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Title: Effects of Substrate Relief, Light Intensity and Herbivory
on the Distribution and Abundance of Periphyton in Laboratory
Streams.

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C. David McIntire

Effects of substrate relief, irradiance and herbivory on the
temporal and spatial patterns of algal development were investigated
in four experiments using laboratory streams.

Hydrologic differences created by current flow over substrate
blocks significantly affected the distribution of algal biomass.
Low shear velocities in areas recessed between substrate blocks
promoted algal colonization and caused biomass initially to
accumulate faster on recessed surfaces than on surfaces exposed to
higher shear velocities on top of the blocks. Once the algal
assemblages became established, growth of assemblages in fast
current regimes was greater than in slow current regimes.
Successional changes on all substrate surfaces were similar with the
exception that recessed surfaces had significantly greater abundance
of the filamentous chlorophyte Stigeoclonium tenue.

Differences in biomass accumulation between top and recessed
surfaces were significantly affected by irradiance level.

Irradiance had a greater effect than current regime on biomass and succession. Assemblages at high irradiances (385 and 90 uE m^{-2} s^{-1}) had greater biomass accumulation, and a greater percentage of mobile diatoms and of Stigeoclonium than assemblages at low irradiance (20 uE m^{-2} s^{-1}). These patterns of algal development were greatly altered by the grazing of the snail Juga silicula (375 m^{-2}). At all irradiance levels, snail densities were higher and algal biomass was lower on recessed surfaces than on top surfaces. As algal biomass became low on recessed surfaces, grazing tended to increase on top surfaces. Snails had the greatest effect on algal succession at low irradiance and these algal assemblages approached adnate cell forms early in succession.

Patterns of algal succession were affected by the type of herbivore and the time of encounter. The introduction of the caddisfly Dicosmoecus gilvipes (50 m^{-2}) at any stage of algal succession decreased biomass and altered successional trajectories towards adnate taxa to a greater degree than either the snail Juga silicula (500 m^{-2}) or the mayfly Baetis spp. (500 m^{-2}). Baetis did not affect algal development when introduced late in succession, suggesting the assemblage had a size escape from grazing.

The results of these experiments were integrated into a conceptual model describing periphyton succession in streams based on the growth forms of taxa. The model has a hierarchical framework that describes periphyton succession at different temporal and spatial scales.

Effects of Substrate Relief, Light Intensity and Herbivory
On the Distribution and Abundance of Periphyton
In Laboratory Streams

by

Dean M. DeNicola

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CONTRIBUTION OF AUTHORS

C. David McIntire assisted with the experimental design, statistical analyses and interpretation of the results for the four experiments in this disseration, and appears as a co-author on these manuscripts.

The manuscript <u>Temporal</u> <u>patterns</u> <u>of</u> <u>grazer-periphyton</u> <u>interactions</u> <u>in</u> <u>laboratory</u> <u>streams</u> (Chapter V) was based on an experiment that was part of the herbivory project, and Stan Gregory, Gary Lamberti and Linda Ashkenas appear as co-authors. They assisted with the experimental design, set up and running of the streams for this experiment, and offered suggestions on data interpretation.

EFFECTS OF SUBSTRATE RELIEF, LIGHT INTENSITY AND HERBIVORY ON THE DISTRIBUTION AND ABUNDANCE OF PERIPHYTON IN LABORATORY STREAMS

I. INTRODUCTION

Historically, the temporal and spatial distribution of benthic algae in streams has been studied both descriptively and experimentally. Early studies were usually qualitative surveys of algae conducted at large spatial scales. The spatial distributions of algal assemblages were described within a drainage basin or compared for streams from different geographic regions, and the seasonal occurrence of assemblages were often noted (e.g., Budde 1928, 1930, Fritsch 1929, Butcher 1932, Scheele 1952, Blum 1957). These studies led to attempts to classify associations of lotic algae based on geography and general physical habitats (Panknin 1947, Symoens 1951, Margaleff 1960, Blum 1960). Although the identification of algal associations has been useful in a broad sense, streams rarely have extensive areas that are persistently inhabited by homogeneous groups of algal species (Hynes 1970). The spatial scale of environmental heterogeneity in streams is relatively large compared to the size of algal cells or colonies, and algal generation times are short. As a result, stream periphyton is usually distributed as a mosaic of patches in different successional states (Blum 1960, Fisher 1983). A quantitative field study by Douglas (1958) was one of the first attempts to relate the patchy and dynamic nature of lotic periphyton to environmental conditions.

In recent experimental studies of stream periphyton, the effects of environmental factors on the distribution of epilithic algae have been examined at smaller scales than the earlier descriptive studies. Most of these experiments were designed to investigate temporal patterns of algal colonization and succession relative to such factors as current velocity, irradiance, nutrients and herbivory (e.g., McIntire 1966a, Kehde and Wilhm 1972, Lowe et al. 1986, Steinman and McIntire 1987, Lamberti et al. 1989). The algal assemblages produced in such studies were either distributed homogeneously on a flat substrate, or sampled in a manner that blended spatial heterogeneity. Although a spatially heterogeneous distribution of algae has been observed on and between cobble to boulder-size substrates in a stream (Gumtow 1955, Blum 1960, Backhaus 1978), few studies have been designed to examine the heterogeneous distribution of algae at the substrate scale. Of the studies investigating spatial heterogeneity of algae on substrates, most have been concerned with effects created by current flow at the upstream edges of a substrate (Munteanu and May 1983, Korte and Blinn 1983, Hamilton and Duthie 1984).

The general objective of the research in this dissertation was to examine how the temporal and spatial distribution of periphyton on hard substrates in streams is affected by substrate relief, irradiance and herbivory. Effects of these factors were examined in four experiments conducted in laboratory streams. The first experiment (Chapter II) investigated the hypothesis that a heterogeneous distribution of periphyton assemblages in streams may

be partly a result of hydrologic differences created when water flows over cobble-sized substrates. In this experiment, hydrologic parameters, algal biomass accumulation and successional patterns associated with surfaces on top of substrate blocks and with surfaces recessed between substrate blocks were compared to corresponding surfaces in streams with no relief. The second experiment (Chapter III) examined the influence of irradiance level on the patterns of algal biomass accumulation and succession created by current flow over the cobble-size blocks. The third experiment (Chapter IV) investigated how the patterns of algal development created by the conditions in experiment 2 interacted with the grazing behavior of the snail _Juga silicula_ (Gould). Effects of herbivore type, and timing of herbivory on algal distribution were examined in the fourth experiment (Chapter V). In Chapter VI the results of the four experiments were integrated into a conceptual model of periphyton succession based on growth forms of the taxa. In addition, patterns of succession observed in this study were placed within a hierarchical framework for describing algal succession in streams at different spatial and temporal scales.

II. EFFECTS OF SUBSTRATE RELIEF ON THE DISTRIBUTION OF
PERIPHYTON IN LABORATORY STREAMS; HYDROLOGY

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ABSTRACT

We examined the hypothesis that the heterogeneity of epilithic algal assemblages in streams may be partly a result of hydrologic differences created when water flows over a rough substrate. A 32-day experiment was conducted in laboratory streams that contained either 22 x 22 x 4 cm or 7.5 x 22 x 4 cm tile blocks. Free-water velocities in the streams averaged 28 cm s^{-1}. Hydrologic parameters and algal assemblages associated with surfaces on top of blocks and with recessed surfaces between blocks were compared to corresponding surfaces in streams with no relief. In streams with blocks, shear velocities averaged 1.7 cm s^{-1} on the top of blocks and 0.8 cm s^{-1} in the recessed areas. Shear velocity at corresponding surfaces in the control (no relief) streams averaged 1.9 cm s^{-1} and exhibited little variation. The hydrologic differences created by the larger blocks significantly affected the distribution of algal biomass, with recessed areas having an average of 2.6 g m^{-2} ash-free dry weight more biomass than surfaces on the top of blocks. Differences in shear velocities and biomass accumulation between top and recessed areas for the smaller blocks were less than for large blocks. Successional changes on all substrates were similar with the exception that recessed surfaces had a significantly greater abundance of the filamentous chlorophyte Stigeoclonium tenue (Ag.) Kutz. after day 16. The results suggested that in cobble riffle areas of natural streams, the interaction between current flow and substrate relief has the potential to create patches of algae which are different in biomass and taxonomic composition.

INTRODUCTION

A heterogeneous distribution of periphyton on individual stones and between neighboring stones in a stream has been explained in part by the pattern of current flow over the substrate (Fritsch 1929, Gumtow 1955, Blum 1960, Backhaus 1967, Jones 1978). For example, Gessner (1953) observed that the diatom Cocconeis placentula Ehr. was more abundant on the upstream and downstream sides of a vertical pole in a stream rather than on sides parallel to the current. In an attempt to understand the mechanisms underlying such observations, more recent experiments have examined the spatial pattern of periphyton colonization on substrates in a current. At a small scale (10^{-2} m), the zone of turbulence that occurs at the upstream edges of a substrate has a higher diatom colonization rate initially than the region of more laminar flow at the center (Munteanu and Maly 1981, Korte and Blinn 1983, Hamilton and Duthie 1984). At a larger spatial scale (10^{-1} m), Stevenson (1983, 1984) suggested that the temporal and spatial heterogeneity of periphyton assemblages behind an obstruction was related to the current regime just above the substrate. In addition, near-bed hydrologic parameters can change in response to the growth of an algal mat on a substrate, thereby creating an autogenic feedback on further development of the assemblage (Reiter and Carlson 1986, Reiter 1986, 1989).

Water velocity decreases very close to the substrate surface because of frictional effects. The slope of the velocity profile

determines the shear velocity near the substrate surface. In turbulent flow, there is a thin region of relatively laminar flow of low velocity immediately above the bed, referred to as the laminar sublayer (Chow 1959, Vogel 1981). The thickness of the sublayer and the shear velocity describe the flow environment an algal cell must pass through to colonize a substrate, and determine the subsequent drag force that the cell experiences after attachment (Vogel 1981, Silvester and Sleigh 1985). As the free (mean) velocity of the water increases, shear velocity increases and the boundary layer thickness decreases. In regions of flow separation, such as at the upstream or downstream edges of a substrate, flow patterns become more complex, but in general, free velocity decreases (Vogel 1981).

In this study, we investigated the general hypothesis that heterogeneity of epilithic algal assemblages in streams may be partly a result of variations in current regime created as water flows over an irregular substrate (Blum 1960). We examined algal heterogeneity in laboratory streams at a spatial scale comparable to cobble-size stones. Specifically, our hypotheses were: 1) the presence of cobble-size substrates in a current create more heterogeneous algal assemblages than a flat substrate, and 2) the size and spacing of substrate elements affect algal heterogeneity. The degree of algal heterogeneity was determined by the similarity between assemblages on the tops of the substrate elements and assemblages in recessed areas between elements. By carrying the experiment out in laboratory streams, we were able to control factors such that the only difference between treatments was the interaction of current with substrate elements. In regions where

periphyton was sampled, algal development was compared to average values of sublayer thickness and shear velocity for the substrate. Additionally, we estimated hydrologic parameters of mean flow in the laboratory streams so the results could be used to generate hypotheses about areas in natural streams with similar hydrologic descriptions (Statzner et al. 1988, Davis and Barmuta 1989).

MATERIALS AND METHODS

Laboratory Streams and Experimental Design

The experiment was conducted in 9 recirculating, fiberglass laboratory streams. The design of the streams was described in detail by DeNicola et al. (1990). Briefly, each stream was 3 X 0.5 m, with two parallel channels separated by a centerboard that was open at both ends. The streams were supplied with well water at an exchange rate of 2.0 L min^{-1}, and a current was generated by a motor-driven paddle wheel. Nutrient concentrations in the water supply were high (Steinman and McIntire 1986), while water temperature in the streams ranged from 16.0^{o} to 17.5^{o} C. Sixteen 1000-watt Metalarc lamps (Sylvania Corp.) provided a photon flux density of 400 uE m^{-2} s^{-1} at the water surface with a photoperiod of 10L/14D. This irradiance level is above that needed to reach the maximum rate of photosynthesis in lotic periphyton assemblages (McIntire and Phinney 1965). The streams were lined with 7.5 X 7.5 X 1.3 cm unglazed clay tiles which served as surfaces for algal attachment. The flora that develops on such tiles is very similar to that on natural rock surfaces in biomass (Lamberti and Resh 1985) and taxonomic composition (Tuchman and Stevenson 1980).

Each of the 9 streams was randomly assigned one of 3 types of substrate relief with 3 replicate streams per type. The bed of three streams had a single layer of clay tiles with no relief ("control streams") (Fig. II.1). The bed of three other streams ("large block streams") contained a single layer of tiles on top of

Figure II.1 Substrate configurations and sampling sites for large block, small block and control streams.
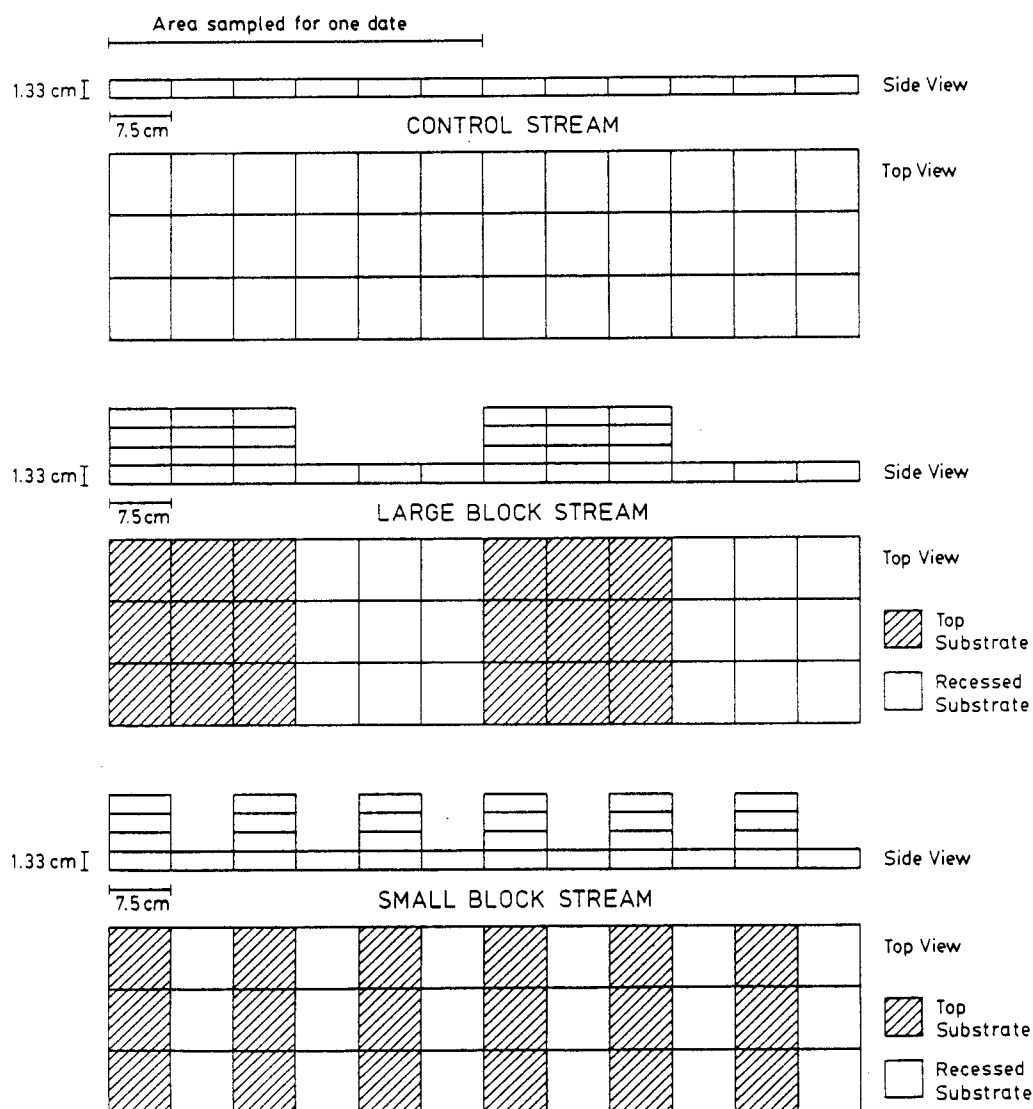
Figure II.1

which were 22.5 cm long, 22.5 cm wide and 4 cm high channel-spanning blocks built of tiles (3 X 3 X 3 tiles). These blocks were spaced 22.5 cm apart (Fig. II.1). The remaining three streams had a bed containing channel-spanning blocks 7.5 X 22.5 X 4 cm (1 X 3 X 3 tiles), spaced 7.5 cm apart ("small block streams") (Fig. II.1). Above the tops of blocks the water depth was 4.4 cm, while between blocks and in the control streams it was 8.4 cm (Fig. II.2).

Sampling

The experiment began on 16 July 1987 and continued for 32 days. On day 1 of the experiment, periphyton was scraped from rocks collected from 3 streams in Benton Co., Oregon (Rock Creek, Oak Creek and the Alsea River). The algal suspension was homogenized for 30 seconds in a 3.8 L Waring blender, and a 1.0 L subsample was added to each laboratory stream. The streams were seeded with algae in this manner once each week during the experiment.

Periphyton from each stream was sampled on days 4, 8, 16, 23 and 32 of the experiment. A failure of the motor which drove the paddle wheels for 6 of the streams resulted in only one stream of each relief type being sampled on day 32. Corresponding locations, equal in total area (6 X 3 tiles, Fig. II.1), were sampled for algae in all streams on each sampling date. In streams with large blocks, the sample area contained two surfaces, top and recessed, which were sampled separately. Algae were scraped from the 9 tiles on top of a block and from the 9 tiles in an adjacent recessed area respectively (Fig. II.1). In streams with small blocks, the sampling location included 3 blocks and 3 adjacent recessed areas. To obtain a sample area equal to the top surface of a large block (9 tiles), scrapings

Figure II.2 Flow patterns over a) small blocks and b) large blocks.

a|

8.4 cm

4 cm

|← 7.5 cm →|← 7.5 cm →|

b|

8.4 cm

4 cm

|← 22.5 cm →|← 22.5 cm →|← 22.5 cm →|
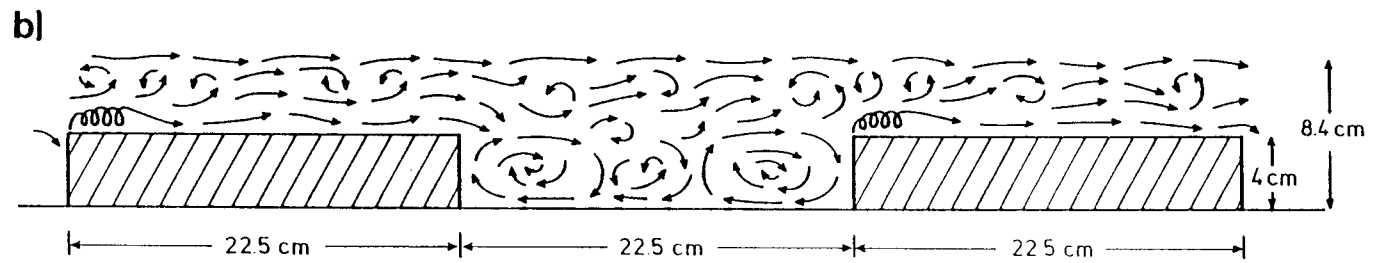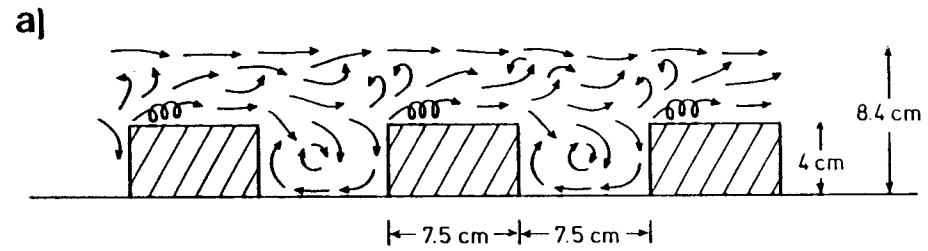
Figure II.2

from the tops of 3 small blocks were pooled. Similarly, samples for recessed surfaces between small blocks were obtained by pooling scrapings from the 9 recessed tiles (Fig. II.1). Streams with no relief provided control samples for effects related to both the relief and spacing of blocks. In the control (no relief) streams, the sampling location yielded 4 samples that were obtained from positions corresponding to the location of block tops and recessed surfaces in large and small block streams. Algae were scraped separately for each row of tiles across the channel in the sampling location. Each of these scrapings was then divided into two equal portions. The scrapings of one portion were pooled into two samples based on how the positions of the rows corresponded to top or recessed surfaces in a large block stream ("large block control samples") (Fig. II.1). Similarly, scrapings from the other portion were combined into two samples according to the row positions of top and recessed substrates in a small block stream ("small block control samples") (Fig. II.1). The area sampled in the streams represented less than 10% of the total stream area.

Each algal sample was subsampled in order to estimate biomass and taxonomic composition. Biomass, expressed as ash-free dry weight, was determined as described by Lamberti et al. (1987). For taxonomic analysis, algal subsamples were settled in 50 ml chambers, and 500 algal units containing chloroplasts were counted at 400X magnification with a Nikon MS inverted microscope (Utermohl 1958). In this count, diatoms were lumped into one category, and all other taxa were identified to species. An algal unit was an individual

cell for unicellular organisms, and a colony or filament for multicellular taxa. After counting, the settled subsample was boiled in concentrated HNO_3, rinsed with distilled water, and 500 cleared diatom valves were identified at 1250X magnification. The proportions of diatom taxa in this count were used to estimate abundances of these taxa in the count of 500 algal units (Steinman and McIntire 1986). On days 23 and 32, filaments of the chlorophyte Stigeoclonium tenue (Ag.) Kutz. were conspicuous in some samples, but the large number of diatoms in the understory mat prevented accurate estimation of its abundance from a count of 500 units. Therefore, the relative abundance of S. tenue on these two dates was determined by a separate count of the total number of S. tenue filaments in the settled subsample.

Data Analysis

Differences in biomass between top and recessed substrates for the streams were tested by a strip plot analysis of variance design, with stream type as the whole plot factor and time as the strip factor (Gill and Hafs 1971). Two separate ANOVAS comparing biomass differences in small block streams to small block controls and large block streams to large block controls were performed because the large and small block control samples were not from independent treatments. Day 32 samples were not included in the analyses because of the loss of 2 sets of replicate streams.

Species composition of the algal assemblages, based on the relative abundances, were compared with the percentage similarity measure of resemblance (Ludwig and Reynolds 1988). Taxonomic diversity of assemblages was expressed by Shannon's information

measure (Peet 1974). The ratio of the relative abundance of
Stigeoclonium tenue on recessed substrates to top substrates on day
23 was compared for small block streams and their controls, and for
large block streams and their controls by t-tests (Snedecor and
Cochran 1980).

Characterization of Flow Environments

Patterns of water flow in streams with substrate blocks were
characterized visually by releasing dye and particles of fine
vermiculite upstream of the blocks. Mean free-water velocities were
measured at 0.4 maximum depth (Smith 1975) in the streams before
algal seeding using midget bentzel tubes (Everest 1967), and a
Montedoro and Whitney model PVM-2 current meter. Measurements of
mean flow velocity were obtained at three sites across the channel
for multiple locations in each stream. The values were averaged to
obtain a mean flow velocity for each stream type.

To calculate parameters of near-bed flow, water velocities were
measured at 1.0 cm above the surfaces sampled for periphyton.
Measurements were taken at 9 sites above the tops of each large
block and at 3 sites above each small block. The respective values
were averaged for the two types of substrates. Water flow above
both large and small recessed substrates contained eddies where the
flow reversed approximately 2 cm above the center of the substrates
(Fig. II.2). We assumed the flow in this 2 cm zone was
unidirectional, and took velocity measurements at 1 cm above the
center of the recessed substrates as representing the average water
velocity.

Several hydrologic parameters were calculated to characterize both the mean flow in the streams and the near-bed flow above substrates sampled for periphyton.

Reynolds number (Re) and Froude number (Fr), were calculated by

$$Re=(UD)/v \qquad (1)$$

and, $Fr=U/\sqrt{gD}$ (2)

where U = the mean free velocity, D = mean depth, v = kenimatic viscosity, and g = acceleration due to gravity. Shear velocity (U*) was calculated by

$$U*=U/2.5 \ln (12 \, D/K) \qquad (3)$$

where K = the height of the substrate elements. K=0.1 cm for the control streams, as abutting tiles were often slightly different in height. Millimeter variations in K have an insignificant effect on estimates of U*. This equation is experimentally based and assumes the scale of the turbulence was proportional to the distance from the bed (Smith 1975).

The roughness Reynolds number (Re*) for the streams was calculated by

$$Re*=U*K/v \qquad \text{(Davis and Barmuda 1989)} \qquad (4)$$

In streams with blocks, the average velocities 1.0 cm above block tops and recessed substrates were used to calculate separate shear velocities for these regions. Since these substrate surfaces were locally flat, K=0.1 cm for equation 3. We assumed that the logarithmic velocity profile above the recessed substrate had a mean water depth of 2 cm (Smith 1975). The depth of the viscous sublayer (d') above the substrates was calculated by

$$d'= (11.5 \, v)/U* \qquad \text{(Smith 1975)} \qquad (5)$$

RESULTS

Flow Characteristics

General current patterns and areas of vortex formation around large and small blocks are indicated in Figure II.2. There was one dominant eddy between small blocks, whereas the pattern of flow between large blocks was more variable.

Mean flow in all three types of streams was characterized as turbulent (Re > 500), and subcritical (Fr < 1) (Table II.1). The presence of blocks in the streams decreased mean water depth and relative roughness (D/K), and increased shear velocity and roughness Reynolds number for mean flow (Table II.1). Relative roughness and roughness Reynolds number indicated streams with blocks were hydrologically rough and that flat control streams were hydrologically transitional between smooth and rough.

Shear velocities and the depth of the laminar sublayer were similar for substrates located on the tops of large and small blocks, and for the control streams (Table II.2). Lower local mean velocities between blocks resulted in lower shear velocities and thicker laminar sublayers above the recessed substrates (Table II.2). In streams with blocks, shear velocity was higher for mean flow (Table II.1) than for local flow over top and recessed substrates (Table II.2). Parameters describing mean flow were influenced by conditions at all substrate boundaries in the streams, including block faces and channel side walls, whereas local flow parameters only described conditions for a given surface.

Table II.1. Characteristics of mean flow for control, large block and small block streams.

Parameter	Control	Large Block	Small Block
Mean velocity (cm s^{-1})	32.5	26.1	25.1
Mean Depth (cm)	8.4	6.4	6.4
Substrate height (cm)	0.1	4.0	4.0
Depth/Height	84.0	1.6	1.6
Reynold's number	27300	16704	16064
Froude number	.36	.33	.32
Shear velocity (cm s^{-1})	1.88	3.53	3.40
Roughness Reynolds number	19	1413	1359
Hydrologic description	Turbulent Subcritical Transitional	Turbulent Subcritical Rough	Turbluent Subcritical Rough

Table II.2. Characteristics of near-bed flow for substrate surfaces.

Parameter	Control	Large Block		Small Block	
		Top	Recessed	Top	Recessed
Mean velocity $(cm\ s^{-1})$	32.5	27.2	-9.54	26.0	-13.2
Mean Depth (cm)	8.4	4.4	4.0^{1}	4.4	4.0^{1}
Substrate height (cm)	0.1	0.1	0.1	0.1	0.1
Shear velocity $(cm\ s^{-1})$	1.88	1.74	0.70	1.65	0.96
Sublayer thickness (mm)	0.61	0.66	1.65	0.69	1.19

[1]2.0 cm used as the depth of the logarithmic profile for the calculation of shear velocity.

Algal Biomass

Algal biomass accumulation on all substrate surfaces during the experiment followed an exponential pattern until day 23 (Figs. II.3a and b). After day 23, algal biomass in the streams with blocks decreased or exhibited little change, while biomass continued to increase in the control streams. Mean biomass accumulation was similar in the large and small block streams for corresponding surfaces. Between days 23 and 32 algae sloughed off the tops of large blocks thereby reducing biomass.

ANOVA indicated that the difference in biomass between top and recessed substrates of large blocks was significantly affected by both the presence of blocks and time, and there was a significant interaction between these main effects (p values < 0.01, Table II.3). The top and recessed substrates of small blocks were not statistically different in their biomass accumulation when compared to the small block controls (0.1 > p > 0.05, Table II.4). On day 16 the mean algal AFDW on recessed substrates was 8.5 g m^{-2} (S.D.=1.5, n=6), whereas it was 6.3 g m^{-2} (S.D.=1.9, n=18) on top and control substrates, which had faster shear velocities. On day 23, the difference in algal biomass in the two types of current regimes was smaller. AFDW biomass on day 23 was 26.2 g m^{-2} (S.D.=3.3, n=6) on substrates in slow shear velocities and 26.5 g m^{-2} (S.D.=4.2, n=18) on substrates in fast shear velocities.

