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RESISTANCE AND RESILIENCE OF LOTIC ALGAL COMMUNITIES: IMPORTANCE OF DISTURBANCE TIMING AND CURRENT[1]

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Abstract. We examined effects of disturbance timing on resistance and resilience of epilithic algal communities growing in fast- (29 cm/s) and slow- (12 cm/s) current outdoor experimental stream channels in Kentucky, USA that were either left undisturbed (control) over 33 d following a simulated spate, or were subjected to an additional spate after either 9, 18, 27, or 33 d. On day 33, all channels were subjected to a final spate to assess effects of short-term disturbance history on resistance, independently of seasonal influences. Succession proceeded from a sparsely populated community dominated by a small, monoraphid diatom (*Achnanthes minutissima*) immediately after the initial spate, to dominance by dense floating mats of filamentous green algae (Zygnematales: *Mougeotia* and *Spirogyra*) and *Synedra* spp. by day 21–24. Resistance was generally lower in slow-current communities, both in terms of cell-density reduction and displacement of taxonomic structure, than in fast-current communities. Resistance in slow-current communities varied temporally, with communities least resistant on day 18, when community composition and physiognomy was changing rapidly, and on day 33, when green algal mats began to senesce. On day 33, slow-current communities that had not been recently disturbed (control, D9) exhibited greatest spate-induced loss of algal biomass. Additionally, slow-current communities with high pre-disturbance phaeophytin content (an indicator of algal senescence) also changed most in diatom assemblage structure across the final spate. No such relationship was noted in fast current, suggesting that autogenic factors influenced communities in slow current more than those in fast. Resilience was higher in slow-current communities than in fast current, with disturbed communities reaching biomass and taxonomic structure similar to controls after 3–9 d. High resilience in slow current resulted from enhanced reproduction in some populations following spate-induced biomass reduction and presumed release from nutrient and light limitation, and low shear stress relative to fast-current channels where biomass accrual was limited by current. Interactions between disturbance timing, successional state, and habitat affect the susceptibility of epilithic algal communities to disturbance and likely influence temporal and spatial heterogeneity in stream ecosystems.

Key words: current; diatoms; disturbance history; disturbance timing; epilithic algae; Kentucky; resilience; resistance; spates; streams; succession; zyngematalean green algae.

INTRODUCTION

Disturbance is an important determinant of community structure and dynamics (e.g., Sousa 1984, Pickett and White 1985, Petraitis et al. 1989). Since communities are not static entities and change both structurally and physiologically during succession, disturbance effects may vary with developmental state. Examples of such dependence can be found in the effects of fire (Romme 1982, Clark 1989) and windthrow (Sprugel 1976, Foster 1988) on forest communities, in effects of wave disturbance on marine intertidal (Sousa

1980, Paine and Levin 1981) and freshwater microalgal (Luttenton and Rada 1986, Peterson et al. 1990) communities, and in the effects of gamma radiation on cyanobacterial cultures (Conter et al. 1987). Community response to disturbance also varies spatially. Environmental patchiness within an ecosystem may affect community structure and function in ways that strengthen or reduce resistance and/or alter the rate and pattern of post-disturbance recovery.

Benthic algal communities in streams are periodically subjected to high-discharge events that vary in effect depending on their frequency and intensity (Tett et al. 1978, Biggs and Close 1989, Grimm and Fisher 1989, Stevenson 1990). These communities can change considerably in structural (Patrick 1976, Steinman and McIntire 1986, Peterson and Stevenson 1990) and physiological properties (Hamilton and Duthie 1984, Aizaki 1985, Steinman et al. 1988) during succession;

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thus the degree to which disturbance affects community structure and function may depend upon disturbance timing as well as intensity.

Lotic algal communities are affected by current, which may also influence their response to disturbance. Current influences algal immigration (Korte and Blinn 1983, Stevenson 1983, Stevenson and Peterson 1989), emigration (McIntire 1968, Bothwell et al. 1989), and reproduction (via variation in nutrient supply rates; Whitford and Schumacher 1961, Vilenken and Pertsov 1983, Horner et al. 1990), as well as attachment strength and community physiognomy (McIntire 1966, Reiter and Carlson 1986, Poff et al. 1990). Current-related differences in algal community structure and physiology may translate into differences in resistance and resilience.

Changes in dominance that occur during benthic microalgal succession in streams are driven by shifts from species that immigrate rapidly, or those that persist through disturbance but are poor competitors, to species that compete well under conditions of resource limitation within high-density, late-successional algal mats (McCormick and Stevenson 1991a, Stevenson et al. 1991, Peterson and Grimm 1992). In lotic systems, where spatial heterogeneity in current maintains an array of habitats and temporal variation in discharge results in periodic disturbance, both of these alternatives represent viable ecological strategies. Under such conditions, variation in disturbance frequency and intensity might strongly affect successional patterns, species-dominance hierarchies, and species diversity (Petraitis et al. 1989). Interactions between biotic processes and abiotic disturbance in streams can, therefore, provide insight into how patterns of temporal and spatial heterogeneity in ecosystems are generated and maintained.

In this study, we employed experimental stream channels, and exposed resident algal communities to simulated spates to examine the implications of temporal and spatial variation on the response of benthic algal communities to spates. Our specific objectives were (1) to determine if community resistance and/or resilience differed as a function of structural or physiological attributes associated with successional change, and (2) to determine how current regime influences these relationships.

We measured resistance in this study as the change in algal biomass and taxonomic structure across a disturbance. As Steinman et al. (1991) eloquently discussed, the choice of a resilience measure can greatly influence the way in which resilience is assessed. Resilience is often defined (e.g., Webster et al. 1975) as the ability of a system to return to some "reference" state following displacement by disturbance. In our system, however, the most appropriate measure of resilience was not return to pre-disturbance state, but rather convergence with a temporally changing undisturbed control community, because successional change

in benthic algae can occur rapidly (Stevenson 1984a, Oemke and Burton 1986, Stevenson et al. 1991). We assessed resilience both in terms of biomass parameters (i.e., cell numbers) and community composition. This option is often unavailable in studies of large-scale disturbance on short-lived organisms because a temporally appropriate reference state for community-structure comparisons does not exist (Stanley and Fisher 1992 but see Boulton et al. 1992).

METHODS

Study site and experimental design

This study was conducted at the University of Louisville's experimental stream facility in Bernheim Forest Nature Preserve (Bullitt County, Kentucky, USA). The facility draws water from Harts Run, a small second-order stream draining a basin of mixed hardwood forest. The headwaters of Harts Run are undisturbed and underlain by Devonian oil shale; the lower reaches, where the facility is located, cut through dolomitic limestone and carry waters that are circumneutral (pH = 7.35). During the study, NO_3-N concentrations in experimental streams ranged from 9.3–19.9 $\mu g/L$ and ortho-phosphate never exceeded 3.0 $\mu g/L$.

The experimental streams used in this investigation are described in detail in Peterson and Stevenson (1990). In brief, stream water was pumped from a large pool in Harts Run into 24 vinyl gutters (3.05 m long, 0.1 m wide). We regulated current in 12 of these channels at 29 cm/s (fast) and maintained a velocity of 12 cm/s (slow) in the remaining channels. Fast- and slow-current channels were alternated across the 24-channel array. Channels were covered with 33% greenhouse shade cloth between samplings to create a light environment similar to that present at the natural stream bed.

Each channel contained 36 unglazed ceramic tiles (5.1 × 5.1 cm), used as substrata for algal colonization, with the first 15 upstream tiles serving as a lead to stabilize current over 20 experimental tiles downstream. The last tile in the series was not sampled. Two tiles were stacked at downstream ends of fast-current channels to maintain a water depth of 2.5 cm. In slow-current channels, cobbles were placed downstream to reduce current velocity; depth in these channels was 6 cm.

Tiles in all channels were precolonized in situ for 5 wk prior to the start of the experiment, which was initiated on 27 April 1988, when all tiles were subjected to a simulated spate. To simulate a severe spate, we removed obstructions from channel ends to increase current (to ≈60 cm/s), then scoured tiles with five passes of a garden hose fitted with a high-pressure nozzle. Obstructions were replaced after 2 h to return flow to pre-disturbance levels.

To determine if algal community resistance and resilience differed as a function of successional changes

TABLE 1.　Schedule for tile collection. × = cell density and phaeophytin samples taken. ×* = cell density, phaeophytin, and ash-free dry mass (AFDM) samples taken. Three replicates unless noted otherwise.

