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Stream periphyton response to grazing and changes in phosphorus concentration

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Abstract

Grazing by the large caddisfly larva, *Dicosmoecus gilvipes* (Trichoptera; Limnephilidae), drastically reduced periphyton biomass in laboratory channels at a current velocity of 20 cm s^{-1}. Reduction in biomass as chl *a* and AFDW ranged from 88 to 93% and 82 to 85%, respectively. On average, grazing rate increased with in-channel SRP (soluble reactive phosphorus) content from 6 to 10 μg l^{-1}. Grazing rates averaged 25.9–29.3 μg chl *a* m^{-2} d^{-1} and 10.8–12.2 μg chl *a* mg^{-1} d^{-1} based on area and grazer biomass, respectively, with most variability among treatments being due to the grazing effect. Grazing tended to shift the algal community increasingly to filamentous blue-green algae regardless of enrichment. After three weeks, *Phormidium* comprised over 61% of the community in grazed treatments but only 35% in ungrazed treatments. The stalked diatom *Gomphonema* comprised only 4% of the grazed community, but 11% in the three ungrazed channels with similar values for *Scenedesmus*. A model that includes grazing was calibrated to the data and produced a reasonable expectation of periphyton biomass over a range in SRP concentrations. While the model with constant grazer abundance predicts a gradually increasing grazed biomass as SRP increases, grazer production in natural streams may actually increase to accommodate the increased food production.

Introduction

The rate of development and ultimate biomass of periphytic algae in both lotic and lentic environments is determined by several factors, including light, current velocity, temperature, suspended solids, substratum type, phosphorus (P), nitrogen (N), carbon (C), pH, and herbivory. Physical factors such as velocity and suspended solids (Seeley, 1986; Horner *et al.*, 1990) or velocity and nutrient enrichment (Veenstra, 1982; Horner *et al.*, 1983) have an interactive effect on periphyton biomass development. From the latter work, conducted in laboratory channels, a steady-state model was calibrated in which periphytic biomass was determined primarily by velocity and P content (Horner *et al.*, 1983). Further work in the same channels suggested that the combination of increased velocity and suspended solids resulted in a synergistic effect, causing greater erosive losses of periphytic biomass than when either factor was examined alone. The experiments also demonstrated that losses were minor unless there was a substantial, abrupt change in velocity. In addition, *in situ* uptake kinetics showed that periphyton uptake was limited at SRP (soluble reactive phosphorus) content less than about 8 μg l^{-1} (Horner *et al.*, 1990).

Grazing by aquatic insects has been shown to have an overriding influence on periphyton in many situations, as evidenced by a decrease in biomass, an altered rate of primary productivity, and/or a change in taxonomic composition and community structure (Hunter, 1980; Kesler, 1981; Lamberti & Resh, 1983; McAuliffe, 1984; Cattaneo & Kalff, 1986; Jacoby, 1987; Lamberti *et al.*, 1987; Steinman *et al.*, 1987a; Steinman *et al.*, 1987b; Hill & Knight, 1988; Feminella *et al.*, 1989; McCormick & Stevenson, 1989; Steinman *et al.*, 1991; Hill *et al.*, 1992). Lack of suitable habitat for grazers was indicated to be an important factor allowing the development of dense mats of fil-

amentous green algae, such as *Cladophora*, in some environments (Welch *et al.*, 1992).

To better understand the influence of insect grazing on stream periphyton, especially filamentous algae, the combined effect of nutrient enrichment and grazing on periphyton biomass development was studied in laboratory channels. The main objective of the work reported here was to determine the role of grazing by *Dicosmoecus gilvipes* larvae, a herbivorous aquatic insect of the order Trichoptera, family Limnephilidae, on temporal variation of periphyton biomass in combination with enrichment with SRP. Estimates of biomass, as chlorophyll *a* (chl *a*) and ash-free dry weight (AFDW), and community composition were determined in experiments involving six combinations of grazing (grazed and ungrazed) and target SRP levels (0, 15, and 25 μg SRP l^{-1}).

The second objective was to include a grazing term, based on the experimental results, into an equation that predicts biomass accumulation of filamentous algae in lotic environments as a function of SRP. That was done by calibrating the steady-state biomass model of Horner *et al.* (1983) incorporating grazing losses with an improved estimate of maximum achievable biomass, one of the model's parameters, determined by Walton (1990).

Material and methods

Experimental design

Two experiments were performed in a set of 12 channels over the course of two consecutive life cycles (two calendar years) of the caddisfly to examine the concurrent effects of grazing and nutrient enrichment on periphyton biomass. In the first of these two experiments, two levels of in-channel SRP concentration (2 μg l^{-1}, which represented no addition to the concentration of the source water, and 11 μg l^{-1}) and two levels of grazing (grazed and ungrazed) were examined. Each treatment, SRP and grazed/ungrazed, was replicated with a separate channel. Unfortunately, N was not added, and so it was limiting. Therefore, only data for the no SRP addition treatments are reported. In the second grazing experiment, with surplus N added, in-channel SRP concentrations of about 2, 5 and 10 μg l^{-1} were evaluated. These in-channel SRP concentrations resulted from inflow concentrations of about 2, 8 and 15 μg l^{-1}. In both experiments, grazer densities were maintained at 100 larvae m^{-2}, or 20 organisms per grazed channel (0.2 m^2). Velocity was held constant at 20 cm s^{-1} in both grazing studies.

Apparatus

Laboratory channels were used to grow periphyton under constant levels of light, current velocity, nutrients, and grazing and at ambient, but nearly constant temperature. The characteristics of these recirculating channels are detailed elsewhere (Horner *et al.*, 1983, 1990). Briefly, eight to twelve Plexiglas^{TM} channels, 100 cm long, 20 cm wide, and 12 cm in height, were used in all experiments. The channels were arranged on tables in banks of three and shared a common air line and light supply. The water supply was piped to the laboratory under gravity flow from a concrete-lined pond. The pond water was low in nutrient concentration (0.5–2.5 μg SRP l^{-1} and 60 μg NO_3-N l^{-1}) and therefore was ideal for nutrient addition experiments.

Pond water was piped into a series of dilution cells where nutrients were added with the mixture flowing to the channels at a rate of 1 l min^{-1}, giving a water residence time of 16 min. The flow-through delivery system is a modification of the Mount and Brungs (1967) proportional diluter (Seeley, 1986). Concentrated stocks of the nutrients tested were stored in light-shielded, 50-l plastic, Nalgene^{TM} carboys and were pumped to the dilution cells using a Cole-Parmer Masterflex peristaltic pump, model 7658, through size 13 Tygon^{TM} tubing. The nutrient stock was delivered to the dilution cells at a constant flow rate of 2.5 ml min^{-1}. The dilution cells served to mix the concentrated nutrient solution with the incoming nutrient-poor pond water. The solution then flowed to the individual channels through light-shielded latex rubber tubing (6.25 mm O.D. × 2.34 mm I.D.). Figure 1 shows the water-nutrient delivery system.

Nutrient stock concentrations were determined using a nutrient mass balance based on the targeted SRP and N concentrations desired and the background pond water SRP and N concentrations. Briefly, using the nutrient mass balances, the amount of P as K_2HPO_4 and N as $NaNO_3$ needed was calculated to attain the target concentrations for the channel inflows. Nitrogen was added in sufficient quantities to attain a N:P ratio of 15:1, which is double the Redfield ratio, so that P would be limiting (Redfield *et al.*, 1963; Rhee, 1978).

Instream velocity was controlled using a compressed air system described by Horner *et al.* (1983).

