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Algal colonization under four experimentally-controlled current regimes in a high mountain stream

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Abstract. Algal colonization and assemblage development were examined on unglazed ceramic tiles in flow-through troughs over a 42-d period (summer 1987) in the regulated upper Colorado River (~2400 m a.s.l.). The unusually constant discharge of the stream, coupled with the trough design, allowed the establishment and maintenance of four controlled current regimes that differed with respect to range of free-stream velocity and associated near-substratum hydraulic conditions: 1) depositional (free-stream current velocity <1 cm/s); 2) slow and hydraulically-smooth (range 14–20 cm/s); 3) fast and hydraulically-smooth (range 36–47 cm/s); and, 4) fast and hydraulically-rough or turbulently mixed (range 15–46 cm/s). Biomass was on average 30–40× higher in the two slow velocity treatments than in the two fast velocity treatments. Chlorophytes, bacillariophytes, and cyanophytes exhibited distinctly different successional trajectories and end-points in all treatments. *Ulothrix zonata*, established by day 4, was the dominant alga at all velocities for the first two weeks, after which it was replaced by a more diverse assemblage of chlorophytes, except in the Fast-rough regime. Diatoms were common in all treatments, but were only numerically dominant during the latter part of the study. Cyanophytes dominated only in the two lowest current regimes and only at the end of the study. Scanning electron microscopy revealed that physiognomy of algal assemblages also varied across current regimes. The two low velocity treatments were characterized by dense, upright filaments within one week, while three-dimensional assemblage structure in the two high velocity treatments did not develop over the 42-d period. Differences in species composition, successional trajectories and physiognomy across treatments demonstrated that current regime (free-stream velocity and pattern of flow) was an important determinant of algal assemblage structure in the absence of hydrologic and grazing disturbances.

Key words: algae, colonization, succession, community structure, physiognomy, current regime.

Spatial patterns of algal species abundance and distribution in lotic systems have long been understood to reflect current velocity patterns (Fritsch 1929, Blum 1960, Jones 1978). In the absence of grazing, algal standing crops represent a dynamic balance between the demographic processes of accrual (immigration, growth/reproduction) and loss (emigration, death, and sloughing). Investigations into how stream current mediates these processes have been conducted in numerous descriptive and experimental studies of the initial colonization and establishment of algae on bare substrata. Recent work has shown that accrual processes are largely regulated by species-specific inter-

actions within the microhydraulic environment of the substratum-water interface (e.g., Stevenson 1983, 1984). Increased velocity enhances impingement rate of algal propagules onto the substratum, but the concomitant increase in shear stress on the surface results in preferential attachment by forms that are small, adnate, and/or mucilaginous (Korte and Blinn 1983, Stevenson 1983). Under these microhydraulic constraints, more algal cells typically accrue initially in lower vs. higher velocity habitats (McIntire 1966, Reisen and Spencer 1970, Stevenson 1984, Oemke and Burton 1986, Steinman and McIntire 1986, Lamb and Lowe 1987). But, over time, the enhanced diffusion and physiological exchange rates associated with higher current habitats (Ruttner 1926, Whitford 1960, Whitford and Schumacher 1961, 1964) can

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enhance cell growth/reproduction to result in greater cell densities relative to slow current habitats (e.g., Reisen and Spencer 1970, Korte and Blinn 1983, Oemke and Burton 1986). These autecological responses are reflected in community organization as well. For example, species richness is often greater under lower current conditions (Korte and Blinn 1983, Stevenson 1984, Lamb and Lowe 1987), due perhaps to the larger pool of species capable of persisting under low velocities (Korte and Blinn 1983, Peterson 1986).

The temporal sequence of species replacements among algae colonizing substrata in streams has also received attention as a test of the universality of ecological succession. Observations of "predictable" transitions from structurally simple, horizontal assemblages characterized by adnate diatoms to more complex vertical ones consisting of an understory of adnate diatoms and an overstory of stalked diatoms and filamentous green and blue-green algae have been made in both lentic (Hoagland et al. 1982) and lotic (Korte and Blinn 1983) systems, and the process might be accelerated (Korte and Blinn 1983) or decelerated (Lamb and Lowe 1987) under faster current. However, the generality of this sequence for lotic periphyton assemblages is not yet clear (e.g., Hamilton and Duthie 1984, Steinman and McIntire 1986).

Studies of the effects of current on algal colonization have been done both under controlled laboratory conditions (e.g., McIntire 1966, Steinman and McIntire 1986) and in the field (e.g., Reisen and Spencer 1970, Munteanu and Maly 1981, Korte and Blinn 1983, Stevenson 1983, Oemke and Burton 1986, Peterson 1986, 1987, Peterson and Stevenson 1989). Laboratory experiments sacrifice realism for control (Allan 1984, Diamond 1986); however, field investigations of algal colonization may fail to maintain a consistent hydraulic environment over the period of study because discharge fluctuations lead to changing velocity and associated microhydraulic variability.

In this study, we attempted to combine the strengths of laboratory and field experiments by taking advantage of the unusually constant summer hydrograph of the upper Colorado River. A colonization experiment was conducted under discharge conditions that ensured minimal temporal variation in current velocity in the stream over the period of the experiment.

The near-constant discharge, coupled with the use of flat troughs paved with artificial substrata, allowed us to establish and confidently maintain different current regimes over a 6-wk period in the field. Although control of current in a turbulent stream channel cannot be as rigorous as control in a laboratory flume, this in-situ field experiment allowed us to take advantage of natural sources and concentrations of colonizing algal propagules under natural current regimes that could be characterized with respect to free-stream velocity and near-substratum hydraulic conditions (i.e., degree of turbulent mixing). Thus, our objectives were to examine how assemblage structure, succession, and growth form (physiognomy) of algae varied over time under four temporally-invariant, distinctly different current regimes in a field setting where hydrologic disturbances did not occur and where grazers were excluded.

Methods

Our study was conducted in the upper Colorado River, ~7 km downstream from the hypolimnial-release Granby Reservoir in Grand County, Colorado (~105°55'W, 40°07'N). The elevation of the site is 2420 m and the mean stream gradient in this reach of the river is ~3.7 m/km. The flow regime of the upper Colorado River, entirely governed by reservoir discharge, is unusual in that the reservoir serves as a trans-basin water supply reservoir. Thus, discharges from the reservoir to the study site represent minimal allowable flows that change according to legally-established time schedules. During the 42-d colonization period (15 June to 27 July 1987), the 24-hr mean discharge in the Colorado River was very stable, ranging from 1.70 to 1.92 m³/s (mean = 1.82; coefficient of variation = 2.8%) (U.S. Bureau of Reclamation, Loveland, Colorado, unpublished data). The slight fluctuations in discharge resulted from variable daily demand from irrigators, whose upstream diversions further dampened these daily discharge fluctuations at the study site.

