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APPLIED ISSUES

Periphyton removal related to phosphorus and grazer biomass level

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SUMMARY

1. The proliferation of nuisance periphyton in enriched streams may be dependent on the biomass of the grazing macroinvertebrates present. In the present study, the effectiveness of grazer size and biomass in controlling periphyton and the extent to which grazing effectiveness was affected by enrichment level were determined.
2. Two sets of experiments with two caddisfly grazers were conducted in laboratory channels during spring and summer 1995 and 1996. The first set tested the combined effect of phosphorus enrichment and grazing, while the second set tested the effect of variable grazer biomass on periphyton biomass.
3. Grazing reduced periphyton biomass in excess of 80%, compared to ungrazed controls. Grazers were equally effective in controlling filamentous green algae, *Stigeoclonium*, diatoms and small colonial greens. Near complete removal of periphyton biomass by grazing occurred at even at the lowest grazer biomass level (750 mg m^{-2}, i.e. approximately one-third of natural levels).
4. Grazing controlled periphyton biomass more than did enrichment with soluble reactive phosphorus (SRP).
5. Grazing rates in the phosphorus-grazing interaction experiments averaged about 6 mg chl *a* g invertebrate^{-1} day^{-1}, which was similar to past work in these channels and elsewhere, while rates were about five-fold higher in the variable grazer biomass experiments.
6. Simulating effects of SRP and grazing with a calibrated model suggests that higher SRP levels would be necessary to exceed a nuisance periphyton biomass level if grazers were present. However, if grazer biomass was more than 1500 mg m^{-2}, a nuisance level would probably not be exceeded at any SRP.

Keywords: filamentous green algae, grazer biomass level, periphyton removal, phosphorus

Introduction

High levels of periphyton biomass have long been recognized as an impairment to water quality and habitat in nutrient-enriched streams (Hynes, 1960; Wharfe, Taylor & Montgomery, 1984; Biggs, 1985). Filamentous green algae (e.g. *Cladophora, Ulothrix* and *Stigeoclonium*) are the most noted nuisance periphyton group and their proliferation is closely tied to enrichment levels (Biggs & Price, 1987; Welch, Horner & Patmont, 1989; Welch, Quinn & Hickey, 1992). Nevertheless, the response of periphyton to increased nutrient loading in streams is not yet predictable. There are many streams enriched sufficiently to promote high periphyton biomass which do not develop significant amounts of periphyton including filamentous green algae (Welch *et al*., 1988; Biggs, 1990; Welch *et al*., 1992). The accumulation of high levels of periphyton biomass in such streams may

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be prevented by other processes which reduce periphyton, such as grazing by invertebrate grazers.

The removal of lotic periphyton by grazing invertebrates is well documented (e.g. Gregory, 1983; Lamberti & Moore, 1984; Colletti *et al*., 1987; Jacoby, 1987; Steinman *et al*., 1987; Power, Steward & Matthews, 1988; Steinman 1991; Feminella & Hawkins, 1995). Earlier studies (reviewed by Gregory, 1983) emphasized grazer preference for diatoms and avoidance of the larger filamentous greens. However, some invertebrates do graze filamentous green algae (McAuliffe, 1984; Jacoby, 1985, 1987; Dudley & Antonio, 1991; Power, 1992; Welch *et al*., 1992), and depending on the type of animal present and its density, can significantly reduce the biomass of some filamentous green taxa (Lamberti *et al*., 1987; Steinman *et al*., 1987; Feminella *et al*., 1989; Walton, Welch & Horner, 1995). In particular, larger invertebrates such as the caddisfly larva, *Dicosmoecus gilvipes* (Hagen), have been found to be more effective grazers of filamentous green algae (Jacoby, 1987; Steinman *et al*., 1987; Feminella *et al*., 1989; DeNicola *et al*., 1990). Grazing by smaller invertebrates (e.g. mayflies and small caddisflies) has generally been shown to be less effective in reducing filamentous greens, possibly because of their smaller mouthparts, which physically cannot handle large filaments (Jacoby, 1987; Hill & Knight, 1988).

The interactive effects of nutrients and herbivory on lotic periphyton have been primarily investigated using large-bodied grazers (Stewart, 1987; Steinman, 1991; Hill, Weber & Stewart, 1992; Walton *et al*., 1995). Walton *et al*. (1995) found that the large, effective grazer *D. gilvipes* controlled periphyton biomass (including filamentous green and blue-green algae) even at high enrichment levels of soluble reactive phosphorus (SRP) ($\leqslant$ 25 μg SRP L^{-1}). However, the effects of nutrient enrichment on periphyton in the presence of smaller grazers is also of interest.

While grazing by large invertebrates is known to control filamentous green algal biomass and small invertebrates may have little effect, knowledge of grazing effectiveness by invertebrates over a range of size and abundance is needed to predict the potential effects of enrichment in streams. Increased enrichment should have less effect on periphyton biomass if grazing pressure is high than if pressure is low (i.e. sparse populations of small grazers). Thus, the absence of nuisance periphyton in enriched streams may be attributed to removal by grazing invertebrates. The hypothesis of the present authors is that the proliferation of nuisance periphyton, especially filamentous green algae, in enriched streams is dependent on the abundance and size of the macroinvertebrate grazers present.

The objectives of the present study were: (1) to determine the effectiveness of grazer size and abundance in controlling periphyton biomass; (2) to determine the extent to which grazing effectiveness is affected by enrichment level; and (3) to modify a previously developed periphyton accrual model (Horner, Welch & Veenstra, 1983; Walton *et al*., 1995) to incorporate grazing rates to predict maximum periphyton biomass. Two sets of experiments were conducted in laboratory channels using two species of fifth instar caddisfly larvae, *D. gilvipes* (24 mg dry - mass individual^{-1}) and *Neophylax rickeri* (Banks) (3.5 mg dry mass individual^{-1}). In the first set, the interactive effects of grazing and nutrient enrichment on periphyton biomass and composition were investigated. In the second set, the effect of grazer biomass level on periphyton biomass and composition at a constant and high nutrient level was evaluated. Incorporating the experimental re-sults in the periphyton accrual model led to better understanding of the interactions between grazer abundance, periphyton biomass and nutrient concentrations.

Materials and methods

Two sets of experiments with two invertebrate grazers were conducted in twelve recirculating channels. Fifth instar *Neophylax* and *Dicosmoecus* were chosen: (1) because these animals are present in streams during periods of accelerated periphyton growth; and (2) so that grazing by herbivores of similar morphology but differing size could be compared. The experiments consisted of colonizing natural cobble substratum with a mixed periphyton community initially dominated by *Stigeoclonium* sp. and then adding grazers after the periphyton mat became established. Periphyton biomass, as chlorophyll *a* (chl *a*), ash-free dry mass (AFDM) and taxonomic composition, was determined at regular intervals until sloughing occurred in the control (ungrazed) channels. The duration of the experiments

ranged from 34 to 40 days, depending on when sloughing occurred.

The combined effects of SRP enrichment and grazing on periphyton biomass and composition were investigated in the first set of experiments (hereafter referred to as phosphorus–grazing interaction experiments). The inflow SRP concentrations were 2, 15 and 25 μg L^{-1}, and grazer biomass (as mg dry weight) was maintained at either 0 or 3000 mg m^{-2}, with each of the six SRP and grazing combinations replicated twice. Nitrogen (N) and phosphorus (P) were added so that P was limiting.

The effect of grazer biomass level on periphyton biomass and composition was investigated in the second set of experiments at an inflow SRP concentration of 10–15 μg L^{-1} (hereafter referred to as variable grazer biomass experiments). Grazer biomass was set at four different levels in the channels: 0, 1500, 3000 and 4500 mg m^{-2} for *Neophylax* and 0, 750, 1500 and 3000 mg m^{-2} for *Dicosmoecus*. Each of the four grazer biomass level treatments was replicated three times. Natural maximum biomass of these two grazers was about 1500 mg m^{-2} in Raging River.

Channels and experimental conditions

Each of the twelve partially recirculating channels was constructed of plexiglass, formed into a rectangle, 1.0 m long, 21 cm wide and 12 cm deep (Walton *et al*., 1995). Air jets, composed of plastic pipettes, connected to rubber tubing and an air supply controlled current velocity (the average channel velocity was ≈ 20 cm s^{-1} at the surface). Fluorescent lights were suspended above the channels yielding an intensity of ≈ 175 μE m^{-2} s^{-1} for 16 h to simulate a Northwest U.S.A. summer photoperiod.

The water used in these experiments was gravity fed from a small concrete pond that contained low-nutrient (2 μg SRP L^{-1} and 60 μg NO_3-N L^{-1}), recirculated city water. Before entering the laboratory holding tank, the water passed through a series of filters of decreasing pore size (100-, 50- and 20-μm Nitex fabric filters) to remove suspended materials. The flow into the chambers was maintained at 1 L min^{-1} to produce a constant hydraulic residence time of 16 min in each channel.