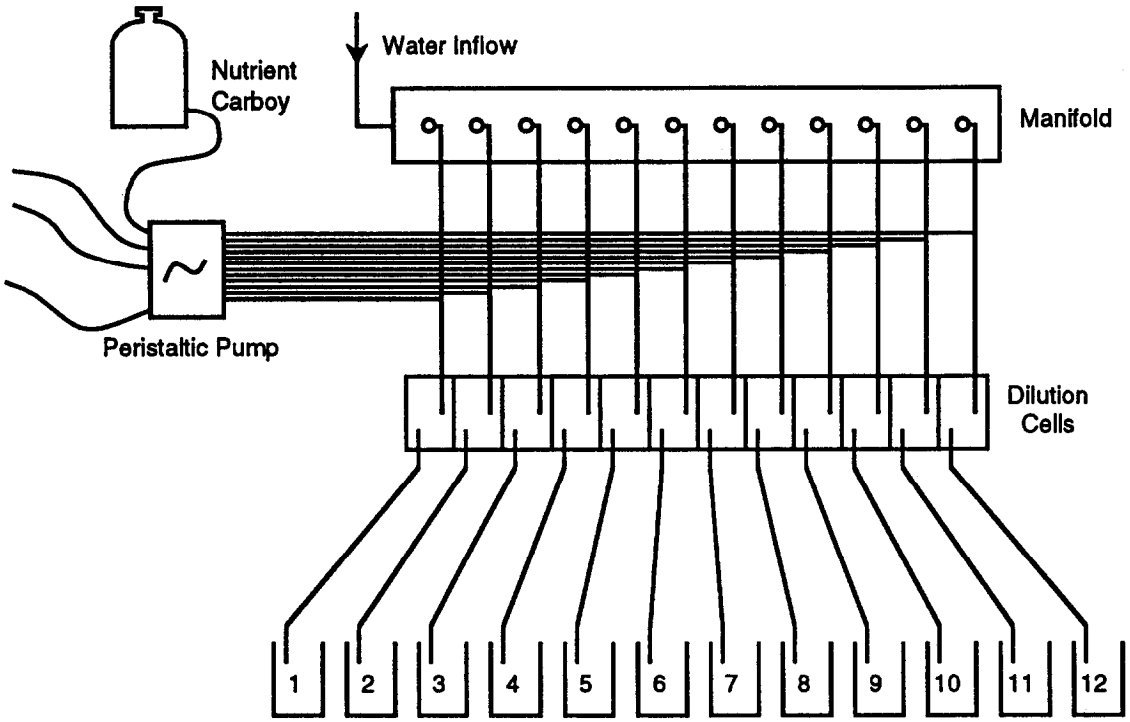

Fig. 1. Nutrient delivery system for laboratory channel experiments.

Briefly, four main feeder lines, connected to the main air supply line (100 psi), were fed into a small manifold made of ABS plastic pipe, 25.4 cm long by 6.35 cm diameter, and capped at both ends. A main air line entered each of the four manifolds at one of the capped ends. Each manifold was fitted with six small Tygon™ tubes (6.4 mm O.D., 3.2 mm I.D.), which entered opposite ends of each channel. A 1-ml plastic disposable pipette was attached to each Tygon™ line and extended horizontally 15 cm into the channel at mid-depth. A stable average velocity produced by the injected air was provided, although a velocity gradient was present in each channel. Velocity was measured in representative channel areas using a Marsh-McBirney flow meter and an average channel velocity calculated. Air-flow was adjusted at one of the four main feeder lines to achieve the target velocity of 20 cm s^{-1} in each set of channels.

Light was provided using four 91.4 cm long Phillips warm white F40 fluorescent bulbs mounted 60 cm above each channel. A 16 hour light and 8 hour dark photoperiod was set and controlled using 24 hour automatic timers. Light was measured using a Spectra Lumicon Series II light meter (Photo Research, Burbank, CA). The readings were taken directly above the water surface of the channels. The average intensity measured was 194 μE m^{-2} s^{-1}, which was consistent with that used in past experiments (Veenstra, 1982; Horner *et al.*, 1983; Seeley, 1986). Water temperature was nearly constant in the two experiments with the same means (19.8 °C) and SDs of 0.6 and 0.9 °C, respectively.

Periphyton colonized natural cobble substrata, which were subsequently sampled for biomass analyses. Cobble size ranged from 35 to 100 mm in length and the stones were arranged to cover the bottom of the channels completely. The total number of stones placed in the individual channels ranged from 56 to 60. A small glass petri-dish filled with sand, from the grazers' parent stream, was placed in all channels so that the larvae could build and repair cases.

The artificial channel substratum was equally divided into six 0.27 × 0.1 m areas containing 9–10 cobbles each, from which biomass was subsampled. The substratum was subdivided and subsampled in order to account for possible variation in periphyton growth due to the velocity gradient created by the air injection system.

To seed the laboratory channels, filamentous periphyton was collected from one of three local streams

(Walton, 1990). Periphyton was removed from heavily colonized rocks by scraping the surface of the rock with a brush or piece of Plexiglass™ into a bucket of stream water. The contents were transported back to the laboratory where the mixture of loose periphyton and stream and pond water was blended for 30 seconds until homogenized (Steinman & McIntire, 1986; Lamberti *et al.*, 1987). The periphyton slurry was added in equal proportions to all of the channels. The actual volume of the homogenized mixture added varied between 500 and 1000 ml for each experiment depending on the dilution volume needed to easily blend the mixture. The chl *a* concentration of the slurry ranged from 90 to 150 mg m^{-3} and the dominant was *Cladophora*.

During the first 1–1.5 hours after channel seeding, current was stopped in order to facilitate the settlement of the added periphyton onto substratum surfaces. During this period of zero velocity, water exchange in the channels continued so that no appreciable increase in temperature occurred. Before treatments were initiated, channel periphyton was allowed to establish for 7–12 days under a 16-hour day photoperiod at a velocity of 20 cm s^{-1}.

Fifth instar larvae of *Dicosmoecus gilvipes* were collected from the Raging River, Fall City, WA, during June 1988 and June 1989 for the two grazing experiments. Twenty larvae of similar size were placed in each channel designated as grazed within 1.5 hours of collection.

Experiment initiation and duration

All experiments began 7–12 days after substrata in the channels had become visibly colonized with the introduction of larvae and nutrient additions. The channel periphyton biomass at experiment initiation varied from 27 to 47 and averaged 39 mg chl *a* m^{-2}.

Both experiments were performed for about a month (28–32 days), which included the initial biomass colonization period. Maximum biomass was assumed to have been reached within that period, as had been shown in previous studies (Horner *et al.*, 1990). The sampling schedule varied slightly for each experiment. Several constituents were examined in each experiment including SRP, TP, nitrate + nitrite-nitrogen ($NO_3 + NO_2$-N), AFDW, chl *a*, and taxonomic composition.

Water quality

Inflow samples for SRP, TP and $NO_3 + NO_2$-N were collected directly from channel inflows. In-channel samples for SRP, TP and $NO_3 + NO_2$-N were collected near the channel outflow. Samples for SRP were collected every three days starting on the second day of nutrient addition. Samples for TP were collected every six days starting on day five. Samples for $NO_3 + NO_2$-N analysis were taken on day 5 and day 20 after nutrient addition.