Flow	Treat-ment†	No. days after initial disturbance												
		0	3	6	9	12	15	18	21	24	27	30	33B	33A
Fast current	Control	×	×	×	×	×	×	×	×‡	×	×§	×	×*	×*
(29 cm/s)	D9				×	×	×	×			×		×*	×*
	D18							×	×	×	×		×*	×*
	D27										×	×	×*	×*
Slow current	Control	×‡	×	×	×	×	×	×§	×	×	×	×	×‡	×*
(12 cm/s)	D9				×	×	×	×			×		×*	×*
	D18							×	×	×	×		×*	×*
	D27										×	×	×*	×*

† D9 tiles were subjected to a simulated spate 9 d into the experiment; D18 disturbed on day 18; D27 disturbed on day 27. 33B samples were collected just prior to a final spate on day 33, 33A samples were taken immediately after that disturbance.
‡ Two replicate phaeophytin samples.
§ Two replicate cell density and phaeophytin samples.

that occurred following the initial disturbance, communities in each current regime were either left undisturbed (control) after this spate or were subjected to an additional spate after 9 (D9), 18 (D18), 27 (D27), or 33 (D33) days of recovery. Three channels, widely separated across the 24-channel array, were designated as replicates for each of these treatments. The additional spates were imposed as described previously, but were less severe than the first, involving only two passes of the high-pressure hose. We sampled communities immediately after each spate and at three subsequent 3-d intervals (Table 1). Recovery was followed for only 6 d after the day-27 spate because of low water in Harts Run.

Resistance of communities in all channels was also examined following a final simulated spate on day 33 (Table 1). The utility of this final disturbance was twofold. First, it enabled us to assess effects of successional state on resistance, independent of potential seasonal influences. While previous spates allowed examination of resistance at different stages of community development, they did not allow us to address adequately the influence of past disturbance events (i.e., time since last disturbance). This is because these spates were temporally separated and disturbed communities were likely affected by changes in day length, temperature, and colonization pool, as well as time since last disturbance. By subjecting all channels to a final disturbance, we were able to examine resistance of communities that had developed concurrently, and therefore differed only in disturbance history. Second, unlike previous disturbances for which control and disturbed tiles were collected from separate channels, this final spate allowed collection of paired samples from each channel before and after the disturbance to assess channel-specific variation within treatments.

Sample collection and processing

On all sampling dates, we collected one tile from each of three channels designated for a given treatment (Table 1). To control for potential bias associated with tile position, one replicate was taken from an upstream channel section (randomly selected among tiles 16–21), one from a mid-channel section (tiles 22–28), and a third from a downstream section (tiles 29–35). The same section of a given channel was never sampled over consecutive dates. Tiles were sampled by scraping material from equal areas (13 cm² each) into two test tubes using a razorblade, toothbrush, and washbottle, then returned to their original position to retain constancy of flow. In the final third of the study, when channels were filled with floating algal mats, we collected both attached and floating material by carefully lifting a tile straight up and cutting the algal mat along tile edges with a razorblade. One scraping from each tile was preserved on site with the fixative M³ (American Public Health Association 1985) for algal cell counts. The second was put on ice, drawn onto a glass-fiber filter (Whatman, GFC) within 6 h, and frozen for later (within 48 h) measurement of chlorophyll a and phaeophytin following methods of Wetzel and Likens (1979). Temporal changes in algal colonization rates were monitored (as described in Peterson and Stevenson 1990) by incubating microbially conditioned tiles in control channels during each of the 11 3-d sampling intervals.

We partitioned samples taken on day 33 into three equal parts; one each for cell counts, pigments, and ash-free dry mass (AFDM), determined as dry mass (dried at 60°C, 24 h) lost upon combustion (combusted at 500°C, 24 h).

Preserved samples were homogenized with a hand-held, variable-speed blender, and a subsample was mounted in syrup medium (Stevenson 1984b) for algal enumeration. Densities of live diatoms (intact frustules containing chloroplasts) and nondiatom algae in each sample were calculated from counts of > 500 cells to estimate densities of subdominant taxa (Stevenson and Lowe 1986). All counts were made at 1000× magnification and at least three 100-μm transects of varying lengths were scanned per slide. For some analyses, we converted species- or genus-specific cell counts to biovolume using formulae of geometric shapes that approximated cell shapes.

Community comparisons and statistical procedures

Resistance.—Resistance within each current regime was assessed using samples collected on the day of each spate and testing for differences (with t tests) between control and disturbed communities in total diatom densities and taxon-specific densities of common algae (all natural-log transformed). Resistance of diatom community composition in each current regime was examined by ordinating samples in species space (using arcsine-square-root transformed relative abundances of the 15 most common diatom taxa) with detrended correspondence analysis (DCA; Hill and Gauch 1980). We gauged resistance of diatom assemblages by comparing mean DCA Axis I and II scores of control samples on a given date with scores of assemblages disturbed on that date using t tests.

Effects of past disturbance and current on characteristics of 33-d communities prior to the final spate were assessed using a two-factor (current × days-since-last-disturbed) ANOVA on cell densities of diatoms and zygnematalean green algae, ash-free dry mass, and phaeophytin content. Differences in resistance to this spate were examined by comparing these community parameters from all treatments before and after the day-33 spate using a single-factor ANOVA followed by a Fisher's least significant difference (LSD) multiple-comparison test.

The relationship between algal senescence and resistance in high-biomass, late-successional communities was assessed by correlating the pre-disturbance levels of phaeophytin (a chlorophyll *a* breakdown product) and AFDM on day 33 with the percent similarity (Ruzicka's Index; Pielou 1984) of diatom assemblages in each channel before and after the final spate. To determine which of these variables (natural log of phaeophytin or AFDM) most influenced resistance, partial correlation coefficients were calculated to relate each variable with diatom similarity before/after this spate while controlling for effects of the other. Although filamentous green algae comprised a large proportion of community biomass on day 33, we chose to assess resistance using changes in diatom assemblage composition because it represented a measure that was somewhat independent from the dominant structural component of the community (i.e., the green-algal matrix).

Resilience.—We assessed resilience by comparing rates of cell accrual on control and disturbed tiles during the 9 d following each simulated spate. Net algal growth rates were estimated with the least-squared solution for the rate of change in natural-log-transformed cell densities during each post-spate recovery period. Differences in cell accrual rates on control and disturbed tiles in each current regime were detected with a test for heterogeneity of slopes of the two regression lines (Freund et al. 1986). We estimated the contribution of new colonists to recovery by comparing the

number of cells accrued on three 3-d colonization tiles collected within each 9-d recovery period with net accumulation of cells on disturbed tiles during that period. Resilience in diatom community composition was examined by comparing trajectories of control and disturbed communities on DCA ordination plots.

RESULTS

Community structure and successional change on control tiles

Over 100 diatom species and 14 nondiatom genera were encountered during the experiment (see Peterson 1989). Of these, we chose 17 taxa that occurred in >65% of the samples and attained a maximum relative abundance of >2.0% for taxon-specific analyses. Prior to the initial (day 0) spate, communities in all channels supported low biomass with no macroscopic evidence of green algal growth. After this initial disturbance, tiles were sparsely populated (fast current mean = 3.25 × 10^4 cells/cm^2 [1 SE = 0.84 × 10^4 cells/cm^2]; slow current mean = 5.84 × 10^4 cells/cm^2 [1 SE = 2.21 × 10^4 cells/cm^2]) and were dominated by *Achnanthes minutissima,* a small (10–15 μm), monoraphid diatom. *A. minutissima* reached a maximum relative numerical abundance of 95.9% (55.9% relative biovolume) on day 12 in fast current and 92.3% (58.2% relative biovolume) on day 6 in slow current (Fig. 1). In fast-current channels, *Gomphonema angustatum* and *Chromulina* cf. *rosanoffii,* a small palmelloid chrysophyte, were also early-successional dominants (Fig. 1).

Diatom abundances approached an asymptote in both current regimes within 2 wk (Fig. 2a, b). Decreases in the relative contribution of early dominants were accompanied by a rise in relative and actual abundances of *Synedra* spp. after day 12 (Fig. 1). Between 18 and 24 d the numerical importance of filamentous green algae (*Mougeotia* and *Spirogyra;* Chlorophyta: Zygnematales) increased, reaching maxima on day 30 of 50.8 and 51.7% in fast and slow current, respectively. These taxa accounted for >98% of total algal biovolume at this time (Fig. 1). Zygnematalean filaments formed dense, floating mats over tiles in all channels, but these mats were more dense and formed earlier in slow current than in fast. Because of their large size, these algae had increased substantially in relative biovolume on substrata by day 12 (Fig. 1), despite sparse population densities (Fig. 2 c, d).

