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## Mechanisms of lotic microalgal colonization following space-clearing disturbances acting at different spatial scales

Christopher G. Peterson

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Diel drift/colonization studies were conducted in Sycamore Creek, Arizona, U.S.A. in late June, 87 d post-spate and, again, 4 d after recession of a large mid-August spate to examine differences in benthic algal colonization of space cleared by small-scale, localized disturbance versus large-scale, system-wide disturbance. Cell densities and species composition in the algal drift pool were quantified with hourly samples, composited every 3 h for 36 h. Diel changes in colonization activity were assessed by sampling ceramic tiles incubated during each of the twelve 3-h periods (instantaneous colonization). Cumulative changes in algal communities were assessed by collecting tiles, introduced at the start of each study, at 3-h intervals for 36 h, then again at 48 and 96 h. Consecutive 3-h measures from instantaneous-colonization samples were summed to compute “expected” cell densities of taxa within different algal divisions, based on short-term colonization alone, after 6 to 36 h, and compared to actual cell densities on cumulative tiles.

Tiles introduced during the June interflood period were colonized much more slowly than in August, and supported assemblages dominated by bluegreen algae. Comparisons of cell densities and changes in taxonomic structure in instantaneous- and cumulative-colonization assemblages indicated that, in June, algal reproductive activity was low and rates of emigration and death were high. In August, diatom and green algal densities in drift and colonization assemblages were significantly higher than in June, and accrual of these taxa on cumulative-colonization tiles exceeded that expected, indicating rapid reproduction. August drift and colonization assemblages exhibited clear diel changes in both cell densities (with mid-day maxima) and taxonomic structure, suggesting that rates of immigration, emigration, and reproduction varied among taxa. In June, mid-day peaks in algal drift activity were caused by passive entrainment of cells into the water column, likely by oxygen bubbles produced by photosynthesis. In August, live diatom cells exhibited higher drift peaks than dead cells, indicating reproductive activity and, likely, changes in cell buoyancy was influential in generating drift maxima. Many diatom taxa displayed clear mid-day minima in colonization efficiency, corresponding to periods of peak drift, suggesting diel changes in cell buoyancy. No such patterns were detected in bluegreen or green-algal taxa.

Rapid recovery of diatom assemblages in Sycamore Creek after spates appears to be driven by rapid reproduction, emigration, and reimmigration of early successional diatom taxa. The rate and pattern of benthic algal colonization of open space in Sycamore Creek, and the mechanisms controlling this process, varied considerably depending on the circumstances under which substrata became available.

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Regeneration of open, colonizable space is a common consequence of physical disturbance on attached communities in many ecosystems. If a disturbance denudes an area of substratum, recovery is driven entirely by the performance of new immigrants, the availability of which is often tied to the spatial extent of the disturbance because this can dictate the proximity of a pool of potential new colonists. These factors, species performance and availability, are key determinants of succession patterns during post-disturbance recovery (Pickett et al. 1987). Whether or not a disturbance alters supply rate and/or performance of new colonists depends, in part, on the nature of the event. Fire in semi-arid woodlands, for example, can induce seed germination in a subset of species within the seed bank (Keeley 1994) while augmenting nutrient supplies in a variety of ways (Wellington and Noble 1985, Christensen 1994). Seeds of terrestrial and aquatic plants, present for years in seed banks, are released when soil is disrupted by animal activity (Burggraaf-van Nierop and van der Meijden 1984) or tillage by humans (Kirkman and Sharitz 1994), yet allogenic nutrient supplies are unaffected by this type of disturbance. Gap-generating disturbances such as windthrow (You and Petty 1991) or landslides (Guariguata 1990) in terrestrial forests produce tree-fall debris that can provide a nutrient pulse for new colonists (Brokaw 1985), but do not enhance propagule supply. Wave disturbance in marine intertidal communities creates gaps of varying size (Sousa 1984), but does not significantly enhance propagule availability or nutrient supply. Understanding the key factors underlying variation in the supply and performance of new colonists is prerequisite to gaining a predictive understanding of post-disturbance recovery in sessile communities.

In stream ecosystems, benthic algal communities are subjected to space-clearing disturbance events that can act at a range of spatial scales. Periodic high-discharge events, or spates, can partially or completely scour algal biomass from large areas of substrata, generating open space for recolonization (e.g., Fisher et al. 1982, Power and Stewart 1987, Biggs and Close 1989). Spates can significantly alter cell densities and species composition in the algal drift pool (Hamilton and Duthie 1987, Cazaubon 1988), the principal source of cells for recolonization of bare substrata (cf. Hoagland et al. 1986). Flood waters often carry high loads of dissolved nutrients (Grimm 1992, Britton et al. 1993), which can remain elevated well after flood recession (Perkins and Jones 1994, Peterson et al. 1994). A spate-induced shift in water-column nutrient regime would be expected to alter species performance during recovery because algal reproductive rates vary substantially among taxa, depending on supply ratios of essential nutrients (e.g., Tilman et al. 1986, Grover 1989).

Localized, small-scale disruptions of attached algal communities occur in streams via activity of macrofauna, either aquatic (e.g., turtles, muskrats, fish) or terrestrial (e.g., herons, humans, cattle). Such disturbances can clear  $\approx 10\text{--}1000\text{ cm}^2$  areas of substrata for new colonization which is also fed by algal drift from upstream sources. Unlike spates, however, these events have little or no effect on either the algal drift pool or allogenic nutrient supply. The implications of these differences on benthic algal community recovery processes have not been elucidated.

Here I report results of two diel algal drift/colonization studies that examined the relationships between propagule availability and patterns of colonization during early stages of algal succession on previously bare substrata, and assessed the influence of disturbance scale on this process. These studies, each spanning 36 h with subsequent sampling of colonist densities after 48 and 96 h, were conducted at the same location in a Sonoran Desert stream under conditions of similar discharge, current speed, and water temperature, but differed in their timing relative to natural spates. The first study, conducted during a long interflood period, allowed assessment of colonization patterns on small patches of bare substrata without concurrent disturbance-induced modification of algal drift or allogenic nutrient regime, conditions analogous to those expected following localized disturbance of stream sediments by animals. The second study followed recession of a natural, substratum-mobilizing spate that greatly elevated concentrations of dissolved nutrients in stream water and denuded much of the stream bed of macroscopic algal growth.

Short-term diel studies of microalgal drift/colonization activity were useful for investigating the importance of variation in supply and performance of algal colonists on successional processes for several reasons. First, the 36-h diel sampling schedule I employed equals or exceeds generation times of freshwater benthic algae reported from laboratory culture studies (Baars 1983) and field studies of early successional algal assemblages (Peterson et al. 1990, McCormick and Stevenson 1991). Thus, the temporal scale used in this research was comparable to that used to study similar processes in sessile communities composed of longer-lived organisms. Second, benthic algae in streams display strong diel variation in drift (Blum 1954, Müller-Haeckel 1976, Stevenson and Peterson 1991) and colonization (Müller-Haeckel 1970) activity. Frequent sampling of drift and colonization assemblages to take advantage of these periodicities allowed better resolution of the connection between propagule availability and colonization activity, and more accurate assessment of performance of new colonists.

## Methods

### Experimental design, sample collection, and processing

The two studies were conducted in summer, 1990 in Sycamore Creek, a spatially intermittent stream in the Sonoran Desert of central Arizona, U.S.A. The first study was initiated on 28 June during midsummer baseflow, 87 d after a spring spate. The second was started on 20 August, 4 d after the stream had returned to baseflow after a series of 3 spates from 12 to 16 August (see Peterson et al. 1994 for a description of these events). Both studies were conducted at the same location in an unshaded, pea-gravel bed reach at an elevation of 650 m.

Unglazed ceramic tiles (28 cm<sup>2</sup>) placed atop 7 flat cinder blocks (20–25 cm long, 20 cm wide, 4 cm deep) were used as substrata for algal colonization. In both studies, tiles were introduced at 0630 h and three replicates (taken from predetermined positions to insure interspersed across the sampler array) were collected every 3 h for 36 h, then again at 48 and 96 h. These samples allowed assessment of *cumulative* changes in algal cell densities and species composition. Diel variation in colonization activity was quantified by collecting three replicate tiles incubated during each of twelve 3-h intervals, giving estimates of 3-h *instantaneous* colonization over the first 36 h of each study. Upon collection, material from each tile was transferred into a vial using a toothbrush and washbottle and preserved, on site, in Lugol's solution (American Public Health Association 1989). A subsample from each vial was later mounted in syrup medium (Stevenson 1984) for quantitative cell counts via light microscopy.

Algal *drift* activity over the initial 36 h of each study was quantified using composites of three 60-ml bulk-water samples collected hourly over the sampler array, leading up to and including the hour of tile collection at the end of each 3-h interval (e.g., triplicate drift samples corresponding to a 0930 h tile collection consisted of subsamples taken at 0730, 0830 and 0930 h). I used composite samples to more accurately estimate average drift densities over each 3-h period than would occur if samples were taken every 3 h. Composite samples were preserved with Lugol's solution. Aliquots of drift samples were filtered in the lab through 0.45 µm cellulose-nitrate filters using a continuous rinse of 95% ethanol, and the filters mounted and cleared in clove oil by methods of Stevenson and Peterson (1989) for quantitative cell counts via light microscopy.

I compared algal accrual on 24-h colonization tiles collected for a separate study on 28 June and 18 August to 24-h cumulative colonization from the diel studies measured on 29 June and 21 August to examine temporal changes in colonization activity during interflood and post-spate periods. Samplers used for the diel

studies were located, at similar depth and current regime, <2 m downstream of the sampler array from which the other 24-h colonization tiles were collected.

Densities and species composition of live diatoms (i.e., those with intact frustules containing chloroplasts) and non-diatom algae in both syrup and clove-oil mounts were determined at 1000× magnification by scanning at least three 100-µm wide transects of various lengths and enumerating, for most samples, ≥ 500 cells. If a scan of 10 long transects failed to yield 500 cells, additional transects were scanned until at least 300 cells had been encountered. Filamentous bluegreen algae (i.e., *Schizothrix* and *Calothrix*) were enumerated as 10-µm lengths since trichome crosswalls were not always evident, precluding reliable cell counts of these taxa. Dead diatom-cell densities were also quantified by counting single diatom valves supporting a central area, and both valves of empty intact frustules, and dividing by two. Dead diatoms were not taxonomically identified.