Algae were allowed to colonize unglazed porcelain tiles (2.3 × 2.3 × 0.5 cm) composed of feldspar and kaolin. The very low permeability (<0.5%) and dark color of the tiles were selected to provide characteristics similar to those of natural granitic substrata in the Colorado River. Tiles were placed in four sheet-met-

al troughs that had been acid-washed and cleaned before introduction to the stream. Troughs were 30 cm wide, 6 cm deep, and at least 90 cm long, with the exception of the trough for the Fast-rough current regime (see below), where the length was 35 cm. A border of at least one row of $4.9 \times 4.9 \times 0.5$ cm tiles was permanently cemented to the bottom adjacent to the walls and the front and back of each trough to reduce edge effects for the sampled tiles, which were fitted in the remaining "central" space (i.e., 8 tiles/row \times 23 rows in all but the Fast-rough trough which had only five rows). Colonized tiles removed during sampling were replaced with bare tiles to maintain a regular surface on the bottom of the trough. Troughs, open at both ends, were secured to concrete blocks which were placed on the stream bottom in locations that differed with respect to free-stream current velocity. Troughs were leveled such that water depth throughout was ~ 3 cm over the tiles. Troughs were placed adjacent to one another ~ 15 m downstream from a turbulent riffle and were presumably exposed to similar concentrations of colonizing propagules. Insolation was not directly measured but was similar in each trough. The long-term, mean daily light energy at a nearby benchmark meteorological station (Grand Lake, Colorado) averaged for June and July is ~ 0.01 cal $\text{cm}^{-1} \text{ s}^{-1}$ (U.S. Department of Commerce 1968).

Water chemistry was determined on day 1 for nitrate ($25 \mu\text{g/L}$), orthophosphate-phosphorous (SRP = $10.2 \mu\text{g/L}$) and pH (7.5). These values were characteristic of summer nutrient levels in Granby Reservoir, the source of water at the study site (U.S. Geological Survey 1987). Spot measurements of water temperature were taken throughout the 42-d colonization period. Diel temperature fluctuations ranged from ~ 4.5 to near 18°C . Suspended solids during the summer season are typically < 3 mg/L, about one-half of which is inorganic (N. J. Voelz, unpublished data).

Free-stream velocity in the troughs was measured with an electronic current meter (Nixon Instrumentation, Ltd., Cheltenham, England) that provides a time-averaged velocity reading at 1-s intervals at ~ 7 mm above the substratum surface. At single locations in the upstream, center, and downstream ends of the troughs, 20–30 readings were taken at the beginning of the study to determine the range of velocity

conditions in the trough. Current measurements within the troughs after day 1 were not taken because water depths in the troughs were observed to remain at ~ 3 cm on 16 d over the course of the experiment (days 1, 2, 4, 8, 13, 14, 21, 28, 29, 30, 31, 34, 35, 36, 41, 42). Thus, according to the continuity principle (e.g., see Roberson and Crowe 1980, p. 110), constant water depths in troughs and constant channel discharge imply constant velocities within troughs. Moreover, because the ranges of current velocities (see below) within troughs were generally small and did not overlap among treatments (with the intentional exception of the variable, hydraulically-rough regime), slight variations in stream discharge would not be sufficient to alter categorical differences among treatments.

One trough had its upstream and downstream ends blocked with unglazed fireplace bricks ($10 \times 10 \times 3$ cm) and was termed the Depositional treatment because flow through the trough was < 1 cm/s (see below). Another trough was placed in slowly moving water (~ 20 cm/s) and a third in fast-flowing water (~ 40 cm/s), both characteristic of much of the stream habitat; these treatments were termed Slow-smooth and Fast-smooth, respectively. The fourth trough was also situated in fast-flowing water, but fireplace bricks partially obstructed its upstream end, and water cascading over these 3-cm high bricks produced a highly turbulent flow regime over the tile substrata. This treatment was termed Fast-rough.

Tiles were allowed to colonize for 4, 8, 14, 30, and 42 d (15 June–27 July 1987) in each velocity treatment except the Fast-rough, where day 42 samples were lost. Sample tiles were collected individually for analysis and were chosen randomly from the "central" portions of the troughs, but with one constraint. At least one tile was collected from the upstream and downstream halves of the trough on each date to compensate for potential position differences within the troughs. During removal and replacement of tiles, flow through the troughs was temporarily blocked to minimize disturbance to remaining tiles. Occasional mobile insects (chironomids and baetids) were observed in the troughs and were removed with forceps on the same 16 days as depth in the troughs was observed (see above). Observed abundances of these animals were always low (< 5 per trough, but typically 1–2) and they were

TABLE 1. Summary of current velocity conditions for each of the four treatment troughs as determined at the beginning of the study.

Treatment	Current Velocity (cm/s)			Coefficient of Variation (%)
	Minimum	Maximum	Mean	
Depositional	<1	<1	<1	—
Slow-smooth	14.3	19.8	17.1	13
Fast-smooth	36.1	47.0	41.6	9
Fast-rough	15.4	46.4	29.2	20

assumed to have insignificant impact on algal colonization dynamics and growth.

Triplicate tiles were randomly collected on days 8, 14, 30, and 42 for periphyton biomass determination. Tiles were individually preserved in the field with 2% formalin and returned to the laboratory where their surfaces were scraped with a razor blade. Scraped material was filtered onto a 0.7- μm glass fiber filter, rinsed with distilled water, dried for 24 hr at 60°C, and weighed to the nearest 0.01 mg to determine dry mass (DM). Samples were then combusted at 500°C for 18 hr to remove the organic fraction from the scraped material (APHA 1980). By difference, the ash-free dry mass (AFDM) was determined.

Duplicate tiles were randomly collected for scanning electron microscopic (SEM) analysis on days 4, 8, 14, 30, and 42. They were preserved in the field in 4% glutaraldehyde and transported to the laboratory, where they were dehydrated in an ethanol series and critical-point-dried with liquid CO₂. Tiles were then mounted directly onto aluminum SEM stubs and sputter-coated with gold-palladium. Tile surfaces were viewed with a Philips 505 scanning electron microscope to locate bacteria, fungi, and algal cells adhering to the surface.

Duplicate tiles were also collected on days 4, 8, 14, 30, and 42 for analysis of algal taxonomic structure. After field preservation in 2% formalin, tiles were scraped with a razor blade in the laboratory, brought up to a standard volume (5 ml), and agitated vigorously by hand to disperse clumps. Wet-mount subsamples (1 ml) were scanned under oil immersion at 1250 \times magnification on a Leitz phase contrast microscope, and cells were identified to lowest prac-

ticable taxon. Species densities (cells/mm²) were calculated using standard strip-count procedures (APHA 1980). Only live diatoms were counted. At least two complete transects and at least 200 cells per sample were counted.

