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Light and a grazing mayfly shape periphyton in a Rocky Mountain stream

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Abstract. To examine the combined effects of light and grazers in structuring periphyton in a subalpine stream, we conducted a field experiment in St. Louis Creek (elevation 3000 m), a 2nd-order Rocky Mountain stream (Colorado, USA). Quarry tiles were placed in the stream for 60 d to colonize with periphyton and then moved into 36 stream channels in which light and grazers were manipulated. Light treatments were high (100% of ambient), intermediate (~40% of ambient), and low light (~5% of ambient). A grazing mayfly, *Rhithrogena robusta*, was maintained inside channels at high (288/m^2), low (96/m^2), or zero densities. After 22–23 d of exposure, mayfly grazing significantly reduced algal biovolume under all light regimes, although species assemblages differed between light treatments. As light levels changed, some algae showed different responses to grazing. *Hydrurus foetidus* (Chrysophyta), for example, was more abundant on grazed substrata relative to non-grazed controls under high light, but it declined in abundance when grazed under intermediate light. Light and grazers also had an interactive effect on periphytic biomass; as light increased, grazers caused greater depletions in periphytic ash-free dry mass. Results suggest that, in subalpine streams, light may be instrumental in establishing periphytic structure and in modifying the impact that grazers have on algae.

Key words: periphyton, algae, herbivory, light, community structure, *Hydrurus foetidus*, *Gomphonema*, subalpine streams, *Rhithrogena robusta*.

Grazers in streams can be a potent selective force shaping the structure and composition of periphytic communities. Herbivory selectively eliminates individual algal cells and can substantially reduce periphytic biomass (Feminella et al. 1989), yet grazing can also have positive, indirect effects on algal communities (e.g., Hart 1985). By removing overstory layers of periphyton, grazers can reduce shading of underlying cells, remove potential competitors for limiting nutrients, and open up space for colonization (Sumner and McIntire 1982, Steinman et al. 1987). Grazers may even add nutrients to periphyton in the form of excreted fecal matter (McCormick and Stevenson 1989). By reducing the abundance of some species relative to others these effects and others allow grazers to alter periphytic assemblages.

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Recent reviews by Cyr and Pace (1993) and Feminella and Hawkins (1995) have emphasized the role of herbivores in structuring aquatic communities. What is less appreciated is how the physical environment might modify herbivory and other biotic interactions, potentially altering their importance or even their outcomes (Dunson and Travis 1991, Hart 1992). Light intensity, by shaping periphytic assemblages, could conceivably determine the impact grazers will have on periphytic algae. Light can be highly variable in streams (DeNicola et al. 1992), and as species composition of the periphyton changes in response to light, so might characteristics that are of consequence to grazers (Stevenson et al. 1991, Steinman 1992). If stalked and erect algae were more abundant under some light intensities, for example, and gelatinous forms were more abundant under others, it might be expected that light level could influence the assemblage's vulnerability to consumers (Steinman et al. 1992).

Here we examine the interactive effects of mayfly grazing and light in structuring an epilithic algal community in a subalpine Rocky Mountain stream. Our objectives were to determine how the effects of mayfly grazing on periphyton, and in particular the algal component of the periphyton, are modified by light availability, and to compare the responses of algal species to grazing under different light regimes. We make the distinction between periphyton (measured as total periphytic ash-free dry mass) and periphytic algae (measured as algal cell biovolume) because algae are just one component, albeit a very important one, of the periphytic matrix. Periphyton is a complex biofilm that consists of bacteria, protozoa, algae, extracellular polysaccharides, detritus, and inorganic material (Lock 1993). We reasoned that as light levels changed, so might the proportion of the periphytic biomass which is made up of autotrophs. We manipulated light level in an attempt to mimic the high intensities found in open canopy stream sections, the intermediate levels found in reaches flowing through forest canopies, and the low light found under heavy riparian cover and beneath or between stream cobbles. We chose a mayfly grazer, *Rhithrogena robusta*, which was abundant and ubiquitous throughout the study stream, and manipulated its density to produce three levels of grazing pressure.

Our first prediction was that light would modify the influence of grazing on algae, causing a shift from abiotic limitation (low influence of grazers) at low light to biotic limitation (grazer controlled) at higher light intensities. Purportedly, losses of algae to mayfly grazing would be least at low light where algae would make up proportionally less of the total periphytic biomass. Others (Lamberti et al. 1989, Steinman et al. 1989, Steinman 1992, Rosemond 1993, Hill et al. 1995) have shown that snail grazers limited algal biomass at high and low light intensities, but mayfly mouthparts are not as efficient at gleaning periphyton from substrata as is a molluscan radula (Arens 1989). Although grazer consumption rates cannot exceed certain maxima (Arens 1989), Scrimgeour et al. (1991) have shown that non-consumptive losses caused by mayfly foraging continue to increase as algal biomass accumulates. Thus, grazers are expected to become more important for reducing algal biovolume and total periphytic biomass at higher light levels.