Peristaltic pumps delivered stock nutrients from a 50-L polyurethane carboy containing KH_2PO4 and $NaNO_3$. Pump flow rates were calculated to deliver target nutrient concentrations in the channels with a N:P ratio of >30:1 to promote P limitation.

Colonization of periphyton

Rocks (diameter ≈ 5 cm), colonized with diatoms and the filamentous green alga *Stigeoclonium*, were collected from a local stream in late March 1995 for the phosphorus–grazing interaction experiments and in late March 1996 for the variable grazer biomass experiments. These seed rocks were placed in the channels and surrounded by 54 uncolonized rocks, arranged into rows of 15, with two rows on each side of the central channel vane; hence, there was a total of 60 rocks $channel^{-1}$. The channels were subsequently filled with enriched water with flow rates (1 L min^{-1}), surface velocities and photoperiod set to prescribed levels. Seed rocks for the *Dicosmoecus* experiments were taken from the ungrazed controls of the *Neophylax* experiments, which were run first because of the earlier entry into diapause of *Neophylax*.

Considerable effort was expended to prevent *Phormidium,* a filamentous cyanobacterium, from colonizing the channels and to encourage *Cladophora*, which is an important nuisance-causing filamentous green algae world-wide. However, *Stigeoclonium* colonized well in the channels, and therefore, was used for both experiments.

Acclimation of grazers

Grazers were collected by hand from Issaquah Creek at Issaquah, Washington, and the Raging River at Fall City, Washington. *Neophylax* larvae were collected in early May 1995 and 1996, while *Dicosmoecus* larvae were collected in late June 1995 and 1996. The animals were acclimated in aerated buckets (initial temperatures around 10 °C) warmed to channel temperature (15–20 °C) for at least 2 h before introduction to the channels.

Gut content analyses

During the second set of experiments, the gut contents of three *Dicosmoecus* larvae collected directly from Issaquah Creek in late June 1996 were compared with five *Dicosmoecus* larvae from the channels (late July)

after 4–5 weeks of grazing. Gut contents were analysed according to Coffman, Cummins & Wuycheck (1971) by: (1) identifying and enumerating constituents on a percentage volume basis; and (2) determining the organic fraction as ash-free dry mass/oven-dry mass (AFDM/ODM).

Dry mass measurements

Dry mass was determined for 30 randomly chosen invertebrates before each experiment by separating them from their cases and drying at 100 °C for 24 h. The average *Neophylax* weighed (± SD) 3.5 ± 0.3 mg, while *Dicosmoecus* dry mass in the phosphorus–grazing interaction experiments was 24.0 ± 3.0 mg per individual. Despite similar larval lengths (≈ 2.5 cm) during 1995 and 1996, *Dicosmoecus* masses for the variable grazer biomass experiments were much higher and more variable. Gut-content analyses revealed that the greater mass was probably a result of ingestion of sand during exceptionally high stream flow before collection. Because the mass of *Dicosmoecus* was influenced by the high and variable amounts of sand within their guts, an individual mass of 24.0 mg was used to stock *Dicosmoecus* in the variable grazer biomass experiment. This mass is consistent with measurements obtained in the phosphorus–grazing interaction experiment, and by Jacoby (1987) and Walton *et al*. (1995).

Channels were stocked for each experiment at respective target caddisfly biomass levels after algal biomass had increased to levels judged to be sufficient to support grazing, but well prior to the maximum potential biomass had been attained. Petri dishes filled with sand and small pebbles were placed in each grazed channel to support the invertebrates' case-building activities.

Periphyton sampling and analysis

Samples were collected in a stratified, random manner by dividing each channel into six sampling zones corresponding to six velocities. One rock was randomly chosen from within each zone so that effects of velocity variation would be adequately represented. Consequently, a total of six rocks was sampled from each channel on each sampling day, which occurred every 2–7 days depending on the changes in periphyton growth.

To collect periphyton, an inverted plastic bottle with the bottom removed was placed on the rock surface. The periphyton mat surrounded by the bottle opening (376 mm^2) was scraped into a plastic dish using de-ionized water and a small wire brush. After sampling, each rock was returned to its original location and not resampled.

The contents of the plastic dish were homogenized in a blender and the resulting slurry was transferred to a graduated cylinder with a final volume of 30 mL. Three 10-mL subsamples were analysed for chl *a*, AFDM and taxonomic composition. Two of the 10-mL subsamples were filtered through 0.45-μm glass fibre filters to be analysed later for chl *a* and AFDM. Chl *a* was analysed using the monochromatic acid-correction method of Lorenzen (1967) with correction for phaeophytin (APHA, 1989) on a spectrophotometer following extraction in 90% buffered acetone. Periphyton AFDM was analysed as gravimetric loss after burning at 550 °C for one hour (APHA, 1989).

After settling for at least one month, concentrated samples to be examined for taxonomic composition and biovolume analysis were placed in a Sedgewick Rafter cell, and algal cells were enumerated at a magnification of × 200. At least five Whipple grids and 250 algal cells were counted, measured and identified. Biovolumes of each taxon (genus) were calculated by multiplying the total number of cells by an estimated taxon volume which was obtained using geometric formulae (Vollenweider, 1974; Wetzel & Likens, 1991).

Nutrient sampling and analysis

Total P (TP), SRP and NO_3-N ($NO_{3^-} + NO_{2^-} - N$) concentrations were determined in the inflows and each channel every 4–7 days to assure maintenance of target concentrations. Samples for SRP and NO_3-N analysis were filtered immediately through a 0.45-μm membrane filter (Millipore Corporation, Bedford, MA) and stored at 0 °C until analysed within 3 days of collection to allow inflow target concentrations to be adjusted if necessary. Soluble reactive phosphorus was measured by the ascorbic acid method (APHA, 1989) with a Spectronic 1001 (Spectronic Instruments Inc., Rochester, NY). Samples for TP were first digested with persulfate and then analysed for SRP. NO_3-N was determined with an ALPKEM RFA-300

ion autoanalyser (OI Analytical, College Station, TX) by the cadmium reduction method (APHA, 1989).

Physical characteristics of the channels

To maintain the desired physical conditions, temperature, current velocity and light intensity were determined at regular intervals. In-channel, mid-day temperature was recorded daily with a hand-held thermometer. During the final *Dicosmoecus* variable grazer biomass experiment, in-channel, daily minimum and maximum temperature were recorded with a thermister. Current velocity was determined initially for all experiments using an open stream velocity meter (Swoffer Instruments Inc., Seattle, WA) and with either a meter or by timing a floating object at irregular times during experiments. Average velocity was computed from six separate meter readings from several points across the channel. Velocity varied greatly with distance from the jets at each end of the channels. Light intensity was determined with a Lambda Instrument Quantum Radiometer-Photometer once during each set of experiments.

Periphyton growth and invertebrate grazing rate

The growth term of an existing periphyton accrual model (Horner *et al*., 1983; Walton *et al*., 1995) was modified to incorporate grazing as observed in the two sets of experiments. This model is a steady-state biomass model which estimates maximum periphyton biomass in mg chl *a* m^{-2} as a function of in-channel SRP, velocity, temperature and grazing.

The exponential period of periphyton accrual was easily distinguishable from the relationships of chl *a* and AFDM versus time in the control (no grazers) channels. The maximum periphyton growth rate ($R_{P,U}$) during this time was calculated as:

$$R_{p,u} = (B_{u,t} - B_{u,o}) / \Delta t \quad (1)$$

where Δt is the length of the exponential period, $B_{U,t}$ is the ungrazed periphyton biomass at the end of the exponential period and $B_{U,o}$ is the ungrazed periphyton biomass at the beginning of the exponential period.

For the phosphorus–grazing interaction experiments, invertebrate grazing rate (R_{gr}) was calculated as an average, linear rate which took periphyton productivity (i.e. the rate of increase in the ungrazed controls) into account, according to the following:

$$R_{gr} = (B_{u,t} - B_{G,t}) / \Delta t \quad (2)$$

where $B_{G,t}$ is the periphyton biomass in grazer channels at the end of the exponential period.

