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Author(s): Patrick J. Mulholland, Alan D. Steinman, Anthony V. Palumbo, Donald L. DeAngelis and Terry E. Flum

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Influence of nutrients and grazing on the response of stream periphyton communities to a scour disturbance

PATRICK J. MULHOLLAND, ALAN D. STEINMAN,
ANTHONY V. PALUMBO, AND DONALD L. DEANGELIS

*Environmental Sciences Division, Oak Ridge National Laboratory,
Oak Ridge, Tennessee 37831-6036 USA*

TERRY E. FLUM

*Department of Biology, University of Tennessee,
Knoxville, Tennessee 37996 USA*

Abstract. We examined the effect of nutrient input and grazing intensity on resistance and resilience of periphyton communities in laboratory streams to a scour disturbance. Previous theoretical studies using stream models indicated that resilience of nutrient-limited streams, as defined by the return time to the initial state, is strongly related to the residence time of nutrients in the system and to the presence of herbivores. To experimentally test this prediction we established two levels of nutrient input by altering the flow regime (once-through flow and 98% recirculated flow) and two levels of grazing intensity by the presence or absence of the snail *Elimia clavaeformis*, resulting in a 2×2 factorial design with two replicate streams per treatment. After the streams reached an approximately stable level of periphyton biomass, a scour disturbance was imposed on all streams. Measures of the resistance and resilience of the periphyton to this disturbance were made.

The resistance of most structural characteristics of the periphyton was significantly higher in streams with snails than in streams without snails. Nutrient input had little effect on resistance of all periphyton characteristics. Resilience was measured by two parameters: rate of increase of a particular characteristic over time following the disturbance (r), and time to return to the pre-disturbance state (T_r). The experimental results on resilience were complex. In general, high grazing intensity resulted in low values of r for most periphyton characteristics, but also shorter T_r for some characteristics. The shorter T_r values were attributed to lower pre-disturbance biomass and metabolism in the streams with snails compensating for lower r for these characteristics following the disturbance. Contrary to model predictions, low nutrient input generally did not result in low resilience for most characteristics in the streams without snails, probably because increased nutrient recycling compensated for low inputs. However, for the streams with snails, resilience of most periphyton characteristics was lower in streams with low nutrient input compared with streams with higher nutrient input. This contrast in resilience suggests a positive feedback between biomass accrual and nutrient recycling that helps maintain high productivity despite low nutrient inputs during recovery of stream periphyton communities from disturbance.

Key words: streams, disturbance, stability, resistance, resilience, herbivory, scour, periphyton, snails.

The effect of disturbance on ecosystem structure and function continues to be an important topic for research in ecology. Studies of disturbance effects on stream ecosystems have been particularly prominent because (1) streams are subjected to a variety of natural disturbances (e.g., spates, droughts) and anthropogenic impacts (e.g., effluents, watershed disturbances), and (2) streams are manageable for study (small systems, usually distinct boundaries).

The response of streams to disturbance can be defined and measured in terms of their re-

sistance and resilience (Webster et al. 1975). Resistance is the ability to maintain structure and function similar to the pre-disturbance state. Resilience is the ability of the system to recover to its pre-disturbance state. Although resistance and resilience are closely related to the type and magnitude (duration, extent) of the disturbance, specific ecosystem characteristics may also define the resistance and resilience properties of different ecosystems. Ecosystem resistance is thought to be related to a large pool of biomass (living or dead) that turns over very slowly and

damps or buffers exogenous changes, whereas resilience is thought to be related to rapid growth and turnover of ecosystem components (O'Neill et al. 1975, Webster et al. 1975, O'Neill 1976). Webster et al. (1975, 1983) have suggested that streams tend to have low resistance because of their dependence on allochthonous inputs and low biomass storage, but generally have high resilience because of high rates of inputs and turnover.

Most studies of disturbance in streams have focused on resilience or rate of recovery after the disturbance has ceased. Stream recovery rates have been related to the proximity of refugia (Sedell et al. 1990), spatial-temporal heterogeneity of physical and biological structure (Poff and Ward 1990, Reice et al. 1990), previous disturbance history (Kaufman 1982, Reice et al. 1990), processes regulating secondary succession (Fisher 1990), nutrient inputs (DeAngelis et al. 1990), and, in the case of watershed disturbances, the rate of recovery of the watershed (Webster et al. 1983). In this paper we focus primarily on the hypotheses of DeAngelis et al. (1990) and experimentally test the relationship between nutrient input and the response of stream ecosystems to a scour disturbance.

Several studies have addressed the effects of and recovery from high-discharge events in natural streams. Power and Stewart (1987) found that differences in the ability of stream algae to withstand spates were largely a result of differential resistance to shear stress, but that recovery patterns following the spate were largely a function of competitive interactions. Grimm and Fisher (1989) studied a number of high-discharge events in a Sonoran Desert stream and concluded that resistance of periphyton was a function of their growth form and mode of attachment, but resilience was a function primarily of nutrient inputs and season. Siegfried and Knight (1977) also noted the importance of energy resources in regulating the recovery of stream macroinvertebrate communities after spates.

In this study we examine the role of nutrients and trophic structure in regulating both the resistance and the resilience of a stream periphyton community to a scour disturbance using replicated laboratory streams. Our objective was to experimentally test previous theoretical predictions that ecosystems with long turnover times of limiting nutrients (due to low input of

nutrients from external sources relative to within-system storage of nutrients in biomass) will recover more slowly following a disturbance that removes biomass from the system than ecosystems with short nutrient turnover times (DeAngelis et al. 1989, 1990). We also test the prediction that ecosystems strongly influenced by herbivory should exhibit higher resilience than ecosystems with low levels of herbivory because herbivores maintain biomass at lower levels (DeAngelis et al. 1989, 1990). In a previous study involving a 3-mo light elimination, we found that neither grazing level nor nutrient input influenced the resistance of autotrophic biomass and production (Steinman et al. 1990), but that resilience of these characteristics was influenced by both grazing level and nutrient input (Steinman et al. 1991). The scour disturbance described in this paper differed from the previous disturbance in that most of the biomass in the system was removed. We predicted *a priori* that the effect of nutrient input on resilience should be more pronounced for this disturbance than for the light elimination disturbance because the removal of biomass during the scour event should reduce nutrient recycling and increase the dependence on external nutrient inputs.

Methods

Experimental design

Eight U-shaped fiberglass laboratory streams, each 0.3 m wide and 22 m long, were supplied with water from a spring-fed pond. Flow was maintained at 0.64 L/s, resulting in a water depth of approximately 5 cm and current velocity of about 22 cm/s. Incoming water was filtered through sand to remove most particulate material before it entered the streams. Light was supplied by 400-watt metal halide lamps, which provided a broad spectrum of photosynthetically available radiation at about 150 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The photoperiod was set at 8L:16D. Unglazed ceramic cylinders (1.6 cm diameter by 1.6 cm length) were placed on the bottom of each stream (18,000 per stream) to serve as substrata for periphyton colonization and units for sampling. The ceramic substrata were placed on the channel bottoms without regard to orientation and covered approximately 95% of the area of each channel. The streams were inoculated with periphyton by adding

rocks collected from Walker Branch, a stream on the U.S. Department of Energy's Oak Ridge reservation. Three to five rocks were placed at the upstream ends of each channel and were left in place for several months.