Triplicate water samples were collected every 3 h, concurrently with tile collections, and analyzed for soluble reactive phosphorus (by methods of Murphy and Riley 1962), nitrate-nitrogen (Wood et al. 1967), ammonium-nitrogen (Solorzano 1969), and specific conductance. Water temperature was recorded at 3-h intervals during the June study. In August, only water temperature extremes were recorded using a minimum/maximum mercury thermometer. A coarse estimate of current speed over the sampler array was obtained at the time of initial tile placement by timing the drift of a floating object over a known distance, using the mean of 3 trials.

### Analytical methods

In each study, temporal variation in physical/chemical variables, the percentage of live diatoms in drift assemblages, and cell densities in instantaneous-, cumulative-colonization, and drift assemblages, were assessed by one-way analysis of variance (ANOVA), with a protected Fisher's Least Significant Difference (LSD) test for multiple comparisons among means. Two-factor (date × time) ANOVA were used to test for differences between studies. Because cumulative-colonization data were taken from spatially interspersed replicate tiles, and because sequential drift and instantaneous-colonization samples represented independent collections, these analyses assume no temporal autocorrelation. Algal densities from 24-h colonization tiles collected on successive dates were compared with t-tests. Natural-log and arcsine-square-root transformations were applied to cell density and percentage data, respectively, to homogenize variances (Zar 1984).

Means from successive 3-h instantaneous-colonization collections were summed to estimate the cell

density "expected" on cumulative-colonization tiles for each 3-h sampling interval. Expected values were then compared to actual densities from cumulative-colonization tiles using a two-factor (treatment [expected or actual]  $\times$  time) ANOVA on natural-log transformed cell-density data.

Temporal changes in taxonomic structure of colonization and drift assemblages were assessed using detrended correspondence analysis (DCA – Hill and Gauch, 1980), run with DECORANA (Hill 1979). Mean DCA axes scores generated from 3 replicate samples from each collection time and assemblage type were plotted in ordination space using species loadings determined from relative abundances of 19–20 common species for each study. Taxa included in this analysis averaged  $\geq 3\%$  of at least one assemblage on at least one sample time. Because taxonomic composition of June and August algal communities differed, a different suite of species was used for each study. Thus, quantitative comparisons of the degree of species-compositional change between studies could not be made. For each study, diel variation in taxonomic structure within each assemblage type was assessed using a one-factor ANOVA with LSD multiple comparisons among sampling times. Differences in ordination scores between assemblages in each study were assessed using a 2-way (treatment  $\times$  time) ANOVA.

All statistical tests were performed using the Statistical Analysis System, Version 6 (SAS Institute 1990).

#### *Determining taxon-specific colonization efficiencies*

The colonization efficiency of each common algal taxon during each 3-h interval was determined by dividing cell density estimates from instantaneous-colonization tiles (cells  $\cdot$  cm $^{-2}$ ) by the number of drifting cells assumed to pass over 1 cm $^2$  of tile surface during the 3 h of incubation. To accomplish this, I assumed that cell densities per unit volume ( $N_d$  – in cells  $\cdot$  ml $^{-1}$ ) estimated from composite drift samples exhibited uniform distribution with depth. I then used my estimate of current speed and employed equations from Silvester and Sleigh (1985) to determine boundary layer thickness and velocity gradient to calculate current speed within 100  $\mu$ m (the length of the largest single-cell alga encountered) of the tile surface ( $CV_b$  – in cm  $\cdot$  s $^{-1}$ ). The supply of potential colonists ( $PC$ ) over each 3-h interval was then calculated as:

$$PC = N_d \times CV_b \times t$$

where  $t = 10\,800$  s.

This estimate, while not necessarily accurate because of the coarse current speed estimates that went into its calculation, allowed precise assessment of diel changes in the colonization activity of individual taxa and comparison of colonization efficiencies among taxa.

Significant diel change in the colonization efficiency of each common taxon was detected with a second-order curvilinear regression of colonization efficiencies calculated for each 3-h interval against time of day (0030–2400 h).

## Results

### Variation in physical/chemical conditions

On 28 June, at the start of the first diel study, Sycamore Creek was at a stable summer baseflow of 0.02 m $^3$   $\cdot$  s $^{-1}$ . Stream depth at the study site was 15.0 cm (10.5 cm to tile surface) and current speed was 6.43 cm  $\cdot$  s $^{-1}$  ( $\pm 0.24$  se). At the start of the second study, on 20 August, stream depth (15.3 cm/10.8 cm to tile surface) was similar to, and current speed (4.95 cm  $\cdot$  s $^{-1}$   $\pm 0.04$  se) was slightly lower than June values. Discharge on 20 August, while stable at 0.08 m $^3$   $\cdot$  s $^{-1}$ , was elevated relative to June levels as a consequence of stream channel recharge during the August spates.

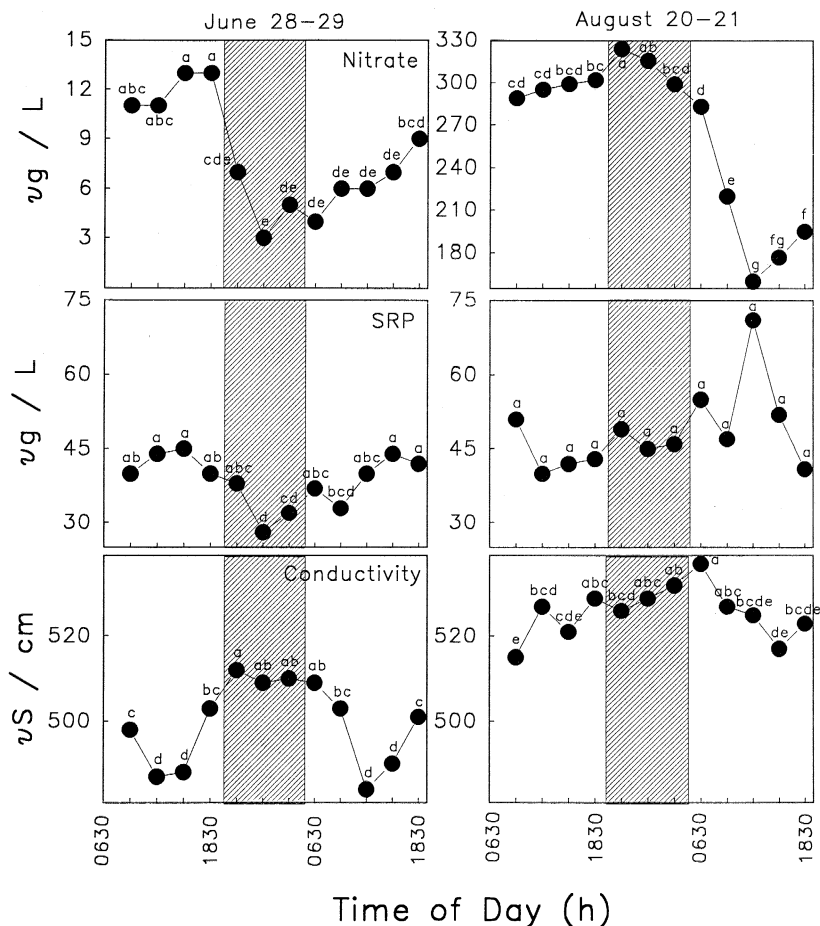
Climatic conditions were similar during the two studies. Daylength between 28–29 June (14:22 h) was  $\approx 1$  h longer than in August (13:18 h). In both studies, tiles were exposed to full sun at ca 0700 h and were shaded, well before sunset, at ca 1800 h in June and at 1630 h in August. Except for 2–3 h of overcast conditions during each of the mornings of 28 June and 21 August, skies were clear for the duration of both studies. Water temperatures ranged from 29.4°C (at 1530 h) to 21.7°C (at 0330 h) in June and from 32.2 to 22.2°C in August.

Water chemistry differed significantly between the two study dates. Specific conductance, NO $_3$ -N, and soluble-reactive phosphorus were significantly higher in August than in June (all  $p < 0.001$ ), particularly NO $_3$ -N, which was still at elevated post-spate levels in August (Fig. 1). Diel variation in these variables was more pronounced in June than in August, with distinct maxima (for conductivity,  $p < 0.001$ ,  $F = 14.2$ , d.f. = 11, 24), or minima (for NO $_3$ -N [ $p < 0.001$ ,  $F = 6.9$ , d.f. = 11, 24] and SRP [ $p = 0.002$ ,  $F = 4.2$ , d.f. = 11, 24]) in samples collected at night (Fig. 1). Ammonium concentration did not differ between months (June: 41  $\mu$ g  $\cdot$  L $^{-1}$   $\pm 7$  se, August: 31  $\mu$ g  $\cdot$  L $^{-1}$   $\pm 5$  se) or with time of day.

### Diel and between-study variation in drift and colonization activity

Significant diel periodicities in collective drift and instantaneous colonization of taxa in each of the 3 major algal divisions were observed in both June and August (Table 1), but cell densities and taxonomic representation in these assemblages differed between studies (Figs 2 and 3). In June, bluegreen algae (primarily

Fig. 1. Diel changes in nitrate-nitrogen, soluble reactive phosphorus (SRP), and specific conductance during June and August studies. Note between-study difference in scale for nitrate concentration. Shade regions denote night. Within each panel, symbols labeled with the same letter do not differ significantly ( $p > 0.05$ , LSD comparisons).



*Schizothrix* and *Anabaena*) were most influential in producing mid-day peaks in algal drift (Fig. 2, Table 2), which reached maxima of 1243 ( $\pm 68$  se) and 1631 ( $\pm 345$  se) cells  $\cdot$  ml $^{-1}$  at 1230 h on 28 and 29 June, respectively. During the first 36 h of the June study, both instantaneous- and cumulative-colonization assemblages were comprised of approximately equal proportions of diatoms, green algae, and bluegreen algae. In contrast, diatoms and green algae dominated August assemblages (Fig. 3), and peak drift densities were more than double those observed in June (Tables 2 and 3). Diatoms were most important in generating mid-morning/early afternoon drift peaks in August, but the highest taxon-specific drift peak was produced by a large pulse of 5- $\mu$ m green-algal zoospores that entered and left the water column between 0630–0930 h on 21 August (Fig. 3, Table 3). Diatoms and green-algal densities on instantaneous-colonization tiles in the August study exceeded those in June by 2–36 $\times$ , whereas accrual of bluegreen algae on 3-h tiles did not differ between studies (Figs 2 and 3).

