Ecology, 70(6), 1989, pp. 1840–1856

PRODUCTIVE CAPACITY OF PERIPHYTON AS A DETERMINANT OF PLANT–HERBIVORE INTERACTIONS IN STREAMS[1]

GARY A. LAMBERTI,[2] STANLEY V. GREGORY, AND LINDA R. ASHKENAS
Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

ALAN D. STEINMAN[3] AND C. DAVID MCINTIRE
Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. To investigate the influence of plant productivity on plant–herbivore interactions in stream ecosystems, we varied the productive capacity of algal assemblages by exposing periphyton to three levels of irradiance and two levels of grazing. We studied interactions between algal assemblages (grown from algae obtained from four Oregon streams) and herbivorous snails (*Juga silicula*) in 15 laboratory streams containing either 250 snails/m^2 or no snails. Biomass, production, export, and taxonomic structure of the algal community were measured at intervals throughout the 75-d study. Ingestion rate and assimilation efficiency of snails also were measured on six different dates using dual-isotope labeling, and snail growth was measured at the end of the experiment.

Rates of primary production, algal biomass accumulation, and dominance by chlorophytes generally increased with higher irradiance, although these patterns were modified by herbivores. Ungrazed periphyton at low irradiance (photon flux density: 20 μmol·m^{-2}·s^{-1}) accumulated little biomass, which was further reduced by grazing snails. At intermediate (100 μmol·m^{-2}·s^{-1}) and high (400 μmol·m^{-2}·s^{-1}) irradiance, snails delayed the accumulation of algal biomass but did not affect the final biomass attained. After 43 d, net primary production (NPP) at high irradiance was unaffected by grazing, whereas grazing increased NPP at both low and intermediate irradiance. Algal export increased with both irradiance and the presence of grazers and constituted a significant loss of plant biomass from the streams. Grazing by *Juga* delayed algal succession and altered algal taxonomic structure and assemblage physiognomy by reducing the relative abundance of erect and non-attached algae, while increasing the abundance of adnate diatoms.

Snails grew slowly at low irradiance, due to scant food resources, but had high growth rates at intermediate and high irradiance, probably because food was not limiting. Assimilation efficiencies for snails generally varied from 40 to 70% and were highest at low irradiance. At low irradiance, 90% of benthic production was harvested by grazers, whereas only 10% accumulated as attached biomass or was exported. At higher irradiances, <15% of primary production was harvested by grazers, and >85% persisted as attached algae or was exported.

In these stream ecosystems, the biomass and production of grazers were influenced by abiotic constraints placed on algal productive capacity (i.e., the ability of a plant assemblage to generate biomass). The structure and metabolism of algal assemblages were affected, in turn, by consumptive demand of herbivores. The productive capacity of periphyton modified the nature and outcome of plant–herbivore interactions. This capacity therefore has important implications for the operation of stream ecosystems.

Key words: algae; benthos; chlorophyll a; *feeding; grazing; herbivory; ingestion;* Juga; *Oregon; streams; periphyton; primary production.*

INTRODUCTION

Herbivory is an interactive process involving a plant component capable of synthesizing organic matter and a consumer component capable of ingesting that material. The productive capacity of the autotrophic component, i.e., the ability of a plant assemblage to generate biomass, therefore may influence the outcome of this interaction (Crawley 1983). Because streams vary considerably in their capacity to produce plant biomass (Minshall 1978), usually as benthic algae (Whitton 1975), the productivity of algal assemblages establishes the templet for grazer–algal interactions in stream ecosystems. To date, however, there have been few experimental investigations of the influence of algal productivity on plant–herbivore interactions in stream ecosystems (see reviews by Gregory 1983, Lamberti and Moore 1984).

[1] Manuscript received 2 February 1988; revised 1 November 1988; accepted 5 January 1989.

[2] Present address: Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA.

[3] Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831 USA.

In this study, we varied the productive capacity of grazed algal assemblages in 15 laboratory streams by exposing periphyton to three irradiance levels ranging from extreme light limitation of primary production to photosynthetic saturation. We hypothesized that if algal production were regulated by grazing (i.e., consumption equaled or exceeded net primary production), then stimulation of primary production by light would result in increased biomass of herbivores but only slightly greater biomass of primary producers. Alternatively, if net primary production exceeded consumption, then stimulation of primary production by light would be expressed as an increase in biomass of primary producers but not in biomass of herbivores. To test these hypotheses, we determined (1) responses in algal assemblages with differing productive capacities to similar levels of grazing, and (2) bioenergetic responses of the herbivore population to different levels of primary production.

Many previous studies have shown that irradiance (e.g., Lyford and Gregory 1975, Shortreed and Stockner 1983, Steinman and McIntire 1986, 1987) and grazing (e.g., Hunter 1980, Lamberti and Resh 1983, McAuliffe 1984) can influence the structure and dynamics of lotic algal assemblages. Productivity of stream algae also is influenced by factors including nutrient concentration (Elwood et al. 1981, Grimm and Fisher 1986), temperature (Darley 1982), current velocity (Whitford and Schumaker 1961, 1964), substrate composition (Bott 1983), and disturbance (Fisher 1983). In this paper, we demonstrate the importance of the interaction between grazing and irradiance (as a determinant of productive capacity) to algal assemblages and grazer bioenergetics in stream ecosystems.

We used the snail *Juga silicula* (Gould) as the herbivore in the laboratory streams. Previous studies have identified *Juga* as a key herbivore in many streams of the Pacific Northwest (Sumner and McIntire 1982, Gregory 1983, Hawkins and Furnish 1987) and other snail species are important consumers in streams throughout North America (Kehde and Wilhm 1972, Hunter 1980, Elwood et al. 1981, Mulholland et al. 1983). *Juga* densities in coastal Oregon streams usually vary between 100 and 500 snails/m^2 (G. A. Lamberti et al., *personal observation*), although densities as high as 1500 snails/m^2 have been reported (Hawkins and Furnish 1987). At higher densities, *Juga* often is the dominant herbivore, constituting >90% of the total invertebrate biomass (Hawkins and Furnish 1987). *Juga* prefers to feed on periphyton, although it will consume coarse and fine detritus when algae is sparse (Anderson et al. 1978, Hawkins and Sedell 1981).

Methods

Experimental design

The 15 laboratory streams were 3.0 × 0.5 × 0.2 m deep recirculating fiberglass channels with current (10 cm/s) provided by a motor-driven paddlewheel (Lamberti et al. 1987*a*). Each stream was filled to a depth of 10 cm with well water delivered at a rate of 2 L/min so that total stream volume (150 L) was replaced once every 75 min. Water temperature was 13 ± 1°C and nutrient levels in the well water were relatively high (NO_3-N: 6.499 mg/L; NH_3-N: 0.002 mg/L; PO_4-P: 0.096 mg/L; molar N:P = 150:1). The substrate consisted of abutted 7.4 × 7.4 cm unglazed clay tiles on the bottom and 15 × 15 cm tiles along the sides. Total wetted area of each stream, including sides, was 2.0 m^2. Light energy was supplied with 1000-W Metalarc lamps (Sylvania Corp.), which provided a broad spectrum of photosynthetically active radiation. Two lamps were positioned longitudinally over each pair of laboratory streams. The daily photoperiod was set at 10L: 14D.

Grazed streams were stocked with 500 snails (≈10 g tissue dry mass), each of 10–15 mm in shell length, which is equivalent to 250 snails/m^2 or an aggregate consumer tissue dry mass of 5 g/m^2. This density was chosen (1) to apply a moderate level of grazing to algal assemblages, as verified by previous experiments (Lamberti et al. 1987, Steinman et al. 1987*a*), and (2) because it falls within the range of natural snail densities found in coastal Oregon streams. Snail densities were maintained at 250 snails/m^2 throughout the experiment by replacing dead snails daily. Mortality accounted for <5% of the population over the duration of the experiment, and no reproduction by the snails occurred.

Irradiance (photon flux density) was varied by placing different density shade-screen over some of the streams to generate three different light regimes: (1) low irradiance (20 μmol·m^{-2}·s^{-1}), (2) intermediate irradiance (100 μmol·m^{-2}·s^{-1}), and (3) high irradiance (400 μmol·m^{-2}·s^{-1}). These three irradiances represented extreme light limitation, slight light limitation, and light saturation, respectively, for algae in our system (Steinman and McIntire 1987). Fifteen laboratory streams were used in this experiment. Five streams were assigned to each light treatment. Four of the five streams contained 250 snails/m^2. The fifth stream in each set had no snails and served as an ungrazed comparison. One of the four grazed streams was not sampled, but instead was used to generate tiles to replace those removed from the study streams. Replacement tiles were selected based on similarity in algal standing crop and community structure to sampled tiles (judged by macroscopic appearance), thereby maintaining similar abundance and type of food for herbivores. These tiles were marked and not resampled.

All streams were inoculated with a mixture of benthic algae on the first day of the experiment, 3 November 1985. Inoculum was prepared by scraping periphyton from rocks collected from four streams in Benton County, Oregon. The scrapings were homogenized for 30 s in a Waring blender and brought to a volume of

15 L with water; a 1-L aliquot was added to each of the 15 streams. Algae were allowed to become established in the streams in the absence of snails for 11 d. This period was sufficient for obvious establishment of algae (≈2 g/m²), but was prior to the exponential growth phase of algae that could obviate grazer influence on those assemblages. Snails were introduced on day 11, at which time shade-screens also were placed on the streams. The experiment lasted 75 d, which included the inoculation and colonization period (11 d) and the grazing period (64 d).

Sampling strategy and analytical methods

Periphyton.—Algal assemblages were sampled on day 11 just before snails were introduced and at discrete intervals after grazing was initiated. Sampling was more frequent at the beginning of the grazing period to document the rapid changes normally associated with early stages of algal development. Algal biomass and chlorophyll *a* were sampled on days 11, 15, 19, 23, 27, 35, 43, 59, and 75. Algal metabolism was measured on days 11, 19, 27, 43, and 75. Algal export was measured on days 11, 18, 26, 42, and 74 (i.e., prior to benthic disturbance associated with routine sampling). Taxonomic structure was examined on days 19, 43, and 75.