Community resistance

Temporal change during succession.—Resistance of algal communities was greater in fast current than in slow and generally decreased with successional time. Total diatom densities were unaffected by the spate on day 9 (Fig. 2a, b), showing no significant reduction in either fast (P = .608) or slow (P = .677) current. Three common diatom taxa were reduced in density by this spate in each current regime, but their 9-d abundances
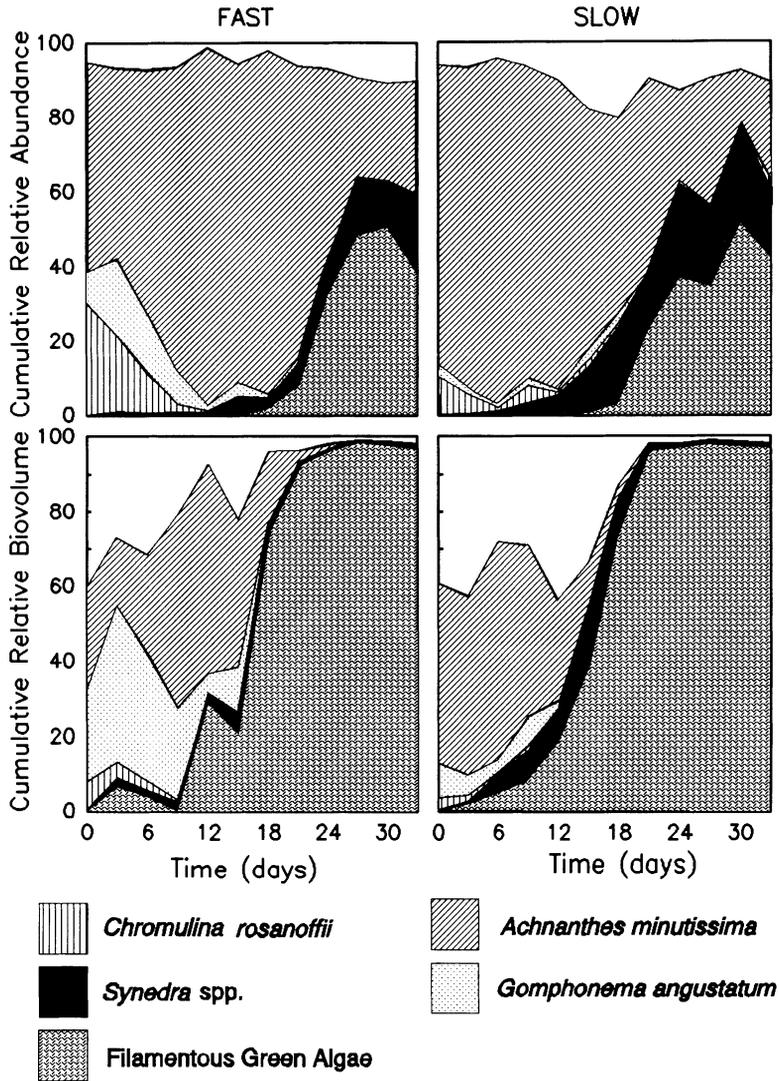
FIG. 1.   Cumulative relative numerical abundance and relative biovolume of dominant taxa on control tiles in fast and slow current. Data are means from each collection date. *Synedra* spp. includes: *S. famelica, S. filiformis* var. *exilis, S. radians, S. rumpens* var. *familiaris,* and *S. tenera.*

were too low to affect the diatom assemblage as a whole (Tables 2 and 3). Green-algal densities were low on day 9 and unaffected by disturbance (fast, $P = .806$; slow, $P = .976$).

On day 18, high variability among replicate control and D18 tiles precluded detection of any significant disturbance effect on total diatom densities (slow current, $P = .103$; fast current, $P = .123$), but density reductions were observed for three diatom taxa in fast current (Table 2) and 11 of 16 common algal taxa in slow current (Table 3). The day-18 spate removed a large proportion of the developing zygnematalean mat in slow current, creating a mosaic of green-algal aggregates on most D18 tiles and significantly reducing zygnematalean density (Fig. 2d, Table 3). In fast current, zygnematalean mats had yet to develop and no signif-

icant spate-induced reduction occurred (Fig. 2c, Table 2).

The day-27 spate did not significantly reduce diatom densities on slow-current tiles ($P = .163$) (Fig. 2b). The only spate-induced reductions observed in this flow regime were in the abundances of zygnematalean green algae, and two large *Synedra* species (Table 3). In fast current, the day-27 spate significantly lowered densities of four diatom taxa (Table 2), resulting in a reduction in total diatom densities ($P = .057$) (Fig. 2a).

By day 33, condition of the dense filamentous green-algal mats that dominated all channels had degenerated; upper layers of these mats changed from a cohesive texture and grass-green color at 27–30 d to a bleached, yellow-green color with a loose, bubbly texture. Zygnematalean density in control channels was
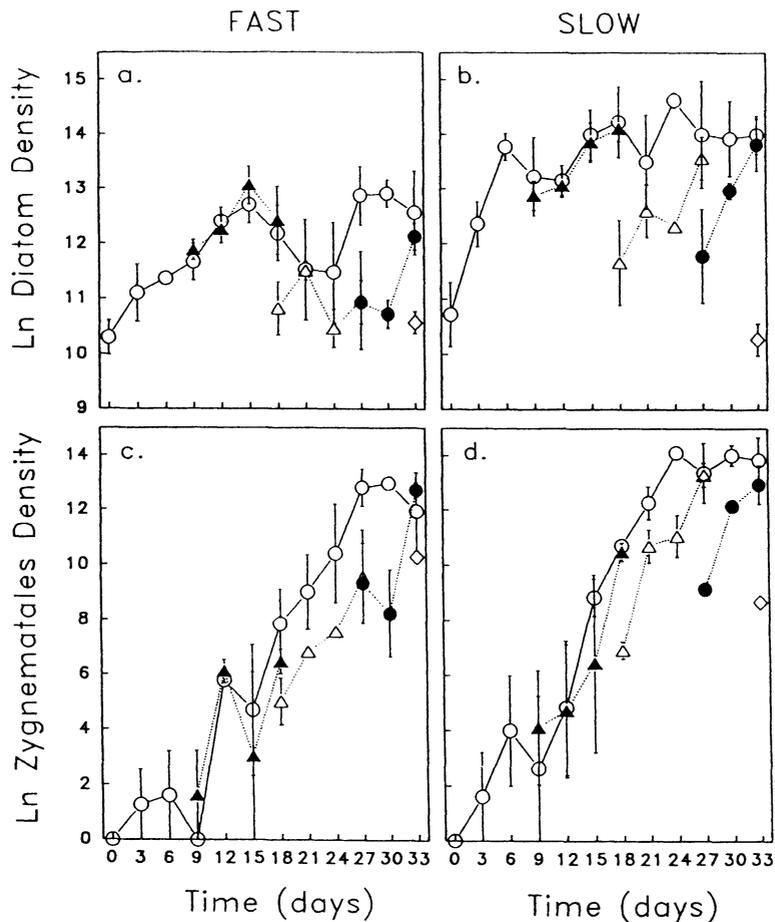
FIG. 2. Densities of diatom cells (a, b) and zygnematalean green algal cells (c, d) (both measured as cells/cm^2, and shown as means ± 1 SE) on control and disturbed substrata in fast and slow current. O = control, ▲ = D9, △ = D18, ● = D27, ◇ = D33. n for all means = 3, except as noted in Table 1.

significantly reduced by the day-33 spate in slow current, but not in fast (Fig. 2, Tables 2, 3). Disturbance of slow-current control communities on day 33 resulted in significant reductions in 59% of the common algal taxa (Table 3), while only 17.6% of the 17 common taxa were affected in fast current (Table 2).

DCA ordinations indicated that simulated spates generally reset diatom assemblage composition to early successional stages, but to different degrees depending on current and community age (Figs. 3 and 4). In both flow regimes, control samples moved from low to high scores on DCA Axis I during succession, reflecting early dominance by *Achnanthes minutissima,* mid-successional influence of *Nitzschia* and *Navicula* species, and strong dominance by *Synedra* spp. late in the sere (Figs. 3 and 4). On all disturbance dates, spates displaced community composition back along DCA Axis I towards ordination space characterized by *A. minutissima.* The most extreme and only statistically significant (P = .006) displacement occurred when slow-current communities were disturbed on day 18

(Fig. 4), a period when development of floating mats of zygnematalean algae had just begun.