The effects of herbivory and nutrient input on resistance and resilience of periphyton communities were examined by manipulating the density of grazing snails and water circulation while maintaining similar flow rates and other physical factors among streams. Four treatments (with two replicates per treatment) were imposed on the streams in a 2×2 factorial design involving the presence or absence of snails and two types of water circulation: (1) no snails, once-through flow (NS-OT); (2) no snails, recirculated flow (NS-REC); (3) snails, once-through flow (S-OT); and (4) snails, recirculated flow (S-REC). In streams with once-through flow, all water made only one pass through the channel. In the recirculated streams, 98% of the flow was recirculated, resulting in reduced supplies of new nutrients to these streams. The recirculated water was cooled by an independent cooling system for each stream to match the temperature of the incoming water. Incoming water from the pond varied in temperature from 10 to 16°C during the course of the experiment, and temperatures of recirculated streams generally were within 1°C of those in once-through streams.

The snail *Elimia clavaeformis* Lea was added to four of the eight streams at a density of 1000/m², a density commonly found in Walker Branch (Burris et al. 1990; Amy Rosemond, Department of Biology, Vanderbilt University, personal communication). Although the other streams contained no snails, chironomid larvae and microfauna were present in all streams, so even the streams without *Elimia* were exposed to a low level of grazing.

The streams had been in use for >1 yr before this experiment. Nine months previously they had been exposed to an experimental scour event (DeAngelis et al. 1990) and 3 months previously to an experimental elimination of light (Steinman et al. 1990). At the time our experiment began the streams had been recovering from the light elimination for 76 d. Measurements of biomass and primary productivity prior to the experiment showed that the streams had recovered to an approximate steady-state condition (Steinman et al. 1991).

On 17 April 1989 an experimental scour disturbance was imposed on all streams. This disturbance consisted of increasing the flow by about a factor of 5 and vigorously overturning and rubbing against each other all the ceramic substrata in each stream over a period of several hours. The disturbance was begun at the upstream end of each channel and extended downstream so that all material dislodged was transported out of the channels. Snail densities were also intentionally reduced to 600/m² in the streams with snails, to simulate reductions in herbivore density from the disturbance. A number of structural characteristics and process rates were measured before the disturbance and at intervals of 1–2 wk beginning 1–2 d after the disturbance.

Sampling design and analytical methods

Water samples were collected weekly at upstream and downstream ends of each stream, but not all chemical characteristics were measured every week. Samples were filtered through washed glass fiber filters (Gelman type A/E, pore size 1 μ m). Concentrations of soluble reactive phosphorus (SRP), ammonium nitrogen (NH₄-N), and nitrate plus nitrite nitrogen (NO₂ + NO₃-N) were measured in the filtrate. SRP was measured using the molybdenum blue method (APHA 1985). NH₄-N was measured by automated phenate colorimetry (Technicon TRAACS 800 auto analyzer), and concentrations of NO₂ + NO₃-N by Cu-Cd reduction followed by automated colorimetry (U.S. Environmental Protection Agency 1983).

Ash free dry mass (AFDM), chlorophyll *a*, periphyton biovolumes, bacterial cell numbers, autotrophic carbon fixation rates, phosphatase activity, and exoproteolytic activity of attached communities growing on the ceramic cylinders were measured prior to the disturbance, within one or two days after the disturbance, and at intervals increasing from 1 wk to 4 wk over the next 23 wk. Detailed methods were given in Steinman et al. (1990) and Mulholland et al. (1991) and will only be reviewed briefly here. All measurements involved randomly selecting 8–12 cylinders from each stream (half from the upstream end and half from the downstream end of each channel) for analysis.

AFDM was determined gravimetrically after

drying (24 h at 60°C) and combusting (475°C) individual cylinders. For algal enumeration, attached material was scraped from cylinders and fixed in a modified Lugol's solution; algal cells were microscopically enumerated according to the methods of Stevenson (1984). Cell counts for each species were converted to biovolume using combinations of simple geometric shapes according to Stevenson et al. (1985). Bacteria were enumerated from samples used to enumerate algae after sonication using the acridine orange direct count technique (AODC) (Hobbie et al. 1977).

Autotrophic carbon fixation rates were determined from uptake of H^{14}CO_3 in recirculating chambers over 3-h periods at ambient light and temperature. Incorporated ^{14}C and chlorophyll *a* were extracted in dimethyl sulfoxide (DMSO) overnight and measured by scintillation counting (^{14}C) and spectrophotometry (chlorophyll) according to the methods of Palumbo et al. (1987). Water samples for total inorganic carbon were collected from each chamber and analyzed using an OI Corporation Model 700 Total Carbon Analyzer. Autotrophic carbon fixation rates were computed on an areal and chlorophyll-specific basis.

Phosphatase activity was determined from rates of hydrolysis of an introduced organic phosphorus substrate (para-nitrophenyl phosphate, NPP) measured spectrophotometrically after 30-min incubations of cylinders and stream water. For each cylinder used in the phosphatase assay, chlorophyll *a* was determined spectrophotometrically after extraction in DMSO overnight at room temperature (Shoaf and Lium 1976). Phosphatase activity was normalized per unit chlorophyll *a*.

Exoproteolytic activity was determined using a modification of the method of Somville and Billen (1983) which is based on production of a fluorescent product after hydrolysis of the peptide-like bond in L-leucyl-B-naphthylamide (LLBN). Four cylinders were randomly collected from each stream and each was incubated in 30 ml of filtered stream water in stirred glass chambers maintained within 1°C of ambient stream water temperature. Sixty μl of a 0.1-M LLBN solution were added to each chamber, and subsamples of water were collected and fluorescence determined at 4-min intervals over a 32-min period. Subsamples were returned to

the chambers to maintain constant volume. Rates of exoproteolytic activity were determined from linear regressions of the fluorescence measurements over time and were expressed per unit surface area of cylinders used in the incubation.

Rates of phosphorus uptake by the periphyton were determined prior to the disturbance by measuring uptake of $^{33}\text{PO}_4$ in 1-h incubations of cylinders and stream water in stirred chambers at ambient stream temperatures. Total uptake of phosphorus normalized by periphyton AFDM was determined using the first-order uptake rate coefficient calculated from the decline in radiotracer concentration in water, AFDM of periphyton used in the incubation, and stream water SRP concentration. Whole stream total phosphorus uptake rates were calculated using the AFDM-normalized uptake rates and total AFDM on all cylinders in the stream. Whole stream net phosphorus uptake rates were calculated as the difference in SRP concentrations at the upstream and downstream ends of the channel multiplied by the discharge. The ratio of total phosphorus uptake : net phosphorus uptake was calculated as an index of phosphorus recycling.

Nitrogen and phosphorus contents of periphyton and detritus on the stream bottom were determined on material scraped from cylinders and collected from the stream bottom just before the disturbance. Bottom detritus was quantitatively sampled by placing an open cylinder (0.008 m²) on the stream bottom, carefully removing all ceramic substrates within it, and pumping the remaining material into a bottle. The detritus so collected was filtered onto pre-ashed and tared glass fiber filters (Gelman A/E), dried (60°C for 48 h), weighed, combusted (475°C), and reweighed to determine AFDM. Nitrogen was determined on dried (60°C for 24 h) material using a Carla Erba CNS Analyzer (Model NA 1500). Phosphorus content was determined after combusting (475°C) the dried material, extracting phosphorus from the ash in hot 1N HCl, and measuring the extracted phosphorus using the molybdenum blue method as described above. Residence times of nitrogen and phosphorus in each stream were calculated by dividing the total N and P in periphyton and detritus on the stream bottom by the rate of input of inorganic N (NH_4 plus NO_2 + NO_3 concentrations times discharge) and P (SRP

concentration times discharge) in new water entering each stream.