Samples were collected in acid-washed 250 ml or 500 ml polyethylene bottles. Samples for SRP and $NO_3 + NO_2$-N were immediately passed through 0.45 μm Millipore filters, which had been presoaked in deionized water for 12–24 hours. The filtrate was transferred to individually labeled 120 ml polyethylene bottles and frozen until analyzed. Samples for TP were transferred directly to 120 ml bottles, containing 1 ml of concentrated sulfuric acid and stored frozen.

SRP was determined to a detection limit of 2 $\mu g\ l^{-1}$ by the ascorbic acid-molybdenum blue method (APHA, 1985) with absorbance determined at 850 nm on a Spectronic 2000 spectrophotometer. Samples for TP were digested with persulfate prior to analysis for SRP. $NO_3 + NO_2$-N was analyzed to a detection limit of 10 $\mu g\ l^{-1}$ using the cadmium reduction method on an ALPKEM RFA-300 autoanalyzer.

Periphyton

Samples for periphyton biomass (as chl *a* and AFDW) and taxa composition were removed from six stones during each sampling date. Each single stone was randomly selected from one of the six sub-areas per channel. Biomass was removed from a 1.25 cm^2 area of stone surface enclosed by an inverted 60-ml polyethylene bottle with its bottom removed and scraping the area outlined with a stiff brush. A partial collection of two stones per channel was made on day 1 of each experiment to determine initial biomass. Complete biomass and taxonomic samples from six stones per channel were collected 10–14 days after nutrient addition with subsequent collections continuing on a weekly basis for two additional weeks. Sampled stones were returned to their respective channels and were not resampled.

Periphyton was scraped from sample stones and gently rinsed into a 133 ml amber jar and then vacuum filtered directly onto a 25 mm glass fiber filter. For chl *a*, one drop of 1% $MgCO_3$ solution was added

to the filter prior to filtration. The filters were stored frozen in desiccant in the dark until analyzed. Samples were similarly collected for AFDW analysis, except samples were filtered onto pre-ashed (15 minutes at 500 °C) and tared 25 mm glass fiber filters.

The sample for taxa composition also was removed from each stone and stored in the dark in a 133 ml amber glass bottle preserved with 15 drops/100 ml of Lugol's solution. Samples for each channel were composited before analysis.

Chl *a* was determined with a Perkin-Elmer Lambda 3 Scanning Spectrophotometer, following an 18–24 hour extraction in 90% acetone (APHA, 1985). Chl *a* concentration was calculated using a modification of the Lorenzen (1967) method with correction for phaeophyton (APHA, 1985).

Filters for AFDW were dried for 24 hours at 105 °C and weighed to the nearest 0.1 mg. The samples were ashed for one hour at 500 °C, after which they were transferred to a desiccator before weighing. AFDW was determined as the difference between weight after one hour at 500 °C and the pre-weighed sample and expressed as mg AFDW m^{-2} (APHA, 1985).

Samples for taxonomic analysis were concentrated to 25 ml after settling for at least one week. Subsamples were diluted as needed to contain at least 250 live algal units, which were defined as a single cell, a single filament or multiple cells in the case of some diatom clumps. Units were identified and enumerated along transects across the width of a Sedgewick-Rafter counting cell at 200 ×, and the resulting data in algal units were used to calculate percent dominance.

Grazing rates

Areal grazing rates were determined as the difference between periphyton biomass (mg chl *a* m^{-2} and g AFDW m^{-2}) in the ungrazed and grazed treatments. The difference in biomass was assumed to approximate the amount of periphyton grazed in a 0.2 m^2 area at a grazer density of 100 larvae m^{-2}. For time t then, periphyton removal rate is equal to

$$(B_{ug} - B_g)/t,$$

where t is the number of days of growth, B_{ug} is the ungrazed biomass and B_g is the grazed biomass. Grazing rates per dry weight of grazer (mg chl *a* mg DW^{-1} d^{-1}) were approximated by assuming a mean dry weight (DW) of 24±4 mg per fifth instar larva (Jacoby, 1986). For time t, the removal rate is equal to

$$[(B_{ug} - B_g)/t]/[GD * DW],$$

where GD is the density of grazers in no. m^{-2}.

Statistical treatment

A two-factor ANOVA was used to evaluate the significance of SRP, grazing, and SRP × grazing interaction on periphyton biomass. Subsamples were combined into a single datum for each experimental unit (channel) and formal analyses of subsamples were omitted (Hurlbert, 1984). Standard errors of the biomass means (chl *a* or AFDW) were calculated for all duplicated treatments ($n = 2$) and for water quality samples collected over the course of the experiment. Multiple comparisons among treatment means were made for both chl *a* and AFDW results using the Tukey test (Zan, 1984).

The index of AFDW/chl *a* was used to evaluate the nutritional state of ungrazed versus grazed periphyton communities over time. AFDW/chl *a* is recognized as an autotrophic index with tresholds established for organic pollution (Collins & Weber, 1978).

Experimental results

In-channel removal of SRP

Mean channel nutrient concentrations are shown in Table 1. Average unenriched inflow SRP in the control channels was 2 $\mu g\ l^{-1}$. In-channel concentrations without enrichment were reduced by about 10%. N/P ratios in the enriched channels were well above the target 15/1, averaging 34±5. Ratios averaged 11±4 in the unenriched channels.

SRP removal, calculated as the difference between channel inflow and in-channel concentrations, increased over time until day 14 in the enriched treatments in experiment 2. In contrast, removal in the control channel (2 $\mu g\ l^{-1}$) remained near zero for the entire experiment (Fig. 2). Utilization of SRP in the grazed treatments with added SRP was consistently lower than that found in the ungrazed treatments. A similar pattern of low removal was observed for the unenriched treatments in experiment 1.

TP concentration among all channels, whether enriched or not, remained rather consistent (mean 45±9 $\mu g\ l^{-1}$).

Table 1. Mean inflow and channel nutrient concentrations (+/-1 SE) during two grazing experiments.

C[a]	Inflow SRP[b]	Channel SRP[b]	Channel NO_3[b]	N:P	Channel Tp[b]
Experiment 1 (*n*)	8	8	2	3	
PW	2.6(0.4)	*	69.2(1.0)	26.6	23.8(2.2)
1G	2.3(0.3)	2.1(0.2)	58.1(7.2)	28.1	21.5(1.1)
6UG	2.3(0.3)	1.6(0.2)	47.8(28.9)	29.9	22.6(1.7)
7UG	2.1(0.3)	1.6(0.2)	42.0(15.1)	26.2	22.1(1.6)
8G	2.2(0.3)	1.6(0.2)	44.3(16.0)	27.5	22.7(1.6)
Experiment 2 (*n*)	7	7	2	3	
PW	1.6(0.1)	*	36.1(0.3)	22.6	34.8(3.7)
1G	1.8(0.1)	2.0(0.1)	20.7(10.0)	10.4	34.3(2.4)
2UG	14.3(1.0)	8.6(0.8)	309.9(18.0)	36.0	47.0(2.6)
3G	15.0(1.1)	10.0(0.8)	313.1(18.2)	31.3	54.9(5.7)
4UG	15.1(1.0)	9.5(0.6)	336.7(33.6)	35.4	52.1(3.3)
5UG	8.4(0.7)	4.7(0.2)	201.9(14.9)	43.0	46.6(5.9)
6G	8.6(0.7)	6.8(0.7)	201.8(8.0)	29.6	51.9(4.1)
7G	8.1(0.7)	6.0(0.7)	190.4(2.9)	31.7	59.3(10.5)
8UG	8.4(0.6)	4.0(0.3)	142.6(3.9)	35.7	43.3(9.1)
9G	1.6(0.1)	1.7(0.1)	27.4(3.92)	16.1	37.3(1.8)
10UG	2.0(0.5)	1.8(0.1)	15.7(5.0)	8.7	32.7(4.3)
11UG	1.6(0.1)	1.8(0.1)	16.0(9.8)	8.8	34.1(2.9)
12G	13.8(1.0)	9.9(1.0)	290.7(0.0)	29.4	51.3(3.5)

a - number indicates channel (C)
b - concentrations in $\mu g\ l^{-1}$
n - sample site per treatment
- measurement not taken
G - grazed treatments
UG - ungrazed treatments
PW - pond water

