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Effects of three herbivores on periphyton communities in laboratory streams

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Abstract. The effects of grazing on algal assemblages by three different stream herbivores, the mayfly *Centroptilum elsa*, the snail *Juga silicula*, and the caddisfly *Dicosmoecus gilvipes*, were studied during a 48-d experiment in six laboratory streams. Compared with ungrazed control streams, grazing by *Centroptilum* (500/m²) modified algal community structure slightly but had little effect on periphyton biomass and chlorophyll *a*. Grazing by *Juga* (350/m²) reduced periphyton biomass and chlorophyll *a* by nearly 50%, but increased the rate of primary production by up to 25%. *Juga* also prevented significant accumulation of cyanophytes and some diatom species. Grazing by *Dicosmoecus* (200/m²) reduced periphyton biomass and chlorophyll *a* to less than 5% of the ungrazed levels, but primary production declined by only 50%. Only adnate algal cells and short filaments persisted on substrates grazed by *Dicosmoecus*. Algal export rates were increased by all three herbivores.

Modification of algal growth patterns by both consumption and dislodgement, and dampening of temporal fluctuations were key mechanisms by which these herbivores altered periphyton communities. Primary production was stimulated by low rates of grazing by *Juga* in the laboratory streams, possibly as a result of increased light intensity in lower strata of the periphyton or removal of senescent algal cells. Algal assemblages displayed both community-level responses (e.g., biomass, production) and species-level responses (e.g., taxonomic composition) that should be considered in other studies of stream herbivory.

Key words: herbivory, stream, periphyton, benthic algae, grazing, *Centroptilum*, *Juga*, *Dicosmoecus*, primary production, chlorophyll *a*, export.

Guilds of grazing invertebrates in streams usually consist of a suite of species, each of which uses a unique feeding morphology and foraging behavior to harvest algal resources (Gregory 1983, Lamberti and Moore 1984). Interactions of herbivores often make it difficult, or impossible, to ascribe periphyton grazing responses to particular herbivore species. Consequently, most previous investigations of grazing effects on stream periphyton communities have focused on a single species either in laboratory channels (e.g., Gregory 1983, Kehde and Wilhm 1972, Sumner and McIntire 1982) or, more rarely, in natural streams where a single species can be experimentally manipulated (e.g., Hart 1985, Lamberti and Resh 1983, McAuliffe 1984). These studies delimit the effects of a predominant grazer on periphyton assemblages, but generate little information on the range of effects that coexisting, but functionally dissimilar, species can exert on periphyton. An essential step in evaluating grazer guild effects on algal assemblages is to assess how the specific abilities of different herbivores influence those assemblages.

In this study, we examined the separate effects of three functionally different herbivores on periphyton assemblages in laboratory streams. These invertebrate grazers were the mayfly *Centroptilum elsa* Traver, the caddisfly *Dicosmoecus gilvipes* (Hagen), and the snail *Juga silicula* (Gould). This study was designed to characterize the range of responses to grazing in the algal assemblages, and to generate hypotheses that could be tested in future experiments. Our specific objectives were (1) to describe the effects of each species' grazing activities on periphyton biomass, chlorophyll

a, metabolism, export, and taxonomic composition, and (2) to compare the effects of the three herbivores and relate observed differences to grazer functional morphology.

The Herbivores

The three herbivores used in this study are abundant in streams throughout the Pacific Northwest, where they commonly coexist. Because of morphological differences in feeding structures (see below) and possible differences in ingestion rate, food selectivity, and foraging behavior, we postulated that their individual grazing activities should elicit different responses by the algal assemblage.

The mayfly *Centroptilum* (Ephemeroptera:Baetidae) functions as a scraper and a collector-gatherer (Edmunds 1984). *Centroptilum* nymphs have mouthparts fringed with brushlike hairs, allowing them to browse periphyton from the substrate. The caddisfly larva *Dicosmoecus* (Trichoptera:Limnephilidae) uses robust bladelike mandibles and other mouthparts, which have limited setation, to scrape periphyton (Wiggins 1984). The radula of the snail *Juga* (Gastropoda: Pleuroceridae) is equipped with many fine teeth to scrape or rasp substrates for adherent algae. Thus, these herbivores represent contrasting feeding morphologies and methods of food acquisition (browsing, scraping, or rasping) that may affect periphyton communities differently.

Centroptilum nymphs and *Juga* snails were collected from Oak Creek, a third-order stream in the coastal mountains of Oregon, and *Dicosmoecus* larvae were collected from Big Elk Creek, a fourth-order stream also in the Oregon coastal mountains. We used late instar *Centroptilum* nymphs, snails of intermediate size (10–15 mm total shell length), and third and fourth instar *Dicosmoecus* larvae in the laboratory streams. The animals were held for no more than two days before introduction to the laboratory streams.

Methods

Laboratory streams

This experiment was conducted in six fiberglass laboratory streams, each 3 m long, 0.5 m wide, and 0.2 m deep (ca. 2 m^2 surface area, including sides). Each recirculating stream had two parallel channels (each 0.25 m wide) separated by a centerboard that was open at both ends. A stainless steel paddlewheel, located at one end and connected by a steel shaft to a variable speed gearmotor, circulated water continuously at a velocity of 10 cm/s at the substratum. Well water was supplied continuously at a rate of 1.5 L/min, which replaced water that drained from the streams through a standpipe that maintained water depth at 10 cm. Total stream volume (0.15 m^3) was replaced about once every 100 min and water temperature was kept at 13 ± 1°C. Light energy was provided by six 1000-watt HID lamps (Sylvania Metalarc), which generated a photon flux density of 400 μEinsteins $m^{-2}\,s^{-1}$ at the water surface. We used a photoperiod of 8L:16D. Nutrient concentrations in the well water were high (NO_3-N: 6.499 mg/L; NH_3-N: 0.002 mg/L; PO_4-P: 0.096 mg/L).

