

Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season

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Abstract. Field experiments were conducted to examine the effects of disturbance frequency on invertebrates and periphyton colonizing bricks in a third order Rocky Mountain (USA) stream. After an initial colonization period (30 days), sets of bricks were turned over at intervals of 0, 3, 9, 27, or 54 days. Invertebrate species richness and density were reduced as disturbance frequency increased. These trends were evident for both seasons (summer and fall) and sites (open vs. closed canopy). Invertebrate species diversity (H') displayed no effect during the fall experiment; however, H' was reduced at high frequencies of disturbance during the summer experiment. *Baetis tricaudatus* was the most abundant invertebrate on the substrata at both sites and seasons. *Alloperla*, *Baetis*, *Cinygmula*, Chironomidae, *Drunella grandis*, *Hydropsyche*, and *Seratella tibialis* increased in absolute abundances as disturbance frequency decreased. Four other abundant taxa (*Capnia*, *Cleptelmis*, *Glossosoma*, and *Isoperla*) displayed no clear response to disturbance in either absolute or relative abundances. Species in low abundance tended to colonize only the less frequently disturbed bricks. During both seasons, periphyton biomass increased as disturbance frequency decreased at the open canopy site, while no trend was apparent at the closed canopy site. Periphyton accumulation monitored over time and among treatments revealed that frequent disturbances maintained low standing crops at an open canopy site. These data suggest that disturbance frequency can directly influence the benthic community at the scale of individual rock "islands" by reducing invertebrate richness, total animal density, and periphyton biomass. The effect of disturbance on species diversity (H') was seasonal, further emphasizing the importance of considering seasonality in stream field studies.

Key words: disturbance, community structure, invertebrate, streams, season, canopy cover, periphyton.

A variety of mechanisms have been posited to be important in the structuring of stream benthic communities. Opinions differ as to whether biotic or abiotic factors play a greater role (e.g., Hart 1983, Reice 1984, 1985), although both have been shown to be important (McAuliffe 1983, 1984, Shiozawa 1983). Recent studies have demonstrated that physical disturbance may be a mechanism controlling stream community structure. Reice (1984) suggests the primacy of physical disturbance (i.e., floods) in maintaining nonequilibrium conditions and thus high diversity in streams. Hemphill and Cooper (1983) document how disturbance may override the competitive interactions between two lotic filter-feeders. They found that the abundance of *Simulium virgatum* increased and *Hydropsyche oslari* decreased on substrata that were periodically disturbed, while on substrata left undisturbed *H. oslari* (the superior competitor) remained dominant.

Physical disturbance, such as a spate, may affect not only invertebrates but also periphyton

assemblages and biomass in streams. The effect is due mainly to severe scouring of the substratum (Fisher et al. 1982, Guntow 1955). Periphyton is an important food resource for invertebrates (Gregory 1983), and numerous studies have shown dramatic effects on periphyton by invertebrate grazers. Hart (1985) documents how the sessile caddisfly, *Leucotrichia*, actually "farms" the periphyton resource within its territory. Lamberti and Resh (1983) and Vaughn (1986) demonstrate that algal standing crops directly influence grazer distribution. Richards (1986) found that densities of baetid nymphs on rocks were correlated to periphyton abundance. Gregory (1983) and Lamberti and Moore (1984) review plant-animal interactions in streams. Few stream studies, however, have examined the effect of disturbance frequency on periphyton standing crops on stones (but see Kaufman 1982).

On a larger scale, Ward and Stanford (1983) suggest that Connell's (1978) intermediate-disturbance hypothesis—that high species diver-

sity is maintained through intermediate frequencies of disturbance—may pertain to lotic ecosystems. As disturbance frequency decreases, competitive exclusion becomes an important community structuring mechanism, and species diversity is reduced by monopolization of resources by the competitive dominant(s). The opposite extreme, frequent disturbance, also tends to reduce species diversity because only species that have evolved appropriate life history patterns are capable of maintaining viable populations. Reice (1985) contends that the hypothesis does not apply to lotic systems, because a competitive hierarchy has yet to be demonstrated in streams (but see McAuliffe 1983, 1984).

Streams may indeed go through periods of environmental equilibrium and nonequilibrium. Competition and other biotic factors (e.g., predation) probably are important in structuring stream benthic communities during stable environmental conditions, while nonequilibrium conditions operate in a changing environment (see Minshall et al. 1985). In fact, Reice (1984, 1985) states that physical disturbance, in the form of a spate, is an important reset mechanism in streams. In a recent paper, Minshall and Petersen (1985) suggest that stream macroinvertebrate communities on rock "islands" (sensu MacArthur and Wilson 1963, 1967) are the "result of an interplay between stochastic and deterministic forces", and that during development, communities on rocks are initially at a stage of species nonequilibrium where environmental factors predominate. Over time, stones reach a state of dynamic species equilibrium, whereupon biotic factors become important. If this is the case then the phasing of disturbance becomes important because a certain time is needed for equilibrium conditions to occur (Abugov 1982).