Variation in resistance to the day-33 spate. — Prior to the day-33 spate, slow-current channels supported greater densities of zygnematalean algae (Table 4, P = .022, two-factor ANOVA, effects of current speed) and diatoms (P =.002), and contained more biomass (P =.022) and higher phaeophytin concentrations (P = .064) than fast-current channels, but differences among disturbance treatments were not detected for any of these parameters ($P > .10$; days-since-last-disturbance [dld] effects).

Zygnematalean algae were the principal contributors to community structure on day 33, accounting for >98% of algal biovolume. Differences between current regimes in both the amount of standing crop lost and the amount remaining after the spate indicated that communities in fast current, regardless of disturbance history, were more resistant than those in slow current. Slow-current communities that had not been recently disturbed (control and D9) lost more green algal bio-
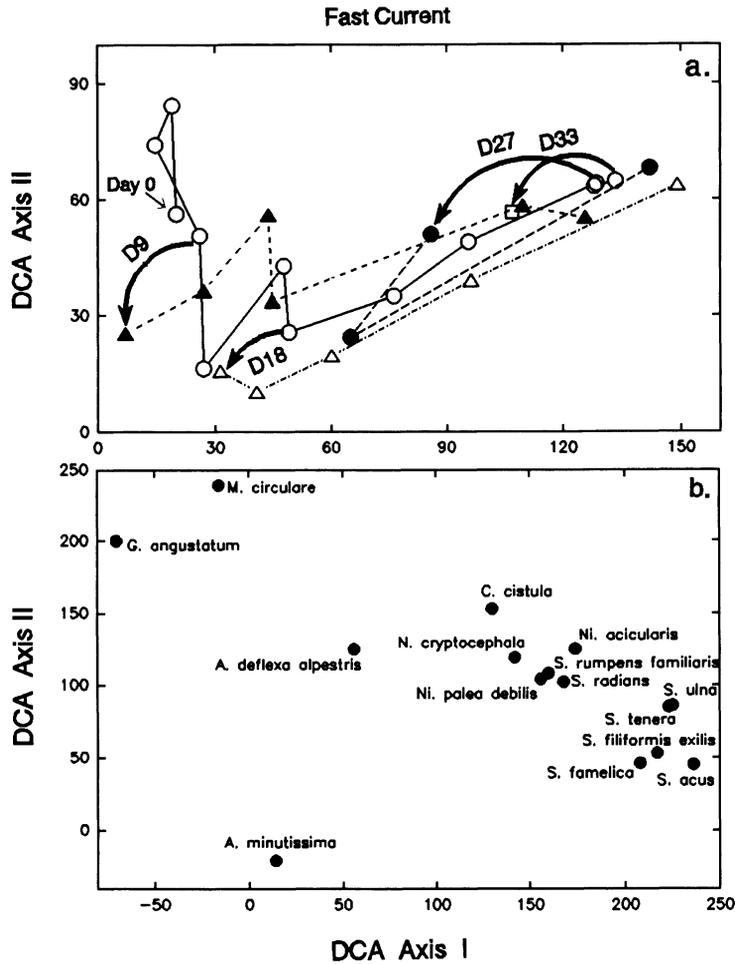
Fast Current

FIG. 3. Detrended correspondence analysis (DCA) ordination of samples in diatom species space (a) and simultaneous ordination of species in sample space (b) for fast-current channels. Symbols in upper panel (O = control, ▲ = D9, △ = D18, ● = D27, □ = D33) represent mean DCA Axis I and II scores of three replicates. Solid arrows show displacement of disturbed samples from control samples on the same date. For each treatment, consecutive samples in the successional sere are connected.

mass during the day-33 spate than communities from other current/disturbance conditions (Table 4). Fast-current control tiles supported the highest zygnematalean biomass after this disturbance. Slow-current communities last disturbed on day 9 supported lower (LSD, $P < .05$) zygnematalean densities than all other treatments (Table 4). This observation, plus the occurrence of a significant current × dld interaction ($P = .027$) suggested that effects of disturbance history were greatest in slow current. Diatom densities exhibited highly significant spate-induced reductions on day 33 in all slow-current channels (control and D9, $P = .001$; D18, $P = .006$; D27, $P = .026$), while significant reductions in fast current were noted only in control ($P = .067$) and D27 channels ($P = .065$).

The degree to which diatom assemblage composition was displaced by the day-33 spate was influenced by current and disturbance history, but varied considerably among channels (Fig. 5a, b). In fast current, the only significant displacement of taxonomic structure

occurred in D27 channels ($P = .008$, Fig. 5a). Slow-current assemblages were strongly displaced by disturbance in D9 channels ($P = .002$), less strongly displaced in D18 ($P = .089$) and D27 ($P = .096$) channels, and unaffected by the spate in control channels ($P = .140$) (Fig. 5b). In many cases, failure to detect displacement of diatom assemblage composition across the final spate statistically was due not to consistently high resistance within a given treatment, but rather to high variability among replicate tiles within a treatment (Fig. 5a, b). For example, 2 of 3 replicates from control channels (open circles in Fig. 5) in each current regime show spate-induced displacement that is consistent in direction and magnitude. However, pre-spate samples from a third replicate do not share high Axis I scores with the other two, and diatom assemblages within these channels were not significantly displaced by the day-33 spate.

The position of day-33 samples (both pre- and post-spate) in ordination space along DCA Axis I, a space

TABLE 2. Densities (10^4 cells/cm^2) of common taxa in fast-current channels before (B) and after (A) spates on days 9, 18, 27, and 33. Symbols between pre- and post-spate densities indicate significant reductions: $>>>$ = reduction significant at $\alpha < .01$; $\gg = .05 > \alpha > .01$; $> = .10 > \alpha$. df for all comparisons = 3 unless otherwise noted in Table 1.

Taxon	Statistic	9 d B		9 d A	18 d B		18 d A
		Age of community at spate					
		9 d			**18 d**		
		B		A	B		A
Achnanthes deflexa var. *alpestris* Lowe et Kociolek	Mean (SE)	0.13 (0.05)		0.09 (0.01)	0.20 (0.14)		0.10 (0.08)
A. minutissima Kütz.	Mean (SE)	11.56 (5.04)		13.93 (3.33)	27.72 (9.64)		5.80 (2.11)
Cymbella cistula (Ehr.) Kirchn.	Mean (SE)	0.01 (0.01)		0 (0)	0.05 (0.03)		0.006 (0.004)
Gomphonema angustatum (Kütz.) Rabh.	Mean (SE)	0.82 (0.23)		0.75 (0.29)	0.31 (0.20)		0.07 (0.04)
Meridion circulare (Grev.) Ag.	Mean (SE)	0.13 (0.08)		0.06 (0.03)	0.04 (0.03)		0.002 (0.001)
Navicula cryptocephala Kütz.	Mean (SE)	0.01 (0.007)		0.002 (0.002)	0.03 (0.02)	$>>>$	0 (0)
Nitzschia acicularis W. Sm.	Mean (SE)	0.19 (0.17)	$>>>$	0 (0)	0.11 (0.08)	$>$	0.008 (0.003)
Ni. palea var. *debilis* (Kütz.) Grun.	Mean (SE)	0.02 (0.01)		0 (0)	0.05 (0.04)		0.005 (0.004)
Synedra acus Kütz.	Mean (SE)	0 (0)		0 (0)	0.02 (0.01)		0 (0)
S. famelica Kütz.	Mean (SE)	0 (0)		0.004 (0.004)	0.03 (0.02)		0.004 (0.002)
S. filiformis var. *exilis* Cl.	Mean (SE)	0 (0)		0 (0)	0.13 (0.12)		0.006 (0.002)
S. radians Kütz.	Mean (SE)	0.03 (0.002)	$>>>$	0 (0)	0.41 0.37)		0.014 (0.01)
S. rumpens var. *familiaris* (Kütz.) Hust.	Mean (SE)	0.03 (0.002)	$>>>$	0 (0)	0.13 (0.08)	$>$	0.007 (0.002)
S. tenera W. Sm.	Mean (SE)	0.02 (0.02)		0.013 (0.013)	0.12 (0.11)		0.01 (0.008)
S. ulna (Nitz.) Ehr.	Mean (SE)	0 (0)		0 (0)	0.04 (0.03)		0.002 (0.002)
Chromulina cf. *rosanoffii* (Wor.) Bütschli	Mean (SE)	0.26 (0.03)		0.64 (0.33)	0.06 (0.02)		0.13 (0.005)
Zygnematalean green algae*	Mean (SE)	0 (0)		0.004 (0.004)	0.76 (0.53)		0.03 (0.01)
Number of significant reductions		3			3		

* *Mougeotia* and *Spirogyra*.

defined by *diatom* assemblage composition, is strongly correlated with green-algal biovolume in both fast (r = 0.906) and slow current (r = 0.833) (both $P < .001$) (Fig. 5c, d). To determine if differences in resistance of diatom assemblage composition were attributable simply to the amount of biomass within communities or to variation in community condition, we ran partial correlations relating change in diatom species composition across the final spate with either AFDM (our biomass estimate) or phaeophytin (an indicator of community condition), controlling for effects of each of these variables on the other. In slow current, both pre-spate phaeophytin content and AFDM were strongly and negatively correlated with spate-induced changes in diatom taxonomic structure (Fig. 6, Table 5). The significant negative correlation between AFDM and the resistance of diatom assemblages disappeared when effects of phaeophytin were controlled; phaeo-

phytin effects persisted when AFDM effects were controlled. In fast current, a weaker relationship was noted between these variables and assemblage resistance (Fig. 6, Table 5). However, correlations between pre-spate phaeophytin content and assemblage resistance became nonsignificant when AFDM effects were controlled, whereas a weak correlation between resistance and AFDM persisted when the influence of phaeophytin was controlled (Table 5).