The bottom of each stream was lined with 7.4 × 7.4-cm unglazed ceramic tiles (55 cm^2 each), which served as surfaces for algal growth and as sampling units. One out of six tiles had an upturned end ("cove" tile) to generate micro-current heterogeneity. The stream sides were lined with 15 × 15-cm tiles to ensure uniform substrate throughout the stream, though these tiles were not sampled.

Experimental design

On the first day of the experiment, 7 April 1985, periphyton was scraped from rocks collected from four streams in Benton County, Oregon. The scrapings were homogenized for 30 s in a Waring blender, brought to a volume of 6 L with water, and a 1-L aliquot was added to each of the six experimental streams. Herbivores were introduced into three of the streams nine days later, 16 April, leaving three flumes as ungrazed controls. Each of the grazed streams was stocked with one herbivore species at the following density: 1) 500 *Centroptilum*/m^2 (ca. 0.5 g ash-free dry mass/m^2), 2) 350 *Juga*/m^2 (ca. 4.0 g AFDM/m^2), or 3) 200 *Dicosmoecus*/m^2 (ca. 2.5 g AFDM/m^2). These densities roughly corresponded to field densities observed at the collection sites. The experiment was terminated on 25 May, 48 d after inoculation.

Chlorophyll *a* standing crop was measured at 4, 8, 12, 16, 24, 32, and 48 d after inoculation. Periphyton biomass was measured at 8, 12, 16, 24, 32, and 48 d. Rates of primary production

and respiration were measured at 9, 16, 34, and 48 d, and taxonomic structure of periphyton was determined at 8, 16, 32, and 48 d. Export was measured at 7, 11, 15, 23, and 46 d, one to two days before any disturbance resulting from routine sampling.

Three tiles were randomly selected from each stream on each sampling date for measurement of chlorophyll *a* and periphyton biomass. Periphyton was removed from the upper surface of each tile with a razor blade, homogenized with a small-volume blender, and split into two equal portions. Each portion was filtered onto a separate Millipore filter (0.45 μm pore size). For chlorophyll *a* analysis, one filter was ground and pigments extracted in buffered 90% acetone for 3 hr. The scraped tile was also soaked in 90% acetone for 24 hr to extract any residual pigment. Chlorophyll *a* was measured with a spectrophotometer using the trichromatic method (Strickland and Parsons 1968). For determination of periphyton biomass as ash-free dry mass, the pre-weighed second filter was dried at 55°C for 24 hr, weighed, combusted at 500°C for 24 hr, and reweighed.

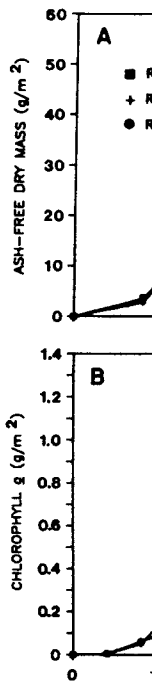
Primary production of periphyton was determined using recirculating chambers similar in design to those of McIntire and Wulff (1969). Three randomly selected tiles from a stream were placed in the 2-L plexiglass chamber. The chamber was sealed and water was circulated with a submersible pump. Three water samples were drawn from the chamber after each of two consecutive 2–3-hr incubations: community respiration (dark run) and net community primary production (light run). Algal assemblages were allowed to adjust to the light for 30 min before the primary production incubation began. Oxygen concentration in each sample was measured with an Orbisphere oxygen meter. Hourly rate of gross primary production was calculated by adding the loss of dissolved oxygen in the dark to the net production of dissolved oxygen in the light and dividing by the incubation time. Daily gross primary production and daily net community primary production were determined based on 8 hr of primary production and 24 hr of community respiration per day. Light energy, nutrient concentrations, current velocity, and temperature were maintained as close as possible to conditions in the laboratory streams. Two complete incubations with different sets of tiles were conducted for each stream. Macroinvertebrates were removed from the tiles before each incubation. Chlorophyll *a* was measured for each set of tiles and used in calculations of assimilation number.

Taxonomic structure of algal assemblages was determined by scraping the surfaces of two randomly selected tiles from each stream into a single pooled sample. Taxonomic composition was determined quantitatively according to the method described in detail in Steinman and McIntire (1986). In brief, periphyton assemblages were fixed in Lugol's solution, settled in 50-ml chambers, and 500 algal units per sample were counted at 400× with a Nikon MS inverted microscope. All algae were identified to species in this step, except diatoms which were counted and identified at 1250× with a Zeiss RA microscope. An algal unit was an individual cell or valve if the taxon was unicellular, or an individual filament or colony if it was multicellular. Mean biovolume of each algal taxon was determined from measurements of at least 10 cells per taxon using standard geometric formulae. The biomass of each algal taxon was estimated by multiplying the taxon's proportion of the community biovolume by the total community biomass.

Export of particulate organic matter (POM > 10 μm) from the streams was measured by placing a 10-μm mesh bag under the standpipe, which filtered all effluent water for a given time interval (30–60 min; 45–90 L volume). Export was measured simultaneously for all streams at mid-morning (0900–1000 hr) on each sampling date. Each sample was analyzed for ash-free dry mass as described for epilithon samples. Influent well water contained no POM.