Three tiles were randomly selected from each stream on each sampling date for measurement of algal biomass and chlorophyll *a*. Algae were 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 determination of algal biomass as ash-free dry mass, one filter was dried at 55°C for 24 h, weighed, combusted at 500° for 24 h, and reweighed. For chlorophyll *a* analysis, the second filter was ground and the pigments extracted in buffered 90% acetone for 4 h. The scraped tile was also soaked in 90% acetone for 24 h to extract any residual pigment. Chlorophyll *a* was measured with a spectrophotometer using the trichromatic method (Strickland and Parsons 1968).

Metabolism of the periphytic community was measured using closed plexiglass chambers in which water was recirculated with a submersible pump. Each of the six 2-L chambers held three tiles; two sets of three tiles were sampled for each stream (i.e., two chambers were used per stream). All snails were removed from the tiles prior to the incubations, but periphyton was otherwise undisturbed. Consecutive 2–3 h incubations were conducted in the dark and in the light. During light incubations, shade-screen was suspended over chambers that held tiles from shaded treatments to ensure that irradiance was the same as in the laboratory streams. Nutrient concentrations, current velocity, and temperature in the chambers also were maintained as close as possible to conditions in the laboratory streams. Following each incubation three water samples were drawn from each chamber and dissolved oxygen concentration was measured with an Orbisphere model 2607 oxygen meter (Geneva, Switzerland).

From the incubations, net primary production was measured as the production of oxygen in the light. Community respiration was measured as the consumption of oxygen in the dark. Gross primary production was calculated as the consumption of oxygen in the dark added to the production of oxygen in the light. Net primary production, as measured by changes in dissolved oxygen concentration, represents the amount of primary production by autotrophs in excess of respiration by both the autotrophic and heterotrophic components of the periphyton. Daily net primary production and production/respiration ratio were calculated based on 10 h of gross primary production minus 24 h of community respiration.

Export of particulate organic matter (predominantly algae) from the streams was measured by filtering effluent water from each stream through a 10-μm mesh bag for 30–60 min (60–120 L volume). Export was measured simultaneously for all streams during the light period between 0900–1000 on each sampling date and analysed for ash-free dry mass (AFDM) as described for periphyton samples. Because the streams recirculated water and suspended matter, this short-term measurement integrated the export that occurred over a longer period of time, thus minimizing the effects of diel variation in export on the estimates. Total export from a stream was divided by total stream area (2 m²) to express export on an areal basis.

Taxonomic structure of algal assemblages was determined quantitatively according to the methods of Steinman and McIntire (1986). Algal assemblages were scraped from two tiles from each stream on each sampling date. The pooled sample was 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. An algal unit was defined as an individual cell if the taxon was unicellular, or a filamentous thallus or colony if multicellular. All algae were identified to species in this step except diatoms, which were cleaned, mounted, and identified at 1250× with a Zeiss RA microscope. Biovolume of each taxon was determined from measurements of at least 25 cells using standard geometric formulae.

Herbivores.—Growth rates of herbivores were determined by individually marking 50 snails from each stream (10% of total) with numbered bee tags. Blotted wet mass of each marked snail was measured at day 11, and wet mass and tissue dry mass were determined at day 75. Initial wet mass was converted to tissue dry mass using regression equations generated from final measurements.

Ingestion rates, assimilation rates, and assimilation efficiencies of the snails were measured on days 11, 19, 27, 35, 43, and 75 using the dual-isotope method developed by Calow and Fletcher (1972) and modified at McCullough et al. (1979*a*,*b*). In this method algae

are labeled with both ^{14}C, as an absorbed marker, and ^{51}Cr, as a non-absorbed surface label. Herbivores assimilate ^{14}C as they feed whereas ^{51}Cr passes through the gut unabsorbed. Rate of ^{51}Cr passage yields ingestion rate and proportion of ^{14}C assimilated yields assimilation efficiency. Assimilation rate is the ingestion rate multiplied by the assimilation efficiency. Assumptions inherent in this technique are discussed by Calow and Fletcher (1972), and appropriate corrections were made for both ^{51}Cr decay and ^{51}Cr absorption in the gut.

In our analyses algae on two tiles from each grazed stream were labeled with $^{14}CO_2$ for 12 h in the light within circulating water baths. This period was sufficient for significant incorporation of ^{14}C by the algae, but too short for substantial algal growth (which could have altered algal biomass or composition). Periphyton was then labeled with $^{51}CrCl_3$ for 12 h in the dark by applying a layer of aqueous $^{51}CrCl_3$ to the surface of each tile and then covering the tile with parafilm to ensure even distribution of the isotope. All tiles were then washed free of unbound isotopes and small scrapes of periphyton were taken from each tile to determine specific activity of ^{14}C and ^{51}Cr.

Animals were fed the remaining dual-labeled algae in circulating water baths in the light. Ingestion rate was determined by removing snails at consecutive time intervals (10–120 min) and measuring ^{51}Cr burden until a steady state was reached. Because ^{51}Cr accumulation was generally linear over time until gut filling, ingestion was calculated from the inflection point of the ingestion curve. Two sets of three snails (one set on each tile) were analyzed for each stream on each sampling date. The snails were then placed on unlabeled algae for 24–48 h for elimination of gut contents as fecal pellets. The samples of labeled algal food and snail feces were analyzed separately for ^{51}Cr by gamma spectroscopy and then dried, weighed, oxidized, and analyzed for ^{14}C by liquid scintillation. Ingestion rate was determined as the mass of algae (with known ^{51}Cr specific activity) consumed per unit time (measured as ^{51}Cr in the animal at a given time). Assimilation efficiency (AE), in percent, was determined by comparing the ratio of ^{51}Cr to ^{14}C in the food to that in the feces with the equation (Calow and Fletcher 1972):

$$AE = \left(1 - \frac{(^{51}Cr/^{14}C)_{food}}{(^{51}Cr/^{14}C)_{feces}}\right) \times 100,$$

where radionuclide activity is measured in becquerels ($1\ B_q = 1$ disintegration/s).

Statistical analyses

We examined statistical differences (1) among grazed streams at different irradiances, and (2) between grazed and ungrazed streams at each irradiance. We used one-way ANOVA to examine these differences at four points during the experiment: (1) day 19, shortly after grazer introduction, (2) day 27, during the exponential growth phase of algae at intermediate and high irradiance, (3) day 43, at asymptotic algal accumulation at intermediate and high irradiance, and (4) day 75, at the end of the experiment. These dates were selected to represent distinct phases of periphyton–grazer interaction in our system (Fig. 1A). The Student-Newman-Keuls (SNK) procedure was used for a posteriori contrasts to identify where differences among the grazed streams resided. Log transformations were applied to adjust for non-normality and heteroscedasticity in the data, except for percentages, which were arcsine square-root transformed.

Replicaton of the grazed streams ($n = 3$) at each irradiance level allowed us to attribute differences among grazed systems to the treatment (light). Contrasts were made between grazed and ungrazed streams using within-stream variance, where $n = 6$–9 for grazed streams and $n = 2$–3 for ungrazed streams. However, because the ungrazed streams were not replicated, differences between grazed and ungrazed streams can be detected but cannot be attributed to treatment. However, previous studies in our system of replicated ungrazed streams have indicated that different streams receiving the same light treatment generate very similar algal assemblages for at least 32–48 d (Steinman and McIntire 1986, 1987, Lamberti et al. 1987*a*). For example, coefficients of variation over 32 d for three replicate ungrazed streams ranged from 4–13% for algal biomass, 7–21% for chlorophyll *a*, and 9–17% for gross primary production (Lamberti et al. 1987–*a*).

Similarity in taxonomic composition of algal assemblages in different streams was determined with the SIMI measure of community similarity (matrices of similarity values based on percent biovolume) (McIntire and Moore 1977). The SIMI value can range from 0 to 1.0, where 0 indicates two communities have no species in common, and 1.0 indicates they are identical in both species composition and relative abundance. SIMI values were based on algal biovolume (Steinman and McIntire 1986).

RESULTS

Periphyton abundance

Biomass.—Accumulation of algal biomass increased significantly with irradiance level on most dates (Table 1), reaching the highest levels of 70–80 g/m^2 at high irradiance between 43 and 59 d (Fig. 1A). However, after 59 d biomass at high irradiance declined substantially, and streams at intermediate irradiance supported the highest algal biomass at day 75. At intermediate irradiance, biomass stabilized after 35 d at 20 g/m^2. Low amounts of algal biomass (<5 g/m^2) accumulated at low irradiance, but were increasing gradually at the end of the experiment.

Snails had different effects on algal biomass depending on irradiance. Snails maintained algal biomass at very low levels (<1 g/m^2) at low irradiance, but were less effective in limiting algal accumulation at inter-