Species Composition and Physiognomy

Algal assemblages on all substrates had similar changes in the relative abundances of the dominant taxa during the experiment

Figure II.3 Biomass accumulation on substrate surfaces for a) large blocks and large block controls and b) small blocks and small block controls.

a]

Large Blocks

b]

Small Blocks
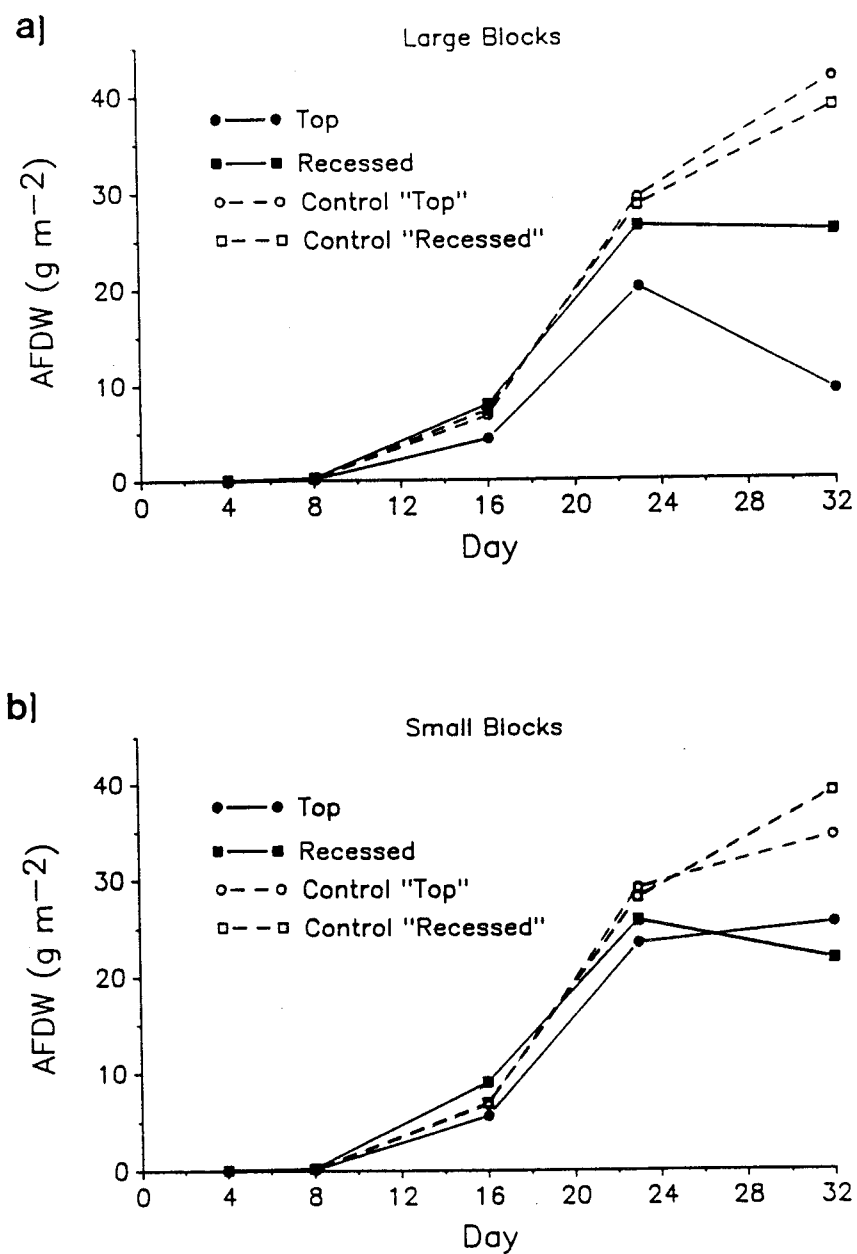
Figure II.3

Table II.3. The ash-free biomass difference (g m^{-2}) between top and recessed substrates (recessed-top) in large block streams and large block controls. Values are means, n=3. Fisher's protected least significant difference values (FPLSD) are given to compare means.

	Day			
	4	8	16	23
Large blocks	0.0156	0.1504	3.6601	6.4103
Large block controls	0.0046	-0.1109	0.5371	-0.8000

To compare means in a column, FPLSD$_{.05}$= 2.5235; and

in a row, FPLSD$_{.05}$= 1.1268.

Table II.4. The ash-free biomass difference (g m^{-2}) between top and recessed substrates (recessed-top) in small block streams and small block controls. Values are means, n=3.

	Day			
	4	8	16	23
Small blocks	0.0624	0.1504	3.4947	2.4000
Small block controls	0.0406	0.0070	0.3675	-0.9778

Standard Errors: Time= 0.5221, Blocks= 0.3221,

Time X Blocks= 0.7273. Effects of factors not

significant at $p < 0.05$.

(Figs. 11.4 and II.5). _Oscillatoria agardhii_ Gomont and _Fragilaria_ _vaucheriae_ (Kutz.) Peters were the most abundant taxa on days 4 and 8. _Oscillatoria agardhii_ was less abundant on the recessed substrates than on substrates located on the tops of blocks or in the control streams. By day 16, the relative abundance of _Nitzschia_ _oregona_ Sov. had increased and comprised 65% or more of the assemblages on all substrates for the remainder of the experiment. _Achnanthes lanceolata_ (Breb.) Grun. reached a maximum relative abundance of approximately 10% on all substrates on day 16. On days 23 and 32 the relative abundance of _A. lanceolata_ was less than 10%, whereas _Navicula arvensis_ Hust. comprised 15 to 30% of the assemblages. Species diversity was highest on all substrates on day 4 and generally decreased with time during the experiment (Figs. II.4 and II.5).

Values of percentage similarity indicated that for all substrates the change in taxonomic structure was greatest between days 8 and 16 (Table II.5), the period corresponding to the increase in _Nitzschia oregona_. Algal assemblages on substrates in the control streams were very similar on each sample date (Table II.6). Assemblages on all substrate surfaces in both the block and control streams generally became more similar during the course of the experiment. However, sloughing of algal mats from substrates on top of blocks between days 23 and 32 accounted for a decrease in the similarity between these assemblages and those on all other substrates.

Compared to the control streams, _Stigeoclonium tenue_ was significantly more abundant on recessed substrates than on top

Figure II.4 The relative abundance of <u>Oscillatoria</u> <u>agardhii</u> (OSCAGR), <u>Fragilaria</u> <u>vaucheriae</u> (FRAVAU), <u>Nitzschia</u> <u>oregona</u> (NITORE), <u>Achnanthes</u> <u>lanceolata</u> (ACHLAN) and <u>Navicula</u> <u>arvensis</u> (NAVARV) on substrate surfaces for large blocks and large block controls. H" for the assemblages are written above each bar. Values are means (n=3) for days 4 to 23; n=1 for day 32.
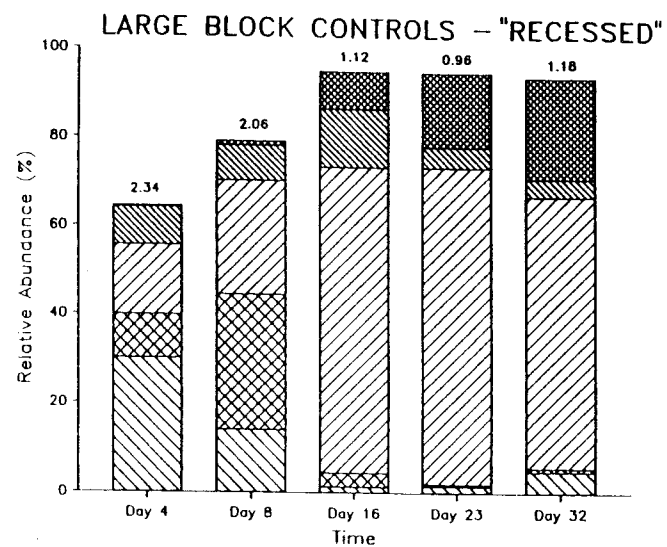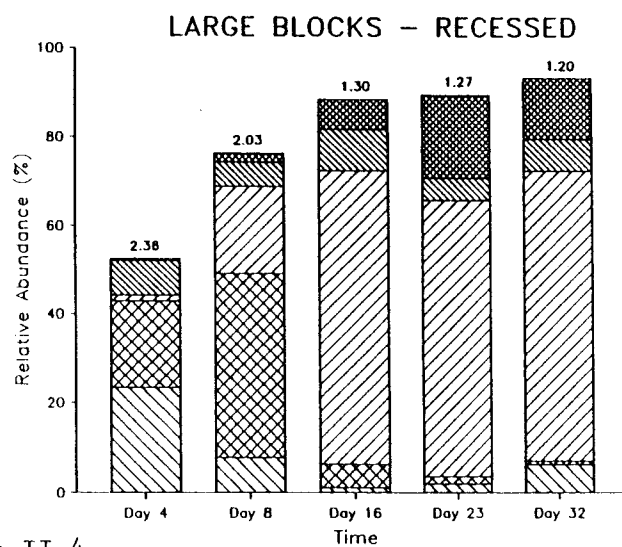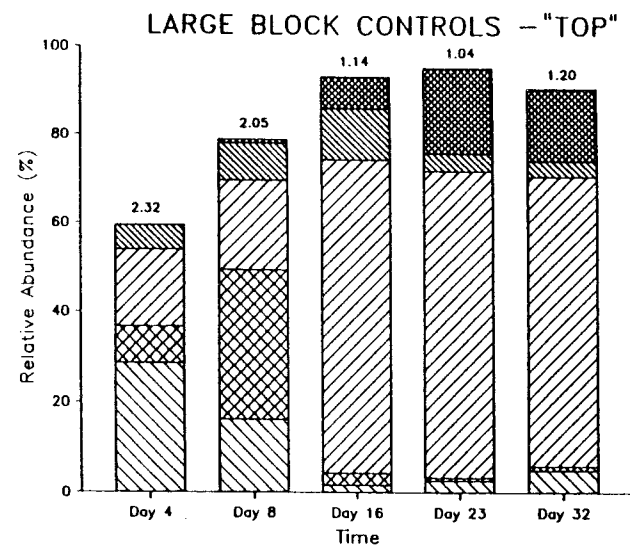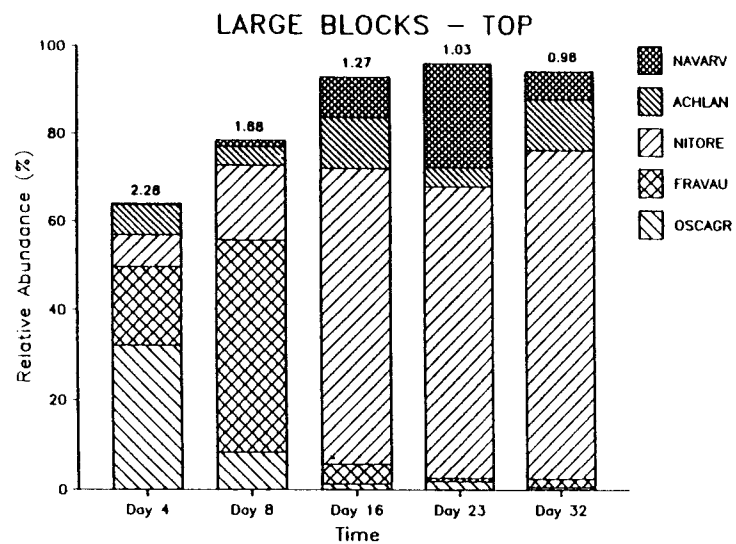
Figure II.4

Figure II.5 The relative abundance of <u>Oscillatoria</u> <u>agardhii</u>
(OSCAGR), <u>Fragilaria</u> <u>vaucheriae</u> (FRAVAU), <u>Nitzschia</u> <u>oregona</u>
(NITORE), <u>Achnanthes</u> <u>lanceolata</u> (ACHLAN) and <u>Navicula</u> <u>arvensis</u>
(NAVARV) on substrate surfaces for small blocks and small block
controls. H" for the assemblages are written above each bar.
Values are means (n=3) for days 4 to 23; n=1 for day 32.
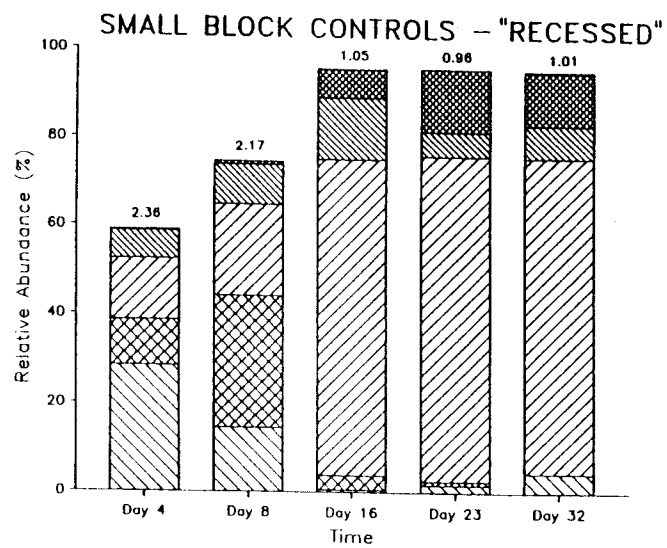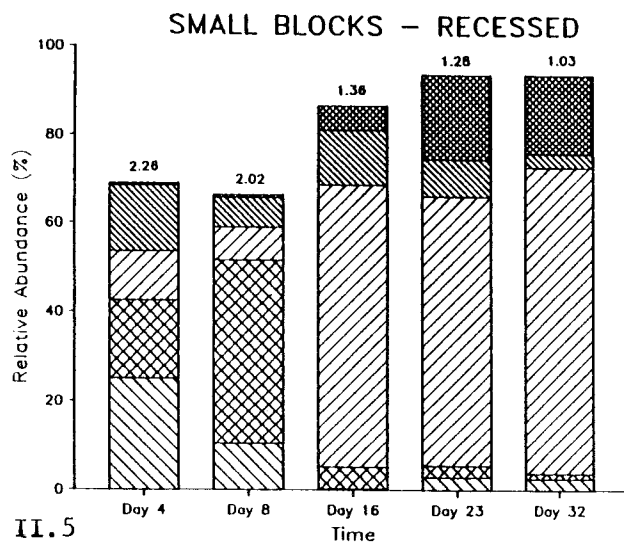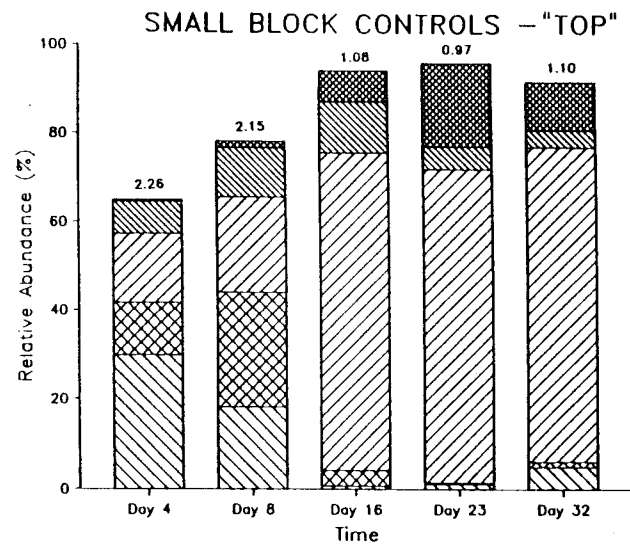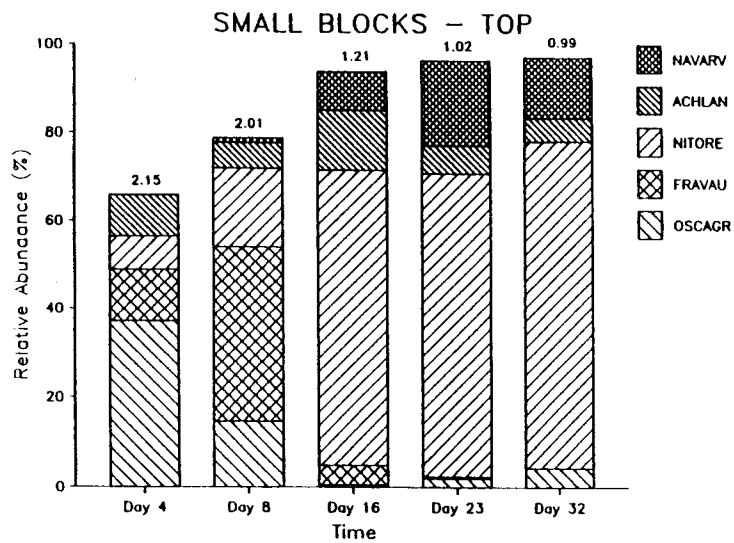
Figure II.5

Table II.5. Similarity values (percentage similarity) of algal assemblages pooled by sampling date.

Day	4	8	16	23	31
4	100.0				
8	64.7	100.0			
16	33.3	40.5	100.0		
24	26.6	34.5	87.6	100.0	
31	28.8	36.8	88.1	95.0	100.0

Table II.6.   Similarity matrices (percentage similarity) for the algal assemblages on each sample date pooled by substrate surface.

DAY 4	Block top	Block recessed	Control top	Control recessed
Block top	100.0			
Block recessed	80.6	100.0		
Control top	79.6	83.1	100.0	
Control recessed	79.9	83.4	93.5	100.0
DAY 8				
Block top	100.0			
Block recessed	91.1	100.0		
Control top	81.9	81.9	100.0	
Control recessed	82.3	81.9	93.0	100.0
DAY 16				
Block top	100.0			
Block recessed	92.6	100.0		
Control top	94.1	91.5	100.0	
Control recessed	94.9	90.4	97.4	100.0
DAY 23				
Block top	100.0			
Block recessed	91.9	100.0		
Control top	96.5	91.7	100.0	
Control recessed	93.0	88.9	95.3	100.0
DAY 32				
Block top	100.0			
Block recessed	90.3	100.0		
Control top	89.2	96.1	100.0	
Control recessed	88.8	96.9	94.0	100.0

Figure II.6 The ratio of <u>Stigeoclonium</u> <u>tenue</u> abundance on recessed substrates to top substrates on day 23 (relative abundance ratio) in large block, small block and control streams. Values are means ± 1 SE, (n=3).
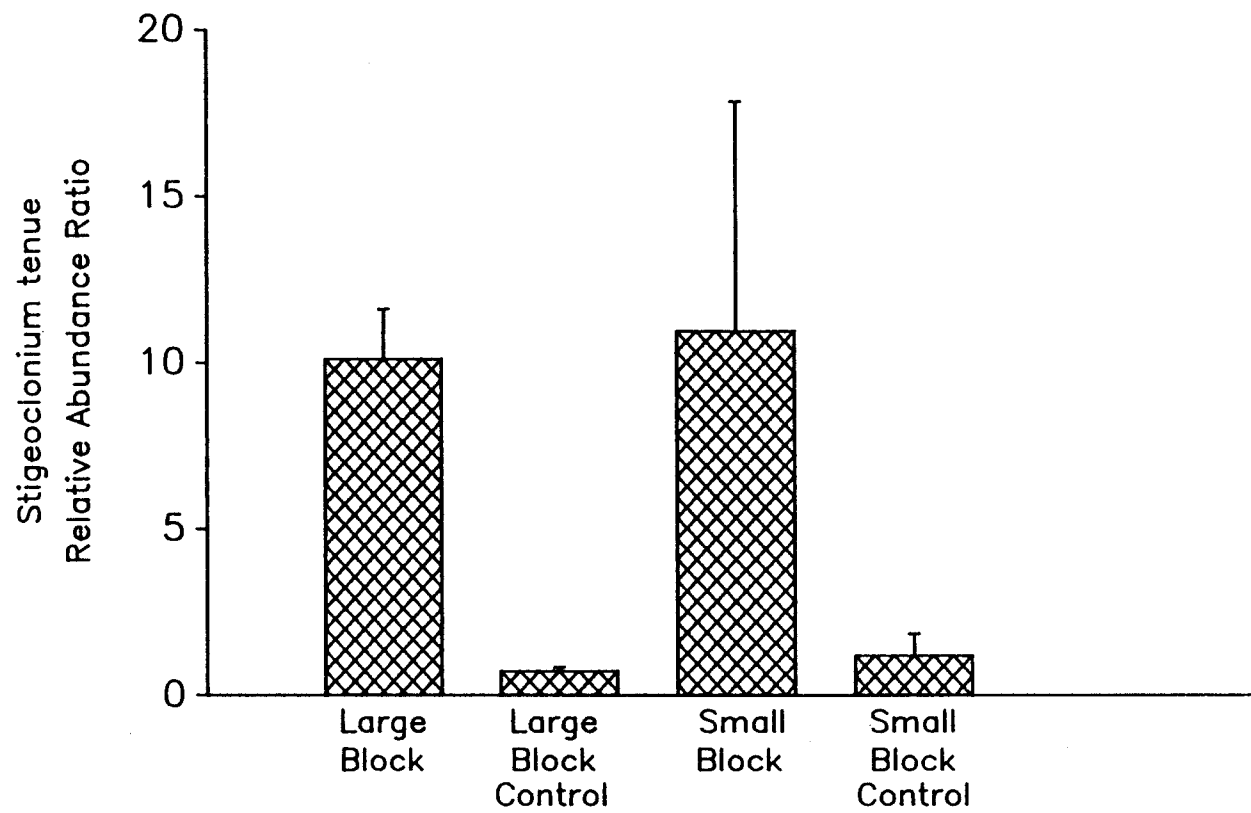
Figure II.6

substrates in both the large and small block streams ($p < 0.05$, Fig. II.6). The presence of S. tenue after day 16 had a great effect on the physiognomy of the assemblages. The tops of large and small blocks were composed of a mat of diatoms and interwoven cyanobacterial filaments, whereas on recessed substrates the mat had an overstory of S. tenue filaments. In control streams the mature assemblages were primarily a diatom-cyanobacteria mat with widely scattered S. tenue filaments.

DISCUSSION

Algal Biomass

The exponential rate of increase in periphyton biomass on all substrates in this experiment was consistent with the results of several studies that have examined periphyton colonization on bare substrates in the absence of grazers (McIntire 1966a, Hamilton and Duthie 1984, Stevenson 1984, Oemke and Burton 1986, Steinman and McIntire 1986). After the first 16 days, periphyton accumulation was initially greater on recessed substrates behind blocks than on substrates either on the tops of blocks or in the flat control streams. The higher water velocities above the substrates on top of blocks and in the control streams increased the rate at which algal cells flowed over them, but the relatively unidirectional flow and higher shear velocities may have inhibited cell attachment. In contrast, the zone of flow separation behind blocks had multidirectional flow with lower shear velocities, which apparently enhanced the deposition and attachment of algal cells (Munteanu and Maly 1981, Vogel 1981, Stevenson 1983, Silvester and Sleigh 1985). Within a recessed substrate, algae colonized the region of relatively still water immediately behind a block before accumulating on the rest of the recessed substrate.

McIntire (1966a) found algal biomass initially accumulated faster in laboratory streams at 9 cm s^{-1} than at 38 cm s^{-1}, but that the trend reversed after 21 days as biomass became greater on substrates in the faster current. This pattern has also been found in several other studies examining periphyton accumulation at

different current velocities (Reisen and Spencer 1970, Korte and Blinn 1983, Stevenson 1984, Omeke and Burton 1986, Steinman and McIntire 1986). By day 16 in our experiment, biomass had accumulated to a greater extent on recessed substrates than on substrates in faster current regimes. However, on day 24 this difference was smaller, indicating the rate of biomass accumulation on substrates in faster shear velocities had become greater relative to the rate of accumulation in slow shear velocities. Studies which show that current flow enhances nutrient uptake, respiration, photosynthesis and growth in algae (Odum and Hoskin 1957, Whitford 1960, Whitford and Schumacher 1961, McIntire and Phinney 1965, McIntire 1966b, Lock and John 1979) support the hypothesis that biomass accumulation rates of periphyton should be higher in faster current regimes after initial establishment.

The presence of blocks significantly affected the difference in biomass accumulation between top and recessed substrates for large blocks but not for small blocks. This may be because the difference in average shear velocity between the two surfaces was greater for large blocks than small blocks. However, dissimilarities in biomass accumulation between the two sizes of blocks may also have been related to their edge areas. Small areas of turbulence at the upstream edges of a substrate enhance cell colonization (Munteanu and Maly 1981, Korte and Blinn 1983, Hamilton and Duthie 1984). As cells accumulate at an edge, downstream turbulence extends over a greater area promoting accumulation from the edges towards the center of the substrate (Stevenson 1983). The upstream edges of

block tops were initially colonized faster than the central area, but biomass may have accumulated faster on small tops than on large tops because small tops had a relatively greater amount of upstream edge area. This would have caused the biomass difference between top and recessed substrates to be less for small blocks.

Reiter and Carlson (1986) and Reiter (1989) suggested that the thickness (biomass) of an algal mat in a current is inversely proportional to the shear stress at the top of the mat. However in our experiment, similar initial shear velocities for control and block top substrates resulted in different final (before sloughing) biomass values. We calculated an initial shear velocity before colonization, whereas Reiter and Carlson (1986) measured the increase in shear velocity as the mat developed. The large difference in water depth between our top (4.4 cm) and control (8.4 cm) substrates may have differentially affected the manner in which mat growth increased shear velocities.

Species Composition

Algal succession was similar on all substrates in this study with the early colonizers, Fragilaria vaucheriae and Oscillatoria agardhii, being replaced by Achnanthes lanceolata, Navicula arvensis and Nitzschia oregona. Stevenson (1986a, 1986b) suggested that pioneer species are able to immigrate onto substrates rapidly but are replaced by taxa with faster growth rates. This pattern may be related to the growth forms of the diatom taxa (Hudon and Legendre 1987). Araphid diatom taxa in general, and F. vaucheriae in particular, were early colonists on bare substrates in several studies (McIntire 1966a, Reisen and Spencer 1970, Hamilton and

Duthie 1984, Stevenson 1984, Omeke and Burton 1986, Hudon et al. 1987, Stevenson and Peterson 1989). These taxa are linear in shape, which may enhance immigration by increasing sinking rates (Stevenson and Peterson 1989). However, araphid diatoms also may be more susceptible to detachment if they extend out of the boundary layer because they have a relatively small area of adhesion in relation to the size of the frustule. The initial accumulation rate of fast immigrating taxa may be enhanced if they grow colonially (Hudon et al. 1987), but the decrease in surface area-volume ratio as the colony grows may make it more susceptible to nutrient limitation (Hudon and Legendre 1987). Therefore, taxa such as F. vaucheriae may be opportunistic, rapidly immigrating onto bare substrate to sequester relatively available nutrients for reproduction followed by a period of increasing vulnerability to resuspension as shear stress at the developing mat front increases. A similar strategy may account for the temporal distribution of O. agardhii in this study. In contrast, firmly attached, solitary monoraphid taxa with high surface area-volume ratios (e.g., A. lanceolata) may be adapted for persistence in an algal mat. More mobile biraphid taxa, such as N. arvensis and N. oregona, may be able to move within a mature mat to obtain resources (Hudon and Legendre 1987). In this and other studies (Marcus 1980, Eloranta and Kunnas 1979, Stevenson 1983, Omeke and Burton 1986), species diversity declined as the periphyton assemblages developed, implying dominance by superior competitors may increase as nutrients and light become limiting in an algal mat.

Results of this study are similar to those of Stevenson (1984)

in that substrates in different current regimes had very similar
assemblages. In our study initial taxonomic differences between the
assemblages were mainly a result of differences in the abundance of
Oscillatoria agardhii. However, like Omeke and Burton (1986), and
Reiter and Carlson (1986), we also observed that assemblages in
different current regimes became more similar over time. We did not
observe an increase in abundance of small adnate diatoms in the
faster currents (Stevenson and Peterson 1989, Omeke and Burton
1986). Comparisons between all these studies are complicated by the
fact that the algae were subjected to different absolute velocities.

The major difference in taxonomic composition of substrates in
this study was the significantly greater abundance of Stigeoclonium
tenue on recessed substrates towards the end of the experiment.
Late successional filamentous chlorophytes, including Stigeoclonium
spp., have been found to be more abundant at relatively low current
velocities (McIntire 1966a, Eloranta and Kunnas 1979, Antoine and
Benson-Evans 1982, Steinman and McIntire 1986). However, Lindstrom
and Taaen (1984) reported some filamentous chlorophytes that
initially appeared at slow current sites were eventually more
abundant at sites with faster velocity. By the end of our
experiment S. tenue began to appear on substrates in the faster
current regimes, suggesting that the successional sequence was the
same in the two current regimes but occurred at different rates with
respect to S. tenue.

Implications for Natural Streams

Based on the parameters in Table II.1, the hydrologic
conditions of mean flow in the laboratory streams were similar to

low order natural streams with shallow depths and subcritical flow (Statzner et al. 1988). Mean flow in the control laboratory streams corresponded most closely to flow over a hard substrate of very low relief (e.g. a bedrock ledge). The large and small block laboratory streams had a mean flow characteristics analogous to a riffle unit with cobble-size substrate. Higher roughness Reynolds number in streams with blocks indicated that the flow environment was patchy, containing zones which differed in local flow (Davis and Barmuda 1989).

Periphyton had a more heterogeneous distribution when current flowed over substrate elements than when it flowed over a flat bed. The main effect of substrate relief initially was to delay periphyton biomass accumulation on substrates in fast current regimes relative to substrates in backwater areas. Moreover, algal assemblages in the two current regimes were slightly different in their patterns of succession. At the end of the experiment, biomass and taxonomic differences may have started to converge but further changes were prevented when assemblages on the tops of blocks began to slough. Similar mechanisms could, in part, account for the differences in periphyton composition and biomass around individual rocks observed by Gumtow (1955), Blum (1960) and Backhaus (1967). These patterns suggest estimates of algal biomass and composition should depend on whether the area sampled is within a single current regime that contains a relatively uniform algal assemblage, or if it includes several algal patches created by different current regimes.

Flow patterns for the two different size blocks appeared to

differ mainly in the degree of vortex formation between substrates. This difference had only a small affect on periphyton development because corresponding assemblages for large and small blocks were very similar in succession and differed only slightly in their patterns of biomass accumulation. The effect of substrate elements on algal development in streams may vary with the free-water velocity, and the spacing and height of the elements. If substrates are very close together, the flow will essentially skim over the tops of the elements, and relatively dead water with stable eddies will form between them. The degree of patchiness may be different when elements are spaced further apart, permitting the wake produced at a block face to increase turbulence in the flow between blocks (Morris and Asce 1955). The latter condition may have been the case for both sizes of our substrate blocks, although the relatively shallow depth of flow probably made flow conditions more complex than those described by Morris and Asce (1955) (Smith 1975, Davis and Barmuda 1989).