Statistical analyses

The goal of our experiment was to obtain a broad view of the grazing process by evaluating three different herbivores and to generate testable hypotheses for future experiments. Because this approach sacrificed treatment replication for breadth (i.e., different herbivore streams were not replicated), grazing effects could not be examined with inferential statistics. However, replication of the ungrazed streams ($n = 3$) provided a basis for comparing streams that received the same treatment (i.e., degree of inter-stream variability), and indicated that there was little difference among those



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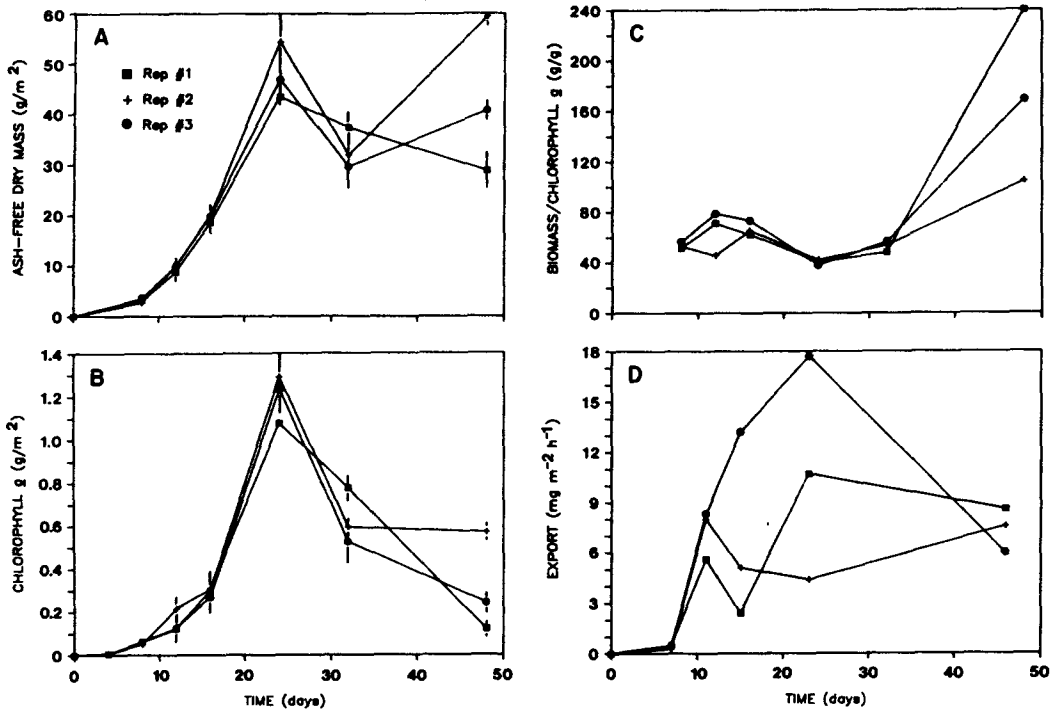

FIG. 1. Periphyton dynamics in three replicate streams containing no herbivores, presented as (A) algal biomass, (B) chlorophyll *a*, (C) biomass : chlorophyll ratio (jointly measured beginning on day 8), and (D) POM export. Values presented are means (±1 SE; $n = 3$, for A, B) of within-stream samples.

streams (see Results). Previous studies in our system have verified that different streams receiving the same treatment produce similar algal assemblages (Steinman and McIntire 1986, 1987). As a basis for representing intra-stream variation, we present the standard errors of measured periphyton attributes (biomass, chlorophyll *a*, gross primary production, community respiration) on each sampling date. Summary statistics based on means (biomass : chlorophyll ratio, production : respiration ratio, assimilation number), pooled samples (individual algal taxa), or time-interval samples (export) are treated as single measurements on each sampling date.

Taxonomic composition of algal assemblages in different streams was compared by the SIMI measure of community similarity (McIntire and Moore 1977). The SIMI value can range from 0 to 1, where 0 indicates two communities have no species in common, and 1 indicates they are identical in both species composition and relative abundance. SIMI values were based on algal biovolume (Steinman and McIntire 1986).

Results

Periphyton development in ungrazed streams

Three streams were used to assess development of benthic algal assemblages in the absence of herbivores. Development of the algal assemblage in terms of algal biomass was consistent with a logistic growth model (Fig. 1A). The initial rate of accumulation was slow (days 0–8), followed by a period of rapid biomass accumulation (logarithmic growth phase; days 8–24), and finally a period of relatively constant biomass (asymptotic phase; days 24–48). Variability among replicates streams in biomass accumulation was low, at least until day 32. After day 32, algal senescence occurred, as shown by chloroplast degradation and decline in mat cohesiveness. This deterioration of the periphyton community resulted in spatial heterogeneity or patchiness in the assemblage (see Steinman and McIntire 1987) and probably accounted for differences in mean biomass among the ungrazed streams by day 48.

Standing crops of chlorophyll *a* peaked in all three streams at day 24, then declined rapidly through day 48 (Fig. 1B). This decline in chlorophyll *a* probably reflects the senescence of the algal assemblage. The biomass-to-chlorophyll ratio remained relatively constant until day 32 (Fig. 1C), then increased markedly through day 48. Allocation of photosynthate into storage products, lower photosynthetic activity, and decreased pigment synthesis are typical of late stages of algal community development (Wetzel and Westlake 1969), and are all processes that could result in increased ratios of biomass to chlorophyll *a*.

Export measured POM >10 μm that was carried with the current and passed out of the streams. Some algae (e.g., single cells < 10 μm) undoubtedly passed through the collection net, which would result in an underestimate of export. However, most taxa were probably retained by the net either because they had a filamentous or colonial growth form, were intertwined with other algal taxa, or because individual cells were large. Consequently, underestimates of algal export were probably minor. Export rates generally increased with biomass accumulation in the ungrazed streams (Fig. 1D). Rates of export varied more than biomass or chlorophyll *a* among replicate streams, possibly because of occasional sloughing of large algal clumps during the 30–60 min sampling period.