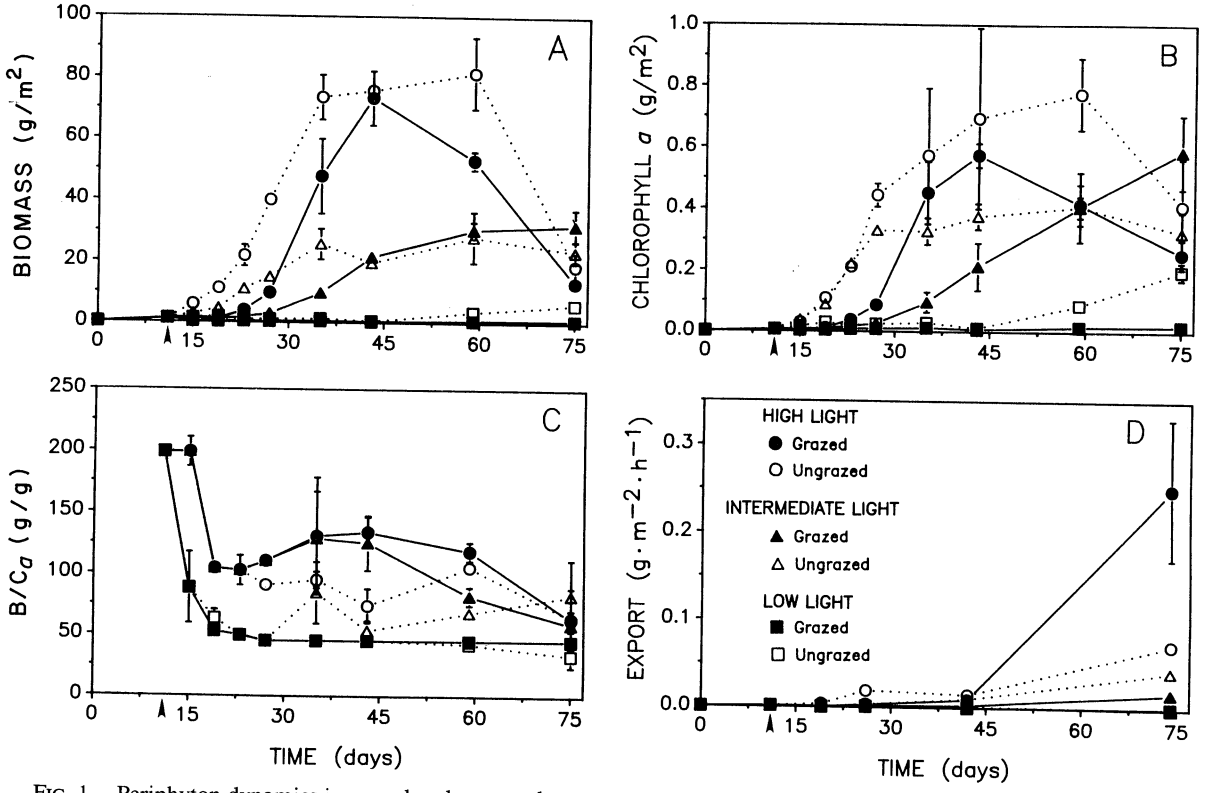

FIG. 1. Periphyton dynamics in grazed and ungrazed streams at three different irradiances (photon flux densities) (Low = 20 μmol·m^{-2}·s^{-1}; Intermediate = 100 μmol·m^{-2}·s^{-1}; High = 400 μmol·m^{-2}·s^{-1}): (A) algal ash-free dry biomass; (B) chlorophyll *a*; (C) mass ratio of ash-free dry biomass (B) to chlorophyll *a* (C_a); (D) export of algal ash-free dry biomass. Values are means ± 1 SE of among-stream variation for grazed streams (n = 3) and within-stream variation for ungrazed streams (n = 3). Arrowhead beneath the horizontal axis indicates date of herbivore introduction and application of shade. Symbol key is provided in part D.

mediate and high irradiance (Fig. 1A). At intermediate irradiance, biomass accumulated more slowly in the grazed streams than in the ungrazed system, but by day 43 there was no difference between grazed and ungrazed streams (Table 1). At high irradiance, biomass was generally 20–30% lower in grazed streams than in the ungrazed stream, except on days 43 and 75 when these differences were not statistically significant (Table 1).

Chlorophyll a.—At low irradiance, abundance of chlorophyll *a* increased slowly in the ungrazed stream but remained low in the grazed streams (Fig. 1B). In the ungrazed stream at intermediate irradiance, abundance of chlorophyll *a* reached an asymptote after only 27 d, whereas it continued to increase in the grazed streams. At high irradiance, amounts of chlorophyll *a* generally increased in grazed and ungrazed systems until 43 and 59 d, respectively, and then declined, though this decline was not as marked as for biomass. Highest chlorophyll *a* values generally were associated with ungrazed streams, but at 75 d, the highest value was observed in grazed streams at intermediate irradiance. Abundance of chlorophyll *a* did not oscillate over time to the extent of algal biomass, which included live, dead, and senescent algal material (Fig. 1A, B). Thus, chlorophyll *a* was a less sensitive indicator of changes in total benthic organic matter than biomass in our system.

Biomass/Chlorophyll a *Ratio.*—Ratios of algal biomass (B) to chlorophyll *a* (C_a) were high (B/C_a = 200) prior to grazer introduction, but then declined rapidly at all irradiances after grazers were introduced on day 11 (Fig. 1C). There was little temporal variation in B/C_a from 19 to 59 d over all treatments. From 59 to 75 d, B/C_a ratios declined at high irradiance, possibly due to sloughing of senescent algal material that had a low chlorophyll content. In general, B/C_a ratios were lowest (B/C_a < 50) at low irradiance and higher at intermediate and high irradiance (B/C_a = 75–125). At all irradiances, grazed streams generally had higher B/C_a ratios than did ungrazed streams (Fig. 1C).

Export.—Organic matter export was minimal at low irradiance (<0.01 g·m^{-2}·h^{-1}), and somewhat higher at intermediate irradiance (0.01–0.05 g·m^{-2}·h^{-1}) (Fig. 1D). At high irradiance, export remained low until day 43 but thereafter increased substantially, especially in the grazed stream. Rates of export at day 75 in high-irradiance, grazed streams (0.24 g·m^{-2}·h^{-1}) were 5–20 times higher than in other streams. This increase in export between 43 and 75 d was associated with a decline in algal abundance (Fig. 1A). Thus, export constituted an important flux in algal dynamics at high

TABLE 1. Results of ANOVA and Student-Newman-Keuls (SNK) tests of periphyton parameters (excluding ratios) on four dates during the 75-d experiment. Untransformed means are presented.

Day	Parameter*	Units	Irradiance† Low G		Low U	Intermediate G		Intermediate U	High G		High U	SNK‡
19	Biomass	g/m²	0.27	★	1.88	0.97	★	4.59	1.16	★	11.27	L I H
	Chl. *a*	g/m²	0.01	★	0.03	0.01	★	0.09	0.01	★	0.11	L I H
	Export	mg/m²	0.20	§	0.64	0.66	§	0.33	0.37	§	3.41	L I H
	GPP	g·m⁻²·h⁻¹	0.00	★	0.03	0.00	§	0.20	0.13	★	0.40	L I H
	CR	g·m⁻²·h⁻¹	0.05		0.04	0.02	§	0.06	0.04	★	0.09	L H I
	NPP	g·m⁻²·d⁻¹	−1.14	★	−0.69	−0.55	§	0.64	0.43	★	1.96	L I H
27	Biomass	g/m²	0.40	★	1.13	2.89	★	14.89	9.75	★	40.02	L I H
	Chl. *a*	g/m²	0.01	★	0.03	0.03	★	0.33	0.09	★	0.44	L I H
	Export	mg/m²	0.81	§	1.13	1.45	§	3.23	3.15	§	17.56	L I H
	GPP	g·m⁻²·h⁻¹	0.08		0.06	0.02	★	0.25	0.34	★	0.65	L I H
	CR	g·m⁻²·h⁻¹	0.09	★	0.00	0.07	★	0.08	0.13		0.10	L I H
	NPP	g·m⁻²·d⁻¹	−1.33	★	0.54	−1.54	★	0.36	0.39	★	4.21	L I H
43	Biomass	g/m²	0.37	★	0.57	21.41		19.52	73.27		75.74	L I H
	Chl. *a*	g/m²	0.01	★	0.02	0.21		0.38	0.58		0.70	L I H
	Export	mg/m²	1.31	§	1.03	2.51	§	9.46	8.80	§	14.06	L I H
	GPP	g·m⁻²·h⁻¹	0.01		0.01	0.27		0.23	0.79		0.86	L I H
	CR	g·m⁻²·h⁻¹	0.01	★	0.03	0.06		0.07	0.11		0.15	L I H
	NPP	g·m⁻²·d⁻¹	−0.25	★	−0.98	1.84	★	0.68	5.20		5.08	L I H
75	Biomass	g/m²	0.85	★	6.13	32.02		23.44	13.25		18.77	L I H
	Chl. *a*	g/m²	0.02	★	0.20	0.59		0.33	0.26		0.41	L I H
	Export	mg/m²	1.16	§	0.10	16.23	§	39.86	238.00	§	68.25	L I H
	GPP	g·m⁻²·h⁻¹	0.02	★	0.10	0.31		0.25	0.32	★	0.48	L I H
	CR	g·m⁻²·h⁻¹	0.03	★	0.09	0.08		0.08	0.07	★	0.13	L I H
	NPP	g·m⁻²·d⁻¹	−0.49	★	−1.06	1.12	★	0.58	1.40		1.63	L I H

* GPP = gross primary production; CR = community respiration; NPP = net primary production.
† Significantly different grazing treatments (ANOVA $P < .05$) at each irradiance are indicated in each irradiance column by a star (★) between grazed (G) and ungrazed (U) means.
‡ Significantly different irradiance treatments (SNK $P < .05$) for *grazed* streams are indicated by different underscores of low (L), intermediate (I), and high (H) irradiance.
§ Insufficient sample size to perform this significance test.

irradiance near the end of the experiment. Periphyton was both sloughed from tiles and dislodged by grazing snails. We observed that snails dislodged algae during their movement and feeding; the large increase in export in grazed streams at high irradiance implicates dislodgement as a major mechanism in algal export.

Benthic metabolism

Gross primary production and community respiration.—Rates of gross primary production (GPP) and community respiration (CR) were related primarily to irradiance and were influenced secondarily by grazing. Both GPP and CR were extremely low ($O_2 < 100$ mg·m^{-2}·h^{-1}) at low irradiance throughout the experiment (Fig. 2A, B). Even long (6–8 h) algal incubations at low irradiance resulted in minimal (<0.2 mg/L) or undetectable changes in oxygen concentrations in the chambers. There were no consistent differences in GPP or CR between grazed and ungrazed streams at low irradiance, although at day 75 GPP and CR were significantly higher in the ungrazed stream (Table 1). At intermediate irradiance, GPP and CR in the ungrazed stream remained relatively constant after 19 d at about O_2 flux rates of 225 and 75 mg·m^{-2}·h^{-1}, respectively. In contrast, GPP and CR in the grazed streams were suppressed by grazing through day 27 but then increased rapidly to O_2 flux rates of about 300 and 75 mg·m^{-2}·h^{-1}, respectively, between 27 and 43 d. At high irradiance, GPP increased through 43 d in both grazed and ungrazed streams but declined from 43 to 75 d. CR also declined after day 43, but to a lesser extent than GPP. GPP and CR generally were lower in grazed streams than in ungrazed streams at high irradiance (Table 1).

Comparison of GPP and CR for all three irradiances indicates that both metabolic rates increased with irradiance (Fig. 2A, B). Differences due to irradiance were maximized at day 43, but declines in GPP and CR at intermediate and high irradiance from 43 to 75 d resulted in greater similarity among treatments at day 75. As with algal biomass, grazing initially delayed increases in GPP and CR, but both measures approached or exceeded those of ungrazed streams by day 43.