In June, all algal divisions had densities on cumulative-colonization tiles that were significantly lower than

expected based on summation of densities from instantaneous-colonization tiles (Table 4, Fig. 2), indicating high cell loss via emigration or mortality. Accrual of dead diatoms on cumulative-colonization tiles was also significantly lower than expected ( $p < 0.001$ , data not shown). In contrast, following the August spate, green-algal and diatom densities on cumulative tiles greatly exceeded that expected from additive instantaneous colonization alone (Table 4, Fig. 3), suggesting rapid reproduction and/or facilitation of immigration. Cumulative bluegreen-algal densities and additive instantaneous-colonization estimates did not differ in the August study (Table 4, Fig. 3).

Changes in community structure among sample times and assemblages also differed in degree and pattern between studies (Figs 4 and 5). In DCA ordinations from both studies, drift clearly separated from colonization assemblages on DCA axis 1 ( $p < 0.001$ ). In June, significant variation in taxonomic structure of drift assemblages among sample times was noted on both DCA axis 1 ( $p < 0.001$ ,  $F = 6.3$ , d.f. = 11, 24) and 2 ( $p = 0.030$ ,  $F = 2.5$ ), but diel patterns of change, while evident, were relatively weak (Fig. 4). Temporal varia-

Table 1. Results of 1-factor ANOVA of differences among sampling times (3–36 h) collective ln-transformed cell densities of taxa within each of the 3 major algal divisions. Degrees of freedom for all ANOVAs = 11, 24.

		June			August		
		Diatoms	Green algae	Bluegreen algae	Diatoms	Green algae	Bluegreen algae
Drift	<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	0.042
	<i>F</i>	8.3	7.3	25.5	26.8	17.9	2.3
Instantaneous colonization	<i>p</i>	0.001	0.001	0.001	<0.001	<0.001	0.030
	<i>F</i>	4.3	4.4	4.6	28.8	7.0	2.5
Cumulative colonization	<i>p</i>	0.002	<0.001	0.001	<0.001	<0.001	0.054
	<i>F</i>	4.0	6.4	4.4	27.9	13.5	2.2

tion in ordination of June drift samples was strongly influenced by the colonial bluegreen alga, *Agmenellum*, which drifted in relatively high densities during daylight hours, particularly morning, but was sparse or absent in the nocturnal drift. Separation of June drift samples from colonization samples on axis 1 arose from relatively high contribution of bluegreen algae and colonial and/or coenocytic chlorophytes in drift assemblages compared to more diatoms and filamentous green algae in colonization assemblages (Table 5). Ordination of cumulative- and 3-h instantaneous-colonization samples differed on axis 1 ( $p = 0.010$ ,  $F = 2.3$ , d.f. = 22, 46), but not axis 2 ( $p = 0.162$ ; 48- and 96-h samples excluded from this analysis because instantaneous colonization samples were not collected at these times) (Fig. 4). No significant ( $p > 0.05$ ) diel variation in community structure on 3-h instantaneous-colonization tiles was detected on either DCA axis. Significant ( $p < 0.001$ ,  $F = 5.5$  and  $3.9$  for axes 1 and 2, respectively; d.f. = 13, 28) variation in cumulative-colonization samples on DCA axes was due, primarily, to increased importance of filament and basal cells of the chlorophyte, *Stigeoclonium*, in 36–48 h assemblages (Fig. 4, Table 5).

Taxonomic changes in algal drift and colonization assemblages after the August spates (Fig. 5) differed from those observed in June (Fig. 4) in three ways. First, August drift and instantaneous-colonization assemblages exhibited diel patterns of taxonomic change that were more pronounced than in June. Second, these assemblages tracked one another more closely in August (DCA axis 2 score for drift vs instantaneous colonization, Pearson correlation coef. [ $r$ ] = 0.914,  $p < 0.001$ ,  $n = 12$ ) than in June ( $r = 0.021$ ,  $p = 0.949$ ,  $n = 12$ ). No significant correlation between drift and instantaneous-colonization ordination scores on axis 1 were detected in either study. Third, unlike in June, August cumulative- and instantaneous-colonization assemblages began to diverge will within the first 24 h of colonization (Fig. 5). Diel changes in August drift were manifested along DCA axis 2 and reflected strong post-sunrise pulses of 5- $\mu$ m green-algal zoospores, followed by increased influence, during late morning and early afternoon, of a suite of diatom taxa. Also evident, were nocturnal increases in the importance of the filamentous bluegreen alga, *Schizothrix* (Table 6). Sig-

nificant ( $p < 0.001$ ,  $F = 16.7$ , d.f. = 22, 46) separation of drift and instantaneous-colonization assemblages along axis 1 was due to a higher contribution of diatoms to late-morning, afternoon, and night instantaneous-colonization samples, and apparent conversion, upon colonization, of flagellated green-algal zoospores to three size classes (3-, 5-, and 8- $\mu$ m) of unicellular chlorococcalean green algae (Table 6). Divergence of cumulative-colonization samples 12–15 h after tile introduction (following sundown) appeared to reflect increased importance of colonial chlorococcalean green algae, and *Stigeoclonium* basal cells and filaments (Fig. 5, Table 6). Taxonomic shifts back along DCA axis 1 between 48–96 h were produced by large increases in both relative and actual abundance of the stalked diatom *Gomphonema parvulum* (increased from relative abundance of  $3.8\% \pm 1.0$  at 48 h to  $16.2\% \pm 0.4$  at 96 h), and *Schizothrix* ( $2.9\% \pm 1.1$  se at 48 h to  $19.6\% \pm 4.1$  at 96 h).

Variability in taxonomic structure among replicate samples, measured as coefficient of variation of mean DCA ordination scores, was much higher in June collections than in August, and generally lower in colonization assemblages than in the drift (Table 7).

Of 48 common taxa (29 diatoms, 12 green algae, 6 bluegreen algae, and 1 cryptophyte) analyzed for diel change in colonization efficiencies, 8 diatom taxa and 2 green algae exhibited highly significant ( $p < 0.05$  – significance of curvilinear regression coef.) mid-day minima in the propensity of a drifting cell to colonize (see Fig. 6 for representative taxa). Three additional diatom taxa exhibited similar, but marginally significant ( $0.05 > p > 0.10$ ), diel variation in colonization efficiency. Of the 13 taxa for which significant diel patterns in colonization efficiency were detected, only 2 (*Epithemia sorex* and *Cyclotella meneghiniana*) exhibited such patterns during the June study (Fig. 6).

### Temporal changes in colonization activity following spates

Comparison of algal densities on substrata colonized in separate 24-h periods, one to three days apart, showed a strong temporal increase in colonization activity after

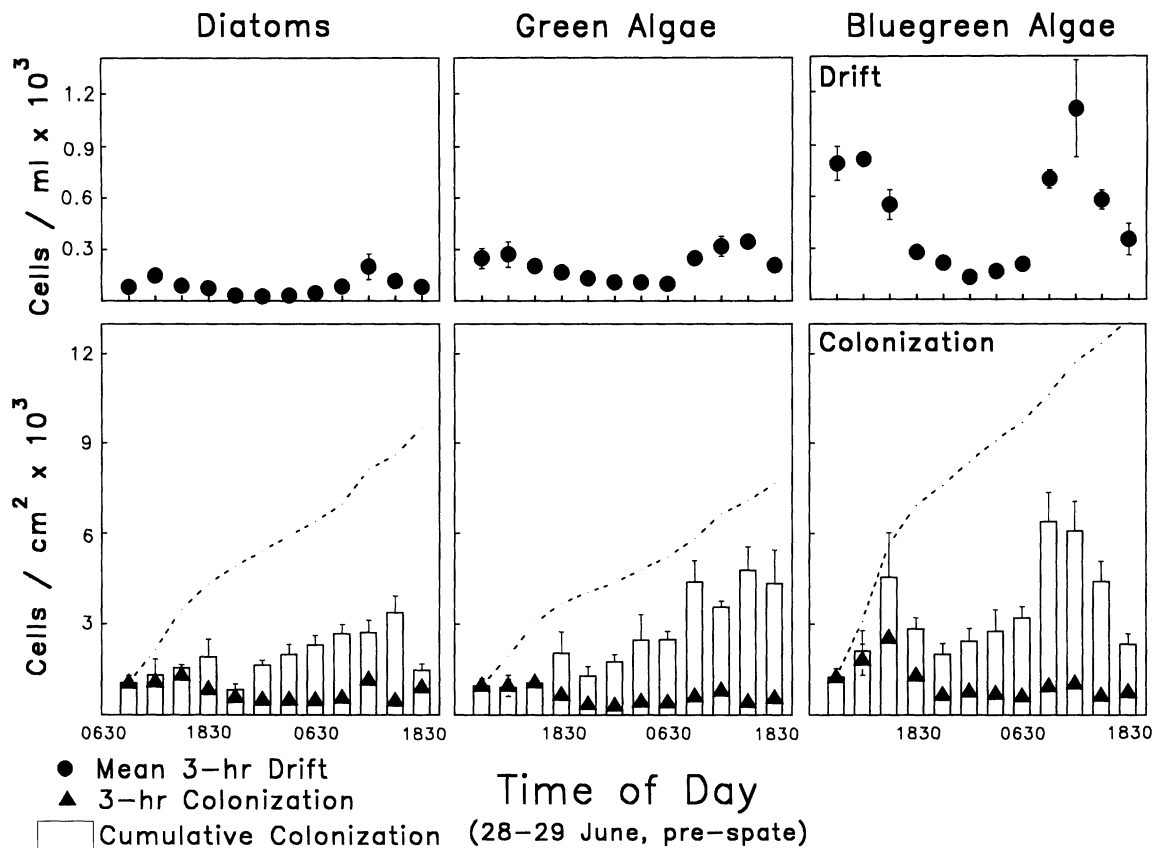


Fig. 2. Diel changes from 28–29 June in mean algal cell density ( $\pm$ s.e.) in the drift (upper panels – closed circles), on 3-h instantaneous-colonization tiles (lower panels – closed triangles), and cumulative-colonization tiles (lower panels – open bars) for each of three major algal divisions. Dashed line in lower-panel plots is the “expected” cumulative cell densities, calculated as the cumulative sum of sequential 3-h instantaneous-colonization densities.

the August spates, but not during the June interflow period (Fig. 7). In June, tiles incubated for 24 h and collected one day apart accrued algae of similar density or taxonomic composition, although both of these 24-h assemblages contained a much higher diatom component than older (84 d) assemblages at the same site (Peterson, unpubl.). Striking differences in short-term colonization rates were noted after the August spates. Tiles introduced on 17 August, one day after the return of Sycamore Creek to baseflow, supported nearly 18 000 cells  $\cdot$  cm $^{-2}$  which were numerically dominated by the same bluegreen algal taxa that dominated assemblages collected immediately before the spates (Peterson unpubl.). In contrast, 24-h accrual on tiles introduced just 3 d later supported an order of magnitude more cells, significantly fewer bluegreen algae ( $p = 0.027$ ,  $t = -2.2$ , d.f. = 5), and much higher numbers of diatoms ( $p < 0.001$ ,  $t = -11.6$ ) and green algae ( $p < 0.001$ ,  $t = -7.3$ ) (Fig. 7).