This calculation assumes that periphyton biomass is not depleted below levels which allow effective grazing during the time that the rate is calculated. However, periphyton in the variable grazer biomass experiments was grazed down to a level which probably inhibited further consumption before the end of the exponential growth period. To account for this occurrence, only the first 2 days of grazer presence were used to calculate grazing rate because periphyton biomass was considered to be still high enough during this period to support relatively uninhibited grazing. This grazing rate was calculated as:

$$R_{gr} = R_{p,u} - R_{p,g} \quad (3)$$

where $R_{p,u}$ is the periphyton growth rate, as shown in Eqn 1, and

$$R_{p,g} = (B_{G,t+2} - B_{G,t}) / \Delta t$$

where t is the day of grazer addition to the channels (day 13) and

$$\Delta t = 2 days$$

These areal grazing rates (mg m^{-2} day^{-1}) were normalized to grazing rates per unit dry weight of invertebrate (mg g invertebrate^{-1} day^{-1}) by dividing by the grazer biomass level (g invertebrate m^{-2}). These grazing rates are actually periphyton removal rates because these make no distinction between ingestion and mechanical dislodgement of the periphyton.

Results

Phosphorus–grazing interaction

Environmental conditions

Target concentrations of low, medium and high SRP (2, 15 and 25 μg L^{-1}) were achieved most of the time,

as indicated by treatment means (± SD) of 2 ± 0.3, 17 ± 2.6 and 28 ± 6.5 μg L^{-1} in the *Neophylax* experiment, and 3 ± 0.3, 14 ± 3.6 and 25 ± 4.3 μg L^{-1} in the *Dicosmoecus* experiment. Target NO_3-N concentrations (30, 225 and 375 μg L^{-1}) were also achieved, providing an average N:P ratio of 14.5 (by mass) in all treatments. The difference between mean SRP concentrations (inflow or in-channel) in grazed and ungrazed channels was not significant during either the *Neophylax* or the *Discosmoecus* experiments (α = 0.05) (Schimek, 1996).

Midday water temperatures in channels ranged from 18 to 26 °C during the two experiments, but were relatively stable during the first few days after grazers were stocked. Temperature gradually increased from 21 to 24 °C after the addition of *Neophylax*. Temperatures increased from 24 initially to 26 °C by the end of the experiment with *Dicosmoecus*. The means for the experiments (± SD) were 21.8 ± 2.2 °C with *Neophylax* and 24.7 ± 1.0 °C with *Dicosmoecus*.

The grazer biomass level was initially 3000 mg m^{-2} in both experiments. By the cessation of periphyton exponential growth (day 29), the active biomass of *Neophylax* biomass had decreased to 2500 mg m^{-2} as a result of mortality and the onset of diapause. *Dicosmoecus* biomass decreased to 2400 mg m^{-2} when periphyton exponential growth ended (day 18) as a result of mortality only. Invertebrates were subsequently restocked to restore target biomass levels.

Effect on periphyton biomass

Grazing by both *Neophylax* and *Dicosmoecus* substantially reduced periphyton biomass, as chl *a* and AFDM, at all SRP levels, as indicated by the difference between grazed and ungrazed biomass on most sampling days (Fig. 1). Average percentage reductions in periphyton biomass over all sampling days after stocking were 69, 86 and 62 mg chl *a* m^{-2} at the low, medium and high SRP levels, respectively, for *Neophylax* and 72, 39 and 67 mg chl *a* m^{-2}, respectively, for *Dicosmoecus*. The relatively low percentage reduction by *Dicosmoecus* at the medium SRP level was associated with high sloughing in the ungrazed channels after day 23.

Soluble reactive phosphorus enrichment also substantially increased periphyton biomass during both experiments, as indicated by the difference in maximum chl *a* among the low, medium and high SRP levels in both grazed and ungrazed channels (Fig. 2). However, the decreased incremental change in periphyton biomass with increased SRP from 15 to

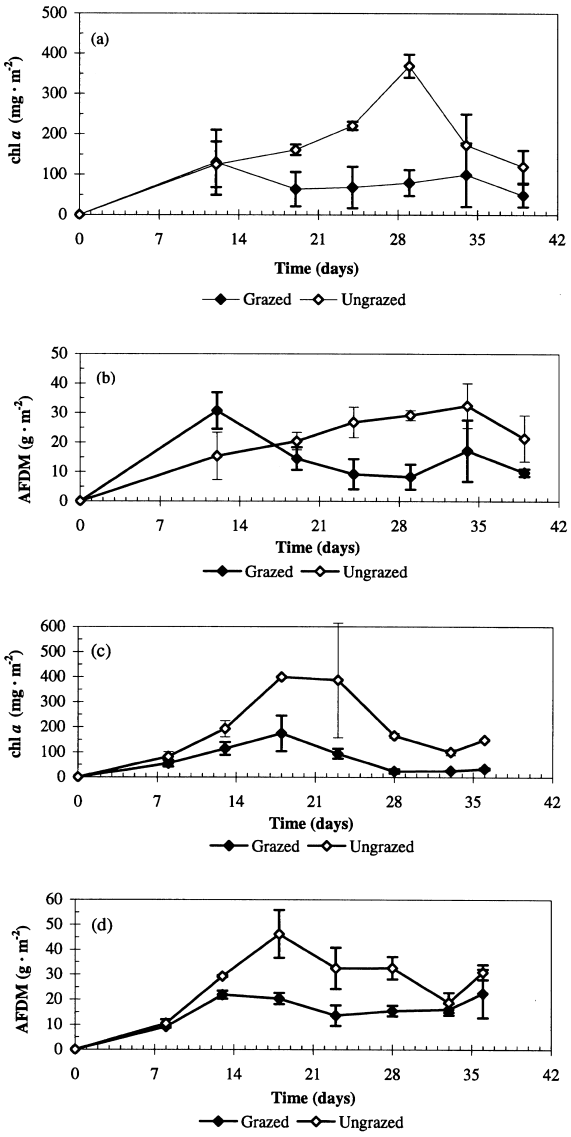

Fig. 1 Effect of *Neophylax* and *Dicosmoecus* grazing on periphyton biomass at high SRP: (a) *Neophylax*, chl *a*; (b) *Neophylax*, AFDM; (c) *Dicosmoecus*, chl *a*; and (d) *Dicosmoecus*, AFDM. The mean values are the average of two treatment replicates and the replicates are the average of six substratum samples. The error bars for treatment means indicate ± 1 SE. *Neophylax* larvae were stocked initially at 3000 mg m^{-2} in the grazed treatments on day 12 of each experiment. *Dicosmoecus* larvae were stocked initially at 3000 mg m^{-2} in the grazed treatments on day 8 of each experiment.

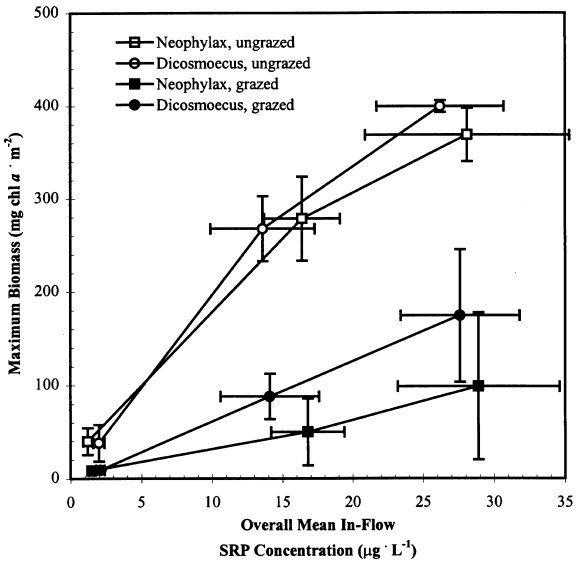

Fig. 2 Combined effect of SRP enrichment, grazing and grazer size on maximum periphyton biomass. The maximum biomass at each SRP level is the mean of two sample replicates. The overall mean inflow SRP values were calculated from all the days in each experiment. The error bars indicate ± 1 SE in both the *x*- and *y*-variables. The initial invertebrate biomass was the same for both experiments (3000 mg m^{-2}).

25 μg L^{-1} in ungrazed channels indicates that periphyton approached SRP saturation. Enrichment with SRP was clearly insufficient to compensate for the dominant effect of grazing by *Neophylax* or *Dicosmoecus* (Fig. 2).

For each experiment, differences in mean chl *a* across the three SRP levels and across the two grazing levels were evaluated with a two-factor analysis of variance (ANOVA) on log-transformed data (ANOVA; $\alpha = 0.05$) on day 29 for *Neophylax* and on day 22 for *Dicosmoecus*. These days showed the largest difference in periphyton biomass between grazed and ungrazed channels, and closely corresponded to the time of maximum periphyton biomass in ungrazed channels.

In both experiments, the reduction in periphyton biomass from grazing and the increase in periphyton biomass caused by SRP enrichment were significant ($\alpha = 0.05$). However, the interaction of grazing and SRP enrichment was not significant ($\alpha = 0.05$). The results of a Tukey test showed that the effect of SRP enrichment from 0 to 15 μg L^{-1} on periphyton biomass was significant within each grazed and ungrazed treatment, while enrichment from 15 to 25 μg L^{-1} was not (Schimek, 1996).