Gross primary production (GPP) generally increased

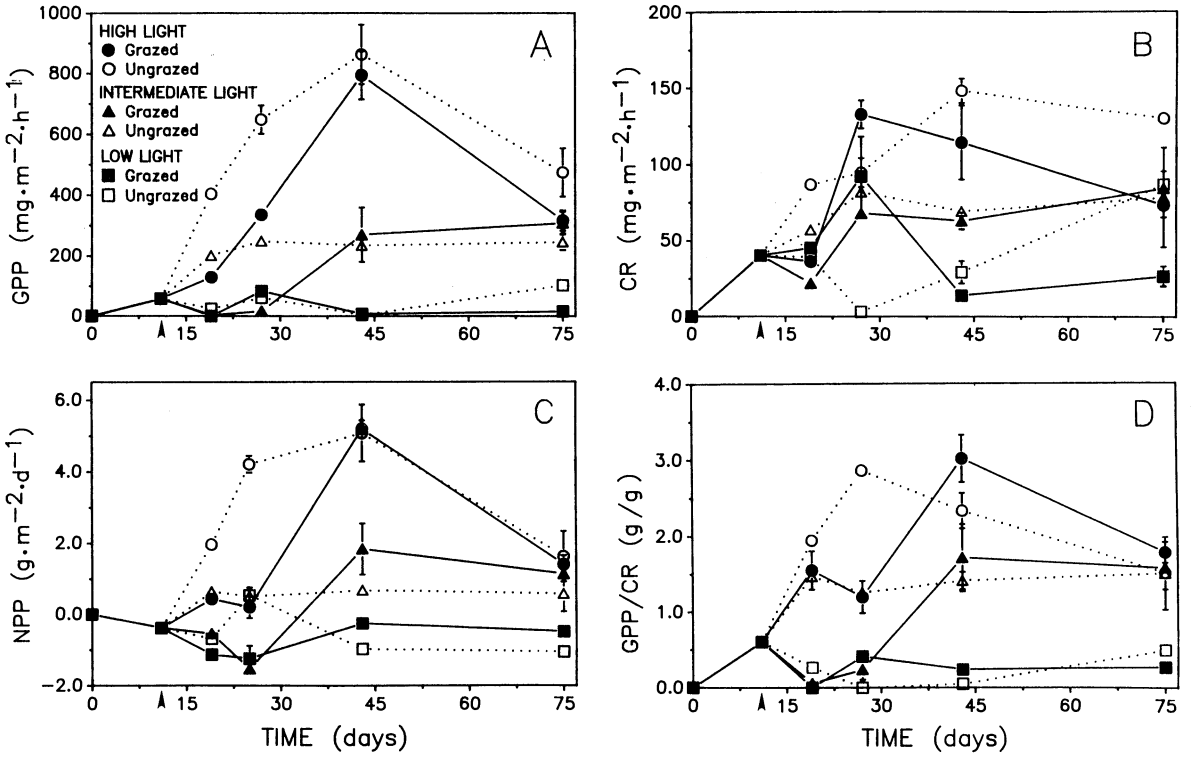

FIG. 2. Production dynamics in grazed and ungrazed streams at three different irradiances (photon flux densities): (A) gross primary production (GPP); (B) community respiration (CR); (C) daily net primary production (NPP), based on 10 h of GPP and 24 h of CR per day; (D) daily production/respiration ratio. All quantities are expressed as O_2 fluxes. At 11 d, all streams were high-irradiance, ungrazed systems; herbivores and shade were applied after day 11 (arrowhead beneath horizontal axis) measurements. Values are means ± 1 SE of among-stream variation for grazed streams (n = 3) and within-stream variation for ungrazed streams (n = 2). Symbol key is provided in Part A.

with algal biomass for all treatments (Fig. 3). However, at low irradiance, there was no significant relationship between GPP and biomass for grazed assemblages because algal biomass was kept within a narrow range by grazing (Fig. 3A). At intermediate irradiance, grazed algae had a broad range of abundances and showed a strong positive relationship between GPP and biomass (Fig. 3B), whereas GPP of ungrazed algae was not significantly related to biomass. At high irradiance, both grazed and ungrazed algae showed a similar positive relationship between GPP and biomass (Fig. 3C). These results indicate that grazing influenced the relationship between GPP and biomass at low and intermediate irradiances by modifying algal abundance, but not at high irradiance where both grazed and ungrazed algae had a broad range of abundance.

Net primary production.—Daily net primary production (NPP, measured as O_2 release) increased with irradiance (Fig. 2C), as also observed for GPP. NPP ranged from -1 g·m^{-2}·d^{-1} at low irradiance to >4 g·m^{-2}·d^{-1} at high irradiance. Negative NPP values at low irradiance indicate that respiration exceeded benthic primary production at low irradiance, whereas production far exceeded respiration at higher irradiances. At both low and intermediate irradiances, NPP in grazed streams was significantly higher than in ungrazed streams at 43 and 75 d (Table 1). At high irradiance, grazing suppressed NPP through day 43, but there was no difference in NPP between grazed and ungrazed streams after day 43.

P/R ratio.—The production/respiration ratio (P/R) was <1.0 for both grazed and ungrazed streams at low irradiance (Fig. 2D). Apparently the combination of very low rates of primary production and respiration by heterotrophs kept P/R at low levels. At intermediate and high irradiance P/R generally ranged from 1.0 to 3.0 and reached the highest levels between 27 and 43 d.

Algal community structure

Algal assemblages at all irradiances were dominated by early colonizing diatoms during the first 19 d of community development. After 19 d, intermediate and high irradiances stimulated the growth of green algae (particularly *Stigeoclonium tenue* and *Scenedesmus obliquus*) in the laboratory streams. Stimulation of chlorophyte production at high irradiance is consistent with the results of other studies conducted in lotic ecosystems (Shortreed and Stockner 1983, Steinman and McIntire 1987). In contrast, assemblages at low irradiance remained dominated by adnate and erect dia-

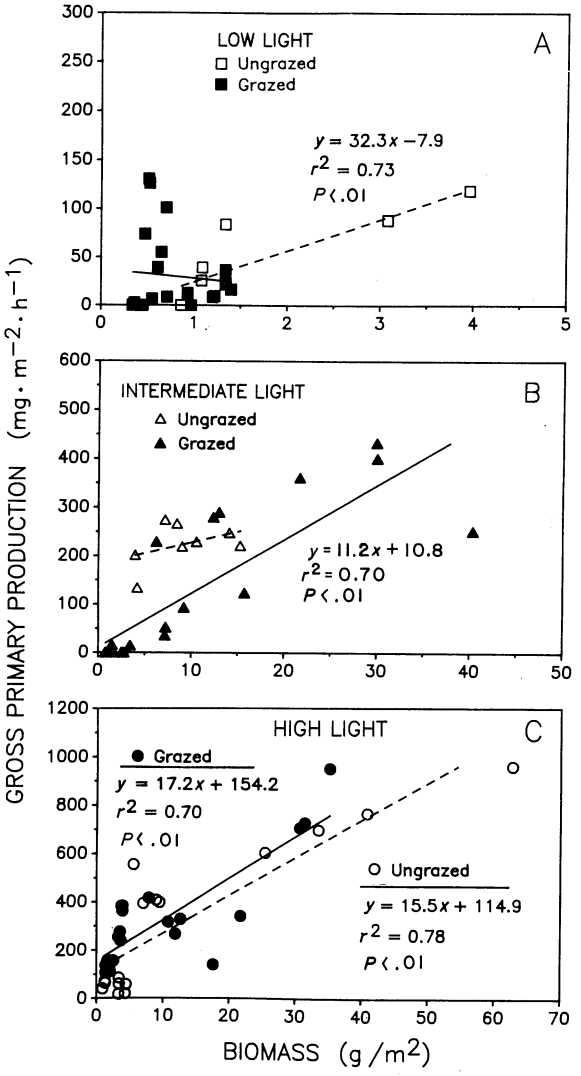

FIG. 3. Relationship between GPP (as O_2 released) and algal ash-free dry biomass in grazed and ungrazed streams at three different irradiances. Simple linear regression lines, significant regression equations (H_0: $b \neq 0$), and significant coefficients of determination (r^2) are presented.

toms after day 19. Grazer-induced changes in algal community structure were greater at low irradiance than at higher irradiances, probably because herbivores harvested a much larger proportion of the total algal biomass at low irradiance than at higher irradiances.

Physiognomy.—Periphyton physiognomy was strongly affected by grazing (Fig. 4). Grazed assemblages were distinguished from ungrazed assemblages by a greater relative abundance of adnate diatoms such as *Cocconeis placentula* and *Achnanthes lanceolata,* filamentous chlorophytes such as *Stigeoclonium tenue,* and prostrate cyanophytes such as *Phormidium tenue.* In contrast, ungrazed assemblages had high relative amounts of non-adnate (erect) diatoms such as *Synedra ulna, Nitzschia linearis,* and *Gomphonema parvulum,* and non-filamentous chlorophytes such as *Scenedesmus obliquus* and *Characium* sp. Filamentous chlorophytes in grazed assemblages were mostly present as basal cells and short, cropped filaments in contrast to long filaments present in ungrazed assemblages.

Taxonomic structure.—The effect of irradiance on community structure varied with time and grazing treatment (Table 2). On day 19, ungrazed algal assemblages at different irradiances all were taxonomically similar (SIMI > 0.8) (block 1 in Table 2). These assemblages then assumed different successional trajectories, as indicated by low taxonomic similarity on day 43 (SIMI < 0.4). By day 75, however, ungrazed assemblages at intermediate and high irradiance converged in taxonomic structure (SIMI = 0.833) whereas assemblages at low irradiance remained taxonomically distinct (SIMI < 0.3).

Grazed assemblages at different irradiances became progressively dissimilar through 43 d (block 2 in Table 2), except for assemblages at low and intermediate irradiances, which were kept similar by grazing (SIMI > 0.9). However, after day 43 assemblages at intermediate light "escaped" grazer influence and most closely resembled high-irradiance assemblages at day 75 (SIMI = 0.887).

