.

Algal species response to concurrent grazing:

Total algal biovolume was significantly reduced by introducing *Baetis* as a second grazer. Our data on the quantitative change of algal biomass due to concurrent grazing are hindered by possible uneven grazing intensity and lack of *Baetis* alone treatment. However, qualitatively, the preferential grazing effect on algae was evident. *Baetis* grazed primarily on *Synedra* and had no effect on *Cocconeis*. These differential grazing effects by *Helicopsyche* and *Baetis* on algae may be a function of differences in their mouth structure, grazing efficiencies, and mobility. *Baetis* can graze on loosely attached overstory algal species with collector-gatherer mouthparts (Merritt & Cummins, 1984). On the other hand, *Helicopsyche* is a scraper with sclerotized mandibles. They move slowly (4.4 cm/h) (Williams *et al.*, 1983) and can scrape periphyton from hard surfaces of the substrates. They may only forage in a limited area due to slow movement and create algal patches. With high mobility, *Baetis* can actively drift and search for food (Kohler, 1985). In a confined space such as our experimental chamber, *Baetis* may graze on tiles repeatedly even when algal densities were very low. A feeding experiment by Scrimgeour *et al.* (1991) indicated that grazing efficiency of *Baetis* increased when algal density was low. Patchy *Synedra* which may possible escape *Helicopsyche* grazing may be preferentially grazed by highly mobile *Baetis*.

Relative importance of nutrient and grazing:

Periphytic algal biomass in the East Branch of the Maple River seems to be regulated by both P and grazing. Enhancement of algal biomass by P enrichment in the absence of grazers represents the growth potential of this community. Such an increase can be dampened or canceled out by grazing activities, implying that grazing may exert a much stronger regulatory impact on algal biomass than nutrients (Stewart, 1987; McCommick &Stevenson, 1989; Hart & Robinson, 1990; Winterrbourn, 1990; Mulholland *et al.*, 1991).

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