Diel drift patterns of live and dead diatoms also suggest significant spate-induced changes in diatom reproduction (Fig. 8). During the initial 36 h of the June study, only 35.3% ( $\pm$  2.1% se) of drifting diatom cells

contained intact chloroplasts, compared to 73.1% ( $\pm$  2.3% se) in August. Live and dead cells exhibited similar diel periodicities in June, attaining mid-day peaks of similar magnitude on successive days (1-way ANOVA, LSD comparison,  $p > 0.05$ ), but live cell densities fell more rapidly from these maxima than dead cells (Fig. 8). In contrast, drift maxima of live diatoms in August were ca 3–6  $\times$  higher than dead-cell maxima. Moreover, the mid-day drift peak of live diatoms on 21 August was nearly double that observed during the same time interval the day before (LSD,  $p < 0.05$ ). No differences were detected in successive drift peaks of dead diatom cells (Fig. 8), green algae, or bluegreen algae (Fig. 3).

Temporal changes in algal drift activity were also evident from taxonomic variation in the drift assemblage on successive days during the August study. In both June and August, movement of drift samples along DCA axes 1 and 2 indicated that the drift assemblage returned to similar taxonomic structure at the same time period on consecutive days (LSD,  $p > 0.05$ ; Figs 4 and 5). Temporal resilience in June drift samples was also apparent on DCA axis 3 (Fig. 9). In August,



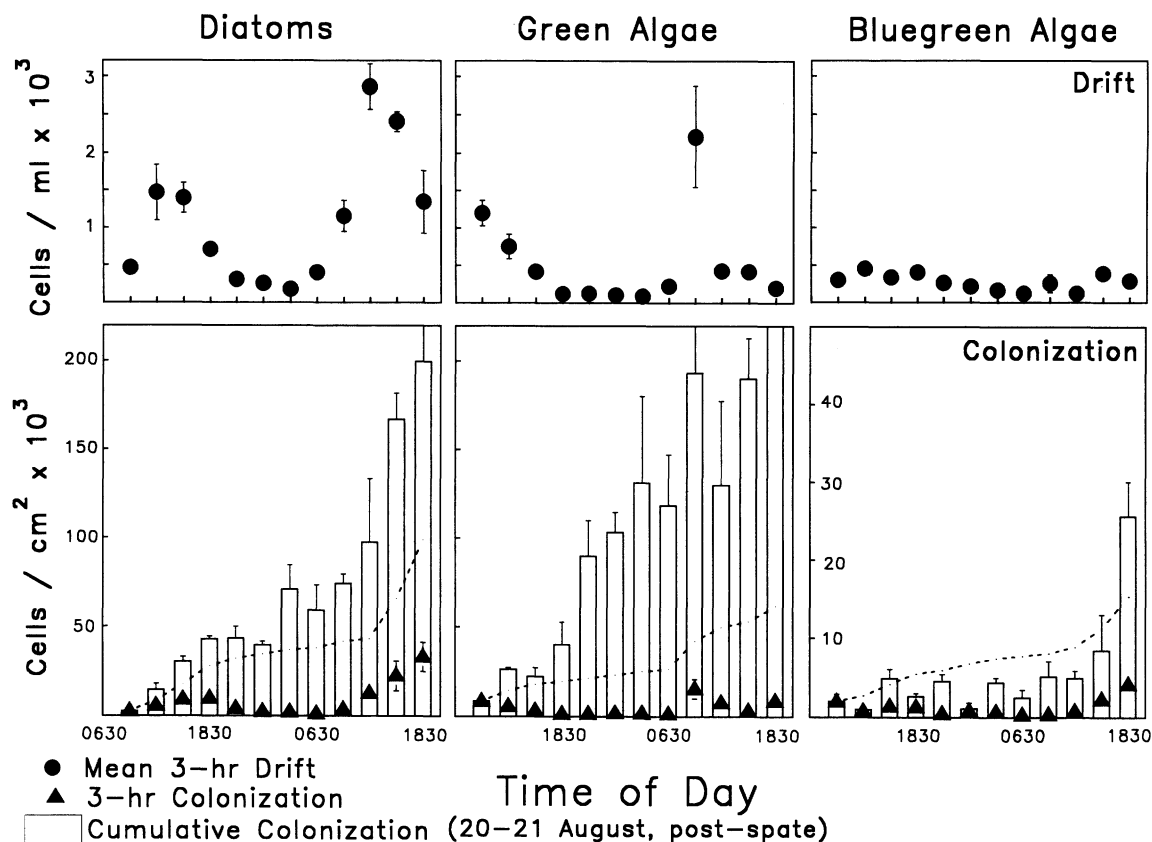


Fig. 3. Diel changes from 20–21 August in mean algal cell density ( $\pm$ s.e.) in the drift (upper panels – closed circles), on 3-h instantaneous-colonization tiles (lower panels – closed triangles), and cumulative-colonization tiles (lower panels – open bars) for each of three major algal divisions. Dashed line in lower-panel plots is the “expected” cumulative cell densities, calculated as the cumulative sum of sequential 3-h instantaneous-colonization densities.

however, axis 3 reveals significant displacement of taxonomic structure of the late-morning/early-afternoon drift samples collected on 21 August, relative to the same time intervals the previous day (LSD,  $p < 0.05$ , Fig. 9). Species loadings on axis 3 suggest that these differences resulted from increased importance of diatom taxa, particularly *Gomphonema parvulum* and *Navicula minusculus* during the second day (Table 7).

## Discussion

Results of these studies show that benthic algal colonization of open space in Sycamore Creek, and the mechanisms controlling this process, varied considerably depending on the circumstances under which cleared substrata became available, and the composition of the extant community. In August, following a system-wide, substratum-mobilizing spate, cell densities in both drift and colonization assemblages were high and algal accrual was strongly influenced by rapid reproduction of diatoms and green algae. Distinct diel patterns in the August study were noted not only in cell

densities of drift and colonization assemblages, but also in changes in the taxonomic structure of these assemblages. This finding suggests interspecific differences in the timing and magnitude of immigration, emigration, and reproduction. Substrata introduced into Sycamore Creek during the June interflood period, analogous to space opened by small-scale, localized disturbance, were colonized much more slowly than in August. Cell accumulation patterns in June suggested slow algal reproductive rates and high rates of emigration. Differences between algal colonization patterns in June and August likely reflected differences in propagule availability and species performance under the vastly different nutrient regimes between these two dates.

It should be noted that microalgal colonization is not limited by availability of space, per se. Algal cells readily attach to detritus, other algae, or algal/bacterial mucilage in addition to inorganic surfaces (Rosowski et al. 1986a, Oppenheim and Paterson 1990), particularly in slow-current habitats (Lamb and Lowe 1987). If motile, individuals can move through the developing milieu of biotic and abiotic material. However, physical and chemical changes that occur on a substratum dur-

Table 2. Mean and maximum cell densities in drift and 3-h instantaneous-colonization assemblages for the most abundant algal taxa, and all taxa combined, observed during the June study. Taxa listed include those with the 5 highest mean abundances in either drift or instantaneous-colonization assemblages across all time intervals. Subscripts on 'time of maximum' abundance: 1 = 28 June, 2 = 29 June. B = bluegreen alga (Cyanophyceae), G = green alga (Chlorophyceae), D = diatom (Bacillariophyceae).  $n = 36$  for 36-h means,  $n = 3$  for 3-h maxima.

Species	Drift (cells · ml <sup>-1</sup> )			3-h instantaneous colonization (cells · cm <sup>-2</sup> )		
	36-h mean (se)	3-h maximum (se)	Time of maximum	36-h mean (se)	3-h maximum (se)	Time of maximum
<i>Agmenellum</i> – B	63 (13)	143 (82)	0930 <sub>2</sub> –1230 <sub>2</sub>	60 (23)	258 (123)	1230 <sub>2</sub> –1530 <sub>1</sub>
<i>Anabaena</i> – B	147 (21)	353 (80)	0930 <sub>2</sub> –1230 <sub>2</sub>	68 (17)	163 (93)	1230 <sub>1</sub> –1530 <sub>1</sub>
<i>Chroococcus</i> – B	101 (11)	187 (65)	0930 <sub>2</sub> –1230 <sub>2</sub>	379 (47)	879 (314)	1230 <sub>1</sub> –1530 <sub>1</sub>
<i>Schizothrix</i> – B	153 (14)	282 (19)	0930 <sub>1</sub> –1230 <sub>1</sub>	455 (46)	952 (36)	1230 <sub>1</sub> –1530 <sub>1</sub>
3- $\mu$ m <i>Chlorococcus</i> – G	18 (2)	34 (15)	0930 <sub>2</sub> –1230 <sub>2</sub>	208 (20)	382 (56)	1230 <sub>1</sub> –1530 <sub>1</sub>
green-algal zoospores – G	63 (5)	103 (21)	0930 <sub>2</sub> –1230 <sub>2</sub>	20 (3)	57 (14)	1230 <sub>1</sub> –1530 <sub>1</sub>
<i>Epithemia sorex</i> – D	11 (2)	26 (3)	0930 <sub>1</sub> –1230 <sub>1</sub>	167 (17)	332 (44)	1230 <sub>1</sub> –1530 <sub>1</sub>
<i>Fragilaria pinnata</i> – D	5 (1)	13 (9)	1230 <sub>1</sub> –1530 <sub>1</sub>	134 (19)	273 (127)	1230 <sub>1</sub> –1530 <sub>1</sub>
Total cells	787 (77)	1631 (345)		2532 (207)	4948 (499)	

§ Density measured as 10- $\mu$ m trichome lengths.

ing early stages of colonization can alter the rate and pattern of algal immigration (Stevenson 1983, Vadas et al. 1992), and density-dependent interactions among early colonists can alter algal reproduction rates (Huang and Boney 1985, Peterson and Stevenson 1989, McCormick 1996). Such interactions may drive the evolution of interspecific differences in the ecological strategies that benthic algae employ (Stevenson et al. 1991).