Our study had three primary objectives: 1) To quantify changes in the macroinvertebrate communities colonizing bricks subjected to different frequencies of disturbance at an open canopy site and a closed canopy site. 2) To examine seasonal differences in the responses of invertebrate assemblages to disturbance. 3) To quantify differences in periphyton biomass on substrates treated to different disturbance regimes and to monitor changes in periphyton standing crop among the different disturbance frequencies over time. A separate paper will

address the impact of disturbance frequency on the diatom community colonizing individual substrata.

Methods

Study sites

Experiments were conducted at three sites within the Mink Creek drainage, a 3rd order stream located in the Caribou National Forest, Bannock County, Idaho (112°23'W longitude; 42°48'N latitude). The climate of the area is characterized by hot dry summers and long cold winters. The three sites, each approximately 20 meters in length, were similar in all measured physical and chemical parameters except the amount of solar radiation reaching the stream bottom. An unshaded area of the main stem provided an open canopy site (OCS), and a heavily shaded reach on the East Fork was a contrasting closed canopy site (CCS). Another unshaded site was the South Fork (SFS). Physically, the stream bottom at each site was characterized by a pebble-cobble matrix. Mean current velocities ranged from 55 cm/s at OCS, to 64 cm/s at CCS, and 141 cm/s at SFS. Little variation in stream discharge occurred during the study periods. During summer, daily maximum stream temperatures were 18–20°C and minima were 8–12°C. Water chemistry was analyzed in the field with a HACH kit. The sites were similar chemically with pH at 8.9, hardness at 220 mg/L (CaCO₃), ortho-phosphate at 1.0–1.7 mg/L (PO₄), nitrate at 13–17 mg/L, and turbidity at 10 FTUs. Solar radiation was measured with a Lambda light meter (Model LI-185). During the experimental periods, solar radiation at the closed canopy site (CCS) ranged from 80 to 260 μE/m²/s, while at the open canopy sites (OCS and SFS) levels were 310–2180 μE/m²/s. Riparian vegetation at CCS was predominantly hawthorn (*Crataegus*), dogwood (*Cornus stolonifera*) and aspen (*Populus tremuloides*) whereas at OCS and SFS riparian vegetation was dominated by sagebrush (*Artemisia tridentata*) and willow (*Salix exigua*).

Disturbance experiments

Field experiments were conducted at OCS and CCS during fall 1983 and summer 1984 to account for seasonal changes in abundance occurring within the invertebrate assemblage. The

fall experiment began on 1 July 1983 and was completed 14 November 1983. The summer experiment began on 4 June 1984 and was completed 30 August 1984. Bricks were used as substrata to simplify experimental manipulation and to minimize physical variation (e.g., substratum complexity) among samples. Artificial substrata have been used extensively in empirical stream studies (e.g., Hart 1978, Lamberti and Resh 1985, Shaw and Minshall 1980, Wise and Molles 1979), and their use in freshwaters has been reviewed by Rosenberg and Resh (1982). We used locally-manufactured ($4 \times 10 \times 15$ cm) half-bricks (Suenaga Company, Pocatello, Idaho). A pilot study during June 1983 examined colonization differences by invertebrates between the half-bricks and natural substrata. No significant differences were observed in species richness, animal density, or species diversity (Chi square; $p < 0.05$, $n=6$). In addition, Tuchman and Stevenson (1980) have documented good comparability of diatom communities between clay tiles and natural mineral substrata in a Michigan stream.

Before each experiment, 50 bricks were placed in the stream at each site (OCS and CCS). Bricks were labelled with a numbered plastic tag stuck to a brick's side with epoxy glue. The bricks were placed at least 0.5 m away from each other to minimize accidental disturbance to neighboring bricks during the manipulative phase of an experiment. Variation observed in completion times of colonization by macroinvertebrates ranged from eight days to over 60 days (see review by Minshall 1984). We allowed substrata to be colonized for 30 days before experimental manipulation.

During this 30-day period, current velocities were measured immediately above each brick using a small Ott C-1 current meter, and a detailed map of brick locations was drawn for each site. After the colonization period, groups of 10 randomly selected bricks within each site were disturbed at frequencies of every 0, 3, 9, 27, or 54 days, during the fall experiment, and every 0, 3, 9, or 27 days, during the summer experiment. A disturbance was created by physically turning over an individual brick and placing it upside down in the identical location. No invertebrates were intentionally removed from the brick, and care was taken to minimize disturbing the substratum around an individual brick. This form of disturbance was

meant to be analogous to "natural" stone tumbling in streams, in that once being disturbed, the top of the brick would subsequently become the bottom until the next disturbance event. During each season, all bricks were in the stream for the entire experimental period. Only the frequency of disturbance was different among groups of bricks.