Spate-induced changes in diatom species composition were generated by differences in susceptibility among populations (Fig. 7). *Achnanthes minutissima*, an adnate taxon more likely to be associated with benthic substratum, consistently increased in relative abundance across the day-33 spate. In contrast, *Nitzschia acicularis* and *Synedra radians*, larger unattached species that might be expected to inhabit interstices within floating algal mats, were present in much

TABLE 2. Continued.

| Age of community at spate | | | | | |
| 27 d | | | 33 d | | |
B		A	B		A
0.26 (0.12)		0.06 (0.04)	0.23 (0.19)		0.07 (0.04)
22.94 (11.13)	>	4.50 (1.78)	16.58 (8.84)		2.48 (0.27)
0.03 (0.03)		0.06 (0.04)	0.05 (0.04)		0.03 (0.01)
0.27 (0.01)		0.20 (0.10)	0.45 (0.20)		0.08 (0.03)
0.13 (0.01)		0.02 (0.01)	0.12 (0.06)		0.02 (0.01)
0.69 (0.43)		0.06 (0.03)	0.54 (0.27)		0.06 (0.02)
2.55 (1.66)		0.16 (0.08)	1.14 (0.74)	≫	0.04 (0.02)
0.68 (0.30)		0.07 (0.03)	0.54 (0.43)		0.04 (0.03)
1.68 (0.98)		0.07 (0.04)	1.25 (0.74)		0.05 (0.03)
0.69 (0.13)		0.08 (0.04)	1.61 (1.12)		0.09 (0.04)
4.72 (2.01)	>	0.23 (0.11)	7.98 (4.48)		0.30 (0.05)
2.68 (0.97)	>	0.17 (0.08)	2.23 (1.01)	≫	0.08 (0.04)
0.76 (0.06)		0.10 (0.04)	1.23 (0.63)		0.10 (0.07)
3.94 (2.93)		0.20 (0.10)	7.18 (3.49)	>	0.22 (0.06)
0.70 (0.70)		0.02 (0.005)	1.47 (0.80)		0.02 (0.01)
0.14 (0.14)		0.05 (0.04)	0.27 (0.15)		0.04 (0.01)
49.92 (27.5)		3.64 (2.41)	43.38 (21.4)		2.91 (1.01)
4			3		

higher relative abundances in pre- than post-spate communities (Fig. 7).

Community resilience. — Resilience, measured as post-disturbance change in both cell densities and diatom species composition, was generally higher in slow current than in fast and did not vary appreciably with successional time. In slow current, both diatom and green-algal densities returned rapidly to control levels following disturbance on all dates (Fig. 2). These patterns were less pronounced in fast current. Net growth of a number of taxa was enhanced by spates, particularly in slow-current channels (Table 6). *Nitzschia acicularis* exhibited the highest net growth in disturbed communities in both current regimes following the day-9 spate. In slow current, accumulation of *N. acicularis* was also more rapid on disturbed tiles relative to controls after spates on days 18 and 27. Accrual of *Synedra filiformis* var. *exilis, S. tenera,* and *S. ulna* was simi-

larly enhanced following disturbance of slow-current communities (Table 6). Net growth of zygnematalean algae was more rapid on disturbed substrata than controls in slow current on days 18 and 27, but was unaffected by spates in fast current (Table 6).

High resilience reflected elevated reproduction more than immigration. Accumulation of diatom cells on 3-d colonization tiles collected between 9 and 18 d accounted for only 16.1 and 17.6% of post-spate accumulation in fast and slow current, respectively. For later spates, we could not use estimates of new colonization to assess recovery because colonization tiles were collected from control channels where cell accumulation was heavily influenced by green algal mats.

Diatom assemblage composition was highly resilient (Figs. 3 and 4). Communities displaced by spates typically recovered to control conditions within 3–6 d. Post-spate convergence of disturbed and control assemblages was more rapid and more true in slow current than in fast. These patterns were particularly striking following the day-18 spate, which strongly displaced diatom species composition in slow-current channels; these communities shared nearly identical ordination space with the control just 3 d later on day 21 (Fig. 4). By day 33, diatom species composition did not differ among treatments in either fast or slow current.

DISCUSSION

Algal community resistance

Resistance of algal communities changed considerably over successional time and differed with current regime. The mechanisms behind this variation were tied to changes in biomass, availability of secondary habitat, and the amount of senescing material within communities.

Early-successional (9-d-old) communities were highly resistant to spate-induced loss of standing crop and change in taxonomic structure, presumably due to their low biomass (cf. Douglas 1958) and simple physiognomy, dominated by *Achnanthes minutissima.* Changes in relative abundance of *A. minutissima* across our day-33 spate also indicate high resistance of this taxon, suggesting that its dominance early in succession was generated by a high resistance to scour relative to other algal taxa. Studies on the effects of scour on microalgal communities growing in cobble- (Rounick and Gregory 1981) and sandy-bottomed streams (Cox 1988), in estuaries (Delgado et al. 1991), and on macroalgal substrata in large rivers (Luttenton and Rada 1986), have yielded similar results. Small, adnate algae, like *A. minutissima,* are also resistant to removal by grazing (e.g., Sumner and McIntire 1982, Peterson 1987*a,* Barnese et al. 1990) suggesting that the same properties that impart resistance to scour also impart resistance to ingestion by grazers.

Increases in structural complexity during succession between days 9 and 18 altered diatom habitat avail-

TABLE 3. Densities (10^4 cells/cm^2) of common taxa in slow-current channels before (B) and after (A) spates on days 9, 18, 27, and 33. Symbols between pre- and post-spate densities indicate significant reductions: $>>>$ = reduction significant at $\alpha < .01$; $\gg$ = $.05 > \alpha > .01$; $>$ = $.10 > \alpha$. df for all comparisons = 3 unless otherwise noted in Table 1.

| | | Community age at spate | | | |
| | | 9 d | | 18 d | |
Taxon	Statistic	B	A	B	A
Achnanthes deflexa var. *alpestris*	Mean	4.10		1.72	34.1	0.89
	(SE)	(2.25)		(0.67)	(33.0)	(0.65)
A. minutissima	Mean	68.28		39.72	85.13	15.99
	(SE)	(29.02)		(11.03)	(28.23)	(6.89)
Cymbella cistula	Mean	0.45		0.12	1.53	>	0.01
	(SE)	(0.24)		(0.03)	(0.98)		(0.01)
Gomphonema angustatum	Mean	0.89	>>>	0.20	3.44	$\gg$	0.06
	(SE)	(0.20)		(0.03)	(1.56)		(0.03)
Meridion circulare	Mean	0.58		0.03	1.26		0.02
	(SE)	(0.30)		(0.02)	(0.82)		(0.01)
Navicula cryptocephala	Mean	0.18		0.03	2.22	>>>	0.02
	(SE)	(0.14)		(0.03)	(1.12)		(0.01)
Nitzschia acicularis W. Sm.	Mean	1.19	$\gg$	0.006	4.20		0.045
	(SE)	(0.60)		(0.006)	(2.88)		(0.03)
Ni. palea var. *debilis*	Mean	0.18		0.014	0.69	>>>	0.03
	(SE)	(0.10)		(0.007)	(0.14)		(0.01)
Synedra acus	Mean	0.11		0.006	0.32	>	0.005
	(SE)	(0.05)		(0.006)	(0.10)		(0.005)
S. famelica	Mean	0.14		0.01	1.07	>>>	0.02
	(SE)	(0.08)		(0.005)	(0.18)		(0.007)
S. filiformis var. *exilis*	Mean	0.34	$\gg$	0.003	9.76	$\gg$	0.05
	(SE)	(0.17)		(0.003)	(7.33)		(0.04)
S. radians	Mean	1.81		0.08	18.08	$\gg$	0.11
	(SE)	(0.91)		(0.02)	(12.35)		(0.05)
S. rumpens var. *familiaris*	Mean	0.65		0.02	5.69	$\gg$	0.16
	(SE)	(0.49)		(0.015)	(3.48)		(0.07)
S. tenera	Mean	0.68		0.009	10.72	>	0.05
	(SE)	(0.39)		(0.005)	(9.29)		(0.05)
S. ulna	Mean	0.06		0.003	0.06		0.02
	(SE)	(0.06)		(0.003)	(0.06)		(0.02)
Chromulina cf. *rosanoffii* (Wor.) Bütschli	Mean	6.04		3.56	3.18		0.27
	(SE)	(4.16)		(0.80)	(3.07)		(0.13)
Zygnematalean Green Algae*	Mean	0.09		0.03	4.58	>>>	0.11
	(SE)	(0.09)		(0.02)	(0.83)		(0.04)
Number of significant reductions		3			11	