### Factors affecting the algal drift pool

Strong diel periodicity in algal drift densities was noted in both June and August, with drift maxima occurring between 0930–1530 h for all common taxa. Similar patterns have been reported from other lotic systems (e.g., Blum 1954, Müller-Haeckel 1966, 1970, Hamilton and Duthie 1987, Stevenson and Peterson 1991; but see Barnese and Lowe 1992). While the phenomenon of periodicity in microalgal drift is cosmopolitan, the mechanisms behind these patterns are varied and include both active and passive processes (Stevenson and Peterson 1991). Algal cells dislodged from the benthos into the drift by base-level activity of fish or invertebrates (Scrimgeour et al. 1991, Lamberti et al. 1995), or via current shear (Cushing et al. 1993), contribute to baseline drift densities. Mechanisms that increase algal drift densities above this baseline include passive entrainment of cells by oxygen bubbles produced by photosynthesis (Blum 1954, Müller-Haeckel 1966), or increased algal emigration during periods of cell division (Müller-Haeckel 1966), due either to higher susceptibility of new cells to removal by current (Rosowski et al. 1986b, Peterson and Stevenson 1990) or to changes in cell buoyancy (as noted in phytoplankton; Eppley et al. 1967). Nocturnal increases in feeding activity of benthic macroinvertebrates (Huhta et al. 1995) or algiv-

orous fish (Fisher et al. 1981), or increases in stream discharge resulting from night-time reduction in evapotranspiration of riparian vegetation (Kobayashi et al. 1990), also contribute to diel variability in algal drift densities, but these mechanisms would not be expected to induce daytime drift peaks. Similarly, temperature-induced variation in density of stream water should promote shorter residence times in the drift for benthic algal cells, and thus lower drift densities during the day, when stream water viscosity is lowest, particularly at the 22–32°C summer temperatures in Sycamore Creek (Cole 1994).

Differences in drift patterns of live and dead diatoms between my two studies suggest that mid-day increases in algal drift were probably caused by different mechanisms. In June, live and dead diatom cells exhibited similar magnitudes and timing of change between daily drift minima and maxima, strongly suggesting passive entrainment into the water column, likely from O<sub>2</sub> bubbles generated by benthic photosynthesis or advection induced by changes in water temperature. The more rapid decrease in live-cell drift (see Fig. 8), however, indicates that buoyancy changes in live diatoms also occurred. August drift was clearly also influenced by passive entrainment mechanisms, but the higher drift maxima of live diatoms relative to dead (by 3–6 $\times$ ) indicates that drift and benthic algal reproduction were tightly coupled. Increased drift activity of live diatoms probably did not stem from heightened post-reproductive susceptibility of new cells to removal by current shear, given the slow (ca 5 cm · s<sup>-1</sup>) current (Peterson and Stevenson 1990). Instead, diatom drift peaks may have been tied to increases in cell buoyancy associated with reproduction, or, perhaps, rapid diatom reproduction within the drift itself. Stevenson and Peterson (1991) used a mathematical model and algal drift data collected during interflood periods in Michigan and Kentucky streams to show that cell division by drifting

Table 3. Mean and maximum cell densities in drift and 3-h instantaneous-colonization assemblages for the most abundant algal taxa, and all taxa combined, observed during the August study. Taxa listed include those with the 5 highest mean abundances in either drift or instantaneous-colonization assemblages across all time intervals. Subscripts on 'time of maximum' abundance: 1 = 20 August, 2 = 21 August. B = bluegreen alga (Cyanophyceae), G = green alga (Chlorophyceae), D = diatom (Bacillariophyceae).  $n = 36$  for 36-h means,  $n = 3$  for 3-h maxima.

Species	Drift (cells · ml <sup>-1</sup> )			3-h instantaneous colonization (cells · cm <sup>-2</sup> )		
	36-h mean (se)	3-h maximum (se)	Time of maximum	36-h mean (se)	3-h maximum (se)	Time of maximum
§ <i>Schizothrix</i> – B	235 (20)	370 (47)	0930 <sub>1</sub> –1230 <sub>1</sub>	754 (125)	2612 (478)	1530 <sub>2</sub> –1830 <sub>2</sub>
3-µm <i>Chlorococcus</i> – G	28 (5)	93 (34)	0630 <sub>1</sub> –0930 <sub>1</sub>	1899 (409)	7665 (2746)	0630 <sub>2</sub> –0930 <sub>2</sub>
green-algal zoospores – G	323 (87)	1660 (465)	0630 <sub>2</sub> –0939 <sub>2</sub>	499 (138)	2194 (1068)	0630 <sub>2</sub> –0930 <sub>2</sub>
<i>Cyclotella meneghiniana</i> – D	294 (36)	654 (32)	1230 <sub>2</sub> –1530 <sub>2</sub>	1317 (174)	3469 (793)	1530 <sub>2</sub> –1830 <sub>2</sub>
<i>Nitzschia palea</i> – D	82 (12)	215 (19)	1230 <sub>2</sub> –1530 <sub>2</sub>	922 (229)	3982 (919)	1530 <sub>2</sub> –1830 <sub>2</sub>
<i>N. palea</i> var <i>debilis</i> – D	247 (38)	648 (99)	0930 <sub>2</sub> –1230 <sub>2</sub>	2771 (611)	10975 (2687)	1530 <sub>2</sub> –1830 <sub>2</sub>
Total cells	1891 (209)	3420 (167)		15627 (2250)	45834 (10547)	

§ Density measured as 10-µm trichome lengths.

diatoms was insufficient to produce observed drift peaks. Whether the same holds true in pre- and post-spate conditions in Sycamore Creek is the subject of future study (Peterson unpubl.).

Diel changes in the taxonomic structure of drift assemblages support interpretations of diatom drift data described above. Entrainment of algal cells into the drift via passive mechanisms should be relatively non-selective, displacing cells at or near the biofilm surface, regardless of taxonomic identity, although interspecific differences in cell size and shape among algal taxa may influence susceptibility to dislodgement somewhat. The highly variable, diel shifts in taxonomic structure evident from DCA ordinations of June drift data are consistent with such random displacement. In contrast, diel changes in the taxonomic structure of August drift assemblages were sharp and regular, returning to the same ordination space in successive days. This suggests predictable taxonomic shifts associated with diel variation in activity among algal populations.

Live/dead cell data cannot be used to infer drift mechanisms in non-diatom algae, because most non-diatom cells degrade after death. However, two lines of evidence suggest that drift of bluegreen and most green algal taxa was controlled, primarily, by passive mechanisms. First, unlike diatoms, drift densities and the magnitude of diel changes in drift of these groups differed little between the two studies. An exception was noted for green algal zoospores, which were apparently released in large quantities just after sunrise during the August study and colonized the benthos within 3 h. Second, colonization efficiencies of all bluegreen algae and all but one green algal taxon did not change on a diel basis in either study. That is, the probability of a drifting bluegreen or green alga successfully colonizing the benthos was unaffected by time of day. In contrast, many diatom taxa exhibited significant mid-day minima in colonization efficiency, corresponding to the timing of drift peaks, strongly suggesting that diel

changes in cell buoyancy contributed to mid-day peaks in diatom drift. Others have documented changes in diatom buoyancy with the onset of adverse environmental conditions (Bothwell et al. 1989) or according to endogenous diel cycles (Eppley 1977).

#### Variation in colonization activity and post-immigration performance

Separation of drift and instantaneous-colonization samples on ordination plots in both studies showed that immigration and emigration activities varied interspecifically. Stevenson and Peterson (1991) noted a similar disparity between the species composition of drift samples, averaged over a day, and 24-h colonization samples taken from two north-central U.S. streams. Differences, between June and August, in performance of initial algal immigrants in Sycamore Creek resulted in vastly different colonization dynamics.

In June, comparisons between 3-h instantaneous- and cumulative-colonization assemblages indicated that algal community dynamics within the first 24 h of colonization were driven by emigration and immigration, with little or no replacement by reproduction. The lack of divergence in ordinations of these two assemblages (see Fig. 4) supports this interpretation. Divergence of taxonomic structure from that of an initial immigration assemblage would be expected if immigrants were reproductively active, because taxa with different autecologies have different growth rates (McCormick and Stevenson 1991, Stevenson et al. 1991). During the June study, Sycamore Creek supported a benthic algal community dominated by late-successional species of bluegreen algae, many of which were nitrogen fixers. These taxa also comprised the largest component of the drift pool. Common diatoms included *Epithemia sorex*, a species also able to fix N<sub>2</sub> by virtue of endosymbiotic bluegreen inclusions, and *Fragilaria pinnata*, a small,

Table 4. Results of 2-factor (Time = 3–36 h, Treatment = expected or actual) ANOVA examining differences between collective In-transformed cell densities of taxa within each of the 3 major algal divisions on cumulative substrata versus densities that would be expected from additive accumulation from 3-h instantaneous colonization. Degrees of freedom for all Main effects = 23, 24; for Time effects = 11, 24; and for Treatment effects = 1, 24. Treatment × Time interactions were not significant in any instance and, thus, are not reported.