Our second prediction was that algal species would differ in response to grazing across light intensities. We based this prediction on 2 assumptions. First, by altering assemblage structure, light would make some algae either more or less vulnerable to grazing. Second, light intensity could shift the equilibrium between an algal species' recruitment and its losses to grazing. Under optimal light intensities, for example, some algae may be able to grow, reproduce, and colonize substrata at a rate equal to or above that at which they are removed by grazing.

Methods

Study site

The study was conducted in St. Louis Creek, a 2nd-order stream at Fraser Experimental Forest, draining approximately 9300 ha of alpine meadow and subalpine forest in the Rocky Mountains of Colorado, USA. Substrata in the stream channel are predominantly cobbles, gravel, and sand, with occasional boulders. Discharge in Colorado Rocky Mountain streams is strongly influenced by the temperate climate and the snow pack in the alpine zone, with approximately 95% of stream run-off derived from spring snow melt, and 5% from summer rainfall (Adenlof and Wohl 1994). The annual hydrograph is dominated by one large peak resulting from snowmelt (Poff and Ward 1989). Peak discharge in St. Louis Creek generally occurs in mid June and then rapidly decreases, reaching base flow in August.

The subalpine riparian forest consists of lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), and fir (*Abies lasiocarpa*). Where the stream flows through wet meadows, the canopy is open and dominated by grasses and low willow shrubs (*Salix* spp.). Diatoms are the predominant algae in the stream, but the chrysophyte *Hydrurus foetidus* may be very abundant, and chlorophytes and cyanobacteria (primarily *Chamaesiphon incrustans*) are also important. Ephemeroptera larvae are the primary grazers, making up 53% of the total number of macroinvertebrates collected in July 1994. Among mayfly grazers, *Baetis* spp. were most abundant (19%), followed by *Rhithrogena robusta* (13%), *Epeorus deceptivus* (12%), and *Cinygmula* spp.

(8%). *Rhithrogena robusta* was the largest of these mayflies and probably accounted for most of the grazer biomass during July. This species also proved to be the easiest to maintain in the experimental enclosures used in the study.

Grazer

Members of the genus *Rhithrogena* feed on epilithon, employing labial brushes and maxillary palps to scrape algae and detritus from substrata (McShaffrey and McCafferty 1988). We used final-instar nymphs, determined by wing-pad development, for our study. Individuals averaged 10.5 ± 0.2 mm (mean ± SD; n = 22) in length without cerci, and 4.0 ± 3.4 mg (n = 129) in dry weight. Seven Surber samples taken from a riffle immediately upstream of the study site showed mean densities in early July 1994 to be 96 ± 34 individuals/m^2. *Rhithrogena robusta* were hand-collected from St. Louis Creek on 2 July 1994 and added to the experimental channels to yield treatments of either zero, 8 nymphs/channel (mean streambed density), or 24 nymphs (3× mean density) per channel. These densities were within the naturally occurring range for *R. robusta* in St. Louis Creek during July 1994.

Experimental design

We examined the effects of 3 light levels (high, intermediate, and low) and 3 mayfly densities (none, ambient, and 3× ambient) on periphyton grown in St. Louis Creek. Light and grazers were manipulated within 36 stream channels in a 3 × 3 factorial experiment. There were 4 replicates of each combination.

Stream channels were constructed of 95-cm sections of 21.5-cm diameter PVC duct pipe that had been sectioned lengthwise. Each half formed a trough whose sides were extended with PVC panels, giving a completed round-bottomed channel that measured 21 (width) × 24 (depth) × 95 (length) cm. Channels were bolted to cement blocks which anchored them approximately 20 cm above the streambed. Nylon mesh (2 mm) glued to the channel ends prevented *Rhithrogena robusta* from escaping or entering. The channels were positioned in flows that produced a mean current velocity of 0.28 ± 0.06 m/s (mean ± SD; n = 36) within the channels. These velocities were similar to those found in slower moving reaches of St. Louis Creek. When necessary, channels were moved to maintain proper water velocity and a ca. 10-cm depth. Mean natural current velocity within the study reach was 0.53 ± 0.18 m/s (n = 35).

We used unglazed quarry tiles (15.0 × 15.0 × 1.0 cm) as substrata. On 2 May 1994, 144 tiles were placed in an open section of St. Louis Creek to initiate periphytic colonization. Tiles were strapped to 60 × 60 cm mats of wire hardware cloth with nylon cable ties. Each mat held 9 tiles, and 16 mats were constructed and staked to the streambed to prevent displacement during peak flow. After 60 d the tiles were detached from the mats and placed inside the stream channels. Three tiles were positioned end to end at the center of each of the 36 channels, and 8–10 cobbles taken from a dry, exposed gravel bank were stacked in front and behind the tiles to hold them in place and to provide additional refuge for *R. robusta* nymphs. Mayfly densities established within channels were based on the upper surface area of 3 clay tiles, the same surfaces which were sampled at the end of the experiment.