Response to nutrients and grazing

Grazing also had a substantial effect on periphyton biomass expressed either as chl *a* or AFDW throughout the experimental period (Fig. 3). Reduction in biomass as chl *a* determined weekly averaged 90±3% and about 84±2% as AFDW. As much as 485 mg chl *a* m^{-2} was removed at the medium level of enrichment. Chl *a* was similarly reduced in experiment 1 (unenriched) from 287 mg chl *a* m^{-2} in the ungrazed treatment to 9.7 mg chl *a* m^{-2} in the grazed treatment. AFDW was reduced from 28.9 g m^{-2} to 3.5 g m^{-2}.

Differences in treatment means for chl *a* and AFDW data on day 21 were tested by two-factor analysis of variance (ANOVA). Chl *a* data were log transformed to meet the test assumption for homogeneous variances of treatment means. Transformation was unnecessary for AFDW data. The reduction in biomass, as chl *a* (Fig. 3a), due to grazing was highly significant ($p<<0.0005$). The increase in biomass (chl *a*) due to SRP enrichment was also significant ($p<0.01$). No significant interaction between grazing and SRP was found (Table 2). Based upon multiple comparisons among treatment means, biomass (chl *a*) values were not significantly different ($p<0.05$) among grazed, unenriched treatments. For grazed, enriched treatments, however, chl *a* was significantly different ($p<0.05$) from grazed, unenriched treatments. No significant differences ($p<0.05$) in biomass as AFDW in grazed or ungrazed, enriched treatments were observed (Fig. 3b).

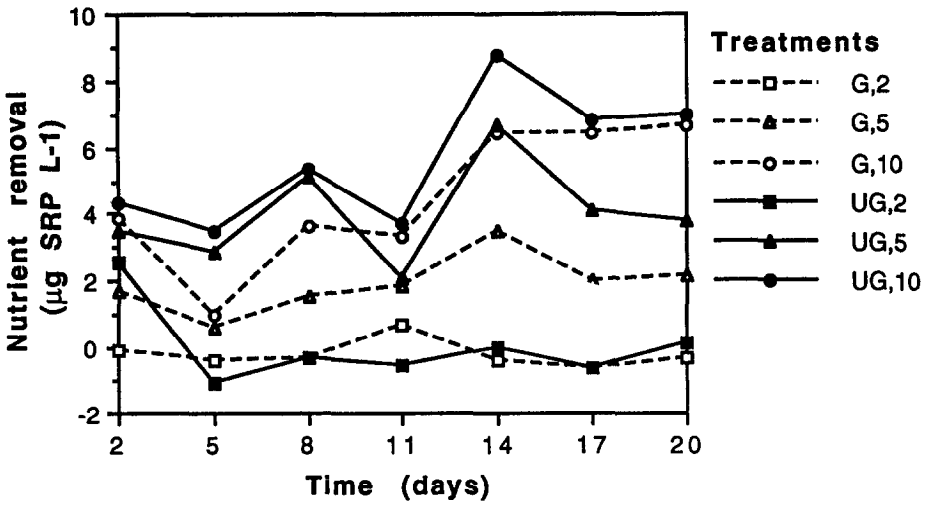

Fig. 2. SRP removal, calculated as inflow channel concentration minus in-channel concentration for grazed (G) and ungrazed (UG) treatments at three levels of enrichment (2, 5 and 10 are approximate in-channel SRP concentrations in μg SRP l^{--1}). Plotted values have SE_s that average ±7.5% of the mean (see Table 2).

Table 2. ANOVA for $\log_{10}$ transformed chl *a* data from the grazing experiment.

Source	DF	MS	F
Total SS	11		
Cells SS	5		
Grazing	1	2.93	226.3*
Phosphorus	2	0.16	14.1**
G*P	2	0.03	2.9
W/I Cells	6	0.01	

* $p \ll 0.0005$
** $p < 0.01$

Table 3. Mean AFDW/chl *a* ratios for experiment 2 for days 7, 14 and 21 in enriched (5,10 μg l^{-1} SRP) and unenriched (2 μg l^{-1}) channels.

	Grazed	Ungrazed
Enriched (n = 12)	113±38	74±11
Unenriched (n = 6)	257±210	130±25

Enrichment tended to decrease the AFDW/chl *a* ratio in the ungrazed treatments. With grazing, however, the ratios at all enrichment levels were similar to those in ungrazed channels without added enrichment (Table 3). Thus, grazing seemed to decrease the chl *a* content of the periphyton, probably by continual removal of the surface layer, which would contain the actively growing cells.

Taxonomic composition

Although *Cladophora* was dominant in the seed, pennate diatoms, including *Fragilaria* and *Scenedesmus* were the dominant genera in unenriched treatments, both grazed and ungrazed, throughout experiment 1. However, the filamentous cyonbacerium, *Phormidium*, became a larger component of the community in grazed treatments over the course of the experiment, while the percentages of diatoms decreased.

The dominant algal genera in experiment 2, which represented at least 5% of abundance, were *Phormidium*, *Fragilaria*, *Synedra*, *Gomphonema*, *Scenedesmus* and *Asterionella* (Fig. 4). Abundance of the different genera varied with treatment and over time. *Phormidium* became a larger fraction in both the grazed and ungrazed treatments over the course of the experiment, but was relatively more abundant in the grazed than ungrazed channels. In the grazed treatments, *Phormidium* comprised over 50% of the algal composition on days 14 and 21, while in the ungrazed treatments, it remained at less than 50% throughout the experiment and showed a slight positive response to enrichment (Fig. 4). There was a slight increase in taxon richness (comprising at least 5%) over time. On day 7, only four genera were present (≥5%) while six genera were present by day 21.