Results

Statistical analysis

Resistance and resilience were measured for AFDM, chlorophyll *a*, autotrophic carbon fixation rates (areal), bacterial numbers, and exoproteolytic activity. Resistance was quantified by calculating the percentage decline in each characteristic from the pre-disturbance measurement to the lowest post-disturbance value. For some characteristics, declines continued for up to 4 wk after the disturbance. To quantify resilience, a first order model ($X = X_0 e^{rt}$) was fitted to the data for each characteristic (X) beginning with the lowest value (X_0) following the disturbance and continuing until there was evidence of an inflection point leading to an asymptote in recovery. At least three data points and in most cases 5–7 data points were used in all model fits. The exponential rate of increase (r) and the nominal time to return to the measured pre-disturbance value (T_s), as determined from extrapolation of the fitted first order model, were used as measures of resilience for each characteristic.

The effects of snails (grazing intensity) and water circulation (nutrient input) on pre-disturbance measures of nutrient recycling were analyzed using a two-way analysis of variance (ANOVA, $df = 1,4$) (SAS 1988). Data were log-transformed prior to ANOVA to correct for heterogeneity of variances. Effects of snails and water circulation on measures of resistance and resilience were also analyzed using a two-way ANOVA. Resistance measures were arcsin-square root transformed and T_s values were log-transformed prior to analysis. Pairwise comparisons between treatments ($df = 1,2$) were also performed using the contrast statement in the SAS GLM procedure (SAS 1988).

Changes in algal taxonomic structure were evaluated with the SIMI index of similarity (Steinman and McIntire 1986). This measure ranges from 0 to 1, where a value of 0 indicates that a given pair of assemblages have no taxa in common, while a value of 1 indicates that the two assemblages have identical species compositions and proportional abundances. All analyses were based on biovolume data.

Pre-disturbance characteristics

Before the scour disturbance, presence of snails had a significant effect ($p < 0.05$) on AFDM, chlorophyll *a*, bacterial numbers, and areal carbon fixation rate, with higher values for each of these characteristics in the streams without snails (NS treatments) compared with the streams with snails (S treatments) (Fig. 1). The effect of water circulation on these characteristics was generally not significant.

The physiognomy and species composition of algal communities were influenced primarily by snails and secondarily by water circulation. Algal communities in the S streams were almost exclusively prostrate forms, dominated by basal cells and short filaments of the chlorophyte *Stigeoclonium* sp. (>70% of biovolume in all S streams, >95% in S-REC streams). The cyanophyte *Chamaesiphon incrustans* made up approximately 17% of community biovolume in the S-OT streams. Algal taxonomic similarity between S-OT and S-REC treatments, as determined from the SIMI index, was high (0.91). Algal communities in the NS streams were dominated by filamentous and erect growth forms and were somewhat more diverse than the S streams. The diatoms *Synedra ulna* (20% of total biovolume) and *Amphipleura perpusilla* (7%), the chlorophytes *Mougeotia* sp. (19%) and *Stigeoclonium* sp. (15%), and the cyanophyte *Oscillatoria tenuis* (6%) each made up at least 5% of the community biovolume in the NS-OT streams. The NS-REC streams were somewhat less diverse, being dominated by the diatoms *Epithemia turgida* (67%) and *Fragilaria capucina* var. *mesolepta* (7%), and the chlorophyte *Stigeoclonium* sp. (11%). Algal taxonomic similarity between NS-OT and NS-REC treatments was low (SIMI < 0.19). Taxonomic similarity also was low between treatments with similar circulation regimes but different grazing intensities (S-OT vs. NS-OT: SIMI = 0.30; S-REC vs. NS-REC: SIMI = 0.09).

Nutrient concentrations before the disturbance were lower in the REC treatments than in the OT treatments, regardless of grazing intensity (Fig. 2). Snails had little effect on $\text{NO}_2 + \text{NO}_3$ concentrations, as indicated by similar reductions in concentrations with recirculation

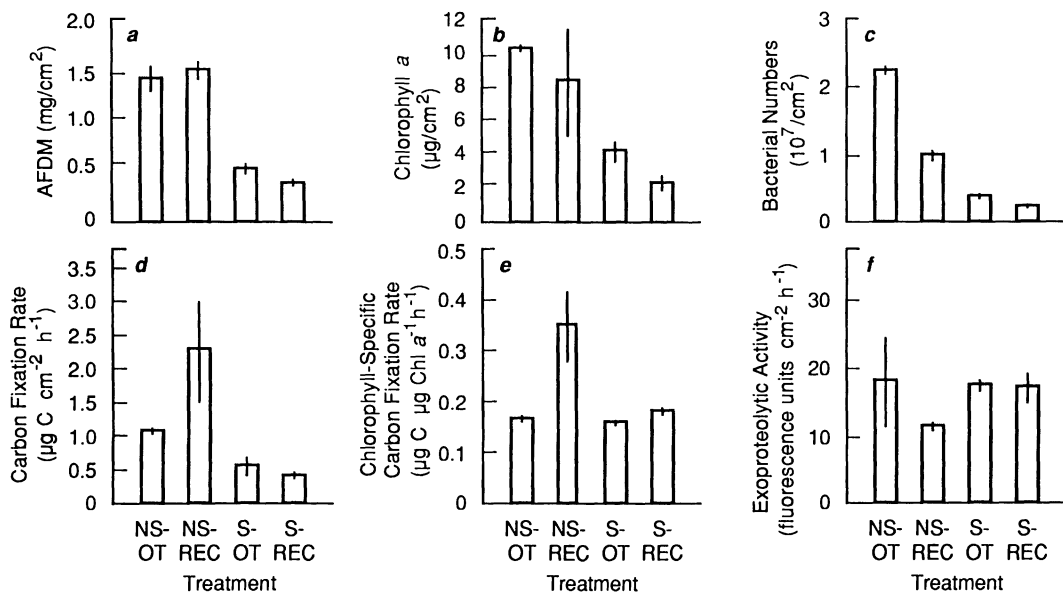


FIG. 1. Measures (mean \pm 1 SD) of biomass and metabolism of the periphyton community before the scour disturbance, based on two replicates of each treatment. Treatments are no snails and once-through flow (NS-OT), no snails and recirculated flow (NS-REC), snails and once-through flow (S-OT), and snails and recirculated flow (S-REC). Results of ANOVA ($df = 1,4$) showed that the effect of snails was significant for AFDM, chlorophyll *a*, bacterial numbers, and carbon fixation rate per unit area ($p < 0.05$).

in S and NS streams (Fig. 2a). However, presence of snails partially compensated for the effect of recirculation on SRP concentrations, resulting in smaller reductions in SRP concentrations with recirculation in the S streams than in NS streams (Fig. 2b).

Several indices of nutrient recycling were significantly influenced by snails and by water circulation (Table 1). Phosphatase activity normalized per unit chlorophyll (chlorophyll-specific phosphatase) was significantly higher in NS streams than in S streams ($p < 0.05$, pairwise comparisons). Consistently higher values of chlorophyll-specific phosphatase activity in the NS-REC streams were marginally significant in a pairwise comparison ($F = 6.19$, $p = 0.068$, $df = 1,2$). Residence times for P and N were significantly longer in NS streams compared with S streams and significantly longer in REC streams than in OT streams ($p < 0.05$, pairwise comparisons). The ratio of total P uptake from water, as determined from the radiotracer studies, to the net depletion of P from upstream to downstream (total:net P uptake) was significantly affected only by water circulation ($p < 0.05$, Table 1), with significantly higher values

in the REC streams than in the OT streams, but only for the NS streams ($F = 13.56$, $p = 0.02$, $df = 1,2$).