Light levels within the channels were controlled with shading cloth attached to the tops of the channels. The 3 light treatments were: high light (no covering), intermediate light (covered with Dewitt Sudden Shade™ plastic shading cloth), and low light (covered with tent canvas). Light was measured on 24 and 25 July 1995 inside channels with a Licor™ spherical quantum sensor and a LI–1000™ data logger. Light measurements were recorded every 2 h by placing the sensor at the center of each channel just above the water surface and taking the average of 4 readings. Mean light levels (μmol m^{-2} s^{-1}, n = 32) over the day were 1367 for high light, 524 for intermediate light, and 25 for low light (Fig. 1).

The experiment lasted for 22–23 d. During this time the channel screens were cleaned twice daily (morning and evening) with a soft-bristle brush to remove accumulated detritus. *Rhithrogena robusta* nymphs that had died or emerged (as determined from dead nymphs or exuviae found on the downstream screens) were replaced with fresh individuals. Each week, inner channel surfaces were carefully scrubbed with a scouring pad to remove algae and accumulation on any surface other than the tiles, and old cobbles were replaced with new dried cobbles.

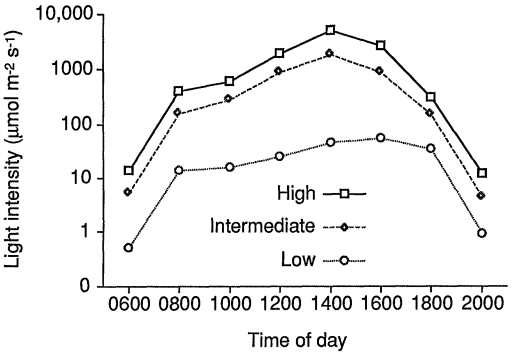

FIG. 1. Mean light levels (μmol m^{-2}, s^{-1}) taken every 2 h in the air just above the water surface within each channel for low, intermediate, and high light treatments (n = 12 for each treatment) on 24 and 25 July 1994. Standard error bars are too small to be visible in the figure.

To eliminate position effects, tile positions were rotated weekly. Periphyton was sampled from tiles on 24 and 25 July 1994.

Algal sampling and analysis

Periphyton was removed from the upper surface of each tile with a toothbrush and squirt bottle. Material scraped from the 3 tiles collected from each channel was pooled to constitute a single sample. In the laboratory, within 2 h of sampling, periphytic suspensions were brought up to a constant volume of 150 mL in a 300 mL flask. Three 50-mL sub-samples were withdrawn from each suspension to determine chlorophyll *a* concentration, ash-free dry mass (AFDM), and algal identity and abundance (cell density and biovolume). Sub-samples were rapidly extracted 1 cm from the bottom of the flask with a 50-mL, wide-bore pipette after vigorously shaking the flask 3 times. The 1st sub-sample was filtered (Gelman A/E glass fiber filter) and frozen, and chlorophyll *a* was extracted with 90% buffered acetone and spectrophotometrically analyzed using the acidification method (American Public Health Association 1985). The 2nd sub-sample was filtered onto pre-weighed glass fiber filters, and AFDM was determined by taking the difference between dried (at 60°C for 24 h), and ashed (480°C for 2 h) sample weights. The remaining sub-sample was preserved in 2% formalin and used to determine composition, density, and biovolume of algal species. Density and biovolume estimates were based on counts of intact, protoplast-containing (i.e., live) cells using an inverted phase-contrast Leitz microscope. Cell density and species composition were estimated by counting at least 300 cells from each sample. Large algal cells were counted at 125× magnification; cyanobacteria and small diatoms were counted at 1250×. Diatom species identifications were made at 1250× magnification on Hyrax-mounted slides from material cleared in 30% hydrogen peroxide before mounting. Cell dimensions were measured with an ocular micrometer, and cell volume was estimated by applying average dimensions of a minimum of 20 cells per species per sample to the geometric shape best approximating the cell shape of each species (Wetzel and Likens 1979).

Statistical analysis

We analyzed the effects of light level and grazer density, and the interaction of these 2 factors on algal biovolume, AFDM, species richness, and cell size with a 2-way analysis of variance (ANOVA) using the General Linear Models (GLM) procedure on SAS (Release 6.03, SAS Institute, Cary, North Carolina). Planned comparisons of grazer effects within light treatments were made using the LSMEANS (least squares means) statement in the GLM procedure (Freund and Littell 1981). Multiple contrasts of grazer and light effects alone were made using Tukey's test (Zar 1984). Algal biovolume data were log-transformed so that they fit homogeneity of variance and normality assumptions, as determined by Bartlett's and Shapiro-Wilk's test, respectively. AFDM, species richness, and algal cell size data fit these assumptions without need for transformation. Chlorophyll *a* data were inconsistent with algal biovolume values, and we suspect samples degraded during storage, so these data are not presented.