* *Mougeotia* and *Spirogyra*.

ability and affected resistance. In slow current, day 18 marked initial development of floating green-algal mats. Although mat formation was incomplete at that time, generation of new metaphytic habitat increased habitat complexity, expanding the area available for diatom colonization and growth (McCormick 1989, Peterson and Stevenson 1990, Dodds 1991). When disturbed, however, this rapidly changing community was readily displaced back to low biomass and dominance by *Achnanthes minutissima*. Thus, transition from predominance of benthic habitat to predominance of metaphytic habitat appeared to represent a window of instability within the successional sere. It is unclear whether a similar unstable period occurred in fast current, since zygnematalean mats had not yet formed when fast-current communities were disturbed on day 18 and these mats had fully developed prior to the day-27 spate.

By day 27, neither fast- nor slow-current communities were greatly affected by disturbance. Zygnematalean density in slow-current channels was reduced significantly by the day-27 spate, but only to levels well above post-spate densities on day 18 (see Fig. 2d). This suggests that the cohesive floating green-algal mats present in all channels by day 27 mitigated disturbance effects for other components of the community. Once fully developed, these mats increased deposition of diatom cells onto tiles (Peterson and Stevenson 1990). Although a significant amount of green-algal biomass was lost from slow-current channels during the day-27 spate, the dense mat may have partially sheltered benthic substrata from full scour. This sheltering, coupled with the association of diatom cells with resistant mat material, reduced disturbance effects on the diatom assemblage.

During the first 27 d of succession, resistance in both

TABLE 3. Continued.

27 d		33 d	
B	A	B	A
3.75	1.10	3.37	0.43
(2.10)	(0.74)	(2.47)	(0.24)
76.65	14.14	56.15 $>>>$	1.74
(31.5)	(9.77)	(19.5)	(0.24)
0.95	0.37	0.85 $\gg$	0.07
(0.93)	(0.22)	(0.50)	(0.06)
1.83	0.20	0.84 $>>>$	0.03
(1.05)	(0.09)	(0.12)	(0.01)
1.60	0.04	0.07	0.002
(1.54)	(0.03)	(0.07)	(0.002)
4.25	0.40	1.81	0.09
(3.10)	(0.27)	(1.41)	(0.04)
8.58	0.24	2.32 $\gg$	0.01
(4.43)	(0.11)	(1.38)	(0.006)
5.67	0.15	0.75	0.04
(3.23)	(0.08)	(0.56)	(0.04)
2.64 $\gg$	0.09	3.79	0.01
(1.64)	(0.04)	(1.95)	(0.004)
10.36	0.19	4.11 $>>>$	0.06
(5.71)	(0.13)	(1.64)	(0.03)
23.01	0.72	20.9 $>>>$	0.18
(11.1)	(0.28)	(8.67)	(0.07)
36.77	1.92	13.13 $>>>$	0.09
(20.9)	(1.37)	(8.29)	(0.05)
16.96	0.94	10.46 $>>>$	0.14
(10.9)	(0.58)	(6.79)	(0.04)
16.12	0.60	11.31 $>>>$	0.11
(9.14)	(0.28)	(3.78)	(0.05)
1.42 $>>>$	0	2.53	0.003
(0.97)	(0)	(1.28)	(0.003)
0.56	0.19	24.30	0.20
(0.54)	(0.16)	(24.8)	(0.12)
133.98 $\gg$	1.00	183.53 $>>>$	0.61
(63.6)	(0.25)	(118.6)	(0.10)
3		10	

current regimes appeared to be controlled primarily by structural attributes of the community. By day 33, current-related differences in the physiological properties of algal communities increased in importance. In both

TABLE 5. Correlation and partial correlation coefficients relating percent similarity (Ruzicka's Index) of diatom assemblages before and after the day-33 spate to the natural logs of pre-disturbance phaeophytin concentrations measured in $\mu g/cm$ and pre-disturbance ash-free dry mass measured in mg/cm^2.*

Variable	Fast current		Slow current	
	Total	Partial	Total	Partial
Phaeophytin				
Mean	−0.574	−0.407	−0.873	−0.699
(SE)	(0.051)	(0.214)	(<0.001)	(0.024)
AFDM				
Mean	−0.658	−0.544	−0.734	0.087
(SE)	(0.020)	(0.084)	(0.007)	(0.812)

* Values are $r_{ij} \cdot x$ (probability of equality to zero), where i is percent similarity, j is the independent variable (i.e., phaeophytin or AFDM), and x is the independent variable controlled for when not directly involved in the correlation. df = 8–10.

fast and slow current, diatom assemblage composition was coupled with zygnematalean biomass (see Fig. 5c, d). In fast current, partial correlation results indicated that diatom resistance to the day-33 spate varied as a function of biomass with less influence of community condition (measured as phaeophytin content). In contrast, resistance of diatom assemblages in slow current exhibited a strong inverse relationship with pre-spate phaeophytin content, indicating that resistance of diatom assemblages in this regime was reduced by senescence within the community, either directly as senescence of diatoms themselves, or through breakdown and lower resistance of their principal habitat (i.e., the green-algal matrix). Similar patterns were noted by Biggs and Close (1989), who observed that actively growing epilithon, identified using the ratio of AFDM to chlorophyll a, was less affected by spates than communities with high AFDM/chl a ratios.

Both physical and physiological mechanisms contribute to current-related differences in resistance. As in our study, others have found that epilithic algae growing in areas of high shear stress attach more strongly (Keithan and Lowe 1985, Reiter and Carlson 1986, Horner et al. 1990) and exhibit higher resistance to scour (Horner and Welch 1981, Lindström and Traaen

TABLE 4. Abundances of zygnematalean green algae* (10^4 cells/cm²) on tiles from each disturbance treatment and current regime on day 33, before and after the final disturbance. Treatment codes are: S = slow current; F = fast current; C = control tiles; 9, 18, and 27 = tiles disturbed on days 9, 18, or 27. Densities that did not differ based on LSD multiple comparisons following ANOVA are connected with a horizontal line beneath treatment codes. ANOVA and LSD tests were performed on natural-log-transformed data.

Before	S9	S18	SC	S27	F18	FC	F9	F27
Mean	275.88	263.3	183.53	61.39	49.11	43.38	41.62	36.53
(SE)	(105.92)	(76.7)	(118.63)	(27.42)	(17.47)	(21.37)	(20.82)	(11.01)

After	F9	F18	S27	FC	S18	F27	SC	S9
Mean	6.16	4.15	3.25	2.91	2.66	2.46	0.61	0.58
(SE)	(2.19)	(1.70)	(1.71)	(0.10)	(1.24)	(0.24)	(0.10)	(0.15)