		June			August		
		Diatoms	Green algae	Bluegreen algae	Diatoms	Green algae	Bluegreen algae
Main effects	<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	ns
	<i>F</i>	6.6	5.1	5.4	17.2	8.7	1.2
Time	<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	ns
	<i>F</i>	5.7	7.9	6.1	34.3	13.8	1.9
Treatment	<i>p</i>	<0.001	<0.001	<0.001	0.001	<0.001	ns
	<i>F</i>	73.5	24.2	45.5	14.3	36.4	2.7

non-motile chain-forming species often associated with bluegreen algal mats in Sycamore Creek (Peterson et al. 1994). Late-successional taxa are well adapted for nutrient-poor conditions (Stevenson et al. 1991, Peterson and Grimm 1992) but do not proliferate rapidly as colonists of open space (cf. Stevenson et al. 1991). Patterns of algal colonization into localized gaps of open stream substrata is strongly affected by the taxonomic composition of the algal drift pool, and this is dictated by the successional state of the extant benthic algal community.

Algal colonization dynamics 4 d after Sycamore Creek had receded to baseflow after spates that mobilized, scoured, and reworked the pea-gravel stream bed, differed greatly from those observed in June, 7.5 wk earlier. Differences between algal cell densities on 3-h instantaneous- versus cumulative-colonization tiles indicated rapid reproduction of diatoms and, to a lesser extent, green algae. Although algal colonization can be facilitated by flow interruptions produced as microtopography develops in early stages of benthic algal community development (Stevenson 1983, McCormick 1991), there are several lines of evidence that indicate algal reproduction was the primary contributor to accrual of high cell densities on cumulative-colonization tiles. First, while the facilitative effects of flow interruption on algal colonization rates are very pronounced in fast current, such effects are minimal or undetectable in the kinds of slow-current habitats present in this study (Korte and Blinn 1983, Peterson and Stevenson 1989, McCormick 1991). Second, facilitative effects, if influential, should have affected all algal taxa, not just diatoms and green algae, and should have also been evident in the June study, but were not. Third, the large increases in diatom drift peaks from one day to the next during the August study, when algal accrual on cumulative tiles greatly exceeded expected levels, and the order-of-magnitude increase in 24-h diatom colonization rates on successive days, strongly suggests diatom reproduction at this time was high, and was feeding the drift.

In August, differences in cell densities between cumulative- and instantaneous-colonization tiles were evident within 6 h of tile placement. The magnitude of cell-density changes over successive 3-h intervals suggested that most green-algal cell division occurred at night, as has been previously reported for lotic green algae (Müller-Haeckel 1976). Diatoms, in contrast, divide just before sunrise (Sicko-Goad et al. 1988) and in the hours immediately after reillumination (Eppley 1977). Blue-green algae, which dominate late-successional, summer assemblages in Sycamore Creek when N:P ratios in stream water are low (Grimm and Fisher 1986, Peterson and Grimm 1992, Peterson et al. 1994), changed little in the nitrate-rich waters that characterize post-spate conditions in this stream (Peterson et al. 1994).

Separation of taxonomic structure between August instantaneous- and cumulative-colonization assemblages occurred, as with cell densities, within 6 h of tile introduction, but became pronounced after sunset, presumably due to the nocturnal pulse of green algal reproduction. However, post-sunrise convergence of taxonomic structure in these two assemblages on the second day of the study suggests that cumulative assemblages were still influenced, somewhat, by immigration. Estimates of benthic algal immigration, as  $\text{cells} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$ , are often calculated from cell densities accrued on substrata incubated for 24 h (Müller-Haeckel and Håkansson 1978, Stevenson 1983, Stevenson and Peterson 1989). A mathematical model applied to algal colonization data collected in  $27\text{--}33 \text{ cm} \cdot \text{s}^{-1}$  currents during winter baseflow in a Michigan stream showed that >90% of algal biomass accrued on a substratum in 24 h could be attributed to immigration (Stevenson 1986). In the slow current, warm temperature, and rich nutrient regime of post-spate Sycamore Creek, reproduction of new immigrants appears to be more influential in determining cell density and taxonomic structure, even in the very early stages of algal succession.

Colonization and proliferation of the filamentous green alga, *Stigeoclonium*, was extremely rapid in August. Transition from drifting green-algal zoospores to

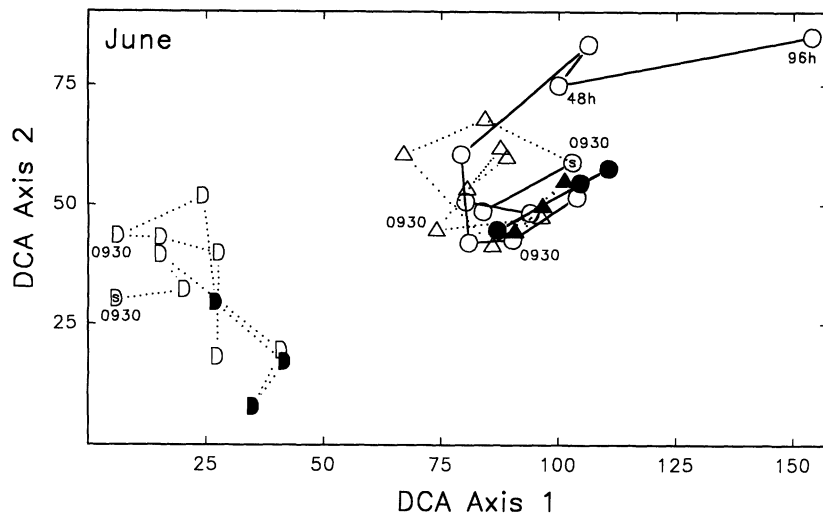


Fig. 4. DCA Ordination of sample means from the June study illustrating temporal changes in algal taxonomic structure in drift (D), 3-h instantaneous-colonization (triangles), and cumulative-colonization (circles) assemblages. Initial samples, taken at 0930 on 28 June, are labeled "S" – samples collected at 0930 on 29 June are also labeled. Connected points represent sequential samples for each assemblage. Filled symbols denote night collections. Species loadings for DCA axes are provided in Table 5.

unicellular chlorococcalean cells (presumably newly colonized deflagellated zoospores) to aggregates of *Stigeoclonium* basal cells and vegetative filaments was clearly evident from DCA ordination scores, and occurred within 48 h. The August spates elevated discharge from a baseflow of  $<0.01 \text{ m}^3 \cdot \text{s}^{-1}$  to  $>60 \text{ m}^3 \cdot \text{s}^{-1}$  and extensively scoured and redistributed substrata, making it likely that most *Stigeoclonium* that persisted through these events did so not as filaments

but as basal cells, which are resistant to removal by abrasion (Mulholland et al. 1991, Rosemond 1993). This situation should constrain the recovery of *Stigeoclonium* because this alga must generate new filaments from basal cells before zoospores can be produced (Entwistle 1989). Results reported here indicate that progression from basal cells to production of reproductive propagules can occur quickly.

In both studies, taxonomic structure of assemblages on cumulative colonization tiles diverged from that of younger assemblages 36–48 h after tile introduction. This divergence was caused, in large, by substantial increases in a subset of taxa that had previously comprised a relatively minor component of the community (i.e. *Stigeoclonium* in both studies, and *Gomphonema parvulum* and *Schizothrix* in August). Despite occurring very early in community development, it is plausible that these shifts reflected a response to autogenic changes in the community that favored later-successional taxa.

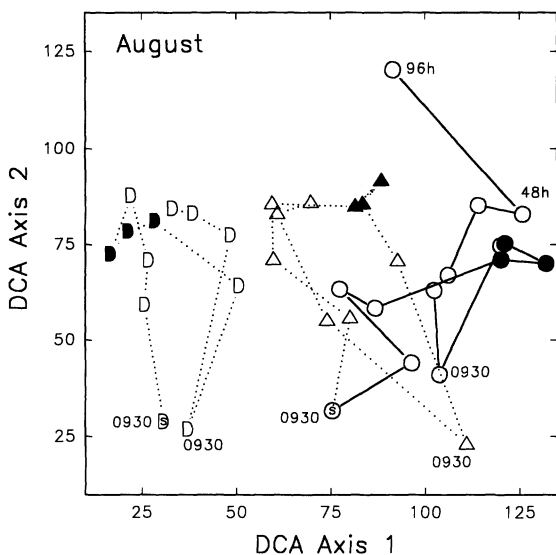


Fig. 5. DCA Ordination of sample means from the August study illustrating temporal changes in algal taxonomic structure in drift (D), 3-h instantaneous-colonization (triangles), and cumulative-colonization (circles) assemblages. Initial samples, taken at 0930 on 20 August, are labeled "S" – samples collected at 0930 on 21 August are also labeled. Connected points represent sequential samples for each assemblage. Filled symbols denote night collections. Species loadings for DCA axes are provided in Table 6.