Grazer effects on periphyton biomass, pigment, and export

All three types of grazers, the mayfly *Centroptilum*, snail *Juga*, and caddisfly *Dicosmoecus*, depressed periphyton biomass to some degree relative to ungrazed algal assemblages (Fig. 2A). Grazing by *Centroptilum* slowed the rate of biomass accumulation after day 16, resulting in slightly less biomass at the asymptotic phase than that of the ungrazed streams; this difference (about a 20% reduction) persisted throughout the experiment. *Juga* reduced the rate of biomass accumulation soon after introduction. Grazing by the snails maintained periphyton biomass at 15–20 g/m² after day 16, about one half of the biomass in the ungrazed streams. *Dicosmoecus* larvae reduced algal biomass immediately after their introduction, and, unlike the other herbivores, resulted in a net decline in periphyton biomass to very low levels (<1 g/m²) for the duration of the experiment.

Compared with standing crops of pigment in the ungrazed streams, the amount of chlorophyll *a* was also reduced by each type of grazer (Fig. 2B). *Centroptilum* and *Juga* reduced the maximum level of chlorophyll *a* by about 40% and 60%, respectively, whereas grazing by *Dicosmoecus* reduced chlorophyll *a* by over 95%. The decline in chlorophyll *a* abundance observed in the ungrazed streams after day 24 also occurred in two of the grazed systems (*Centroptilum, Juga*). In these latter cases, senescence of the algal assemblage apparently contributed to the dynamics of chlorophyll *a*.

The biomass-to-chlorophyll ratio was similar in the ungrazed, *Centroptilum*, and *Juga* streams, generally ranging from 50 to 80 during the first 32 d of the experiment (Fig. 2C). Following the deterioration in the algal community, when chlorophyll *a* declined but biomass remained relatively constant, this ratio increased to >100 in these three systems. The biomass-to-chlorophyll ratio was consistently low (<30) in the stream grazed by *Dicosmoecus*.

Export rates of periphyton increased in all three streams soon after herbivore introduction (Fig. 2D). By day 15, export rates in the grazed streams were several times higher than export in the ungrazed systems. Patterns of export reflected the extent of reduction of algal abundance by herbivores; export was highest for the *Dicosmoecus* treatment, indicating that these animals were most disruptive of the algal assemblage, and intermediate for the *Juga* and *Centroptilum* systems. Export rates declined between days 15 and 46 in the grazed streams, but did not change appreciably in the ungrazed streams (Fig. 2D). Biomass remained relatively constant in all streams over this same period (Fig. 2A), indicating that biomass-specific export rates (i.e., export per unit attached biomass) also declined in the grazed streams.

Grazer effects on periphyton metabolism

Rates of primary production and respiration were measured for the ungrazed, *Juga*, and *Dicosmoecus* streams. Rates of gross primary production (GPP) increased in all three systems during the course of the experiment (Fig. 3A). Grazing by *Dicosmoecus* reduced GPP by about 50% as compared with the ungrazed streams,

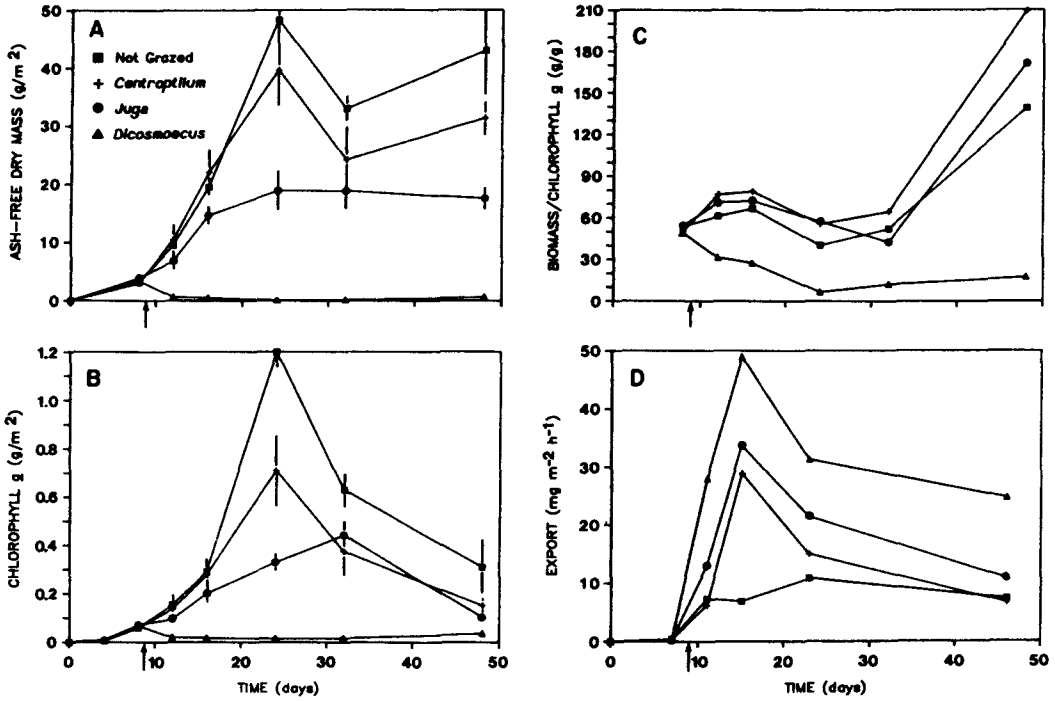

FIG. 2. Periphyton dynamics in streams containing either *Centroptilum* mayflies, *Juga* snails, or *Dicosmoecus* caddisflies, compared with a mean of the three ungrazed streams. A–D as in Figure 1. Arrow shows date of animal introduction.

but grazing by *Juga* actually stimulated GPP by about 25% over that in the ungrazed streams after day 16.