Comparison of grazed vs. ungrazed assemblages over time (block 3 in Table 2) shows that grazers initially changed the taxonomic structure of algal assemblages

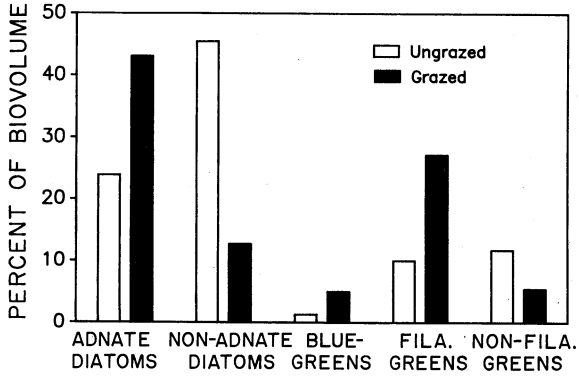

FIG. 4. Relative abundance of dominant algal taxa classified according to growth form under grazed and ungrazed conditions pooled over time and irradiance ($n = 27$ for grazed bars; $n = 9$ for ungrazed bars). Adnate diatoms include *Achnanthes lanceolata, Cocconeis placentula* var. *euglypta,* and *Navicula minima.* Non-adnate diatoms include *Fragilaria vaucheriae, Gomphonema parvulum, Nitzschia lancettula, N. linearis, N. oregona,* and *Synedra ulna.* Cyanophytes (blue-green algae) include *Phormidium uncinatum* and *P. tenue.* Filamentous chlorophytes include *Klebsormidium fluitans, Stigeoclonium tenue,* and *Ulothrix aequalis.* Non-filamentous chlorophytes include *Characium* sp. 1, *Scenedesmus obliquus,* and *Stigeoclonium tenue* basal cells. Filamentous chlorophytes in grazed treatments were generally short (5–20 cells long) and formed thin "lawns," whereas those in ungrazed treatments were much longer (>100 cells) and grew in clumps. These 16 taxa accounted for 93.4% and 92.4% of total community biovolume in the grazed and ungrazed treatments, respectively.

TABLE 2. Matrices of taxonomic similarity values (SIMI) for algal assemblages at 19, 43, and 75 d. SIMI values are based on percent biovolume.* Treatment key: Low = low irradiance, Int = intermediate irradiance, High = high irradiance; G = grazed, U = ungrazed.

Day	Treatment	Treatments					
		Low–G	Int–G	High–G	Low–U	Int–U	High–U
19	Low–G	1.000					
	Int–G	0.961	1.000				
	High–G	0.575	0.643	1.000			
			(2)				
	Low–U	**0.475**	0.302	0.238	1.000		
	Int–U	0.387	**0.276**	0.296	0.931	1.000	
	High–U	0.305	0.189	**0.270**	0.842	0.936	1.000
			(3)			(1)	
43	Low–G	1.000					
	Int–G	0.905	1.000				
	High–G	0.424	0.374	1.000			
			(2)				
	Low–U	**0.871**	0.932	0.132	1.000		
	Int–U	0.156	**0.303**	0.118	0.116	1.000	
	High–U	0.320	0.304	**0.821**	0.254	0.243	1.000
			(3)			(1)	
75	Low–G	1.000					
	Int–G	0.516	1.000				
	High–G	0.509	0.887	1.000			
			(2)				
	Low–U	**0.305**	0.270	0.355	1.000		
	Int–U	0.361	**0.708**	0.732	0.271	1.000	
	High–U	0.296	0.642	**0.812**	0.193	0.833	1.000
			(3)			(1)	

* Different SIMI blocks (numbered in parentheses) at a specific date separate comparisons of (1) ungrazed assemblages at different irradiances, (2) grazed assemblages at different irradiances, and (3) grazed vs. ungrazed assemblages at all irradiances. Boldface SIMI values show comparisons of grazed and ungrazed streams at the same irradiance.

at all irradiances (day 19; SIMI < 0.5). Assemblages at day 43 were in a period of transition, as indicated by SIMI values that ranged from 0.118 to 0.932, and grazers appeared to delay emergence of the distinct trajectories displayed by ungrazed assemblages at day 43. At 75 d, effects of light generally prevailed over grazer effects, as assemblages at intermediate and high irradiance were similar (SIMI > 0.6) regardless of grazer treatment. However, grazers still affected taxonomic structure at low irradiance, as reflected in low similarity of grazed assemblages to all other assemblages (SIMI < 0.4).

Herbivore growth and bioenergetics

Growth.—Snails had similar rates of growth in tissue dry mass at intermediate and high irradiance (Fig. 5A), averaging about 1.4 $mg \cdot g^{-1} \cdot d^{-1}$. However, snails in the stream exposed to low irradiance did not show appreciable gain in mass during the experiment (<0.02 $mg \cdot g^{-1} \cdot d^{-1}$) and some of the snails lost mass during the study period. There was more variation in individual growth for snails at low irradiance than at higher irradiances.

Ingestion.—Ingestion rates were similar for snails at intermediate and high irradiance for much of the experiment, generally varying between 1 and 2 $mg \cdot g^{-1} \cdot h^{-1}$ (Fig. 5B). In contrast, snail ingestion rates at low irradiance were substantially higher (4–8 $mg \cdot g^{-1} \cdot h^{-1}$) than those for snails at the other irradiances, even though growth rates were minimal. These differences were statistically significant on several dates (Table 3). At intermediate and high irradiance, ingestion rates increased gradually between 19 and 43 d (Fig. 5B).

Assimilation.—Assimilation efficiencies were high (70-80%) for snails at all irradiances shortly after the snails were placed in the streams, but declined at all irradiances over the course of the experiment (Fig. 5C). In general, assimilation efficiency was higher for snails at low irradiance than under intermediate or high irradiance (Table 3). At the end of the experiment, assimilation efficiency ranged from 37% at high irradiance to 61% at low irradiance.

Assimilation rates (the product of ingestion rate times assimilation efficiency) were highest for snails at low irradiance, but lower and about equal for snails at high and intermediate irradiance (Fig. 5D; Table 3). Assimilation remained relatively constant at intermediate and high irradiances between 19 and 75 d (Table 3). This occurred because ingestion rates increased over that period while assimilation efficiencies declined.

Mass balance analysis

Ingestion rate and export rate were integrated over the entire experiment for each treatment (ungrazed streams had no ingestion term) and converted to areal

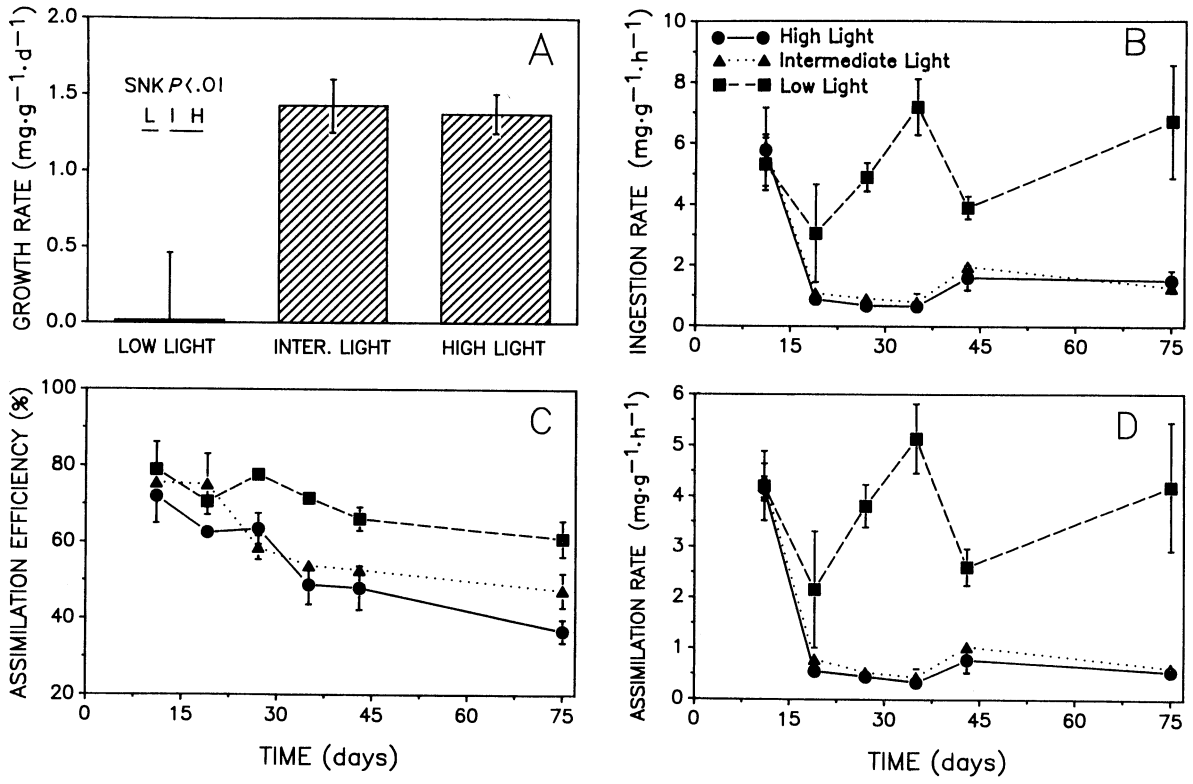

FIG. 5. Bioenergetics of *Juga silicula* snails at three different irradiances: (A) growth rate during the interval 11–75 d, with results of Student-Newman-Keuls (SNK) test; (B) ingestion rate; (C) assimilation efficiency; (D) assimilation rate. All rates are related to tissue dry mass. Values are means ±1 SE for among-stream variation (n = 3). Symbol key for parts B–D is provided in part B.

ash-free dry mass to determine the total amount of algal biomass that was consumed or exported during the 75-d period. These quantities were compared to the mean standing crop of algal biomass present in each treatment on day 75 in order to partition algal biomass into its three principal fates (accumulation, consumption, export) within the stream (Fig. 6). All data were normalized to represent a proportion of total biomass at each irradiance. At low irradiance, herbivores consumed 89% of algal biomass in the grazed streams whereas 76% of algal biomass accumulated in the ungrazed stream; export was a minor portion (7–24%) of the mass balance. Thus, when herbivores were present at low irradiance, the majority of algal biomass was

TABLE 3. Results of Student-Newman-Keuls (SNK) tests of herbivore bioenergetic parameters on four dates during the 75-d experiment. Significantly different irradiance treatments (SNK $P < .05$) are indicated in the right-hand column by different underscores of low (L), intermediate (I), and high (H) irradiance. Non-transformed means are presented.