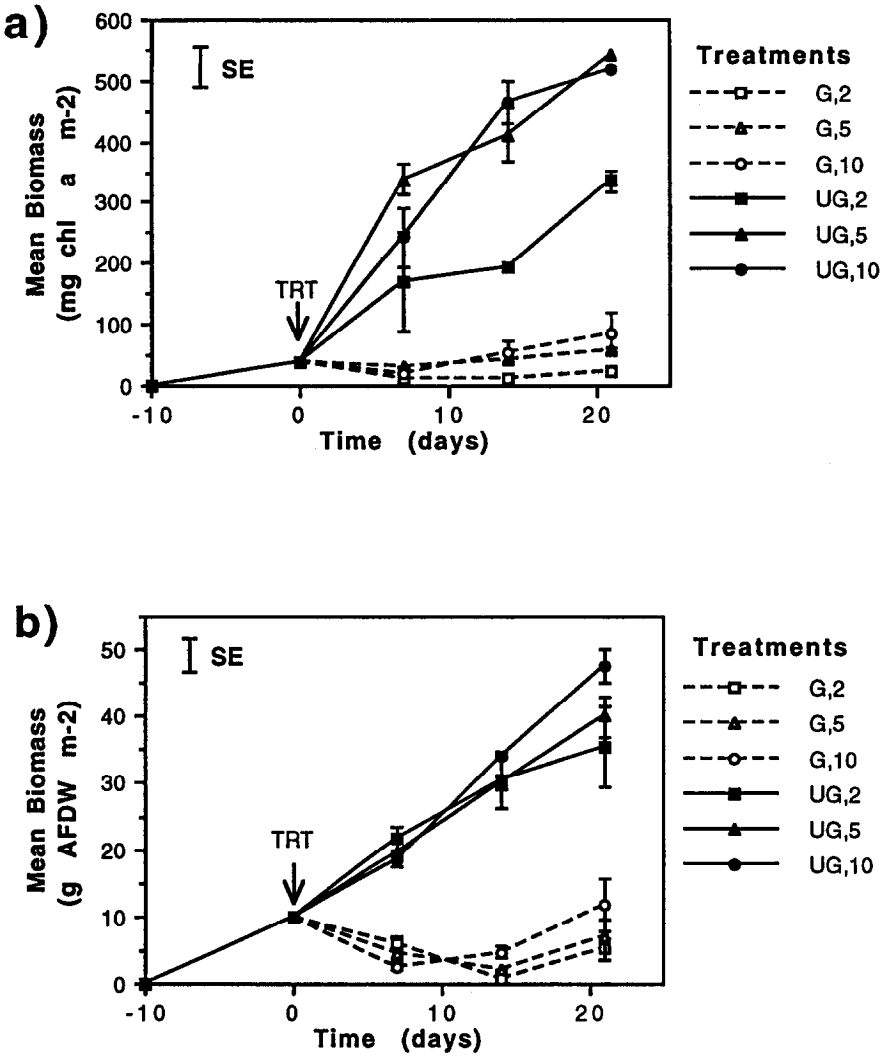

Fig. 3. (a) Mean chl *a* in mg m^{-2} for grazed (G) and ungrazed (UG) treatments at three levels of enrichment (2, 5 and 10 are in-channel SRP concentrations in $\mu g\ l^{-1}$). (b) Mean AFDW in g m^{-2} for grazed (G) and ungrazed (UG) treatments at three levels of enrichment (2, 5 and 10 are in-channel SRP concentrations in $\mu g\ l^{-1}$).

Grazing rates

Grazing of periphyton was indirectly a function of SRP concentration, because the amount of periphyton available for grazing was related to nutrient content. Periphyton removal rates were highest at the two elevated SRP concentrations of 5 and 10 $\mu g\ l^{-1}$ (Table 4a). Grazing rates per unit grazer biomass were also greatest at the two elevated SRP concentrations (Table 4b). Except for the unenriched treatment (experiment 2), grazing rates based on AFDW also were greater at higher SRP concentrations (Table 4a, b).

Modeling

Data from the grazing and maximum biomass experiments were evaluated further using a periphyton accrual model. The model is a mechanism-based formulation originally proposed by Horner *et al.* (1983), but modified here to include grazing and a higher, more realistic maximum biomass resulting from supplementary experiments reported by Walton (1990). Table 5 lists the values for constants and functions in equations 1 through 4 which follow below:

$$dB/dt = K_1 \mu L(k_f + k_{fo})(B_{max} - B) - K_2 V^{\Theta} \quad (1)$$

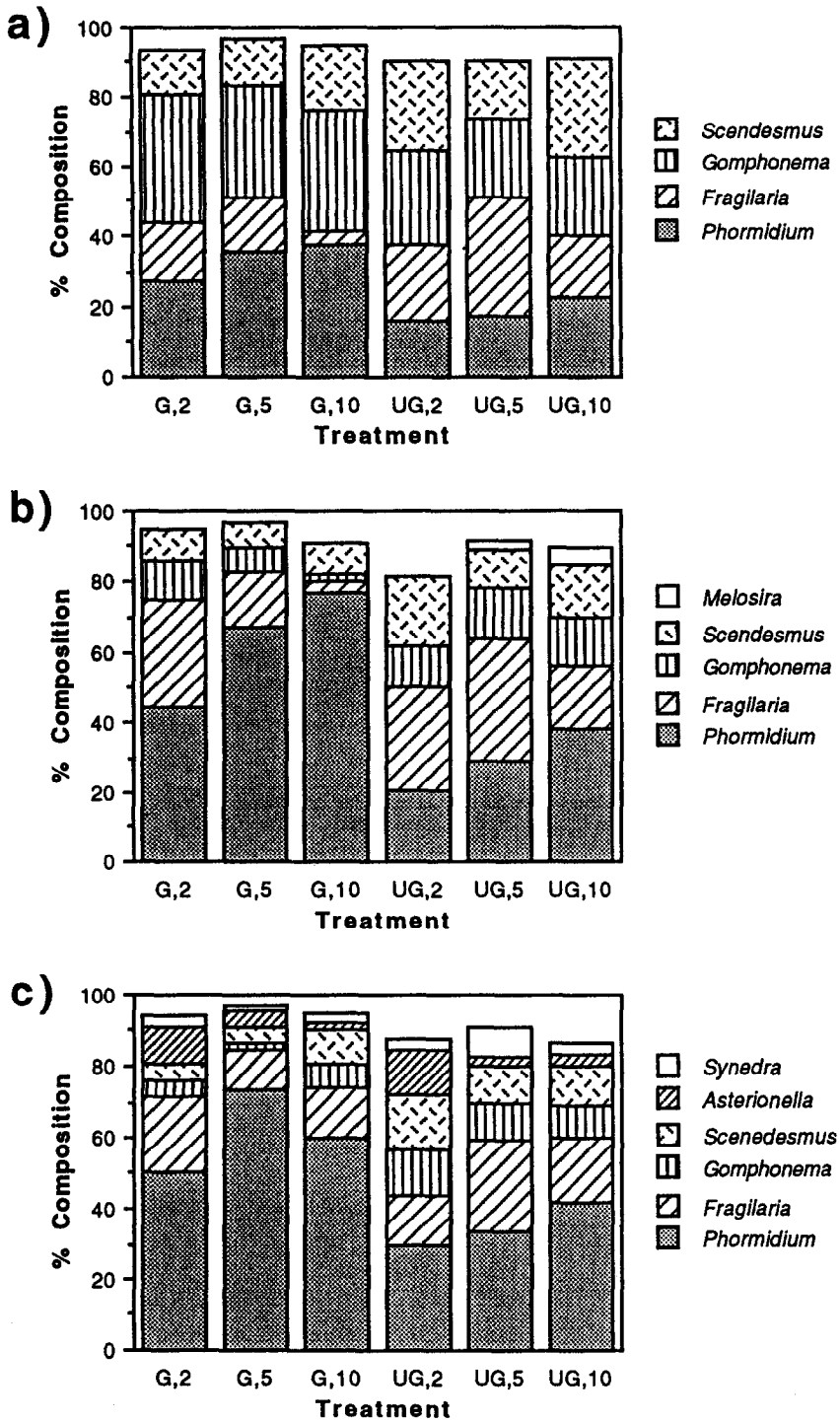

Fig. 4. Percent composition for experiment 2, for grazed (G) and ungrazed (UG) treatments at in-channel SRP levels of 2, 5 and 10 $\mu g\ l^{-1}$. Genera shown represent those present at a level of 5% or more in at least one treatment: (a) day 7; (b) day 14 and (c) day 21.

Table 4. a) Mean areal rate of periphyton removal calculated for grazer density of 100 m^{-2} (n=3) and b) mean grazing rates for periphyton removal as a function of grazer dry weight (n=3) (b). SRP concentrations listed are approximate in-channel values.

