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Herbivory and irradiance shape periphytic architecture in a Swiss alpine stream

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Abstract

The effects of herbivory and light on epilithic periphyton from Minor Creek (2,200 m above sea level), a Swiss alpine stream, were examined by manipulating light intensity and the densities of two abundant grazers in streamside channels. We hypothesized that the high light intensities in Minor Creek (exceeding 2,000 μmol m^{-2} s^{-1} on the stream bed) would cause photoinhibiton and thus regulate algal composition and biomass accrual. After 18 d, full sunlight had negative effects on all measures of periphytic abundance in streamside channels. A five-level light gradient experiment in Minor Creek corroborated these findings: full sunlight suppressed periphytic accumulation.

To test the interactive effects of grazing and light, we used two herbivorous insects with distinctly different feeding structures. *Ecdyonurus* sp. (Heptageniidae) possesses brushing mouthparts; *Drusus lateralis* (Limnephilidae) has scraping mandibles. In accordance with a conceptual model that predicts algal physiognomy and herbivore feeding mode regulate algal susceptibility to grazing, we hypothesized that *Ecdyonurus* would primarily reduce physiognomies composing the periphytic overstory (e.g., stalked and filamentous algae), whereas *Drusus* would have greater access to understory physiognomies (e.g., prostrate forms). In addition, we hypothesized that tall physiognomies would be less abundant under full sunlight due to the exposure of the periphytic mat to photoinhibiting irradiance. Thus, we expected *Ecdyonurus* to have a smaller effect on periphyton at high light intensities.

Light in channels did not directly modify grazing effects; however, the data suggest light intensity altered periphytic susceptibility to grazing. Channels receiving full sunlight had less periphyton, yet grazer weights did not differ between light treatments despite the fact that weight gain for each grazer was negatively correlated with conspecific biomass, implicating competition for limited periphytic food. Algal responses were most pronounced under grazing by *Ecdyonurus,* which was associated with decreases in the abundance of six of the seven algal physiognomies. Contrary to model predictions, *Ecdyonurus* reduced low-lying as well as overstory physiognomies. *Drusus,* by contrast, was associated with reductions in only four physiognomies. Results from this study suggest that understanding periphytic community responses to grazing will require more sophisticated models of periphytic structure.

Herbivory and light limitation present an adaptive dilemma for periphytic algae in streams. Both light and herbivores penetrate periphytic mats from above. One has a positive influence, the other negative, and together they exert antagonistic selective pressures on algal evolution. This results from an alga's need for adequate light, often satisfied by high placement in the periphytic mat, and its need to survive herbivory, often satisfied by low placement in the mat (Gregory 1983, Lamberti et al. 1987*a*, Steinman and McIntire 1987, Steinman et al. 1987).

Like terrestrial plant communities, periphytic assemblages are three-dimensional structures that may exhibit a proportionately large vertical component (Hoagland et al. 1982). Consequently, light attenuation within the algal mat increases with mat thickness, and in complex assemblages only a few weeks old, photon flux may be decreased by 65–95% at the substratum-mat interface (van Dijk 1993). Thus, euphotic zones are typically restricted to the upper few millimeters of the mat (Meulemans 1987, Dodds 1992). To position themselves within this photic zone, algae have evolved strategies such as forming mucilaginous stalks, possessing a filamentous structure, or growing perpendicular to the substratum. These traits confer a competitive advantage where low light limits growth and reproduction, but they could be detrimental in an ecological setting where grazing is important (Gregory 1980; Hudon and Bourget 1983; Steinman and McIntire 1987; Steinman et al. 1989; Stevenson et al. 1991; Steinman 1992; Wellnitz and Ward 1998).

A model of periphytic structure proposed by Gregory (1980) and detailed by Steinman (1996) makes predictions about algal susceptibility to grazing based on two factors, algal physiognomy and herbivore feeding mode (Fig. 1). According to this model, the interaction between algal growth form and grazer mouthpart structure determines to what degree algal biomass will be removed and which physiognomies will be susceptible to grazing. Periphytic architecture is analogized to canopy layers in a terrestrial plant community (Hoagland et al. 1982), with physiognomy determin-

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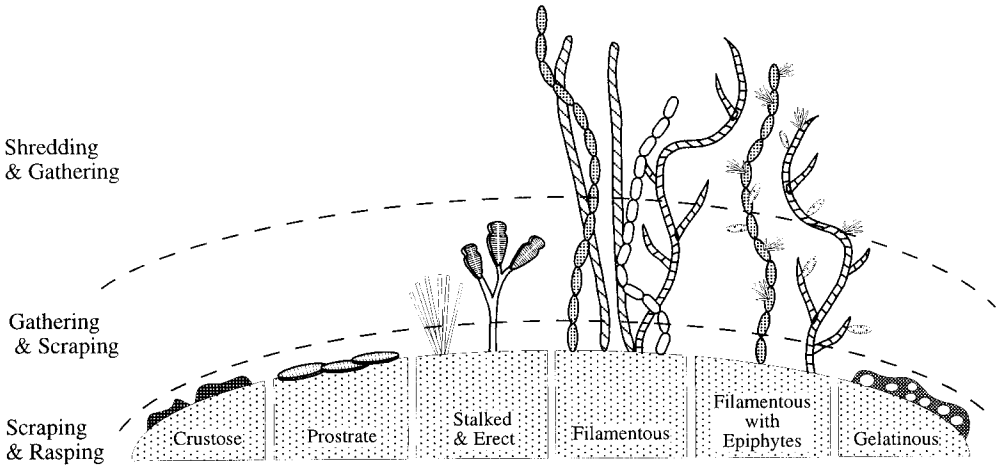

Fig. 1. The major physiognomies of periphytic algae, illustrating the variation in shape and vertical layering. Algal vulnerability to consumers is hypothesized to be influenced by these structural attributes (from Steinman 1996, after Gregory 1980). Physiognomies extending into the shredding and gathering zone will be vulnerable to grazers possessing brushing or gathering mouthparts, such as heptageniid and baetid mayflies, respectively. Algal physiognomies within the gathering and scraping layer will be exposed to grazers with gathering mouthparts or to grazers that use mandibles to scrape the substratum (e.g., glossosomatid caddisfly larvae). Physiognomies in the lowest layer, the scraping and rasping zone, will be vulnerable only to grazers possessing scraping mandibles or a molluscan radula.

ing the layers an alga will occupy. Filamentous forms reach into the upper-most layers of the assemblage and sometimes support epiphytic species. Stalked and erect forms (e.g., the diatoms *Gomphonema* and *Synedra*) extend into the intermediate layers of the matrix and comprise the understory canopy. Prostrate or adnate, low-lying physiognomies (e.g., the cyanophyte *Chamaesiphon* and diatoms *Achnanthes* and *Navicula*) are the undergrowth of the periphytic community, maintaining close proximity to the substratum and occupying the lowest layers of the mat.