Resistance

Resistance of most structural characteristics and metabolic processes was significantly affected by snails and relatively little affected by water circulation (Table 2). Resistance of all characteristics was significantly greater (percentage reductions were lower) in the S streams compared with the NS streams. Effects of water circulation were significant only for bacterial numbers, with lower reductions (higher resistance) in the REC streams than in the OT streams. The significant treatment interaction for chlorophyll *a* resistance was the result of significantly greater chlorophyll reductions (lower resistance) in the OT compared with the REC streams for the S treatments ($F = 12.04$, $p = 0.026$, $df = 1,2$) but significantly greater reductions (lower resistance) in the REC than in the OT streams for the NS treatments ($F = 15.73$, $p = 0.017$, $df = 1,2$).

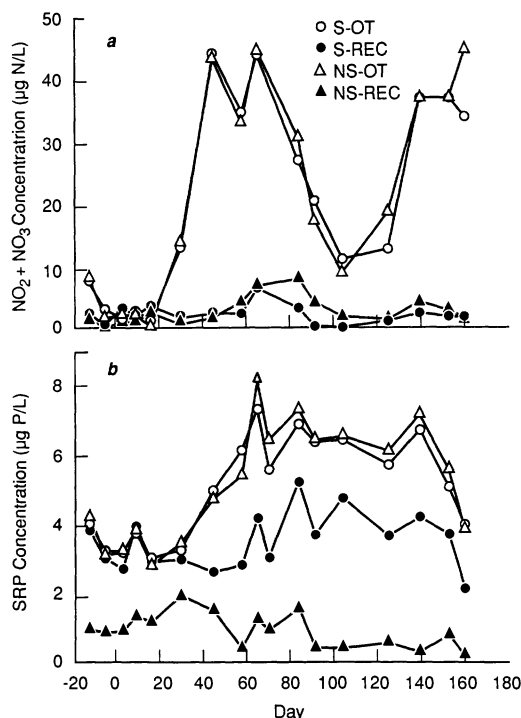


FIG. 2. Concentrations of (a) $\text{NO}_2 + \text{NO}_3$ and (b) SRP in stream water for the different treatments over time. Data points are mean concentrations of the two treatment replicates at the upstream ends of the channels (error bars have been omitted for clarity). The scour disturbance took place on day 0. See Figure 1 for treatment abbreviations.

Resistance of algal taxonomic composition determined from SIMI values in each stream between the pre-disturbance date and day 1 following the disturbance was significantly affected by snails ($F = 651.6$, $p = 0.0001$, $df = 1,4$), being higher in the S streams (SIMI values > 0.98) than in the NS streams (SIMI values ranging from 0.14 to 0.30). The low SIMI values in the NS streams were primarily the result of a loss of almost all taxa except *Stigeoclonium* sp. after the disturbance. On day 1, *Stigeoclonium* sp. made up 97% of the biovolume in the NS-OT streams and 90% of the biovolume in the NS-REC streams. The effect of water circulation on taxonomic resistance was marginally significant only among the NS streams ($F = 5.23$, $p = 0.084$, $df = 1,2$), with greater resistance in the OT treatment (SIMI = 0.245) compared with the REC treatment (SIMI = 0.145).

Resilience

The temporal patterns of recovery of AFDM, chlorophyll *a*, and bacterial numbers were generally similar among treatments (Fig. 3). In most cases there was a lag period of 8–32 d following the disturbance before biomass characteristics began to increase. In the NS-OT streams, biomass eventually increased to levels exceeding pre-disturbance values and declined in the later portion of the study. Biomass also eventually exceeded the pre-disturbance level in the S-OT streams and NS-REC streams (chlorophyll *a* and bacteria only in the latter). In the S-REC streams, AFDM and chlorophyll *a* remained low

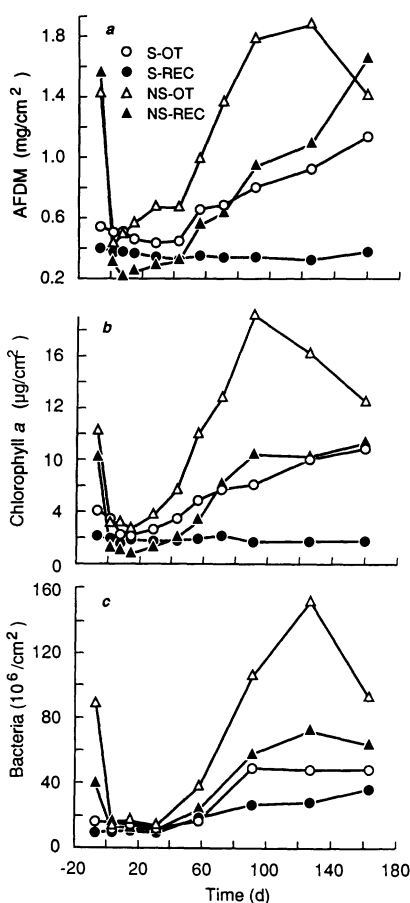


FIG. 3. Three different expressions of periphyton biomass for the different treatments over time. Data points are mean values of the two treatment replicates. (a) Ash-free dry mass (AFDM); (b) Chlorophyll *a*; (c) Bacterial cell numbers. See Figure 1 for treatment abbreviations.

TABLE 1. Nutrient recycling indices measured during the week before the scour disturbance. Results of an ANOVA for grazing level (GRLEV) and water circulation (WATCIRC) treatments and their interaction (GRLEV \times WATCIRC) are also given (df = 1,4). Treatments were: snails and once-through flow (S-OT), snails and recirculated flow (S-REC), no snails and once-through flow (NS-OT), and no snails and recirculated flow (NS-REC).

Characteristic	Treatment	Mean	ANOVA (F)		
			GRLEV	WATCIRC	GRLEV \times WATCIRC
Chlorophyll-specific phosphatase [$\mu\text{mol mg Chl a}^{-1} \text{ h}^{-1}$]	S-OT	1.30	46.8**	1.23	5.82
	S-REC	0.74			
	NS-OT	4.54			
	NS-REC	13.8			
P residence time (d)	S-OT	2.4	142.2**	654.4**	12.1*
	S-REC	56.2			
	NS-OT	8.1			
	NS-REC	498			
N residence time (d)	S-OT	17.0	100.3**	599.7**	3.74
	S-REC	630			
	NS-OT	60.4			
	NS-REC	4386			
Total : Net P uptake	S-OT	2.95	0.04	7.89*	5.76
	S-REC	3.48			
	NS-OT	1.34			
	NS-REC	7.62			

** $p < 0.01$.
* $p < 0.05$.

throughout the study, although bacterial numbers increased steadily.

Temporal patterns of recovery of areal carbon fixation rates were also similar among treatments (Fig. 4a). In all treatments carbon fixation rates exceeded pre-disturbance levels by day 60 and declined from their maximum post-disturbance value in the later stages of the study period. The lag in recovery evident in biomass characteristics was not evident in carbon fixation data. The temporal pattern in chlorophyll-specific carbon fixation rate was complex, but generally increased after the disturbance, peaked about day 56, and then declined (Fig. 4b).

Exoproteolytic activity followed a temporal pattern similar to that of bacterial numbers, with an extended lag period, and peak activities were reached only late in the study period (Fig. 4c). There appeared to be a greater stimulation effect by snails on exoproteolytic activity compared with areal carbon fixation rate. Rates of exoproteolytic activity in S streams were as high or higher than rates in NS streams of the same water circulation treatment.