Periphyton growth and invertebrate grazing rates

Both periphyton growth rate ($R_{p,u}$), as mg chl *a* m^{-2} day^{-1}, and invertebrate grazing rate (R_{gr}), as mg chl *a* g^{-1} day^{-1}, increased with SRP enrichment during both experiments (Table 1). *Dicosmoecus* grazing rates (R_{gr}) were higher than those for *Neophylax* at the medium and high SRP levels by ≈ 46% and 36%, respectively. The R_{gr} for both invertebrates was lower at the low SRP level, indicating that grazing was limited to some extent by periphyton production. Grazing rates of ≈ 6 mg chl *a* g^{-1} day^{-1} have been reported in past work with *Dicosmoecus* (Jacoby, 1987; Walton *et al.*, 1995).

Taxonomic composition

The periphyton was composed of a mixture of taxa with five being dominant (by percentage biovolume):

Table 1 Periphyton growth and invertebrate grazing rates for *Neophylax* and *Dicosmoecus* for the SRP and grazing combined experiment. Grazing rates (mg chl *a* g invertebrate^{-1} day^{-1}) are expressed as grams dry weight present in the channels: (L) lowest level of SRP enrichment (2 μg L^{-1}); (M) middle level of SRP enrichment (15 μg L^{-1}); and (H) highest level of SRP enrichment (25 μg L^{-1}). Grazing rates for *Neophylax* were calculated using day 29 data, while those for *Dicosmoecus* were calculated using day 18 data

Invertebrate grazer	SRP level	Mixed periphyton growth rate(mg chl *a* m^{-2} day^{-1})	Grazing rate(mg chl *a* g invertebrate^{-1} day^{-1})
Neophylax	L	1.98	0.8
	M	7.18	4.9
	H	14.38	6.1
Dicosmoecus	L	0.75	0.4
	M	19.91	7.2
	H	31.75	8.3

the diatom *Fragilaria*, the filamentous green alga *Stigeoclonium* and *Microspora*, the colonial green alga *Scenedesmus*, and the cyanobacterium *Lyngbya*. *Stigeoclonium* and *Fragilaria* were the most abundant taxa in all treatments. *Stigeoclonium* percentage biovolume was somewhat higher in grazed channels during the *Neophylax* experiment and approximately equal during the *Dicosmoecus* experiment, whereas *Fragilaria* percentage biovolume was slightly higher in the ungrazed channels during both experiments (Fig. 3). In spite of the greater absolute representation by diatoms, filamentous green algae were more visible to the present authors.

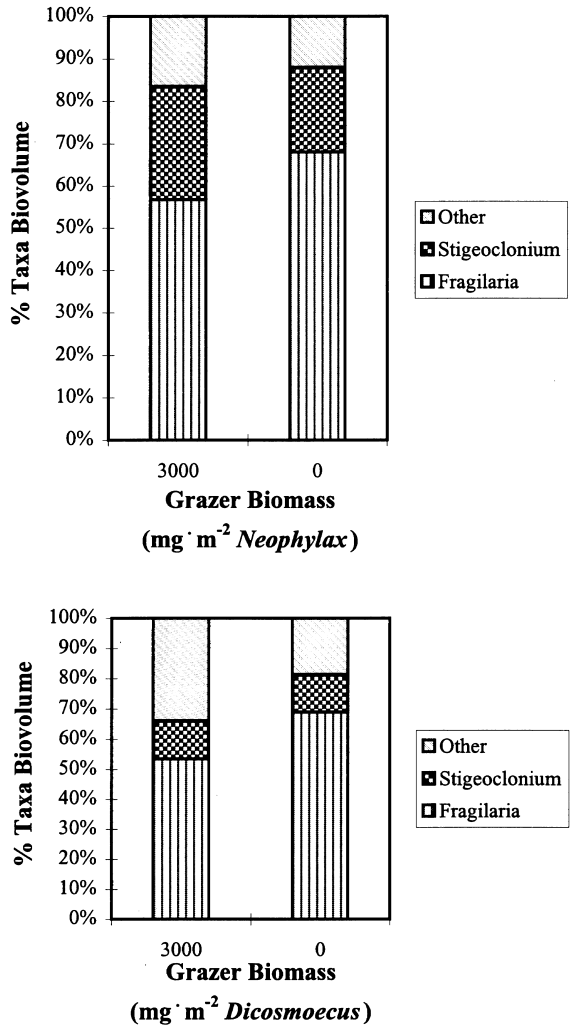

Fig. 3 Mean percentage biovolume of the dominant periphyton taxa in grazed and ungrazed treatments across all three SRP levels on day 22 of the phosphorus-grazing interaction experiment with *Neophylax* (top) and *Dicosmoecus* (bottom).

Variable grazer biomass

Environmental conditions

Mean inflow SRP (± SD) was 10.7 ± 1.5 μg L^{-1} for the experiment with *Neophylax* and 14.8 ± 3.0 μg L^{-1} for the experiment with *Dicosmoecus*. Inflow SRP was not significantly different ($\alpha = 0.05$) among the twelve channels during either experiment (Anderson, 1997). The difference in mean SRP between experiments was negligible because the absolute difference among in-channel values was only 1–2 μg L^{-1}. This small difference had no effect on periphyton biomass because growth has previously been shown to saturate at SRP > 10 μg L^{-1} (Walton *et al.*, 1995). NO_3-N content produced N:P ratios which averaged 13.8, indicating that P was almost certainly the limiting nutrient throughout the experiments.

In-channel temperature was relatively consistent during both experiments, except for a warm period during days 25–30 of the experiment with *Dicosmoecus* when temperature increased to 23 °C. Thus, the mean temperature during the *Neophylax* experiment (17.4 ± 1.0 °C) was lower than that during the *Dicosmoecus* experiment (20.8 ± 1.3 °C). This 3 °C temperature difference between experiments should have had a minimal effect on grazing rate (Anderson, 1997).

Initial biomass levels for *Neophylax* were maintained until day 20, when the first pupa was observed. Nevertheless, *Neophylax* larvae were not restocked as pupation increased; thus, grazer biomass decreased proportionally at all biomass levels. This decline in biomass level did not significantly affect results because only the first few days of grazing were used to calculate invertebrate grazing rates. *Dicosmoecus* did not begin to pupate until the very end of the experiment. Mortality was minimal for both grazers.

Effect of grazer biomass level

Periphyton biomass was dramatically reduced by both grazers at all grazer biomass levels (Figs 4 & 5). At all grazer biomass levels, *Neophylax* reduced algal biomass by at least 36% after only 2 days of grazing. After 7 days of grazing, periphyton biomass was reduced by 84–98% at all levels of *Neophylax* with no significant difference among the treatments ($\alpha = 0.05$).

At a lower grazer biomass of 750 mg m^{-2}, *Dicosmoecus* reduced periphyton biomass by an average of