Herbivore feeding characteristics are the second aspect of the Gregory–Steinman model (Fig. 1). Stream grazers exhibit diverse modes of feeding that include rasping (e.g., snails), gathering or brushing (e.g., heptageniid mayflies) and scraping (e.g., glossosomatid caddisflies; Arens 1989; Merritt and Cummins 1996). Head orientation, mouthpart morphology, motility, and foraging behavior can influence how a grazer feeds and to what level of periphyton it will have access (Lamberti et al. 1987*a*; Hill and Knight 1988*a*; Karouna and Fuller 1992; Lamberti et al. 1995; Wellnitz and Ward 1998). Gregory (1980) and Steinman (1996) predict that upper layers of the mat will be vulnerable to gathering and shredding herbivores; intermediate layers will be susceptible to gathering and scraping; and the lower-most layers will be vulnerable to scraping and rasping grazers. There is overlap between these feeding zones and, in general, taller growth forms will be more vulnerable to more herbivores. Snails with rasping mouthparts, for example, are capable of feeding on prostrate algae, but also can remove large quantities of periphytic overstory (Sumner and McIntire 1982). Of course, the influence a particular herbivore will have on periphytic community structure depends not just its mode of feeding, but also on total herbivore biomass and density (Hill and Knight 1987; Steinman et al. 1987) and productive capacity of the system to accrue biomass (Lamberti et al. 1989).

In the present study we examine how light intensity and two grazers with different feeding modes influence periphyton growing in an alpine stream. Light intensity is typically associated with greater algal biomass, but light can be excessive as well as limiting (Guasch and Sabater 1995; Hill 1996). Previous work has indicated higher irradiance in mountain streams may have a null or inhibitory effect on algal growth (Wellnitz et al. 1996*a*; Wellnitz et al. 1996*b*). Photoinhibition within an algal assemblage may be due to damage by ultraviolet radiation, photorespiration, photosystem saturation by excessive electron flux or a combination of these processes (Smith et al. 1980; Pahl-Wostl and Imboden 1990; Boston and Hill 1991; Bothwell et al. 1994; Hill et al. 1995; Hill 1996; Beardall et al. 1997). In the high light environment found in mountain streams, photoinhibition may be a factor approaching light limitation in its importance for constraining algal growth. Within the context of light acquisition and herbivory, strong photoinhibition could shift the balance of ecological and selective forces acting on algal growth form towards low-lying physiognomies. Moreover, because light can influence the taxonomic and physiognomic make-up of periphytic assemblages, and thus, shape periphytic architecture, it may modify the response that assemblages show to grazing (Hudon and Bourget 1983; Lowe et al. 1986; Stevenson et al. 1991; Wellnitz et al. 1996*b*; Wellnitz and Ward 1998).

The grazers used in this study were the mayfly *Ecdyonurus* spp. (Heptageniidae) and the caddisfly *Drusus lateralis* (Limnophilidae). These herbivores differed in three important respects: size, foraging behavior and mouthpart structure. *Ecdyonurus* is the larger of the two herbivores used in the experiment, measuring 8–10 mm in length and having

approximately 5 × the biomass of larval *Drusus* during September (when the study was conducted). *Ecdyonurus* is an errant mayfly that can move rapidly across substrate surfaces or enter the drift to make large scale movements. This genus exhibits a clinging mode of existence (Merritt and Cummins 1996) and possesses a dorsal-ventrally depressed head with prognathous mouthparts. Its brush-like labial palps are used in broad sweeping motions to harvest periphyton from substrata. By contrast, *Drusus* is a small caddisfly (3–5 mm in length) that inhabits a mineral case and is relatively sedentary. *Drusus* possesses an orthognathous head posture and uses mandibles to scrape periphyton from substrata. This head posture dictates that only the tips of mandibles are brought in contact with the substratum, suggesting this species may apply more concentrated force in removing periphyton as compared to *Ecdyonurus*, and also may exert greater selectivity on algae because of the smaller feeding area (Arens 1989).

We hypothesize that *Ecdyonurus* and *Drusus* utilize two distinct grazing strategies that we refer to as ''extensive'' and ''intensive'' feeding. Because mayflies are highly motile and may respond rapidly to resource patches (Richards and Minshall 1988), we hypothesize that *Ecdyonurus* graze periphyton *extensively*, removing overstory physiognomies and then moving on, leaving behind algae that is less accessible. *Drusus*, alternatively, being slower and less agile, but also capable of taking deep bites of periphyton, may find it energetically more efficient to graze *intensively*, taking what food is at hand, and cleaning periphyton from patches thoroughly before moving to the next patch. We predict that (1) because *Ecdyonurus* is larger and mobile than *Drusus*, it will have a greater effect on total periphytic biomass; (2) *Ecdyonurus* will reduce primarily stalked, erect and filamentous physiognomies and should have little effect on prostrate forms; (3) *Drusus*, by virtue of its feeding structures, will cause greater reductions in prostrate and low-lying physiognomies.

We also hypothesize that the high light intensities common in our study stream (sometimes exceeding 2,000 μmol m^{-2} s^{-1} on the stream bed at midday) are great enough such that photoinhibiton is an important process for structuring the algal community and controlling biomass accrual. If photoinhibition is important in Minor Creek then (1) algal biomass accumulation in the stream should be greatest at some intermediate irradiance between full sunlight and growth-limiting shade; (2) tall physiognomies will be less abundant under full sunlight because upper layers of the periphytic mat will be exposed to photoinhibiting irradiance; (3) grazer growth rates will be reduced under full sunlight because food will be more limiting (less algae) and less accessible (lower growth forms).

Methods

Study site—Minor Creek is a second-order alpine stream in the Bernina Massif, Engadine region of the Swiss Alps (10° 00′E, 46° 25′N). The stream drains a narrow, 8.5 km^2 valley of alpine meadow and is fed by two small lakes at the upper end of the catchment and by intermittent tributaries along its length. The stream is 3,050 m above sea level at its source and flows approximately 3 km before joining the Bernina River at 2,100 m. Vegetation in the valley is predominantly grasses, and in summer the catchment is grazed by free-ranging cattle. Stream substrata are comprised of rubble, cobble, and gravel with small amounts of sand. Water in Minor Creek is clear and cold (2–9°C during the study) and nitrate values were high, probably due to the influence of cattle. Total dissolved nitrogen during the study period ranged from 239 to 314 $\mu g^{-1}L$; total phosphorous ranged from 2 to 5 $\mu g^{-1}L$; and dissolved organic carbon ranged from 0.23 to 1.28 $\mu g^{-1}L$.