Chlorophyll-specific phosphatase activity (CSPA) was not greatly affected by the disturbance, except in the NS-OT streams (Fig. 5). In the S streams it was low before the disturbance and remained low following the disturbance. In the NS-REC streams where it was highest before the disturbance, CSPA increased during the first 60 d following the disturbance and remained high relative to the pre-disturbance values. CSPA gradually increased in the NS-OT streams following the disturbance.

Resilience of most biomass characteristics and metabolic processes, as determined by the rate of increase (r) following the disturbance, was significantly affected by snails (Table 3). For all characteristics but exoproteolytic activity, pairwise comparisons showed that r was significantly lower in S streams than in NS streams of the same water circulation treatment ($p < 0.05$). For exoproteolytic activity, r was significantly lower in the S streams than in the NS streams for the OT treatment ($F = 10.33$, $p = 0.0325$), but not for the REC treatment ($F = 0.27$, $p = 0.63$).

Overall, water circulation had a significant

TABLE 2. Resistance of several characteristics of the periphyton community to the scour disturbance. Reductions are percentages calculated from differences between the pre-disturbance and lowest post-disturbance measurement. Percentages were divided by 100 and arc-sin transformed prior to ANOVA ($df = 1,4$). See Table 1 for treatments and abbreviations.

Characteristic	Treatment	Reduction (%)	ANOVA (F)		
			GRLEV	WATCIRC	GRLEV \times WATCIRC
AFDM	S-OT	19.3	76.4**	1.82	2.26
	S-REC	18.9			
	NS-OT	69.8			
	NS-REC	87.1			
Chlorophyll <i>a</i>	S-OT	45.8	155.2**	0.12	27.6**
	S-REC	27.0			
	NS-OT	74.2			
	NS-REC	91.2			
Bacteria	S-OT	33.1	89.1**	11.23*	2.72
	S-REC	7.5			
	NS-OT	86.2			
	NS-REC	76.4			
Carbon fixation rate	S-OT	16.0	33.9**	4.39	0.69
	S-REC	25.4			
	NS-OT	66.8			
	NS-REC	92.7			
Exoproteolytic activity	S-OT	26.4	13.9*	0.29	5.30
	S-REC	38.4			
	NS-OT	69.1			
	NS-REC	48.9			

** $p < 0.01$.

* $p < 0.05$.

effect on r for chlorophyll *a*, bacterial numbers, and exoproteolytic activity, but not for AFDM and areal carbon fixation rate (Table 3). In S streams, pairwise comparisons showed that r 's for chlorophyll *a*, bacterial numbers, and carbon fixation rates were significantly greater in the OT treatment than in the REC treatment ($F = 118.4$, $p = 0.0004$ for chlorophyll *a*; $F = 148.9$, $p = 0.0003$, for bacterial numbers; $F = 16.5$, $p = 0.0154$ for carbon fixation rate). In addition, r for AFDM was substantially greater in S-OT than in S-REC streams, although the differences were not significant ($F = 4.40$, $p = 0.104$). In the NS streams, r for chlorophyll *a* was significantly greater in the REC streams than in the OT streams ($F = 25.1$, $p = 0.007$). In contrast, r 's for bacterial numbers and exoproteolytic activity in the NS streams were significantly lower in the REC streams compared with the OT streams ($F = 60.7$, $p = 0.0015$ for bacterial numbers; $F = 12.4$, $p = 0.024$ for exoproteolytic activity).

The second characteristic describing resilience, the time to reach the pre-disturbance value (T_s) as determined from application of the first-order model for recovery, gave somewhat different results from those for r . T_s was significantly affected by snails or water circulation only for AFDM and bacterial numbers (Table 4). In pairwise comparisons, T_s for AFDM was significantly shorter in S streams than in NS streams, but for the OT treatment only ($F = 43.5$, $p = 0.007$), and was significantly longer in REC streams than in OT streams, but for the NS treatment only ($F = 15.4$, $p = 0.029$). Because r for AFDM in the S-REC streams was negative (i.e., AFDM declined slightly during the period after the disturbance), T_s for AFDM was undefined for this treatment and pairwise comparisons could not be made using S-REC streams. For bacterial numbers, T_s was significantly shorter in the S streams compared with the NS streams, but only for the REC treatment ($F = 16.87$, $p =$

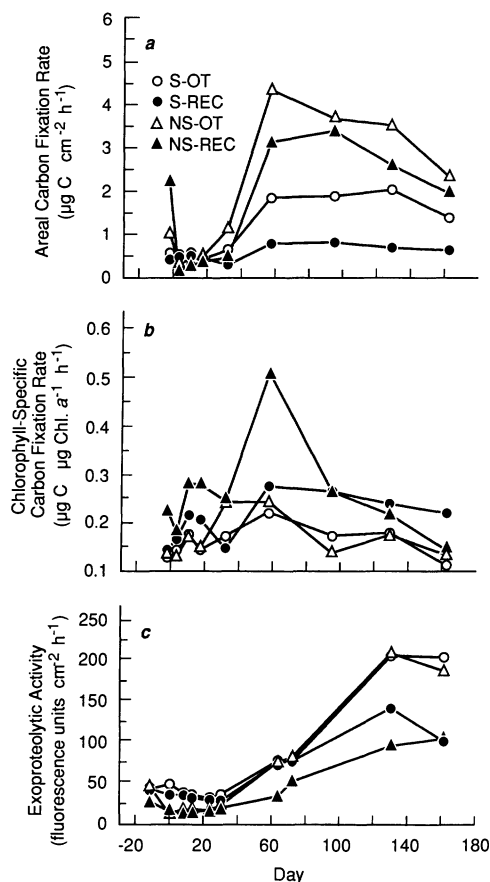


FIG. 4. Three different expressions of periphyton metabolism for the different treatments over time. Data points are mean values of the two treatment replicates (error bars have been omitted for clarity). (a) Areal carbon fixation rates; (b) Chlorophyll-specific carbon fixation rates; (c) Exoproteolytic activity. See Figure 1 for treatment abbreviations.

0.015), and was significantly shorter in the REC streams than in the OT streams, but only for the S streams ($F = 16.69$, $p = 0.015$).

Discussion

Treatment effects on structure and processes

Presence of snails and water circulation had large effects on biomass, species composition, carbon fixation, nutrient concentrations, and nutrient recycling. In general, snail grazing resulted in lower periphyton biomass, a simplified algal community consisting of prostrate

cells, lower areal rates of carbon fixation, and less recycling of nutrients within the streams as indicated by lower chlorophyll-specific phosphatase levels and shorter N and P residence times.

Reduced nutrient input as a result of water recirculation resulted in substantial changes in algal species composition, lower bacterial numbers and exoproteolytic activity, lower nutrient concentrations in stream water, and greater recycling of nutrients as indicated by increased chlorophyll-specific phosphatase levels, longer N and P residence times, and higher total : net P uptake ratios. However, these effects were largely confined to the streams with no snails (NS treatment). Presence of snails compensated to some extent for the reduction of nutrient inputs from external sources (new water) by reducing periphyton biomass (and consequently nutrient demand) and presumably by increasing remineralization of N and P. However, the significantly lower level of chlorophyll in the S-REC treatment compared with the S-OT treatment suggests that nutrient remineralization via snail feeding did not entirely compensate for reduced nutrient input due to water recirculation.