Results

Efficacy of manipulations

The stream channels formed effective barriers to *Rhithrogena robusta* movement. Although most channels required mayfly replacement following death or emergence, no immigration into or emigration out of the channels occurred. At the end of the experiment, high-density treat-

TABLE 1. *F* values from analysis of variance of light and grazer effects on algae taken from tiles after 22–23 d in stream channels.

Factor (df)	AFDM	Biovolume	Species richness	Mean cell size
Light (2, 27)	68.13**	65.51**	12.42**	3.42*
Grazers (2, 27)	16.18**	23.89**	19.55**	7.93**
Light × grazers (4, 27)	3.36*	2.86	2.37	0.53

* $p < 0.05$, ** $p < 0.005$

ments had lost an average of 3.7 *R. robusta* individuals per channel and low-density treatments lost 0.8. Most individuals were lost to emergence, however, and mortality did not appear to be greater in high density treatments. Other invertebrates entered the channels only in small numbers. Early instar mayflies (primarily Baetidae) and small stoneflies (e.g., *Sweltsa* sp. and *Zapada* sp.) were occasionally seen on tiles but their small size (~1–3 mm) and low number (<12 per channel) suggest that their effects on algae were negligible compared with *R. robusta* effects. Grazer controls did not have more invertebrate immigrants than did other treatments (ANOVA, $F_{2,27} = 0.93$, $p = 0.07$).

Light effects

Periphytic AFDM, algal biovolume, and algal species richness were greater at the 2 higher light intensities (Tables 1 and 2), although intermediate light produced the greatest values. This trend was significant, however, only for periphytic AFDM (ANOVA, $F_{2,27} = 68.13$, Intermediate > High > Low, Tukey's test, $p < 0.05$; Table 2). Mean cell size was greatest at intermediate light and did not differ between low and high light treatments (Table 2).

Light level had a strong effect on the abundance of common algae. The most common algae under intermediate light were 3 species of *Gomphonema* (*G. affine*, *G. angustatum*, *G. olivaceum*) and *Hydrurus foetidus*, which made up 26% and 24% of algal biovolume, respectively. *Hydrurus foetidus* (42% of algal biovolume across grazer treatments) was most abundant at high light, and *Diatoma mesodon* (34%) and Chlorophytes (30%) were the most abundant algae in the low light treatment (Table 3). Across all light treatments *Gomphonema* spp. were the most common algae, making up 23% of total algal biovolume after 22–23 d.

Differences in mean algal size between treatments were due to variation in algal species composition among assemblages. Large diatoms, primarily *Gomphonema affine* (average cell volume > 1000 μm^3) predominated under intermediate light whereas *Chlorella* sp. and *Mariellopsis* sp., the two small chlorophytes common under low light, had cell volumes that averaged around 10 and 100 μm^3, respectively. The most common alga under high light, *H. foetidus*, had a mean cell size of 125 μm^3.

Grazer effects

Periphyton grazed by *Rhithrogena robusta* had less AFDM, less algal biovolume, lower algal species richness, and smaller algal cell size than did non-grazed treatments (Tables 1 and 4). Each increase of *R. robusta* density, from no mayflies to ambient, and from ambient to 3×

TABLE 2. Light effects across grazer treatments. Mean (±1 SE) values for periphytic biomass (AFDM), algal biovolume, species richness, and mean cell size for the 3 light treatments. Different superscript letters indicate significant differences between light treatments ($p < 0.05$, Tukey's test).

Parameter (units)	Low	Intermediate	High
AFDM (mg/cm^2)	4.4 ± 0.2^a	10.9 ± 0.4^b	9.2 ± 0.9^c
Biovolume ($\mu m^3/cm^2 \times 10^7$)	0.87 ± 0.46^a	19.01 ± 5.81^b	11.62 ± 2.85^b
Algal richness (no. of species)	8.1 ± 0.7^a	12.7 ± 1.3^b	10.9 ± 0.9^b
Mean cell size (μm^3)	345 ± 63^a	543 ± 71^b	514 ± 68^a

TABLE 3. The most abundant algal species on tiles at the start of the experiment (Initial conditions), and after 22–23 d exposure to various grazer × light treatments. 0x, 1x and 3x refer to grazer densities where x = mean ambient density of *Rhithrogena robusta*/m² at the start of the study. Values are the mean percent abundance in biovolume for each species. The mean biovolume for each treatment is given in the last row.