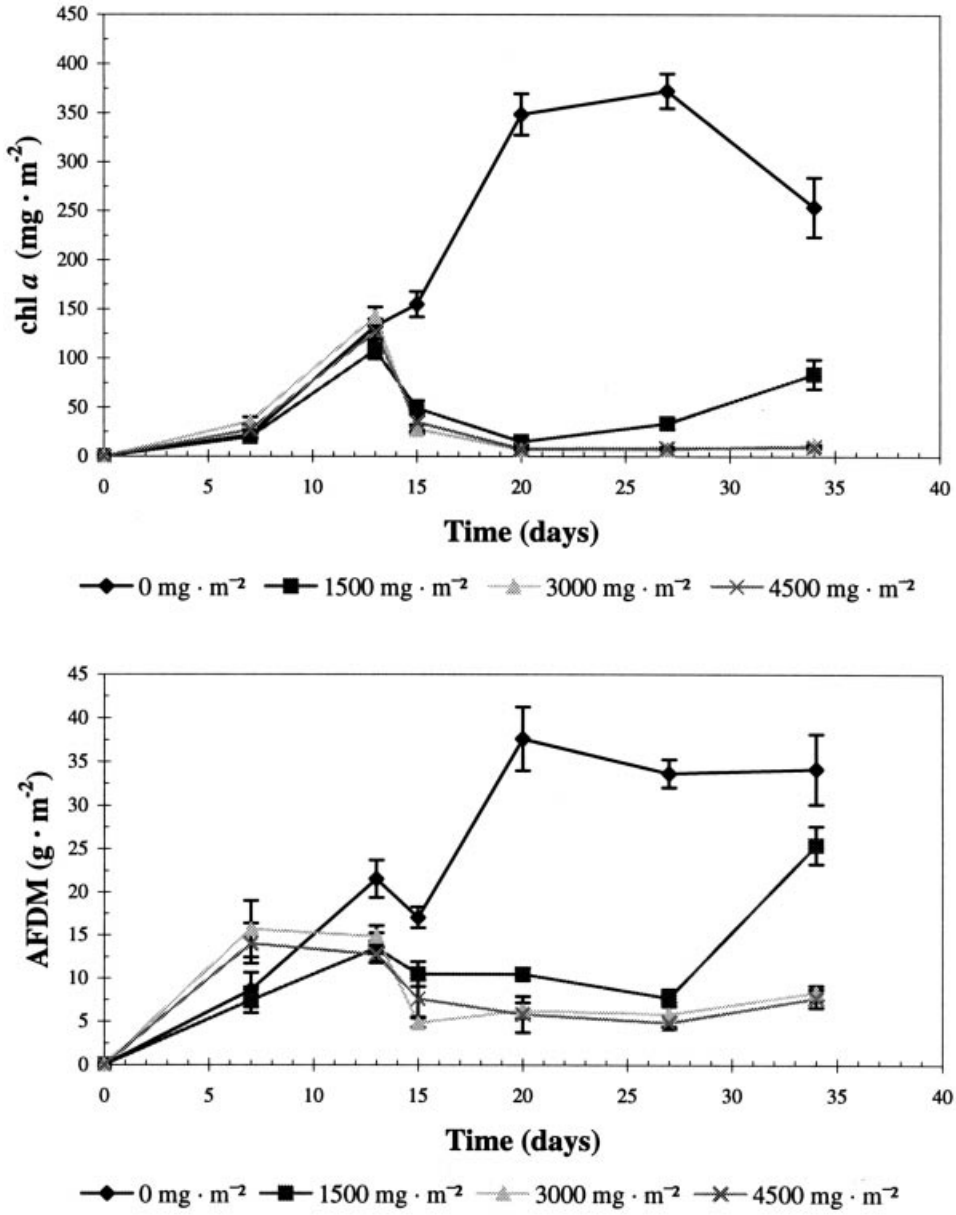

Fig. 4 Effect of grazer biomass level (*Neophylax*) on periphyton biomass (chl *a*, top; AFDM, bottom). The values for the 0, 3000 and 4500 mg m^{-2} grazing levels represent the means of eighteen sample replicates (six from each replicate channel). The values for the 1500 mg m^{-2} grazing level represent a mean of only twelve sample replicates since one set of data was discarded as a result of mayfly presence in the channel. The error bars show ± 1 SE for each mean value. Larvae were added after sampling on day 13.

only 48% after 2 days, whereas periphyton biomass was reduced by ≈ 87% at the two higher grazer biomass levels (1500 and 3000 mg m^{-2}). At the highest biomass levels, *Dicosmoecus* reduced periphyton biomass by at least 94% after 5 days. Periphyton biomass reduction at the lowest stocking biomass of 750 mg m^{-2} was significantly less (79%) than that at the higher biomass levels ($\alpha = 0.05$). By day 23, grazers at the higher biomass levels reduced periphyton biomass by 95%, while reduction at the 750 mg m^{-2} level was still significantly less (88%) ($\alpha = 0.05$) (Anderson, 1997). However, periphyton biomass began to increase from that point until day 34 when the experiment ended.

Taxonomic composition

Fragilaria, *Diatoma*, *Stigeoclonium* and *Scenedesmus* were the dominant periphyton taxa in terms of percentage biovolume in the *Neophylax* and *Dicosmoecus* experiments (Fig. 6). The diatom *Melosira*, other pennate diatoms and the cyanobacterium *Phormidium* were present to a lesser degree. Although not dominant in terms of biovolume, filamentous green algae were visually apparent in all of the channels.

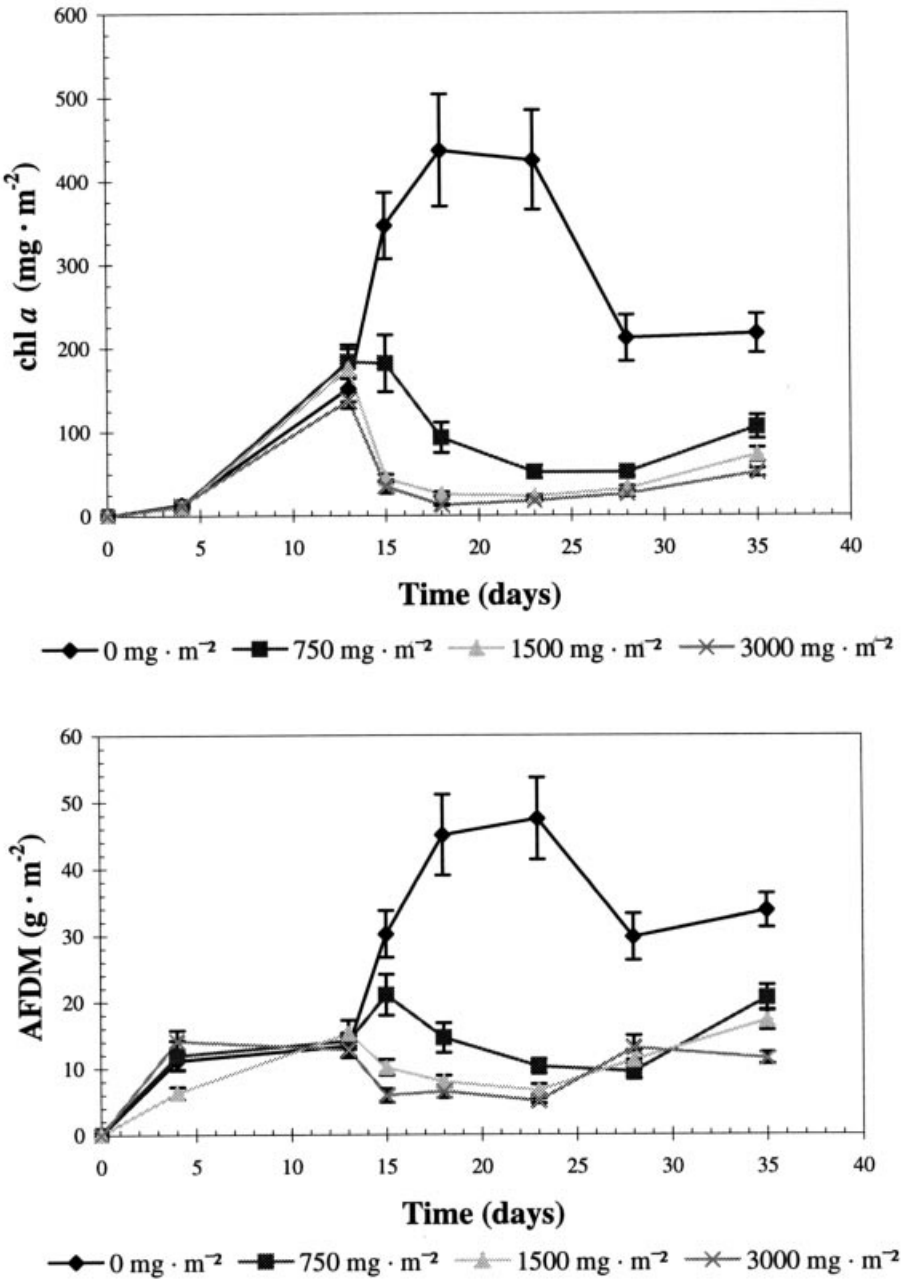

Fig. 5 Effect of grazer biomass level (*Dicosmoecus*) on periphyton biomass (chl *a*, top; AFDM, bottom). The values for all grazing levels represent the mean of 18 sample replicates (six from each replicate channel). The error bars show ± 1 SE for each mean value. Larvae were added after sampling on day 13.

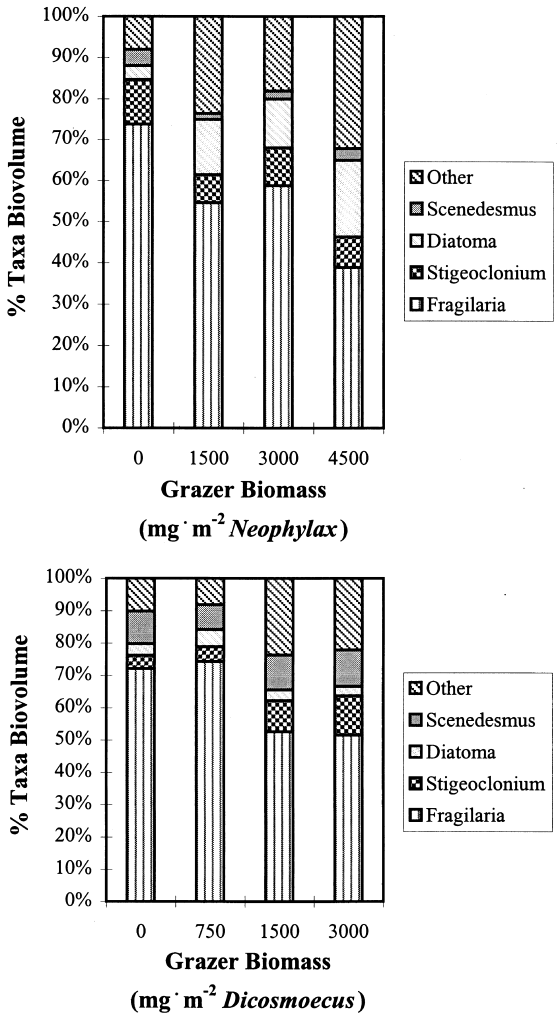

Fig. 6 Mean percentage biovolume of the dominant periphyton taxa for each of the grazer biomass level treatments on day 20 of the variable grazer biomass experiment with *Neophylax* (top) and *Dicosmoecus* (bottom).