In the absence of snails, reduced nutrient input had little effect on autotrophic biomass but resulted in changes in algal taxonomy and somewhat higher rates of areal carbon fixation. Increased importance of *Epithemia* sp. in the recirculated streams may be a response to low nitrogen concentrations in water in these streams. The capability of *Epithemia* to fix nitrogen due to inclusions of endosymbiotic cyanobacteria (Drum and Pankratz 1965, Geitler 1977) may have given this species a competitive advantage in the REC streams. Areal carbon fixation rates were higher in the recirculated streams as a result of higher chlorophyll-specific carbon fixation rates rather than differences in algal biomass. The higher chlorophyll-specific carbon fixation rates may be a result of taxonomic differences (e.g., high chlorophyll-specific carbon fixation rates of *Epithemia*), although it is unclear why reduced nutrient input would result in increased photosynthetic capacity. We observed no significant differences in areal and chlorophyll-specific carbon fixation rates in an earlier study (Mulholland et al. 1991) with a somewhat lower level of water recirculation (90%) than that used in the present study.

TABLE 3. Resilience of several characteristics of the periphyton communities as defined by the first-order rate of increase (r , units of d^{-1}) following the disturbance. Treatment abbreviations as in Table 1.

Characteristic	Treatment	Mean r	ANOVA (F)		
			GRLEV	WATCIRC	GRLEV \times WATCIRC
AFDM	S-OT	0.0058	42.5**	0.49	5.15
	S-REC	-0.0009			
	NS-OT	0.0154			
	NS-REC	0.0190			
Chlorophyll a	S-OT	0.0146	654.8**	17.2*	126.3**
	S-REC	0.0016			
	NS-OT	0.0266			
	NS-REC	0.0326			
Bacteria	S-OT	0.0258	148.9**	126.2**	0.04
	S-REC	0.0164			
	NS-OT	0.0358			
	NS-REC	0.0266			
Carbon fixation rate	S-OT	0.0359	39.6**	3.59	14.79*
	S-REC	0.0155			
	NS-OT	0.0446			
	NS-REC	0.0514			
Exoproteolytic activity	S-OT	0.0172	3.63	12.42*	6.96
	S-REC	0.0160			
	NS-OT	0.0231			
	NS-REC	0.0151			

** $p < 0.01$.

* $p < 0.05$.

Higher chlorophyll-specific but not areal carbon fixation rates were observed with 95% water recirculation just prior to the previous light elimination disturbance (Steinman et al. 1990). In other respects, however, the treatment effects on periphyton structure and processes in the present study were similar to those in the previous studies (Mulholland et al. 1991, Steinman et al. 1990).

Treatment effects on resistance

Our results showing much greater resistance to scour of structural and functional characteristics of periphyton in streams with snails than in streams without snails are consistent with those of Power and Stewart (1987) who found that short turfs of *Spirogyra* had greater resistance than longer, more mature filaments to spates in a stream in Oklahoma. Intense herbivory should lead to greater resistance of periphyton to scour because the resultant community usually consists of a thin layer with

prostrate growth forms (Steinman et al. 1987, Lowe and Hunter 1988). This type of community will be exposed to lower shear stress during spates (Steinman and McIntire 1990). In our study snail grazing resulted in a periphyton community dominated by basal cells of *Stigeoclonium* which proved to be the taxon most resistant to scour in all streams. Thus, our results indicating high resistance of streams with snails to a scour disturbance support the conclusions of Grimm and Fisher (1989) that resistance of the autotrophic components of the periphyton to spates is largely a result of growth form and mode of attachment.

Kaufman (1982) conducted disturbance studies involving copper additions to experimental streams and found an inverse relationship between resistance and successional age of the periphyton community. Our results are also consistent with Kaufman's findings. Intense grazing by snails maintained the periphyton communities in S streams in a young successional state highly resistant to disturbance.

Water circulation had little effect on resis-

TABLE 4. Resilience of several characteristics of periphyton communities as defined by the time to recover to the pre-disturbance value (T_r , units of d) following the disturbance. Treatment abbreviations as in Table 1.

Characteristic	Treatment	Mean T_r	ANOVA (F)		
			GRLEV	WATCIRC	GRLEV \times WATCIRC
AFDM	S-OT	38.2	97.6**	15.4*	—
	S-REC	—			
	NS-OT	78.1			
	NS-REC	119.6			
Chlorophyll <i>a</i>	S-OT	54.3	0.14	2.19	0.61
	S-REC	179.7			
	NS-OT	63.8			
	NS-REC	85.0			
Bacteria	S-OT	83.6	9.83*	9.63*	7.15
	S-REC	25.4			
	NS-OT	85.1			
	NS-REC	78.3			
Carbon fixation rate	S-OT	57.4	0.22	0.03	5.24
	S-REC	22.8			
	NS-OT	27.8			
	NS-REC	53.0			
Exoproteolytic activity	S-OT	36.9	1.66	0.12	0.81
	S-REC	45.0			
	NS-OT	54.8			
	NS-REC	48.0			

** $p < 0.01$.

* $p < 0.05$.

tance of periphyton characteristics in streams with and without snails. The lack of an effect of water circulation in the streams with no snails, despite taxonomic differences between NS-OT and NS-REC streams, further supports the conclusion that growth form was most important in defining resistance. The higher resistance of bacterial numbers in the REC compared with the OT streams was probably a result of lower bacterial numbers in the REC streams before the disturbance. The scour event resulted in a small remnant population of bacteria and so differences in resistance were related more to differences in initial populations than to differences in the post-disturbance populations.

The results of the scour disturbance on resistance are different in two respects from those from an earlier 3-mo light elimination (Steinman et al. 1990). In the light elimination experiment, differences in resistance between streams with and without snails were not nearly as large as in the present study. This probably reflects the greater importance of growth form in resistance to scour than to other types of

disturbances. Also, resistance of structural characteristics (AFDM, chlorophyll *a*, taxonomic composition) was higher than that for process rates (carbon fixation) in the light elimination study in contrast to similar resistance of these characteristics in the study described here. This contrast is not surprising considering that the light elimination disturbance should directly affect photosynthesis and only gradually influence biomass of algae. A scour disturbance would directly affect biomass. Therefore, the present results support the conclusions of Steinman et al. (1990) that ecosystem resistance to different disturbances reflects differences in the characteristics of the disturbances more so than attributes of the ecosystem.

One interesting similarity in the results of Steinman et al. (1990) and the present study is the high resistance of the basal form of the alga *Stigeoclonium* to both disturbances. Although the high resistance to scour disturbances is intuitively reasonable given its prostrate growth form, it is unclear why *Stigeoclonium* should be so highly resistant to light elimination as well.

Treatment effects on resilience

We predicted *a priori* that: (1) reduced input of nutrients resulting in increased dependence on nutrient recycling, as indicated by increased nutrient residence time, would result in lower resilience as defined by increased time to recovery, but (2) addition of herbivores would increase resilience (DeAngelis et al. 1990). Our experimental reduction of nutrient input by water recirculation resulted in streams with increased residence times for N and P compared with streams with once-through flow, and thus allowed us to explicitly test hypothesis 1. With rate of increase (r) as the measure of resilience following the scour disturbance, we would reject hypothesis 1 for the algae-related characteristics (AFDM, chlorophyll a , and carbon fixation) but would not reject it for bacteria-related characteristics (bacterial numbers, exoproteolytic activity). For the latter characteristics, r values were lower in the REC streams (long nutrient residence times) than in the OT streams (short nutrient residence times) as hypothesized. However, if we consider time to return to the pre-disturbance state (T_s) as the measure of resilience, then our results on AFDM, chlorophyll a , and carbon fixation rate are consistent with hypothesis 1 (i.e., longer T_s in the REC streams). This apparent contradiction is the result of differential resistance of NS-REC and NS-OT streams. Although the rate of increase of algae-related characteristics was similar to slightly higher in REC streams compared with OT streams, it took longer for these characteristics to recover to pre-disturbance levels (longer T_s) in REC streams because they were depressed to lower levels by the disturbance. These results reflect the difficulty of separating resistance and resilience in ecosystems unless measurements of each are carefully defined. In our study, r is probably a better measure of resilience for testing the hypothesis of DeAngelis et al. (1990) because these authors assumed that the disturbance resulted in equal displacement from the pre-disturbance state. The lower resilience hypothesized for the model streams with high rates of nutrient recycling (long nutrient residence times) was therefore the result of lower r in these streams when nutrient recycling was disrupted (DeAngelis et al. 1990).