Multivariate statistical techniques were used to examine algal species associations within and between current treatments over time. TWINSPAN (Hill 1979b) is a divisive, hierarchical clustering algorithm that is frequently used to assist in interpretation of algal species assemblage structure (e.g., Metcalfe 1988). Detrended Correspondence Analysis (DCA) is an ordination technique (Hill 1979a) that can be useful in assessing successional trajectories through time (Steinman and McIntire 1986). In both procedures, species abundances were based on densities of algal cells.

Results

Current regimes

Current velocity readings measured at 7 mm above the tiles within each trough at the upstream, central, and downstream sections were similar and were pooled. The four treatments were characterized by current regimes that differed with respect both to free-stream velocity and to inferred near-substratum hydraulic characteristics. Minimum, mean, and maximum 1-sec velocities varied among the Depositional, Slow-smooth, and Fast-smooth troughs and were non-overlapping (Table 1). The range of velocities in the Fast-rough trough was large and overlapped both the Slow-smooth and Fast-smooth treatments because of turbulent mixing induced by the bricks in the upstream section of the trough. These free-stream velocity ranges within troughs were maintained over the course of the study period (see Methods).

Differences among troughs in free-stream velocities and in specific trough geometries also allowed some inferences to be made about important, general differences in microhydraulic characteristics among the treatments. Where substratum roughness elements (vertical surface irregularities) are small relative to water depth, so-called "hydraulically-smooth" flow can occur (Davis and Barmuta 1989). Under these conditions, turbulent boundary layers (with a viscous sublayer immediately adjacent to the substratum surface) develop because large-scale

TABLE 2. Total number of algal taxa identified in each of the four current regimes for five sampling times over the 42-d colonization period. (Day 42 samples from the Fast-rough current were lost.)

Days Colonized	Current Regime			
	Depositional	Slow-smooth	Fast-smooth	Fast-rough
4	13	13	15	13
8	17	17	18	17
14	17	14	14	17
30	17	20	21	19
42	32	24	21	—

turbulent eddies that disrupt boundary layer formation are not generated by flow over the smooth surface. The development of turbulent boundary layers downstream from the leading edge of flat plates positioned parallel to the direction of turbulent, open-channel flow is empirically well-described (e.g., Roberson and Crowe 1980). Turbulent boundary layers should have developed downstream from the inlet of both the Slow-smooth and Fast-smooth troughs because the height of the tile roughness elements was small ($<100 \mu\text{m}$) relative to water depth ($\sim 3 \text{ cm}$) and thus the troughs were essentially flat plates exposed parallel to the flow (Jon Peterka, Department of Civil Engineering, Colorado State University, personal communication). Theoretical characteristics of the developing boundary layers (see Roberson and Crowe 1980, p. 323 ff. for equations) can be compared between the Slow-smooth and Fast-smooth troughs to illustrate initial micro-hydraulic differences among the current regimes. Using the maximum velocities from Table 1 in the calculations, the depths of the viscous sub-layers of the turbulent boundary layers ranged from 0.7 to 1.1 mm (at 8 and 61 cm downstream from the leading edge of the trough) for the Slow-smooth trough and from 0.3 to 0.6 mm (at 8 and 61 cm) for the Fast-smooth trough. The corresponding upstream-downstream range in shear velocities (a function of shear stress on the substratum) was 1.0–0.6 cm/s for the Slow-smooth and 1.9–1.1 cm/s for the Fast-smooth troughs. These non-overlapping theoretical values illustrate initial hydraulic differences between the Slow-smooth and Fast-smooth troughs. The hydraulic gradients within the troughs (due to the downstream development

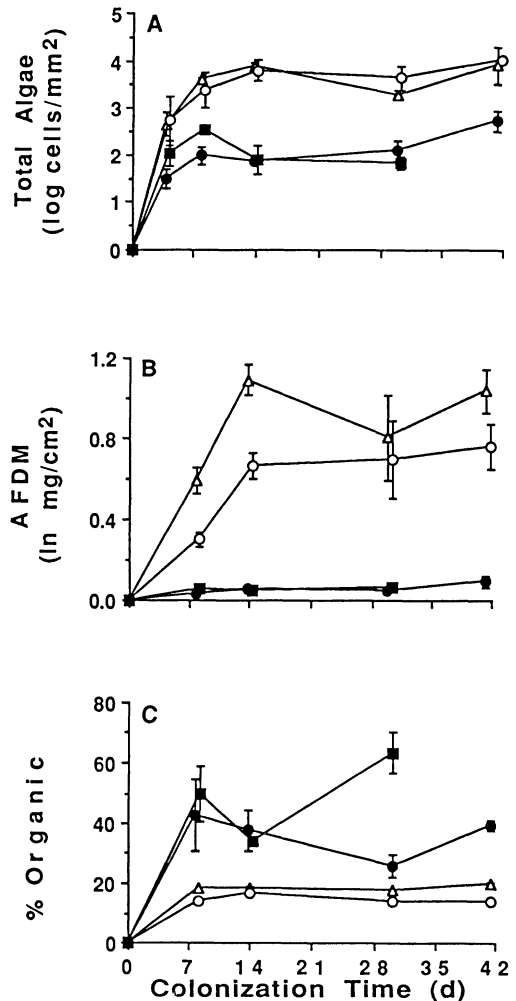


FIG. 1. Temporal pattern for A) total algal cells, B) periphyton ash-free-dry-mass, and C) percent organic fraction of total periphyton dry mass accumulating on initially bare substrata over a 42-d period under four current regimes (— Δ — Depositional; — \circ — Slow-smooth; — \bullet — Fast-smooth; — \blacksquare — Fast-rough). All values plotted as $\bar{x} \pm 1 \text{ SE}$. Symbols slightly offset to avoid overlap of error bars, which when not visible are smaller than the corresponding symbol.

of the turbulent boundary layers) also illustrate potentially important position differences that might affect algal colonization.

In the Fast-rough trough, "hydraulically-rough" flow (cf. Davis and Barmuta 1989) would have occurred because the obstructing bricks at the upstream entrance induced large-scale turbulent eddy formation in the trough. Boundary

TABLE 3. Relative abundances of major algal taxa and total cells (number/cm²) for four current regimes at five colonization times. Golden-brown algae were rare and are not included. (Day 42 samples from the Fast-rough current were lost.)