Epilithic algal assemblages in the creek were predominantly diatoms, which composed approximately 60% of the biomass, followed by cyanophytes (~30%) and the chrysophyte, *Hydrurus foetidus* (~10%). Minor Creek supported a macroinvertebrate herbivore fauna that included heptageniid (e.g., *Ecdyonurus* and *Rhithrogena* spp.) and baetid mayflies, limnephilid caddisflies (e.g., *Drusus* sp.) and chironomid midges. The grazer guild was dominated in terms of biomass and numbers by heptageniids and *Drusus* in September.

Stream-side channel design and operation—Thirty-two artificial stream channels were constructed of Plexiglas. Each circular channel was 17 cm in diameter, 8 cm deep, and had a 4 × 9 cm (diameter × height) standpipe mounted at the center (see Wellnitz and Ward 1998 for additional details). Water entered each stream through a submerged nozzle positioned to provide current, and exited through drainage holes cut into standpipes. The drainage holes maintained a water depth of 5.5 cm and were covered by screen collars (1-mm mesh) to prevent herbivores from being washed out of channels.

Water for the artificial streams was taken from Minor Creek and gravity-fed into a 800 l reservoir mounted 10 m uphill from and 1.5 m above the channels. Before entering the reservoir, water passed through a net (250-μm mesh) to remove macroinvertebrates, detritus, and other large suspended particles. The reservoir filter was cleaned of accumulated particulates every 2–3 d. Water flowed downhill from the reservoir through flexible plastic pipe into two 6-cm (inner diameter) PVC tubes fitted with spigots. These were mounted to the rear of two tables set next to the bank of Minor Creek, with each table supporting 16 channels. Tygon tubing (1 cm inner diameter) connected individual spigots to the 32 channels; current velocity within each stream channel was controlled by adjusting the spigots. Water exchange rates in channels were 2.16 ± 0.12 l min^{-1} (n = 32; mean ± SD) and current velocity was maintained between 10 and 12 cm s^{-1} and was within the velocity range experienced by the grazers in the stream (see below). Water temperatures in the channels were within ±0.5°C of Minor Creek during the study.

Stream-side channel experiment—Two light treatments (open and shaded) and four densities each of *Ecdyonurus* and *Drusus* were applied to the 32 channels in a 2 × 4 × 4 factorial design. Light treatments were replicated; grazer treatments were not. Instead, grazer densities were applied to channels in nested gradients following the design of Hill and Knight (1988*a*). We designed our experiment so that the

data could analyzed using multiple regression. Regression analysis permits a statistical evaluation of relationships (as opposed to differences) between dependent and independent variables (e.g., algal biomass and *Ecdyonurus* density), and can be appropriately used if the data are independent and linearly distributed (Sokal and Rohlf 1995).

Light intensity was manipulated by using shading screens that reduced irradiance to approximately 20% of ambient. Shaded channels ($n = 16$) were covered with two layers of nylon screening (1-mm mesh) supported on a wire frame. Channels were grouped in pairs with shaded and open treatments alternating across the channel array (and thus $n = 8$ for light treatments instead of 16). Light intensity was measured on 17 and 18 September 1996. Two LiCor spherical quantum sensors mounted level with channels, one placed adjacent to the shaded and the other adjacent to the open channels, measured photosynthetically active radiation (PAR) every 15 min. Mean PAR during the day were 814 μmol m^{-2} s^{-1} for open channels and 168 μmol m^{-2} s^{-1} for shaded channels.

Grazer densities were established at 0, 2, 4, or 10 nymphs per channel for *Ecdyonurus* and 0, 4, 7, or 20 larvae per channel for *Drusus.* These densities corresponded to 0, 0.6, 1.2, and 3.0 times the ambient density of *Ecdyonurus,* and 0, 0.5, 1.0, and 2.7 times the ambient density of *Drusus* in Minor Creek during September 1996. Grazer densities in the stream were determined from 12 Suber samples (Merritt and Cummins 1996) collected from a 15-m stream section containing riffles and runs. Current velocity 5 cm above the stream bed was 15.8 $\pm$ 9.8 cm s^{-1} ($n = 12$; mean $\pm$ SD) as determined with a Marsh-McBirney current meter. Mean *Drusus* densities were 345 $\pm$ 41 individuals m^{-2}; *Ecdyonurus* densities were 157 $\pm$ 23 individuals m^{-2}. Grazer densities within the experimental streams were calculated using the channel's bottom surface area (214 cm^2).

Substrata for channels were taken directly from Minor Creek. Channel bottoms were lined with 1 cm of gravel sieved so that particle size ranged from 8 to 16 mm. Small, flat cobbles (each approximately 8 $\times$ 8 $\times$ 2 cm) were then collected from the stream bed and, after removal of all macroinvertebrates, were placed four to a channel. Exposure of both gravel and cobbles to air was minimized to preserve periphyton assemblages.

Stream light gradient experiment—To assess the influence of light intensity on periphytic development in Minor Creek, 45 ceramic tiles (surface area = 225 cm^2) were placed in the stream on 29 August 1996 to initiate colonization. Tiles were assembled into five groups of nine tiles each and randomly assigned to one of five light treatments, either unshaded or shaded with one, two, three, or four layers of shading screens. Screens were attached to 1 m^2 metal frames and suspended ca. 20 cm over the stream surface. Shading screens were added on 10 September. PAR irradiance was measured twice hourly from 24 to 27 September at the stream surface above unshaded tiles and above tiles shaded with one screen. PAR was measured under the remaining three light treatments (i.e., those with 2, 3, and 4 shades) at 1000, 1200, 1400, and 1600 h on 24 September. Values collected during these times were used to calculate percent reduction in ambient PAR and used to extrapolate intensities for the entire day. The resulting light gradient reduced ambient PAR irradiance by 0, 41, 69, 78, and 86% for zero, one, two, three, and four screens, respectively. After 35 d in the stream, four tiles were selected randomly from each light treatment and sampled for periphyton.

Periphyton sampling and analysis—Periphyton was sampled from the channels 18 d after grazer introduction. Periphyton in experimental channels was removed from the upper surface of three cobbles (chosen at random from four) with a razor blade, toothbrush, and wash bottle. Sample area was determined by outlining the cobble surface on drawing paper, cutting out the paper template, and then weighing the template. A weight-area regression based on weighed paper of known area was used to determine the surface area for each template.