Species	Initial conditions	Low light			Intermediate light			High light		
		0x	1x	3x	0x	1x	3x	0x	1x	3x
Bacillariophyta										
Achnanthes minutissima	5	5	5	6	6	3	7	1	<1	1
Cymbella minuta	<1	8	3	3	<1	0	0	1	0	6
Diatoma mesodon	0	43	2	0	6	<1	0	1	<1	0
Gomphonema affine	0	0	0	10	4	9	40	12	3	8
Gomphonema angustatum	<1	16	10	1	11	28	27	13	3	2
Gomphonema olivaceum	0	<1	<1	1	2	7	11	2	<1	2
Fragilaria arcus	2	0	19	<1	25	19	3	46	5	<1
Nitzschia paleacea	0	<1	0	7	2	1	0	0	0	0
Pinnularia sp.	4	0	0	0	0	0	0	0	0	0
Chlorophyta										
Chlorella sp.	0	11	26	31	<1	1	<1	<1	0	1
Muriellopsis sp.	0	13	26	27	<1	0	0	0	0	0
Chrysophyta										
Hydrurus foetidus	73	0	2	0	29	21	7	19	81	70
Cyanophyta										
Chamaesiphon incrustans	15	1	1	5	<1	7	8	1	6	5
Total mean biovolume ($\mu m^3/cm^2 \times 10^7$)	1.27	2.14	0.33	0.21	40.19	8.72	8.16	21.38	11.42	2.07

TABLE 4. Grazer effects across light treatments. Mean (±1 SE) values for periphytic biomass (AFDM), algal biovolume, species richness, and mean cell size for the 3 grazer treatments. Grazer densities are listed as 0x, 1x, and 3x where x = the average density of *Rhithrogena robusta* on the St. Louis Creek streambed at the start of the study. Superscripts show whether grazer effects were significant across light treatments. Different letters indicate significant differences ($p < 0.05$, Tukey's test).

Parameter (units)	0x grazers	1x grazers	3x grazers
AFDM (mg/cm²)	9.8 ± 1.1[a]	8.3 ± 0.9[b]	6.5 ± 0.8[c]
Biovolume (μm³ cm² × 10⁷)	21.23 ± 6.02[a]	6.82 ± 1.77[b]	3.47 ± 1.24[c]
Algal richness (no. of species)	13.8 ± 1.2[a]	9.8 ± 0.8[b]	8.1 ± 0.6[b]
Mean cell size (μm³)	649 ± 84[a]	396 ± 42[b]	343 ± 40[b]

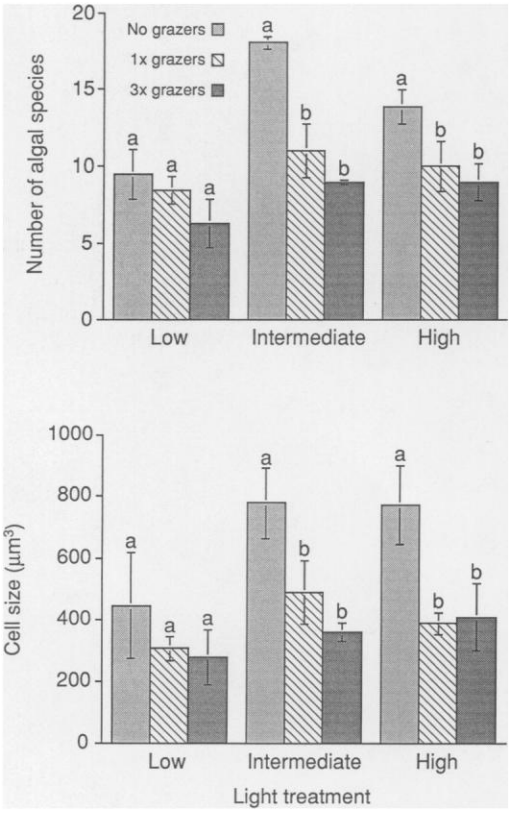

FIG. 2. Algal species richness and cell size (μm³) responses to *Rhithrogena robusta* grazing under the 3 light treatments. Bars = ±1 SE. Grazer densities are listed as 0x, 1x and 3x where x = the average density of *Rhithrogena robusta* on the St. Louis Creek streambed at the start of the study. Within light treatments, means of bars having the same letter are not significantly different (least squares means test, $p < 0.05$).

ambient, resulted in significantly less periphytic AFDM and algal biovolume ($F_{2,27}$ = 16.18 for AFDM and 23.89 for biovolume, Tukey's test; $p < 0.05$; Table 4). There were no differences between 1× and 3× mayfly treatments in species richness and cell size (Fig. 2, Table 1).

We considered species to be tolerant to grazing if they did not decline in either relative or absolute abundance across grazer treatments within a given light treatment. Tolerant species included small forms such as *Chamaesiphon incrustans* (Cyanophyta), *Chlorella* sp., and *Muriellopsis* sp. at low light, and also the stalked and relatively large *Gomphonema* spp. at intermediate light, and the gelatinous *Hydrurus foetidus* (Chrysophyta) under high light (Table 3, Fig. 3). Species that were not resistant to grazing tended to be large diatoms like *Fragilaria arcus* and *D. mesodon*. However, the response of some taxa to grazing changed with light intensity (e.g., *Gomphonema* spp. and *H. foetidus*; see below).