Day	Parameter	Units	Irradiance			SNK
			Low	Intermediate	High	
19	Ingestion rate	mg·g⁻¹·h⁻¹	3.06	1.08	0.89	L I H
	Assimilation rate	mg·g⁻¹·h⁻¹	2.16	0.78	0.55	L I H
	Assim. efficiency	%	70.6	75.1	62.5	L I H
27	Ingestion rate	mg·g⁻¹·h⁻¹	4.90	0.91	0.69	L I H
	Assimilation rate	mg·g⁻¹·h⁻¹	3.81	0.53	0.45	L I H
	Assim. efficiency	%	77.7	58.5	63.5	L I H
43	Ingestion rate	mg·g⁻¹·h⁻¹	3.91	1.97	1.61	L I H
	Assimilation rate	mg·g⁻¹·h⁻¹	2.61	1.03	0.77	L I H
	Assim. efficiency	%	66.1	52.7	48.0	L I H
75	Ingestion rate	mg·g⁻¹·h⁻¹	6.72	1.29	1.52	L I H
	Assimilation rate	mg·g⁻¹·h⁻¹	4.19	0.62	0.55	L I H
	Assim. efficiency	%	60.9	47.3	36.6	L I H

consumed. At intermediate irradiance, there was about equal accumulation and export of algae in the ungrazed stream. In grazed streams, accumulation accounted for two-thirds of algal biomass, whereas 22% of algal biomass was exported and 13% was consumed. At high irradiance, export dominated the mass balance of both grazed and ungrazed streams, accounting for 72% of the total biomass of ungrazed streams and 84% of algal biomass in grazed streams. Ingestion removed only about 4% of the algal biomass, and 11% and 28% of algal biomass accumulated in grazed and ungrazed streams, respectively.

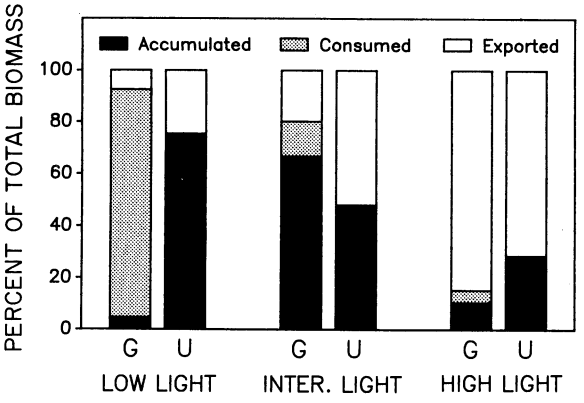

FIG. 6. Primary production partitioned into its three principal fates (accumulation, consumption, export) in grazed (G) and ungrazed (U) streams at three different irradiances during the 75-d experiment. Total algal biomass produced, considering all fates, at low, intermediate, and high irradiance, was 22.0, 48.6, and 154.5 g/m^2, respectively, for grazed streams, and 8.1, 50.0, and 67.6 g/m^2 for ungrazed streams. All quantities were normalized to a percentage of this total biomass. Key: Accumulated = biomass of attached algae at the end of the 75-d experiment; Consumed = biomass of ingested algae integrated over the 75-d period; Exported = biomass of exported algae integrated over the 75-d period.

DISCUSSION

Responses to herbivory

Plants.—The productivity of algal assemblages in the laboratory streams was affected by both irradiance and grazing. Rates of primary production, biomass accumulation, and export increased with irradiance. However, herbivores modified plant productivity by harvesting standing crop and altering community structure. Herbivores had the greatest relative effect on plant assemblages with low productivity. For example, at low irradiance the maximum standing crop of grazed algae was only 14% of that of ungrazed algae, whereas at higher irradiances the biomass of grazed algae exceeded 90% of ungrazed algal biomass. Net primary production increased in response to grazing at low and intermediate irradiance, whereas at high irradiance grazers had no appreciable effect on net primary production. Further, only at low irradiance was community structure of grazed and ungrazed algal assemblages substantially different at the end of the experiment. Grazers both consumed and dislodged algae, with the relative importance of each process being related to the magnitude of algal production. For example, consumption was the predominant process at low primary production, whereas export (some of which was due to dislodgement by grazers) was more important at high production.

All algal assemblages exhibited a period of grazer limitation (i.e., reduction of algal biomass by the herbivores) during the experiment. At low irradiance, this limitation in algal accrual persisted throughout the experiment. At intermediate and high irradiance, limitation was evident until halfway (43 d) through the experiment, at which time grazed assemblages "caught up" with ungrazed communities. Despite this delay in community development, grazed assemblages with higher productivities eventually displayed a structure and standing crop that was similar to ungrazed systems.

At the end of the experiment, algal assemblages at the three irradiance levels exhibited strikingly different rates of biomass accrual. Algae at low irradiance continued to accumulate biomass very slowly because of the overriding influence of severe light limitation. At intermediate irradiance a steady state in standing crop (no net accrual) was approached in 35 d as biomass gains (NPP) were balanced by losses (consumption and export). Grimm and Fisher (1986) observed a similar steady state in nitrogen-enriched periphyton within 21 d. At high irradiance, biomass accumulated rapidly and then plummeted as losses exceeded gains near the end of the experiment. Thus two of the three treatments failed to reach a steady state during the 75-d experimental period. These patterns also resulted in algal standing crops that were more similar over all irradiances at 75 d than earlier in the experiment, which emphasizes the importance of frequent sampling of periphyton. For example, a single measurement of standing crop taken at either 43 or 75 d would have yielded far different results of treatment effects.

The marked decline in biomass seen at high irradiance in this experiment has been reported rarely in previous studies of periphyton (but see McIntire and Phinney 1965, Stockner and Shortreed 1978). At high irradiance, algae deteriorated and sloughed after 43–59 d, as shown in declining biomass and increasing export. During the sloughing process we observed that large patches of thick algae lifted from the tiles (often underlain by gas bubbles), eventually detached, and were transported by the current out of the streams. Apparently senescence and death of algae (especially basal cells) reduced the resistance of the algal mat to shear stress and grazer-induced dislodgement in the laboratory streams. In previous studies in our system, we have observed similar declines in algal biomass after 32 d at high irradiance (Steinman and McIntire 1986, Lamberti et al. 1987*a*). Stockner and Shortreed (1978)

also reported that sloughing occurred after 40 d in streamside channels. Such oscillation is a normal feature in the dynamics of productive algal assemblages, although it may not be revealed in the short-term (<40 d) experiments usually conducted for periphyton. This process may be similar to the collapse of periphyton "blooms" in natural streams that occur in the absence of intervening physical disturbance (e.g., Fisher et al. 1982).

Export was an important facet of periphyton dynamics in the laboratory streams, especially where consumption was a small fraction of total algal production. Grazers increased export at high standing crops of algae because they dislodged deteriorating algae. Algal export clearly can provide a source of inocula for downstream reaches, but also can be an important food resource for primary consumers. Algal detritus transported by currents can be collected and consumed by filter-feeding invertebrates (Benke and Wallace 1980, Wallace and Merritt 1980) or can accumulate in depositional areas of pools and along stream margins, thereby providing a nutritious food resource for detritivores (Lamberti and Moore 1984). Algal dislodgement by mobile grazers may be important in a variety of aquatic ecosystems because of the ease with which moving water can transport consumer-dislodged algae. For example, redistribution of algae dislodged by marine benthic herbivores is important to deposit-feeders in soft-bottom habitats (Lopez and Levinton 1987).

Grazing maintained algal assemblages, at least temporarily, in an early successional stage. Grazed and ungrazed assemblages at low irradiance remained dissimilar throughout the experiment, suggesting that different seral stages were expressed even at 75 d. In contrast, grazed and ungrazed assemblages at intermediate and high irradiances were similar at day 75, suggesting that similar successional stages had been reached. Thus, grazer influence on community structure was greatest at low irradiance, further demonstrating the strong interaction between algal production and herbivore consumptive demand. In general, herbivores appeared to abbreviate algal succession at low irradiance but only to delay succession at higher irradiances. This may be analogous to terrestrial ecosystems, where herbivory has been shown to retard or alter successional seres (Watt 1981, Brown 1985).

Herbivores.—Growth rates of the snails reflected the difference between productive capacity of each algal assemblage and consumptive demand. Snails had very slow growth rates at low algal abundance but rapid growth rates at higher algal abundances. Given these differences, it is surprising that snails at low irradiance had higher ingestion rates than those at higher irradiances. Interactions among behavior, feeding activity, and metabolism of the snails may account for this apparent contradiction.

Most snails at intermediate and high irradiance foraged for only short periods interspersed among much longer periods of inactivity, as indicated by both day and night observations (J. Li, *unpublished data*). Inactive snails were either completely withdrawn into their shells or passively attached to the substrate with their mouthparts retracted. In contrast, snails at low irradiance foraged almost continuously and had higher movement rates ($\bar{X} \pm$ SE, 0.40 ± 0.09 cm/min; $n = 9$), and therefore potentially higher metabolic costs, than foraging snails at intermediate irradiance (0.18 ± 0.03 cm/min; $n = 9$) (J. Li, *unpublished data*). Snails also left behind a mucous trail as they moved, an additional loss of organic material. Previous studies have shown that up to one-third of the total energy budget for freshwater snails may be expended in mucous production (Calow 1974). Thus, although snails at low irradiance had high ingestion rates, respiratory and other metabolic costs associated with foraging may be responsible for the low growth rates.

It is also possible that duration of the isotope feeding studies contributed to apparent low ingestion values for snails at intermediate and high irradiance. Our short-term (<2 h) feeding studies may have reflected satiation level more than long-term consumption patterns. For example, if ingestion rates of satiated snails were measured during a period of relative inactivity (a likely case at intermediate or high irradiance), then overall ingestion rates might be underestimated. Nonetheless, ingestion and growth rates were clearly related to algal productive capacity, with food limitation occurring at low irradiance but not at higher irradiances.

Initial assimilation efficiences of 70–80% for snails were higher than those reported in previous studies of algal assimilation by benthic invertebrates, which generally range from 30–60% (see review by Pandian and Marian 1986). However, at the end of the experiment, efficiencies had declined to about 40–60%. This decline in efficiency corresponded to an increase in ingestion rates at higher algal abundances, which resulted in relatively constant assimilation rates. Thus the herbivores may have compensated for declining assimilation efficiencies by increasing their ingestion rates.

The decline in assimilation efficiency may reflect changes in the community structure and physiological condition of the algal assemblages. Early algal assemblages were composed mostly of diatoms and unicellular green algae whereas late communities were dominated by senescent filamentous green and blue-green algae. Differences in biochemical and structural properties of these taxa, as well as changes in algal physiological condition, may have been responsible for declining assimilation efficiencies. For example, senescent filamentous algae may be less nutritious to grazers than vigorously growing diatoms (Lamberti and Moore 1984, Steinman et al. 1987*b*). In general, the implications of changing food composition to herbivore bioenergetics are poorly understood, yet remain a cornerstone of trophic relationships in stream ecosystems. Further study in this area is greatly needed.