(a) μg SRP L^{-1}	Periphyton removal mg chl a m^{-2} d^{-1}	Periphyton removal g AFDW m^{-2} d^{-1}
2^1	11.3	1.3
2^2	16.0	1.8
5^2	29.3	1.8
10^2	25.9	1.9
(b) μg SRP L^{-1}	Grazing rate mg chl a mg^{-1} d^{-1}	Grazing rate g AFDW mg^{-1} d^{-1}
2^1	4.7	0.52
2^2	6.7	0.77
5^2	12.2	0.75
10^2	10.8	0.80

[1] Data from experiment 1
[2] Data from experiment 2

The integral form of this model, with initial condition $B=0$ at $t=0$, is the linear differential equation:

$$B = [B_{max} - K_2V^{\Theta}/K_1\mu L(k_f + k_{fo})] \quad (2)$$
$$[1 - e^{-K_1\mu L(k_f+k_{fo})t}].$$

This model was modified to include a grazing component as follows:

$$dB/dt = K_1\mu L * (k_f + k_{fo})(B_{max} - B) - \quad (3)$$
$$K_2V^{\Theta} - K_3B,$$

where the integral form, with initial condition $B=0$ at $t=0$, is the linear differential equation

$$B = [K_1\mu l(k_f + k_{fo})B_{max} - K_2V^{\Theta}]/ \quad (4)$$
$$[K_1\mu l(k_f + k_{fo}) + K_3][1 - e^{-K_1\mu l(k_f+k_{fo})+k_3t}].$$

Values for k_f, k_{fo}, L, K_2, and Θ were taken from a previous calibration using channel data (Horner *et al.*, 1983). The nutrient uptake rate, μ, was described using the Michaelis-Menton formulation. K_1, K_3, B_{max}, and V were determined from observation and calibration with data reported here (Table 5). Based on results from ungrazed channels, the growth coefficient, K_1, was recalculated using equation 4, with K_3 set equal to zero. K_1 was plotted against SRP concentration to evaluate the relationship between the two variables. The linear regression of K_1 on SRP resulted in a significant slope ($p<0.05$) and correlation coefficient ($r^2=0.69$; Fig. 5). From the calibrated K_1 results using equation 2, the grazing coefficient, K_3, was calculated. That calculation was performed by using the grazed biomass from experiment 2, equation 4 and the regression equation for K_1. The regression of K_3 on SRP has a significant slope ($p<0.05$) and correlation coefficient ($r^2=0.81$).

From the regression equations for K_1 and K_3, and the periphyton accrual model with grazing equation 4), biomass was calculated as a function of SRP. Figure 6 shows predicted and actual biomass for grazed and ungrazed treatments in experiment 2.

The output of this model was compared for a wide range in SRP concentration, with and without grazing, using the constants and functions listed in Table 5. These results show that ungrazed biomass should approach a maximum at around 15–20 μg SRP l^{-1} (Fig. 7). As expected, the predictions without grazing correspond closely to the maximum biomass levels observed for in-channel SRP concentrations of 2–86 μg l^{-1} reported by Walton (1990). However, predicted grazed biomass in Fig. 7 increases gradually over the whole range in SRP to about 300 mg chl a m^{-2} at an in-channel concentration of 150 μg SRP l^{-1}. These projections suggest that such elevated SRP concentrations will still have a positive effect on algal biomass in the presence of grazing.

Discussion

Biomass

Grazing pressure exerted by the caddisfly, *D. gilvipes*, resulted in a substantial reduction of periphytic biomass in laboratory channels. Reduction in biomass (chl *a*) of the mixed assemblage of filamentous and non-filamentous forms was about 90% from that in ungrazed channels. This reduction was even greater than observed *in situ* (64%) with the same species of caddisfly in a stream dominated by diatoms (Jacoby, 1987). Areal grazing rates generally increased with increasing enrichment, most likely due to the increased biomass available for grazing. The areal grazing rates of 11.3–29.3 μg chl a m^{-2} d^{-1} and 1.5–1.9 g AFDW

Table 5. Summary of constants and functions from the periphyton steady-state biomass model (equation 4).

Symbol	Definition	Unit	Form or value	Source
B_{max}	Maximum sustainable chl *a* biomass	mg m^{-2}	1000	W
K_1	Growth coefficient	–	3.2+0.24*P	Data
K_2	Scour coefficient	–	0.3	H
K_3	Grazing coefficient	–	0.0013+0.005*P	Data
Θ	Velocity exponent	–	0.45	H
μ	Nutrient uptake rate	day^{-1}	$\frac{\mu_{max} * P}{K_s + P}$	M-M
μ_{max}	Maximum growth rate	day^{-1}	$.22e^{T/10}$	E
K_s	Phosphorus half-saturation constant	μg SRP l^{-1}	10	Data
P	Phosphorus	μg SRP l^{-1}	varied	Data
V	Velocity	cm s^{-1}	varied	Data
T	Temperature	°C	19.1	Data
L	Light factor	–	0.755	H
k_f	Mass transfer coefficient	cm s^{-1}	$(D*V/pi)\cdot^5$	C-W
D	Diffusion coefficient	cm^2 s^{-1}	$1.5*10^{-5}$	P-G
k_{fo}	Mass transfer	cm s^{-1}	$009*(1.018)^{(T-20)}$	C-W

W - Walton (1990)
H - Horner *et al.* (1983)
M-M - Michaelis-Menten formulation
E - Eppley (1972)
C-W - Canale and Weber (1972)
P-G - Pasciak and Gavis (1974)

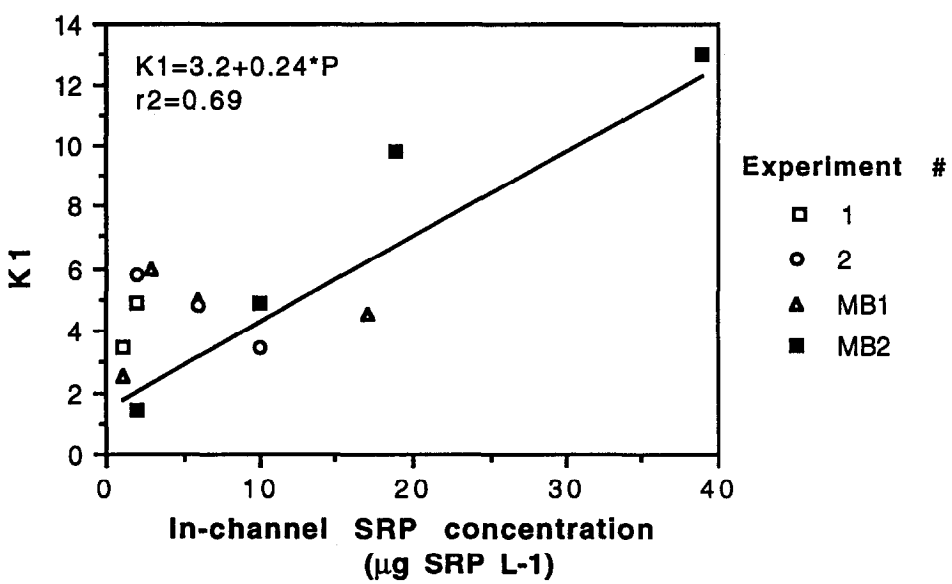

Fig. 5. Algal growth coefficient (K_1) calibrated against SRP in equation. Data shown for MB1 and MB2 are from Walton (1990).