Periphyton from the three cobbles was combined in a beaker and the resulting suspension brought up to 150 ml with filtered water. This suspension was mixed and divided into three 50-ml subsamples to determine Chl *a*, ash-free dry mass (AFDM), and algal species biovolume. Samples for chlorophyll were filtered onto glass fiber filters (pore size 45 μm; Schleicher and Schuell No. 6). Chlorophyll (Chl) *a* was extracted in 90% ethanol and then quantified using high-performance liquid chromatography (Meyns et al. 1994). AFDM samples were filtered onto glass fiber filters, and AFDM was determined as the difference between dried (at 60°C for 24 h) and ashed (480°C for 2 h) sample weights. Periphyton collected for species composition was preserved in 2% formalin and used to determine the 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 $\times$125 magnification; Cyanophyta and small diatoms were counted at $\times$1,250. Diatom species identifications were made at $\times$1,250 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 1991).

To assess the impact of grazers and light on periphytic architecture, algae species were categorized as belonging to one of six physiognomic groups (Table 1). Physiognomy refers to the structure and form of algal cells as they occur in nature and includes orientation to the substrate (e.g., prostrate vs. erect), special structures (e.g., stalks) and cell size (Whittaker 1975; Steinman 1996). To this definition is sometimes added cell motility (Molloy 1992; Wellnitz and Ward 1998). Although algal motility is a functional rather than a morphological attribute, it is nevertheless a trait that can influence an algal cell's position within periphytic mats. Our intent was to identify algal characteristics that could influence vertical placement within the periphyton, access to light and vulnerability to herbivory. Algal motility is capable of

Table 1. Seven categories of algae distinguished on the basis of motility and morphological characteristics.

Physiognomic category	Distinguishing features and typical genera and species
Prostrate/nonmotile	Small size, monoraphid, generally prostrate orientation to substrate: *Achnanthes* spp.
Prostrate/motile	Generally prostrate and frequently motile: *Cymbella cistula, Navicula minuscula.*
Stalked	Arborescent or stalk-forming genera: *Gomphonema, Cymbella* spp.
Erect	Perpendicular to substrata without stalks; forming rosettes, ribbonlike colonies or short chains: *Diatoma, Fragilaria, Hannea, Meridion, Synedra, Nitzschia* spp.
Gelatinous	Colonies of cells imbedded in mucilaginous pads or thalli, can assume either a prostrate, adherent, or extended morphology: *Hydrurus foetidus.*
Rod clusters	Small, erect, cylindrical cyanobacteria, found in clusters on substratum or growing epiphytically: *Chamaesiphon* sp., *Clastidium* sp.
Filamentous cyanophytes	Small filaments of blue-green algae, often motile: *Leptolyngbya, Phormidium* spp.

satisfying these criteria (Round and Palmer 1966; Hudon and Bourget 1983; Pringle 1990; Hill 1996).

For the light gradient experiment periphyton from stream tiles was removed in the same manner as from cobbles, but suspensions were divided in half and assayed only for Chl *a* and periphytic AFDM. Ash-free dry mass and chlorophyll samples were analyzed as described above for cobbles in the channel experiment.

Grazer analysis—At the end of the experiment all insects were collected from channels and preserved in 5% formalin. In the laboratory, *Drusus* and *Ecdyonurus* from were separated by species, placed on glass fiber filters, and dried. AFDM was determined as the difference between dried (at 60°C for 24 h) and ashed (480°C for 2 h) sample weights.

Statistical analysis—We analyzed the effects of light level and the two grazers on channel periphyton using the multiple regression module in Statistica (StatSoft, Tulsa, OK, USA). Periphyton parameters examined were AFDM, Chl *a*, algal biovolume and species richness. For each parameter we used the multiple regression equation

$$Y = B_0 + B_{\mathrm{Ecd}}X_1 + B_{\mathrm{Drus}}X_2 + B_{\mathrm{Light}}X_3,$$

where Y is the periphyton parameter from each channel, B_0 is the regression constant, and B_{Ecd}, B_{Drus}, and B_{Light} were the regression coefficients for *Ecdyonurus, Drusus,* and light, respectively. Values for X_1 and X_2 were the AFDM (measured in milligrams) of *Ecdyonurus* and *Drusus* from each channel, and X_3 represented light level. We used 0 and 1 as dummy variables to represent shaded and open light levels, respectively. Interactions among factors were examined by adding the appropriate interaction terms to the regression equation (e.g., X_1X_2, X_2X_3), but because these were never significant, only main-factor effects were used in the final regression model. The effect of grazer biomass and light on individual grazer weight was analyzed using the same regression equation, except that Y was used to represent the average AFDM per individual of either *Ecdyonurus* or *Drusus.* As with periphyton parameters, interactions were not significant so only main factors were included.

The unique contribution of each factor (e.g., grazers, AFDM, light level, etc.) for predicting measures of periphytic abundance was examined using partial regression coefficients. Partial regression coefficients quantify the relationship between the respective factor and the parameter of interest adjusted by all the other variables (Sokal and Rohlf 1995). Data were log-transformed or, for percentage of abundance, arcsine-transformed prior to analysis to ensure that the assumption of linearity was met.

For the light gradient experiment we analyzed the effects of light level on stream using simple regression. Parameters examined were periphytic AFDM and Chl *a*. These data were log-transformed prior to analysis to insure linearity for the regression analysis.

Results

Light effects on channel periphyton—Greater light intensity produced significant reductions in all measures of periphytic abundance; periphytic AFDM, algal biovolume and chlorophyll were all lower in open than in shaded treatments (Table 2). In addition, fewer diatom species were found in the open than in the shade (18 versus 26 species, respectively), but algal species richness did not differ significantly between light treatments (Table 2). There was a trend toward greater abundance of some algal species in the shade. The cyanophyte *Clastidium* sp., for example, was approximately four times more common in the shade than the open, and all

Table 2. Regression coefficients for effects of *Ecdyonurus* and *Drusus* and light on periphytic abundance and species richness. Data were log-transformed prior to performing the regression.

Parameter	F	B_0	*Drusus*	*Ecdyonurus*	Light
AFDM	6.34**	0.06	NS	−0.623***	−0.337*
Biovolume	26.78****	6.27	−0.650***	−0.850****	−0.649***
Chl *a*	34.22****	1.34	−0.717****	−0.850****	−0.790****
Species richness	11.68****	1.31	−0.556**	−0.708****	NS

**** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, not significant.

Table 3. Regression statistics for grazer and light effects on algal biovolume as grouped by physiognomic form. Partial correlation coefficients are shown for *Drusus*, *Ecdyonurus*, and light. Data were log transformed prior to performing the regression. The percentage abundance for each physiognomic type is given in the last column.