At the end of each experiment, bricks were sampled for invertebrates and periphyton. Individual bricks were collected by placing a fine-meshed net (250 μ m) directly downstream of the brick and quickly placing the brick into the net. All invertebrates from the brick and the net contents were preserved in 10% formalin. In the laboratory, invertebrates were identified to species (except for chironomids, which were identified to family) and enumerated using a dissecting microscope at $10 \times$ magnification.

Immediately following the collection of invertebrates, three 5-cm² samples of periphyton were removed from each brick by scrubbing a known area using a technique derived from Stockner and Armstrong (1971). A 35-ml syringe tube was reduced to 5 cm in length by removing the "needle" end, and a neoprene gasket (made from 0.5-cm wet-suit material) was glued to the flared "plunger" end. During sampling, the apparatus was pressed onto the substratum surface, the rubber gasket creating a seal, and the periphyton was scrubbed into a slurry with a coarse brush. This slurry was then pipetted into a storage vial, placed on ice, and returned to the laboratory. In the laboratory, samples were vacuum filtered (103.5 kPa) through 2.4-cm Whatman GF/C filters (pore size 0.45 μ m), and immediately stored at -20°C for chlorophyll *a* analysis.

Chlorophyll *a* was extracted by grinding the previously frozen filter in 3 ml of reagent-grade acetone (100%), transferring the extractant to a centrifuge tube, filling the tube to 10 ml with acetone, and refrigerating the mixture at 4°C for 24 hr. Chlorophyll *a* and phaeopigment concentrations were determined with a Turner Model 111 fluorometer by multiplying the fluorescence readings by a calibration factor derived with a Beckman Instruments Model-DB spectrophotometer (Anonymous 1980). The remaining solution from each sample was then used for measurement of total organic matter (ash-free dry weight). Samples were oven-dried to constant weight at 60°C , cooled to room tem-

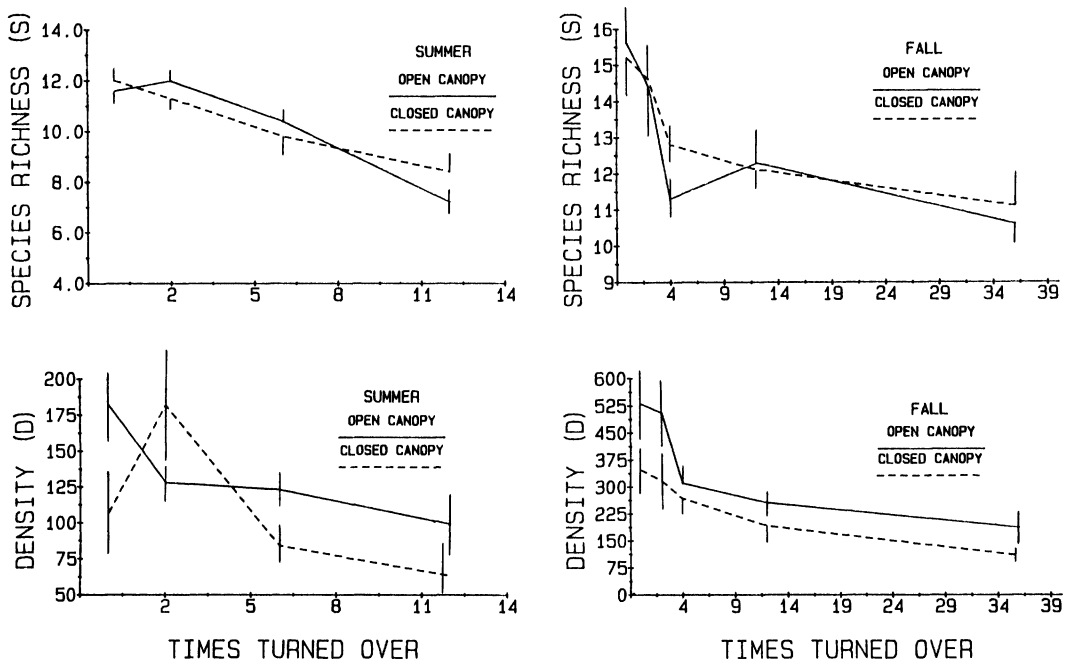


FIG. 1. Effects of disturbance frequency (times brick turned over) on invertebrate species richness (S) and animal density (D). Bars represent standard error of the mean. $n=7$. F values for treatment effects: CCS fall $R=5.31$, $p>0.003$; CCS fall $D=2.68$, $p>0.05$; OCS fall $R=4.34$, $p>0.008$; OCS fall $D=8.66$, $p>0.0001$; CCS summer $R=6.33$, $p>0.006$; CCS summer $D=4.51$, $p>0.04$; OCS summer $R=25.7$, $p>0.0001$; OCS summer $D=3.51$, $p>0.04$.

perature, weighed, ashed at 550°C for 2 hr, rehydrated, redried at 60°C, and reweighed.