Fates of algal production.—The mass balance analysis of algal biomass revealed that different processes were dominant at different algal productive capacities. Consumption declined in importance with increasing productive capacity; >90% of algal biomass was consumed at low irradiance compared to <5% consumed at high irradiance. In contrast, export increased greatly with increasing algal abundance, accounting for the fate of >80% of algal biomass at high irradiance compared to <10% at low irradiance. Relative to the other processes, accumulation of algal biomass was the dominant fate of algae only at intermediate irradiance. These results highlight the fact that standing biomass of periphyton may represent only a small fraction of total plant production in streams (Gregory 1983). Our experiment demonstrated that other processes, such as ingestion and export, may account for the fate of a large proportion of algal production.

Assessment of study hypotheses.—We postulated that stimulation of less productive algal assemblages, relative to consumption, would be manifested in higher biomass of consumers rather than in increased biomass of plants. In our experiment, stimulation provided by a shift from low to intermediate irradiance (20 to 100 μmol·m^{-2}·s^{-1}) resulted in a significant increase in both consumer growth rates and algal biomass. This degree of stimulation was sufficient to raise productive capacity in excess of consumptive demand. Thus, increased algal production was expressed as both herbivore and plant biomass.

We also postulated that stimulation of more productive algal assemblages, relative to consumption, would be expressed as higher biomass of plants rather than as increased biomass of herbivores. As hypothesized, stimulation resulting from a shift from intermediate to high irradiance (100 to 400 μmol·m^{-2}·s^{-1}) produced greater biomass of plants but did not change herbivore growth. Consumptive demand of the herbivores was met by the production level at intermediate irradiance and further increases in productive capacity were expressed as additional plant growth or export of plant biomass.

Significance to stream ecology

Productive capacity of benthic algae in natural streams often is limited by the quantity and quality of solar radiation. Light limitation of primary production is common in small streams where dense canopies of riparian vegetation intercept much of the light energy before it reaches the streambed (e.g., Fisher and Likens 1972, Gregory 1980, Minshall et al. 1983). This condition is similar to the low-irradiance treatment in our laboratory experiment. However, under the more open canopies of larger streams, higher light levels can saturate the photosynthetic rates of aquatic primary producers. This condition was simulated by the high-irradiance treatment in the laboratory streams. Our intermediate irradiance level was designed to simulate partial shading by riparian vegetation.

Differences in irradiance may affect algal productive capacity considerably. A number of descriptive studies of open and shaded stream reaches have reported higher amounts of primary and secondary production in open reaches. Increased primary production associated with light-saturated reaches results in increased densities and biomass both of total invertebrates (Minshall 1978, Newbold et al. 1980) and of herbivorous macroinvertebrates (Burky 1971, Durrant 1977, Hawkins and Sedell 1981, Towns 1981, Hawkins et al. 1982). In addition, herbivores in open reaches grow faster than those in shaded reaches (McMahon et al. 1974, Cummins 1975, McMahon 1975, Fuller et al. 1986). The results of our laboratory experiment suggest, as do these field studies, that the productive capacity of autotrophs is a major determinant of the distribution and production of consumers in stream ecosystems.

As hypothesized in our experiment, changes in the productive capacity of streams may be expressed as biomass of herbivores rather than as algal biomass. For example, because of high algal turnover rates, streams may have a small amount of algae but high herbivore biomass (Douglas 1958, Elwood and Nelson 1972, Lamberti and Resh 1983, McAuliffe 1983), resulting in an "inverted trophic pyramid" (Gregory 1983, Lamberti and Moore 1984). Computer simulation of the herbivory process by McIntire (1973) has shown that a small amount of benthic algae, with a high turnover rate, could support a biomass of grazers twenty times greater than its own. In our experiment, the biomass of herbivores at low irradiance (5 g/m^2) was 7 times greater than the average biomass of algae (0.7 g/m^2). This biomass was sufficient to sustain the herbivores, although growth rates were low. Other laboratory studies have confirmed that algal assemblages can support 10 to 20 times their own mass in herbivores (McIntire 1975, Gregory 1980). However, when consumptive demand greatly exceeds productive capacity, grazers may compete for limited food resources (Hart 1987, Lamberti et al. 1987*b*).

In streams with high productive capacity, herbivores may have little apparent effect on algal assemblages (Collins et al. 1976, Stockner and Shortreed 1976), as occurred at high irradiance in our experiment. These conditions are met when algal assemblages grow rapidly ("bloom") in favorable environments, thereby developing sufficient biomass to escape regulation by herbivores. However, such "windows" may close rapidly as herbivores respond numerically (e.g., via reproduction or immigration) or functionally (e.g., via increased consumption) to abundant periphyton, or as physical factors such as floods reset algal assemblages to low levels (Fisher et al. 1982). In the laboratory streams, reproduction by *Juga* snails did not occur during the 75-d experiment, because *Juga* reproduces only in the spring. However, given an experiment long enough to

encompass the reproductive period of *Juga,* recruitment to the snail population may be sufficient to limit algal biomass even at high irradiance.

Ecosystem implications

Production and grazing.—The productive capacity of plant assemblages provides the context for viewing the process of herbivory. Productive capacity determines the relative contribution of primary production to consumer growth or to additional plant biomass. In stream ecosystems with low productive capacity, even a low density of herbivores may limit the biomass and production of algal assemblages, although the herbivores themselves may be food limited. At high rates of algal production, grazers may have little effect on periphyton because their nutritional demands are met by a small portion of the production. As demonstrated in our experiment and in other lotic studies, herbivore growth and biomass may be linked directly to productive capacity.

In contrast to other ecosystems, the proportion of the total plant assemblage consumed by grazers often is high (>50%) in streams (Wiegert and Owen 1971). For example, in the laboratory streams, snails consumed almost 90% of the plant biomass at low irradiance. In terrestrial (e.g., forests, grasslands) and coastal marine (e.g., salt marshes, rocky intertidal zones) ecosystems, herbivores generally consume a small fraction (<30%) of the total plant biomass but may be limited by the nutritional quality of plants (Murdoch 1966, Janzen 1970, Lopez and Levinton 1987) or the susceptibility of plants to grazing (Sinclair 1975, Levin 1976, Lubchenco and Gaines 1981, Steinberg 1985). In planktonic systems, plant biomass also generally exceeds that of consumers, although periods of heavy grazing may temporarily change these conditions (Porter 1977, Raymont 1980). Although the linkage between productive capacity and consumptive demand exists in all ecosystems, streams appear to be unique in the large proportion of plant production consumed by herbivores (Gregory 1983, Lamberti and Moore 1984).

Studies of lotic herbivory rarely consider the influence of plant productivity on observed patterns of both plants and herbivores, even though the linkages between production and consumption are recognized in most ecosystems. For example, in terrestrial ecosystems, fertilization of pastures to increase grass production is a standard practice to improve growth rates of livestock (Crawley 1983). Complexity of trophic structure in unmanaged terrestrial ecosystems has been related to the capacity for plant production (Oksanen et al. 1981). In marine ecosystems, natural nutrient infusion (upwelling or river discharge) to nearshore areas may be expressed as increases in both phytoplankton and phytoplanktivorous infauna (Dayton and Oliver 1977). Experimental fertilization of salt marshes (Valiela et al. 1975) or unshaded streams (Perrin et al. 1987) leads to changes in plant composition and production that are expressed at several trophic levels. In the laboratory streams, stimulation of primary production by light was reflected clearly in increased herbivore growth and plant biomass.

Grazer stimulation of primary production.—Enhancement of primary production by grazing has been the subject of considerable debate in ecology (e.g., McNaughton 1979, 1986, Belsky 1986, 1987, Paige and Whitham 1987). The fundamental question is whether consumption of plants or their parts can increase the overall productivity of a plant assemblage. In freshwater ecosystems, stimulation of primary production by grazing has been demonstrated occasionally in lake littoral zones (Flint and Goldman 1975), ponds (Osborne and McLachlan 1985), and microcosms (Cooper 1973, McDonald 1985). Lamberti et al. (1987*a*) observed slight stimulation of GPP by grazing snails in laboratory streams. The current experiment demonstrated that NPP was slightly greater in grazed streams at low and intermediate irradiance but not at high irradiance. In many cases, however, lotic grazing results in younger algal assemblages with higher *biomass-specific* rates of primary production but not necessarily greater GPP or NPP (e.g., Gregory 1983, Lamberti and Resh 1983).

In streams the potential for enhancement of primary production by grazing is greater than in ecosystems with long-lived plants because of rapid turnover rates (hours to days) of algae. Thus, losses of algae to grazing are partially compensated by rapid algal growth. At high rates of consumption, productivity of periphyton most often declines because of greatly reduced algal abundance (Lamberti and Moore 1984). However, algal assemblages that have only a small portion of their biomass harvested may become more productive if they are "thinned" of less productive plants (cells) that only shade or otherwise inhibit photosynthesis by viable plants. Recent studies of marine sediment (Connor et al. 1982) and coral reef (Carpenter 1986) communities also suggest that low levels of grazing stimulate production of microalgae, though not necessarily that of macroalgae. Thus, low rates of grazing relative to productive capacity may stimulate primary production due to (1) removal of dead or senescent algal cells by consumption or dislodgement, (2) shifts in assemblage composition to more photosynthetically active species (e.g., diatoms), (3) increased light penetration and nutrient diffusion to lower plant strata because grazers create gaps in the algal matrix, and (4) nutrient renewal by grazer waste products. In our experiment, we observed slight stimulation of NPP by grazing but no stimulation of GPP. This occurred because respiration rates declined in grazed assemblages, which would result if unproductive (but respiring) cells were removed by grazing (1, above). Grazed algal assemblages also had higher proportions of adnate diatoms, which may increase assemblage productivity (2, above). We could

not test reasons 3 and 4 in our system because nutrient concentrations were high, but both potentially contribute to enhanced NPP of grazed algal assemblages.

The herbivory process in stream ecosystems is shaped by the array of environmental factors influencing both plants and herbivores. The productive capacity of the system can modify the degree of interaction between plants and herbivores, which may be intense at low capacities but relatively benign at high capacities. Consideration of productive capacity in the evaluation of lotic processes is essential to improve our understanding of the organization and operation of stream ecosystems.