Algal physiognomy	F	B_0	*Drusus*	*Ecdyonurus*	Light	% total biovolume
Rod clusters	5.90**	5.34	NS	NS	−0.598***	23.6
Erect	8.10***	5.62	NS	−0.683****	NS	20.7
Stalked	13.65****	5.59	−0.544**	−0.752****	NS	20.3
Prostrate/nonmotile	27.83****	5.54	−0.591***	−0.849****	−0.578***	12.1
Prostrate/motile	9.61***	5.83	−0.486**	−0.670****	−0.374*	8.7
Gelatinous	4.38**	4.64	NS	−0.567**	NS	8.4
Filamentous cyanophytes	11.48****	4.91	−0.400*	−0.728****	NS	6.2

**** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, not significant.

but one of the six *Achnanthes* species were more than three times more abundant in the shade than in the open.

Of the seven algal physiognomies, light influenced the abundance of three: rod clusters, prostrate/nonmotile, and prostrate/motile diatoms (Table 3). In each case, abundance was negatively correlated with the higher light intensity. Collectively, these three physiognomies composed 44% of the algal biovolume across treatments.

Light significantly influenced the percent representation of two physiognomies on cobbles, prostrate/nonmotile and the gelatinous type (Table 4). Light intensity was positively correlated with a decreased percent of prostrate/nonmotile physiognomy but was positively correlated with an increased percent in the gelatinous form (i.e., *Hydrurus foetidus*).

Grazer effects on channel periphyton—The mayfly *Ecdyonurus* had a greater impact on periphyton than did the caddisfly *Drusus* in terms of the number of parameters affected and the extent of those effects (Fig. 2). *Ecdyonurus* biomass was correlated with reductions in all measures of periphytic abundance and lower species richness, whereas the caddisfly reduced algal biovolume, chlorophyll, and species richness, but not periphytic AFDM (Table 2). For those parameters affected by both grazers, the magnitude of the partial regression coefficients suggested *Ecdyonurus* effects were greater.

Grazers influenced six of the seven algal physiognomic categories; the exception was the rod cluster type, which neither grazer affected (Table 3). *Ecdyonurus* was associated with reductions in all six of the susceptible forms. *Drusus* was associated with reductions in four physiognomies: stalked, prostrate/nonmotile, prostrate/motile, and filamentous cyanophytes. *Ecdyonurus* effects appeared greater than *Drusus* on these four physiognomies. Partial regression coefficients for *Ecdyonurus* ranged between −0.670 and −0.849, whereas *Drusus* coefficients ranged between just −0.400 and −0.591 (Table 3).

Algal physiognomies varied in their susceptibility to grazing as indicated by changes in their percentage representation on cobbles (Table 4). Increases in the relative abundance of the rod cluster physiognomy, for example, was associated with increasing biomass of both grazers, and *Ecdyonurus* grazing was associated with a percent increase in the gelatinous form. Conversely, *Ecdyonurus* grazing produced relative decreases in the representation of erect, prostrate/nonmotile and prostrate/motile diatoms. As was true for other periphytic parameters, *Ecdyonurus* effects were greater where both grazers had influence (i.e., rod cluster and erect forms), and were more extensive, affecting five physiognomies whereas *Drusus* affected only two.

Grazer and light effects on grazers—Individual weights of *Ecdyonurus* and *Drusus* were negatively correlated with increasing conspecific biomass, but not with the biomass of the other grazer species (Fig. 3, Table 5). Therefore, intraspecific competition may have been more important than interspecific competition for determining final grazer weights.

Table 4. Regression statistics for grazer and light effects on the percent abundance of algal physiognomies. Partial correlation coefficients are shown for *Drusus*, *Ecdyonurus*, and light. The percentage abundance for each physiognomic type is given in the last column. Data were arcsine transformed prior to performing the regression. The regression constant (B_0) and partial correlation coefficients are not shown if the F value for the regression was not significant.

Algal physiognomy	F	B_0	*Drusus*	*Ecdyonurus*	Light	% of total biovolume
Rod cluster	16.61****	0.11	0.471*	0.799****	NS	23.6
Erect	10.61****	0.20	NS	−0.736****	NS	20.7
Stalked	1.09	—	—	—	—	20.3
Prostrate/nonmotile	6.16**	0.19	NS	−0.584***	−0.414*	12.1
Prostrate/motile	4.66**	1.11	−0.368*	−0.527**	NS	8.7
Gelatinous	10.37***	0.01	NS	0.530**	0.679***	8.4
Filamentous cyanophytes	0.99	—	—	—	—	6.2

**** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, not significant.

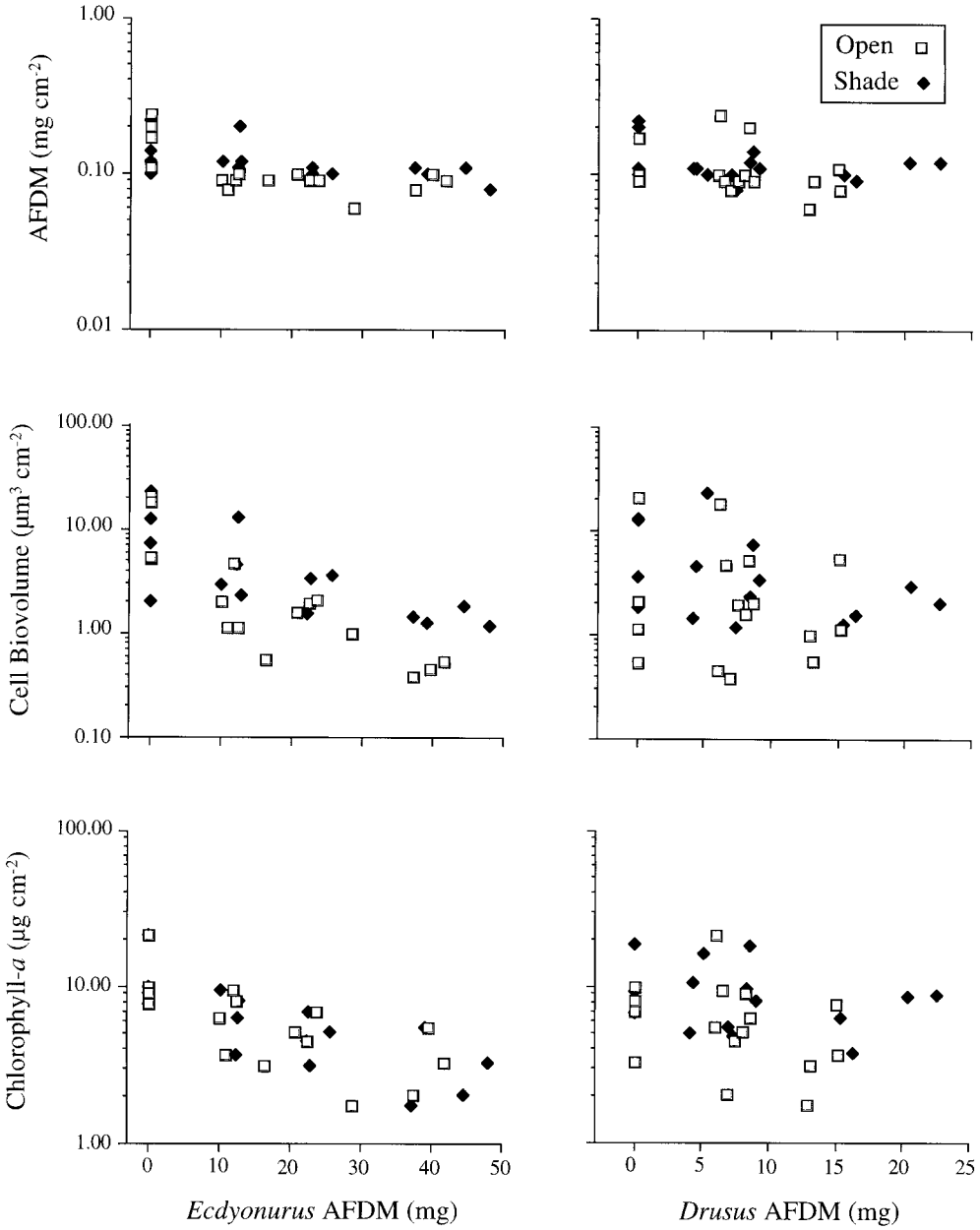

Fig. 2. Periphyton biomass parameters versus biomass of *Ecdyonurus* and *Drusus* in each channel at the end of the experiment.

Light treatment did not significantly effect the biomass of either grazer (Table 5), however, the short (3-week) duration of the channel experiment may not have allowed sufficient time for light effects to manifest themselves.

Light gradient experiment—Periphytic chlorophyll was inversely correlated with light level and this relationship was highly significant ($F = 72.31$, $p < 0.0001$; Fig. 4A). Periphytic AFDM responses to decreasing light were more complex. Although the linear regression performed on log-transformed AFDM data indicated a significant inverse relationship between light intensity and periphytic biomass ($F = 7.41$, $p = 0.01$), the regression line that best fit the nontransformed data was a hump-shaped curve (Fig. 4B). The r^2 value for a humped curve described by a second-order polynomial was 0.54, whereas a linear model had an r^2 value of only 0.029. These data suggest that the highest light level (unshaded tiles) produced the least periphyton, and there was a trend for decreasing periphyton at the lowest light level. Thus, intermediate irradiance appeared to produce the most periphyton.

Discussion

The two factors that had the largest influence on algal abundance in the experimental channels were light intensity and

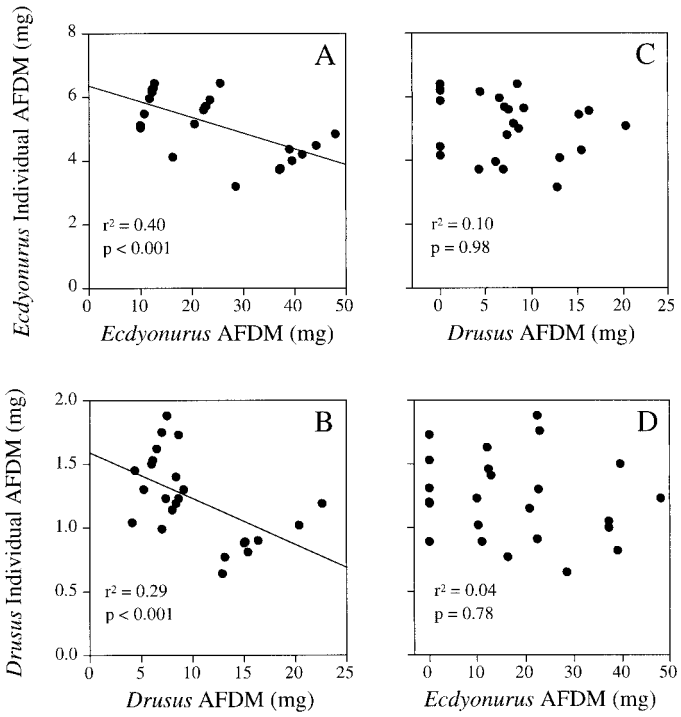

Fig. 3. Final weight of individual *Ecdyonurus* and *Drusus* larvae as a function of total biomass for *Ecdyonurus* (A and D) and *Drusus* (B and C). The regression lines and r^2 values are given for the untransformed data.

grazing by *Ecdyonurus.* In each case, the influence was negative. Both factors were associated with decreased periphytic AFDM, Chl *a*, algal biovolume, and, where effects were significant, the abundance of physiognomic types. We had predicted that *Ecdyonurus* would have a greater influence than *Drusus* on periphytic biomass by virtue of its size and mobility, and the data support this. We had also hypothesized that photoinhibition is an important process structuring the periphytic community in this alpine stream. Evidence from the channel experiment and the in situ study offer compelling evidence that it is. Other work in high mountain streams have shown that the high light intensities common to unshaded reaches do not necessarily produce more periphyton (Wellnitz et al. 1996*a*; Wellnitz et al. 1996*b*). What sets the present study apart is the consistently negative effects of greater irradiance on measures of periphytic and algal biomass.

In the light gradient experiment conducted in Minor Creek, it was not surprising that periphytic chlorophyll had an inverse relationship to light; cellular chlorophyll can increase to compensate for lower light intensities (Falkowski and LaRoche 1991). What is striking was that AFDM values were clearly lower under ambient light in Minor Creek than the diminished light beneath artificial shades. The greatest AFDM values produced in the stream were found at intermediate light intensities. Periphytic AFDM showed a hump-shaped response to irradiance that echoed the findings of a Rocky Mountain stream study (Wellnitz et al. 1996*a*) where intermediate light levels produced more periphyton than did natural light in open and closed canopy reaches. These data

Table 5. Regression statistics for grazer and light effects on the individual grazer AFDM. Partial correlation coefficients are shown for *Drusus*, *Ecdyonurus*, and light. Grazer factors refer to the total AFDM for each grazer species in each channel. Data were log transformed prior to performing the regression.