Light and grazer effects on periphytic and algal biomass

Grazers had a greater negative impact on AFDM at higher light intensities, causing a significant interaction between the effects of light and grazing ($F_{4,27}$ = 3.36, $p < 0.05$; Table 1). Under low light, grazers had no effect on AFDM; under intermediate light, grazers reduced periphytic biomass, but only at high (3x) densities; at high light levels, grazers reduced periphytic biomass at high and low densities and each increase in grazer density caused a significant reduction in AFDM (least squares means test, $p < 0.05$; Fig. 4). The greatest reduction in periphytic AFDM by grazing occurred at high light.

Algal biovolume response was different from periphytic AFDM. Mayfly grazing caused re-

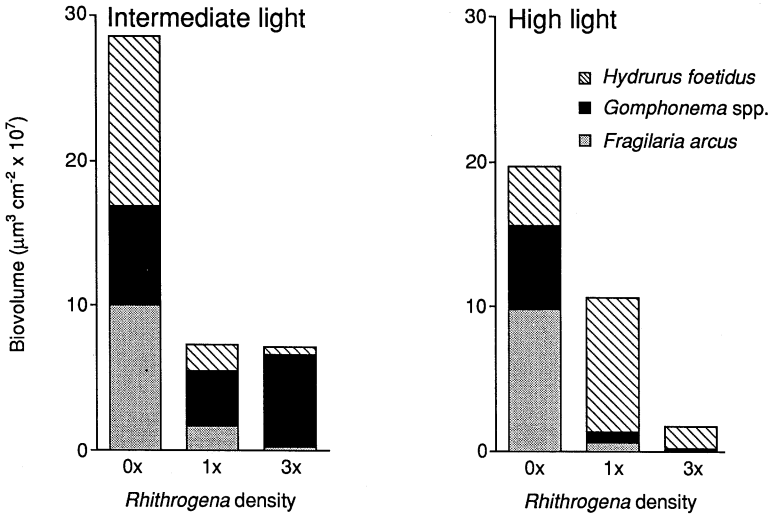

FIG. 3. Total algal biovolume ($\mu m^3/cm^2 \times 10^7$) of the 3 dominant algae (*Hydrurus foetidus*, *Gomphonema* spp., and *Fragilaria arcus*) under different grazer regimes in intermediate and high light treatments. Grazer densities are listed as 0x, 1x and 3x, where x = the average density of *Rhithrogena robusta* on the St. Louis Creek streambed at the start of the study.

ductions in algae at all light levels, with no differences in algal biovolume noted between 1x and 3x grazer densities at low and intermediate light. At high light levels, however, algal biomass was significantly reduced only at the 3x grazer density (Fig. 4). *R. robusta* grazing caused the greatest absolute reduction in algal biovolume at intermediate light, but proportional reductions at higher grazer densities were approximately the same between the light treatments (Fig. 4).

Light and grazer effects on algal species composition

At the beginning of the experiment, algal assemblages on tiles were dominated by *Hydrurus foetidus* (Chrysophyta) and *Chamaesiphon incrustans* (Cyanophyta; see Initial conditions, Table 3). After 22–23 d, diatoms were the most commonly encountered taxa, but chlorophytes were abundant in low light and chrysophytes maintained dominance at high light (Table 3).

Grazer-free tiles in the low light were dominated by *Diatoma mesodon* and *Gomphonema angustatum* (Bacillariophyta), and *Chlorella* and *Muriellopis* spp. (Chlorophyta). Diatom biomass in this light treatment decreased progressively as mayfly densities increased, declining from 73% of all algae on non-grazed tiles to 39% and 28% for 1x and 3x *R. robusta* densities, respectively. At the highest (3x) grazer density, *D. mesodon* was not encountered and *G. angustatum* was rare. Relative abundance of chlorophytes increased on grazed substrata (Table 3).

Under intermediate light, *F. arcus* and *H. foetidus* were the most abundant taxa on non-grazed substrata, but both became less common in the presence of grazers (Table 3 and Fig. 3). *Gomphonema* spp., conversely, were not diminished by grazing (ANOVA, $F_{2,9} = 0.57$, $p = 0.58$; Fig. 3), and became relatively more abundant at higher grazer densities (Table 3). *Gomphonema* spp. made up 17% of the algal biovolume on non-grazed tiles, 44% at low mayfly densities and 78% at high mayfly densities.

At high light, the diatoms *G. affine*, *G. angustatum*, and *F. arcus*, and the chrysophyte *H. foetidus* were the most commonly encountered taxa on non-grazed tiles. With grazing, these diatoms were less prevalent, whereas *H. foetidus* became very abundant (Table 3 and Fig. 3).