Community respiration (CR) increased in the ungrazed and *Juga* streams between days 9 and 16 and then remained steady (Fig. 3B); in the *Dicosmoecus* stream CR gradually increased from days 16 to 48. The production-to-respiration ratio (P/R) was slightly greater than one (1.06) when the animals were introduced (Fig. 3C). P/R increased in all treatments during the experiment. By day 48, GPP was more than double the respiratory demands of the community in the ungrazed and *Dicosmoecus* streams, and more than triple the CR in the *Juga* stream. Daily net community primary production (the absolute difference between daily GPP and daily CR) on day 48 was 3.6 g O_2 m^{-2} d^{-1} in the ungrazed streams, 5.2 g O_2 m^{-2} d^{-1} in the *Juga* stream, and 1.7 g O_2 m^{-2} d^{-1} in the *Dicosmoecus* stream.

Patterns of algal production (Fig. 3A) did not display the extreme differences shown in algal abundance (Fig. 2A). For example, though standing crops of chlorophyll *a* were much greater in the ungrazed streams than in the *Dicosmoecus* stream, rates of GPP in the ungrazed streams were only slightly more than twice the production in the *Dicosmoecus* stream. This response reflects the influence of grazing on the rate of primary production per mass of chlorophyll *a* (chlorophyll-specific primary production) in the algal assemblage. At the light intensities used in this experiment (400 μEinsteins m^{-2} s^{-1}) photosynthesis was almost certainly saturated (Jasper and Bothwell 1986), so chlorophyll-specific primary production represents assimilation number. Assimilation number was always higher in the grazed streams than in the ungrazed streams (Fig. 3D). Thus, reductions in algal abundance did not cause equivalent declines in primary production. In fact, reductions in biomass and chlorophyll *a* in the *Juga* stream were accompanied by increases in gross primary production.

Grazer effects on algal community structure

A total of 46 algal species was identified during the experiment. The number of taxa was relatively consistent for each treatment: 33

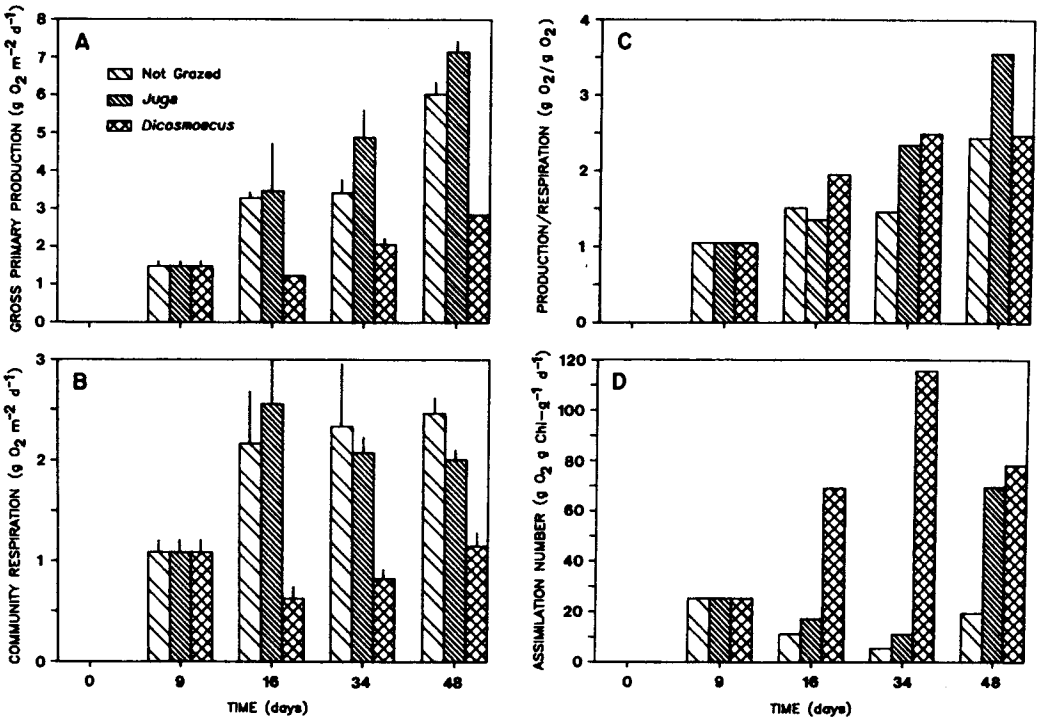

FIG. 3. Metabolism of periphyton grazed by *Juga* snails, *Dicosmoecus* caddisflies, or ungrazed, for five sampling dates during the experiment, presented as (A) rate of gross primary production ($\bar{x}$ + 1 SE; n = 2), (B) community respiration, (C) 24-hr production:respiration ratio, and (D) assimilation number. Animals were introduced after measurements on day 9.

species were found in the ungrazed stream, 35 species in the *Centroptilum* stream, 37 species in the *Juga* stream, and 29 species in the *Dicosmoecus* stream.

Greater than 90% of the periphytic material by mass consisted of identifiable algae. Examination of live and fixed samples by light microscopy revealed very few bacterial cells or fungal hyphae. In addition, observation of tiles with scanning electron microscopy failed to reveal significant amounts of non-algal biomass (Steinman and McIntire 1986, 1987). This may be related to a lack of microbial inocula in the water supply. The small amount of detritus present was therefore of algal origin. Assuming a detrital composition similar to the live algal community, specific biomasses could be estimated from individual biovolumes and total community biomass (Fig. 4).

The three dominant diatom taxa responded differently to the experimental treatments. *Nitzschia oregona* and *Achnanthes lanceolata* were most abundant in the ungrazed streams, where they increased throughout the experiment (Figs. 4A, B). These taxa also increased in the *Centroptilum* and *Juga* systems until day 32 and then declined; both taxa were sparse in the *Dicosmoecus* stream after day 16. The diatom *Synedra ulna* showed high biomass in the ungrazed and *Centroptilum* streams, intermediate in the *Juga*, and low in the *Dicosmoecus* (Fig. 4C). *Synedra ulna* was dominant in early algal assemblage development in all treatments, peaking at day 16 and then declining.