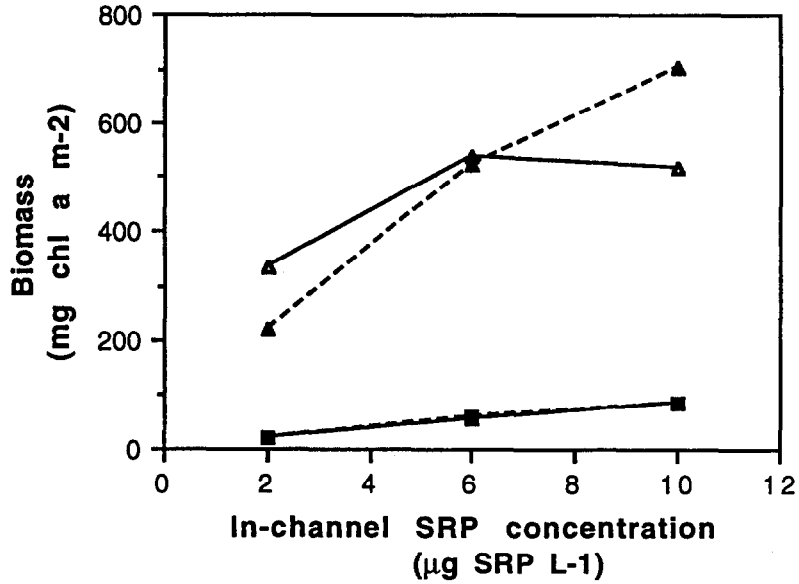

Fig. 6. Actual (solid lines) and predicted (dashed lines) biomass for grazed (squares) and ungrazed (triangles) treatments using the calibrated model (equation 4) and experiment data.

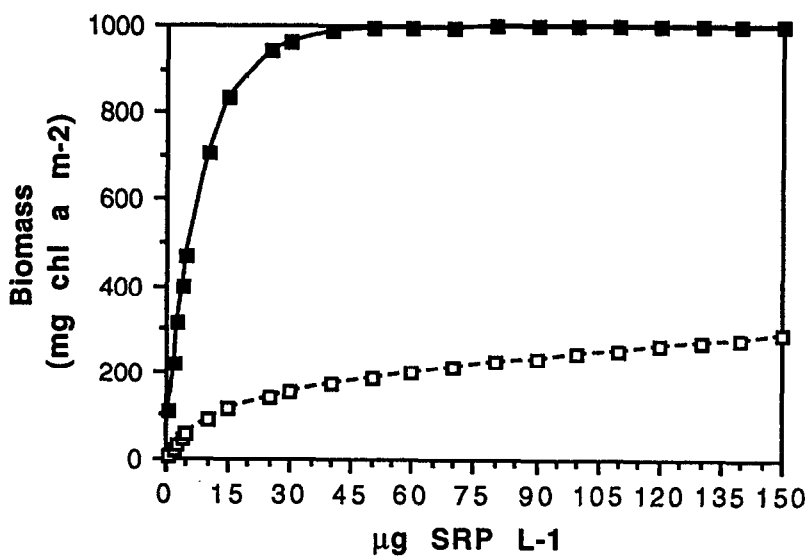

Fig. 7. Prediction of periphyton biomass with (dashed line) and without (solid lines) grazing using equation 4 for in-channel SRP concentrations of 1–150 $\mu g\ l^{-1}$. Constants and functions for the model are listed in Table 5.

$m^{-2}\ d^{-1}$ were in close agreement with the previous rates of 37 μg chl *a* $m^{-2}\ d^{-1}$ and 6.4 g AFDW $m^{-2}\ d^{-1}$ determined for *D. gilvipes* in the laboratory (Jacoby, 1986). Grazing rate, expressed per unit animal, ranged from 4.7–10.7 μg chl *a* $mg^{-1}\ d^{-1}$ and 0.52–0.80 mg AFDW $mg^{-1}\ d^{-1}$ and again increased with increasing enrichment. These rates are also very close to the previous values of 4.6 μg chl *a* $mg^{-1}\ d^{-1}$ and 0.83 mg AFDW $mg^{-1}\ d^{-1}$ determined by Jacoby (1986).

The response to grazing pressure, in combination with SRP enrichment, suggests that the effect of biomass loss through grazing decreased with increasing enrichment. That was evident in the gradually increasing level of grazed biomass predicted throughout a large range in SRP, as well as observed high-

er biomass in grazed treatments with increased SRP (Fig. 7). That effect may not happen in nature, however, because the grazer population should compensate for the increased food resource, given other factors being favorable (Elwood *et al.*, 1981). Those circumstances would result in a higher abundance of grazers with residual periphyton biomass nearly as low as in unenriched streams and also, possibly, of altered composition. A natural stream is characterized by a mixed assemblage of invertebrates, or a guild of grazers, which simultaneously utilize the periphyton resource, with abundance of individual species probably varying with resource availability. In the channel experiments, however, grazer abundance was held constant. Therefore, the predicted increased biomass in an enriched stream would have supported a larger population of caddisfly larvae, as well as other grazers, thereby reducing periphyton biomass to similar pre-enriched levels. Following factorial experiments examining the roles of nutrients on herbivory or periphyton, Steinman *et al.* (1991) advanced a hypothesis in agreement with this analysis: A factor like light or nutrient concentration could allow periphyton production to exceed consumption in the short run, but grazer recruitment should ultimately restore the herbivores to the dominant role.

The grazer abundance used in this study ($100\ m^{-2}$), was typical of the observed range reported in the literature ($40–200\ m^{-2}$) for this and comparable grazers (Hart, 1981; Jacoby, 1987; Lamberti *et al.*, 1987; Steinman *et al.*, 1987a). This range in densities suggests some ability of the population of grazers to adjust to resource availability. Hart (1981) assessed the rate of periphyton removal relative to resource renewal rates and suggested that periphyton was the limiting resource for which *D. gilvipes* larvae exploitatively compete for survival. If this is indeed the case, then periphyton resources in a natural system should be depleted even under enriched conditions. If periphyton resources are overutilized, we would expect to see a downward adjustment of natural abundance of *D. gilvipes* as the population ages. Predation and other causes of death, as well as downstream drift, are also important losses which reduce population abundance.

The effect of grazing on periphyton biomass in lotic environments also has been shown to vary with the invertebrate species present (Lamberti *et al.*, 1987; Jacoby, 1987; Hill & Knight; 1988). Benthic grazers (mollusks and crayfish) were found to effectively reduce the biomass of marine algae (Creese, 1988) and macrophytes in lakes (Flint & Goldman, 1975). *D. gilvipes* is a large grazer which has been demonstrated in this and other work to be an effective remover of periphyton (Jacoby, 1987; Steinman *et al.*, 1987a; Feminella *et al.*, 1989). Work showing the effectiveness of grazing over a range in grazer type, size, abundance, and density is obviously needed to predict grazing loss in nature.

Grazing by invertebrates in lotic systems presents a possible explanation for the paradox that exists for the relationships between SRP and biomass in running water. Nuisance biomass levels of algae are not simply correlated with increasing P concentration (either SRP or TP) as in lentic systems (Welch *et al.*, 1988). Some of that difference is due to the physical differences between the availability of nutrient and the measured biomass forms in the two environments. But factors other than nutrients, such as sloughing, grazing, temperature, light and substratum type, are more prominent in streams than lakes and interact to create a favorable or unfavorable environment for periphyton accrual. This and previous work in these channels suggests that given favorable and constant current velocity, light, temperature, natural substrata, and abundant nutrients, grazing can be a dominant force in controlling even filamentous periphyton.