Treatment	Algal Group	Days of Colonization				
		4	8	14	30	42
Depositional	diatoms	0.038	0.103	0.445	0.591	0.389
	green algae	0.946	0.897	0.555	0.292	0.056
	blue-green algae	0.016	0.000	0.000	0.117	0.555
	total cells	892	8131	15,824	3933	16,333
Slow-smooth	diatoms	0.923	0.149	0.242	0.198	0.188
	green algae	0.073	0.678	0.758	0.410	0.301
	blue-green algae	0.004	0.077	0.000	0.391	0.511
	total cells	1061	4784	12,374	8579	20,518
Fast-smooth	diatoms	0.492	0.383	0.338	0.814	0.364
	green algae	0.508	0.418	0.581	0.070	0.385
	blue-green algae	0.000	0.199	0.081	0.116	0.251
	total cells	61	196	148	242	1074
Fast-rough	diatoms	0.175	0.124	0.596	0.676	—
	green algae	0.787	0.598	0.314	0.023	—
	blue-green algae	0.038	0.278	0.000	0.301	—
	total cells	211	684	156	123	—

layer formation in this trough was likely to be transient at best and could not be inferred (Jon Peterka, personal communication). In this Fast-rough treatment, the bricks appeared to create a hydraulic jump that formed a standing wave which moved slowly from the downstream end to the upstream end of the trough before being swept away by a surge of fast water. This unsteady flow pattern was continually repeated with a period of ~10 s, over which time a wide range of near-substratum shear stresses was likely to have occurred.

Algal colonization

Taxonomic structure and biomass.—Eighty-eight species of algae were identified for the 42-d experimental period. Four main groups were Bacillariophyta (diatoms, 57 species), Chlorophyta (green algae, 21 species), Cyanophyta (blue-green algae, 8 species), and Chrysophyta (golden-brown algae, 2 species). The numbers of taxa identified from the different treatments were similar over the 42-d period and ranged from 13 on day 4 to 32 on day 42 (Table 2).

Algal cell densities increased rapidly in all current treatments and reached asymptotic values by day 8 (Fig. 1A). Cell densities in the

Depositional and Slow-smooth treatments were similar at all times, and were one to two orders of magnitude greater than those in the Fast-smooth and Fast-rough treatments, which were themselves similar. All four troughs rapidly accumulated biomass initially and reached asymptotic values within 14 d. The Depositional and Slow-smooth treatments accumulated 30–40× as much biomass (Fig. 1B), comprising a greater inorganic fraction (Fig. 1C), than did the Fast-smooth and Fast-rough treatments.

Patterns of algal colonization and assemblage composition varied among the treatments, as indicated by differences in relative abundances both of major algal groups throughout the 42-d period (Table 3) and of major individual taxa at days 30 and 42 (Table 4). The Depositional treatment was initially colonized by green algae, followed by diatoms and blue-green algae, which replaced green algae after day 30. *Ulothrix zonata* was the dominant green alga through day 14; *Microspora* sp. was abundant on day 30; and the blue-green algae, *Oscillatoria* sp. and *Anabaena* cf. *affinis*, characterized the assemblage at day 42 (Table 4). Early diatom colonists included *Melosira italica* and *Nitzschia palea*, whereas *Fragilaria pinnata* became numerically abundant toward the end of the period.

TABLE 4. Relative abundances for common taxa (>4% of total live cells) after 30 d and 42 d of colonization under four current regimes (DP = Depositional, SS = Slow-smooth, FS = Fast-smooth, FR = Fast-rough). See Table 2 for total cell densities on corresponding dates. (Day 42 samples from the Fast-rough current were lost.)

Taxon	30 days				42 days		
	DP	SS	FS	FR	DP	SS	FS
Bacillariophyta							
<i>Fragilaria pinnata</i>	0.072	—	—	—	0.163	—	—
<i>Achnanthes minutissima</i>	0.117	0.043	—	0.128	—	—	—
<i>Achnanthes lanceolata</i>	—	—	0.041	0.143	—	0.045	—
<i>Cymbella minuta</i>	—	—	0.046	—	—	—	—
<i>Cymbella sinuata</i>	—	—	—	—	—	—	0.226
<i>Gomphonema angustatum</i>	—	—	—	0.090	—	—	—
<i>Gomphonema</i> sp.	—	—	0.083	—	—	—	—
<i>Navicula</i> sp.	—	—	—	—	—	—	0.057
<i>Nitzschia palea</i>	0.129	0.056	—	—	0.080	0.063	—
<i>Nitzschia paleacea</i>	—	—	0.467	0.128	—	—	0.040
<i>Synedra rumpens</i>	0.082	—	—	—	—	—	—
Chlorophyta							
<i>Coleochaete</i> sp.	—	—	—	—	—	—	0.328
<i>Cladophora</i> sp.	—	0.123	—	—	—	0.045	—
<i>Microspora</i> sp.	0.211	—	—	—	—	—	—
<i>Pediastrum boryanum</i>	—	0.072	—	—	—	0.072	—
<i>Scenedesmus obliquus</i>	0.047	—	—	—	—	0.054	—
<i>Zygnema</i> sp.	—	0.072	—	—	—	0.072	—
<i>Ulothrix zonata</i>	—	0.219	0.054	—	—	—	—
Cyanophyta							
<i>Anabaena</i> cf. <i>affinis</i>	—	0.257	0.083	0.301	0.473	0.511	—
<i>Oscillatoria limnetica</i>	—	0.129	—	—	—	—	—
<i>Oscillatoria</i> sp.	0.094	—	—	—	0.451	—	—
<i>Phormidium</i> sp.	—	—	—	—	—	—	0.223

The Slow-smooth treatment was initially colonized by diatoms which were quickly followed by green algae. Blue-green algae did not appear in appreciable numbers until the end of the study (Table 3). Early diatom colonists included *M. italica* and *Fragilaria* spp. Towards the end of the study, *Achnanthes minutissima*, *A. lanceolata*, and *N. palea* were relatively abundant. *Ulothrix zonata* was the dominant green alga until day 30, after which a diverse group of chlorophytes occurred. By day 42, the cyanophyte *Anabaena* cf. *affinis* was the dominant alga (Table 4).

Diatoms and green algae were the initial colonists in the Fast-smooth trough, and they were abundant throughout the study period. *Hannaea arcus* was a conspicuous early diatom colonist, as were *Cocconeis placentula*, *M. italica*, *Synedra fasciculata*, and others. *Nitzschia paleacea* was the

most abundant diatom by day 30, though *Gomphonema* sp. was also well represented; but by day 42, *Cymbella sinuata* was numerically dominant. As in the Slow-smooth treatment, *Ulothrix zonata* was the dominant green alga early, but by day 42 it had been replaced by *Coleochaete* sp. Blue-green algae became established in this current regime by day 8 (*Oscillatoria* sp.), and *Phormidium* sp. was dominant by the end of the study (Table 4).