The cyanophyte *Phormidium tenue* and chlorophytes *Scenedesmus* spp. showed little accumulation until day 32, after which *P. tenue* accumulated substantial biomass in the ungrazed and *Centroptilum* streams (Fig. 4D). *Scenedesmus* increased rapidly in all but the *Dicosmoecus* treatment (Fig. 4E), representing one third to one half of total community biovolume by day 48 (Table 1).

The biomass of filamentous chlorophytes, predominantly *Stigeoclonium tenue*, peaked at day 32 in the ungrazed, *Centroptilum*, and *Juga* treat-

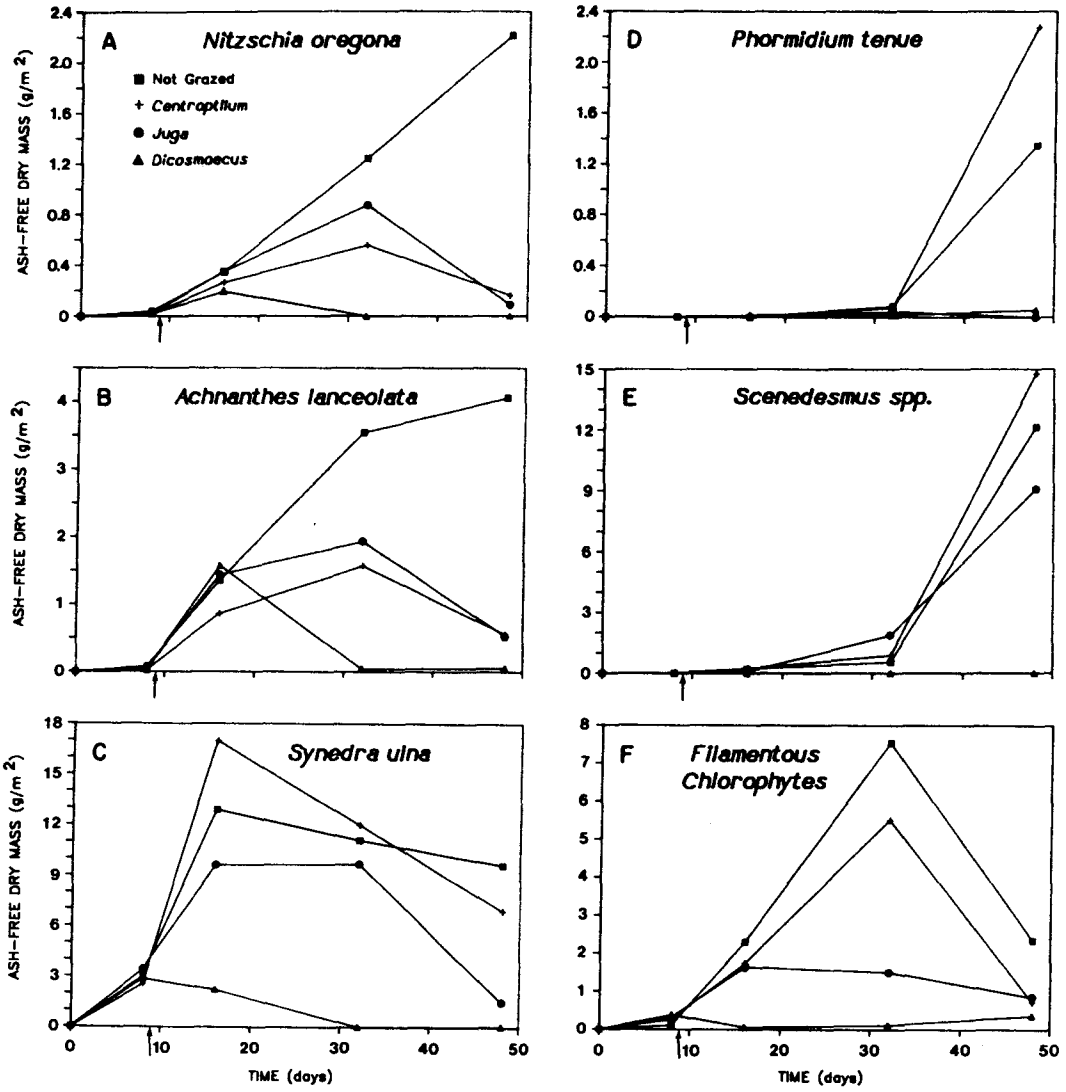

FIG. 4. Biomass accumulation for the six dominant algal taxa in streams containing either *Centroptilum* mayflies, *Juga* snails, or *Dicosmoecus* caddisflies, compared with a mean of the three ungrazed streams. Arrow shows date of animal introduction.

ments (Fig. 4F). Though no algal taxon accumulated much biomass in the *Dicosmoecus* stream owing to heavy grazing pressure (Fig. 2A), the filamentous forms did account for >50% of the total community biovolume in that system on day 48 (Table 1). In general, the pattern of algal succession in the streams included early colonization and dominance by *Synedra*, growth of *Stigeoclonium*, *Achnanthes*, and *Nitzschia* at mid-successional stages, and late growth of *Scenedesmus* and *Phormidium*.

SIMI measures of algal community similarity at day 8 showed that there was a high degree of similarity (SIMI > 0.99) among the four treatments before grazer introduction (Table 2). By day 16, algal community structure in the *Dicosmoecus* stream began to diverge, but the other treatments remained similar. On day 32, algal assemblages grazed by *Centroptilum* and *Juga* remained quite similar to each other (SIMI = 0.96) but differed from the control streams (SIMI < 0.40). The algal community grazed by *Dicos-*

TABLE 1. Relative abundance, as percent of total community biovolume, of the six dominant algal taxa in each treatment at day 48.