### Mechanisms behind rapid post-spate colonization

Post-spate recovery of diatom assemblages in Sycamore Creek is extremely rapid, with diatom films visible on scoured gravel within 1–2 d of spate recession (Fisher et al. 1982, Grimm and Fisher 1989). Data presented here suggest that such rapid recolonization is not driven by reproduction of cells that remained attached to substrata through the spate (my data were from previously clean substrata). The large taxonomic and density differences between 24-h colonization assemblages collected on 18 August, 2 d after spate recession, and on 21 August (see Fig. 7) show that post-spate recolonization patterns did not stem directly from immigration of cells suspended by the spate. Similarity in taxonomic

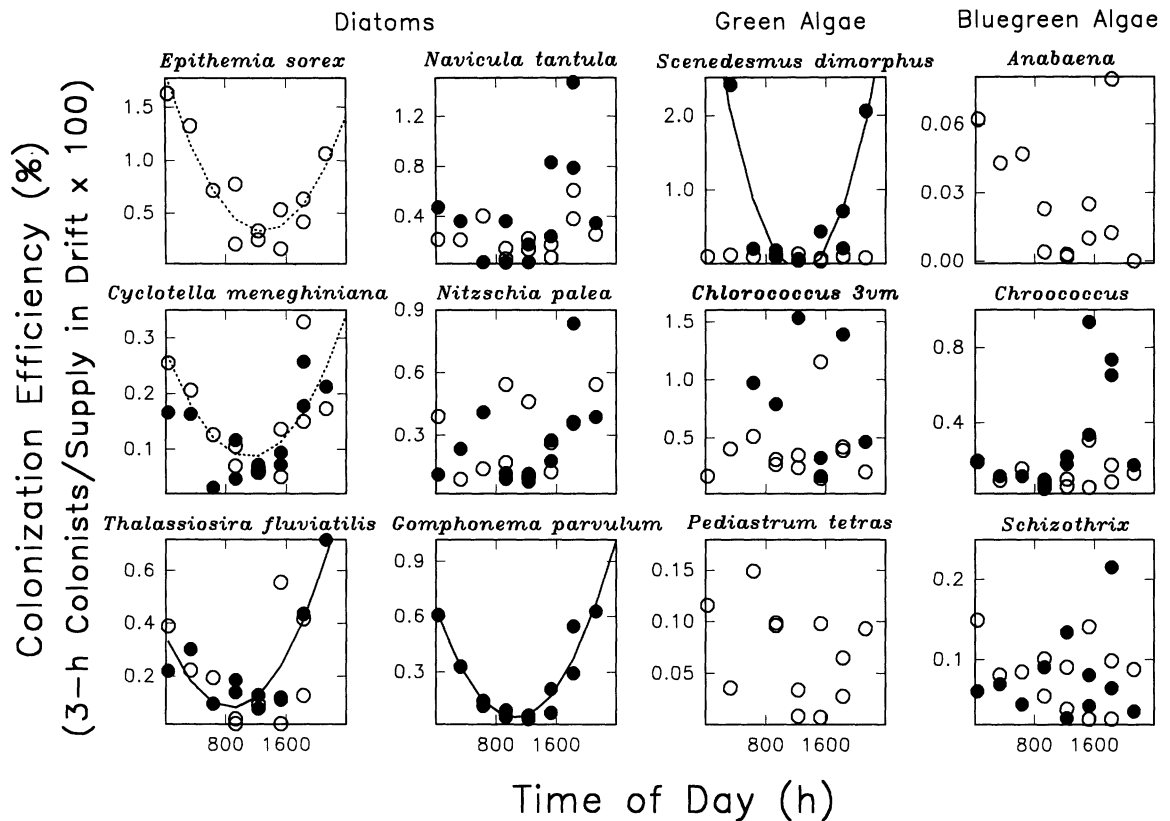


Fig. 6. Patterns of diel change in colonization efficiencies of 12 algal taxa during the June (open symbols) and August (closed symbols) studies. Solutions to significant ( $p < 0.05$ ) curvilinear regressions of colonization efficiency against time of day are denoted by either dashed (June study) or solid (August study) lines.

composition between 24-h colonization assemblages collected immediately post-spate and 132-d old assemblages sampled just before the spate (Peterson unpubl.) does, however, suggest that reimmigration of cells dislodged by the spate did occur.

Rapid recovery of benthic algal communities following the August spates appeared to be produced by a cascade effect, whereby emigrants from a rapidly dividing subset of taxa in the initial immigration assemblage augment the drift pool and accelerate recovery via reimmigration (Fig. 10). Measurements of short-term colonization made immediately after spates and again several days later, have shown dramatic temporal increases in densities of algal colonists (Stevenson 1990, August study – this paper). Similar successive measurements made in systems not influenced by recent spates, have shown no significant temporal change in colonization activity (Oemke and Burton 1986, McCormick and Stevenson 1991, June study – this paper). In addition, diatom densities in the drift and on 3-h instantaneous-colonization tiles increased greatly from one day to the next during the August study, but showed no similar temporal changes during the June interflood period. Comparisons of live/dead ratios between my two stud-

ies, and differences in patterns of diel change in living and dead diatom cells showed strong evidence for post-spate stimulation of diatom reproduction, a response not shared by bluegreen and most green algae. Interspecific differences in response to post-spate conditions were also reflected in taxonomic changes in drift composition between days (see Fig. 9 – DCA axis 3), and provides additional evidence for cascade effects.

Operation of this mechanism for rapid post-spate recovery of benthic algal communities is most plausible under conditions that favor diatom growth, following a disturbance event that thoroughly scours algal biomass from a large percentage of the stream bed. Many diatoms, particularly lightly silicified *Nitzschia* like those common in the drift during the August study, reproduce rapidly on clean substrata (Peterson and Stevenson 1989, Peterson et al. 1990), and are more prone to drift than many other diatoms (Roeder 1977, Peterson et al. 1990). On substrata that retain attached algae through a spate, algal reproductive rates are inversely related to the amount of persistent biomass present (Stevenson 1990, Uehlinger 1991, Peterson et al. 1994). Strong cascade effects and consequent rapid accrual of algal biomass, therefore, are most probable

Table 5. Species loadings and ranks for axis of DCA plots (Figs 4 and 9) generated by analysis of relative abundance data from drift, instantaneous-colonization, and cumulative-colonization samples from the June study. B = bluegreen alga (Cyanophyceae), G = green alga (Chlorophyceae), D = diatom (Bacillariophyceae), C = cryptophyte (Cryptophyceae).

Species	Axis 1 Eig. val. = 0.134		Axis 2 Eig. val. = 0.029		Axis 3 Eig. val. = 0.022	
	Loading	Rank	Loading	Rank	Loading	Rank
<i>Stigeoclonium</i> basal – G	305	1	251	2	–75	18
<i>Stigeoclonium</i> filament – G	216	2	120	4	0	26
<i>Fragilaria capucina</i> – D	201	3	81	10	90	10
15- $\mu$ m Cryptophyte – C	183	4	137	3	99	9
<i>Fragilaria pinnata</i> – D	166	5	107	5	102	7
3- $\mu$ m <i>Chlorococcus</i> – G	165	6	51	13	43	12
<i>Synedra ulna</i> – D	164	7	25	16	124	4
<i>Epithemia sorex</i> – D	137	8	77	11	75	11
<i>Cocconeis placentula</i> var. <i>lineata</i> – D	117	9	93	8	37	13
<i>Cyclotella meneghiniana</i> – D	96	10	44	15	116	5
<i>Chroococcus</i> – B	54	11	48	14	8	15
<i>Schizothrix</i> – B	53	12	–18	17	9	14
<i>Scenedesmus dimorphus</i> – G	34	13	56	12	109	6
<i>Calothrix</i> – B	32	14	101	6	–25	17
3 $\mu$ m-celled colonial green alga – G	24	15	98	7	393	1
<i>Scenedesmus bijuga</i> – G	3	16	87	9	182	3
<i>Pediastrum tetras</i> – G	–4	17	–74	19	206	2
green-algal zoospores – G	–82	18	–28	18	101	8
<i>Anabaena</i> – B	–94	19	–164	20	–128	20
<i>Agmenellum</i> – B	–152	20	363	1	–103	19

Table 6. Species loadings and ranks for axis of DCA plots (Figs 4 and 9) generated by analysis of relative abundance data from drift, instantaneous colonization, and cumulative colonization samples from the August study. B = bluegreen alga (Cyanophyceae), G = green alga (Chlorophyceae), D = diatom (Bacillariophyceae).

Species	Axis 1 Eig. val. = 0.121		Axis 2 Eig. val. = 0.046		Axis 3 Eig. val. = 0.031	
	Loading	Rank	Loading	Rank	Loading	Rank
3 $\mu$ m-celled colonial green alga – G	285	1	228	2	219	3
<i>Stigeoclonium</i> basal – G	227	2	338	1	65	9
3- $\mu$ m <i>Chlorococcus</i> – G	196	3	–25	17	81	
<i>Stigeoclonium</i> filament – G	180	4	104	9	71	8
5- $\mu$ m <i>Chlorococcus</i> – G	178	5	–33	18	60	10
<i>Fragilaria pinnata</i> – D	147	6	150	5	227	2
8- $\mu$ m <i>Chlorococcus</i> – G	128	7	–12	16	–73	17
<i>Nitzschia kutzingiana</i> – D	120	8	108	8	24	13
<i>Thalassiosira fluviatilis</i> – D	93	9	86	11	25	12
<i>Gomphonema parvulum</i> – D	67	10	194	3	–92	18
<i>N. palea</i> var. <i>debilis</i> – D	53	11	89	10	–39	15
<i>N. palea</i> – D	46	12	78	13	–40	16
<i>Chroococcus</i> – B	23	13	145	6	178	4
<i>Cyclotella meneghiniana</i> – D	15	14	73	14	27	11
<i>N. accommodata</i> – D	12	15	84	12	–3	14
green-algal zoospores – G	–9	16	–132	19	166	5
<i>Calothrix</i> – B	–79	17	6	15	274	1
<i>Navicula minusculus</i> – D	–85	18	139	7	–165	19
<i>Schizothrix</i> – B	–116	19	161	4	146	6

after spates that leave large expanses of “clean” substrata, and that recede quickly to low current velocity. Reproduction and subsequent emigration from pockets of persistent biomass would be less than that observed on initially clean substrata. In fast-flowing stream

reaches, immigration and initial accrual of benthic algae, particularly light, non-attaching taxa, should be significantly curtailed (cf. Reisen and Spencer 1970), likely negating effects of colonization cascades and slowing post-spate recovery.

Table 7. Average coefficients of variation ( $\pm 1$  s.e.) about mean DCA ordination scores from analyses of taxonomic change in drift and colonization assemblages during the June and August diel studies. Values are means of coefficients of variation of three replicates taken at each sampling interval. For drift and instantaneous colonization,  $n = 12$ . For cumulative colonization,  $n = 14$ .