Statistical analysis consisted mainly of One-Way Analysis of Variance (ANOVA) on transformed $[\log(x+1)]$ data sets (Zar 1984) using the "PROC GLM" procedure of the Statistical Analysis System (SAS Institute 1982). Treatment means were then discriminated with Tukey's HSD (honestly significant difference) test with $\alpha = 0.05$ (Zar 1984). All values are expressed as nontransformed means. Other statistical tests performed are addressed in the text.

Periphyton accumulation experiment

During the summer of 1984 an experiment was conducted at the unshaded South Fork Site (SFS) to quantify changes in periphyton standing crop within and between treatments over time. Labeled bricks were placed into the stream in a 4×7 matrix configuration (i.e., seven rows of four bricks each). Groups of seven bricks (one from each row) were disturbed, as described above, at frequencies of every 0, 3, 9, or 27 days, respectively. Before each distur-

bance one periphyton sample was removed from the brick and analyzed for chlorophyll *a*. For example, a brick that was turned over every three days had one periphyton sample removed every three days immediately before being turned over. The experiment was terminated on day 54. These data were analyzed first using a randomized block ANOVA (Zar 1984) with no differences found within treatments among rows. Therefore, treatments were pooled by date and a Two-Way Analysis of Variance was performed on the transformed $[\log(x+1)]$ data set as described above.

Results

Macroinvertebrate community response to disturbance frequency

Frequent disturbances maintained mean species richness and mean total densities of invertebrates at low levels. As the frequency of disturbance decreased, species richness and density significantly increased (Fig. 1). These trends were similar for both the fall and summer experiments at both sites. Generally, there

was an addition of five species and a two-fold increase in total numbers as experimental disturbance intervals decreased from every three days to zero days (Fig. 1). In addition, Tukey's HSD test (Zar 1984) revealed no differences in species richness or animal density among the low disturbance frequencies, i.e., ≥ 27 days (Fig. 1). This implies that physical disturbance had a profound effect on the invertebrate community only at the more frequent intervals, i.e., < 27 days, by reducing species richness and invertebrate densities.

A different outcome was observed for species diversity (H') (Fig. 2). Species diversity was calculated using the Shannon-Wiener Index (Shannon and Weaver 1949, Pielou 1966). This index takes into account both the number of species and their respective abundances. When used in conjunction with other community parameters, e.g., species richness and total density, the index can aid in providing information into causal mechanisms of community structuring phenomena. The frequency of disturbance had no effect (at CCS $p > 0.07$, at OCS $p > 0.07$) on H' during the fall experiment regardless of site; however, during the summer experiment H' increased as disturbance frequency decreased (at CCS $p < 0.02$, at OCS $p < 0.04$; Fig. 2).

A closer look at invertebrate abundance and richness, between seasons and by treatment, reveals a possible explanation for the seasonal modification of disturbance frequency on H' . Greater numbers (as much as $3\times$) and greater species richness (approximately three additional species) occurred during the fall experiment (Fig. 1). Invertebrate taxa also were more evenly divided in the fall than in summer as indicated by equitability values (after Lloyd and Ghelardi 1964) of 0.60 and 0.52, respectively. Thus, seasonal changes in macroinvertebrate abundances may modify the effects of disturbance frequency on community parameters, because at times of high density, space may be limiting and may indirectly influence colonization rates. For example, an open patch (i.e., disturbed stone) may be colonized much more quickly during periods of high animal abundance than at times of low animal abundance. Two recent studies (Ciborowski and Clifford 1984, Lake and Doeg 1985) showed that lotic invertebrates can quickly colonize substrata, and that relatively little change occurred in species richness and

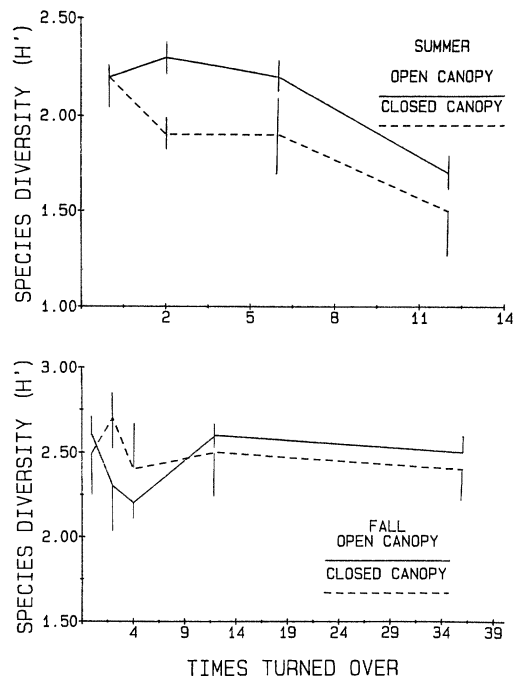


FIG. 2. Effects of disturbance frequency (times brick turned over) on invertebrate species diversity (H'). Bars represent standard error of the mean. $n=7$. F values for treatment effects: CCS summer = 2.01, $p > 0.02$; OCS summer = 7.2, $p > 0.04$; CCS fall = 0.18, $p > 0.95$; OCS fall = 2.08, $p > 0.07$.

density after only two days of colonization. This implies that a greater frequency of disturbance, perhaps even a 24-hr interval or less, is needed to show an effect on the invertebrate community especially during periods of high animal density.