Individual grazer AFDM	F	B_0	*Drusus*	*Ecdyonurus*	Light
Ecdyonurus	9.89***	1.10	NS	−0.691***	NS
Drusus	7.52**	0.57	−0.626**	NS	NS

*** $P < 0.001$; ** $P < 0.01$; NS, not significant.

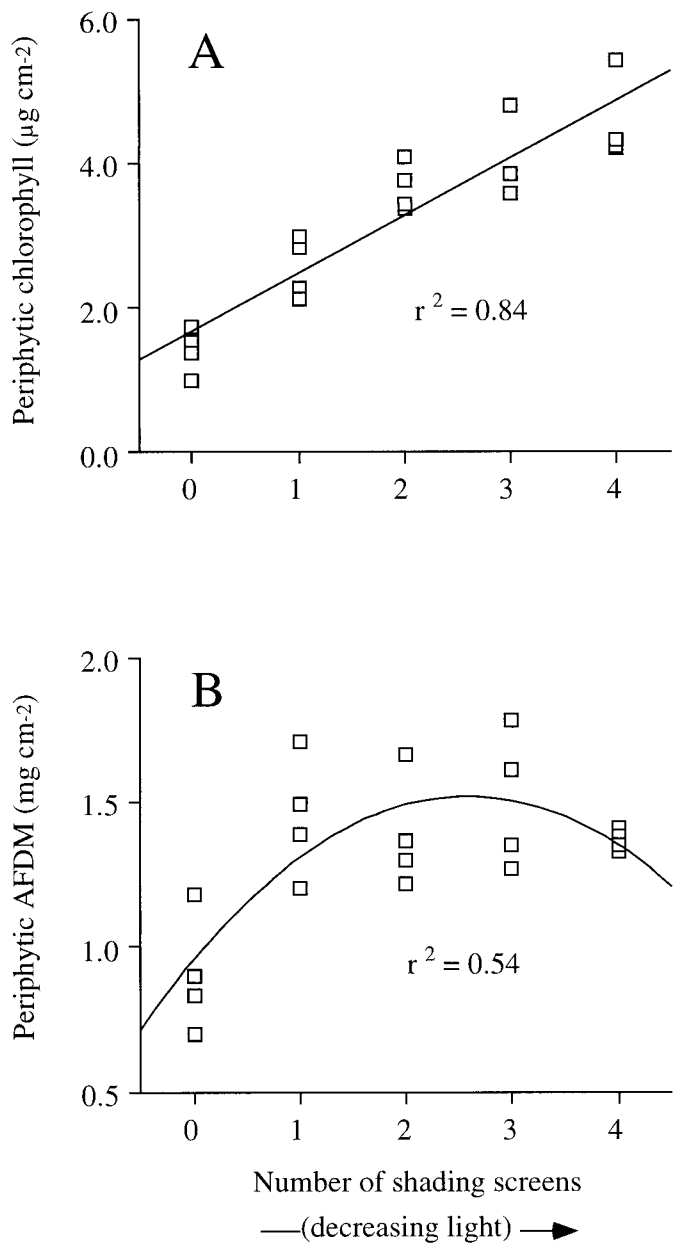

Fig. 4. (A) Periphytic Chl *a* collected from tiles that were unshaded or shaded by one, two, three, or four layers of shading screen. (B) Same as above, but for AFDM. Lines fitted to data reflect best fits based on r^2 values (shown in figures).

lend support to the idea that light in high mountain streams may have a very different role in structuring periphytic assemblages from that of lowland streams. Whereas natural irradiance is frequently limiting at low elevations because of its scarcity, particularly in streams shaded by riparian canopies (Hill and Harvey 1990; Hill and Knight 1988*b*), full sunlight may constrain algae and periphyton where it is excessive (Guasch and Sabater 1995; Hill et al. 1995). Evidence from this study and others (e.g., Wellnitz et al. 1996*a*; Wellnitz et al. 1996*b*) suggest that photoinhibition may be particularly important for structuring periphytic communities in high mountain streams where high irradiances are common.

Light reduced the abundance of specific physiognomies, but not the ones we had predicted. Rather than decreasing the abundance of upright forms, only low-lying physiognomies declined in response to high irradiance. We attribute this decrease to a decline in adnate forms occurring epiphytically, however, we cannot be certain of this because periphytic structure becomes disrupted when removed from substrata. Nevertheless, when light had a significant influence on physiognomic abundance it was always negative.

Ecdyonurus had a considerably larger influence on periphyton than *Drusus. Drusus* larvae had no effect on total periphytic biomass and influenced the abundance of just four of the seven algal physiognomies. By contrast, *Ecdyonurus* reduced all physiognomies except for the rod cluster type. Not only did this mayfly deplete physiognomies that are typically raised off the substratum (e.g., erect and stalked diatoms), *Ecdyonurus* also was correlated with reductions in adnate forms (e.g., prostrate/nonmotile and prostrate/motile algae).

We had hypothesized that *Ecdyonurus* was an ''extensive'' grazer, one that would have a greater influence on total algal biomass than *Drusus,* but primarily by depleting taller rather than low-lying physiognomies. According to the model of algal vulnerability proposed by Steinman (Gregory 1980; Steinman 1996), mayfly feeding should be largely confined to more accessible upper or middle layers of the periphytic matrix. The premise of this model is that physiognomy dictates the vertical position of an alga within the periphytic mat and herbivore mouthpart structure will determine how deeply into the mat and to which physiognomies grazers will have access. In this study and in other work (Wellnitz and Ward 1998), we have found that algal physiognomy is in fact a poor predictor of vulnerability to consumers. There are at least two possible explanations to account for this. One possibility is that physiognomy does not necessarily dictate an alga's vertical position within the periphytic matrix. Many algae are epiphytic on other algae or attached to detritus, a situation that could position algal cells higher, regardless of their physiognomy. Another possibility is that herbivore feeding structures may not constrain consumers as much as is generally believed. Herbivore behavior, for example, may alter the intensity or the mode of feeding. The heptageniid *Rhithrogena pellucida* employs at least two modes of feeding, using its maxillary palps to ''scrape'' and its labial palps to ''brush'' periphyton from substrata (McShaffrey and McCafferty 1988). Nor were this mayfly's feeding activities confined to its mouthparts; *R. pellucida* could use its forelegs as auxiliary feeding appendages to dislodge tightly adherent periphyton as well. Herbivore hunger level may also alter grazing intensity. Steinman (1991) found that starved snails removed more prostrate *Cocconeis placentula* diatoms than did fed snails, suggesting that after susceptible growth forms had been removed, hungry snails continued to feed and consumed more adherent physiognomies.