Taxon	Relative Abundance (%)			
	Ungrazed	*Centroptilum*	*Juga*	*Dicosmoecus*
Nitzschia oregona	5.1	0.5	0.5	0.1
Achnanthes lanceolata	9.0	1.8	3.0	8.5
Synedra ulna	19.6	22.1	8.5	7.5
Phormidium tenue	3.1	7.2	0.0	19.0
Scenedesmus spp.	32.3	47.0	51.6	0.0
Filamentous chlorophytes	5.1	2.3	4.8	57.2
All other algal taxa	25.8	19.1	31.6	7.7
Total	100.0	100.0	100.0	100.0

TABLE 2. Matrices of similarity values (SIMI) of algal community structure for grazing treatments by sampling date. A single randomly selected stream was used to represent the ungrazed treatment on each date.

	Ungrazed	*Centroptilum*	*Juga*	*Dicosmoecus*
Day 8				
Ungrazed	1.000			
Centroptilum	0.998	1.000		
Juga	0.998	0.999	1.000	
Dicosmoecus	0.995	0.999	0.999	1.000
Day 16				
Ungrazed	1.000			
Centroptilum	0.955	1.000		
Juga	0.969	0.993	1.000	
Dicosmoecus	0.863	0.840	0.882	1.000
Day 32				
Ungrazed	1.000			
Centroptilum	0.393	1.000		
Juga	0.380	0.958	1.000	
Dicosmoecus	0.299	0.324	0.296	1.000
Day 48				
Ungrazed	1.000			
Centroptilum	0.763	1.000		
Juga	0.748	0.899	1.000	
Dicosmoecus	0.129	0.148	0.101	1.000

moecus was distinct from all other streams (SIMI < 0.35). At day 48, similarity increased between both the *Juga* and *Centroptilum* treatments and the ungrazed streams (SIMI > 0.70). Algal community structure in the *Dicosmoecus* system continued to be distinct throughout the 48 d (SIMI < 0.20).

Discussion

Laboratory stream experiments cannot reproduce the degree of natural variation and environmental heterogeneity imposed by natural systems. However, laboratory studies profit from the ability to maintain certain environmental parameters constant (such as light, nutrients, flow, and substrate in our study) while manipulating key features of interest (type of herbivore in our study). In natural streams where the herbivore community may consist of many species, it may be difficult to ascribe responses in the periphyton community to individual grazer species. The laboratory streams allowed us to study a single species in isolation, to accurately describe its grazing effects, and to identify important relationships for examination in subsequent experiments.

Our primary objective was to compare the relative effects of three different grazers on stream periphyton communities. We used three herbivore species that are widely distributed and frequently abundant in streams of the Pacific Northwest. In addition, two of these species (*Dicosmoecus gilvipes* and *Juga silicula*) have been identified previously as key herbivores in western streams (Gregory 1983, Hart 1981, Hawkins and Furnish 1987, Sumner and McIntire 1982), and functionally analogous species can be found in other geographical areas (Kehde and Wilhm 1972, McAuliffe 1984, Mulholland et al. 1983).

Previous investigations have demonstrated that stream herbivores can affect periphyton biomass (Lamberti and Resh 1983, McAuliffe 1984, Power et al. 1985), rates of production (Gregory 1983, Lamberti and Resh 1983), taxonomic structure (Hart 1985, Sumner and McIntire 1982), export (Mulholland et al. 1983, Sumner and McIntire 1982), and nutrient cycling (Mulholland et al. 1983). However, most previous studies have documented the response in only one or two periphyton parameters, such as biomass accumulation or pigment concentration, rather than examining the array of features that characterize plant-herbivore interactions (Gregory 1983). This study has demonstrated that measuring a variety of features in the periphyton community may be necessary to ade-

quately characterize algal response to grazing. A single feature (e.g., biomass, pigment, productivity, or taxonomy) would have described only a small fraction of the observed responses of the algal assemblage. For example, periphyton biomass alone was not a suitable measure from which to infer chlorophyll *a*, metabolism, export, or community structure.

Grazer regulation of algal biomass and export

The three herbivores examined in this study had differing effects on the accumulation of algal material. Grazing by *Centroptilum* only slightly reduced algal biomass below levels in the ungrazed streams. However, we observed that individual *Centroptilum* could clear periphyton from small patches (<2 cm in diameter) immediately around themselves, and other baetid mayflies produce similar patches in benthic algal assemblages (Wiley and Kohler 1984). Grazing by *Juga* greatly reduced the maximum standing crop attained and resulted in an algal community with biomass and pigment intermediate between that of *Centroptilum* and *Dicosmoecus*. Similar reductions of algal biomass by *Juga* have been observed in stream diversions (Hawkins and Furnish 1987) and in other laboratory channels (Gregory 1983, Sumner and McIntire 1982). Grazing by the caddisfly *Dicosmoecus* immediately reduced algal biomass and pigment to extremely low levels and prevented any accumulation of algal material. Some scraping Trichoptera have been shown to have such a prevailing effect on algal accumulation in other systems as well (Hart 1981, Lamberti and Resh 1983, McAuliffe 1984).

The wide fluctuations in biomass and pigment observed during the asymptotic phase of algal assemblage development in the ungrazed streams did not occur in the streams grazed by *Juga* and *Dicosmoecus*. After day 24, the benthic algal assemblage of the ungrazed streams became senescent, as shown by a rapid increase in the biomass:chlorophyll ratio. Grazing by *Dicosmoecus* and *Juga* dampened these fluctuations during the asymptotic phase of assemblage development and produced relatively stable standing crops of algae throughout the experiment. Algal assemblages in these treatments never became thick mats of algae. In general, the three herbivores produced a gradient in grazing pressure ranging from strong reduction of algal biomass by *Dicosmoecus* to the relatively weak influence of *Centroptilum*.