Macroinvertebrate taxon response to disturbance frequency

Ten taxa formed greater than 90% of the community assemblage colonizing the bricks at a site (Table 1); the remaining taxa typically were represented by only a few individuals. Data analysis was conducted on these 10 most abundant taxa. The grazing mayfly, *Baetis tricaudatus*, was predominant on all bricks regardless of site or disturbance frequency. This species made up about 30% of the community at CCS and about 60% at OCS. *Baetis* increased in absolute numbers as disturbance frequency decreased at both sites and during both seasons; however, its relative abundance displayed no response. Six

TABLE 1. Effects of disturbance on absolute and relative numbers (per brick) of the 10 most abundant taxa, by site and by season. Asterisks mark taxa whose absolute numbers were significantly different at different disturbance frequencies: * significant at $p=0.10$, ** significant at $p=0.05$. Relative abundances were not significantly different at $p=0.05$.

Species	Disturbance Interval (days)									
	3		9		27		54		108	
	No.	%	No.	%	No.	%	No.	%	No.	%
OPEN CANOPY SITE—SUMMER										
<i>Baetis tricaudatus</i> *	37.6	38	44.2	36	53.6	42	78.6	43		
Chironomidae	33.0	33	40.2	33	34.5	27	53.0	29		
<i>Glossosoma</i> spp.	18.0	18	17.8	14	15.7	12	3.2	2		
<i>Alloperla</i> spp.**	2.6	3	3.4	3	2.7	2	19.8	12		
<i>Isoperla</i> spp.**	0.4	0	3.6	3	1.9	1	0.4	0		
<i>Drunella grandis</i> **	1.0	1	3.6	3	1.0	1	8.4	5		
<i>Serratella tibialis</i> **	1.0	1	3.0	2	6.5	5	9.8	5		
<i>Cleptelmis</i> spp.	1.2	1	3.1	2	5.2	4	1.6	1		
<i>Hydropsyche</i> spp.	1.0	1	0.6	0	1.0	1	0.9	0		
<i>Simulium</i> spp.	0	0	0	0	0	0	0	0		
Others	3.0	3	4.0	3	5.0	4	4.0	2		
CLOSED CANOPY SITE—SUMMER										
<i>Baetis tricaudatus</i>	49.8	79	52.6	63	117	64	65.5	61		
Chironomidae**	3.4	5	10.6	12	22.8	12	12.8	12		
<i>Glossosoma</i> spp.	0	0	0	0	0	0	0	0		
<i>Alloperla</i> spp.	1.6	2	1.0	1	3.2	2	1.5	1		
<i>Isoperla</i> spp.	1.0	1	0.8	1	1.0	0	1.8	1		
<i>Drunella grandis</i> *	0	0	0	0	0	0	0.75	1		
<i>Serratella tibialis</i> *	0	0	3.4	4	3.8	2	5.5	5		
<i>Cleptelmis</i> spp.	0	0	1.6	2	1.2	1	1.0	1		
<i>Hydropsyche</i> spp.*	1.4	2	5.2	6	8.8	5	8.0	7		
<i>Simulium</i> spp.*	0	0	1.6	2	11.5	6	4.5	4		
Others	7.0	11	7.0	9	11.0	6	5.0	5		
OPEN CANOPY SITE—FALL										
<i>Baetis tricaudatus</i> *	50	27	59	23	114	35	126	25	145	27
Chironomidae**	56	30	67	26	41	13	114	23	141	27
<i>Glossosoma</i> spp.	32	17	49	19	100	31	123	24	86	16
<i>Alloperla</i> spp.	12	6	19	7	22	7	34	7	33	6
<i>Isoperla</i> spp.*	13	7	19	7	18	5	34	7	33	6
<i>Drunella grandis</i> **	1	0	2	1	2	1	4	1	8	2
<i>Serratella tibialis</i> **	7	4	19	7	6	2	28	5	40	7
<i>Hydropsyche</i> spp.*	1	0	1	0	2	2	4	1	4	1
<i>Capnia</i> spp.	8	4	4	2	2	1	4	1	6	1
<i>Cinygmula</i> spp.	2	1	2	1	7	2	9	2	9	2
Others	7	4	18	7	6	2	20	4	21	4
CLOSED CANOPY SITE—FALL										
<i>Baetis tricaudatus</i>	53	49	102	53	143	53	165	52	211	61
Chironomidae**	5	5	8	4	10	4	17	5	16	5
<i>Glossosoma</i> spp.**	1	1	2	2	2	1	3	1	1	0
<i>Alloperla</i> spp.	5	5	7	4	9	3	9	3	11	3
<i>Isoperla</i> spp.**	5	5	6	3	12	4	11	3	7	2
<i>Drunella grandis</i>	0	0	0	0	0	0	0	0	0	0
<i>Serratella tibialis</i>	5	5	7	4	10	4	9	3	13	4
<i>Hydropsyche</i> spp.**	1	1	3	2	6	2	7	2	15	4
<i>Capnia</i> spp.	8	7	8	4	10	4	10	3	7	2
<i>Cinygmula</i> spp.**	9	8	11	6	21	8	28	9	24	7
Others	9	9	36	19	45	17	60	19	42	12