ACKNOWLEDGMENTS

We thank Judy Li, Dale McCullough, Kelly Moore, and Randy Wildman for their assistance in various phases of this research. Craig McFarlane and Carlos Wickliff (USEPA), Mike Conrady (OSU), and Carl Schreck (OCFRU) kindly provided access to isotope-counting instruments. Comments by Stuart Fisher and two anonymous reviewers improved an earlier version of this paper. This study was supported by research grants BSR-8318386 and BSR-8508356 from the National Science Foundation. This is Technical Paper 8882 of the Agricultural Experiment Station of Oregon State University.

LITERATURE CITED

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist **100**:64–82.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. American Naturalist **127**:870–892.

———. 1987. The effects of grazing: confounding of ecosystem, community, and organism scales. American Naturalist **129**:777–783.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology **61**:108–118.

Bott, T. L. 1983. Primary productivity in streams. Pages 29–53 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum, New York, New York, USA.

Brown, V. K. 1985. Insect herbivores and plant succession. Oikos **44**:17–22.

Burky, A. J. 1971. Biomass turnover, respiration, and interpopulation variation in the stream limpet *Ferrissia rivularis* (Say). Ecological Monographs **41**:235–251.

Calow, P. 1974. Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods, *Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn. Oecologia (Berlin) **16**:149–161.

Calow, P., and C. R. Fletcher. 1972. A new radiotracer technique involving ^{14}C and ^{51}Cr, for estimating the assimilation efficiencies of aquatic, primary consumers. Oecologia (Berlin) **9**:155–170.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs **56**:345–363.

Collins, N. C., R. Mitchell, and R. G. Wiegert. 1976. Functional analysis of a thermal spring ecosystem, with an evaluation of the role of consumers. Ecology **57**:1221–1232.

Connor, M. S., J. M. Teal, and I. Valiela. 1982. The effect of feeding by mud snails, *Ilyanassa obsoleta* (Say), on the structure and metabolism of a laboratory benthic algal community. Journal of Experimental Marine Biology and Ecology **65**:29–45.

Cooper, D. C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. Limnology and Oceanography **18**:31–37.

Crawley, M. J. 1983. Herbivory. The dynamics of animal–plant interactions. University of California Press, Berkeley, California, USA.

Cummins, K. W. 1975. Macroinvertebrates. Pages 170–198 *in* B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California, USA.

Darley, W. M. 1982. Algal biology: a physiological approach. Blackwell Scientific, Oxford, England.

Dayton, P. K., and J. S. Oliver. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. Science **197**:55–58.

Douglas, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. Journal of Ecology **46**: 295–322.

Durrant, P. M. 1977. Some factors that affect the distribution of *Ancylus fluviatilus* (Muller) in the river systems of Great Britain. Journal of Molluscan Studies **43**:67–78.

Elwood, J. W., and D. J. Nelson. 1972. Periphyton production and grazing rates in a stream measured with a ^{32}P material balance method. Oikos **23**:295–303.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology **62**:146–158.

Fisher, S. G. 1983. Succession in streams. Pages 7–27 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum, New York, New York, USA.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs **52**:93–110.

Fisher, S. G., and G. E. Likens. 1972. Stream ecosystem: organic energy budget. BioScience **22**:33–35.

Flint, R. W., and C. R. Goldman. 1975. The effects of a benthic grazer on the primary productivity of the littoral zone of Lake Tahoe. Limnology and Oceanography **20**: 935–944.

Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. Journal of the North American Benthological Society **5**:290–296.

Gregory, S. V. 1980. Effects of light, nutrients, and grazing on periphyton communties in streams. Dissertation. Oregon State University, Corvallis, Oregon, USA.

———. 1983. Plant–herbivore interactions in stream systems. Pages 157–189 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum, New York, New York, USA.

Grimm, N. B., and S. G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society **5**:2–15.

Hart, D. D. 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia (Berlin) **73**: 41–47.

Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos **49**:209–220.

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology **63**:1840–1856.

Hawkins, C. P., and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology **62**:387–397.

Hunter, R. D. 1980. Effects of grazing on the quantity and quality of freshwater aufwuchs. Hydrobiologia **69**:251–259.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist **104**:501–528.

Kehde, P. M., and J. L. Wilhm. 1972. The effects of grazing by snails on community structure of periphyton in laboratory streams. American Midland Naturalist **87**:8–24.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987*a*. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society **6**:92–104.

Lamberti, G. A., J. W. Feminella, and V. H. Resh. 1987*b*. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia (Berlin) **73**:75–81.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers. Pages 164–195 *in* V. H. Resh and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York, USA.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology **64**:1124–1135.

Levin, D. A. 1976. The chemical defenses of plants to pathogens and herbivores. Annual Review of Ecology and Systematics **7**:121–159.

Lopez, G. R., and J. S. Levinton. 1987. Ecology of deposit-feeding animals in marine sediments. Quarterly Review of Biology **62**:235–260.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics **12**:405–437.

Lyford, J. H., and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **19**: 1610–1616.

McAuliffe, J. R. 1983. Competition, colonization patterns, and disturbance in stream benthic communities. Pages 137–156 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum, New York, New York, USA.

———. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos **42**:327–333.

McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979*a*. Bioenergetics of a stream "collector" organism, *Trichorythodes minutus* (Insecta: Ephemeroptera). Limnology and Oceanography **24**:45–58.

McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979*b*. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. Ecology **60**:585–596.

McDonald, M. E. 1985. Growth of a grazing phytoplanktivorous fish and growth enhancement of the grazed alga. Oecologia (Berlin) **67**:132–136.

McIntire, C. D. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. Ecological Monographs **43**:399–420.

———. 1975. Periphyton assemblages in laboratory streams. Pages 403–430 *in* B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California, USA.

McIntire, C. D., and W. W. Moore. 1977. Marine littoral diatoms: ecological considerations. Pages 333–371 *in* D. Werner, editor. The biology of diatoms. University of California Press, Berkeley, California, USA.

McIntire, C. D., and H. K. Phinney. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecological Monographs **35**:237–258.

McMahon, R. F. 1975. Growth, reproduction and bioenergetic variation in three natural populations of a freshwater limpet *Laevapex fuscus* (C.B. Adams). Proceedings of the Malacological Society of London **41**:331–351.

McMahon, R. F., R. D. Hunter, and W. D. Russell-Hunter. 1974. Variation in aufwuchs at six freshwater habitats in terms of carbon biomass and carbon:nitrogen ratio. Hydrobiologia **45**:391–404.

McNaughton, S. J. 1979. Grazing as an optimization process: grass–ungulate relationships in the Serengeti. American Naturalist **113**:691–703.

———. 1986. On plants and herbivores. American Naturalist **128**:765–770.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. BioScience **28**:767–771.

Minshall, G. W., R. C. Peterson, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs **53**:1–25.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, and C. L. Hom. 1983. The effect of grazing intensity on phosphorous spiralling in autotrophic streams. Oecologia (Berlin) **58**:358–366.

Murdoch, W. W. 1966. Community structure, population control, and competition—a critique. American Naturalist **100**:219–226.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences **37**:1076–1085.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemala. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Osborne, P. L., and A. J. McLachlan. 1985. The effects of tadpoles on algal growth in temporary, rain-filled rock pools. Freshwater Biology **15**:77–87.

Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. American Naturalist **129**:407–416.

Pandian, T. J., and M. P. Marian. 1986. An indirect procedure for the estimation of assimilation efficiency of aquatic insects. Freshwater Biology **16**:93–98.

Perrin, C. J., M. L. Bothwell, and P. A. Slaney. 1987. Experimental enrichment of a coastal stream in British Columbia: effects of organic and inorganic additions on autotrophic periphyton production. Canadian Journal of Fisheries and Aquatic Sciences **44**:1247–1256.

Porter, K. G. 1977. The plant–animal interface in freshwater ecosystems. American Scientist **65**:159–170.

Raymont, J. E. G. 1980. Plankton and productivity in the oceans. Second edition. I. Phytoplankton. Pergamon, Oxford, England.

Shortreed, K. S., and J. G. Stockner. 1983. Periphyton biomass and species composition in a coastal rainforest stream in British Columbia: effects of environmental changes caused by logging. Canadian Journal of Fisheries and Aquatic Sciences **40**:1887–1895.

Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. Journal of Animal Ecology **44**:497–520.

Steinberg, P. D. 1985. Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. Ecological Monographs **55**:333–349.

Steinman, A. D., and C. D. McIntire. 1986. Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. Journal of Phycology **22**:352–361.

Steinman, A. D., and C. D. McIntire. 1987. Effects of irradiance on the community structure and biomass of algal assemblages in laboratory streams. Canadian Journal of Fisheries and Aquatic Sciences **44**:1640–1648.

Steinman, A. D., C. D. McIntire, S. V. Gregory, G. A. Lamberti, and L. R. Ashkenas. 1987*a*. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. Journal of the North American Benthological Society **6**:175–188.

Steinman, A. D., C. D. McIntire, and R. R. Lowry. 1987*b*. Effects of herbivore type and density on chemical composition of algal assemblages in laboratory streams. Journal of the North American Benthological Society **6**:189–197.

Stockner, J. G., and K. R. S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. Journal of the Fisheries Research Board of Canada **33**:1553–1563.

Stockner, J. G., and K. R. S. Shortreed. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. Journal of the Fisheries Research Board of Canada **35**:28–34.

Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Sumner, W. T., and C. D. McIntire. 1982. Grazer–periphyton interactions in laboratory streams. Archiv für Hydrobiologie **93**:135–157.

Towns, D. R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. New Zealand Journal of Marine and Freshwater Research **15**:185–192.

Valiela, I., J. M. Teal, and W. J. Sass. 1975. Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge. Biomass, production and species composition. Journal of Applied Ecology **12**:973–982.

Wallace, J. B., and R. W. Merritt. 1980. Filter-feeding ecology of aquatic insects. Annual Review of Entomology **25**: 103–132.

Watt, A. S. 1981. A comparison of grazed and ungrazed grassland A in East Anglian Breckland. Journal of Ecology **69**:499–508.

Whitford, L. A., and G. J. Schumacher. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnology and Oceanography **6**:423–425.

Whitford, L. A., and G. J. Schumacher. 1964. Effects of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology **45**:168–170.

Whitton, B. A. 1975. Algae. Pages 81–105 *in* B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California, USA.

Wiegert, R. G., and D. F. Owen. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. Journal of Theoretical Biology **30**:69–81.