Periphyton distribution in streams is often a mosaic of assemblages on different successional trajectories (Fisher 1983) with the degree of patchiness usually related to spatial and temporal variation in the environment (e.g., Parker et al. 1973, Jones 1978, Tett et al. 1978, Busch 1979, Blinn et al. 1980). Succession within a patch is bounded by the composition of the species pool and the physiological characteristics of the species (Patrick 1976), and it is influenced by the interaction of factors such as invasion rate, nutrients, light, temperature, current, substrate and herbivory. Disturbance can impart a stochastic nature

to some of these factors, altering the timing of their interactions and giving periphyton patches a probabilistic distribution (Fisher et al. 1982, DeAngelis and Waterhouse 1987, DeNicola et al. 1990). This study indicated that current flow around substrates may, at least temporarily, generate algal patches within a riffle unit when other factors are held constant. The degree to which algal patches created by the interaction between current and substrate elements converge or diverge may be affected by other factors, such as irradiance level, herbivory and nutrient regime.

ACKNOWLEDGMENTS

III. EFFECTS OF SUBSTRATE RELIEF ON THE DISTRIBUTION OF
PERIPHYTON IN LABORATORY STREAMS;
INTERACTIONS WITH IRRADIANCE

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ABSTRACT

Laboratory streams were used in a 42-day experiment designed to investigate how the spatiotemporal distribution of lotic periphyton created by current flow over cobble-size substrates is affected by irradiance. The streams contained 22 X 22 X 4 cm substrate blocks and were exposed to either 385, 90 or 20 uE m^{-2} s^{-1}. We monitored periphyton succession in fast current regimes on top of blocks and in slower current regimes at surfaces recessed between blocks.

The absolute differences in AFDW algal biomass between top and recessed substrates were significantly affected by irradiance and time. At the end of the experiment, biomass in streams exposed to 20 uE m^{-2} s^{-1} was approximately 5 and 8 times less than in streams exposed to 90 and 385 uE m^{-2} s^{-1}, respectively. Differences in biomass were greater between irradiance levels than between top and recessed substrates within an irradiance level. Irradiance also had a greater effect than current regime on the taxonomic composition of assemblages. Oscillatoria agardhii Gomont and Navicula minima Grun. characterized assemblages at 20 uE m^2 s^{-1}, whereas Fragilaria vaucheria (Kutz.), Nitzschia oregona Sov., Navicula arvensis Hust. and Stigeoclonium tenue (Ag.) Kutz. were more abundant at the two higher irradiances. Detrended correspondence analysis indicated that the rate of succession was accelerated for assemblages at high irradiance and in the slow current regimes between blocks. The results suggested that in natural streams, patches of periphyton produced by large differences in irradiance should be more

heterogeneous than patches within them induced by current flow over cobble-size substrates. Moreover, irradiance level influences the heterogeneity of algal patches produced by hydrologic differences over a substrate.

INTRODUCTION

Differences in light energy at a stream bed can generate a
spatial distribution of periphyton that is heterogeneous in biomass,
taxonomic composition, and productivity (Yount 1956, Parker et al.
1973, Lyford and Gregory 1975, Murphy and Hall 1981, Rounick and
Gregory 1981). The spatial scale of algal patches can depend on the
size of the shaded area. For example, light gaps in a partially
closed canopy may produce algal patches the size of a pool or riffle
unit (Yount 1956, Hill and Knight 1988), or entire segments in a
stream system may have completely open or closed canopies (Rounick
and Gregory 1981). At a smaller scale, a heterogeneous algal
distribution may also occur as a result of hydrologic differences
created when water flows around cobble to boulder-sized substrates
(Gumtow 1955, Blum 1960, Backhaus 1967, Stevenson 1983, DeNicola and
McIntire 1990a). In a hierarchical spatial organization of stream
habitats, microhabitats defined by substrate size develop within the
constraints of habitats defined at a larger spatial scale by
riparian vegetation (Frissell et al. 1986, Minshall 1988). The
objective of this study was to examine how the spatiotemporal
distribution of periphyton is affected by the interaction between
current flow over cobble substrates and irradiance.

Previous studies in laboratory streams indicated that, for a
flat substrate, the effect of current velocity on periphyton
succession depends on the irradiance level (McIntire 1968a, Steinman
and McIntire 1986). In an experiment conducted at a single, high
irradiance (400 uE m^{-2} s^{-1}), DeNicola and McIntire (1990a) found

that differences in current flow over cobble-size substrates created a heterogeneous distribution of periphyton within laboratory streams. In that study, assemblages exposed to fast shear velocities on top of substrate blocks had different patterns of succession than assemblages located in slower shear velocities between the blocks. In the present study, we examined periphyton succession in these two flow regimes at three levels of irradiance. Specifically, our hypotheses were: 1) irradiance has a greater effect on algal succession than current regime; and 2) the effect of current regime on succession depends on the irradiance level.

MATERIALS AND METHODS

Laboratory Streams and Experimental Design

The experiment was conducted in 9 recirculating fiberglass laboratory streams (DeNicola and McIntire 1990a). Well water was supplied to each stream at an exchange rate of 2.0 L min^{-1}, and current was provided by a variable speed, motor-driven paddle wheel. Light energy was provided by sixteen, 1000 W metalarc lamps (Sylvania Corp.), each mounted in a Maxigro reflector. Timers were set to produce 10 hours of light and 14 hours of darkness each day.

The streams were lined with 7.5 long X 7.5 wide X 1.3 cm thick unglazed clay tiles, which served as surfaces for algal attachment. The bed of each stream contained 22.5 cm long, 22.5 cm wide and 4 cm high channel-spanning blocks built of tiles (3 X 3 X 3 tiles). The blocks were spaced 22.5 cm apart (Fig. III.1). The water depth was 4.4 cm above the top surface of the blocks and 8.4 cm above the recessed substrates between blocks.

Free-water velocities were measured in the stream channels before algal seeding at 0.4 maximum depth (Smith 1975) using midget bentzel tubes (Everest 1967) and a Montedoro and Whitney model PVM-2 current meter. The speeds of the paddle wheels were adjusted until the mean free-velocity in all the streams was 27 cm s^{-1}. Patterns of water flow and near-bed hydrological parameters were previously determined for substrates on block tops and between blocks at this mean free-water velocity (DeNicola and McIntire 1990a).

Each of the 9 streams was randomly assigned one of 3 levels of light energy, with 3 replicates per treatment. The photon flux

Figure III.1 Substrate blocks, and locations of top and recessed substrates.

1.33 cm

7.5 cm

LARGE BLOCK STREAM

Side View

Top View

Top Substrate

Recessed Substrate
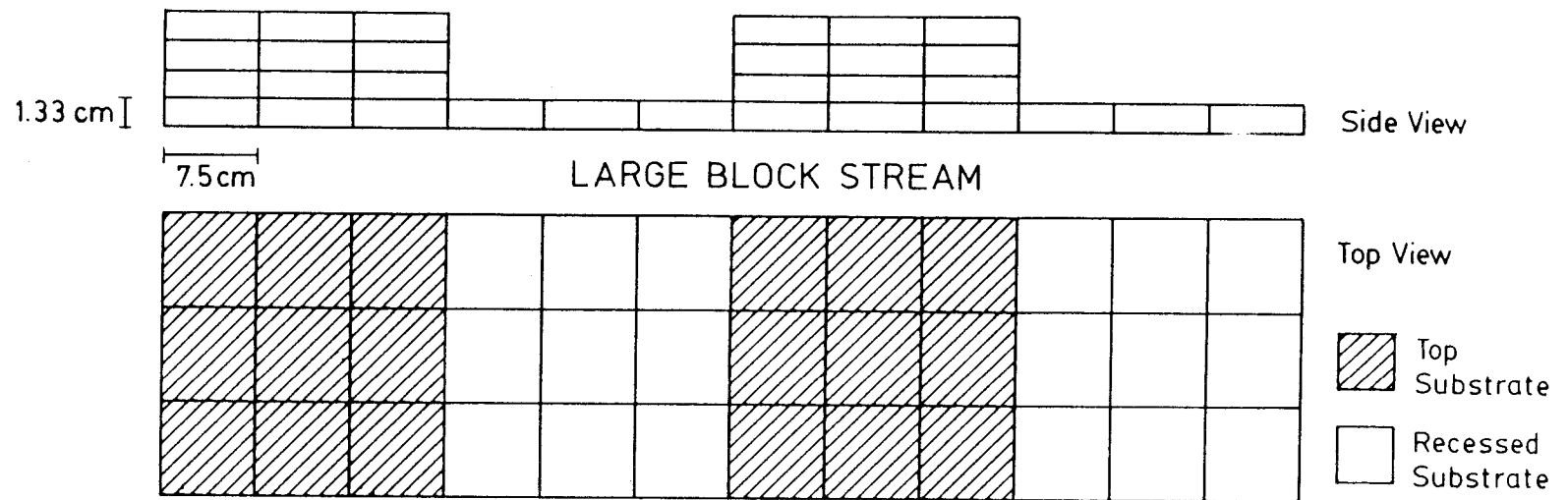
Figure III.1

densities (PFD) of the three irradiance levels were 385, 90 and 20 uE m^{-2} s^{-1} (high, intermediate and low irradiance). Photon flux densities were obtained by adjusting the height of the lamp fixtures and, for the two lower irradiances, by placing green Chicopee screen of the appropriate mesh size over streams. The PFD values represent averages of readings taken at the top of blocks and in the recessed areas between blocks in each stream with a LI-COR Model LI-185 photometer. A PFD of 385 uE m^{-2} s^{-1} is above the saturation intensity of photosynthesis for lotic periphyton (McIntire and Phinney 1965, Jasper and Bothwell 1986). The two lower PFD levels simulated irradiance levels that occur in naturally shaded Oregon streams (Gregory 1983a).

<u>Sampling</u>

The experiment was initiated on 5 September 1987 and continued for 42 days. The streams were seeded on day 1 and once each week during the experiment with periphyton scraped off rocks from local streams (DeNicola and McIntire 1990a). Algal biomass accumulation and taxonomic composition were monitored for surfaces on top of blocks and in recessed areas between blocks in all streams. Periphyton from each of the 9 streams was sampled on days 8, 16, 24, 32 and 42 of the experiment by scraping tiles with a razor blade. On each date in each stream, tiles comprising the top of one block (506 cm^2) and tiles contained in an adjacent recessed area (506 cm^2) were sampled separately (Fig. III.1). Each sample was divided volumetrically to obtain subsamples for estimating algal biomass and taxonomic composition. Biomass, expressed as ash-free dry weight,

was determined by the method described by Lamberti et al. (1987).
Subsamples for taxonomic analysis were preserved in Lugol's
solution. Procedures for microscopic examination and enumeration of
samples for taxonomic composition were outline by Steinman and
McIntire (1986).

Data Analysis

The absolute differences in algal biomass between top and
recessed substrates in the streams were examined by a strip-plot
analysis of variance design with the whole plot factor as PFD level
and the strip factor as time (Gill and Hafs 1971). The sample-
species data matrix for taxonomic analyses contained the relative
abundance of each species based on counts of 500 algal units. An
algal unit was an individual cell for unicellular organisms, and a
colony or filament for multicellular taxa. Taxonomic diversity of
the algal assemblages was expressed by Shannon's information measure
(Peet 1974). Successional changes in the assemblages were examined
by detrended correspondence analysis (DCA) (Hill and Gauch 1980).
Successional trajectories were obtained by plotting a temporal
sequence of the mean sample scores for each treatment relative to
DCA axes 1 and 2.

RESULTS

Algal Biomass

Algal biomass increased on both top and recessed substrates in all streams during the experiment (Fig. III.2). On day 42, biomass values in streams exposed to 20 uE m^{-2} s^{-1} were approximately 5 and 8 times less than in streams exposed to 90 and 385 uE m^{-2} s^{-1}, respectively. Differences in biomass were generally greater between PFD levels than between top and recessed substrates within a PFD level. Biomass accumulated faster on recessed substrates than on top substrates for all three PFD levels until day 24. On day 42, biomass values on top substrates were greater than on recessed substrates with intermediate and high irradiances, but the two substrate types had similar biomass values with low irradiance. Analysis of variance indicated that the absolute difference in biomass between top and recessed substrates was significantly affected by the interaction of irradiance and time (p < 0.01). The main effects of these two factors were also significant (p < 0.01) (Table III.1).

Taxonomic Composition and Species Heterogeneity

The cyanophyte Oscillatoria agardhii Gomont and zoospores of chlorophytes were the most abundant taxa on both top and recessed substrates on day 8 in streams exposed to low irradiance (Fig. III.3a and b). By day 16 in these streams, O. agardhii had decreased slightly in relative abundance and no zoospores were found. Concurrently, there was an increase in diatoms, especially Fragilaria vaucheriae (Kutz.) and Achnanthes lanceolata (Breb.)

Figure III.2 Biomass accumulation on top (T) and recessed (R) substrate surfaces at 385, 90 and 20 uE m^{-2} s^{-1}. Values are means (n=3).
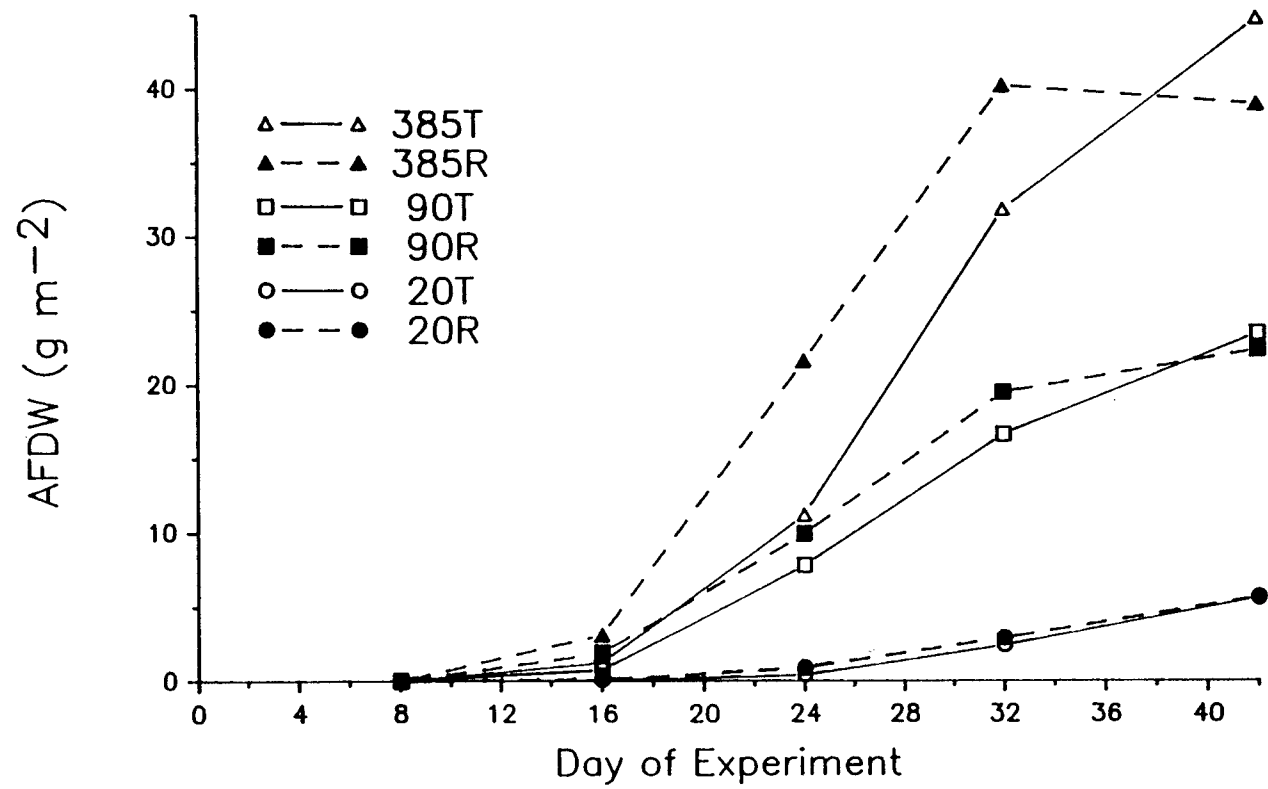
Figure III.2

Table III.1. The absolute value of the difference in ash-free biomass (g m^{-2}) between top and recessed substrates. Values are means, n=3. Fisher's protected least significant difference values (FPLSD) are given to compare means.

			Day		
PFD	8	16	24	32	42
20	0.0246	0.0915	0.5073	0.5117	0.1923
90	0.0308	1.1746	2.1380	2.8443	1.3000
385	0.0304	1.8421	10.4667	8.4167	15.4830

To compare means in column, FPLSD$_{.05}$ = 1.8613;

and in a row FPLSD$_{.05}$= 1.1291.

Figure III.3 The relative abundance of zoospores (ZOOSP),
Oscillatoria agardhii (OSCAGR), Fragilaria vaucheriae (FRAVAU),
Navicula arvensis (NAVARV) and Stigeoclonium tenue (STITEN). a)
Top substrates at 20 uE m^{-2} s^{-1}. b) Recessed substrates at 20 uE
m^{-2} s^{-1}. c) Top substrates at 90 uE m^{-2} s^{-1}. d) Recessed
substrates at 90 uE m^{-2} s^{-1}. e) Top substrates at 385 uE m^{-2} s^{-1}.
f) Recessed substrates at 385 uE m^{-2} s^{-1}. H" for each of the
assemblages is written above the bar. All values are means (n=3).
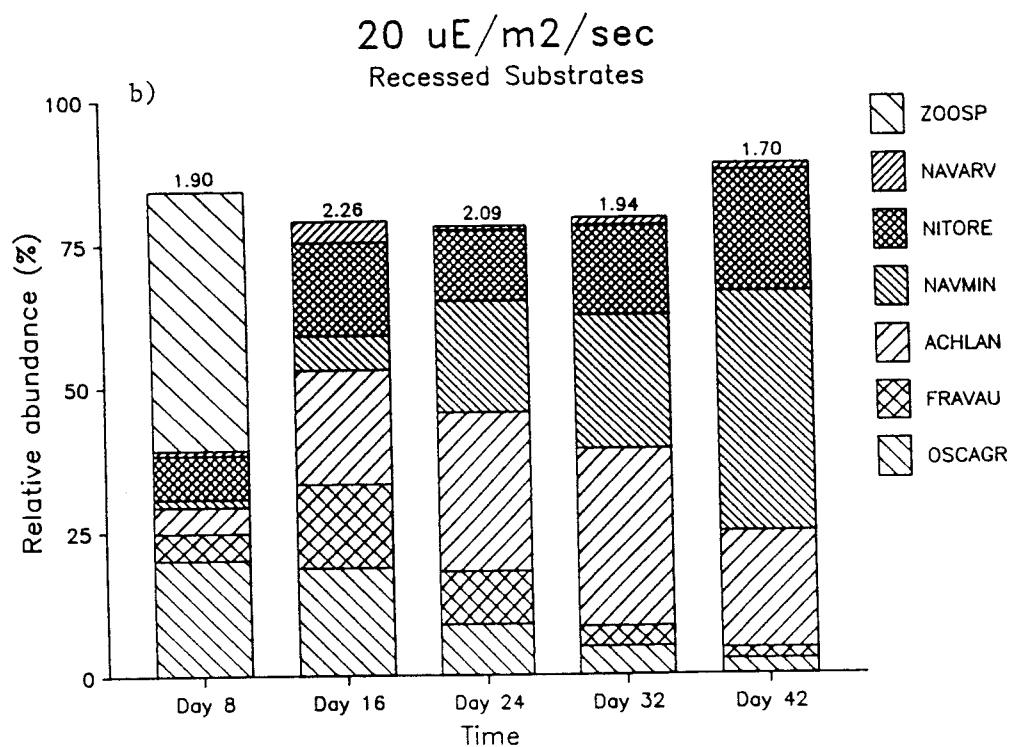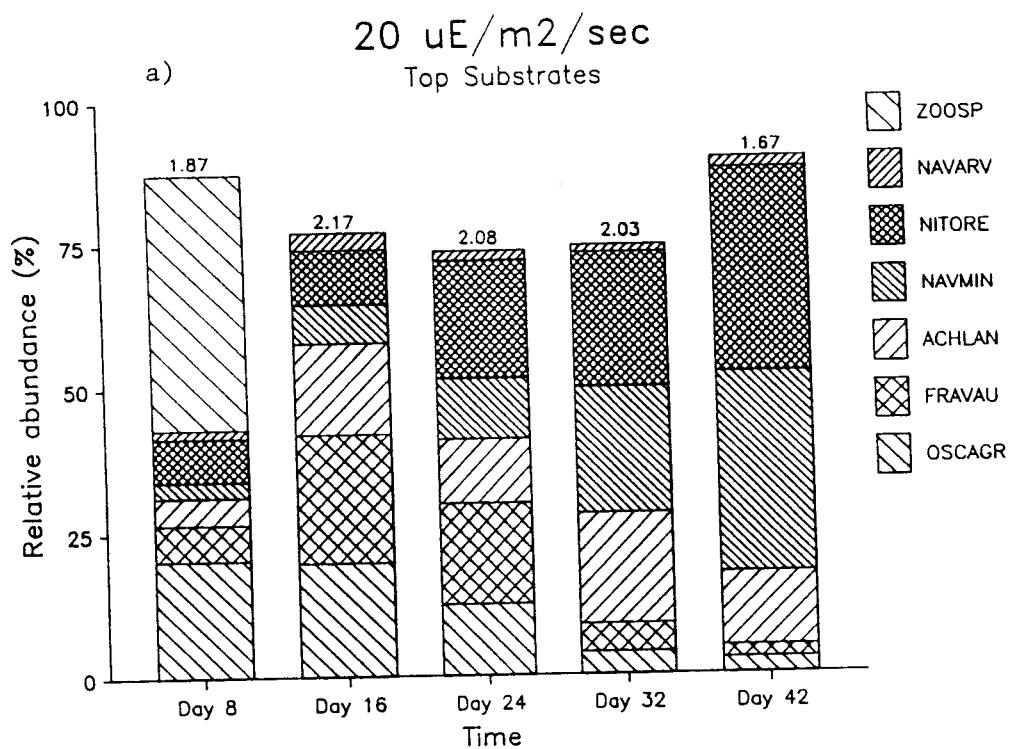
Figure III.3

Figure III.3 contd.

385 uE/m2/sec

e) Top Substrates

385 uE/m2/sec

f) Recessed Substrates
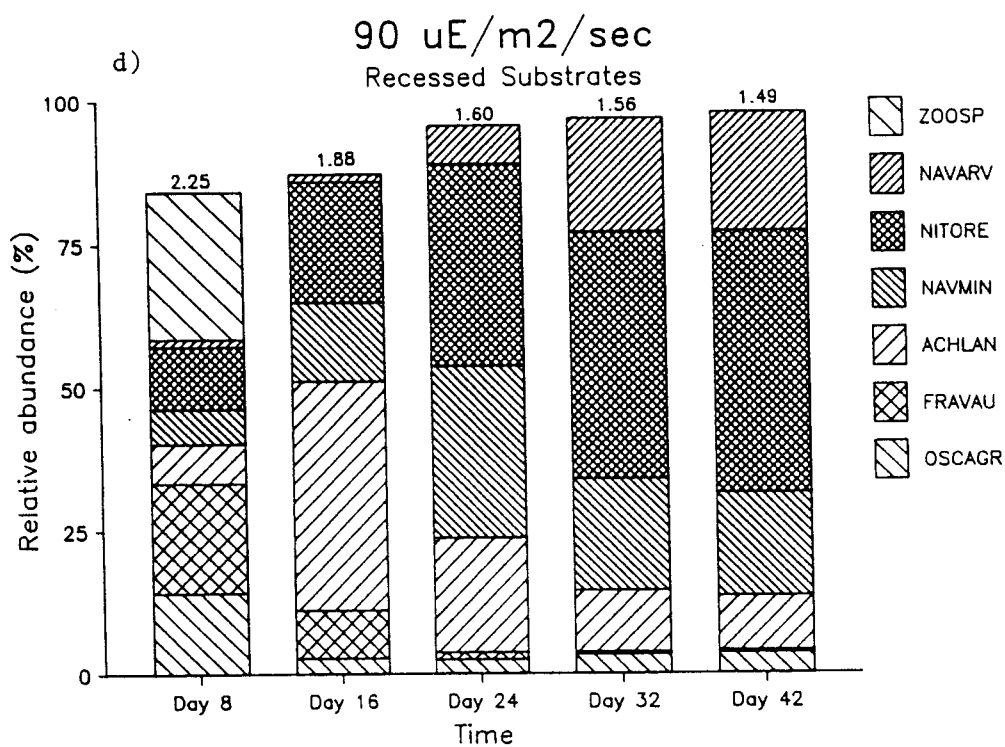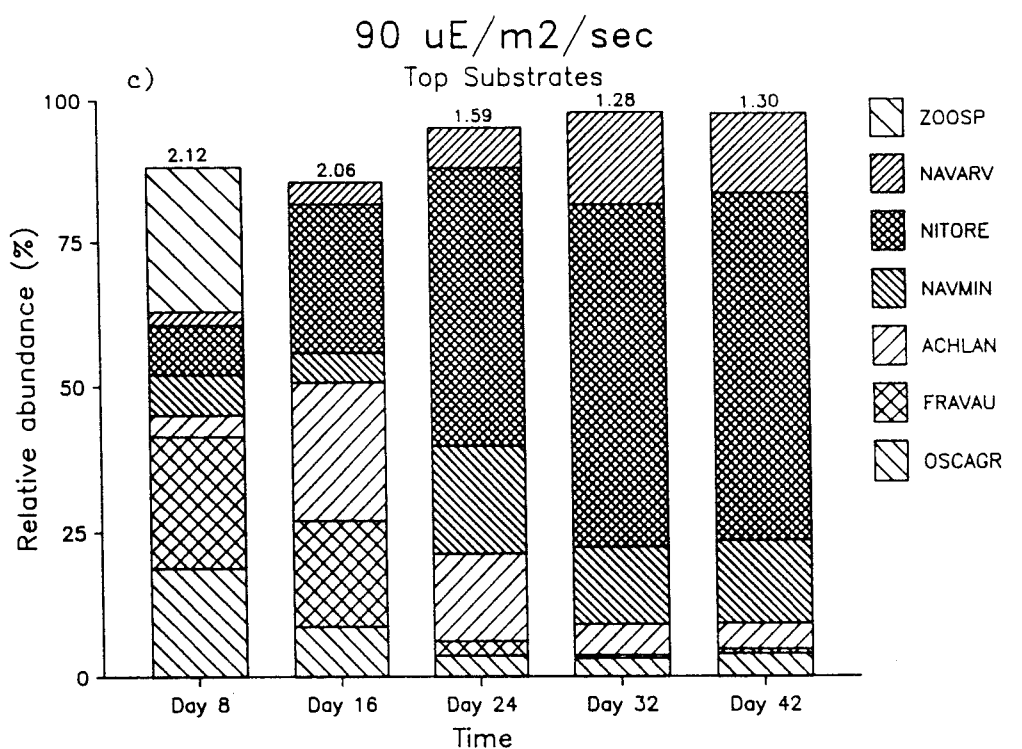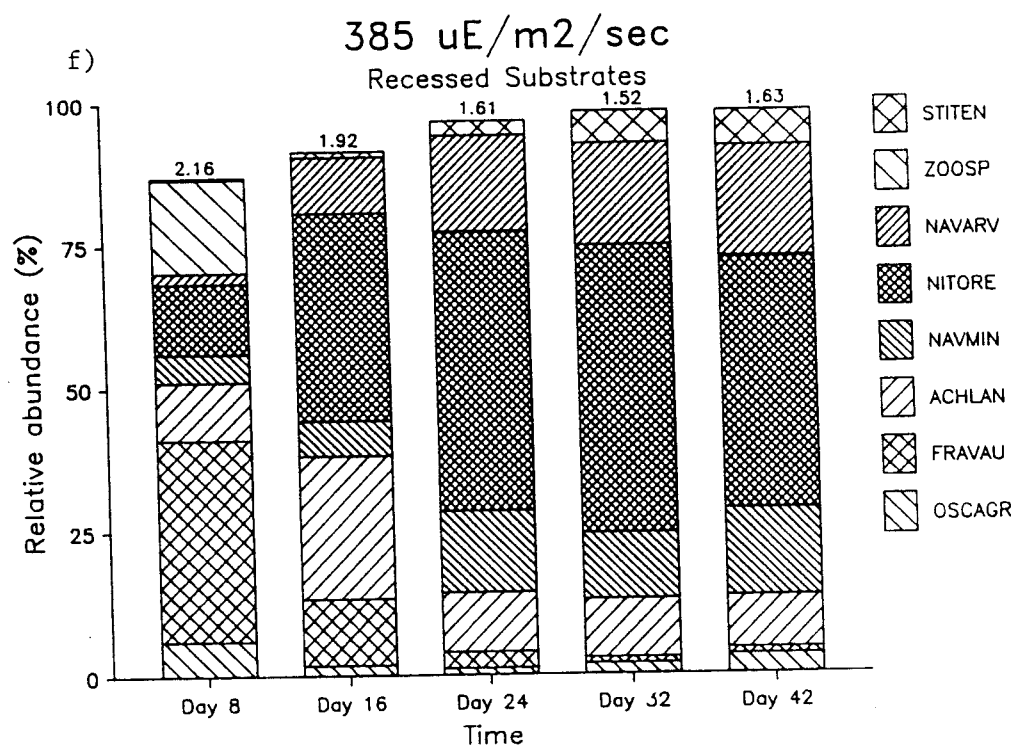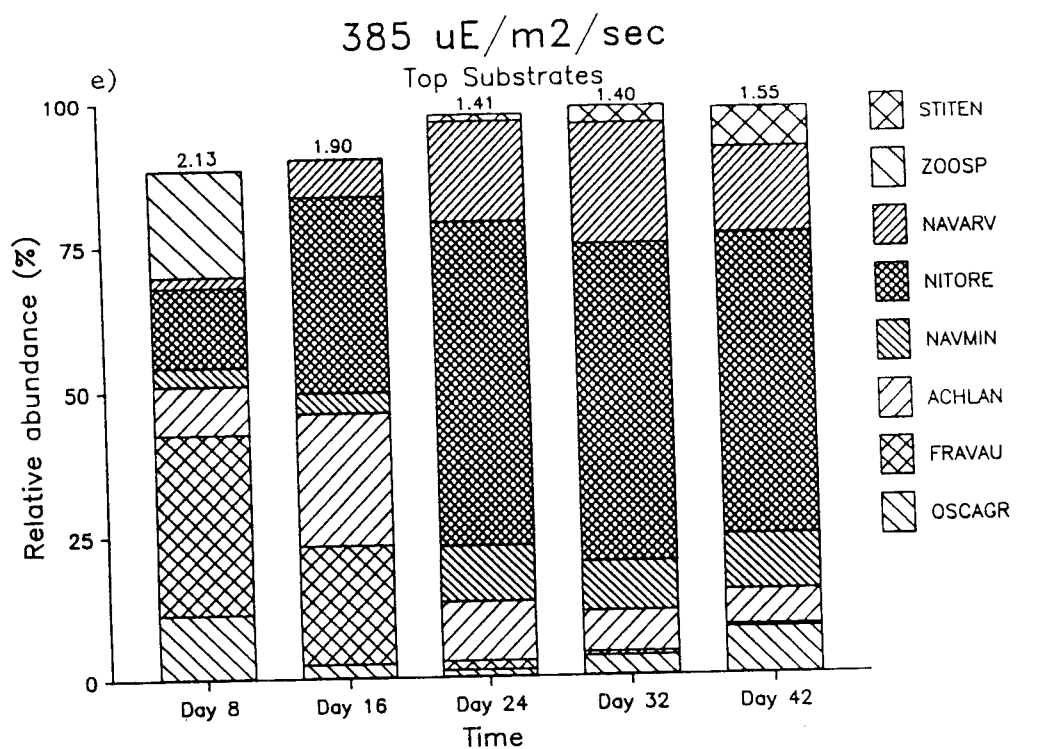
Figure III.3 contd.