other taxa (*Hydropsyche*, *Alloperla*, *Drunella grandis*, *Cinygmula*, Chironomidae, and *Serratella tibialis*) increased in absolute abundances as the frequency of disturbance decreased, although again no response was evident in relative numbers (Table 1). Clearly, frequent disturbance reduced the absolute abundances of these organisms. The lack of response in their relative numbers may be attributed to the increase in species richness and total numbers on the less disturbed substrata (Fig. 1).

The remaining four abundant taxa (*Capnia*, *Cleptelmis*, *Glossosoma*, *Isoperla*) showed no clear response to disturbance in either absolute or relative abundances. At OCS, *Glossosoma* decreased in absolute and relative abundance as disturbance frequency decreased during the summer experiment; however, this species increased in relative abundance during the fall experiment. The density of *Glossosoma* also was greater (2–4 \times) during the fall experiment (Table 1). No other taxa showed a positive response to an increase in disturbance. This suggests that these abundant taxa are capable of colonizing the bricks even at the three-day disturbance interval. As mentioned above, species richness increased as disturbance frequency decreased indicating that frequent disturbance may have a greater impact on rare taxa. Indeed, a greater number of rare species were present on the less frequently disturbed bricks (Fig. 1).

Periphyton response to disturbance frequency

The responses of periphyton standing crops to disturbance were similar between seasons but different between sites (Fig. 3). At OCS, chlorophyll *a* levels increased as disturbance frequency decreased (fall $p < 0.0001$, summer $p < 0.01$). At this site, chlorophyll *a* values increased from 0.22 to 0.74 $\mu\text{g}/\text{cm}^2$ in the summer experiment and from 5.6 to 11.3 $\mu\text{g}/\text{cm}^2$ in the fall experiment as the frequency of disturbance decreased. Indeed, although all bricks were in the stream for the same length of time per season, low algal standing crops were maintained on the frequently disturbed substrata. At the closed canopy site no differences were observed between treatments during the summer experiment ($p > 0.12$). However, during the fall experiment an increase in chlorophyll *a* was observed on substrata at the intermediate frequency of disturbance ($p < 0.01$) although no differences existed between the other treat-

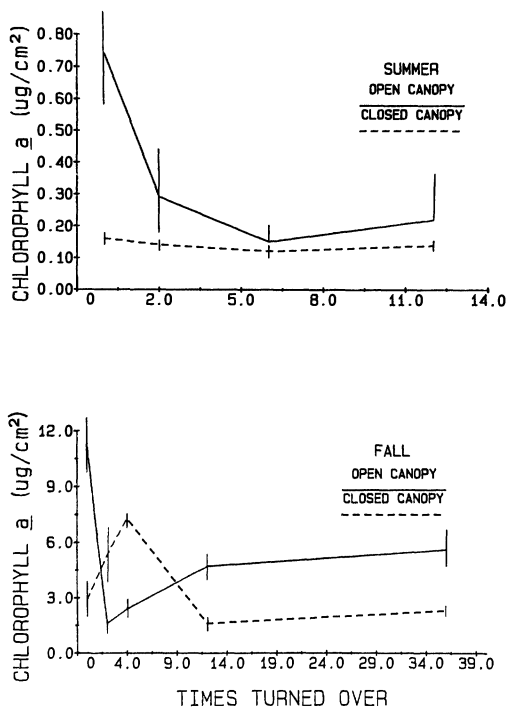


FIG. 3. Effects of disturbance frequency (times brick turned over) on periphyton standing crop as chlorophyll *a* ($\mu\text{g}/\text{cm}^2$). Bars represent standard error of the mean. $n=10$. F values for treatment effects: CCS summer = 2.08, $p > 0.12$; OCS summer = 4.12, $p > 0.01$; CCS fall = 4.2, $p > 0.01$; OCS fall = 13.6, $p > 0.0001$.