Periphyton growth and invertebrate grazing rate

The maximum periphyton growth rate ($R_{p,u}$) in the experiment with *Neophylax* was 31 mg chl *a* m^{-2} day^{-1}, while the maximum $R_{p,u}$ with *Dicosmoecus* was 57 mg chl am^{-2} day^{-1} (Table 2). The mean water temperature was 3 °C higher during the second experiment, but this difference could only have increased periphyton productivity by about 20%, assuming a Q_{10} of 2. Therefore, the difference in growth rates probably cannot be attributed solely to temperature. However, the first periphyton growth rate was calculated over a 7-day period, whereas the second rate was calculated over a 5-day period. Hence, if the length of the exponential period were similar and relatively short, some of the difference in growth rates could be an artifact of the length of observation period (i.e. the denominator of Eqn 1).

These periphyton growth rates are comparable to rates calculated from outdoor stream channels in full sunlight. Experiments conducted in outdoor channels in Montana during July and August 1996 (water temperature = 15 °C, velocity = 15 cm s^{-1}, SRP = 10 μg L^{-1} and *Ulothrix* dominant) had periphyton growth rates of 16 and 57 mg chl *a* m^{-2} day^{-1}, respectively (Welch *et al.*, in preparation).

The grazing rates calculated for both *Neophylax* and *Dicosmoecus* (mg chl *a* m^{-2} day^{-1} and mg chl *a* g invertebrate^{-1} day^{-1}) are presented in Table 2. These rates are much higher (approximately five-fold for similar grazer biomass) than any previous grazing rates observed in these or the outdoor channels cited above.

Prediction of periphyton biomass

The purpose of the modelling effort in the present study was to modify the grazing term of an existing periphyton growth model (Horner *et al.*, 1983; Walton *et al.*, 1995) to vary as a function of grazer and periphyton biomass. For that purpose, a Michaelis–Menten formulation was included to represent grazing rate that: (1) approached a maximum, zero-order rate at high periphyton biomass; (2) depended on periphyton biomass at intermediate periphyton biomass; (3) equalled the periphyton growth rate when biomass was at or below some low biomass threshold; and (4) would proportionally increase or decrease depending on grazer biomass level. The complete model is represented as:

$$B_{i+1} = \Delta t\left[\begin{array}{l} K_1\mu L(k_f + k_{fo})(B_{\max} - B_i) - K_2V^{\theta} \\ -\left(g_{\max}\left(\dfrac{B_i}{K_{ab} + B_i}\right)B_g\right) \end{array}\right] \quad (5)$$

where grazing rate = $R_{gr} = g_{\max}\left(\dfrac{B_i}{K_{ab} + B_i}\right)B_g$

periphyton growth rate =

$R_p = [K_1mL(k_f + k_{fo})(B_{max} - B_i)]$

scouring loss rate = K_2V^{θ}, and Δt = 1 day.

Table 2 Calculated grazing rates for *Neophylax* and *Dicosmoecus* (mg chl *a* m^{-2} day^{-1} and mg chl *a* g $invertebrate^{-1}$ day^{-1}) for the variable grazer biomass experiment

Invertebrate grazer	Grazing level (mg m^{-2})	Mixed periphyton growth rate (mg chl *a* m^{-2} day^{-1})	Grazing rate (mg chl *a* g $invertebrate^{-1}$ day^{-1})
Neophylax	0	31	
	1500		40
	3000		29
	4500		17
Dicosmoecus	0	57	
	750		77
	1500		82
	3000		36

The definitions of all the model variables and constants, and their sources are listed in Table 3. All parameters except g_{max} and K_{ab} have been defined previously (Horner *et al*., 1983; Walton *et al*., 1995).

No sloughing term was included because predictions beyond maximum periphyton biomass were not considered. Also, B_{max} was set at 600 mg chl *a* m^{-2}, consistent with most observations in these channels

Table 3 Definition and sources of model constants and variables: SRP

Parameter/constant	Definition	Unit	Value	Reference
B	Periphyton biomass	mg chl *a* m^{-2}		
t	Time	days		
k_f	Mass transfer coefficient (turbulent diffusion)	cm s^{-1}	$(D \times V \times \pi^{-1})^{0.5}$	Horner *et al*. (1983)
k_{fo}	Mass transfer coefficient (non-turbulent condition)	cm s^{-1}	$0.009 \times 1.018^{(T-20)}$	Horner *et al*. (1983)
μ	Nutrient uptake rate	day^{-1}	$\mu_{max} \times SRP\ (K_s + SRP)^{-1}$	Michaelis–Menten formulation
μ_{max}	Maximum nutrient uptake rate	day^{-1}	$0.22 \times e^{T/10}$	Horner *et al*. (1983)
T	Temperature	°C		Data
SRP	Average in-channel SRP concentration	μg SRP L^{-1}		Data
K_s	SRP half-saturation constant	μg SRP L^{-1}		Calibrated
L	Light factor		0.755	Walton (1990)
B_{max}	Maximum sustainable biomass	mg chl *a* m^{-2}	600	Data with literature guidance
V	Current velocity	cm s^{-1}		Data
D	Diffusion coefficient	cm^2 s^{-1}	1.5×10^{-5}	Horner *et al*. (1983)
Theta	Velocity exponent		0.5	Calibration by Horner *et al*. (1983)
K_1	Periphyton growth coefficient			Calibrated
K_2	Scour coefficient		0.34	Calibration by Horner *et al*. (1983)
B_g	Grazer biomass	g DW invertebrate m^{-2}		Data
K_{ab}	Algal biomass at which grazing rate = 0.5 g_{max}	mg chl *a* m^{-2}		Calibrated
g_{max}	Maximum possible grazing rate	mg chl *a* g $invertebrate^{-1}$ day^{-1}		Calibrated

(Walton *et al*., 1995) and natural streams (Watson, 1989; Lohman, Jones & Perkins, 1992; Watson & Gestring, 1996). Although values on the order of 1000 mg chl *a* m^{-2} have been observed occasionally in channels and natural streams (Welch *et al*., 1992; Walton *et al*., 1995), such high levels occur too rarely to be generally applicable. During the second set of experiments, periphyton was not grazed to below 10 mg chl *a* m^{-2} at any grazer biomass levels. Consequently, an if/then statement was included to reduce the grazing rate (R_{gr}) to equal the net periphyton growth rate (R_p – scouring loss rate) if periphyton biomass (B) was grazed to 10 mg chl *a* m^{-2} or lower during any time step.

The values for T, SRP and V were determined from experimental data. The values for k_f, k_{fo}, L, θ and K_2 were taken from the calibration by Horner *et al*. (1983). Nutrient uptake rate was determined from the Michaelis–Menten equation shown in Table 3 with μ_{max} as a function of T.

The model was calibrated with data from the first set of experiments only since these produced grazing rates similar to those reported previously in these channels (Walton *et al*., 1995) and elsewhere (Jacoby, 1987). Since K_s was unknown, it was estimated from the data in each experiment. Therefore, K_s was calibrated simultaneously with K_1 by iteration using ungrazed data, assuming that K_s was between 1 and 10 μg L^{-1} SRP. K_s was allowed to vary among experiments, because each experiment had different water temperatures and taxonomic composition among periphyton communities. However, K_1 was calibrated until one common value satisfied predictions for all experiments. After K_1 and K_s were determined by calibration to ungrazed data, g_{max} and K_{ab} were calibrated to the grazed data by iteration. The maximum grazing rate (g_{max}) was 30 mg chl *a* g^{-1} day^{-1} for *Neophylax* and 45 mg chl *a* g^{-1} day^{-1} for *Dicosmoecus*.

Data from Walton's (1990) grazing experiment with *Dicosmoecus* were used for model verification. K_s was assumed to be 5 μg L^{-1}, the value used by Walton *et al*. (1995), and this estimate is consistent with experimental data (Walton, 1990). Model output agreed well with experimental data at all SRP concentrations; a comparison is shown for 10 μg L^{-1} only (Fig. 7).