It is important to note the different response shown by *Gomphonema* spp. and *H. foetidus* to mayfly grazing at intermediate and high light levels (Fig. 3). *Gomphonema* spp. abundance remained stable relative to grazer controls when grazed under intermediate light (least squares means test, $p > 0.05$), but declined dramatically

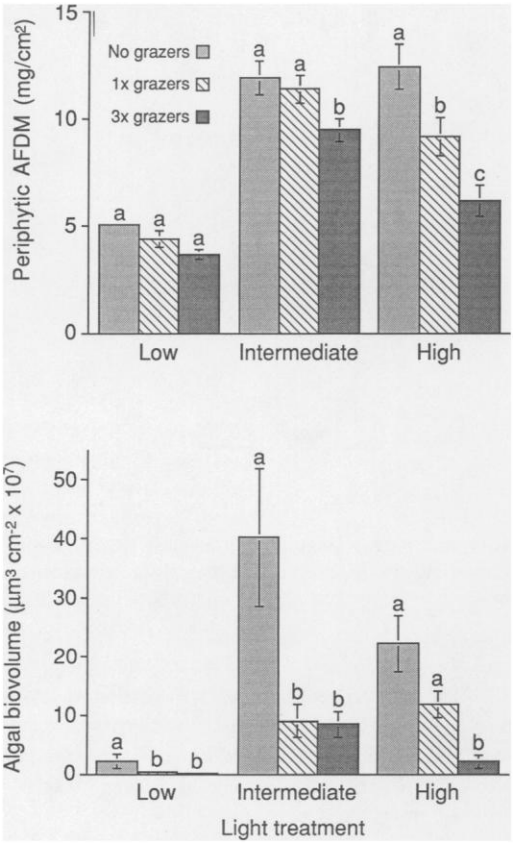

FIG. 4. Periphytic (AFDM; mg/cm²) and algal biomass (biovolume; $\mu m^3/cm^2 \times 10^7$) responses to *Rhithrogena robusta* grazing under the 3 light treatments. Bars = ±1 SE. Grazer densities are listed as no grazers, 1x and 3x, where x = the average density of *Rhithrogena robusta* on the St. Louis Creek streambed at the start of the study. Within light treatments, means of bars having the same letter are not significantly different (least squares means test, $p < 0.05$).

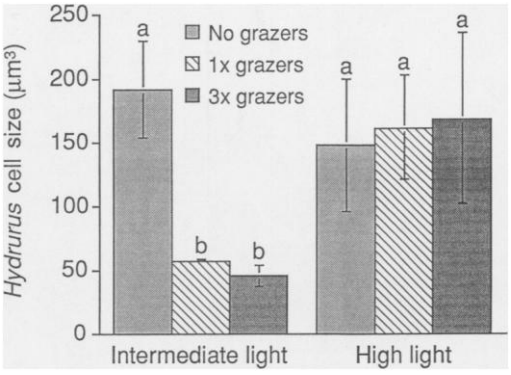

FIG. 5. Mean cell size (μm^3) of *Hydrurus foetidus* in response to *Rhithrogena robusta* grazing under intermediate and high light treatments. Grazer densities are listed as 0x, 1x and 3x, where x = the average density of *R. robusta* on the St. Louis Creek streambed at the start of the study. Bars = ±1 SE. Means of bars having the same letter are not significantly different (least squares means test, $p < 0.05$). Note the decrease in *H. foetidus* cell size on grazed substrata under the intermediate light treatment.

with increased grazer densities under the high light treatment (ANOVA, $F_{2,9} = 9.95$, $p \leq 0.005$). *Hydrurus foetidus*, in contrast, was less abundant on grazed tiles at intermediate light (ANOVA, $F_{2,9} = 4.52$, $p = 0.04$), but became more abundant at ambient grazer density under high light (ANOVA, $F_{2,9} = 5.65$, $p < 0.05$: 1x grazers > no grazers = 3x grazers; Table 3). Though *H. foetidus* was lower in absolute abundance at 3x mayfly densities, it was still the most common species in this treatment, composing 70% of the algal biovolume. In addition to this response, *H. foetidus* cell size was smaller on grazed than on non-grazed substrata at intermediate light, (ANOVA, $F_{2,15} = 4.63$, $p \leq 0.03$; Fig. 5), a change not seen at high light.

Discussion

Our prediction that increased light would invariably produce more periphytic biomass, primarily from enhanced algal growth, was not supported. Algal biovolume did not differ significantly between intermediate- and high-light treatments, and periphytic AFDM was actually greater under intermediate light than high light. Algal biovolume showed a non-significant trend of higher values at intermediate light, however, and we suspect it was this and the greater impact that grazers had on periphytic biomass under high light that caused AFDM values to be greater at intermediate light.

Several possible explanations exist for the failure of our highest light treatment to produce more algal biomass. Increased algal productivity at high light might have been sloughed off and lost, and therefore not recorded. We consider this unlikely. Periphyton in St. Louis Creek is a tightly adherent slime and lacks the loose overstory layer common in some lowland streams (e.g., Hill and Knight 1988). Removal of periphyton from experimental substrata at the end of the experiment involved repeated scrub-

bings and rinsings, and losses of periphyton during handling and transfer during sampling were not noticeable.