In the Fast-rough regime, the initial colonizers were mostly green algae, but by day 30 (the last sample day for this treatment) diatoms and blue-green algae dominated (Table 3). Early diatom colonizers included *Hannaea arcus*, *Synedra fasciculata*, *Cocconeis placentula*, and *M. italica*. By day 30, several species were numerically abundant (Table 4). Among the green algae, *Ulothrix zonata* dominated throughout, but it declined

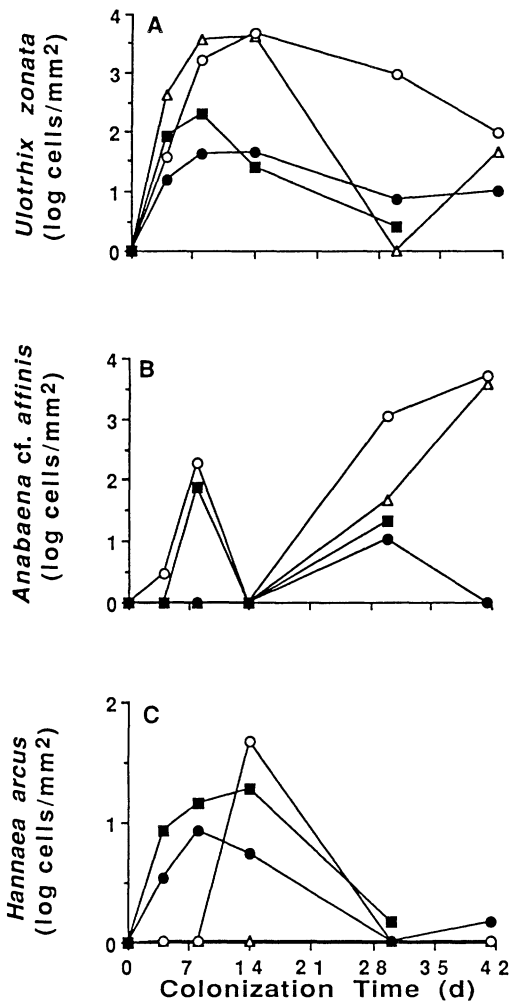


FIG. 2. Temporal pattern of mean density of A) *Ulothrix zonata* (Chlorophyta), B) *Anabaena cf. affinis* (Cyanophyta), and C) *Hannaea arcus* (Bacillariophyta) over a 42-day period under four current regimes (—△— Depositional; —○— Slow-smooth; —●— Fast-smooth; —■— Fast-rough). Each symbol represents the mean of two samples.

after day 14 (see Fig. 2A). Among the blue-green algae, *Anabaena cf. affinis* was dominant by day 8, but *Oscillatoria* sp. and *Phormidium* sp. were also present.

The numerically dominant taxa showed temporal abundance patterns that varied among the current treatments. For example, *Ulothrix zonata* was initially abundant in all treatments. Although its trajectory was generally similar across all current regimes, this species attained much

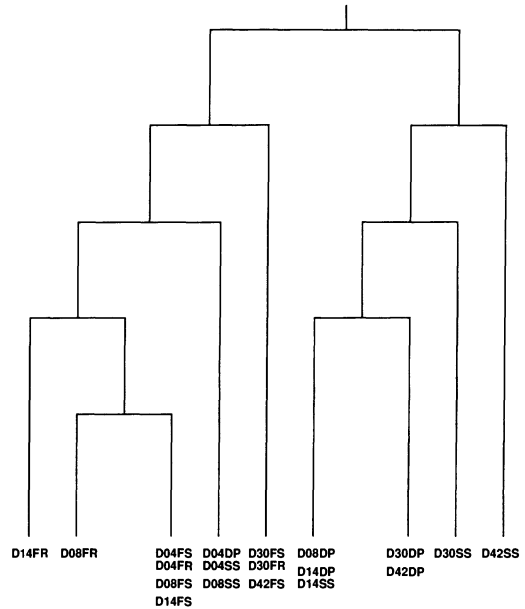


FIG. 3. TWINSpan dendrogram showing affiliations among 19 day \times current algal assemblages. The first three symbols in the five-character alpha-numeric represent days of colonization (e.g., D08 = 8 d). The last two letters refer to the current regime (DP = Depositional; SS = Slow-smooth; FS = Fast-smooth; FR = Fast-rough).

greater abundance in the slow velocity treatments (Fig. 2A). The trajectory of *Anabaena cf. affinis* was more complicated (Fig. 2B), owing largely to the unexplained absence of this species on day 14; by the end of the study, it attained great abundance only in the two slow velocity treatments. Patterns exhibited by individual diatom species were not as clear as for dominant green and blue-green algae. However, the trajectories of *Hannaea arcus* across the current treatments (Fig. 2C) illustrate the general similarity between the two fast current regimes and the two slow ones, at least during the early part of the colonization period.

TWINSpan was used to facilitate detection of patterns among the combined species assemblages. The affiliation between "sites" (19 day \times current combinations) in species space was evaluated on the raw data set (Fig. 3). The first major division in the dendrogram largely separated the Depositional and the Slow-smooth colonization sites (right trunk) from the remaining treatment combinations (left trunk). The last division within the right trunk sepa-

rated the "late" (≥ 30 day) and "early" (≤ 14 day) slow-velocity treatment combinations. In the left trunk, the first two branches also separated the "late" assemblages in the Fast-smooth and Fast-rough regimes from the "early" assemblages in the Depositional and Slow-smooth regimes. The remaining treatment combinations consisted of "early" assemblages in the Fast-smooth and Fast-rough regimes, with Fast-smooth combinations remaining affiliated through the last division.

The successional trajectories in each of the four current regimes were also examined with detrended correspondence analysis, which showed the similarities between treatment combinations in species space. The first two DCA axes explained 77% of the variance (i.e., that provided by the four largest eigenvalues determined by the program). Assemblage trajectories in the four regimes were initially different (day 4), passed through a period of species similarity on days 8 and 14, and diverged in species space at days 30 and 42 (Fig. 4). The Depositional and Slow-smooth regimes tended to be characterized by similar trajectories until day 42. The assemblage trajectory in the Fast-smooth regime appeared to have diverged substantially by day 42 from those in the slow velocity regimes. Interestingly, the Fast-rough assemblage tracked the trajectory in the Fast-smooth regime relatively closely, at least until day 30, at which time it was intermediate between the trajectory of the Fast-smooth and the common trajectory of the slow current regimes. (But note that the Fast-rough regime clustered with the Fast-smooth regime in Fig. 3.) Because no samples from the Fast-rough regime were recovered on day 42, it could not be determined whether this assemblage was becoming taxonomically more similar to those of the slow velocity treatments or not.

Physiognomic characteristics.—Representative examples of the physiognomy of algal assemblages at early and late developmental stages are shown for each of the four current regimes in Figures 5–8. In the Depositional treatment upright filaments of *Ulothrix zonata* were dominant by day 4, although particles of detritus and assorted diatoms (e.g., *Cocconeis*, *Fragilaria*, *Cymbella*) were also present (Fig. 5A). By day 14 the surface of the tile was virtually covered by a dense matrix of *U. zonata* filaments and associated entangled detritus and diatoms (e.g.,

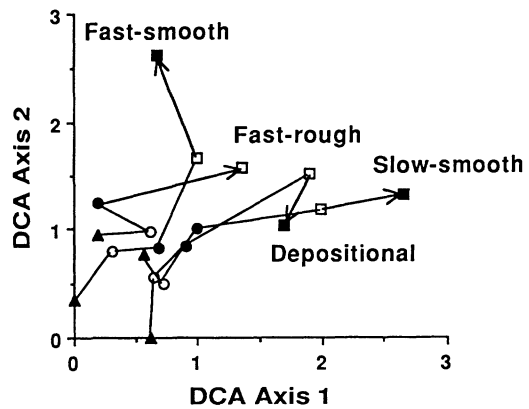


FIG. 4. Sample ordinations by detrended correspondence analysis showing successional trajectories of algal assemblages exposed to four current regimes. Arrows indicate temporal direction of succession for 4 (\blacktriangle), 8 (\circ), 14 (\bullet), 30 (\square), and 42 (\blacksquare) days of colonization.