Steinman et al. (1991) measured resilience to a light elimination disturbance in the same streams used in the present study and found

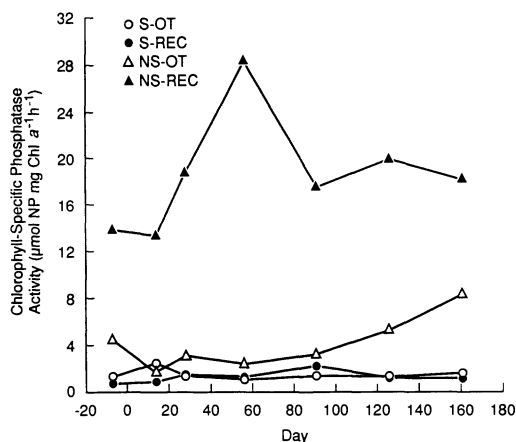


FIG. 5. Chlorophyll-specific phosphatase activity of periphyton for each treatment over time. Data are mean values of the two treatment replicates (error bars have been omitted for clarity). See Figure 1 for treatment abbreviations.

that r for most characteristics was higher in the OT than in the REC streams, results consistent with hypothesis 1. We expected that there would be an even greater effect of recirculation in the present study because, in contrast to the study of Steinman et al. (1991), much of the biomass (living and dead) was removed from the system in the scour disturbance. This removal of biomass should have reduced the potential for high rates of nutrient recycling that could compensate for lower nutrient input in the REC streams following the disturbance. However, the increase in chlorophyll-specific phosphatase activity in the REC streams in the first 60 d following the disturbance (Fig. 5) may indicate that biomass-specific nutrient recycling was maintained and perhaps even increased in the REC streams, thus allowing relatively high r in spite of low nutrient inputs.

The fact that hypothesis 1 was supported in the case of r for the bacterial characteristics suggests that regrowth of bacteria was influenced more by nutrient input than regrowth of algae. This may reflect higher nutrient limitation of bacteria than of algae due to a lower affinity for nutrients or to reduced availability of nutrients in the water to bacteria, perhaps because of their position within the polysaccharide matrix of the biofilm.

The effects of snail herbivores on resilience of several characteristics (hypothesis 2) were different depending on whether r or T_s was

used as a measure of resilience. Considering first the results for r , presence of snails resulted in lower r for all characteristics in the OT streams (S-OT vs. NS-OT, Table 3) and therefore, rejection of hypothesis 2. Steinman et al. (1991) also found lower rates of recovery in the streams with snails following the light elimination disturbance and attributed this primarily to depensatory grazing by the snails (i.e., snails harvested an increasing proportion of algal production as production declined). Depensatory grazing appears to have occurred in the present study as well, as indicated by the virtual lack of recovery in the S-REC streams. With respect to T_s , snails resulted in longer values for carbon fixation rate in OT streams. However, T_s values were shorter for AFDM, chlorophyll a , and exoproteolytic activity in the presence of snails (S-OT vs. NS-OT, Table 4), a result consistent with hypothesis 2.

Of the two resilience measures, T_s may be a better measure for testing hypothesis 2. The theoretical basis for this hypothesis is that herbivores should reduce the steady-state periphyton biomass, and that herbivory should act as a compensatory process, removing a constant proportion of algal production and thus resulting in a lower absolute removal rate of periphyton after the disturbance than before (DeAngelis et al. 1989, 1990). Consequently, the rate of recovery (r) of stream periphyton biomass may be reduced somewhat by herbivores, but because steady-state biomass would be considerably lower in herbivore streams, the time to recovery (T_s) should be shorter for these streams than those without herbivores. Although it appeared that snail grazing in this experiment was depensatory rather than compensatory, most of our results are consistent with this interpretation of hypothesis 2.

Perhaps the most interesting result of our experiment was the strong interactive effect of herbivory and nutrient input on resilience. In the absence of snails, resilience generally was not influenced by reduced nutrient input, probably because of high rates of nutrient recycling. However, in streams with snails present, resilience was strongly influenced by nutrient input, being considerably lower in the streams with reduced nutrient input (S-REC) compared with the streams with ambient nutrient input (S-OT). This contrast in resilience suggests a positive feedback between biomass accrual and nutrient recycling during stream recovery from

scour types of disturbances. Intense herbivory can constrain both biomass accrual and nutrient recycling (see also Mulholland et al. 1991), and this effect can lead to very slow recovery in systems with low nutrient input.

The importance of nutrient supply for the recovery of periphyton biomass following scouring during spates in desert streams was noted by Grimm and Fisher (1986). However, in a subsequent study they found that concentrations of dissolved nutrients in water had little effect on periphyton recovery rates but may have indirectly caused a sharp reduction in macroinvertebrate density in the later stages of periphyton recovery due to declines in the nutrient content of periphyton (food quality) at this time (Grimm and Fisher 1989). In our study we observed declines in measures of periphyton biomass and metabolism in the later stages of the recovery period (Figs. 3, 4). These declines were more prominent in streams with no snails, particularly those with once-through flow. Declines in areal carbon fixation rates preceded declines in the biomass-related characteristics, showing that primary production was affected first and probably led to the declines in autotrophic and heterotrophic biomass. This lag in biomass response, in contrast to metabolism, may be because nutrients have a direct influence on metabolism, but only an indirect effect on biomass, which is a product of metabolism. Bothwell (1989) also observed substantial declines in stream periphyton biomass in the later stages of a study that examined the effects of nutrient concentration on periphyton biomass and growth, noting that higher nutrient concentrations were needed to sustain a given level of biomass than to create it.

This overshoot and decline in periphyton biomass during recovery from disturbance or colonization of new substrata may be a consequence of reduced supply of nutrients to lower layers of the periphyton community when biomass accumulations are large. Riber and Wetzel (1987) have shown that nutrient uptake is strongly limited by boundary-layer mass transfer in intact periphyton films. Using autoradiographic techniques, Burkholder et al. (1990) found that underlying adnate cells in a biofilm matrix took up substantially less $^{33}\text{PO}_4$ from water than the loosely attached overstory cells. Rose and Cushing (1970) measured a decline in ^{65}Zn from the surface down through a river periphyton community following addition of the

radiotracer to the overlying water. Pringle (1990) has demonstrated that the understory species in well-developed periphyton communities can be, to a large extent, isolated from nutrients added to the overlying water. These studies suggest that at high periphyton biomass, mass transfer of nutrients to lower layers may be low enough to reduce productivity and viability of these cells, thus eventually increasing loss rates by sloughing. However, in streams with significant populations of invertebrate consumers, such as those studied by Grimm and Fisher (1986, 1989), increasing nutrient limitation of algal and bacterial production within the periphyton mat during the later stages of regrowth may result in reductions in invertebrate densities before reductions in the biomass of periphyton.