* *Mougeotia* and *Spirogyra*.
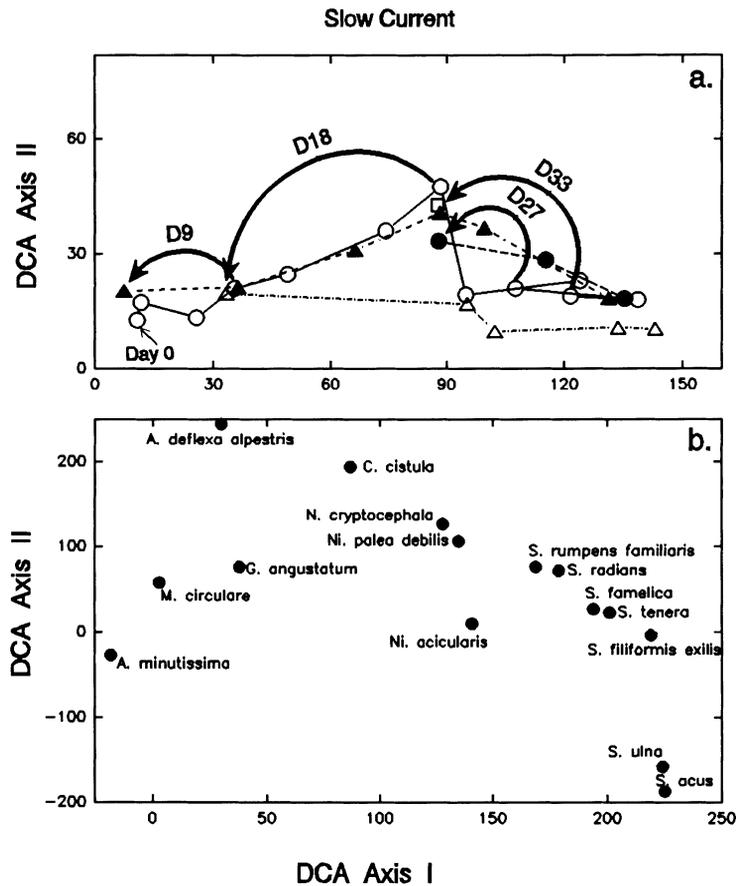
Slow Current

FIG. 4. Detrended correspondence analysis (DCA) ordination of samples in diatom species space (a) and simultaneous ordination of species in samples space (b) for slow-current channels. Symbols and arrows as described in legend for Fig. 3.

TABLE 6. Net growth rates (r) of common algal taxa on control (C) and disturbed (D) substrata over 9-d intervals throughout the 33-d study period. Significance levels of rates in italics = .05, normal type = .05–.10. 0 denotes accumulation rates that do not differ significantly ($P > .10$) from zero. Growth rates of taxa in communities of the same age and current-speed

	Fast current						
	0–9 d	9–18 d		18–27 d		27–33 d	
Taxon	C	C	D	C	D	C	D
Achnanthes deflexa var. *alpestris*	0	0	0.12	0	0	0	0
A. minutissima	0.15	0	0	0	0	0	0
Cymbella cistula	0	0.48	0.49	0	0	0	0
Gomphonema angustatum	0	0	0	0[a]	−0.30[a]	0	0
Meridion circulare	0	0	0	0	0	0	0
Navicula cryptocephala	0	0	0.56	0	0.52	0	0
Nitzschia acicularis	0.55	0[c]	0.91[c]	0	0	0	0
N. palea var. *debilis*	0	0	0.61	0.43	0	0	0
Synedra acus	···†	0.39	0.62	0	0.71	0	0
S. famelica	0	0.49	0	0	0	0	0
S. filiformis var. *exilis*	0	0.74	0.77	0.45	0.31	0	0
S. radians	0	0[b]	0.80[b]	0	0.29	0	0
S. rumpens var. *familiaris*	0	0[b]	0.73[b]	0	0.39	0	0
S. tenera	0	0	0	0.60	0	0	0.60
S. ulna	0	0.48	0.45	0	0	0	0
Chromulina cf. *rosanoffii*	−0.17	0	−0.74	0	0	0	0
Zygnematalean algae*	0	0.76	0	0.53	0.48	0	0

* *Mougeotia* and *Spirogyra*.
† ··· = taxon not encountered.
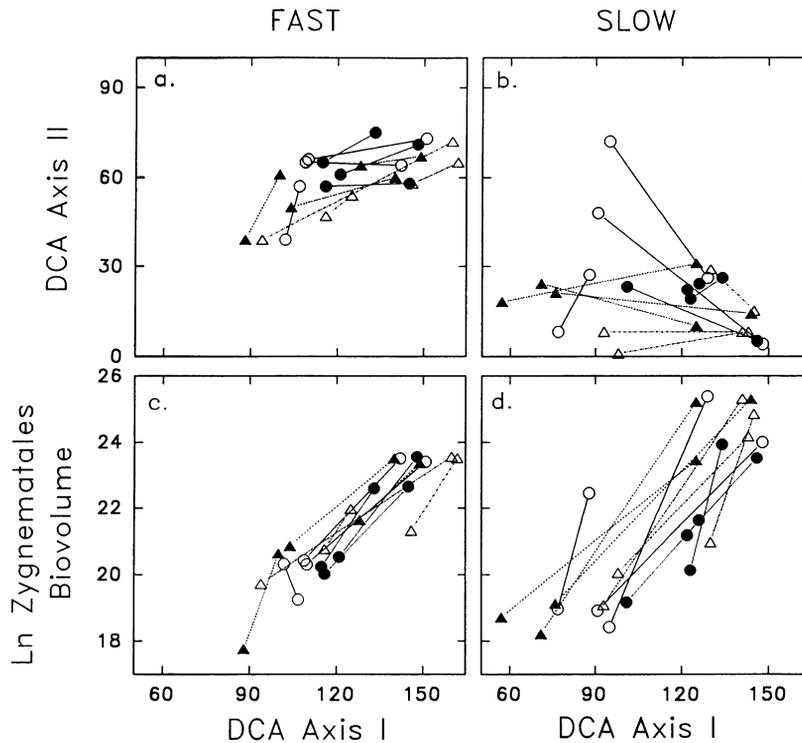
FIG. 5. Detrended correspondence analysis (DCA) ordinations of diatom assemblage structure from paired samples taken from individual channels before and after the day-33 spate (a, b) and plots of DCA Axis I scores with zygnematalean biovolume in each sample (c, d). Symbols refer to disturbance treatments: O = control, ▲ = D9, △ = D18, ● = D27. Pre- and post-spate samples from the same channel are connected; in all cases pre-spate samples exhibit higher DCA Axis I scores than post-spate samples. There are three replicate channels per treatment.

treatment that have a common superscript letter differ significantly from one another: [a] = $.10 > P > .05$, [b] = $.05 > P > .01$, [c] = $P < .01$.

	Slow current					
0–9 d	9–18 d		18–27 d		27–33 d	
C	C	D	C	D	C	D
0.27	0	0.20	0	0	0	0
0.30	0	0.10	0	0	0	0.26
0	0	0	0	0	0	0
0.22	0.18	0.30	0	0.22	0	0
0.39	0[a]	0.61[a]	0	0	0	0
0.50	0.41[a]	0.89[a]	0	0	0	0
0.72	0.27[c]	0.99[c]	0[b]	0.58[b]	0[a]	0.48[a]
0.65	0.29	0.67	0	0	0[a]	0.49[a]
0.56	0	0.76	0.20[c]	0.87[c]	0	0.49
0.58	0.51	0.79	0	0.46	0[a]	0.63[a]
0.60	0.46[b]	0.95[b]	0[b]	0.60[b]	0[a]	0.58[a]
0.83	0.59	0.59	0[b]	0.49[b]	0	0.47
0.56	0.41	0.71	0	0.35	0	0.47
0.77	0.57	0.79	0[b]	0.90[b]	0	0.54
0	0[a]	0.74[a]	0.48	0.76	0[c]	1.60[c]
0	0	0	0	−0.54	0	0
0	0.97	0.71	0.31[b]	0.65[b]	0[b]	0.63[b]

1984) than algae in slow-current habitats. Slow-current communities are strongly influenced by deposition and contain a large proportion of cells that are either unattached, or attached to unattached secondary substrata (cf. Lamb and Lowe 1987). Because of low shear stress, communities growing in slow current typically support high biomass, increasing potential for cells within benthic mats to become nutrient and/or light limited (cf. Stevenson et al. 1991), which leads to higher percentages of dead or dying cells at the base of these communities (Meulemans and Roos 1985, Lamontagne et al. 1986). Density-dependent increases in potential for nutrient limitation are exacerbated by the low nutrient renewal rates in slow-current environments (Whitford and Schumacher 1961, Horner et al. 1990). All of these factors probably reduce the resistance to scour of algal communities growing in slow currents.