Whereas *Ecdyonurus* was thought to graze extensively, we had characterized *Drusus* as an ''intensive'' grazer. Our expectation was that this caddisfly would have less impact on total algal biomass than *Ecdyonurus,* but would be associated with greater decreases in adnate and prostrate physiognomies by virtue of its orthognathous mouthpart orientation and scraping mandibles. Although it was clear that *Drusus* removed less periphyton than *Ecdyonurus,* this caddisfly was not correlated with greater reductions in low-lying forms. As mentioned, *Ecdyonurus* had greater effects on physiognomies influenced by both grazers, which included prostrate/nonmotile and prostrate/motile forms. It is noteworthy, however, that neither grazer was associated with a decrease in the rod cluster form. Rather, both grazers were correlated with an increase in the percent representation of these small cyanophytes. The small size of this group (*Chamaesiphon* spp. were smaller than diatoms by a factor of 10) may have made these algae less susceptible to grazing. Rosemond (1993), for example, found *Chamaesiphon investiens* abundance increased in response to snail grazing and they suggested that there may have been a trade-off between growth and grazer resistance in this alga. Given the equivocal responses of other physiognomies to grazing, however, it is difficult to know whether the rod cluster form was less vulnerable by virtue of its position within the matrix, was somehow more resistant to grazing (e.g., via compensatory growth) or if it was actively avoided by the herbivores. But as Steinman (1996) has pointed out, little is known about grazer selectivity, algal food quality or chemical defenses in freshwater algae.

Herbivore weights measured at the end of the study indicated that competition for periphytic resources occurred in the channels. Although individual grazer weights of the two taxa were not correlated, there was a negative association between grazer weight and conspecific biomass. This result suggests intraspecific rather than interspecific competition was an important factor controlling grazer biomass in our channels and may be an important process structuring these herbivore populations in Minor Creek, as has been shown for herbivores in other streams (Colletti et al. 1987; Hawkins and Furnish 1987; Lamberti et al. 1987*b*; Feminella and Resh 1990).

That *Drusus* had no effect on *Ecdyonurus* was not surprising, given the small influence it had on periphyton. The failure of *Ecdyonurus* to significantly influence *Drusus* weights, however, was striking. There was considerable overlap between the algal forms removed by both herbivores, and *Ecdyonurus* always removed more. In addition, *Ecdyonurus* was approximately five times larger and its average biomass in channels was approximately twice as great across treatments. It seems paradoxical, then, that *Ecdyonurus* did not appear to compete with *Drusus,* especially in

light of the many studies that have shown interspecific competition to be an important process structuring stream herbivore populations (e.g., McAuliffe 1984*a*; McAuliffe 1984*b*; Hart 1987; Hill and Knight 1988*a*; Kohler 1992; Gresens 1995).

Competition between *Drusus* and *Ecdyonurus* may not have occurred in the experimental channels due to spatial partitioning of food resources (e.g., MacArthur 1959). To mimic stream bed architecture, we covered the bottom of each channel with a 1-cm layer of gravel, on top of which were placed the stream cobbles that were sampled for periphyton. The gravel served as a refuge for grazers, but it also supported periphyton, an alternative food source for *Drusus*. Thus, our experiment may have underestimated the effect of *Drusus* by reason of nonrepresentative sampling of periphyton in our channels. However, our experiment was designed to assess the respective roles of *Ecdyonurus* and *Drusus* in shaping periphytic assemblages which grew on the upper surfaces of stream cobbles, and in this regard it is clear that *Ecdyonurus* effects were more important.

Surprisingly, light did not influence grazer weight gain through its regulation of periphytic biomass. We had hypothesized that if photoinhibition was an important factor controlling periphytic biomass accrual, as our data suggest, then grazers in open channels would have been more food-limited, and thus, grazer weight gain should have been less than in shaded channels. But this did not occur. One possible explanation for the failure of light to influence grazer biomass is that the experiment did not run long enough for increased food limitation to become evident. This seems unlikely, however, because our experiment identified interspecific competition as a factor controlling *Drusus* and *Ecdyonurus* weights. For competition to occur, of course, resources—in this case, periphyton—must be limiting.

A more interesting possibility is that light altered periphytic susceptibility to grazing such that periphyton receiving intense, photoinhibiting irradiance were more readily consumed. Were this the case, then differences in grazer weight gain between light treatments may not have occurred if grazers found algae in open channels more palatable. Irradiance is capable of modifying the vulnerability of periphyton to grazing (Hill et al. 1995; Rosemond and Brawley 1996; Wellnitz and Ward 1998). For example, Wellnitz et al. (1996*b*) found that light in a subalpine stream could modify the effect *Rhithrogena robusta* mayfly nymphs had on periphytic biomass; as light increased, grazers caused greater depletions in periphytic AFDM. Although there has been little work exploring the mechanisms underlying this phenomenon (but see Rosemond and Brawley 1996), environmental stress (*sensu* Grime 1979) may be a factor. Light intensities that are sufficient to photoinhibit algae could constitute a such a stress (Boston and Hill 1991; Hill et al. 1995; Wellnitz et al. 1996*a*; Beardall et al. 1997). Stress negatively effects communities (Odum et al. 1979), and exposure to one stressor can make organisms less resistant to others because of the costs associated with stress tolerance. We speculate, then, that grazer biomass did not respond to light-induced changes in periphytic biomass because periphyton in the two light treatments differed in palatability. Although there was less algae in the high light treatment, grazers may have compensated by eating more of it.

Results from this work and a previous study (Wellnitz and Ward 1998) suggest that understanding periphytic community responses to grazing and other constrains may require more sophisticated models of periphytic structure. Rosemond and Brawley (1996) have argued that future models of periphyton need to incorporate both general attributes (e.g., physiognomy) and specific characteristics (e.g., species autecologies) so that we can better predict benthic community responses to anthropogenic eutrophication and other perturbations. To this list of important factors to be acknowledged we should like to add the ''environmental context.'' Accumulating evidence suggests that the physical environment can constrain biotic interactions, potentially altering their importance or even their outcomes in streams (Poff and Ward 1995; Wellnitz et al. 1996*b*) and other ecosystems (Dunson and Travis 1991; Sanford 1999). Although we did not detect significant interactions between light and grazers is this study, knowledge of the role that light had in shaping periphyton—the environmental context—was integral to understanding the role that grazers had in structuring the periphytic community in Minor Creek.

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