All three grazers substantially increased the rate of algal export, because the animals mechanically dislodged algae as they moved across the substrate. *Dicosmoecus* larvae, in particular, disrupted algae by vigorously clawing at the algal material with their front tarsi and by dragging their stone cases as they moved. At times in the laboratory streams, periphyton dislodged may exceed that consumed (Lamberti, unpublished data). In natural streams, dislodgement may be an important mechanism by which stream herbivores regulate periphyton communities while generating high-quality food resources for filter-feeding and deposit-collecting organisms. Herbivore-dislodged benthic algae may be important in the bioenergetics of downstream communities, just as phytoplankton released in the outflows of impoundments can determine the production of filter-feeding caddisflies and blackflies below dams (Ward 1984). Untidy feeders such as *Dicosmoecus* may contribute to the pool of algal seston in a manner disproportionate to their abundance.

Biomass-specific export rates declined over time in all of the grazed streams. This may have been due to declining rates of feeding or movement by the animals, or to shifts in algal composition or physiognomy to forms that resisted export. For example, in the *Dicosmoecus* stream, algal physiognomy shifted from large overstory cells and filaments to adnate forms that probably resisted detachment by herbivore activity.

Grazer regulation of periphyton metabolism

Increases in the production per unit biomass (P/B) of periphyton by grazing have been observed frequently in habitats ranging from lake littoral zones (Flint and Goldman 1975) to natural streams (Lamberti and Resh 1983) and laboratory flumes (Gregory 1983). This increase in algal P/B appears to occur over a wide range of grazing pressure (Lamberti and Moore 1984). However, stimulation of gross primary production of periphyton may occur only under relatively low grazing pressure (Cooper 1973, Flint and Goldman 1975, Hargrave 1970). Moderate to high levels of grazing most frequently result in a decline in gross primary production, as has been demonstrated in ponds (Cuker 1983, Seale 1980) and streams (Lamberti and Resh 1983).

Grazing pressure in most streams is sufficient to reduce absolute rates of gross or net primary production, a condition that has been termed "overgrazing" in aquatic systems (Lamberti and Moore 1984) or "undercompensation" in terrestrial habitats (Belsky 1986). Our experiment, however, suggests that some levels of grazing (e.g., that applied by *Juga*) may increase rates of gross and net primary production.

Grazing by both *Dicosmoecus* and *Juga* increased the production per unit biomass of periphyton. However, *Dicosmoecus* substantially reduced gross primary production compared with ungrazed streams. Only the grazing by *Juga* increased gross primary production over that of the ungrazed algal assemblage. Most explanations for production stimulation by grazing center around nutrient renewal by algal cell disruption and excretion by grazers, or reduced competition for those nutrients (Gregory 1983, Lamberti and Resh 1983). Because of high nutrient concentrations in the laboratory streams, it is doubtful that nutrient supply could explain the enhanced production (i.e., nutrients were probably not limiting at any time). More likely in our system, biomass reduction by the grazers increased light levels in the lower strata of the assemblage. If this were accompanied by removal of senescent cells, either by consumption or dislodgement, then increased rates of primary production could result. Further study is needed to identify the precise mechanisms operating in our system.

Grazer regulation of community structure

Several previous studies have shown that the taxonomic structure of periphyton communities can be altered by either grazing caddisflies (e.g., Hart 1981, Lamberti and Resh 1983, McAuliffe 1984) or snails (e.g., Cuker 1983, Gregory 1983, Sumner and McIntire 1982), and may be modified, at least at a local level, by grazing mayflies (e.g., Wiley and Kohler 1981). The herbivores in our study also influenced the taxonomic structure of the algal community. By day 32, there was little similarity in community structure between any pair of treatments except the *Centroptilum* and *Juga* streams.

Taxonomic structure appeared to be related to the type of grazer and the intensity of harvest. For example, at day 48 the algal assemblage grazed by *Dicosmoecus* was dominated by basal cells and short erect filaments of *Stigeoclonium tenue*, resulting in a relatively homogeneous algal monolayer. In contrast, ungrazed assemblages at that time included large amounts of *Scenedesmus* spp. and several diatom species. Apparently, *Dicosmoecus*, a scraper that possesses robust mandibles, could remove most algae except for basal structures of *S. tenue*. *Juga* feeds with an efficient fine-toothed radula that was particularly effective at removing *Synedra ulna*, a large rosette-forming diatom, and *Phormidium tenue*, a cyanophyte whose loose filamentous form may make it susceptible to grazing or dislodgement. Assemblages grazed by *Centroptilum* had lower abundances of some diatoms, but comparable amounts of filaments, as ungrazed assemblages. The delicate, brushlike mouthparts of the mayflies may be more effective at harvesting diatoms than at removing long filaments. In general, assemblages grazed by *Centroptilum* and *Juga* were more heterogeneous in appearance than those grazed by *Dicosmoecus*, possibly reflecting the lower intensity of grazing by the mayflies and snails that allowed uninterrupted development of certain algal patches.

Closing remarks

Our study demonstrated that each type of herbivore can alter periphyton assemblages, though the effects differ and may be detectable only as community-level responses (e.g., biomass, production) in some cases, or species-level responses (e.g., taxonomic shifts) in other cases. Two of the three herbivores (*Dicosmoecus* and *Juga*) substantially modified patterns of algal growth (community-level response), but this degree of influence was not demonstrated by *Centroptilum*. All three herbivores modified taxonomic composition (species-level response) to some degree and increased algal export. Dislodgement of periphyton into export is a potentially important mechanism of algal community modification that has significant implications for the nutrition of downstream consumers in natural streams. Because this study examined only single densities of three types of herbivores, extension of these results to other systems is limited. Further investigation is needed to determine the effects of a range of densities of different types of herbivores on periphyton assemblages. For example, grazing pressure can

then be varied to bracket the response in primary production and to test hypotheses concerning potential stimulation of primary production by stream herbivores.

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