The relationship between grazing rate and periphyton biomass in the model was demonstrated by

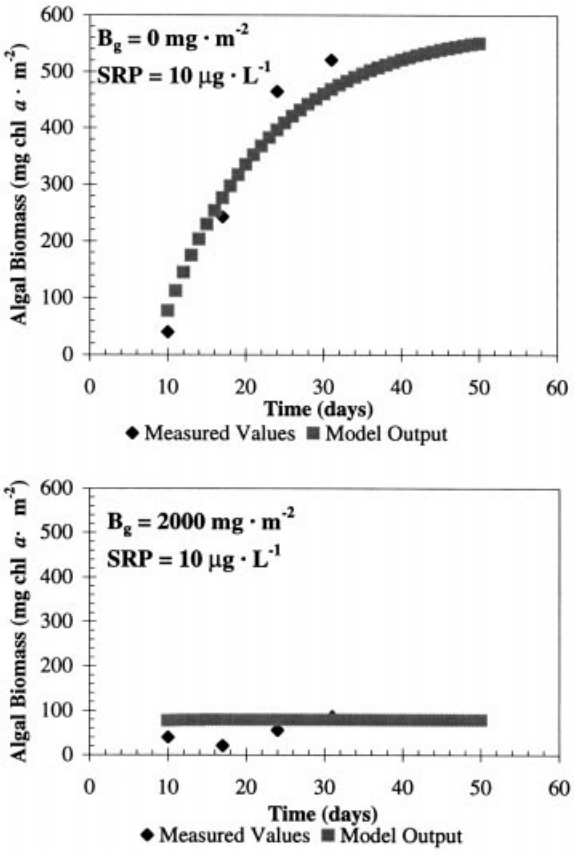

Fig. 7 Results of model verification with data for *Dicosmoecus* from Walton (1990). Grazer biomass levels and in-channel SRP concentrations are shown on each figure. The model constants were as follows: V = 20 cm s^{-1}; T = 19.1 °C; B_{max} = 600 mg chl *a* m^{-2}; K_{ab} = 125 mg chl *a* m^{-2}; K_1 = 5; g_{max} = 45 mg chl *a* m^{-2} day^{-1}; and K_s = 5.0 μg L^{-1}.

entering a high initial periphyton biomass value into the model and recording the subsequent changes in grazing rate as periphyton biomass decreased. This output is shown for a g_{max} value of 45 mg chl *a* g^{-1} day^{-1} (Fig. 8). At high periphyton biomass levels, R_{gr} approaches g_{max}. At lower levels, R_{gr} decreases until periphyton biomass reaches 10 mg chl *a* m^{-2} and R_{gr} is equal to the periphyton growth rate term. Predicted grazing rates, corresponding to the initial periphyton biomass levels observed in the first set of experiments (≈ 50 mg chl *a* m^{-2}), are similar to the calculated grazing rates. Consequently, the range estimated for g_{max}, 30–45 mg chl *a* g^{-1} day^{-1} is considered to be reasonable.

Model sensitivity was roughly quantified by vary-

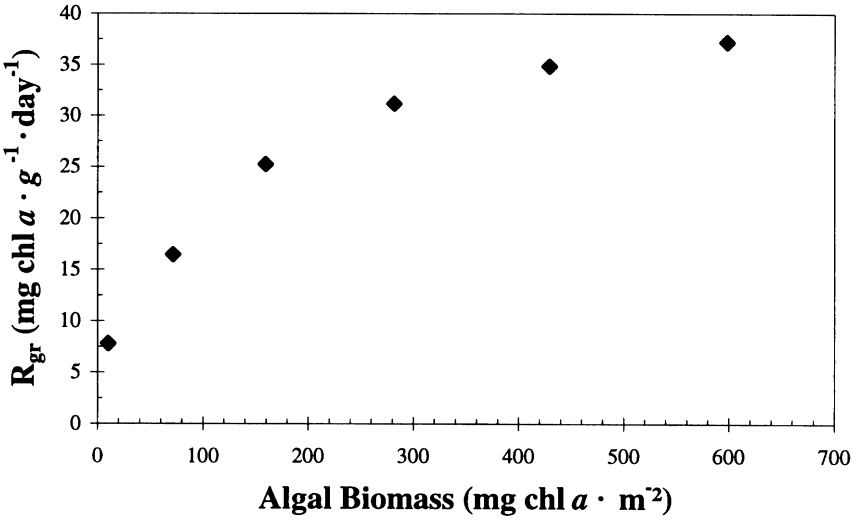

Fig. 8 The relationship between periphyton biomass and grazing rate (g_{max} = 45 mg chl *a* g^{-1} day^{-1}) used for prediction.

ing each calibrated parameter and recording the resulting percentage change in predicted 40-day periphyton biomass. When the algal growth coefficient, K_1, was increased by 10%, periphyton biomass increased by ≈ 13%. When the periphyton biomass half-saturation constant (K_{ab}) was increased by 10%, periphyton biomass increased by ≈ 8%. Also, when K_{ab} = 0 mg chl *a* m^{-2}, periphyton biomass was reduced nearly linearly by grazing. Finally, when g_{max} was increased by 10%, periphyton biomass decreased by ≈ 12%.

Periphyton biomass was predicted after 40 days over a range of SRP concentrations for different grazer biomass levels to evaluate threshold grazer biomass levels with increased enrichment (Fig. 9). The 40-day periphyton biomass was selected because, after that

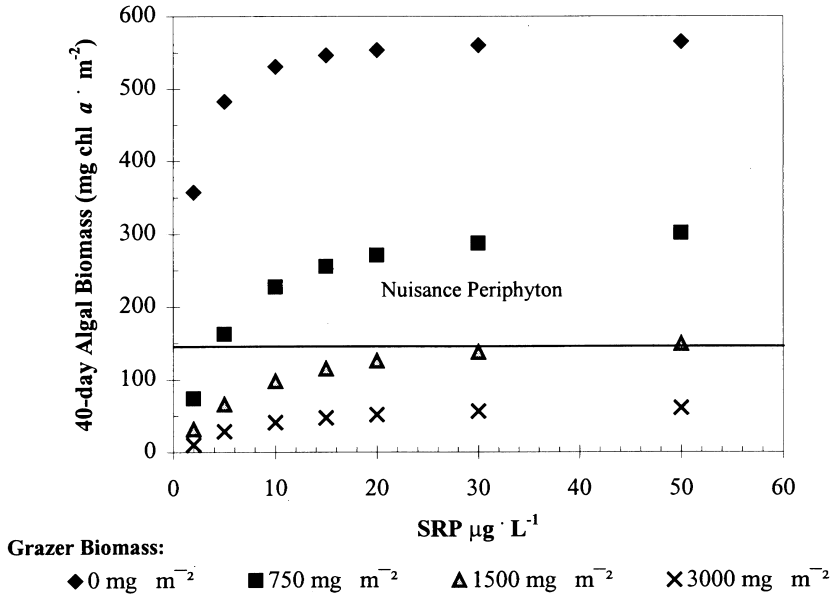

Fig. 9 Model output for 40-day maximum periphyton biomass for a range of SRP concentrations. The straight line represents a proposed threshold for nuisance periphyton biomass (150 mg chl *a* m^{-2}): g_{max} = 35 mg chl *a* g^{-1} day^{-1}; T = 18 °C; K_s = 5 μg L^{-1}; B_{max} = 600 mg chl *a* m^{-2}; V = 20 cm s^{-1}; K_1 = 5; and K_{ab} = 125 mg chl *a* m^{-2}. Grazing was started on day 11.

time and for all model simulations, grazing rate was equal to algal growth rate and algal biomass was constant.

As SRP increases, the grazer biomass level needed to maintain periphyton biomass below nuisance levels increases. For example, at 750 mg invertebrates m^{-2}, SRP concentrations greater than 5 $\mu g\ L^{-1}$ result in nuisance periphyton biomass by day 40. At 1500 mg invertebrates m^{-2}, periphyton biomass approaches nuisance levels only when SRP is $\approx 50\ \mu g\ L^{-1}$. Grazers at 3000 mg m^{-2} control periphyton at well below the nuisance threshold at any SRP concentration. Periphyton biomass in ungrazed simulations rapidly approaches B_{max} as SRP increases to only 10 $\mu g\ L^{-1}$. Predicted biomass without grazing may be overestimated because mat sloughing would probably occur before 40 days and there is no sloughing term in the model. However, given the rate at which maximum periphyton biomass was reached without grazing (Fig. 9), predicted maxima without grazing would be similar for much shorter times than 40 days. Predicted biomass is similar to observed values from the first set of experiments, although grazing is somewhat overestimated by the model (Fig. 8).