ments ($p=0.05$). Chlorophyll *a* values at CCS ranged from 0.14 to 0.16 $\mu\text{g}/\text{cm}^2$ during the summer experiment and from 1.6 to 7.3 $\mu\text{g}/\text{cm}^2$ during the fall experiment. The results observed at CCS are not surprising because, typically, the organic layer on rocks in forested streams consists primarily of bacteria, fungi, and detritus, while in open canopy streams this layer is dominated by diatoms and filamentous algae (Rounick and Winterbourn 1983). In addition, the higher chlorophyll values observed during the fall experiment at both sites may be attributed to the increased solar radiation reaching the stream after autumn leaf fall (Sumner and Fisher 1979, Triska et al. 1983), and to the slower metabolic rates of aquatic insects, i.e., reduction in grazing intensity, in this season (Butler 1984). Correlation coefficients between chlorophyll *a* values and ash weights of individual samples were highly significant (range 0.74–0.85) within seasons and sites, sug-

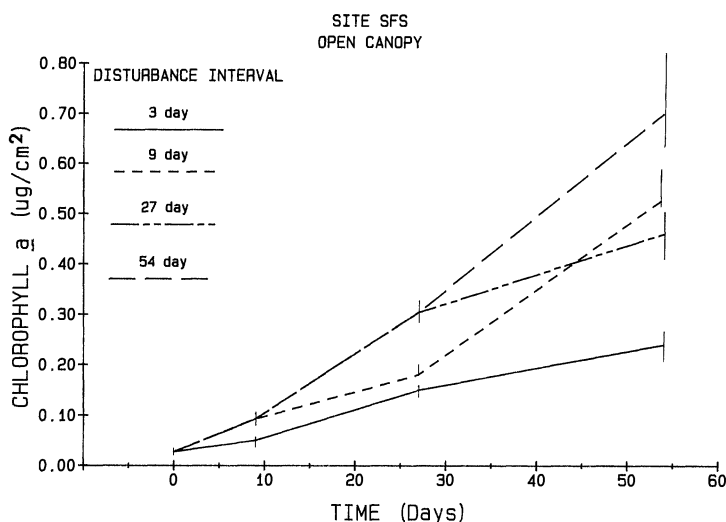


FIG. 4. Accumulation of periphyton standing crop [as chlorophyll *a* ($\mu\text{g}/\text{cm}^2$)] over time among treatments (disturbance frequencies). $n=7$ for each sampling date. F values: treatment = 9.88, $p>0.0001$; date = 117.04, $p>0.0001$; treatment*date = 5.77, $p>0.0001$. Bars represent standard error of the mean.

gesting that chlorophyll *a* accurately represented periphyton biomass on these substrates.

Periphyton accumulation experiment

The study at SFS that monitored periphyton accumulation within and between treatments over time revealed the influence of physical disturbance on stream periphyton development. All independent factors (i.e., treatment, time, and treatment*time) had significant effects on the dependent factor, chlorophyll *a* (Fig. 4). Accumulation of periphyton was greatest on substrata treated to low frequencies of disturbance, while high disturbance frequencies maintained low periphyton standing crops. On the last sampling date, chlorophyll *a* ranged from $0.21 \mu\text{g}/\text{cm}^2$ on the high frequency substrates to $0.65 \mu\text{g}/\text{cm}^2$ on the low frequency substrates (Fig. 4). These values are consistent with those found for the summer experiment at OCS (Fig. 3). Clearly, physical disturbance has the potential to inhibit periphyton development in stream systems.

Discussion

The results of this study demonstrate that physical disturbance, and the frequency thereof, can have dramatic effects on benthic com-

munity structure in streams. In all four cases (2 sites \times 2 seasons) invertebrate species richness and densities decreased as disturbance frequency increased (Fig. 1). These findings are contradictory to those of Reice (1984, 1985), who found no direct impact of disturbance frequency on richness, although significant reductions in total numbers were noted immediately following disturbance. The two studies did differ somewhat in method. One difference is that Reice's (1984, 1985) study consisted of two disturbance events, while ours contained disturbance events periodically throughout the experiments. Another is the unit of sample. In our study the sample unit consisted of individual uniform-sized substrates, while Reice (1984, 1985) used cobble-filled baskets. This difference in scale is of utmost importance when interpreting the results from any study. McAuliffe (1984) demonstrates nicely how the scale of sampling must coincide with the scale of the processes of influence. He found significant interactions only at the smallest unit of scale: individual stones. In addition, individual rocks have been considered as sampling units in many stream studies (e.g., Behmer and Hawkins 1986, Minshall and Petersen 1985, Sheldon 1977, Stout and Vandermeer 1975, Trush 1979). Our study augments this data base and further suggests that physical disturbance is an impor-

tant structuring mechanism at the unit of individual stone "islands". The use of different scales or patch sizes is important in fully understanding community dynamics in streams.