Grun. The relative abundance of the diatoms _Nitzschia oregona_ Sov. and _Navicula minima_ Grun. increased gradually in the assemblages with low irradiance after day 16, while the abundance of _O. agardhii_ and _F. vaucheriae_ decreased. Assemblages exposed to intermediate and high irradiances had lower relative abundances of _O. agardhii_ and zoospores, and more _F. vaucheriae_ on day 8 than assemblages exposed to low irradiance (Fig. III.3c-f). Between days 8 and 16, both _O. agardhii_ and _F. vaucheria_ decreased in assemblages exposed to intermediate and high irradiances, whereas _A. lanceolata_ increased to a maximum relative abundance. Assemblages with intermediate and high irradiances were dominated by _N. oregona_ and the diatom _Navicula arvensis_ Hust. after day 16. In all streams, _N. oregona_ was more abundant on top substrates than on recessed substrates, whereas _A. lanceolata_ and _N. minima_ were more abundant on recessed substrates (Fig. III.3a-f).

The relative abundance of the filamentous chlorophyte _Stigeoclonium tenue_ (Ag.) Kutz. increased throughout the experiment in assemblages exposed to high irradiance, and represented about 1.5% of the algal units at the end of the experiment (Fig. III.3e and f). _Stigeoclonium tenue_ was slightly more abundant on recessed substrates than on top substrates at high irradiance, but this difference decreased with time. Filaments of _S. tenue_ never comprised more than 0.5% of an assemblage with intermediate irradiance and were not found in assemblages exposed to low irradiance. The abundance of _S. tenue_ affected the physiognomy of the assemblages. Final assemblages at low irradiance were a flat

mat of interwoven cyanophyte filaments and diatoms. Final

assemblages with intermediate irradiance contained scattered

filaments of S. tenue (0.2 to 2% of the assemblage biovolume)

extending above the mat, whereas, with high irradiance the mat had a

dense overstory of filaments (27 to 33% of the biovolume).

In general, species diversity of all the assemblages decreased

with time. Species diversity was highest for assemblages exposed to

low irradiance, except on day 8 when zoospores were abundant (Figs.

III.3a-f).

Successional Trajectories

Mean successional trajectories for top and recessed substrates

at the 3 PFD levels are illustrated in Fig. III.4a. Effects of time

and irradiance on succession were separated by ordination axes 1 and

2, respectively. DCA maximizes the correspondence between sample

and species ordinations; therefore, taxa that describe a

successional pattern can be found by comparing the configuration of

the sample ordination scores with corresponding positions in the

species ordination. Tracing the trajectories for all the streams in

the species ordination showed a general temporal change from

assemblages characterized by zoospores, Oscillatoria agardhii,

Cocconeis placentula var. euglypta (Ehr.) Cl. and Fragilaria

vaucheriae to assemblages of mostly Achnanthes lanceolata, Nitzschia

oregona, Navicula minima and Navicula arvensis (Fig. III.4a cf.

III.4b). Oscillatoria agardhii, Phormidium tenue (Menegh.) Gomont,

Achnanthes minutissima Kutz., Achnanthes deflexa Reim. and N. minima

characterized assemblages with low irradiance. Assemblages exposed

to the two higher PFD's had a greater abundance of F. vaucheriae, N.

Figure III.4 a) Successional trajectories of the periphyton assemblages on top (T) and recessed (R) substrates at 385, 90 and 20 uE m^{-2} s^{-1}. Points along the trajectories are mean (n=3) sample scores for days 8, 16, 24, 32 and 42. b) Ordination of species (mean scores, n=3) that had a relative abundance greater than 2 percent. See text for explanation of ordination method.

a) Plot of DCA Axis 2 versus DCA Axis 1 with series: 20 T, 20 R, 90 T, 90 R, 385 T, 385 R.

b) Plot of DCA Axis 2 versus DCA Axis 1 showing species positions: Navicula minima, Achnanthes deflexa, Achnanthes minutissima, Phormidium tenue, Oscillatoria agardhii, Cocconeis placentula var. euglypta, Zoospores, Nitzschia oregona, Achnanthes lanceolata, Navicula arvensis, Stigeoclonium tenue, Fragilaria vaucheria.
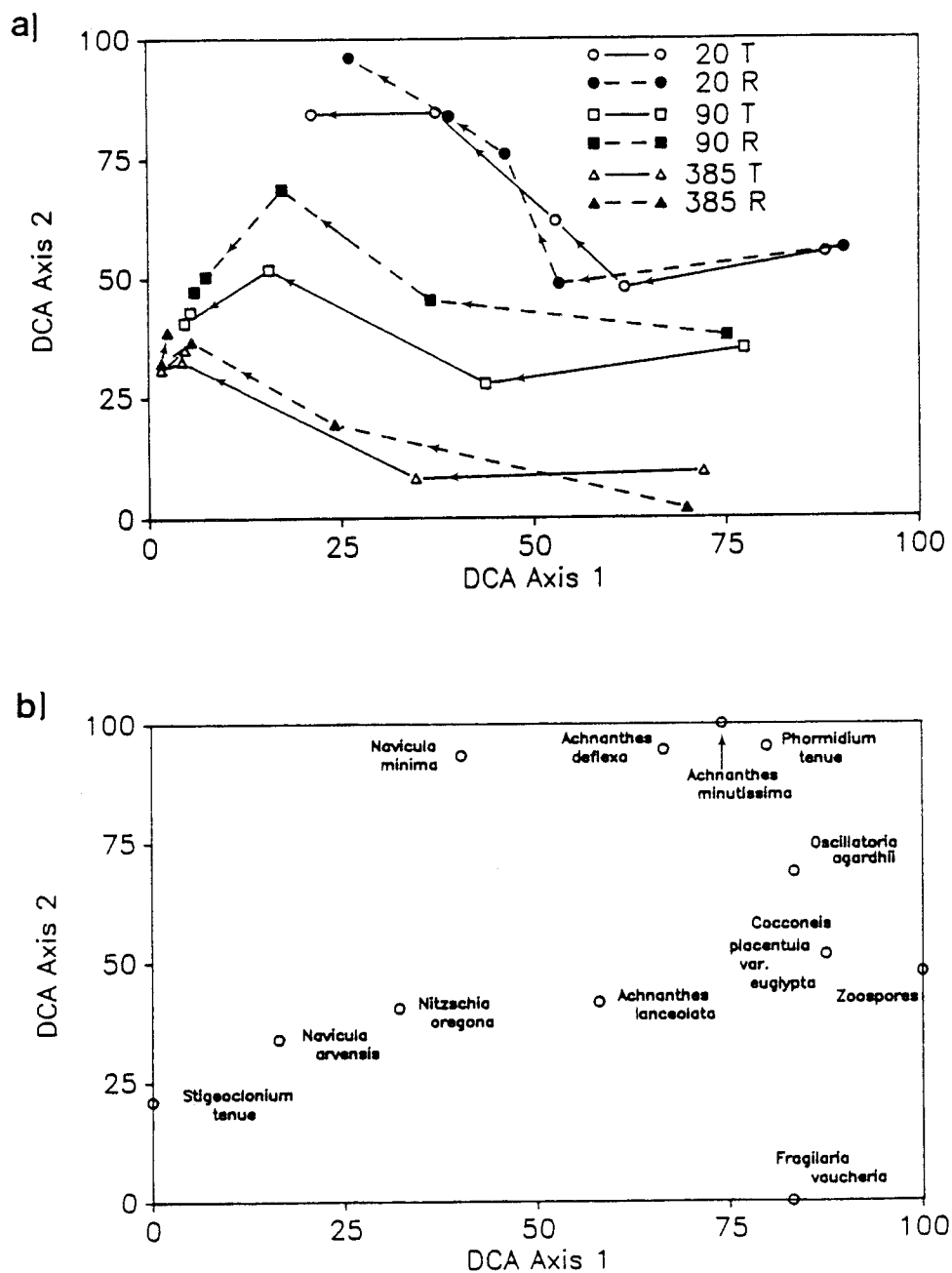
Figure III.4

oregona, N. _arvensis_ and _Stigeoclonium_ _tenue_.

The rate at which successional trajectories approached a "final" assemblage increased with PFD level. For example, there were relatively greater changes in species composition early in succession with higher PFD levels (i.e., the distances between days 8 and 16, and days 16 and 24 in the ordination were larger). Moreover, assemblages with intermediate and high irradiances showed little change in species composition after days 24 and 32, respectively (i.e., their trajectories remained relatively fixed at a "final stage"), whereas assemblages with low irradiance continued to have noticeable changes in composition until the end of the experiment (Fig. III.4a).

For each irradiance, assemblages on recessed substrates usually occupied a higher position in the ordination space than assemblages on top substrates (Fig. III.4a.), indicating that for a given PFD level, recessed substrates usually contained a comparatively greater abundance of taxa characteristic of lower light intensity (Fig. III.4b). This may have resulted from recessed substrates being slightly shaded by the walls of the blocks (< 15% of each ambient PFD). Initially, the rate of succession was faster on recessed substrates than on top substrates for each PFD level. By day 32, assemblages on top and recessed substrates were similar within each irradiance. However, between days 32 and 42, there was a divergence between top and recessed trajectories in streams at low irradiance (Fig. III.4a).

DISCUSSION

Algal Biomass

The rate and degree of algal biomass accumulation in the streams increased with PFD level. A similar effect of irradiance on lotic periphyton biomass has been previously observed in other laboratory experiments (McIntire 1968a, Steinman and McIntire 1986, Steinman and McIntire 1987) and in field situations (Lyford and Gregory 1975, Shortreed and Stockner 1983, Lowe et al. 1986). However, some studies have suggested that, with high irradiance, photoinhibition of photosynthesis can cause periphyton biomass to decrease (Antoine and Benson-Evans 1983, Hill and Knight 1988).

In a previous study employing the same substrate relief in laboratory streams at 400 uE m^{-2} s^{-1}, DeNicola and McIntire (1990a) found the presence of blocks significantly affected the distribution of biomass when compared to streams with no substrate relief. In that study it was suggested that lower shear velocities at recessed substrates relative to top substrates promoted algal deposition and colonization, causing biomass initially to accumulate faster on recessed substrates. However, once the algal assemblages became established, growth of assemblages on top substrates was greater, possibly because the higher flow velocities enhanced nutrient diffusion to cells (DeNicola and McIntire 1990a). While the same patterns were observed in this study, differences in biomass accumulation between top and recessed substrates were smaller with lower PFD levels. This suggested that the effects of the hydrologic differences between the two substrates decreased with a decrease in

irradiance. Similarly, when separate laboratory streams with level substrates were treated with different combinations of light and current velocity, differences in biomass accumulation between fast and slow velocities were smaller with low irradiance (Steinman and McIntire 1986).

Bothwell et al. (1989) found that darkness enhanced the emigration of algal cells after initial attachment to substrates in streams. This may explain why initial differences in biomass between top and recessed substrates (i.e., fast and slow shear velocities) were less with lower irradiances in our experiment. Rates of biomass accumulation in our experiment also suggested that, after colonization, assemblages in fast shear velocities had greater rates of net primary production than those in slow shear velocities, and that the difference was greater with high irradiance. An increase in current velocity, like an increase in CO_2 concentration and temperature (McIntire 1966, 1968b), should enhance the diffusion of nutrients for the enzymatic "dark" reactions of photosynthesis but not effect the reactions limited by light (i.e., the initial slope of the photosynthesis-light curve). Therefore, rates of primary production for two current velocities should only be different when irradiance is high enough to saturate photosynthesis at the slower velocity. The rate of primary production in lotic periphyton has been shown to be affected in this manner when light interacts with assemblages grown with different levels of CO_2 and temperature (McIntire and Phinney 1965), but to our knowledge this hypothesis has not been tested for current velocity. Moreover, effects of current velocity relating to nutrient diffusion within an

algal mat would increase with high irradiance because water must flow through an algal mat of greater biomass.

Taxonomic Composition

The abundance of zoospores in the streams on day 8 most likely represented cells remaining from the algal seed. The greater percentage of zoospores with low irradiance reflected the lower biomass of attached cells in these streams relative to suspended seed cells in the water column. Overall, irradiance had a greater effect on the taxonomic composition of assemblages than current regime. The greater abundance of the filamentous chlorophyte Stigeoclonium tenue with higher irradiance was consistent with previous observations in laboratory streams (Steinman and McIntire 1986 and 1987). Similarly, in field studies, filamentous chlorophytes increased in abundance following canopy removal (Hansmann and Phinney 1972, Lyford and Gregory 1975, Shortreed and Stockner 1983, Lowe et al. 1986). Chlorophytes may be restricted to environments of high irradiance due to their lack of pigment diversity (Lowe et al. 1986, Steinman and McIntire 1987).

In this study, and in Steinman and McIntire (1986), the diatom Nitzschia oregona was more dominant with high irradiance and fast current regime. These environmental conditions were associated with a relatively high (final) algal biomass. N. oregona may have had an advantage over other diatoms in the thicker algal mats because the possession of a keel raphe provides greater motility in fine-particle environments (Hill and Knight 1987, Hudon and Legendre 1987). Similar reasoning may explain why there was a general shift

from the less motile araphid and monoraphid diatom taxa to the more

motile biraphid taxa as biomass increased within an algal mat.

Successional trajectories of the assemblages in this experiment

indicated that assemblages with high irradiance had accelerated

initial rates of species replacement and took less time to reach a

"final" stage. Discounting the effect of zoospores on day 8, the

accelerated trajectories for assemblages exposed to high irradiance

also decreased faster in species diversity. Yount (1956) observed

similar effects in a spring when he compared the rate of succession

and the diversity of diatom assemblages on glass slides at a site

with high irradiance to a shaded site. Steinman and McIntire (1987)

found that the initial rate of periphyton succession increased with

irradiance for assemblages exposed to 15, 50 and 150 uE m^{-2} s^{-1},

although the rate of succession was slower with 450 uE m^{-2} s^{-1} than

with lower irradiances. Grime (1979) suggested that in highly

productive terrestrial environments the initial rate of plant

succession should be more rapid than in unproductive habitats.

Additionally, more productive environments should tend to have lower

species diversity relative to unproductive habitats because the

faster population growth rates would increase the rate of

competitive exclusion (Huston 1979).

In this experiment, the initial rate of succession in

assemblages on the recessed substrates was greater than that for

assemblages on top substrates. Possibly, the enhanced colonization

in the slower current velocities of recessed areas accelerated

autogenic successional changes within the assemblages (Stevenson

1983). DeNicola and McIntire (1990a) found that assemblages on top

and recessed substrates with 400 uE m^{-2} s^{-1} had very similar floras, but succession proceeded at a slightly faster rate on recessed substrates, especially with respect to the development of _Stigeoclonium_ _tenue_. Similarly, Oemke and Burton (1986), and Steinman and McIntire (1986) found that rates of periphyton succession were initially faster in slow current than in fast current regimes.

The degree of similarity between periphyton successional trajectories on top and recessed substrates in this experiment depended on the irradiance level. Ambient irradiance may have interacted with effects of flow regime on succession, as well as effects related to the shading of recessed substrates by block walls. McIntire (1968a) suggested that the abundances of some lotic algal taxa can be affected by the interaction between current velocity and irradiance. To our knowledge no one has examined lotic periphyton succession at a gradient of irradiance that is fine enough to determine if shading effects in our experiment may have caused an interaction between substrate type and ambient light.

Implications for Natural Streams

In natural streams periphyton can be distributed as a mosaic of patches, which may be on different successional trajectories or at different stages of the same trajectory (Busch 1979, Fisher 1983). Spatial heterogeneity in the distribution of algal assemblages in a stream depends upon the scale of the observations, with patches at smaller scales developing within the constraints of conditions forming the larger patches. In this study we assumed that the area

of an open or shaded patch in a stream is much larger than the size
of substrates in the stream, and that within a light-induced patch a
second level of heterogeneity may occur as a result of current flow
around cobble-sized substrates. Based on the results of this
experiment, one would predict that in natural streams patches of
periphyton produced by large differences in irradiance should be
more different than the smaller patches within them induced by
current flow over cobble-sized substrates. However, the degree of
heterogeneity produced by hydrologic differences over substrates may
depend upon the irradiance level of the light patch. For example,
differences in biomass due to current flow around the substrates
were greater at high irradiance in this experiment. Irradiance has
also been shown to interact with other factors that affect the
distribution of periphyton in streams, such as nutrient regime
(Stockner and Shortreed 1976, Sumner and McIntire 1982, Lowe et al.
1986, Hill and Knight 1987), herbivory (Sumner and McIntire 1982,
Steinman and McIntire 1989, Lamberti et al. 1989) and disturbance
(Douglas 1958, Busch 1978, Jones 1978, Rounick and Gregory 1981,
Fisher et al. 1982). The effects of these interactions on the
spatial distribution of periphyton may also vary temporally in
response to seasonal changes in ambient sunlight and canopy closure
(Sherman and Phinney 1971, Lyford and Gregory 1981). In order to
more completely understand the distribution of periphyton in
streams, the strength of the interactions of all these factors at
different temporal and spatial scales must be established.

ACKNOWLEDGMENTS

IV. EFFECTS OF SUBSTRATE RELIEF AND IRRADIANCE ON
GRAZER-PERIPHYTON INTERACTIONS IN
LABORATORY STREAMS

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ABSTRACT

A 54-day experiment was conducted in laboratory streams to examine the relationships between temporal and spatial patterns of algal development, and the grazing behavior of the snail _Juga silicula_ in a patchy physical environment. The streams contained 22 X 22 X 4 cm substrate blocks and were exposed to a photon flux density of either 375, 90 or 20 uE m^{-2} s^{-1}. We monitored periphyton succession and the number of snails in fast current regimes on tops of blocks and in slower current regimes on surfaces recessed between blocks.

At the end of the experiment, algal biomass in streams exposed to high irradiance was approximately 8 and 80 times higher than in streams with low and intermediate irradiance, respectively. Growth rates of _Juga_ in streams with high and intermediate irradiances were similar and approximately 15 times greater than rates at low irradiance. At all irradiances, snail densities were higher and algal biomass was lower on recessed substrates than on substrates on top of blocks. As algal biomass became low on recessed substrates, snails tended to be more abundant on top substrates, and biomass values in the two current regimes became more similar. Differences in algal biomass and snail abundance between the two substrates were greater in streams exposed to high irradiance than for the two lower irradiances. Snails had the greatest effect on algal succession at low irradiance, and these algal assemblages contained adnate cell forms early in succession. At intermediate irradiance, succession in both current regimes moved towards adnate cells, but this

occurred more rapidly on the more heavily grazed recessed substrates. At high irradiance, parts of the algal assemblages in both current regimes remained ungrazed, producing a mix of successional stages on the substrates. Similar interactions may occur in coastal Oregon (U.S.A) streams, because <u>Juga</u> is the competitive dominate herbivore with few predators, and its distribution corresponds mainly to irradiance (a determinant of algal abundance), current regime and substrate size.

INTRODUCTION

The distribution of periphyton on and between cobble to boulder-sized substrates in streams has been observed to be patchy in terms of both biomass and species composition (Frisch 1929, Gumtow 1955, Blum 1960, Backhaus 1967, Jones 1978). The spatial distribution of invertebrate herbivores in streams is often related to the distribution of algal biomass (Hart 1981, Lamberti and Resh 1983, Kohler 1984, Vaughn 1986, Richards and Minshall 1988), and for some types of grazers, algal physiognomy (Dudley et al. 1986). However, invertebrate movement also may be determined by abiotic factors (e.g., current, temperature, and substrate size) and biotic interactions (competition and predation) (Hart and Resh 1980, Peckarsky 1983). Therefore, the probability of algal patches being encountered by herbivores depends on plant abundance, and the environmental and physiological characteristics affecting the foraging range of the herbivores (Lubchenco and Gaines 1983). Models describing foraging patterns in a patchy environment usually assume that the animal chooses whichever option maximizes its chances of survival and reproduction (Stephens and Krebs 1987). The objective of this study was to determine how spatial and temporal patterns of algal development in streams interact with the grazing behavior of the pleurocerid snail _Juga silicula_ (Gould).

Most studies of the effects of herbivory on algal assemblages in streams have assumed that the plant-animal interactions occurred in a homogenous environment (e.g., Kedhe and Wilhm 1972, Sumner and McIntire 1983, Hill and Knight 1987, Steinman et al. 1987, Lamberti

et al. 1989, Lowe and Hunter 1988, McCormick and Stevenson 1989, DeNicola et al. 1990, however see Colletti et al. 1987). Using laboratory streams in a previous study, we found that ungrazed algal assemblages exposed to fast shear velocities on top of substrate blocks had different patterns of succession than assemblages located in slower shear velocities between blocks (DeNicola and McIntire 1990a). Moreover, algal biomass and species composition in the two current regimes depended on the irradiance level (DeNicola and McIntire 1990b). In this experiment, we examined interactions between patterns of algal development and the distribution of _Juga_ in the two current regimes at three levels of irradiance.

Juga often is an abundant invertebrate in streams in the Pacific Northwest, and snails are important consumers in streams throughout North America (Kehde and Wilhm 1972, Hawkins and Furnish 1987, Lowe and Hunter 1988). _Juga_ prefers to feed on periphyton but can consume detritus when algae are scarce (Anderson et al. 1978, Hawkins and Sedell 1981). _Juga_ is usually a competitive dominant herbivore in coastal Oregon streams, comprising over 90% of total invertebrate biomass in some habitats (Hawkins and Furnish 1987). Vertebrate predation on the snails is low and their distribution within streams mainly corresponds to irradiance (a determinant of algal productivity), current, and substrate size (Hawkins and Furnish 1987).

MATERIALS AND METHODS

Laboratory Streams and Experimental Design

The experiment was conducted in 9 recirculating fiberglass laboratory streams. The design of the streams was described by DeNicola et al. (1990). Briefly, each stream was 3 X 0.5 m, with two parallel channels separated by a centerboard that was open at both ends. Well water was supplied to each stream at an exchange rate of 2.0 L min^{-1}, and a current was generated by a variable speed, motor-driven paddle wheel. Nutrient concentrations in the water supply were high (Steinman and McIntire 1986), while water temperature in the streams ranged from 16° to 18.5^{o}C. Light energy was provided by sixteen, 1000 W metalarc lamps (Sylvania Corp.), each mounted in a Maxigro reflector. Timers were set to produce 10 hours of light and 14 hours of darkness each day.

The streams were lined with 7.5 long X 7.5 wide X 1.3 cm thick unglazed clay tiles, which served as surfaces for algal attachment and grazing. The bed of each stream contained 22.5 cm long, 22.5 cm wide and 4 cm high channel-spanning blocks built of tiles (3 X 3 X 3 tiles). The blocks were spaced 22.5 cm apart (Fig. IV.1). The water depth was 4.4 cm above the top surface of the blocks and 8.4 cm above the recessed substrates between blocks.

Free-water velocities were measured in the stream channels before algal seeding at 0.4 maximum depth (Smith 1975) using midget bentzel tubes (Everest 1967) and a Montedoro and Whitney model PVM-2 current meter. The speeds of the paddle wheels were adjusted until the mean free-velocity in all the streams was 26 cm s^{-1}. Patterns

Figure IV.1 Substrate blocks, and locations of top and recessed substrates.

1.33 cm

7.5 cm

LARGE BLOCK STREAM

Side View

Top View

Top
Substrate

Recessed
Substrate
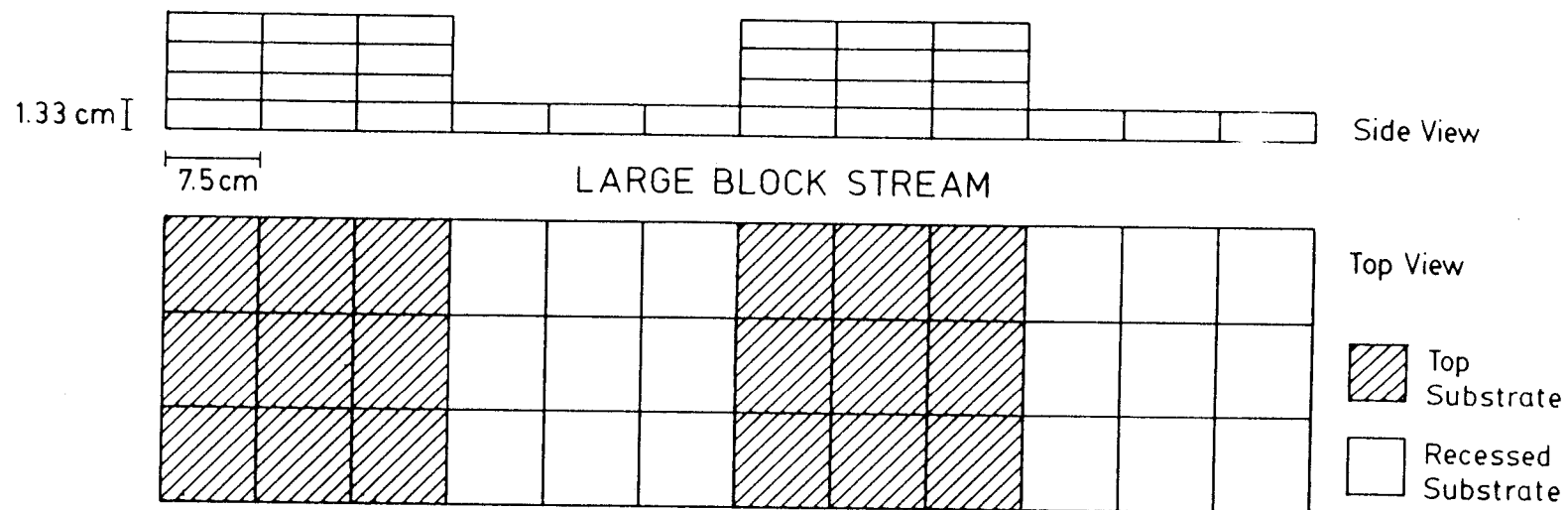
Figure IV.1

of water flow and near-bed hydrological parameters were previously determined for substrates on block tops and between blocks at this mean free-water velocity (DeNicola and McIntire 1990a).

Each of the 9 streams was randomly assigned one of 3 levels of light energy, with 3 replicates per treatment. The photon flux densities (PFD) of the three irradiance levels were 375, 90 and 20 uE m^{-2} s^{-1} (high, intermediate and low irradiance). Photon flux densities were obtained by adjusting the height of the lamp fixtures and, for the two lower irradiances, by placing green Chicopee screen of the appropriate mesh size over streams. The PFD values represent averages of readings taken at the top of blocks and in the recessed areas between blocks in each stream with a LI-COR Model LI-185 photometer. A PFD of 375 uE m^{-2} s^{-1} is above the saturation intensity of photosynthesis for lotic periphyton (McIntire and Phinney 1965, Jasper and Bothwell 1986). The two lower PFD levels simulated irradiance levels that occur in naturally shaded Oregon streams (Gregory 1980).

The experiment was initiated on 30 June 1988 and continued for 54 days. The streams were seeded on day 1 and once each week during the experiment with periphyton scraped off rocks from local streams (DeNicola and McIntire 1990a). Specimens of _Juga silicula_ were collected from the Alsea River in Benton County, Oregon. On day 13 of the experiment, each stream was stocked with 750 snails (375 m^{-2}) that were 10-15 mm in shell length. These densities roughly corresponded to field densities in Coastal Oregon streams (100-500 snails m^{-2}, Lamberti et al. 1990). Snail densities were maintained throughout the experiment by replacing dead individuals (less than

5% of the total).