Observations of high nutrient concentration and low biomass in nature may be explained by the presence of grazer guilds which maintain the periphyton biomass at low levels in spite of the enrichment level. The relatively low SRP concentration ($10–20\ \mu g\ l^{-1}$) without grazing needed to produce a maximum biomass (*i.e.*, saturate growth) in these channel experiments also might explain situations of low nutrient concentration and high biomass in natural streams with an otherwise suitable environment. Bothwell (1989) also found biomass of periphytic diatoms to reach a maximum of relatively low SRP concentration. Furthermore, the converse situation (*i.e.*, low biomass, high nutrient) being caused by grazing is supported by the low biomass levels observed in the grazed channels at an in-channel concentration of $10\ \mu g\ SRP\ l^{-1}$, which produced a biomass of 520 mg chl *a* m^{-2} in the ungrazed channels.

Taxonomic composition

The composition of the ungrazed periphyton community remained rather diverse with no particular taxa dominating. The grazed community, however, showed a substantial increase in the percentage of the filamen-

tous blue-green *Phormidium* and a reduction in the other taxa, which were primarily the diatoms *Synedra*, *Gomphonema*, and *Fragilaria*. The percent increase in *Phormidium* from day 7 to day 21 averaged 28% for the grazed treatments but only 17% for the ungrazed. By the end of the experiment (day 21), the total abundance of *Phormidium* in the grazed treatments ranged from 50–73%, but only 30–42% of the total in the ungrazed treatment.

The substantial increase in the fraction of *Phormidium* with grazing, compared to channels without grazing, as well as the decrease in the remaining diatom genera in the grazed treatments, indicates that grazing may have favored the filamentous form. Other factors could have been important as well, such as a chemical resistance by the cyanobacterium. Gregory (1983) described two mechanisms which might result in the alteration of algal community structure: 1) the active selection by herbivores for or against a particular taxon, and 2) the different vulnerability or tolerance among species to grazing pressure.

Filamentous periphyton is apparently grazed by *D. gilvipes*. *Cladophora*, a filamentous green alga, was heavily grazed by *D. gilvipes* where large detached clumps occurred at the bottom of pools (Hart, 1981). Examining the relationship between foraging and resource patchiness, Hart (1981) described the utilization of food resources which are rarely found in the same place or at the same time as the forager. The lack of availability of *Cladophora* was largely a result of its growth in areas characterized by high current velocity where *D. gilvipes* larvae could not graze. However, the utilization of *Cladophora* as a food resource by *D. gilvipes* larvae was observed in the field (Raging River, WA) and in the laboratory (Jacoby, 1986). Power (1992) also made observations relevant to this point in regulated and unregulated northern California rivers. *Cladophora* blooms occurred in unregulated but not regulated rivers, apparently because of consumer reductions in the former set of streams by winter floods.

The utilization and selectivity of various food resources by most herbivorous invertebrates appears to vary spatially and temporally. Similarly, in these experiments, *D. gilvipes* appeared to exert some selectivity for particular taxa (diatoms) and against others (*Phormidium*). Alteration of community composition by *D. gilvipes* grazing was probably a function of vulnerability of certain taxa specific to this community. For example, the stalked diatom, *Gomphonema*, may be structurally more susceptible to grazing pressure because of its elevated position above the substrata. Steinman *et al.* (1991) observed dominance by prostrate forms over upright taxa with grazing.

Mechanical dislodgement of algal cells could have resulted in an altered community composition and structure. Increased export has been documented in the presence of grazing. Rates of periphyton export were related to the extent of reduction of algal abundance, which was in turn related to herbivore type and density (Lamberti *et al.*, 1987). Loss rates at constant velocity in these channels were found to be minimal (Horner *et al.*, 1990).

Community growth rate

Although periphyton accrual rate over time was not examined specifically, patterns of growth can be inferred. Growth of the periphyton community did not exhibit the same pattern among the three enrichment levels (Fig. 3). At the highest level of enrichment, ungrazed biomass increase exhibited a logistic pattern until day 14, when biomass began leveling off. At the lower enrichment level and unenriched-ungrazed treatments, growth was characterized by a step-like pattern, suggesting the influence of differential growth rates of the individual taxa comprising the periphyton community. However, grazed treatments showed a similar growth pattern for all levels of enrichment, suggesting an overriding influence of grazing pressure.

In contrast, biomass as AFDW exhibited a linear growth pattern for ungrazed treatments at all levels of enrichment. The grazed biomass (as AFDW) at all levels of enrichment, exhibited a much greater initial decrease in biomass than was evident for chl *a*, but then appeared to recover and approach pretreatment biomass levels by the end of the experiment.

Comparison of the two indices of biomass shows the sensitivity of chl *a* to changes in community composition that were not reflected by AFDW. Differential growth rates and changes in community composition were reflected by chl *a* content, whereas biomass as AFDW increased at a constant rate. Moreover, enrichment effects in the ungrazed treatments were only differentiated on day 21 by AFDW, whereas enrichment effects differentiated the treatments by day 7 as chl *a*. The much lower AFDW/chl *a* ratios with enrichment further illustrate the effect.

Increased chl *a*/biomass with grazing observed by Hunter (1980) was not shown here. Rather than the ratio of AFDW/chl *a* being lower with grazing, it

was nearly double that without grazing, regardless of enrichment.

Modeling

The model, recalibrated to include grazing (equation 4), represents an initial step to include grazing to predict the potential biomass expected from a given SRP concentration and other conditions. However, the basis for some of the functions needs broadening. For example, temperature was rather similar for all experiments, averaging 19.1 °C,and that value was used for calibration. The probable dependence of K_1 on temperature suggests the need to examine the effects of a wider range in temperature to improve model application.

Prediction over a wide range in SRP concentration suggests that grazing could substantially reduce biomass levels at the calibrated grazing rate. Again, a larger data set including field observations, would be useful in assessing the relationship between SRP and K_3, the grazing coefficient. The grazing coefficient is hypothesized to reach or approach some maximum value if grazer abundance were held constant. A larger data set which evaluated a wider range of SRP in combination with constant grazing pressure could test such a hypothesis.

Two other aspects of calibrating K_3, which need to be examined, are the effects of grazer type, abundance and size. Abundance of animals in nature is partially dependent on food resource availability. If a site has a large food resource (periphyton productivity high), a large biomass of invertebrates could theoretically still exist even if the periphyton biomass remained low. Grazer size and type vary in streams, and reduction of periphyton biomass by grazing is usually caused by a guild of invertebrate herbivores which utilize different foraging and feeding strategies. The importance of multiple grazers has been examined by several researchers (Georgian & Wallace, 1983; Jacoby, 1987; Lamberti *et al.*, 1987; Steinman *et al.*, 1987a; Steinman *et al.*, 1987b; Hill & Knight, 1988). What has been missing in such studies, however, is an examination of the response of the grazing community to increased periphyton accrual due to enrichment.

B_{max} was set at 1000 mg m^{-2} chl *a*, because that level was attained in experiments utilizing an SRP range up to 100 μg l^{-1} without grazing. However, B_{max} levels only half that were observed without grazing in experiment 2 and in previous studies in which the filamentous green alga *Mougeotia* was dominant on Plexiglas™ substrata (Horner, *et al.*, 1983). Although the 1000 mg m^{-2} channel B_{max} was dominated by diatoms, levels of *Cladophora* to 1200 mg m^{-2} have been observed on natural rock substrata in streams (Welch *et al.*, 1992). Therefore, setting a B_{max} near the apparent maximum potential seems reasonable, although such factors as sloughing, scouring and substratum character may limit the B_{max} attainable in both unenriched and enriched streams.

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