Discussion

Combined effect of SRP and grazing

The high degree of control exerted by the two caddisfly grazers on periphyton, as indicated by the substantial and significant difference in biomass between grazed and ungrazed treatments across all SRP levels, has also been observed elsewhere with these grazers (Jacoby, 1987; Lamberti *et al*., 1987, 1992; Steinman *et al*., 1987; Hill & Knight, 1988; DeNicola *et al*., 1990; Martin, Taylor & Barton, 1991; Hill, 1992; Hill *et al*., 1992; Rosemond, Mullholland & Elwood, 1993). Furthermore, previous work in these channels (Walton *et al*., 1995) showed that *Dicosmoecus* readily controlled periphyton biomass, including a filamentous taxon, at in-channel SRP concentrations of 2, 6 and 10 $\mu g\ L^{-1}$.

In the phosphorus–grazing interaction experiment, *Neophylax* larvae dramatically reduced periphyton biomass in the channels at low, medium and high inflow SRP concentrations. Maximum periphyton biomass in grazed channels never exceeded the nuisance level of 100–150 mg chl *a* m^{-2} (Welch *et al*., 1988) on any day after grazer stocking. However, algal biomass in the ungrazed channels surpassed nuisance levels at medium and high SRP concentrations, which averaged 7 and 12 $\mu g\ L^{-1}$, respectively. Relative to the maximum ungrazed periphyton biomass, biomass reduction by *Neophylax* averaged about 80% across all SRP concentrations.

Dicosmoecus larvae, at a comparable biomass to *Neophylax*, had a similar effect on periphyton biomass at the low, medium and high inflow SRP levels. Maximum chl *a* in grazed channels at low and medium SRP did not exceed nuisance biomass levels at any time during the grazing period. Maximum periphyton biomass in grazed, high SRP channels was significantly lower than that in ungrazed channels, although biomass exceeded nuisance levels in both cases (400 and 170 mg chl *a* m^{-2} in ungrazed and grazed channels, respectively). Biomass reduction by *Dicosmoecus* averaged about 67% across all SRP levels.

Separate effect of SRP

Soluble reactive phosphorus enrichment had a significant and positive effect on periphyton biomass, as indicated by chl *a* and AFDM during the first two experiments. The effect was clearly evident by simply observing mean biomass at low, medium and high SRP. Also, the effect was statistically significant across the two grazing levels for means on individual sampling days as well as for means over the entire grazing period. However, periphyton biomass at the medium and high SRP levels, across the two grazer biomass levels and on several individual sampling days, were not significantly different (Schimek, 1996). This was expected considering past results from these channels which showed that growth of even filamentous greens and blue-greens was saturated at a SRP < 10 $\mu g\ L^{-1}$ (Horner *et al*., 1990; Walton *et al*., 1995).

Effect of variable grazer biomass

Previous grazing rates reported for *Dicosmoecus* have been 6.9 mg chl *a* g^{-1} day^{-1} (Jacoby, 1987), 8.6 mg chl *a* g^{-1} day^{-1} (Walton, 1990) and 5.3 mg chl *a* g^{-1} day^{-1} in the phosphorus–grazing interaction experiments. Comparatively, the rates measured in the variable grazer biomass experiments are extremely high (36–82 mg chl *a* g^{-1} day^{-1}; Table 2). Simi-

larly, the grazing rates of *Neophylax* in variable grazer biomass experiments (17–40 mg chl *a* g^{-1} day^{-1}; Table 2) were much higher than those in the phosphorus–grazing interaction experiment (0.79–6.1 mg chl *a* g^{-1} day^{-1}; Table 1).

The higher rates in the variable grazer biomass experiments may be a result of *Neophylax* and *Dicosmoecus* being in a state of starvation while in Issaquah Creek. The creek had experienced some flooding during winter 1996–1997. There were slope failures in the stream in the area in which *Neophylax* and *Dicosmoecus* were collected, suggesting that scour may have kept periphyton resources low. Gut content analyses showed that *Dicosmoecus* taken directly from Issaquah Creek had 3.6 times more gut mass and 7.5 times more gut volume composed of inorganic matter than *Dicosmoecus* taken from the channels later (26.7% versus 3.5%, respectively). The present authors assumed that *Neophylax* was similarly affected because the larvae were collected from the same area as *Dicosmoecus* larvae only one month earlier.

Nevertheless, other researchers have reported similarly high grazing rates for *Dicosmoecus*. DeNicola *et al*. (1990) and Lamberti *et al*. (1987) observed dramatic reductions of periphyton biomass at grazer biomass levels of 1200 mg m^{-2} (50% reduction after 4 days) and 4500 mg m^{-2} (95% reduction after 3 days). However, the extraordinary environmental conditions which may have caused the elevated rates were not mentioned. The wide range of grazing rates observed here and elsewhere suggests that invertebrate grazers may be affected by the stream conditions where these animals are collected as well as in the experimental environment.

The grazing rate calculation makes no distinction between periphyton loss as a result of consumption and export. Therefore, increased export from the greater activity of starved grazers would have contributed to the calculated grazing rate. Export rates were not determined, but substantial sloughing was observed in the grazed channels soon after stocking. Thus, increased export from grazer activity probably contributed to the high calculated grazing rates as well as increased consumption from starvation.

Ryder (1989) reported that mayflies (*Deleatidium*) grazing on silted and clean periphyton ingested silt in proportion to its concentration in the periphyton. The above author proposed that the larvae could not reject the silt, but instead consumed the silt along with periphyton, suggesting that removal rates of silted periphyton would have to be greater than unsilted periphyton to supply adequate nutrition.

Differences in grazing effectiveness among grazer stocking levels were difficult to distinguish because of this rapid reduction of periphyton to similarly low biomass levels. Consequently, the relative effectiveness of *Neophylax* and *Dicosmoecus* at different stocking levels could not be distinguished readily. However, some researchers have shown that grazing rates decreased with increasing grazer biomass and attributed the effect to increased competition and mechanical energy demand (Brown & Carman, 1994). This same phenomenon might have been evident here had the grazing rates not been so exceptionally high.

Effects of grazer size

The grazing rates for *Neophylax* and *Dicosmoecus*, although differing statistically, were actually quite similar, varying by a factor of only about 1.5, considering that the biomass of *Neophylax* is seven times less than that of *Dicosmoecus* (3.5 versus 24 mg $individual^{-1}$). Thus, grazer size was probably much less significant than biomass in determining areal grazing rate. Hence, grazing by *Neophylax* and *Dicosmoecus* was similarly modelled on a biomass basis.

Steinman (1991) also found that snail (*Elimia*) size did not significantly affect the removal of algal AFDM. Cattaneo & Mousseau (1995) reported that 65% of the variation in removal rates was attributable to differences in grazer biomass. Based on these results, the above authors proposed that removal rate is primarily a function of overall grazer biomass and not grazer size. For example, five, 1-mg caddisflies will graze at approximately the same rate as one, 5-mg caddisfly. Cattaneo & Mousseau (1995) also indicated that there was no significant difference in removal rates between snails and caddisflies despite their differing morphological and behavioural characteristics. Therefore, grazer biomass may be a sufficient indicator to express the grazing effect for predicting maximum periphyton biomass in streams, regardless of grazer size and perhaps taxa, although the latter requires further study.

Prediction of periphyton biomass

The effects of P enrichment and grazer biomass level

were reasonably well simulated for conditions in these experimental channels. Saturation of periphyton biomass at relatively low SRP concentrations was clearly evident in the experimental results and could be predicted as shown previously (Walton *et al*., 1995). Combinations of SRP and grazer biomass that would result in maximum periphyton biomass less than nuisance levels were evident. According to the model, SRP > 5 $\mu g\ L^{-1}$ would probably be required to exceed a nuisance biomass of 150 mg chl *a* m^{-2} if grazing occurred at low levels, and if grazer biomass was >1500 mg m^{-2}, nuisance periphyton biomass would not be exceeded at any concentration of SRP.

To improve model predictions further, a term which decreases grazing efficiency with increased grazer biomass level (as a result of crowding effects) could be added in the form of a second Michaelis–Menten type formulation. This addition could perhaps provide better predictions of algal biomass under highly grazed conditions. If biomass prediction over time, in addition to the maximum, is desired, a sloughing term as a function of algal biomass should be added.

These results indicate that while low concentrations of SRP can result in nuisance biomass levels of periphyton, a relatively low biomass level of grazers may be capable of controlling that biomass, even at high SRP. Therefore, the present research illustrates the potential importance of sustaining invertebrate habitat in enriched stream environments where reducing the limiting nutrient is not an option. If a degraded habitat is significantly improved, the rehabilitated area may attract invertebrates from upstream reaches which could, in turn, graze nuisance periphyton to more acceptable levels.

Acknowledgments

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