Algal Sampling and Analytical Methods

Algal biomass accumulation and taxonomic composition were monitored for surfaces on top of blocks and in recessed areas between blocks in all streams. Periphyton from each of the 9 streams was sampled on days 9, 20, 33 and 54 of the experiment by scraping tiles with a razor blade. On each date in each stream, tiles comprising the top of one block (506 cm^2) and tiles contained in an adjacent recessed area (506 cm^2) were sampled separately (Fig. IV.1). Each sample was divided volumetrically to obtain subsamples for estimating algal biomass and taxonomic composition. Tiles removed from the streams for sampling were replaced with tiles having visually similar algal biomass and composition in order to maintain food density and type for grazers. The source of replacement tiles was two laboratory streams that were not part of the experimental design.

Biomass, expressed as ash-free dry weight, was determined by the method described by Lamberti et al. (1987). Subsamples for taxonomic analysis were preserved in Lugol's solution. For taxonomic analysis, algal subsamples were settled in 50 ml chambers, and 500 algal units containing chloroplasts were counted at 400X magnification with a Nikon MS inverted microscope (Utermohl 1958). For this count, diatoms were lumped into one category, and all other taxa were identified to species. An algal unit was an individual for unicellular organisms, and a colony or filament for multicellular taxa. After counting, the settled subsample was

boiled in concentrated HNO_3, rinsed with distilled water, and 500 cleared diatom valves were identified at 1250X magnification. The proportions of diatom taxa in this count were used to estimate abundances of these taxa in the count of 500 algal units (Steinman and McIntire 1986). Mean biovolumes of cells in an algal unit were estimated using standard geometric formulae. Biovolumes for each taxon in a sample were calculated by multiplying the estimated biovolume per algal unit by the number of algal units in the count of 500.

Differences in algal biomass between top and recessed substrates in the streams were examined by a strip-plot analysis of variance design with the whole plot factor as PFD level and the strip factor as time (Gill and Hafs 1971). The sample-species data matrix for taxonomic analyses contained the relative biovolume of each species based on counts of 500 algal units. Successional changes in the assemblages were examined by detrended correspondence analysis (DCA) (Hill and Gauch 1980). Successional trajectories were obtained by plotting a temporal sequence of the mean sample scores for each treatment relative to DCA axes 1 and 2.

Herbivore Sampling and Analytical Methods

Growth rates of snails were determined by marking 35 individuals from each stream (4.7% of the total) with numbered bee tags. Blotted wet mass and dry mass were determined on day 54. Initial wet mass values were converted to dry mass using regression equations from the final measurements (Lamberti et al. 1987). Effects of PFD level on growth rates were examined by a one-way analysis of variance.

After the introduction of snails on day 13, the number of individuals on top substrates and on recessed substrates were counted between 1200 and 0300 hours on 31 of the remaining 41 days in the experiment. Relative differences (percent) between the number of snails on recessed substrates and on top substrates were examined by a strip-plot analysis of variance design, with the whole plot factor as PFD level and the strip factor as time (Gill and Hafs 1971).

RESULTS

Algal Biomass

At the end of the experiment, algal AFDW in streams exposed to 375 uE m^{-2} s^{-1} were approximately 8 and 80 times greater than in streams exposed to 90 and 20 uE m^{-2} s^{-1}, respectively (Fig. IV.2). After snails were introduced, biomass accumulation was greater on top substrates than on recessed substrates in streams with high and intermediate irradiances. After day 33, biomass continued to increase on recessed substrates but decreased on top substrates in these streams. In streams exposed to low irradiance, biomass initially declined following the introduction of snails. Biomass was greater on top substrates than on recessed substrates on days 33 and 54 with low irradiance (Fig. IV.2). Analysis of variance indicated that the difference in biomass between top and recessed substrates (Table IV.1) was significantly affected by irradiance level ($p < 0.01$), time ($p < 0.05$) and their interaction ($p < 0.01$). The same results were obtained for only grazed assemblages (i.e., day 9 samples excluded).

Taxonomic Composition

The filamentous cyanophyte Oscillatoria agardhii Gomont was the dominant taxon in all assemblages on day 9, the sample date prior to snail introduction (Fig. IV.3a-f). However, day 9 assemblages exposed to intermediate and high irradiances had a greater percentage biovolume of the diatom Fragilaria vaucheriae (Kutz.) than assemblages with low irradiance. Following the introduction of snails, O. agardhii gradually declined in streams with low and

Figure IV.2 Biomass accumulation on top (T) and recessed (R) substrate surfaces at 375, 90 and 20 uE m^{-2} s^{-1}. Values are means (n=3). Arrows indicate the time of snail introduction.
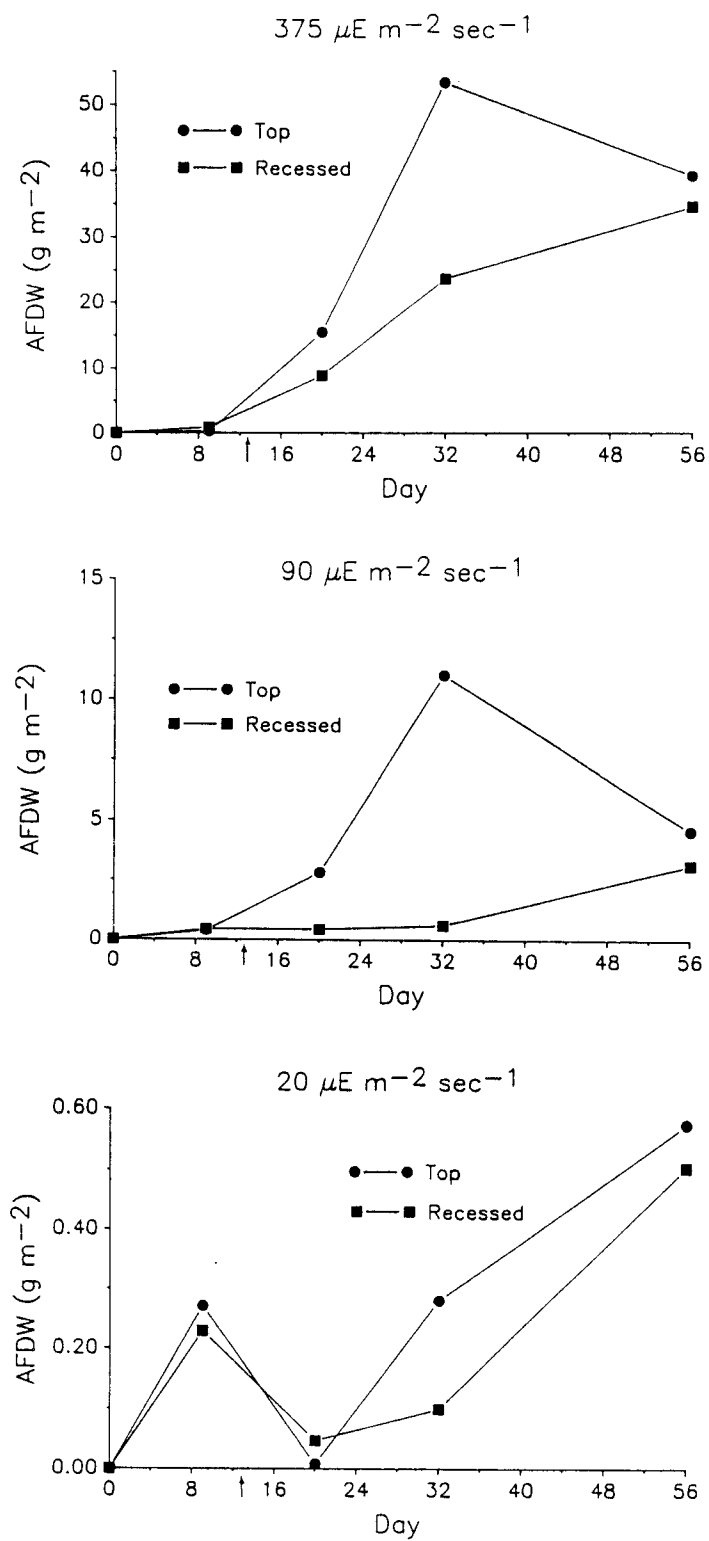
Figure IV.2

Table IV.1. The difference in ash-free biomass (g m^{-2}) between top and recessed substrates (top-recessed). Values are means, n=3. Fisher's protected least significant differences (FPLSD) are given to compare means.

| | | Day | | |
PFD	9	20	33	54
20	0.042	-0.039	0.180	0.071
90	-0.050	2.360	10.416	1.445
375	-0.614	6.544	29.649	4.731

To compare means in column, FPLSD$_{.05}$ = 4.49;

and in a row FPLSD$_{.05}$ = 9.64.

Figure IV.3 The relative abundance of <u>Oscillatoria</u> <u>agardhii</u> (OSCAGR), <u>Fragilaria</u> <u>vaucheriae</u> (FRAVAU), <u>Nitzschia</u> <u>linearis</u> (NITLIN), <u>Achnanthes</u> <u>lanceolata</u> (ACHLAN), <u>Nitzschia</u> <u>oregona</u> (NITORE), <u>Stigeoclonium</u> <u>tenue</u> basal cells (STGBAS), <u>S</u>. <u>tenue</u> filaments (STGFIL), and <u>Chroococcus</u> sp. (CHROOC). a) Top substrates at 20 uE m^{-2} s^{-1}. b) Recessed substrates at 20 uE m^{-2} s^{-1}. c) Top substrates at 90 uE m^{-2} s^{-1}. d) Recessed substrates at 90 uE m^{-2} s^{-1}. e) Top substrates at 375 uE m^{-2} s^{-1}. f) Recessed substrates at 375 uE m^{-2} s^{-1}. All values are means (n=3).

Figure IV.3

90 uE/m2/sec

c)

Top substrates

90 uE/m2/sec

d)

Recessed substrates

Figure IV.3 contd.

375 uE/m2/sec
Top substrates

375 uE/m2/sec
Recessed substrates
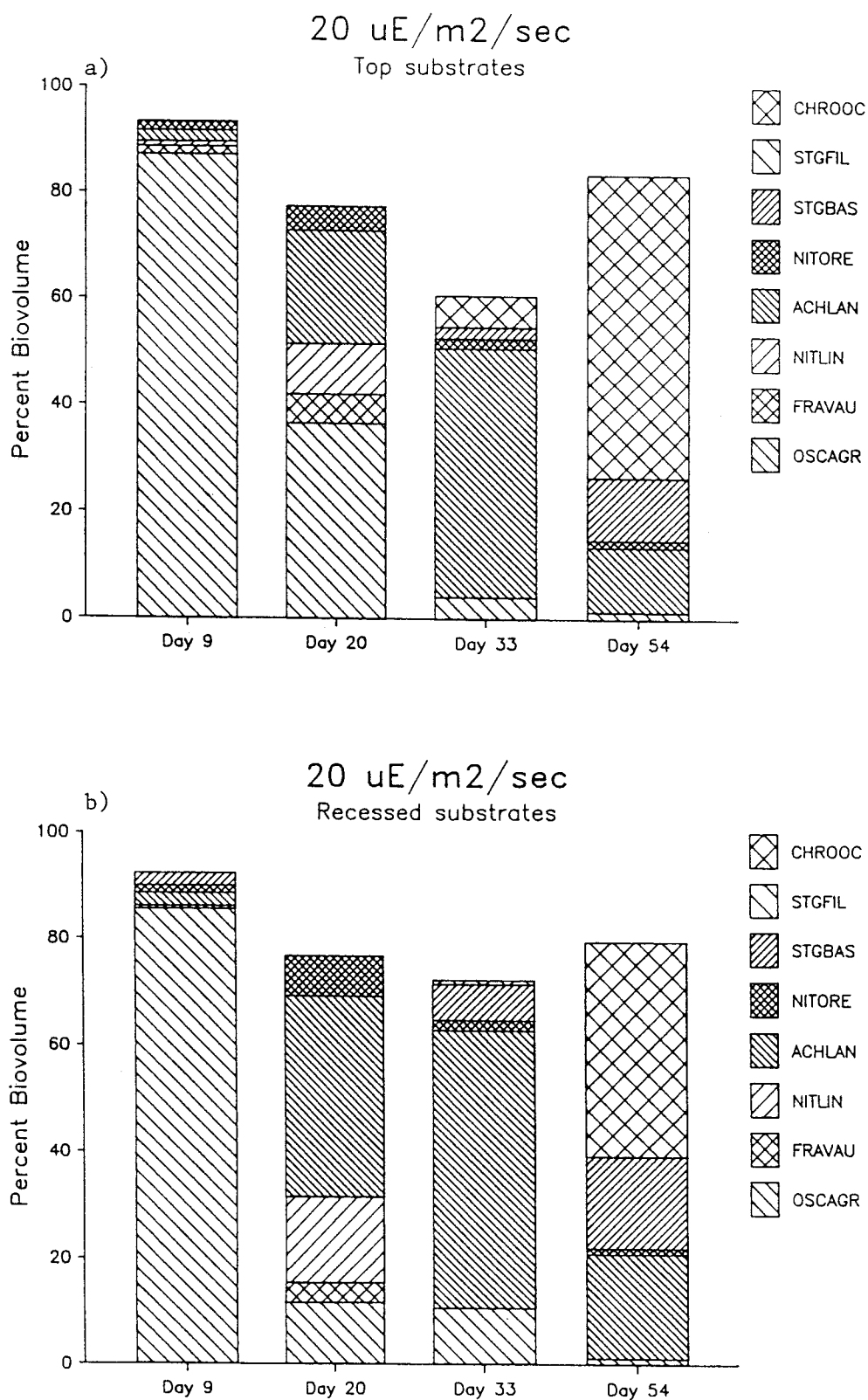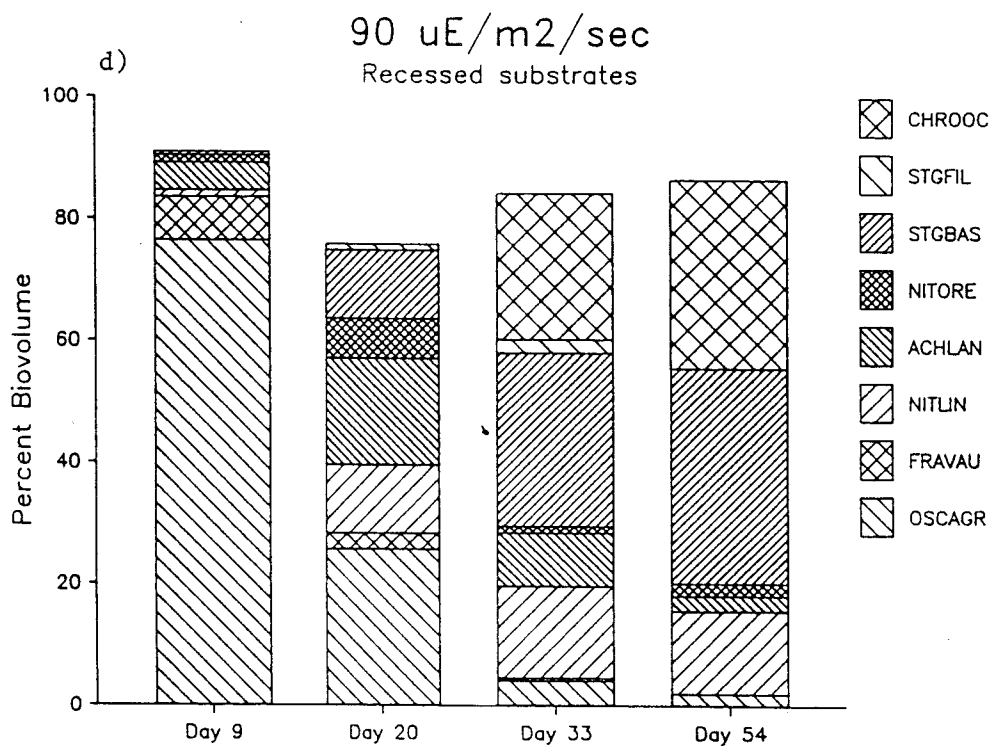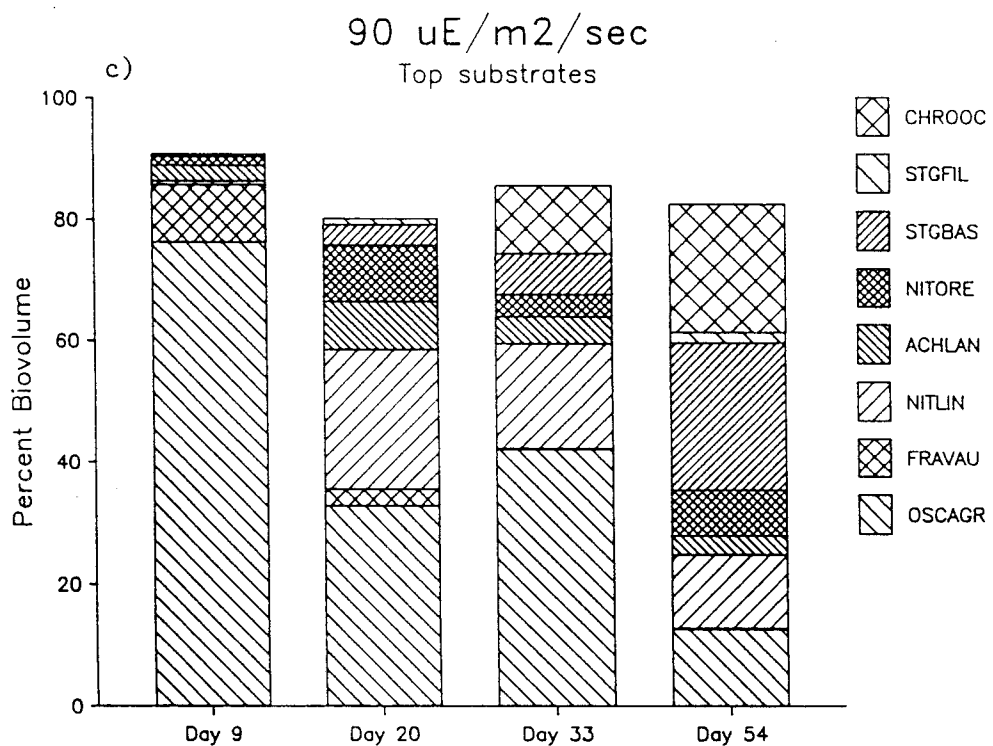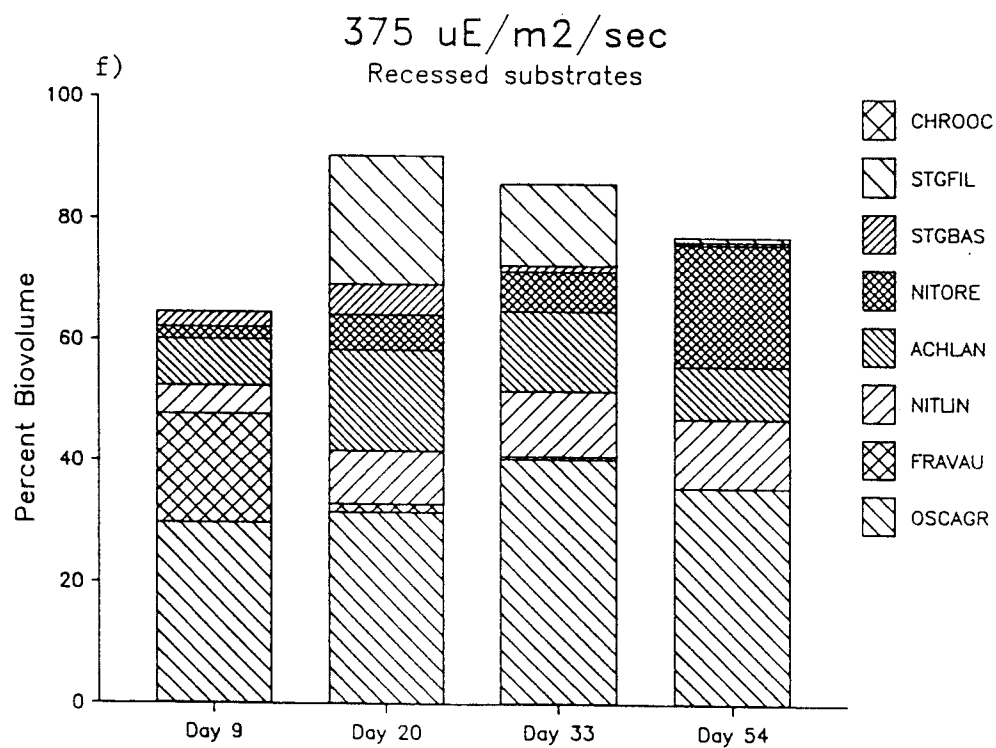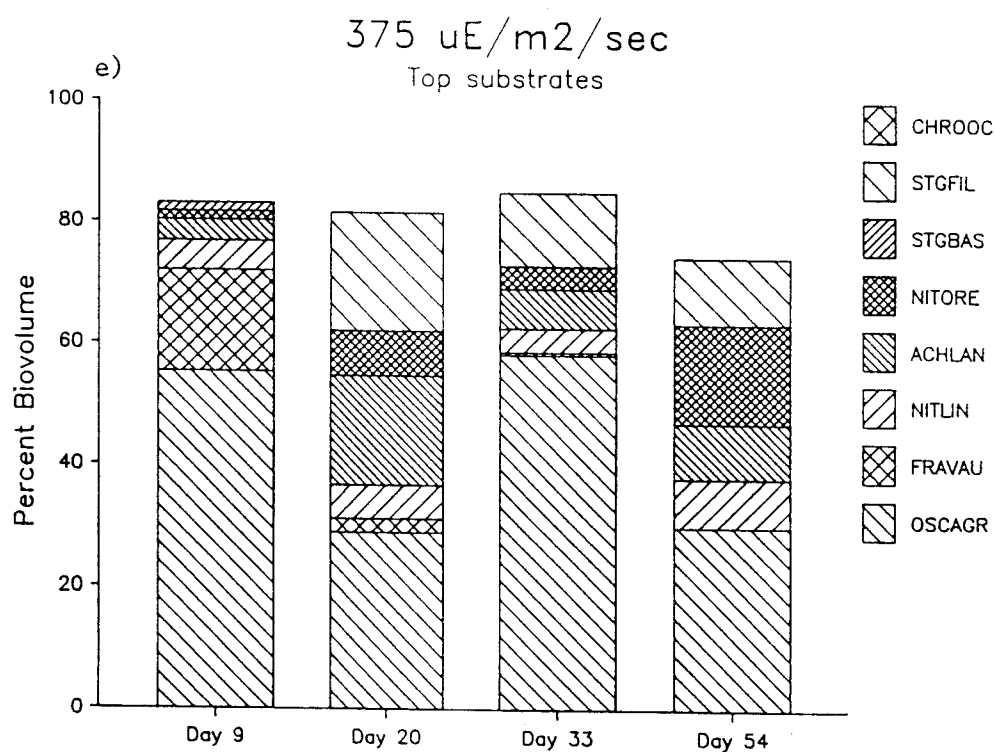
Figure IV.3 contd.

intermediate irradiances. The adnate diatom Achnanthes lanceolata (Breb.) Grun. was abundant in assemblages exposed to low irradiance on days 20 and 33. At the end of the experiment assemblages exposed to low irradiance were predominately the coccoid cyanophyte Chroococcus sp., A. lanceolata and basal cells of the heterotrichous chlorophyte Stigeoclonium tenue (Ag.) Kutz. (Fig. IV.3 a and b). Grazed assemblages with intermediate irradiance had a greater biovolume of S. tenue basal cells and the diatom Nitzschia linearis W. Smith than assemblages in streams with low irradiance (Fig. IV.3 c and d). The relative abundances of O. agardhii, filaments of S. tenue, and the diatom Nitzschia oregona Sov. were greater in streams with high irradiance than in streams exposed to the two lower irradiances following snail introduction (Fig. IV.3 e and f).

The taxonomic composition of assemblages on top and recessed substrates were relatively similar throughout the experiment in streams with low irradiance and with high irradiance. However with high irradiance, there was a greater abundance of S. tenue filaments on top substrates than on recessed substrates on day 54. In streams with intermediate irradiance, O. agardhii, N. oregona and N. linearis comprised a greater abundance of the biovolume on top substrates than on recessed substrates. Conversely, S. tenue basal cells, A. lanceolata and Chroococcus were more abundant on recessed substrates in these streams (Figs. IV.3a-f).

The mean successional trajectories for the algal assemblages on top and recessed substrates for each of the three irradiances are illustrated in Figure IV.4a. Detrended correspondence analysis maximizes the correspondence between sample and species ordinations;

therefore, taxa that describe a successional pattern can be found by comparing the configuration of the sample ordination scores with corresponding positions in the species ordination (Fig. IV.4b). The successional trajectories on both types of substrates for low and intermediate irradiances proceeded from assemblages characterized by O. agardhii, F. vaucheriae and Synedra ulna (Nitz.) Ehr. towards assemblages containing more S. tenue basal cells and Chroococcus sp. (Fig. IV.4a cf. IV.4b). However, the relative biovolumes of the filamentous cyanophyte Phormidium tenue (Menegh.) Gomont, and the diatoms A. lanceolata, Cocconeis placentula var. euglypta (Ehr.) Cl. and Rhoicosphenia curvata (Kutz.) Grun ex Rabh. were greater in assemblages with low irradiance than with intermediate irradiance. Assemblages at intermediate irradiance were more abundant in S. tenue basal cells, and the diatoms N. oregona, N. linearis and Navicula minima Grun. In streams exposed to low and intermediate irradiances, assemblages on recessed substrates generally changed more rapidly between days 9 and 33 than assemblages on top substrates (Fig. IV.4a).

Successional trajectories in streams with high irradiance were quite different from those with the two lower irradiances, primarily because O. agardhii persisted in the assemblages exposed to high light (Fig. IV.4a and b). After snails were introduced into these streams, trajectories proceeded toward assemblages characterized by S. tenue filaments and the diatom Gomphonema parvulum Kutz. However after day 33, the trajectories approached assemblages containing a greater abundance of N. oregona.

Figure IV.4 a) Successional trajectories of the periphyton
assemblages on top (T) and recessed (R) substrates at 375, 90 and
20 uE m^{-2} s^{-1}. Points along the trajectories are mean (n=3) sample
scores for days 9, 20, 33 and 54. b) Ordination of species (mean
scores, n=3) that had a relative biovolume greater than 5 percent.
See text for explanation of ordination method.

a)

b)
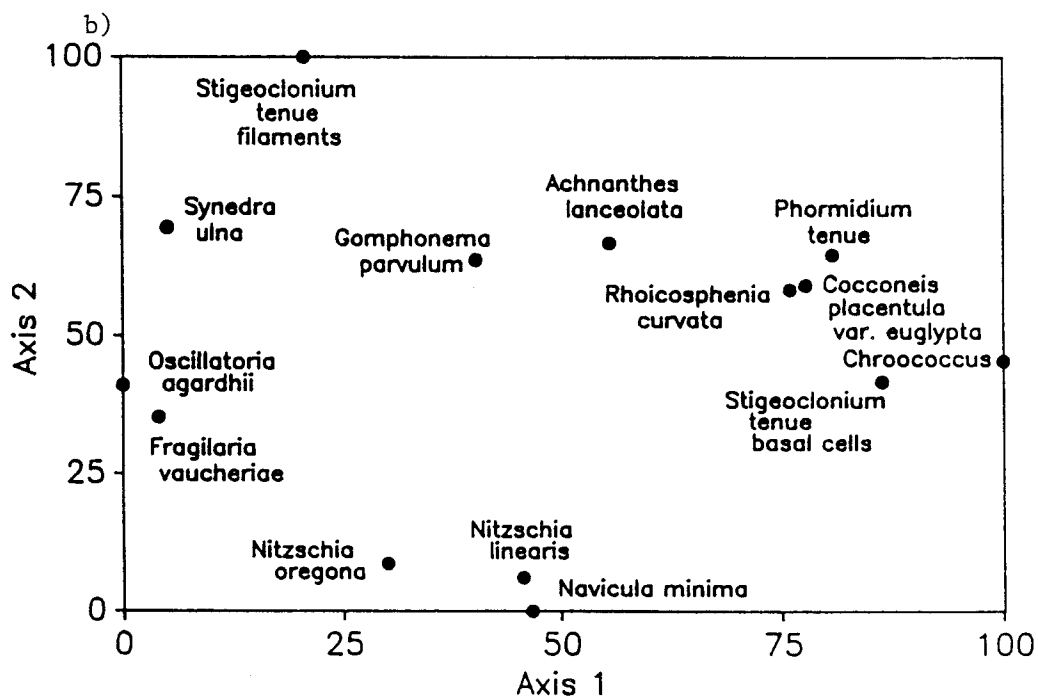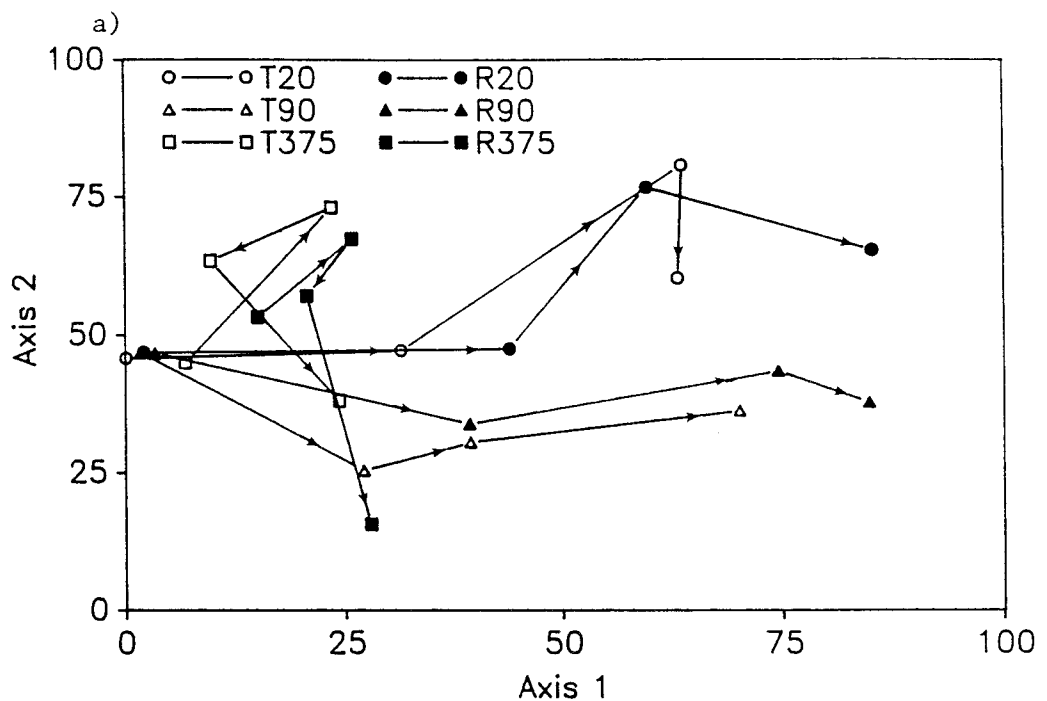
Figure IV.4

<u>Physiognomy</u>

Algal assemblages on both top and recessed substrates exposed to low irradiance were barely visible to the eye throughout the experiment. With intermediate irradiance, assemblages on recessed substrates formed a thin mat; top substrates developed a thicker skin-like mat between days 20 and 33. However, at the end of the experiment, the physiognomy of both assemblages was a thin mat. Assemblages on top substrates in streams exposed to high irradiance developed a thick understory mat composed of <u>Oscillatoria</u> trichomes and diatoms, with tufts of <u>Stigeoclonium</u> filaments forming an overstory. Pieces of the mat began to slough off top substrates after day 33. Recessed substrates in these streams had a thin layer of algae. However, after day 20, patches of mat with <u>Stigeoclonium</u> filaments covered approximately one-third of the area on recessed substrates.