Didymosphenia) (Fig. 5B). Similarly, in the Slow-smooth regime upright filaments of *U. zonata* were abundant by day 4 although adnate diatoms such as *Cocconeis* and *Cymbella* were also present on the exposed surface (Fig. 6A). By day 14, however, the surface was generally covered with *U. zonata* filaments and entangled detritus (Fig. 6B).

Physiognomic characteristics in the high velocity regimes differed greatly from those in the slow velocity regimes. After 8 d in the Fast-smooth treatment, much tile surface remained free of algae or detritus (Fig. 7A). After 30 d, a diverse assemblage of taxa existed, but they were primarily prostrate diatoms (e.g., *Cocconeis*, *Nitzschia*, and *Cymbella*) or short filaments of *U. zonata* (Fig. 7B). Fungal hyphae were also abundant at this time, but much of the tile surface remained sparsely colonized relative to slow velocity treatments. In the Fast-rough treatment little material had accumulated by day 4 (Fig. 8A), but by day 30 numerous taxa were represented (e.g., *Cocconeis*, *Achnanthes*, and clumps of the green alga *Coleochaete*) although growth forms remained relatively prostrate and much tile surface remained open (Fig. 8B).

Sampling position within troughs.—Inferred micro-hydraulic characteristics for the Slow-smooth and Fast-smooth regimes suggested that turbulent boundary layers would increase in depth downstream from the leading edges of the troughs (see above). Given the greater den-

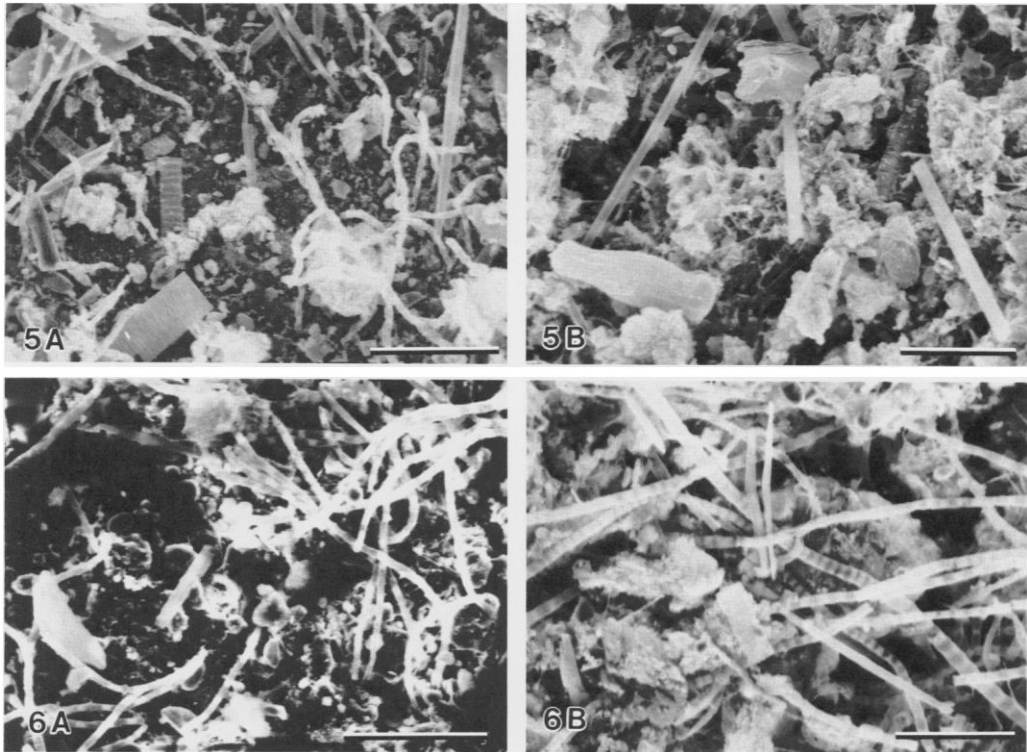


FIG. 5. Scanning electron micrograph from Depositional current treatment at A) 4 days and B) 14 days. Scale bar = 0.1 mm. See text for discussion.

FIG. 6. Scanning electron micrograph from Slow-smooth current treatment for A) 4 days and B) 14 days. Scale bar = 0.1 mm. See text for discussion.

sities of algal cells in the slow vs. fast current regimes (Fig. 1A), a pattern of increasing algae was expected to occur along the downstream gradient of decreasing shear in each of these two troughs. To examine whether algal response depended on sampling position within troughs, differences in cell density were determined for pairs of tiles collected on the same day from the upstream and downstream halves in each trough. Only pairs of tiles separated by at least 25 cm in the upstream-downstream direction were included. Position differences in the Depositional treatment, where no upstream-downstream hydraulic gradient was inferred, were also examined. (No evaluation of longitudinal differences was possible for the Fast-rough trough, which was only 35 cm long.) Cell densities were indeed greater on downstream than on upstream tiles in both the Slow-smooth trough ($n = 4$) and the Fast-smooth trough ($n = 5$), but not in the Depositional trough

($n = 5$) (Fig. 9). Given the near-overlap in inferred shear stress between the upstream section of the Slow-smooth trough and the downstream section of the Fast-smooth trough, one might expect among-trough similarity in cell densities for tiles located in those locations. However, cell densities were uniformly at least an order of magnitude greater on upstream tiles in the Slow-smooth regime than on downstream tiles in the Fast-smooth regime, further indicating the importance of differences in free-stream velocities between the troughs.