Failure to observe increases in algal biomass under more intense light might also indicate light saturation. Light in St. Louis Creek and in other streams at Fraser Experimental Forest can be intense, often exceeding 3000 μmol m^{-2} s^{-1} at the stream surface in open sections. These light levels were much higher than those found by Jasper and Bothwell (1986) to be optimal for summer periphytic populations in a British Columbia stream. Furthermore, although our intermediate light treatment reduced ambient PAR (photosynthetically active radiation) by approximately 62%, average daily light intensity at this level of shading still exceeded 500 μmol m^{-2} s^{-1}, an intensity bright enough to be used as "high" light treatments in similar studies (e.g., Lamberti et al. 1989, Steinman 1992, Hill et al. 1995).

A 3rd hypothesis to explain the similar amounts of algae found under intermediate and high light relates to the productivity of the algal assemblages. The abundance of *Gomphonema* spp. at intermediate light levels was more than double that in high light. Moreover, these taxa were unaffected by mayfly grazing in intermediate light, but declined sharply with increased grazer densities in high light. This result is surprising because these diatoms have a stalked, erect growth form that should make them vulnerable to grazing. Indeed, examination of *R. robusta* gut contents showed that *Gomphonema* spp. were very common amongst ingested algae (T. Wellnitz, personal observation). The fact that *Gomphonema* could persist under grazing at intermediate but not high light suggests that this alga was able to reproduce and colonize rapidly enough at intermediate light to compensate for grazing losses. This rapid turnover of *Gomphonema* may have yielded a more productive assemblage despite lower light levels. Perhaps *Gomphonema* thrived at intermediate light despite grazing because its high profile allowed these diatoms better access to light than low-lying algal species (Hudon and Bourget 1983), giving this alga a competitive advantage. Under high light levels, where such an advantage would be lost, *H. foetidus* became the most abundant alga on grazed substrata while *Gomphonema* declined. *H. foetidus* probably predominated under high light because it was more resistant to grazing. Consequently, high turnover rates would not be required for this species to persist on grazed substrata and productivity here may have been lower.

What is particularly intriguing about the response of *H. foetidus* was that it resisted grazing exceedingly well at high light but failed to do so at intermediate light. *Hydrurus* is commonly considered to be resistant to grazers by virtue of its tough mucilaginous sheaths, a characteristic thought to confer resistance to grazing (e.g., Steinman et al. 1992, Malej and Harris 1993). It is clear from our data, however, that, under intermediate light, grazing caused *H. foetidus* to become less abundant. Under intermediate light, *H. foetidus* cells on grazed substrata were smaller and more tightly packed within their thalli than those on ungrazed tiles, a change that did not occur at high light. Smaller mean cell size could have resulted directly from grazing; as mayflies removed older and larger cells, smaller new cells became proportionately more common. At high light levels, conversely, *H. foetidus* flourished and resisted grazing better than any other algal species, and average cell size remained large. Thus, grazing had less of an impact on *H. foetidus* at high light; where losses did occur from grazing, healthy compensatory growth may have kept average cell size from "shrinking".

We speculate that *H. foetidus* became susceptible to grazing at intermediate light because of structural changes that occur in this alga at low light intensities. *Hydrurus foetidus* is a common alga in cold, well-lit alpine and subalpine streams (Bursa 1934, Ward 1994), but does not tolerate shaded conditions well (Kawecka 1986). Parker et al. (1973) noted that *H. foetidus* exhibited cytological deterioration, decreases in chlorophyll, and lower rates of photosynthesis after 6 d of exposure to light levels that were below those with which *H. foetidus* was commonly associated. If *H. foetidus* was structurally weaker, it may have been easier to consume. Further, because *H. foetidus* does not grow well at lower light intensities, growth under our intermediate light treatment may have been insufficient to compensate for losses incurred by herbivory.

In a recent review of grazer–algal interactions, Feminella and Hawkins (1995) observed that mayflies were the only taxonomic group to have consistently low effects on periphyton relative to other grazers. In many alpine and sub-

alpine streams, however, mayflies dominate the grazer assemblage throughout the year and are the most important group of grazing organisms in terms of biomass. In our study, we used realistic densities of *Rhithrogena robusta*, a common mayfly grazer, and naturally occurring light levels. We have shown that this heptageniid grazer can have significant effects on algal and periphytic biomass and taxonomic structure across a broad range of light regimes. *Rhithrogena robusta* provides an exception to the general conclusion by Allan (1995) that "effective grazers tend to be individually large, relatively slow-moving, and well equipped with scraping mandibles or a radula." Clearly *R. robusta*, a moderately sized fast-moving mayfly that uses labial brushes to feed, has the potential for exerting "top-down" control on subalpine stream periphyton.

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