<u>Snail Growth Rates and Behavior</u>

The mean growth rate of snails was significantly affected by irradiance level ($p < 0.01$). Growth rates of snails in streams with high and intermediate irradiances were similar and approximately 15 times greater than those with low irradiance (Fig. IV.5).

The distribution of snails in the streams was quantified as the percentage of <u>Juga</u> individuals on recessed substrates minus the percentage on top substrates (distribution index, Fig. IV.6). The distributions of snails on the two substrates in the streams were significantly affected by light ($p < 0.01$), time ($p < 0.05$) and their interaction ($p < 0.01$). In all streams there were always more snails on recessed substrates than on top substrates (Fig. IV.6).

Figure IV.5 Growth rates of _Juga_ between days 13 and 54. The
rates are relative to tissue dry mass. Values are means +1 SE,
with comparison of means using Fisher's protected least significant
difference (FPLSD).
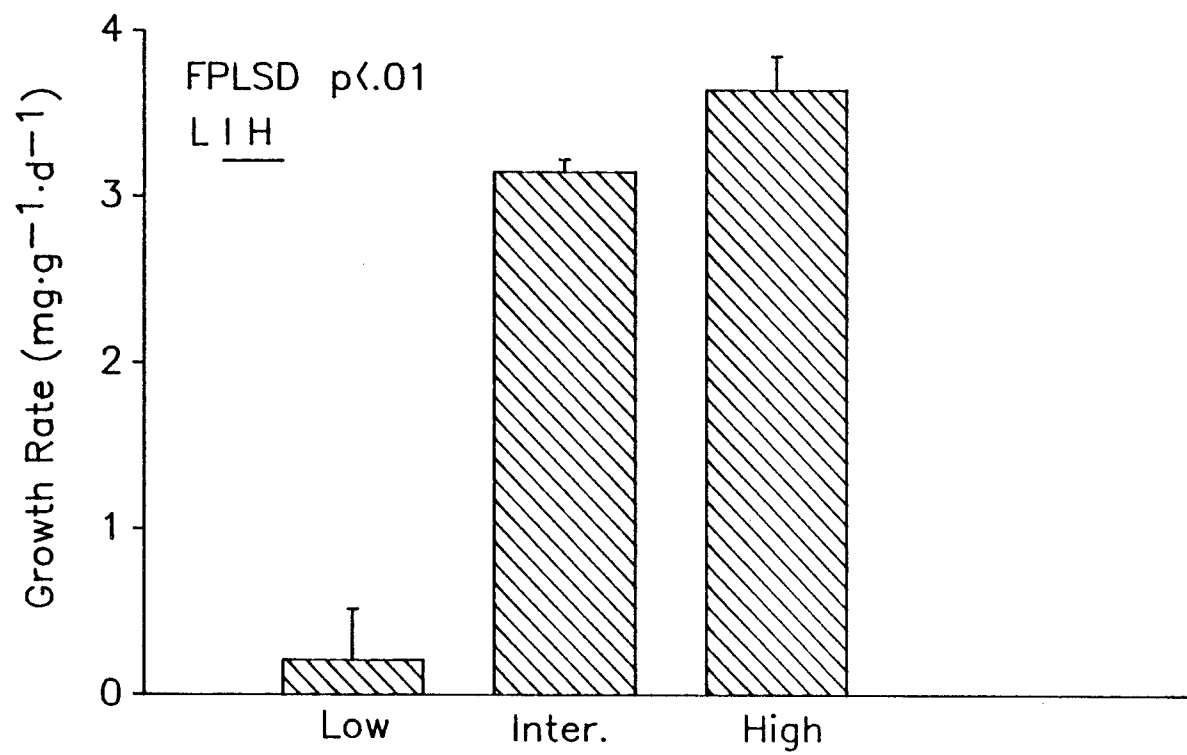
Figure IV.5

Figure IV.6 The difference between the percentage of _Juga_ individuals on recessed substrates and top substrates (recessed - top = distribution index).
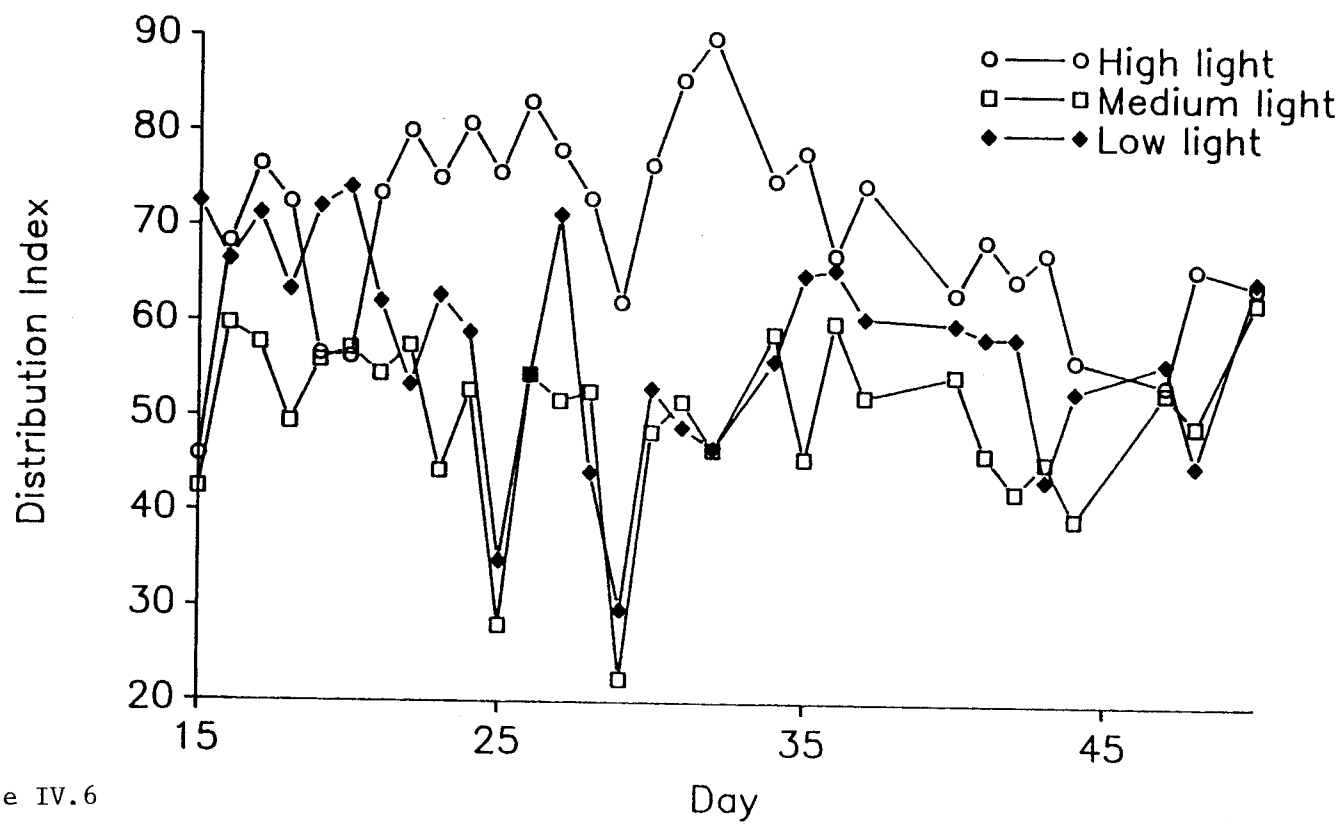
Figure IV.6

In general, the number of snails on recessed substrates, relative to top substrates, was greatest in streams exposed to 375 uE m^{-2} s^{-1} and least in streams with 90 uE m^{-2} s^{-1} (Fig. IV.6).

DISCUSSION

Algal Biomass and Snail Foraging

Algal biomass accumulation in this experiment was a function of algal colonization, algal productivity, snail consumption and algal export. Algal biomass was positively related to irradiance, reflecting the greater productive capacity of algal assemblages at high irradiance. In this experiment, the rates of algal biomass accumulation within a PFD level depended on the position of the substrates. In previous studies employing the same substrate relief without grazers, DeNicola and McIntire (1990a, 1990b) found that lower shear velocities in recessed areas promoted algal deposition and colonization, causing biomass initially to accumulate faster on recessed substrates than on top substrates. However, once the algal assemblages became established, growth of assemblages on top of substrates was slightly greater, possibly because the higher flow velocities enhanced physiological processes within the algal mat. Moreover, the differences in biomass accumulation between top and recessed substrates increased with irradiance level. Before streams were stocked with grazers in this study, initial biomass accumulation was slightly greater on recessed substrates than on top substrates at high and intermediate irradiance. However, when grazers were introduced, the results were unlike responses in the absence of grazing (DeNicola and McIntire 1990a, 1990b), as algal biomass accumulated relatively faster and to a much greater extent on top substrates than on recessed substrates. This pattern occurred because recessed substrates always had a greater number of

snails than top substrates.

Field densities of _Juga_ are high in habitats with current velocities between 5 and 20 cm s^{-1}, with snails avoiding areas of faster velocities (Hawkins and Furnish 1987, Li 1989). In this experiment, mean current velocities were approximately 10 cm s^{-1} in recessed areas and 27 cm s^{-1} on top of blocks (DeNicola and McIntire 1990a). An increase in water movement has been shown to increase the rate of respiration and decrease activity in aquatic snails (Hutchinson 1947, Berg et al. 1958). The relatively high densities of snails on recessed substrates at all irradiances were probably related to the greater metabolic cost associated with attaching and moving in the faster currents on top substrates. In addition, areas between blocks acted as depositional zones for detached snails.

Growth rates of _Juga_ were similar at 375 and 90 uE m^{-2} s^{-1} and much greater than those at 20 uE m^{-2} s^{-1}. The growth rates of _Juga_ were similar to those reported by Lamberti et al. (1989) for streams exposed to 400, 100 and 20 uE m^{-2} s^{-1}. Freshwater snails with low food resources show greater locomotion and more random patterns of movement than satiated snails (Calow 1974, Li 1989). A similar result was seen in this experiment, as snails in streams exposed to high irradiance appeared to forage primarily on recessed substrates, whereas with the two lower irradiances, snails foraged more equally on top and recessed subsrates. However, there were relatively more snails on top substrates in streams with intermediate irradiance than with low irradiance. The very low food density in streams exposed to low irradiance may have limited the degree to which snails could expend the extra energy needed to forage on top

substrates.

The decline in algal biomass on top substrates after day 33 in streams exposed to high and intermediate irradiances appeared to be related to the feeding activity of the snails. The high algal biomass of these assemblages made them susceptible to being dislodged by snails and exported out of the streams. Export of detached algal patches was more likely to occur in the faster current regimes on top of blocks than in the backwater recessed areas. Moreover, the biomass decline on top substrates after day 33 may have been enhanced by a slight increase in the number of snails on top substrates between days 33 and 45. Snail movement to top substrates during this period may have been a response to the increased food density on top substrates relative to recesssd substrates.

Algal Composition and Successional Trajectories

Algal physiognomy and composition in the streams were related to both irradiance and herbivore distributions. The autecologies of many of the dominant taxa found in this study are beginning to become established. The distribution of these taxa corresponded to the following patterns. Linear araphid-diatoms that have high sinking rates, like *Fragilaria vaucheriae* and *Synedra ulna* in this experiment, are often rapid colonizers of bare substrates in streams and occur early in succession (Riesen and Spencer 1970, Stevenson 1984, Omeke and Burton 1986, Steinman and McIntire 1986, 1987, 1989, Stevenson and Peterson 1989, DeNicola and McIntire 1990a, 1990b). In previous studies, we have found *Oscillatoria agardhii* to occur

early in succession and to be more abundant at low irradiance (DeNicola and McIntire 1990a, 1990b). In this experiment, this taxon also was abundant in later stages of succession at high irradiance (see below). Taxa that colonize bare substrates usually adhere weakly to the substrate and are rapidly removed by grazing (Hudon and Legendre 1987).

Adnate monoraphid-diatoms, such as <u>Achnanthes lanceolata</u> and <u>Cocconeis placentula</u> var. <u>euglypta</u> in this study, are usually high in relative abundance at low irradiance and in grazed assemblages (Hudon and Bourget 1983, Sumner and McIntire 1983, Steinman and McIntire 1987, 1989, DeNicola and McIntire 1990b). Many studies have shown that high grazing pressure from snails in streams results in epilithic algal assemblages that have low relief and a greater abundance of small adnate diatoms (e.g., Hunter 1980, Steinman et al. 1987, Lowe and Hunter 1988, McCormick and Stevenson 1989, Steinman and McIntire 1989). Additionally, tightly adhering basal cells of filamentous chlorophytes may increase at high grazing pressure (Lowe and Hunter 1988, McCormick and Stevenson 1989, Steinman and McIntire 1989, this study). Nonmotile, erect diatom forms (e.g., <u>Rhoicosphenia curvata</u>) may be abundant in assemblages in low irradiance (Lowe et al. 1986), but potentially are more susceptible to grazing than prostrate forms.

With higher irradiances, thicker algal mats are more likely to develop and usually contain a greater abundance of the more mobile biraphid and keel-raphid diatoms, such as <u>Nitzschia oregona</u>, <u>Nitzschia linearis</u> and <u>Navicula minima</u> (Lowe et al. 1986, Steinman and McIntire 1986, 1989, Hudon and Legendre 1987, Hill and Knight

1987, DeNicola and McIntire 1990b). Filamentous chlorophytes, such as _Stigeoclonium tenue_, usually occur late in succession in assemblages with high irradiance and low grazing pressure (Shortreed and Stockner 1983, Lowe et al. 1986, Steinman and McIntire 1986, 1987, DeNicola et al. 1990, DeNicola and McIntire 1990b). However, basal cells of _S. tenue_ became abundant in lower irradiance under heavy grazing pressure in this study, and in the study by Steinman and McIntire (1989). Some species of _Chroococcus_ have been reported to occur mixed with other cyanobacteria in epilithic films (West and Fritsch 1927). In this study, this taxon was closely associated with _Phormidium tenue_ and _S. tenue_ basal cells in streams exposed to low and intermediate irradiance.

High grazing pressure can accelerate species replacements by driving succession towards more grazer resistant assemblages (Connell and Slayter 1977, Lubchenco and Gaines 1981). For example, intense herbivory in lotic periphyton assemblages can cause the rapid replacement of early successional taxa that adhere weakly to the substrate with more tightly adhering adnate taxa (Steinman et al. 1987, Lowe and Hunter 1988, Steinman and McIntire 1989, McCormick and Stevenson 1989, DeNicola et al. 1990, this study). However, in terms of periphyton physiognomy, Lamberti et al. (1989), and Steinman and McIntire (1989) considered grazing in streams to delay succession because it maintained a thin mat of diatoms and supressed the development of late successional, filamentous chlorophytes. Many of these effects of herbivory on the rate algal succession in streams are related to the ability of herbivores to

control the rate of biomass accumulation and the autecologies of the algal taxa.

In previous studies, ungrazed assemblages exposed to high irradiance had relatively faster successional changes than assemblages with low irradiance (DeNicola and McIntire 1990b, Steinman and McIntire 1987). The presence of grazers in this study reversed this trend as assemblages exposed to low and intermediate irradiances had more rapid changes in composition than assemblages with high irradiance. Moreover, the higher density of snails on recessed substrates resulted in a more rapid species replacement than in top assemblages with low and intermediate irradiances but not with high irradiance. These results suggested that herbivores had a larger effect on algal assemblages exposed to low irradiance than on the more productive assemblages exposed to high irradiance. At high irradiance, successional trajectories initially reversed after grazers were introduced because areas cleared by grazers permitted early successional taxa (e.g. Oscillatoria) to recolonize the substrate. As succession proceeded, grazers were less capable of keeping pace with algal development, and parts of the assemblages may have temporarily escaped herbivory. Such escapes may be temporary because mature periphyton assemblages probably do not have a size escape from Juga (DeNicola et al. 1990). Therefore, for the same density of grazers, herbivory in streams exposed to high irradiance can appear to delay succession because herbivores create a mosaic of successional stages within the sample area, whereas with low irradiance herbivory tends to drive successional trajectories towards adnate taxa.

Relevance to Natural Streams

In coastal Oregon streams, _Juga_ is a competitive dominant herbivore and vertebrate predation on the snails, primarily by the Pacific Giant Salamander (_Diamptodon ensatus_), maybe low (Hawkins and Furnish 1987). Therefore, the distribution of _Juga_ in natural streams corresponds mainly to irradiance (algal abundance), current speed and substrate size (Hawkins and Furnish 1987). The results of this experiment should provide some insight into grazer-periphyton dynamics in natural streams because the main factors affecting _Juga_ foraging (irradiance and current regime) were controlled in the experiment for a chosen substrate size.

The results of this study suggested that the interaction between algal development and snail grazing on cobble-size substrates depends more on irradiance than on the current regime. At high irradiance, when productivity of algae is greater than the food demand of _Juga_, snails may avoid grazing assemblages in fast currents. However, these assemblages are susceptible to sloughing when biomass becomes high. Algal assemblages in slower current regimes should be preferentially grazed, but the high rates of algal production also may allow portions of the assemblage to eventually overcome the effects of herbivory. Therefore, with high irradiance, assemblages within a current regime around a cobble substrate can become a mix of different successional stages and physiognomies. With low irradiance, the low productivity of the algae may allow the same density of herbivores to suppress assemblages in all current regimes to adnate cells relatively early in succession. At

intermediate irradiances, succession in assemblages in all current regimes may move towards adnate cells, but this should occur more rapidly in slow current regimes. This experiment was not run long enough to determine if the distribution of algal biomass and herbivores in the two current regimes may have approached an equilibrium within an irradiance level. In natural streams, herbivores can migrate to graze in areas of greater algal production. This would tend to equalize algal standing crops in areas of different irradiance. Furthermore, depression of other invertebrate herbivore populations by *Juga* may be less in areas of high algal productivity (Hawkins and Furnish 1987). How these patterns may vary with seasonal changes in algal productivity and herbivore abundance needs to be examined further.

The implications of this study may only apply to *Juga* because the effects of abiotic factors, competition and predation on foraging patterns should be different for other types of lotic herbivores (Peckarsky 1983). In addition, interactions between herbivores and periphyton assemblages in streams are affected by the type of mouthpart morphology and method of food acquisition of the herbivores (Lamberti et al. 1987, DeNicola et al. 1990).

ACKNOWLEDGEMENTS

V. TEMPORAL PATTERNS OF GRAZER-PERIPHYTON INTERACTIONS IN LABORATORY STREAMS

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ABSTRACT

The snail _Juga_ _silicula_ (500 m^{-2}) and the caddisfly _Dicosmoecus_ _gilvipes_ (50 m^{-2}) were introduced into separate laboratory streams on days 1, 9, 16 and 28 of algal development. The mayfly _Baetis_ spp. (500 m^{-2}) was introduced on days 1 and 16, and two streams did not receive grazers. We assessed the interaction between succession in the periphyton, herbivore type and time of encounter in a 40-day experiment.

In ungrazed streams, the chlorophyte _Scenedesmus_ _obliquus_ was the most abundant early colonizer. The relative abundance of diatoms increased after day 9, and at day 40 the algal assemblage consisted of a thick mat of diatoms and _S_. _obliquus_ with an overstory of filaments of the chlorophyte _Stigeoclonium_ _tenue_. In general, introductions of grazers at any stage altered this pattern by removing biomass, accelerating the replacement of _S_. _obliquus_ by diatoms, and suppressing the growth of filaments. Grazing also reduced the relative abundance of the larger diatom _Nitzschia_ _oregona_ but increased the relative abundance of the smaller adnate diatoms _Nitzschia_ _frustulum_ var. _perpusilla_ and _Navicula_ _minima_.

Dicosmoecus decreased algal biomass and altered successional trajectories to a greater degree than either _Juga_ or _Baetis_. _Dicosmoecus_ rapidly grazed the entire substrate, whereas _Juga_ and _Baetis_ only cleared patches in the assemblages. Little alteration in algal development was observed in the _Baetis_ streams after day 16, probably because the periphyton assemblages attained a size and

structure that prevented effective grazing by _Baetis_.

The patchy grazing patterns of _Juga_ and _Baetis_ resulted in more diverse algal assemblages than either the _Dicosmoecus_ grazed or ungrazed streams. In natural streams, the temporal and spatial pattern of grazing relative to the developmental stage of the periphyton may contribute to maintaining a mosaic of algal patches in different seral stages.

INTRODUCTION

Herbivores can alter plant succession by influencing species replacement (Connell and Slatyer 1977), a process that can occur at any stage in a successional sequence (Lubchenco and Gaines 1981). In lotic ecosystems, the effect of herbivores on periphyton succession has been studied primarily after grazers were introduced into early seral stages of algal development (Kehde and Wilhm 1972, Hunter 1980, Steinman et al. 1987), although a few investigators introduced lotic herbivores into the later stages of algal succession (Sumner and McIntire 1982, Jacoby 1985). However, the effects of timing of herbivore introduction on succession in lotic periphyton assemblages has not been examined experimentally.

Although macroinvertebrate herbivores in streams are generally much larger than the plants they consume, and usually graze unselectively on periphyton assemblages (Lamberti and Moore 1984), differences in their mouthpart morphology and feeding behavior can have different effects on algal biomass and taxonomic composition (Steinman et al. 1987, Lamberti et al. 1987). Lotic herbivores also may differ in their ability to harvest algal assemblages that are different in physiognomy (Gregory 1983b). In some microalgal-grazer systems the relatively high biomass and more complex physiognomy of algal assemblages during the later stages of succession may impart some resistance to herbivory (Brown 1961, Castenholtz 1961, McShaffrey and McCafferty 1988). An inference derived from these studies is that the effect of herbivory on periphyton succession in

streams may depend upon the type of herbivore and the seral stage it encounters.

In this study, three herbivores that differed in their mouthpart morphology and method of food acquisition, were introduced into laboratory streams containing assemblages of periphyton at different stages of algal development. The herbivores used in the experiment were the caddisfly _Dicosmoecus_ _gilvipes_ Hagen, which scrapes algae from substrates using its mandibles and tarsal claws, the snail _Juga_ _silicula_ Gould, which rasps the substrate with a radula, and _Baetis_ spp. mayfies, which gather algae with the setae on their mouthparts. The experiment was designed to examine the following hypotheses: (1) successional trajectories in lotic periphyton assemblages are determined in part by the type of herbivore and the seral stage of the periphyton during the encounter; and (2) the type of herbivore, and the spatial-temporal pattern of grazing relative to the developmental stage of the algal assemblage, can interact to maintain patches of algae in different stages of succession.

MATERIALS AND METHODS

Laboratory Streams

The experiment was conducted in 12 recirculating, fiberglass laboratory streams. Each stream was 3 m long, 0.5 m wide and 0.2 m deep (ca. 2 m^2 surface area including sides), with two parallel channels separated by a centerboard that was open at both ends. Each stream was supplied with well water at a rate of 1.5 l min^{-1}, which replaced water that drained from the stream through a standpipe that maintained water depth at 10 cm. The water was circulated in each channel by a rotating paddle wheel connected to a variable speed motor. Free velocity of the water was maintained at 10 cm sec^{-1}, and water temperature remained between 15° and 17^oC. Previous chemical analysis of the water supply (Steinman and McIntire 1986) indicated that nutrient concentrations were relatively high (e.g., PO_4-P: 0.19 mg l^{-1}; silica: 19.2 mg l^{-1}; NH_4-N: 0.01 mg l^{-1}; NO_3-N: 6.25 mg l^{-1}). Light energy was provided by sixteen 1000-watt Metalarc lamps (Sylvania Corp.) that generated a photon flux density of 425 uE m^{-2} s^{-1} at the water surface. This level is above that needed to reach the maximum rate of photosynthesis in lotic periphyton assemblages (McIntire and Phinney 1965). A photoperiod of 10L/14D was used.

Each stream was lined with 7.5 X 7.5 cm unglazed clay tiles which served as surfaces for algal attachment and grazing, and as sampling units for the periphyton. The flora which develops on such tiles is very similar to that on natural rock surfaces in biomass (Lamberti and Resh 1985) and taxonomic composition (Tuchman and

Stevenson 1980). Smaller tiles (1.2 X 1.2 cm) were located throughout each stream and served as sampling units for examination with scanning electron microscopy (SEM).

Experimental Design

The experiment began on 9 July 1986 and continued for 40 days. On the first day of the experiment, periphyton was scraped from rocks collected from three streams in Benton Co., Oregon. The algal suspension was homogenized for 30 seconds in a 3.8 l Waring blender, diluted, mixed, and a 1.0 l subsample was added to each stream.

Herbivores were collected from third and fourth order streams in the Coast Range and Cascade Mountains of Oregon. The snail _Juga silicula_ was introduced at a density of 500 individuals m^{-2} into four of the twelve laboratory streams. The date of introduction, either day 1, 9, 16 or 28 of the experiment, was different in each of the four streams. Similarly, the caddisfly _Dicosmoecus gilvipes_ was introduced (50 individuals m^{-2}) into four of the other streams on either day 1, 9, 16 or 28. Two other streams received a combination of the mayflies _Baetis bicaudatus_ Dodds and _Baetis tricaudatus_ Dodds (500 individuals m^{-2}); in one stream they were introduced on day 1, whereas the other stream was stocked on day 16. The two remaining streams received no grazers during the experiment. Replication offtreatments in the experiment was sacrificed in order to obtain a range of introduction times for the three herbivores.

Juga and _Dicosmoecus_ densities were maintained at the original densities in the stream channels throughout the experiment by replacing dead individuals (less than 5% of the total). Mortality

of the small _Baetis_ mayflies was difficult to quantify in the channels and thus their density varied within 10% of the target density. Densities of all three animals were similar to densities found in nearby streams (Lamberti et al. 1987).

Sampling

Samples for periphyton biomass in each stream were obtained by scraping three randomly selected 7.5 X 7.5 cm tiles with a razor blade on days 4, 9, 16, 28, 32, and 40. Biomass, expressed as ash-free dry weight, was determined as described by Lamberti et al. (1987).

Two other 7.5 X 7.5 cm tiles were selected at random from each stream on days 4, 9, 16, 28 and 40 for analysis of algal taxonomic composition. Algal scrapings from the two tiles were pooled and preserved in Lugol's solution. Procedures for microscopic examination and counting of samples for taxonomic analysis were outlined by Steinman and McIntire (1986).

Samples for SEM analysis of periphyton physiognomy were obtained by removing 2 of the 1.2 X 1.2 cm tiles from streams on days 9, 16, 28 and 40. The tiles were frozen immediately in liquid nitrogen and sublimated. They were coated with Au-Pd by vacuum evaporation, mounted on stubs, and examined with an Amray 1000A SEM at 20 Kv.

Data Analysis

The sample-species data matrix for taxonomic analyses contained the relative abundance of each species based on counts of 500 algal units. An algal unit was an individual cell for unicellular organisms, and a colony or filament for multicellular taxa. Algal

species heterogeneity was expressed by Shannon's information measure (Peet 1974). Ordination of samples and species by detrended correspondence analysis (DCA) were performed using the program DECORANA (Hill 1979).

DCA maximizes correspondence between sample and species ordinations such that corresponding areas in the two ordinations contain sample and species configurations that are maximally correlated (Gauch 1982). The trajectory of taxonomic change in the periphyton assemblage for each stream channel was illustrated by connecting its ordinated sample points sequentially by date (days 4, 9, 16, 28 and 40). The length and direction of a line between points indicates the degree of change in algal composition between sampling dates. The same pattern in the species ordination indicates taxa that were characteristic of the successional trajectory.

RESULTS

Biomass Accumulation

The average biomass accumulation of periphyton in the two unstocked streams closely resembled an exponential curve until day 28, after which time biomass declined slightly due to the sloughing of material from the algal mat (Fig. V.1).

Algal biomass remained very low throughout the experiment in the stream stocked with Dicosmoecus on day 1. In the other streams stocked with Dicosmoecus, the patterns of biomass accumulation were similar to those in the unstocked streams up to the time of animal introduction. However, algal biomass declined greatly soon after the introduction of Dicosmoecus on days 9, 16 and 28 (Fig. V.1).