	Drift		3-h instantaneous colonization		cumulative colonization	
	June	August	June	August	June	August
DCA axis 1	43.1%	36.0%	12.9%	11.1%	13.8%	7.5%
	( $\pm 10.9$ )	( $\pm 7.3$ )	( $\pm 2.2$ )	( $\pm 2.4$ )	( $\pm 1.9$ )	( $\pm 1.0$ )
DCA axis 2	51.0%	10.1%	29.7%	15.5%	21.8%	11.7%
	( $\pm 9.2$ )	( $\pm 1.4$ )	( $\pm 3.9$ )	( $\pm 6.9$ )	( $\pm 2.8$ )	( $\pm 2.2$ )

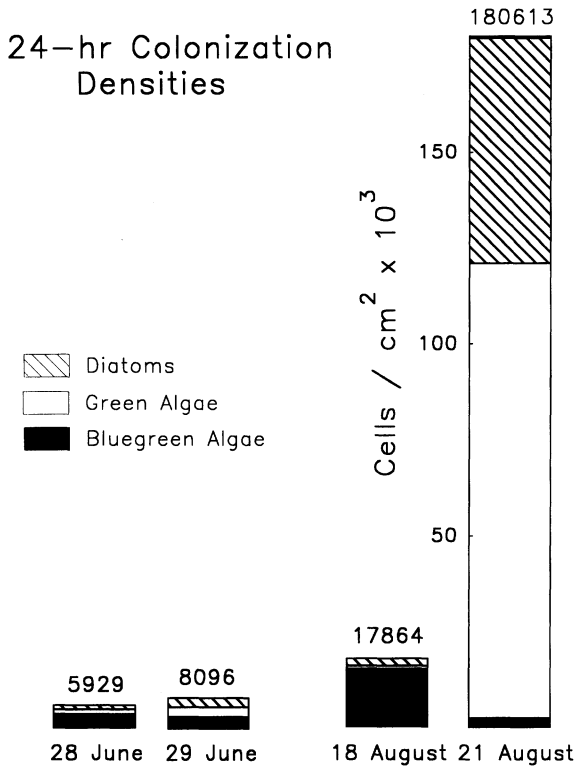


Fig. 7. Mean cell densities for major algal divisions on tiles colonized in Sycamore Creek for 24 h on successive dates during an interflood period in June, and a post-spate period in August. The thin segment at the top of the 21 August bar reflects contribution of taxa not belonging to the three algal divisions listed.

### Concluding remarks

In streams, algal drift provides a continuous supply of potential colonists of newly cleared benthic substrata farther downstream. This differs from other types of sessile communities in which recruitment is linked to specific periods of propagule production (e.g., barnacle assemblages, Gaines and Roughgarden 1985), or stochastic episodes of propagule dispersal via wind or visits by animals (e.g., woody plants, Canham and Marks 1985). Within a given stream, however, the pool

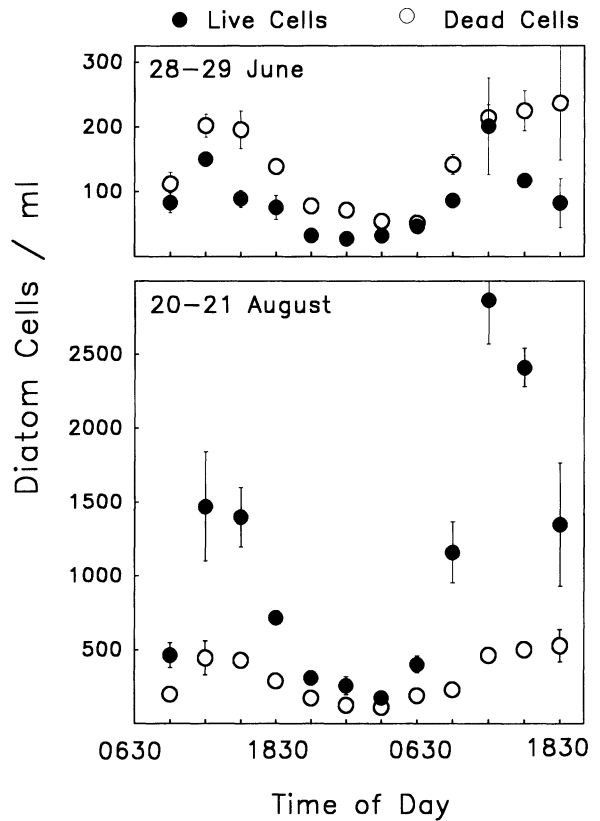


Fig. 8. Diel changes in mean densities ( $\pm$  s.e.) of live and dead diatom cells in drift assemblages during the June and August studies.

of microalgal colonists exhibits significant intraannual variation in density, taxonomic content, and physiological condition (Brettum 1974, Müller-Haeckel and Håkansson 1978, Barnese and Lowe 1992), likely reflecting phenological or successional changes in the benthic algal community. The rates and patterns of recovery of algal communities from localized space-clearing disturbance depend upon the species composition and condition of benthic algae in proximate upstream sources.

My results suggest that algal colonization patterns are affected by the character of the community surrounding the open space, but provide no insight into



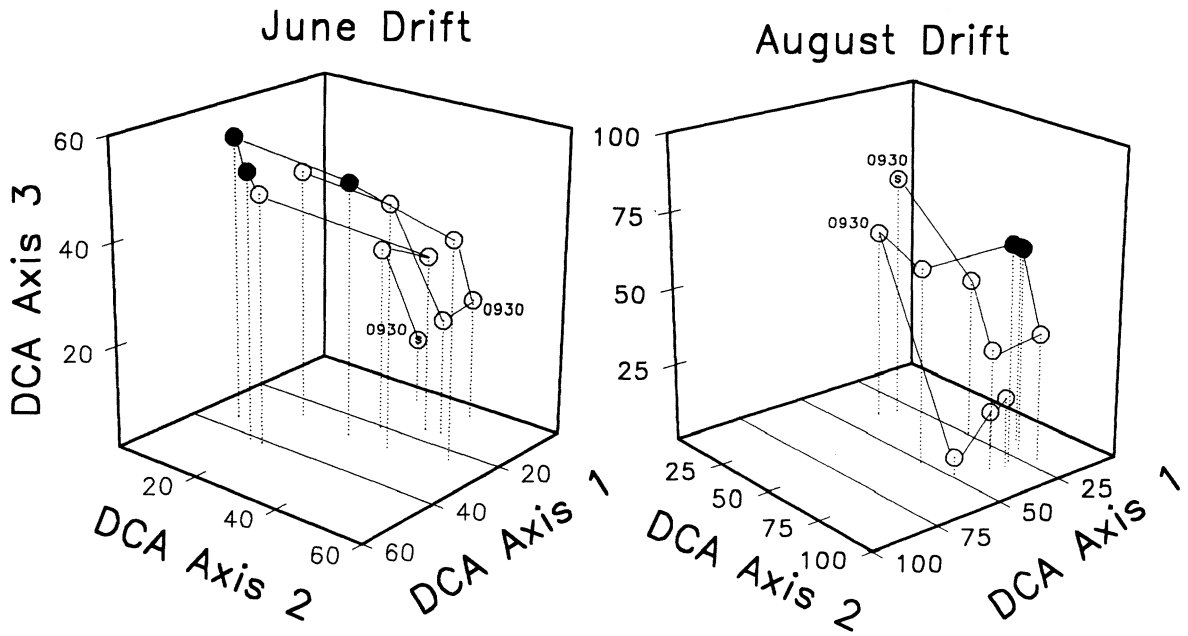


Fig. 9. 3-dimensional DCA Ordinations of sample means from the June and August studies illustrating temporal changes in algal taxonomic structure in drift assemblages. Initial samples, taken at 0930 on the first day of each study are labeled "S" – samples collected at 0930 on the second day are also labeled. Connected points represent sequential samples for each assemblage. Filled symbols denote night collections. Species loadings for DCA axes are provided in Table 5 for the June ordination plot, and Table 6 for the August plot.

the spatial extent of such influence. Müller-Haeckel (1976) used longitudinal changes in colonization rates in stream-side wooden channels to estimate algal drift distances between 18–34 m. Radio-labeled fine-particulate organic matter, including microalgae, in two Idaho streams was transported 580–800 m within a day, with estimated turnover times of 1.5–3 h for material on a given area of benthos (Cushing et al. 1993). Eglishaw and Shackley (1971) noted significant longitudinal change in algal drift composition over several km in a small Scottish stream, suggesting local influences on the drift pool that should, in turn, be reflected in spatial variation in colonization patterns in areas of substratum cleared by localized disturbance. Patterns of benthic algal recovery should exhibit spatial and temporal variation as a function of both proximate community characteristics and variation in physical/chemical parameters, such as current and nutrient supply.

Rates of algal accrual on bare substrata are influenced by local community characteristics because algal taxa employ different ecological strategies and, as a consequence, vary in performance (Stevenson et al. 1991, McCormick 1996). During long interflood periods, in systems with well-developed benthic algal communities, the first colonists in areas denuded by localized disturbance, because of their prevalence in the drift, are likely to be taxa best adapted for slow growth and low resource availability. Under such circumstances, the supply of early successional taxa, which can

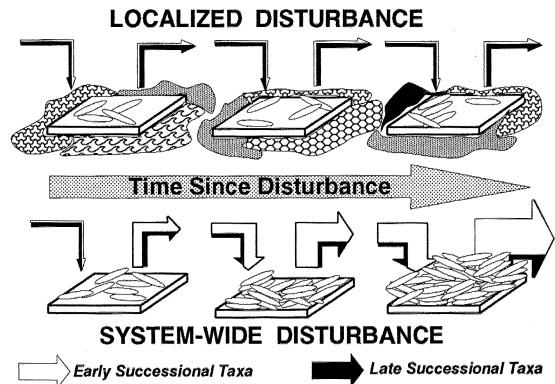


Fig. 10. Conceptual model showing differences in algal colonization mechanisms of newly cleared space following disturbances acting at different scales. Arrows pointing to and from substrata refer to algal immigration and emigration, respectively. Size of arrows correspond to cell densities.

rapidly proliferate under resource-replete conditions, should be insufficient to generate logarithmic growth that drives rapid accrual of algal biomass. Algal colonization of newly opened space should be directly related to the relative availability of early successional taxa, a condition that should vary with time since last large-scale disturbance, or with the prevalence of small, localized disturbances.

Fisher (1987) argued that disturbance effects must be assessed by measuring biotic attributes and independent

variables at a scale appropriate to the spatial range of the disturbance. Brooks and Boulton (1991) subsequently demonstrated a lack of concordance between patterns of macroinvertebrate recovery following simulated and natural spates citing, as cause, differences in pathways and rates of colonization and in sources and faunal composition of recolonists. My results show that algal recovery patterns are sensitive to changes in the quantity and taxonomic composition of the algal drift pool; these are properties affected by both the scale and timing of physical disturbance events in aquatic systems.

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