In summary, our experimental results concerning the resilience of a stream periphyton community following a scour disturbance show that nutrient input and nutrient residence time (nutrient recycling) are important characteristics determining recovery rate, as predicted by modeling studies of DeAngelis et al. (1989, 1990). However, contrary to the model predictions, nutrient input had a greater effect on resilience in streams with intense herbivory than in streams with low levels of herbivory. In the low herbivory streams, the time to recovery following the experimental disturbance was longer for streams with low nutrient input and long nutrient residence times as predicted by the model. However, the experimental results were due to lower resistance of periphyton biomass in the low nutrient streams, not to lower rates of regrowth in these streams compared with those receiving higher nutrient inputs.

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Literature Cited

- APHA. 1985. Standard methods for the examination of water and waste water. 16th edition. American Public Health Association, Washington, D.C.
- BOTHWELL, M. L. 1989. Phosphorus-limited growth dynamics of lotic periphyton diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1293-1301.
- BURKHOLDER, J. M., R. G. WETZEL, AND K. L. KLOMPARENS. 1990. Direct comparison of phosphate uptake by adnate and loosely attached microalgae within an intact biofilm matrix. *Applied and Environmental Microbiology* 56:2882-2890.
- BURRIS, J. A., M. S. BAMFORD, AND A. J. STEWART. 1990. Behavioral responses of marked snails as indicators of water quality. *Environmental Toxicology and Chemistry* 9:69-76.
- DEANGELIS, D. L., S. M. BARTELL, AND A. L. BRENKERT. 1989. Effects of nutrient recycling and food chain length on resilience. *American Naturalist* 134:778-805.
- DEANGELIS, D. L., P. J. MULHOLLAND, J. W. ELWOOD, A. V. PALUMBO, AND A. D. STEINMAN. 1990. Biogeochemical cycling constraints on stream ecosystem recovery. *Environmental Management* 13:685-697.
- DRUM, R. W., AND S. PANKRATZ. 1965. Fine structure of an unusual cytoplasmic inclusion in the diatom *Rhopalodia*. *Protoplasma* 60:141-149.
- FISHER, S. G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management* 14:725-736.
- GEITLER, L. 1977. Zur Entwicklungsgeschichte der Epithemiaceen *Epithemia*, *Rhopalodia*, and *Denticula* (Diatomophyceae) und ihre vermutlich symbiotischen Spharoidkörper. *Plant Systematics and Evolution* 128:259-275.
- 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.
- GRIMM, N. B., AND S. G. FISHER. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293-307.
- HOBBIE, J. E., R. J. DALEY, AND S. JASPER. 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. *Applied and Environmental Microbiology* 33:1225-1228.
- KAUFMAN, L. H. 1982. Stream aufwuchs accumulation: disturbance frequency and stress resistance and resilience. *Oecologia* 52:57-63.
- LOWE, R. L., AND R. D. HUNTER. 1988. Effects of grazing by *Physa integra* on periphyton community structure. *Journal of the North American Benthological Society* 7:29-36.
- MULHOLLAND, P. J., A. D. STEINMAN, A. V. PALUMBO,

- J. W. ELWOOD, AND D. B. KIRSCHTEL. 1991. Role of nutrient recycling and herbivory in regulating periphyton communities in laboratory streams. *Ecology* (in press).
- O'NEILL, R. V. 1976. Ecosystem persistence and heterotrophic regulation. *Ecology* 57:1244-1253.
- O'NEILL, R. V., W. F. HARRIS, B. S. AUSMUS, AND D. E. REICHEL. 1975. A theoretical basis for ecosystem analysis with particular reference to elemental cycling. Pages 28-40 in F. G. Howell, J. B. Gentry, and M. H. Smith (editors). *Mineral cycling in southeastern ecosystems*. U.S. Energy Research and Development Administration. Washington, D.C.
- PALUMBO, A. V., P. J. MULHOLLAND, AND J. W. ELWOOD. 1987. Extraction with DMSO to simultaneously measure periphyton photosynthesis, chlorophyll, and ATP. *Limnology and Oceanography* 32:464-471.
- POFF, N. L., AND J. V. WARD. 1990. Physical habitat template of lotic ecosystems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.
- POWER, M. E., AND A. J. STEWART. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 117:333-345.
- PRINGLE, C. M. 1990. Nutrient spatial heterogeneity: effects on community structure, physiognomy, and diversity of stream algae. *Ecology* 71:905-920.
- REICE, S. R., R. C. WISSMAR, AND R. J. NAIMAN. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management* 14:647-659.
- RIBER, H. H., AND R. G. WETZEL. 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnology and Oceanography* 32:1181-1194.
- ROSE, F. L., AND C. E. CUSHING. 1970. Periphyton: autoradiography of zinc-65 adsorption. *Science* 168:576-577.
- SAS INSTITUTE INC. 1988. SAS/STAT user's guide. Release 6.03 edition. SAS Institute Inc., Cary, North Carolina.
- SEDELL, J. R., G. H. REEVES, F. R. HAUER, J. A. STANFORD, AND C. P. HAWKINS. 1990. Role of refugia in recovery from disturbance: modern fragmented and disconnected river systems. *Environmental Management* 14:711-724.
- SHOAF, W. T., AND B. W. LIUM. 1976. Improved extraction of chlorophyll *a* and *b* from algae using dimethyl sulfoxide. *Limnology and Oceanography* 21:926-928.
- SIEGFRIED, C. A., AND A. W. KNIGHT. 1977. The effects of washout in a Sierra foothill stream. *American Midland Naturalist* 98:200-207.
- SOMVILLE, M., AND G. BILLEN. 1983. A method for determining exoproteolytic activity in natural waters. *Limnology and Oceanography* 28:190-193.
- 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. 1990. Recovery of lotic periphyton communities after disturbance. *Environmental Management* 14:589-604.
- STEINMAN, A. D., C. D. MCINTIRE, S. V. GREGORY, G. A. LAMBERTI, AND L. ASHKENAS. 1987. Effect 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., P. J. MULHOLLAND, A. V. PALUMBO, T. E. FLUM, AND D. L. DEANGELIS. 1991. Influence of nutrients and grazing on the resilience of lotic ecosystems to a light elimination disturbance. *Ecology* (in press).
- STEINMAN, A. D., P. J. MULHOLLAND, A. V. PALUMBO, T. E. FLUM, J. W. ELWOOD, AND D. L. DEANGELIS. 1990. Resistance of lotic ecosystems to a light elimination disturbance: a laboratory stream study. *Oikos* 58:80-90.
- STEVENSON, R. J. 1984. Procedures for mounting algae in a syrup medium. *Transactions of the American Microscopical Society* 103:320-321.
- STEVENSON, R. J., R. SINGER, D. A. ROBERTS, AND C. W. BOYLEN. 1985. Patterns of epipellic algal abundance with depth, trophic status, and acidity in poorly buffered New Hampshire lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1501-1512.
- U.S. ENVIRONMENTAL PROTECTION AGENCY. 1983. Methods for chemical analysis of water and wastes. Report number EPA-600/4-79-020, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio.
- WEBSTER, J. R., J. B. WAIDE, AND B. C. PATTEN. 1975. Nutrient recycling and stability of ecosystems. Pages 1-27 in F. G. Howell, J. B. Gentry, and M. H. Smith (editors). *Mineral cycling in southeastern ecosystems*. U.S. Energy Research and Development Administration. Washington, D.C.
- WEBSTER, J. R., M. E. GURTZ, J. J. HAINS, J. L. MEYER, W. T. SWANK, AND J. B. WALLACE. 1983. Stability of stream ecosystems. Pages 355-395 in J. R. Barnes and G. W. Minshall (editors). *Stream ecology: application and testing of general ecological theory*. Plenum Press, New York.

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