Streams stocked with Juga also had lower algal biomass than the unstocked streams at the end of the experiment. Unlike the pattern associated with Dicosmoecus introductions, biomass continued to increase for a period after the introduction of Juga on days 9 and 16. However, the rate of increase was lower than in the unstocked streams (Fig. V.1). In general, streams grazed by Juga had higher biomass at the end of the experiment (10-20 g m^{-2}) than streams grazed by Dicosmoecus (1-10 g m^{-2}).

Baetis inhibited algal biomass accumulation only slightly. In the stream stocked with Baetis on day 1, algal biomass remained low until day 9 and then increased rapidly (Fig. V.1). Following the introduction of Baetis on day 16, the rate of biomass accumulation was only slightly less than the mean rate for the unstocked streams. After day 28, Baetis mortality in both streams was high, as mayflies

Figure V.1 Biomass accumulation in streams stocked with
<u>Dicosmoecus</u>, <u>Juga</u> and <u>Baetis</u>. The average biomass accumulation for
the unstocked streams is given in each plot. Standard errors for
mean values in the unstocked streams were: Day 4=0.1; Day 9=0.6;
Day 16=2.0; Day 28=0.73; Day 32=4.2; Day 40=10.4.
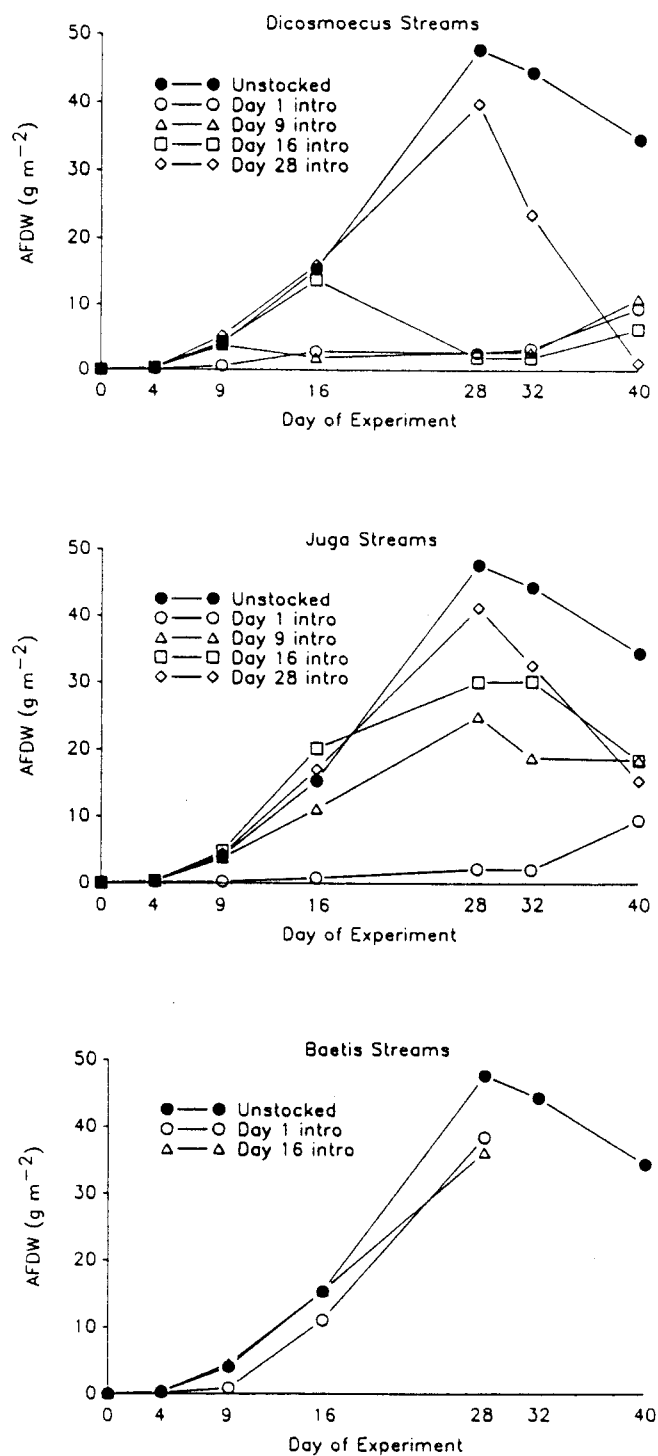
Figure V.1

were apparently unable to harvest the filamentous assemblages present at this stage of development. For this reason the mayfly part of the experiment was terminated on day 28.

Taxonomic Composition and Species Heterogeneity

On days 4 and 9 the periphyton assemblages in the unstocked streams were dominated primarily by the coenobic chlorophyte Scenedesmus obliquus (Turp.) Kutz. (ca. 40% of the algal units), with lesser amounts of the diatom Nitzschia oregona Sovereign and the small adnate diatom Navicula minima Grun. (Table V.1). Between days 9 and 40, the relative abundance of S. obliquus declined by half, whereas that of N. oregona and N. minima increased. The small adnate diatom Nitzschia frustulum var. perpusilla (Rabh.) Grun. never comprised more than 7% of the algal assemblages in the two unstocked streams. Other taxa in the ungrazed streams included the coenobic chlorophytes Characium sp. and Scenedesmus quadricauda (several varieties), the cyanophyte Oscillatoria agardhii Gomont, and the diatom Synedra ulna (Nitz.) Ehr., all of which were found primarily on days 4 and 9. Filaments of the chlorophyte Stigeoclonium tenue (Ag.) Kutz. were present after day 16.

Prior to animal introductions, the streams stocked with Dicosmoecus were similar in taxonomic composition to the unstocked streams in that S. obliquus and N. oregona were the two most abundant taxa (Table V.1). However, following each introduction of Dicosmoecus, the abundances of both taxa were greatly reduced, so that by the end of the experiment they each represented less than 10% of the algal assemblages. In contrast, the abundance of N.

Table V.1. The relative abundance (percent of algal units) of <u>Scenedesmus</u> <u>obliquus</u> (SO), <u>Nitzschia oregona</u> (NO), <u>Navicula minima</u> (NM), and <u>Nitzschia</u> <u>frustulum</u> var. <u>perpusilla</u> (NFP) on days 4, 9, 16, 28 and 40 of the experiment.

	DAY 4				DAY 9				DAY 16			
STREAM*	SO	NO	NM	NFP	SO	NO	NM	NFP	SO	NO	NM	NFP
UNST A	44.0	16.7	7.0	3.8	30.6	25.8	14.8	4.8	22.4	35.3	24.6	7.0
UNST B	39.1	18.8	8.8	1.6	49.3	19.6	8.8	6.2	24.4	29.4	38.6	5.8
MAY 1	22.9	11.3	17.9	4.4	27.1	22.0	20.0	7.4	5.4	9.8	46.8	9.8
MAY 16	28.5	16.9	17.5	3.0	33.7	26.3	7.0	7.4	12.4	26.8	44.8	4.6
JUGA 1	23.8	14.0	26.6	3.2	11.5	9.5	5.4	3.0	9.2	13.8	17.2	5.0
JUGA 9	33.5	20.8	14.2	1.6	56.4	12.9	8.8	2.4	25.2	38.0	17.2	9.0
JUGA16	31.2	15.7	9.8	2.6	36.1	23.4	8.0	4.4	30.3	33.7	24.5	3.6
JUGA28	37.7	19.2	8.4	1.8	34.3	25.7	13.3	6.8	39.8	22.7	20.9	2.4
DICO 1	40.0	15.1	12.2	1.2	43.6	18.1	9.2	5.6	4.0	16.2	40.0	17.2
DICO 9	45.4	13.5	8.4	1.8	35.1	18.0	13.2	7.2	8.8	19.5	40.0	15.7
DICO16	34.9	18.9	7.2	2.4	50.3	18.2	7.0	3.4	27.4	26.6	23.2	11.4
DICO28	28.3	21.8	11.4	2.8	48.7	18.6	9.8	3.4	23.2	34.3	28.9	7.8

	DAY 28				DAY 40			
STREAM*	SO	NO	NM	NFP	SO	NO	NM	NFP
UNST A	19.9	29.5	37.3	2.4	18.2	26.8	44.6	1.8
UNST B	23.4	35.4	29.9	1.0	20.4	25.3	41.6	3.2
MAY 1	22.8	12.4	53.3	1.0	-	-	-	-
MAY 16	23.0	26.0	38.0	1.0	-	-	-	-
JUGA 1	<0.1	1.6	9.0	2.6	<0.1	10.8	22.8	13.4
JUGA 9	27.0	24.8	24.8	4.4	21.2	20.0	37.3	8.0
JUGA16	27.3	27.3	32.7	4.6	13.6	24.6	41.7	7.2
JUGA28	33.9	23.2	34.3	3.0	43.0	21.8	25.6	4.0
DICO 1	1.6	5.2	35.8	42.4	<0.1	5.4	24.5	64.0
DICO 9	<0.1	1.2	17.6	70.2	<0.1	3.8	29.2	59.0
DICO16	7.4	2.6	27.1	39.9	0.0	4.6	15.0	74.7
DICO28	26.6	32.8	32.8	1.4	5.2	8.0	22.6	49.0

*UNST-unstocked, MAY-mayfly stocked, JUGA-<u>Juga</u>
  stocked, DICO-<u>Dicosmoecus</u> stocked. The number
  after the code for grazed streams denotes the
  day of animal introduction.

<u>frustulum</u> var. <u>perpusilla</u> increased after introductions and represented about 50% or more of the algal assemblages by day 40. In general, <u>N</u>. <u>minima</u> initially increased then decreased slightly in relative abundance following an introduction of <u>Dicosmoecus</u>.

After day 4 of the experiment, the algal composition in the stream stocked with <u>Juga</u> on day 1 was quite different from assemblages in all other streams. On day 9, 53% of the algal assemblage in this stream was zoospores of <u>Stigeoclonium</u> <u>tenue</u>. Basal cells of <u>S</u>. <u>tenue</u> together with the filamentous cyanophyte <u>Phormidium</u> <u>tenue</u> (Menegh.) Gom. comprised more than 30% of the assemblage in this stream for the remainder of the experiment.

In the three other streams stocked with <u>Juga</u>, <u>S</u>. <u>obliquus</u> and <u>N</u>. <u>oregona</u> remained abundant throughout the experiment (Table V.1). <u>S</u>. <u>obliquus</u> declined somewhat following introductions of snails on days 9 and 16, whereas <u>N</u>. <u>oregona</u> exhibited little temporal variation. <u>N</u>. <u>minima</u> generally increased in all three streams during the experiment. Although not a common taxon, <u>N</u>. <u>frustulum</u> var. <u>perpusilla</u> was slightly more abundant at the end of the experiment then in the unstocked streams.

The streams stocked with <u>Baetis</u> generally showed similar temporal changes in algal composition as the unstocked streams but <u>N</u>. <u>minima</u> was more abundant in the streams receiving <u>Baetis</u> (Table V.1). Compared to the unstocked streams, the stream stocked with <u>Baetis</u> on day 1 had a low relative abundance of <u>S</u>. <u>obliquus</u> on day 16 and of <u>N</u>. <u>oregona</u> on days 16 and 28. As in the unstocked streams, <u>N</u>. <u>frustulum</u> var. <u>perpusilla</u> always represented less than 10% of the periphyton assemblages.

All samples from streams stocked with the same grazer were pooled to calculate algal species heterogeneity as expressed by Shannon's index. Heterogeneity was highest in streams stocked with Juga and lowest in streams with Dicosmoecus (Fig. V.2). Unstocked streams and those with Baetis had similar intermediate levels of heterogeneity.

Successional Trajectories

The taxomonic composition of the periphyton in the stream stocked with Juga on day 1 was different from that in all other streams. As a result, sample and species ordinations using all the samples were strongly influenced by samples taken from that stream. Consequently, to identify successional patterns in the other streams, sample and species ordinations were determined with the five samples from this stream excluded from the analysis (Figs. V.3a-e).

Trajectories of taxonomic change in the two unstocked streams are shown in Figure V.3a. The downward trajectory between day 4 and day 9 in both unstocked streams was characterized by a change from a Scenedesmus obliquus and Characium sp. assemblage to one with more S. obliquus and less Characium sp. (Fig. V.3a cf. V.3e). The characteristic diatom on days 4 and 9 was Synedra ulna. After day 9, S. obliquus decreased slightly in relative abundance and the trajectories proceeded toward assemblages with more Navicula minima and Nitzschia oregona (i.e., to the upper right in Figs. V.3a and V.3e).

Streams to be stocked with Dicosmoecus displayed similar

Figure V.2 Species heterogeneity (diversity) of algal samples from unstocked, <u>Dicosmoecus</u>, <u>Juga</u> and <u>Baetis</u> stocked streams, pooled for all dates. H" =2.44 instead of 2.22 for the <u>Juga</u> streams if samples from the stream stocked with <u>Juga</u> on day 1 are excluded.
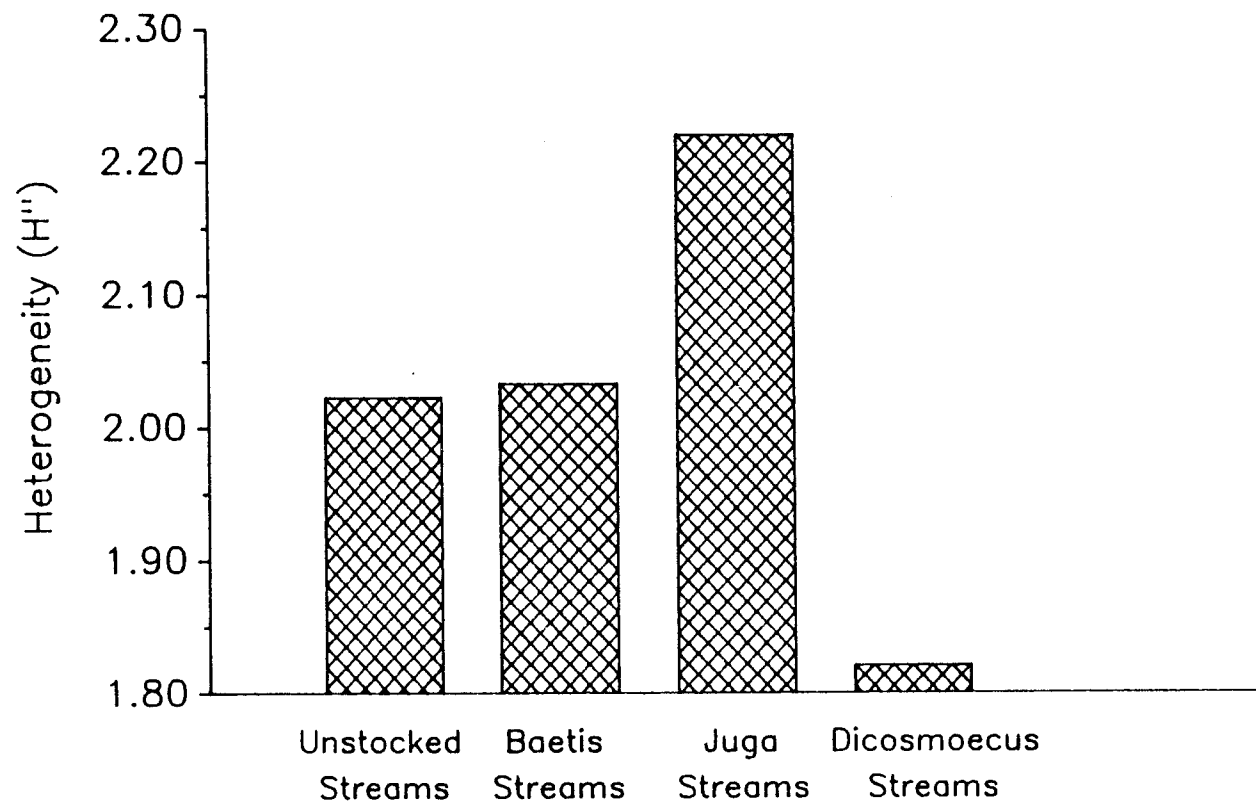
Figure V.2

Figure V.3 Successional trajectories of periphyton assemblages in the a) unstocked, b) <u>Dicosmoecus</u>, c) <u>Juga</u> and d) <u>Baetis</u> stocked streams. A solid symbol indicates a sample that was taken on a date after animals were introduced. e) Ordination of selected species. See text for explanation of ordination method.

Figure V.3

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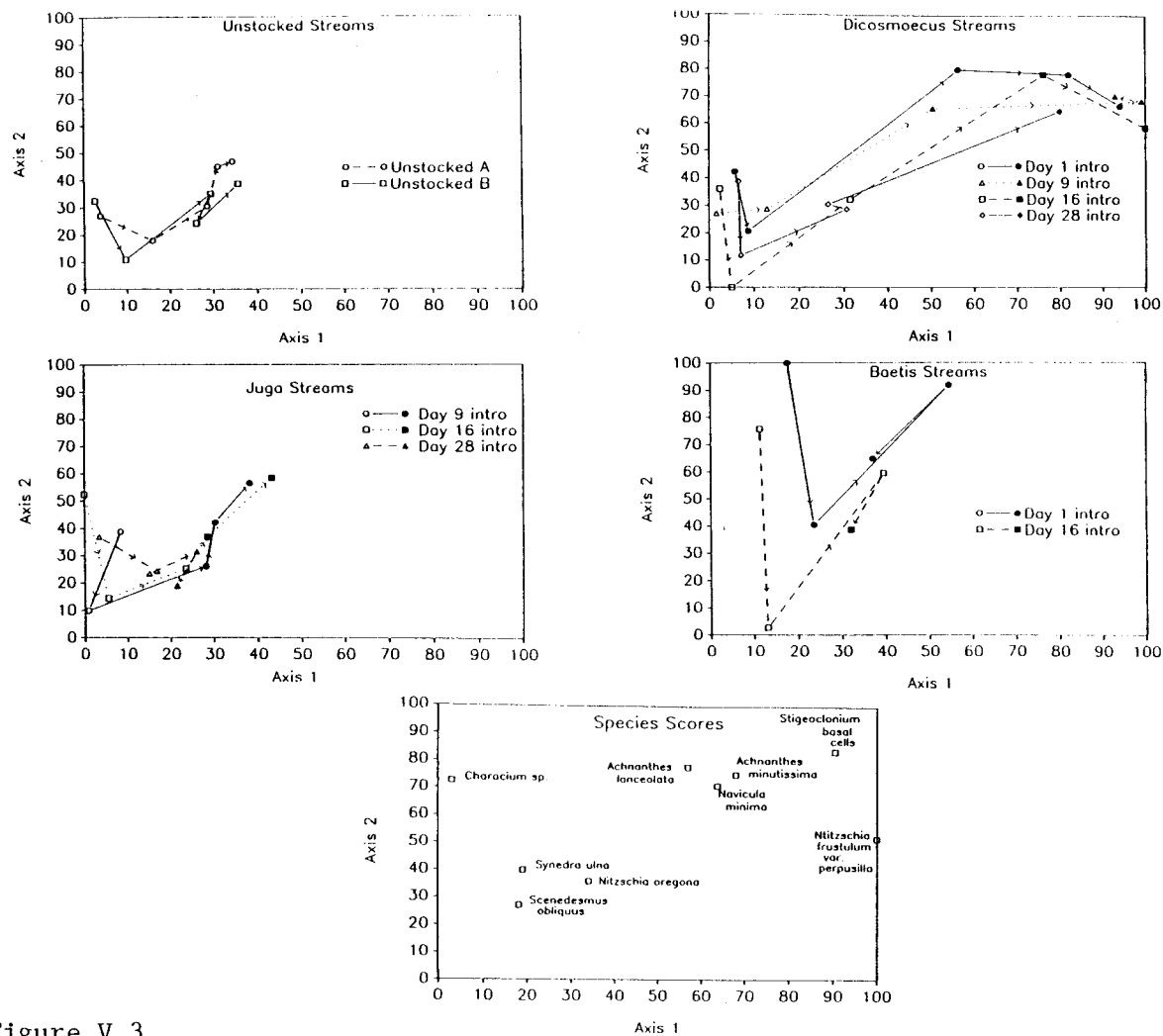
trajectories to the unstocked streams until caddisfly larvae were introduced (Fig. V.3b). Following the Dicosmoecus introductions on days 1 and 9, trajectories deviated from those of unstocked streams and moved toward diatom assemblages of N. minima, N. oregona and Achnanthes minutissima Kutz. All streams stocked with Dicosmoecus, regardless of the date of introduction, were finally characterized by Nitzschia frustulum var. perpusilla, N. minima, and Stigeoclonium tenue basal cells.

Assemblages in the streams stocked with Juga were similar to those in the unstocked streams on days 4 and 9 (Fig. V.3c). When Juga was introduced on days 9 and 16 the algal assemblage shifted away from one dominated by S. obliquus, towards one characterized by N. oregona and N. minima. In the stream stocked with Juga on day 28, the relative abundance of S. obliquus increased slightly after the introduction. Overall, the successional trajectories in the streams stocked with Juga were similar to those in the unstocked streams, but usually extended slightly further toward adnate diatom assemblages because of a small increase in the abundance of N. frustulum var. perpusilla. However, at the end of the experiment, the degree of dominance by small, adnate diatoms was less than in streams stocked with Dicosmoecus.

The two streams receiving Baetis had slightly lower relative abundances of S. obliquus on day 4 than the other streams, but by day 9 S. obliquus increased relative to the other taxa (Fig. V.3d). On day 16, the assemblage of the stream stocked with Baetis on day 1 was characterized by Achnanthes lanceolata (Breb.) Grun. and N. minima. An increase in S. obliquus after day 16 in both the

day 1 and day 16 stocked streams caused their successional trajectories to reverse and approach assemblages more similar in composition to those in the unstocked streams.

Physiognomy

By day 28 of the experiment, algal assemblages in the unstocked streams consisted of a thick mat of diatoms and Scenedesmus obliquus. Although an overstory of Stigeoclonium tenue filaments was conspicuous on days 28 and 40 (Fig. V.4), counts of algal units in these assemblages did not reflect their effect on physiognomic properties because of the large number of diatom cells and S. obliquus colonies in the understory mat. A longitudinal section through the mat revealed the unstructured nature of the mature ungrazed assemblage (Fig. V.7).

Assemblages grazed by Dicosmoecus exhibited a thin layer consisting mainly of the adnate diatoms Nitzschia frustulum var. perpusilla and Navicula minima (Fig. V.8). Whereas Dicosmoecus grazed the entire substrate whenever they were introduced (Fig. V.5), Juga tended to graze in more discrete patches, leaving much of the algal assemblage intact (Fig. V.6). In patches where Juga grazed, algal assemblages were similar to those grazed by Dicosmoecus, and consisted of a monolayer of small adnate diatoms (Fig. V.9).

The stream that received Baetis on day 1 contained a thin layer of Achnanthes lanceolata, N. minima and S. obliquus on day 16 (Fig. V.10). On day 28, algal assemblages in this stream and in the stream stocked on day 16 were similar in physiognomy to the

Figure V.4 Photograph of an unstocked stream on day 40. Note the overstory of filaments of <u>Stigeoclonium</u> <u>tenue</u>.

Figure V.5 Photograph of the day 40 assemblage in the stream stocked with <u>Dicosmoecus</u> on day 28.

Figure V.6 Photograph of the day 40 assemblage in the stream stocked with <u>Juga</u> on day 28. Note the grazed patches.
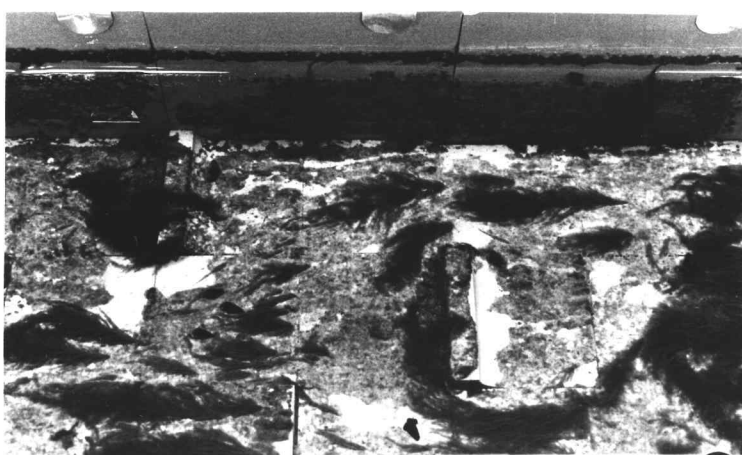
Figures V.4, V.5 and V.6

Figure V.7 SEM of a longitudinal section through the day 40 assemblage from an unstocked stream. Note the unstructured nature of the algal mat. The major taxa are <u>Nitzschia</u> <u>oregona</u> overlying <u>Synedra</u> <u>ulna</u>.

Figure V.8 SEM of the day 40 assemblage from the stream stocked with <u>Dicosmoecus</u> on day 28. The major taxa are the adnate diatoms <u>Nitzschia</u> <u>frustulum</u> var. <u>perpusilla</u>, <u>Achnanthes</u> <u>lanceolata</u> and <u>Navicula</u> <u>minima</u>.

Figure V.9 SEM of the day 40 assemblage from the stream stocked with <u>Juga</u> on day 28. Note the different physiognomies of the grazed (adnate diatoms; lower right) and ungrazed (<u>Scenedesmus</u> <u>obliquus</u>, <u>Nitzschia</u> <u>oregona</u> and <u>Synedra</u> <u>ulna</u>; lower left) regions.

Figure V.10 SEM of the day 16 assemblage from the stream stocked with <u>Baetis</u> on day 1. The major taxa are <u>Achnanthes</u> <u>lanceolata</u>, <u>Scenedesmus</u> <u>obliquus</u> and <u>Navicula</u> <u>minima</u>.
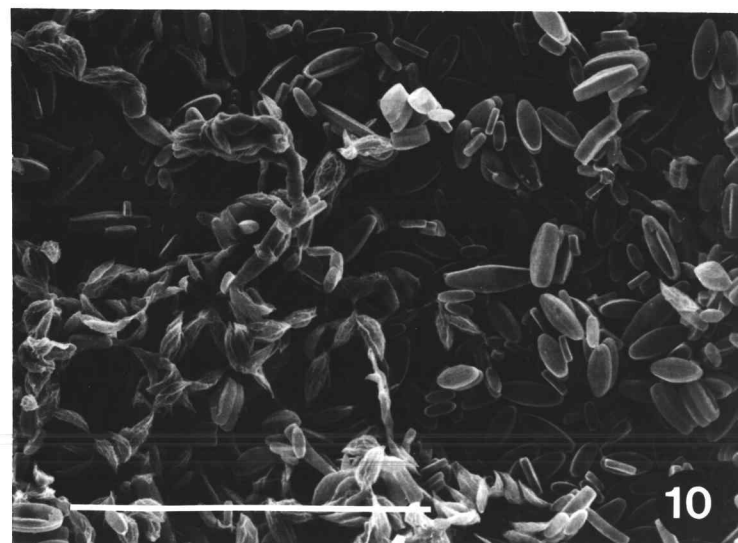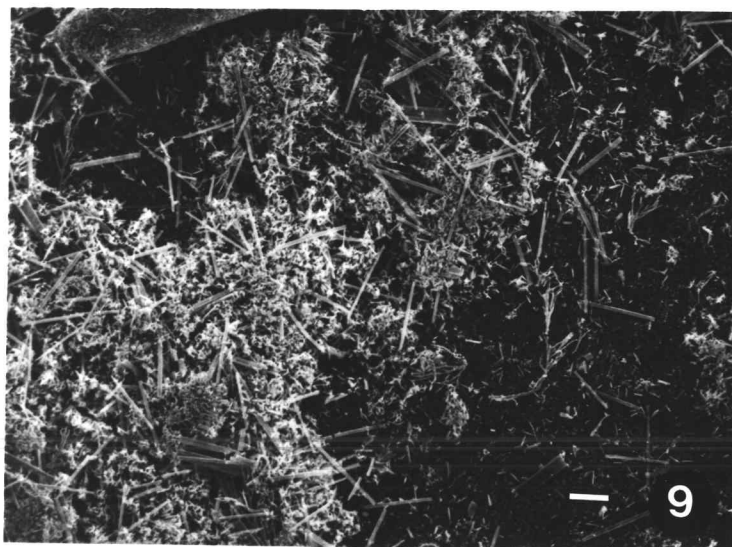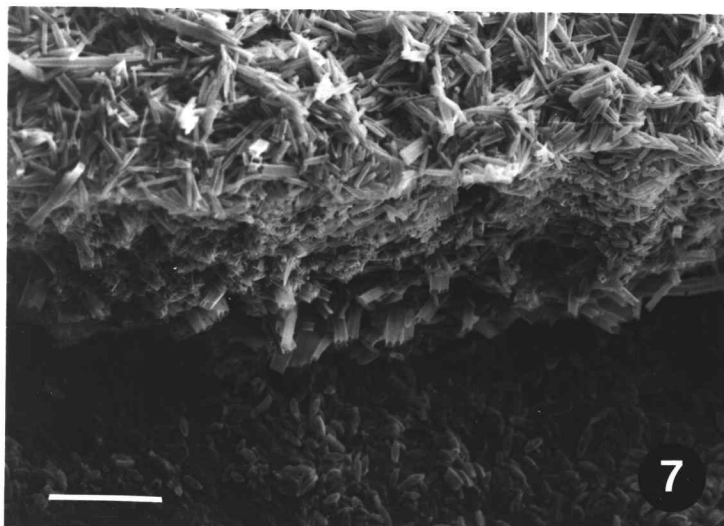
Figures V.7, V.8, V.9 and V.10.

unstocked streams.