One item of interest is that both this study and Reice's (1984, 1985) found no significant impact on diversity (H'); however, in the present study a seasonal component to the disturbance mechanism was found. During summer, when the richness, equitability, and density of invertebrates were low (Fig. 1), species diversity significantly increased as disturbance frequency decreased (Fig. 2). During the fall experiments, when invertebrate richness, equitability, and density were high (Fig. 1), no impact on diversity was observed (Fig. 2). The difference in the responses of these parameters implies that the subsequent colonization of intensely disturbed patches (stones) may be dependent on the abundance of animals. When space is limiting, e.g., during periods of high animal abundance, these highly disturbed patches may be quickly and completely colonized in a matter of hours. In fact, Carl Richards (Idaho State University, personal communication) found that the *Baetis* colonizing his experimental substrata could reach equilibrium numbers in less than a day. It can be speculated further that at times of low invertebrate abundance and equitability, physical disturbance may have a greater impact on the community because of the reduced probability of less abundant taxa to drift onto an open patch. In addition, at periods of low animal abundance, space is not limiting, emigration rates from nondisturbed stones may be low, and thus colonization rates on recently disturbed stones may be slower. These results indicate the importance of considering seasonality when designing a stream field study. The frequency, as well as the magnitude, of disturbance is influential in the structuring of stream invertebrate communities on rocks, and under certain conditions physical disturbance can be an important "reset" mechanism (Reice 1984, 1985). However, the impact of disturbance can be modified both spatially and temporally.

The results concerning periphyton development somewhat confound clear interpretation of the invertebrate results, but again stress the importance of measuring all factors of influence. At CCS no disturbance effect was apparent, whereas at OCS periphyton standing crop

increased significantly as disturbance frequency decreased (Fig. 3). The study at SFS indicated that periphyton development is inhibited by frequent disturbances (Fig. 4). Speculation arises as to whether the actual physical disturbance or the low periphyton levels caused the reduction in invertebrate species richness and density at OCS. The correlation between chlorophyll *a* (as a measure of food quantity) and animal density was high ($r=0.87$) at OCS. The overall number of invertebrates also was greater at OCS than at CCS, corroborating the results found by Behmer and Hawkins (1986) and Hawkins et al. (1982). Further, most grazer species, e.g., *Glossosoma*, were predominant only at OCS. Plant-animal interactions in lotic ecosystems are known to be complex (Gregory 1983, Lamberti and Moore 1984) in that either organism may influence the other (Lamberti and Resh 1983). On the other hand, disturbance frequency directly influenced invertebrate numbers and richness at CCS. Two possibilities exist. One is that a factor other than disturbance frequency was responsible for the trends observed at CCS but was not analyzed. For example, perhaps the less disturbed substrata retained more detrital food or richer growths of fungi and bacteria which were undetected by our methods. Another possibility is that the physical disturbance, by directly influencing periphyton development, also directly influenced the invertebrate community. This implies the necessity for further research into the colonization dynamics of stream macroinvertebrates in relation to disturbance and resource availability.

Our study may not be an adequate test of Connell's (1978) hypothesis because Mink Creek is dominated primarily by mobile species and the hypothesis is based on communities that are inhabited by sessile organisms, for example, tropical forests (Connell 1978) or the marine intertidal (Dayton 1971, Paine 1971, Sousa 1979a, 1979b). The results from our study do provide evidence towards the theory on macroinvertebrate community development proposed by Minshall and Petersen (1985), and further emphasize the importance of frequent physical disturbance as a reset mechanism. In our study species richness was reduced by frequent disturbance; and as disturbance became less frequent (e.g., every 27 days) species richness increased (Fig. 1). There also were no sig-

nificant differences between the 27-day disturbance interval and the 54-day disturbance interval (Tukey's test, $p=0.05$). This implies that frequent disturbances (e.g., >9 but <27 -day intervals) can maintain the system in a phase of nonequilibrium, but that equilibrium conditions can be attained if disturbances are less frequent (e.g., >27 -day intervals). More field research is needed to ascertain whether natural stream substrata are disturbed at frequent enough intervals to maintain the system in a permanent state of nonequilibrium as suggested by Reice (1984, 1985).

Three major conclusions from this study are: 1) Physical disturbance, by acting directly on invertebrates or indirectly through the alteration of the food resource, can be a significant reset mechanism of invertebrate community development. Species richness and invertebrate density were reduced at high frequencies of disturbance. 2) Disturbance frequency can maintain low periphyton standing crops, although the effect appears to be dependent on overhead canopy cover. No quantifiable effect on periphyton biomass was detected at CCS. 3) Frequent disturbances can maintain nonequilibrium conditions on rock "islands" in lotic systems; however, this influence may be modified by seasonal fluctuations in invertebrate abundance. The impact of disturbance on invertebrate diversity was influenced by season.

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