Discussion

This study shows that algal colonization dynamics and assemblage development (both taxonomic and physiognomic) through time differ substantially depending on the current regime (free-stream current velocity and pattern of flow) to which algal species are exposed. Some results

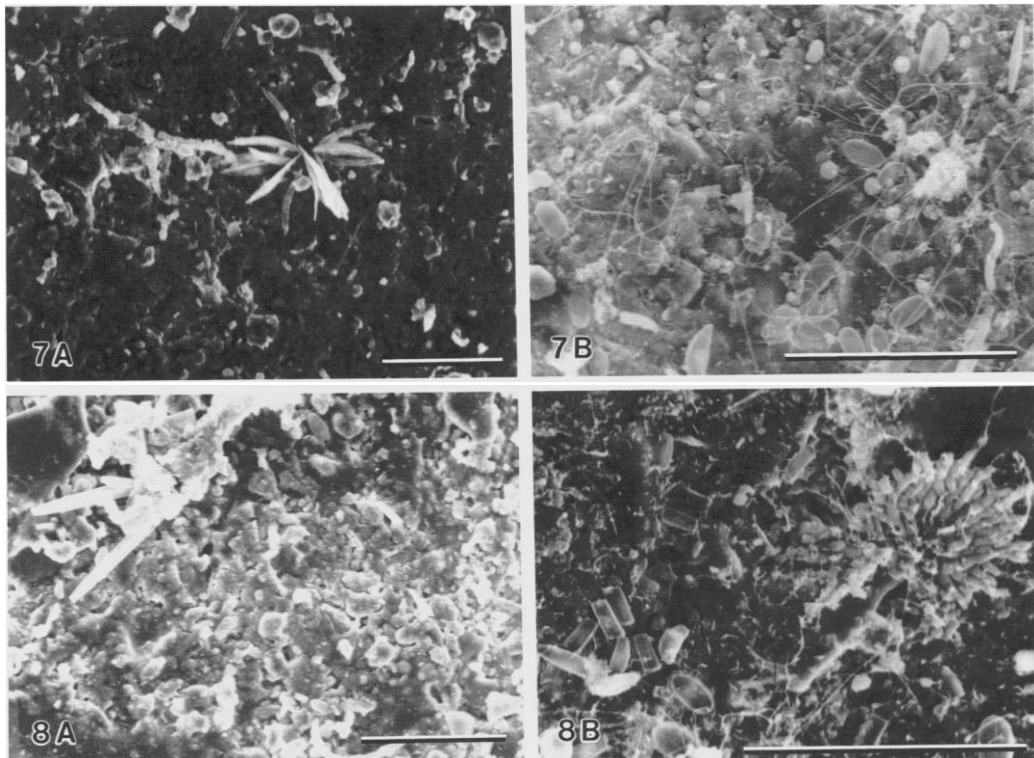


FIG. 7. Scanning electron micrograph from Fast-smooth current treatment for A) 8 days and B) 30 days. Scale bar = 0.1 mm. See text for discussion.

FIG. 8. Scanning electron micrograph from Fast-rough current treatment for A) 4 days and B) 30 days. Scale bar = 0.1 mm. See text for discussion.

are consistent with previous work. For example, biomass (McIntire 1966, Lamberti et al. 1987), cell densities (Oemke and Burton 1986), and species richness (Oemke and Burton 1986) have all been reported to exhibit initial, rapid increases during colonization. Both biomass (McIntire 1966) and algal cell densities (Reisen and Spencer 1970, Oemke and Burton 1986) have been found to be initially lower under high velocity conditions but, over time, to attain similar magnitudes as found under lower velocities. However, this pattern was not observed in our study, where both biomass and cell densities (Fig. 1) remained greater at all times in low vs. high velocity treatments (see also Stevenson 1984, Peterson 1987). Indeed, in many attributes (biomass, species composition, physiognomy) general similarity within slow velocity treatments (Depositional, Slow-smooth) and within high velocity treatments (Fast-smooth, Fast-rough) was notable and persistent. The many

differences between slow and fast regimes suggest that maximum free-stream velocity played a major role in influencing assemblage species compositions and development.

Several factors can modify algal colonization and assemblage development, and many of these are current-dependent. The abilities of colonizing species to attach under different hydraulic conditions are clearly important. Differences among treatments with respect to free-stream velocity and trough design allowed general inferences on important micro-hydraulic conditions such as shear stress and turbulence among and within troughs. Though progressive development of algal mats in the troughs could alter micro-hydraulic characteristics (see Reiter 1989), near-substratum differences among troughs would be important in influencing *initial* algal colonization (cf. Stevenson 1983). For example, *Melosira italica*, a colonial diatom with a filamentous growth form that possesses no

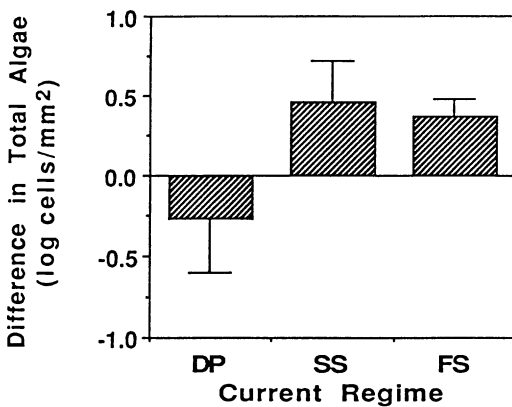


FIG. 9. Mean differences in algal cell densities between downstream and upstream tiles for DP (Depositional), SS (Slow-smooth), and FS (Fast-smooth) current regimes. Bars represent 2 SE.

specialized attachment mechanisms, was the numerically dominant initial diatom colonist in both the Depositional and Slow-smooth current treatments. In the Fast-smooth and Fast-rough treatments, species with specialized attachment mechanisms such as pores (e.g., *Hannaea arcus*) or raphe(s) (e.g., *Cocconeis placentula*) were more abundant, suggesting that higher inferred shear stresses in the high velocity regimes retarded the successful colonization of the substratum by *M. italica*. The abundance of *U. zonata* in the colonization sequences across treatments may reflect the seasonal abundance of dispersing zoospores (Dick Dufford, Department of Biology, Colorado State University, personal communication) and the species' possession of basal holdfasts (Prescott 1980) which provide a morphological mechanism by which filaments could attach. Additionally, the high densities of *U. zonata* and other chlorophytes (especially in the low velocity treatments—see Table 2) were probably stimulated by high light intensities and shallow, clear water in the troughs. Both biomass and growth rates of filamentous chlorophytes respond positively to light intensity (Shortreed and Stockner 1983, Lowe et al. 1986, Steinman and McIntire 1986, 1987).

Chronically low biomass and cell densities in the two fast velocity treatments are consistent with the nutrient-current hypothesis proposed by Horner and Welch (1981), who found that low concentrations (<40 $\mu\text{g/L}$) of orthophosphate-phosphorous reduced accrual rate of al-

gal cells, but only at velocities ~ 50 cm/s or greater. They postulated that under high velocity and low nutrient levels, increased shear overcomes the advantage of improved nutrient diffusion. Thus, while nutrients may be more available at higher velocity (leading to higher individual growth rates), less total assemblage biomass accumulates owing to accelerated emigration. At slower velocities, more biomass accumulates because cell growth exceeds emigration. Maximum velocities of near 50 cm/s in the fast current regimes and the oligotrophic nature of the upper Colorado River (ortho-P $\cong 10$ $\mu\text{g/L}$) provided conditions similar to those described by Horner and Welch (1981).