DISCUSSION

Effects of Herbivore Type on Algal Development

An exponential pattern of increase in algal biomass in the absence of grazers has been reported in previous studies from laboratory streams (Kehde and Wilhm 1972, Sumner and McIntire 1982, Lamberti et al. 1987), outdoor channels (Stockner and Shortreed 1976, Eichenberger and Schlatter 1978) and natural streams (Jacoby 1987). We observed a similar pattern in our unstocked streams, however, there was a slight decline in algal biomass after day 28. Apparently, the production of gas bubbles and senescence of basal cells within the thick algal mat caused patches of the mat to detach and be exported out of the streams (Lamberti et al. 1989). Associated with the biomass increase was the development of an algal assemblage which gradually changed its physiognomy from a thin layer of cells to a thick mat with an overstory of filaments. The unstructured nature of the mature ungrazed assemblage was consistent with observations of Steinman and McIntire (1986) and Steinman et al. (1987) in laboratory streams. In contrast, late stages of periphyton succession on substrates suspended vertically in a lentic habitat (Hoagland et al. 1982) and in an estuary (Hudon and Bourget 1981) have shown more stratified assemblages, with levels of adnate, rosette and stalked diatoms. The development of stratified assemblages may depend on the habitat, the substrate orientation, and the pool of species available for colonization.

Grazers introduced at different stages of periphyton development in this study were exposed to assemblages that differed

in biomass, species composition and physiognomy. Of the three

herbivores examined, <u>Dicosmoecus</u> was the most effective at altering

algal biomass, physiognomy and succession, followed by <u>Juga</u>, and

with <u>Baetis</u> having the least effect. A similar species-related

gradient of grazing intensity was observed for <u>Dicosmoecus</u>, <u>Juga</u> and

the mayfly <u>Centroptilum</u> by Lamberti et al. (1987) when they were

introduced at an early stage of algal succession (day 9).

The ability of the three herbivores to alter the pattern of

algal succession and production was related to differences in their

mouthpart morphology and feeding behavior, particularly when the

animals were introduced at later stages of periphyton development

(days 16 and 28). Using its mouthparts and tarsal claws,

<u>Dicosmoecus</u> rapidly cleared large areas of filamentous overstory and

thick understory mats. Unlike the other two herbivores its feeding

behavior was rather sloppy and resulted in a high loss of undigested

algae through export (see also Lamberti et al. 1987).

<u>Juga</u> cleared patches within the algal mat slowly. SEM

indicated that ungrazed areas of the assemblage were similar to the

unstocked streams in biomass and physiognomy whereas, within a

grazed patch, biomass was reduced and taxonomic composition was

altered toward adnate diatoms. Therefore, samples from streams

stocked with <u>Juga</u> represented a mixture of these two quite different

assemblages.

The stream stocked with <u>Juga</u> on day 1 had a different

successional trajectory than the other streams. Presumably, the

high density of <u>Stigeoclonium</u> <u>tenue</u> zoospores present on day 9

accounted for the subsequent dominance of S. tenue basal cells in this stream. The initial algal seed for this stream may have contained filaments with zoosporangia that were not present in the seed of the other streams. Whether grazing contributed to subsequent zoospore production or release by S. tenue is uncertain. In any case, Juga maintained the assemblage mostly as basal cells, suppressing the growth of filaments.

The 500 Baetis m^{-2} stocked on day 1 were only able to suppress algal biomass accumulation until day 9 suggesting that their rate of harvest could not keep pace with algal growth. In both Baetis stocked streams, biomass continued to increase and filaments of Stigeoclonium tenue developed between days 16 and 28. During this period mortality of Baetis in the streams increased greatly and the algal assemblages may have obtained an escape from herbivory. Size escape from herbivory by plants occurs when either size alone or a size-related factor reduces the ability of a herbivore to consume a plant (Lubchenco and Gaines 1981). Size escape has been observed in phytoplankton communities (Porter 1977), and for macroalgae (Lubchenco 1983) and diatom assemblages (Castenholtz 1961) in intertidal communities. In streams, some macroinvertebrates avoid grazing algal filaments that are large or mucilaginous (Brown 1961, Hambrook and Sheath 1987). McShaffrey and McCafferty (1988) found that Rithrogena pellucida Daggy required algal assemblages of low relief to effectively move their maxillary palps to feed. They suggested that filamentous algal assemblages may interfere with grazing and that the life cycle of this mayfly may be tied to seasonal patterns of succession in the periphyton. The results of

these studies suggest that the late successional, filamentous assemblages that developed in the _Baetis_ streams in our study may have escaped herbivory by becoming large and physiognomically complex, and/or by having a size related change in the food quality of the assemblage.

Herbivory and the Autecology of Algal Taxa

From an algal perspective, the herbivores reduced the relative abundance of the loosely attached chlorophytes _Characium_ sp. and _Scenedesmus_ spp., and the rosette forming diatom _Synedra ulna_, which were replaced by more firmly attached diatoms. The relative abundance of diatoms also increased over time in the unstocked streams, but the changes were much slower than in streams stocked with grazers. Kehde and Wilhm (1972) also observed a grazer-induced decline in the relative abundance of _Scenedesmus obliquus_ after early colonization, followed by an increase in more firmly attached taxa. Species that adhere weakly to the substrate and that are easily resuspended into the water column are highly susceptible to removal by grazing (Gregory 1983b, Lamberti and Moore 1984). However, taxa with these characteristics can also colonize bare substrates rapidly (Hudon and Legendre 1987). Therefore, one would expect taxa such as _Characium_, _S. obliquus_ and _S. ulna_ to occur early in succession, be rapidly removed by herbivores and be replaced by the more firmly adhering diatoms and _Stigeoclonium tenue_.

The diatoms in _Juga_ and _Baetis_ grazed assemblages were mostly _Nitzschia oregona_ and _Navicula minima_, whereas _Nitzschia frustulum_

var. _perpusilla_ and _N_. _minima_ were dominant in _Dicosmoecus_ grazed assemblages. Apparently, the larger _N_. _oregona_ was more susceptible to intense grazing; it also was a major taxon in the ungrazed streams. Several studies of periphyton have documented a decrease in the relative abundance of large diatom taxa concurrent with an increase in small adnate taxa with grazing (Douglas 1958, Nicotri 1977, Hunter 1980, Sumner and McIntire 1982, Hill and Knight 1987, Steinman et al. 1987). In our study, the adnate diatom _N_. _frustulum_ var. _perpusilla_ appeared to be more resistant to grazing by _Dicosmoecus_ than the other adnate taxa.

Stigeoclonium _tenue_ is a heterotrichous alga, i.e., the thallus contains erect and prostrate portions. This structure allowed it to persist as basal cells in _Dicosmoecus_ grazed streams and as filaments in the ungrazed and _Baetis_ streams. Both forms of this taxon were present in the streams with _Juga_ due to the patchy pattern of grazing. The ability of heteromorphic algae to grow from basal cells may confer a competitive advantage during periods when grazing intensity is reduced (Littler and Littler 1980, Lubchenco and Cubit 1980).

The rapid removal of early successional taxa (e.g., _Scenedesmus_ spp., _Characium_ sp., and _Synedra_ _ulna_) by grazers in this study indicated that herbivores can accelerate species replacements and drive succession to later stages. Conversely, because _Dicosmoecus_ could effectively graze later successional stages, this could be viewed as reversion of succession to earlier stages (Lubchenco and Gaines 1981). In reality, the effect of herbivory on periphyton succession depended on the type of herbivore and the time of

encounter, and trajectories directed by herbivory often had assemblages that were different from those at any stage of succession in ungrazed assemblages.

Herbivory and Algal Community Structure

If it is assumed that the ungrazed, Baetis grazed, Juga grazed, and Dicosmoecus grazed streams represented a series of treatments with increasing grazing intensity, the corresponding species heterogeneity of the algal assemblages for these treatments (Fig. V.2) conformed to the predation hypothesis of Paine (1966). This hypothesis predicts that under no or very low grazing pressure, competitive dominants will exclude subordinate taxa and reduce diversity, whereas high grazing intensity results in dominance by a few taxa tolerant of grazing. Therefore, diversity should be highest at intermediate grazing intensity.

In this study, the effect of herbivory on algal species diversity apparently was related to the feeding morphology, behavior and density of the particular grazer. The patchy grazing patterns of Juga and Baetis within a stream channel created different assemblages on individual substrate tiles. Thus, the higher algal diversity in these streams probably reflects sample heterogeneity at this spatial scale. In contrast, the periphyton on substrates grazed by Dicosmoecus consisted of a few homogeneously distributed algal taxa tolerant of grazing. Animal densities in this experiment were within the range of those found in nearby streams. At higher densities of Juga and Baetis, grazed areas may merge quickly, thereby creating a more homogeneous, less diverse assemblage,

similar to that produced by <u>Dicosmoecus</u>. This was observed in laboratory streams by Steinman et al. (1987) for <u>Juga</u>, and by Colletti et al. (1987) for the mayfly <u>Heptagenia criddlei</u> (McD.). Grazers have been reported to increase (Dickman and Gochnauer 1978), decrease (Hunter 1980, Colletti et al. 1987) or have no effect on algal species diversity in streams (Kehde and Wilhm 1972, Sumner and McIntire 1982). Grazer type and density, and the spatial and temporal scales of sampling may help to explain some of these inconsistencies.

<u>Herbivory in Natural Streams</u>

The results from this experiment generate hypotheses concerning the role of herbivory in determining the structure of lotic periphyton communities in natural streams. Periphyton in natural streams often is distributed as a mosaic of patches on different successional trajectories or at different stages of the same trajectory (Fisher 1983). This study indicated that the degree to which the trajectories of algal patches diverge may be influenced by the type of herbivore and the stage of succession it encounters. The extent to which herbivory elicits or suppresses patch formation would affect algal diversity within a stream habitat. A model of an open, nonequilibrium system of patches (Caswell 1978) has been used to explain the maintenance of algal diversity in an assemblage of tide pools (Paine and Vadas 1969) and the coexistence of species in freshwater plankton and terrestrial plant communities (Caswell 1978). If lotic herbivores contributed to patch formation in periphyton assemblages this would promote the coexistence of many algal taxa. Conversely, if herbivory within a stream habitat is

intense, then all algal patches may be suppressed to grazer tolerant assemblages, thereby lowering diversity.

Grazers may not only contribute to the creation of algal patches in streams, but the biomass, physiognomy and composition of a patch may influence grazer distributions. For example, various caddisflies have been shown to selectively graze areas of high algal abundance (Hart 1981, Lamberti and Resh 1983, Dudley et al. 1986, Vaughn 1986). Conversely, patches containing an overstory of mature filaments may have a size-related escape mechanism that excludes grazing by herbivores such as _Baetis_ (this experiment, McShaffrey and McCafferty 1988). Grazing by herbivores such as _Baetis_ may be dependent upon the ability of more effective grazers or abiotic factors (e.g., scour) to generate accessible seral stages of periphyton.

ACKNOWLEDGMENTS

VI. SYNTHESIS

Several types of temporal and spatial patterns in ecosystems have come under the label of succession. Some studies have considered temporal changes in ecosystem processes such as photosynthesis and respiration as a type of succession (Margalef 1968, Odum 1969). In streams, the downstream transport of organisms and organic matter, along with longitudinal changes in physical factors can impart a spatial aspect to community structure that mimics temporal succession. For example, changes in ecosystem processes and species composition that occur longitudinally in a stream have been considered a type of successional sequence (Margalef 1960, Vannote et al. 1980, Fisher 1983). Classically, succession has been defined as the temporal change in community composition at a specific site following a disturbance that clears space (Connell and Slayter 1977). This study examined succession in this sense by investigating temporal changes in periphyton composition on initially bare substrates in specific types of stream habitats.

In the experiments of this study, I have emphasized that successional changes at a site could be viewed as the result of emerging species having growth forms that were better adapted to the changing conditions during community development. Classification of plants by growth forms has been used to simplify descriptions of community structure and development under different conditions for terrestrial (Raunkiaer 1934), macroalgal (Littler and Littler 1980)

and phytoplankton (Margalef 1978) assemblages. Several studies have examined periphytic microalgal assemblages in terms of growth forms (e.g., Hudon and Bourget 1981, 1983, Hoagland et al. 1983, Lowe et al. 1986), and the physiological adaptations and ecological implications associated with the different growth forms was summarized by Hudon and Legnedre (1987). The characteristic properties of the algal growth forms are similar to the "vital attributes" of terrestrial plants described by Noble and Slayter (1981) in that they can determine the successional sequence at a site under a given set of conditions.

In this study, early colonizing species were usually long araphid diatoms that have relatively high sinking rates, and filaments of <u>Oscillatoria</u> that attach prostrately to the substrate. These taxa adhere weakly to substrates suggesting a fugitive life history centered on dispersal and colonization. Shaded assemblages were associated with low rates of biomass accumulation. As biomass increased under these conditions, colonizing species were replaced by more firmly attached, immobile taxa with upright growth forms. The upright growth form allows a cell to have a small area firmly attached to the substrate while extending up to intercept light and nutrients. In addition to erect taxa, assemblages exposed to low irradiance usually had some firmly attached taxa with adnate growth forms. In assemblages exposed to high irradiance, the accumulation of algal biomass was greater and the replacement of colonizing taxa was more rapid than under shaded conditions. Scanning electron microscopy indicated that algal assemblages exposed to high irradiance contained a thick unstructured mat of diatoms. Biraphid

and keel raphid diatoms were abundant in these algal mats because
they are able to move through the mat to utilize resources and avoid
burial. Mature successional stages of assemblages exposed to high
irradiance contained anchored filamentous species that could exploit
resources above the mat. Small, immobile taxa with tightly
adhering, adnate growth forms were more capable of persisting in
heavily grazed assemblages and rapidly dominated assemblages when
herbivory was intense. A summary of the characteristic assemblages
found in this study, the dominant growth forms in the assemblages,
and the conditions leading to the formation of the assemblages are
presented in Table VI.1.

Horn (1975) modeled forest succession at a site as a
probabilistic, plant-by-plant replacement processes. The
successional sequence in the assemblage was determined by the
present distribution and the probability that an individual tree
would be replaced by an individual of new species in the next
generation. Fisher et al. (1983) adapted Horn's model to study the
temporal changes of algal patches in a desert stream following an
intense flood event. In that study, the transition of one patch
type to another was determined empirically and the probabilities
associated with the transitions were estimated for a given time
interval. Similarly, in this study, successional changes for an
assemblage in a particular habitat can be viewed as a series of
transitions between growth forms occurring with a particular
temporal probability. The transition probabilities would be
associated with the arrows in Fig. VI.1. The probability that a

Table VI.1. Characteristic assemblage states in succession.

Assemblage state	Dominant growth forms	Characteristic taxa	Conditions increasing formation
Bare substrate	-	-	scour, slough
Pioneers	immobile, araphid linear-diatoms; low adhesion; colonial?	_Fragilaria vaucheriae_, _Synedra ulna_, _Oscillatoria agardhii_	bare substrate, slow current
Upright	immobile, erect or short-stalked diatoms; some adnate diatoms	_Rhoicosphena curvata_, _Achnanthes lanceolata_, _Achnanthes minutissima_	low light, low biomass
Adnate	small, mono or biraphid diatoms, prostrate on substrate; low mobility	_Cocconies placentula_, _Navicula minima_, _Achanathes deflexa_, _Achnanthes lanceolata_, _Stigeoclonium_ basal cells	grazing, low light, low biomass
Mat with overstory	mobile, biraphid and keel-raphid diatoms; anchored filaments; epiphytes?	_Nitzschia oregona_, _Nitzschia linearis_, _Navicula arvensis_, _Navicula minima_, _Stigeoclonium_ filaments	high light, high biomass

given seral stage of succession would occur in a given physical
habitat would be determined by the characteristics of the growth
forms, the previous assemblage state, factors influencing the rate
of biomass increase or loss, and the degree of herbivory during the
time period (Fig. VI.1). Transitions between successional stages in
this study appeared to be most like Connell and Slayter's (1977)
tolerance model, in that extant species probably did not inhibit or
facilitate recruitment of new species with different growth forms.
Species changes were most likely a result of certain taxa having
life history characteristics that were more tolerant of the changing
conditions (Table VI.1). However, an increase in water turbulence
created by algae colonizing a bare substrate may have facilitated
the recruitment of colonists onto the substrate (Stevenson 1983).

At a landscape perspective, site specific succession in an area
with a heterogeneous environment may produce a mosaic of
successional states. For example, polyclimax and climax-pattern are
terms that describe the distribution of climax successional stages
at local sites or along environmental gradients in an area,
respectively. Watt (1947) emphasized that the interactions between
temporal and spatial patterns in terrestrial plant communities can
produce a mosaic of patches on different successional trajectories
or at different stages of the same trajectory. In contrast to
forests, streams have a spatial scale of environmental heterogeneity
that is relatively large compared to the size of the organisms, and
the life time of the organisms is relatively short. Therefore,
mosaics of successional states in streams are perceived to occur in
very small patches and change over very short time intervals. Algal

Figure VI.1 Possible successional states and their relationships
for the periphytic assemblages observed in this study.
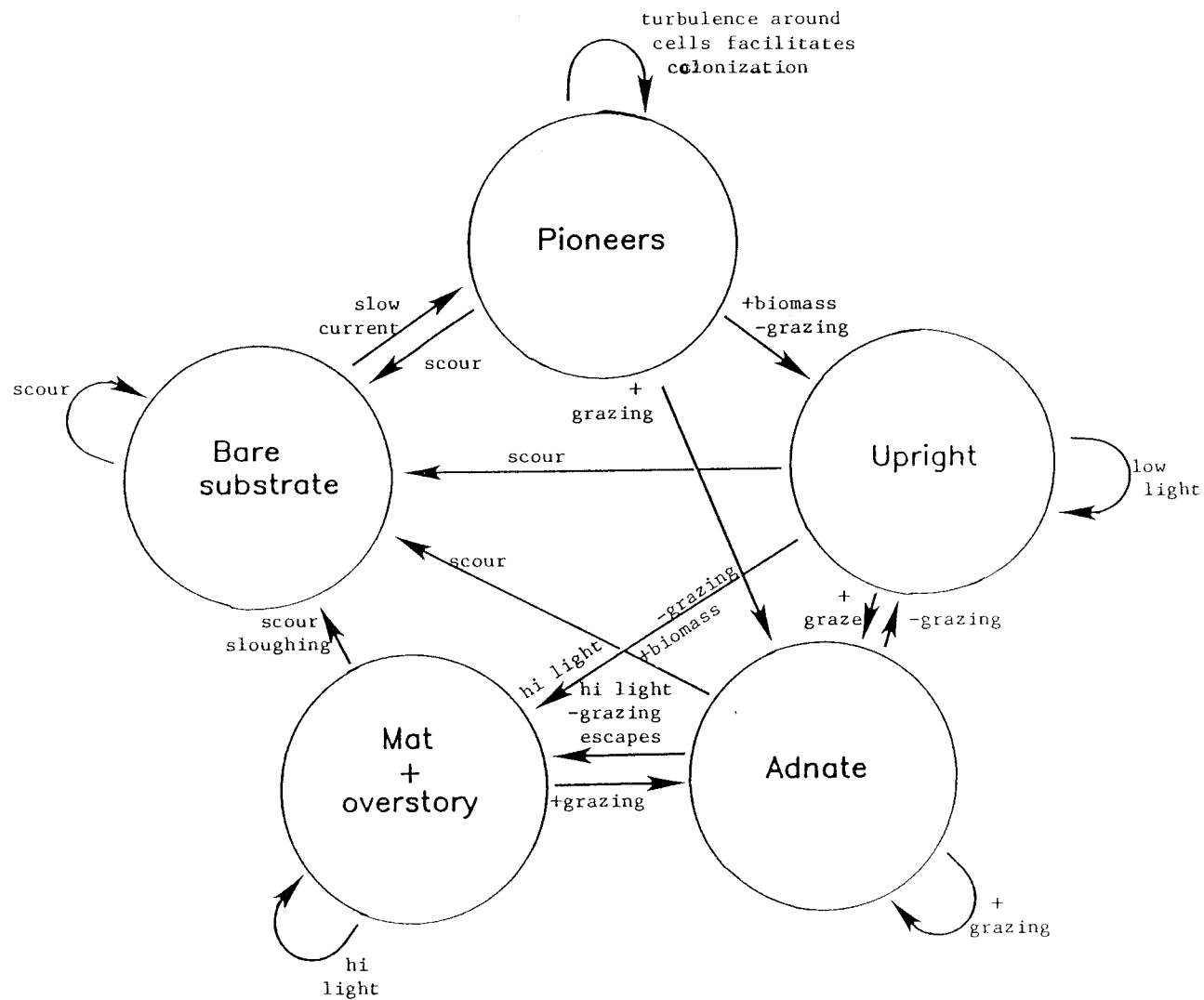
Figure VI.1

succession in streams is frequently compared to plant succession in terrestrial habitats. However, such comparisons have caused confusion because forest succession is traditionally studied at a patch scale, whereas algal succession in streams is often studied at a landscape scale.

Blum (1956) and Patrick (1975) suggested that succession of periphyton in streams is very different from forest succession because the predominance of abiotic factors and high frequency of disturbance in streams prevents species of the moment from determining their successors. This implies that compared to terrestrial plant communities, succession in streams is always at early, immature stages (Patrick 1975). Similarly, Blum (1956) suggested that algal colonization and climax are simultaneous in streams. However, in studies of algal colonization and development examined at small temporal and spatial scales (e.g., Stevenson 1984, Oemke and Burton 1986, this study), there are often predictable species replacements, which are more analogous to succession in terrestrial plant communities. This difference in interpretation mainly arises because of the temporal and spatial scales used in the studies. When succession is studied in a relatively homogeneous patch at scales closer to the size and life time of the organisms, autogenic factors are important. Therefore, successional patterns of periphyton in this study, and other small scale stream studies, appear to be similar to patterns observed in traditional studies of terrestrial plant succession done at a site. When succession is examined at temporal and spatial scales much larger than the scales

of the organisms (landscape scale), species replacements appear more rapid and effects are better related to allogenic than to autogenic effects. This is the scale Blum and Patrick were considering and the reason why streams have been cited as an ecosystem where the traditional concept of succession as a autogenically produced sequence does not hold (Vannote et al. 1980, Wehr 1981). However, similar allogenically related successional patterns can also be seen in terrestrial plant communities if they are examined at a relatively large scale (e.g., palynological studies, O'Neill et al. 1986). Confusion created by studies of lotic periphyton succession that are done at different scales can be resolved by considering the results in a hierarchical framework.

In this study, an algal habitat patch is defined as an area with a relatively uniform physical environment that has the potential to produce a spatially homogenous periphyton assemblage. As a periphyton assemblage in a habitat patch changes through time, it develops only within a set of constraints imposed by its potential capacity, defined as all its possible developmental states (Warren et al. 1979). In turn, the potential capacity of the assemblage is constrained by conditions that determine the habitat patch. For example, factors such as irradiance level and current speed determine that habitat patch. These factors constrain which seral states can occur in the patch and the transition probabilities between possible states (Figs. VI.1 and VI.2). Moreover, habitats in streams are organized in a nested hierarchical structure such that the factors that determine the algal patches develop within the spatiotemporal constraints of the larger scale habitats of which

Figure VI.2 Potential capacities of two patches of periphyton within the hierarchical organization of a stream reach and its habitat subsystems.

Reach Scale;
succession determined
by allogenic factors
determining habitats

Patch Scale;
succession determined
by autogenic factors
and constrained by
habitat

Stream Unit
Scale

Legend
- - - - - - - - - - - - - - - -

P - pool unit

R - riffle unit

(T) - shade tree

(gravel bar) - gravel bar
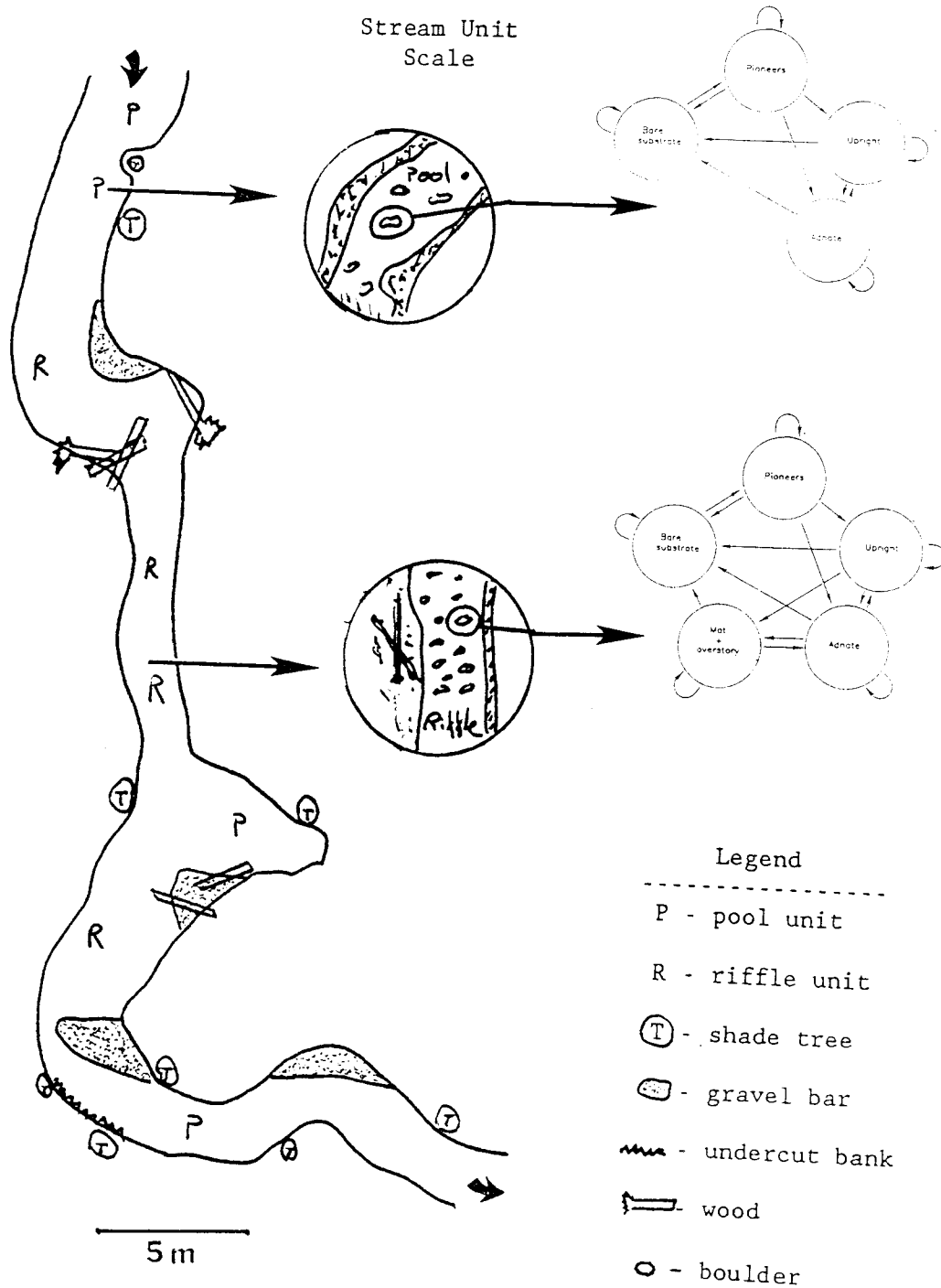
~~~ - undercut bank

wood

O - boulder

5 m

Figure VI.2

they are a part (Frissel et al 1985). Therefore, one way of conceptualizing periphyton succession within a stream is as a series of trajectories in different habitat patches nested within the spatiotemporal constraints of conditions that define the habitats (Fig. VI.2).

By using a hierarchical model of succession in streams, one can choose the level of examination and measure the appropriate variable for understanding succession at that level. For example, at large spatial scales (> substrate size) algal succession in a stream is determined primarily by changes that occur at relatively long frequencies (> months) such as changes in algal species pool, light, temperature, nutrients, current and herbivore abundances. Many of these are allogenic changes, which are related to seasonal effects or to disturbance regimes. These factors affect periphyton by changing the distribution of habitat patches for algae (Fig. VI.2). This would be the level of succession that Blum, Patrick and Wehr were considering. At smaller spatial scales (substrate size) the above parameters can be treated as constants within an algal patch. One must consider variables that change at faster frequencies (days) such as the rate of algal biomass increase from invasion or primary production, the rate of export, and the timing of grazer-periphyton interactions within the patch. Many of these are autogenic factors (Figs. VI.1 and VI.2). This is the level examined in this study and other small-scale experiments (e.g., Stevenson 1984, Oemke and Burton 1986, Steinman and McIntire 1986, 1987, 1989, Colletti et al. 1987).

The experiments in this study indicated that the degree to which herbivore foraging influenced algal succession was determined in part by herbivore type, algal biomass and current speed. In addition, effects of herbivory on succession were greater at low irradiance than at high irradiance. The effects of these factors on herbivory operate at large and small scales. At a large scale, physical factors establish algal habitats, and influence herbivore type and abundance. Within these constraints, patch scale characteristics such as algal biomass and successional state, and their interactions with herbivore foraging, influence the degree of herbivory within an algal patch. Some of the experiments in this study indicated that a heterogeneous distribution of algae also may occur at a level within a habitat patch as a result of algal escapes from herbivory. For example, algal assemblages in relatively uniform physical environments became patchy when algal productive capacity exceeded the consumptive demand of the herbivores. Such algal escapes are a function of herbivore density and type, and the timing of grazer-periphyton interactions.

The examination and understanding of benthic algal distribution in streams can be improved by using a hierarchical conceptual framework that combines both the temporal and spatial aspects of algal succession. The scales within the hierarchy should be defined by functional properties that effect algal distributions. For example, a scale may be defined for surfaces of a substrate element based on hydrologic regime. At a larger scale, algal distribution may be defined for a stream reach based on the geomorphic processes that determine the slope of the bed or riparian cover. Such a

framework indicates the importance and context of variables that affect successional patterns for different scales of investigation.

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