Conditions in fast-current environments are more conducive to establishment of resistant algal communities. In our fast-current channels, aging, senescent cells were likely lost through export (e.g., McIntire 1968), nutrient supply rates were higher, and fresh biomass was maintained by rapid regrowth. Thus, the relationship between phaeophytin and resistance observed in slow current did not hold in fast current, and we observed no legacy of past disturbance in this re-
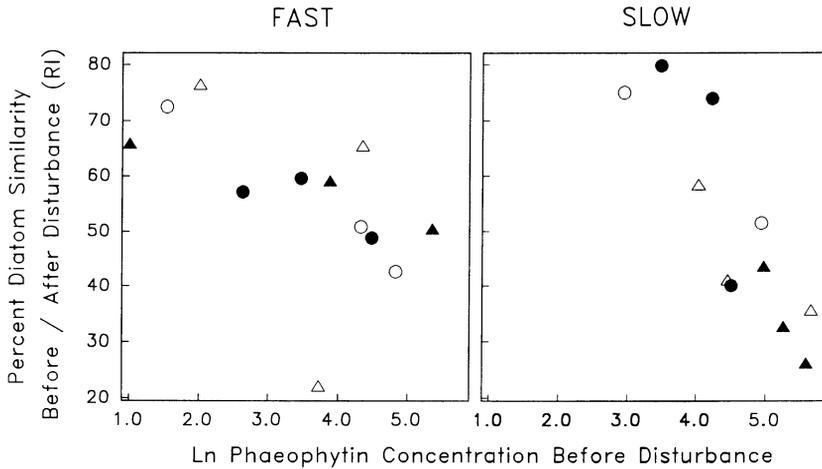
FIG. 6. Relationship between pre-disturbance phaeophytin content on day 33 (measured as μg/cm²) and similarity of diatom assemblages before and after disturbance measured by Ruzicka's Index, RI. Symbols refer to disturbance treatments: O = control, ▲ = D9, △ = D18, ● = D27.

gime. In slow-current channels, communities left undisturbed for extended periods (control, D9) exhibited the greatest loss in green-algal biomass following the day-33 spate, suggesting that in habitats where potential for autogenically induced resource limitation is high, periodic disturbance may delay senescence (cf. Peterson et al. 1990) and confer high resistance to future disturbance. For example, Power and Stewart (1987) found new growth of *Spirogyra* to be much more resistant to removal by flooding than older filaments.

Physical and physiological mechanisms that impart

high resistance to spates on fast-current algal communities may also increase resistance of these communities to other types of disturbance. In areas of fast current, scour disturbance (spates, grazing) represents an elevation of the force (shear stress) to which resident benthic algae are accustomed; high resistance could be a function of physical acclimation. However, Peterson (1987b) demonstrated that epilithic algal communities developed in direct-current environments were more resistant to short-term desiccation than communities developed in sheltered habitats. In that study, higher
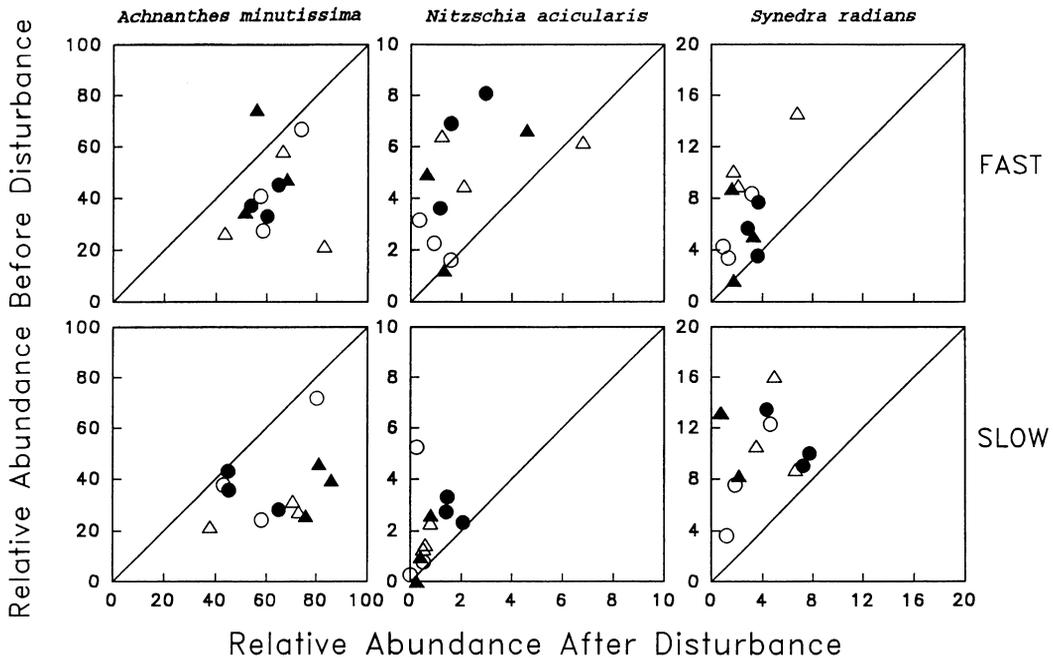
FIG. 7. Percent contribution of three taxa to diatom assemblages in individual fast- and slow-current channels before and after the day-33 spate. Solid lines mark expected distribution of data points if disturbance had no significant effect on relative abundance. Symbols are defined as in legend for Fig. 6.

resistance of communities exposed to high shear stress was attributed to physiological condition of microorganisms tied to resource availability.

Algal community resilience

Effects of successional state and current.—Algal community resilience did not differ appreciably with successional time and was higher in slow current than in fast, with cell densities returning to control levels within 6–9 d. These results support the predictions of Webster et al. (1975) that ecosystem resistance and resilience are inversely related. However, the mechanisms responsible for these patterns deviated from Webster et al.'s predictions that systems with high nutrient supply rates should also exhibit high resilience. Rates of nutrient supply and turnover were likely greater in fast current than in slow (cf. Whitford and Schumacher 1961); these are characteristics that should enhance system resilience (Jordan et al. 1972, Webster et al. 1975, Steinman et al. 1991). Instead, in our system, it seems likely that the resilient capacity of fast-current communities was constrained by physical limitations of shear stress that exported new production from the system (McIntire 1968, Peterson and Stevenson 1990). Similar patterns were reported by Steinman et al. (1991) who found that periphyton developed under conditions of high nutrient supply was highly resilient following a light elimination disturbance, but resilience declined when the community was subjected to heavy grazing by snails. These snail-grazed systems were also more resistant to scour (Mulholland et al. 1991). Thus, the same physical forces that appeared to constrain resilience (i.e., shear stress/grazing) may also alter community properties to confer resistance.

Common to many post-disturbance recovery sequences is an acceleration or pulse of regrowth following release of persistent individuals or new immigrants from competitive constraint (Noble and Slatyer 1980). High productivity and rapid growth of benthic algae is often observed after scouring by spates (Moore 1976, Fisher et al. 1982, Grimm and Fisher 1989) or removal of overstory biomass by grazing (Lamberti and Resh 1983, McCormick and Stevenson 1991*b*). In the present study, net growth of several populations was enhanced by simulated spates. Given that microalgal growth is influenced by algal densities on substrata (Peterson and Hoagland 1990, Stevenson 1990, McCormick and Stevenson 1991*a*), it is likely that spate-induced reductions in cell density increased supplies of nutrients and light to both persistent cells and new immigrants, thereby stimulating reproduction in a subset of populations. This effect was less pronounced in fast current than in slow because cell export limited accrual of algal biomass in fast-current habitats.

The rapid recovery of diatom community composition following disturbance in slow-current channels suggested that structural properties of the habitat and differential species performance influenced resilient ca-

pacity. In the most extreme case, the day-18 spate strongly displaced slow-current diatom assemblages back to dominance by *Achnanthes minutissima*. Within 3 d, however, assemblages had returned to dominance by *Synedra* and *Nitzschia* spp. and were indistinguishable from day-21 control assemblages. In this case, displacement occurred because of the high resistance of *A. minutissima* relative to *Synedra* and *Nitzschia* spp., most likely because these latter taxa inhabited interstices within relatively susceptible zygnematalean mats. Following the spate, however, regeneration of green-algal biomass was rapid and, with this regeneration of habitat, interstitial taxa proliferated while densities of adnate taxa associated with tile surfaces remained relatively unchanged. The fact that assemblage composition was more resilient in slow current than in fast reflects greater influence of physical constraints in fast current.

Conclusions

We have shown that benthic algal communities can vary in resistance based on both the timing of disturbance events with respect to stage of community development and on the current regime in which they develop. Variation in responses to disturbance results from a complex set of underlying mechanisms that controls resistance and resilience. For example, we found that the presence or absence of secondary habitat (i.e., filamentous green-algal mats) strongly influenced disturbance response of diatom assemblages. In addition, communities that appeared taxonomically and morphologically similar differed in resistance depending on short-term disturbance history, but only in slow-current habitats in which biotic control factors were paramount. Knowledge of the interactions between effects of ambient environmental conditions and disturbance regime can contribute much to our understanding of successional dynamics in streams and other ecosystems.

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