Algal colonization rates on substrata with high surface tensions are slow relative to substrata with low surface tensions (Tuchman and Stevenson 1980, Korte and Blinn 1983, cf. Peterson and Stevenson 1989). The high surface tension of tiles used in our study, coupled with the fact that fewer types of algae can "adhere" under conditions of fast flow (Butcher 1932, Stevenson 1983), probably contributed to the relatively slow colonization rates in the high velocity treatments. Moreover, Peterson and Stevenson (1989) found that experimental organic conditioning of tiles significantly enhanced colonization in fast (28 cm/s) but not slow (12 cm/s) current. The absence of initial bacterial-detrital films in our study (based on SEM observations) should have contributed to further reduction in colonization rates on tiles in fast current regimes.

A general model for the colonization and development (succession) of lotic algal assemblages was proposed by Korte and Blinn (1983). Initially, an organic film of detrital mucilage, bacteria, and fungi develops and conditions the substratum within a period of hours. Within days, adnate diatom species become established in a 2-dimensional matrix which characterizes the early seral stage of the assemblage. Vertically-oriented species, including upright diatoms and filamentous algae, invade to produce a 3-dimensional overstory flora that represents the late seral stage. The complex, 3-dimensional matrix of algae, bacteria, fungi, and polysaccharides are frequently observed as mature algal mats (see Lock 1981). Models similar to this one have also been proposed for freshwater lentic (Hoagland et al. 1982) and marine (Hudon and Bourget 1983) algal assemblages.

The results of our study do not generally support this model. Scanning electron microscopy revealed that bacteria were uncommon on bare substrata. Fungi were observed under SEM in appreciable numbers only under high velocity conditions after 30 d, i.e., subsequent to the establishment of diatom and non-diatom species. *Ulothrix zonata* colonized all current regimes within four days. The rapid growth of this species in the Depositional and Slow-smooth treatments resulted in assemblages that were dense and vertically-oriented within 8 d. These assemblages did not go through a 2-dimensional physiognomic or a diatom-dominated taxonomic seral stage. In the high velocity treatments, the persistent high abundance of *U. zonata* and the invasion of blue-green algae by day 8 (Table 2) demonstrated the absence of a diatom-to-filamentous-algae taxonomic sequence as well. However, the physiognomy of the algal assemblages in the Fast-smooth and Fast-rough treatments varied from that in the Depositional and Slow-smooth troughs. Filaments remained relatively short, such that the assemblage never developed the conspicuous vertical structure characteristic of the lower velocities. Interestingly, the occurrence of some upright diatoms (e.g., *Gomphonema* spp.) later in the colonization sequence, suggested that "physiognomic succession" in the fast velocity treatments might be occurring, but at a slow rate (cf. Korte and Blinn 1983).

This study supports the notion that physical environmental heterogeneity in streams contributes directly to spatial variation in algal distribution and abundance. While generally consistent with many field studies, our observations contradict some expectations from controlled studies in laboratory flumes. For example, Reiter and Carlson (1986) found algal assemblage structure converged through time under different current velocities. They hypothesized that algal mats developing under different current regimes in turbulent streams would converge over a period of weeks unless mat development were truncated by disturbances such as spates or grazing. In our field study, hydrologic disturbances did not occur and grazing pressure was relatively low (e.g., dense algal mats similar to those observed in the Slow-smooth treatment were never noted under similar velocity ranges on the stream bottom, where caddisfly, mayfly, and chironomid grazers were abundant during

the time the experiments were performed—N. L. Poff, personal observation). The hydraulic environments in the Slow-smooth and Fast-smooth troughs were very simple relative to most natural flow environments (see Davis and Barmuta 1989), and if temporal convergence were to be detectable in the field, it should be in such simplified current regimes. But differences in physiognomy (Figs. 7, 8), taxonomy (Tables 3, 4) and biomass (Fig. 1) arose and persisted through time for both the Slow-smooth and Fast-smooth troughs. We believe these assemblage divergences reflect complex, integrated algal responses to a suite of ecologically inseparable characteristics that vary naturally with current (i.e., nutrient diffusion, shear stress, sediment transport), and, therefore, convergence of algal mats to similar compositions under different current regimes is not likely in natural settings.

The among-trough and within-trough algal patterns documented here are noteworthy because they show that the hydraulic geometry of the sampling system imposed an important constraint on algal assemblage development. For example, individual tiles were randomly sampled from the troughs and replaced with bare tiles without regard to how such changes might alter bottom roughness and hence potentially modify the micro-hydraulic environment of remaining downstream tiles (cf. Reiter 1989). Quantitative detection of such alterations was beyond the scale of resolution in this study, but it is interesting to note that the *average* responses of algae (i.e., for the 5.29 cm² surfaces of the tile substrata) to different current regimes (among troughs) and to inferred differences in longitudinal hydraulic environment (within troughs) were apparently insensitive to hydraulic modifications occurring at this scale. Nonetheless, algal patchiness was observed at several spatial scales within the troughs. First, on individual tiles, SEM revealed that algal cells were patchily distributed across tile surfaces. Second, enhanced deposition and/or growth of algal cells was seen along the edges of many tiles (especially in the Fast-smooth treatment), apparently due to local variation in shear stresses. Similar small-scale edge effects have been noted elsewhere (e.g., Jones 1978, Munteanu and Maly 1981, Stevenson 1983, Hamilton and Duthie 1984). Third, differences in algal cover were also obvious among different tiles within

a trough. For example, some tiles in the Slow-smooth regime were not uniformly covered with conspicuous mats of *U. zonata* and other filamentous forms. Although not separately analyzed, these smaller patches may have represented an alternative successional trajectory for this current regime. This patchiness appeared to occur randomly throughout the troughs, and is most easily attributed to stochastic colonization and subsequent autogenic processes. Fourth, in the Slow-smooth and Fast-smooth troughs, there was a distinct upstream-downstream gradient in cell density (see Fig. 9). These within-trough position differences were similar to patterns attributed to among-trough hydraulic characteristics, i.e., higher cell densities where inferred shear stresses were lower. Despite these interesting patterns of within-trough variation, among-trough differences were persistent and reflected the overriding influence of free-stream velocity and current regime in influencing algal assemblage development.

Current velocity and flow pattern can directly influence algal assemblage composition and patchiness in streams. However, algal heterogeneity can also result from a variety of other factors, including random colonization processes (Korte and Blinn 1983, Hamilton and Duthie 1984), senescence and sloughing of mats (Lamberti et al. 1987), variable light intensities (Steinman and McIntire 1986), seasonal variation in abundance of colonizing species (Oemke and Burton 1986) and animal grazing (Hart 1985, Colletti et al. 1987, Steinman et al. 1987, Power et al. 1988). The extent to which these factors are themselves mediated by spatial and temporal variation in current regime remains largely uninvestigated.

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