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# Stream Periphyton Development in Relation to Current Velocity and Nutrients<sup>1,2</sup>

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HORNER, R. R., AND E. B. WELCH. 1981. Stream periphyton development in relation to current velocity and nutrients. *Can. J. Fish. Aquat. Sci.* 38: 449–457.

Measurement of chlorophyll *a* accrual on flattened rock substrates placed in streams revealed that a velocity increase up to  $\sim 50 \text{ cm} \cdot \text{s}^{-1}$  enhanced periphytic algae accumulation when orthophosphate-phosphorus concentration exceeded  $40\text{--}50 \mu\text{g} \cdot \text{L}^{-1}$ . At lower P concentrations velocity increases reduced the accrual rate. The erosive effect of current was hypothesized to retard accumulation unless nutrient availability was such that the positive influence of turbulent diffusion of dissolved substances, and consequent cell growth, overcame frictional shear. Velocity increments above  $50 \text{ cm} \cdot \text{s}^{-1}$  eroded an increasingly greater proportion of the periphyton growth. The definition and use of a heterotrophic index as the ratio of adenosine triphosphate to chl *a* demonstrated that current velocity increases assisted the accumulation of the attached consumers relative to that of the primary producers. Comparison of heterotrophic indices before and after elevated storm runoff currents showed smaller reductions in the standing crop of the periphytic heterotrophs than that of the autotrophs.

*Key words:* periphyton, current velocity, nutrients, phosphorus, chlorophyll *a*, adenosine triphosphate, heterotrophs

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Des mesures de chlorophylle *a* sur des substrats de roches plates placées dans des cours d'eau indiquent qu'une augmentation de la vitesse du courant jusqu'à environ  $50 \text{ cm} \cdot \text{s}^{-1}$  favorise l'accumulation d'algues périphytiques quand la concentration de phosphore sous forme d'orthophosphate dépasse  $40\text{--}50 \mu\text{g} \cdot \text{L}^{-1}$ . À de plus faibles concentrations de P, une vitesse de courant accrue réduit le taux d'augmentation. On suppose que l'effet érosif du courant retarde l'accumulation, à moins que la disponibilité de substances nutritives soit telle que l'influence positive de la diffusion turbulente des substances dissoutes, et partant la croissance cellulaire, puissent vaincre les forces de friction. Les augmentations de vitesse au-delà de  $50 \text{ cm} \cdot \text{s}^{-1}$  font disparaître une proportion de plus en plus forte de la croissance périphytique. La définition et l'utilisation d'un indice hétérotrophe comme le rapport adénosine triphosphate à chlorophylle *a*, démontrent que les augmentations de vitesse du courant favorise l'accumulation des consommateurs sessiles par rapport à celle des producteurs primaires. Une comparaison des indices hétérotrophes avant et après une crue soudaine des eaux indique de plus faibles réductions de biomasse d'hétérotrophes périphytiques que celle des autotrophes.

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THIS study was conducted to investigate in the field the development of lotic periphyton in relation to current velocity and nutrients. Though substantial literature documents the association of some measure of periphyton growth or activity with nutrients, velocity, light, and temperature, most research has been conducted in laboratory channels rather than in the field. Previous studies did not encompass wide ranges of both nutrient concentrations and current velocity. This work comprised broad ranges of both variables. It thus offered the

opportunity to refine the conclusions of artificial stream research and to investigate their applicability to natural systems. Including measurements pertinent to both the auto-

<sup>1</sup>Prepared in cooperation with Washington State Transportation Commission, Department of Transportation, and U.S. Department of Transportation, Federal Highway Administration.

<sup>2</sup>The contents of this report reflect the view of the authors, who are responsible for the facts and the accuracy of the data presented herein. The contents do not necessarily reflect the official views or policies of the Washington State Department of Transportation or the Federal Highway Administration. This report does not constitute a standard, specification, or regulation.

trophic and heterotrophic periphyton, the study also permitted observations of the development of both segments of the attached community and the relationships between them. Of principal interest in both cases were the effects of conditions on biomass accumulation over time.

Among the studies illustrating the effect of current on periphyton, Whitford and Schumacher (1964) measured a 40.5–57.1% increase in respiratory rate when velocity was increased from 0 to  $15 \text{ cm} \cdot \text{s}^{-1}$  and an increase in  $^{32}\text{P}$  uptake rate of 5.1–16 times with velocity increases of 0 to  $20 \text{ cm} \cdot \text{s}^{-1}$ . McIntire (1966) compared attached algal growth at 9 and  $38 \text{ cm} \cdot \text{s}^{-1}$  and found equal biomass at the end of the experiment, but more export from the community grown at  $38 \text{ cm} \cdot \text{s}^{-1}$ . Sperling and Hale (1973) and Rodgers and Harvey (1976) both documented substantially greater  $^{14}\text{C}$  accumulation at corresponding higher velocities.

Phaup and Gannon (1967) demonstrated a similar tendency among the lotic heterotrophs, finding that *Sphaerotilus* bacterial biomass increased in proportion to velocity increases between 18 and  $45 \text{ cm} \cdot \text{s}^{-1}$ . The experiments of Wuhrmann (1972) involving sessile decomposers revealed that the rate of sugar metabolism at  $24 \text{ cm} \cdot \text{s}^{-1}$  was more than 12 times that occurring at  $4 \text{ cm} \cdot \text{s}^{-1}$ .

In one of the few previous investigations conducted in the field and including velocities above  $40 \text{ cm} \cdot \text{s}^{-1}$ , Ball et al. (1969) determined that the greatest algal standing crop in the Red Cedar River, Michigan, existed in the range  $30.5\text{--}61 \text{ cm} \cdot \text{s}^{-1}$  and the lowest at  $91.5\text{--}137 \text{ cm} \cdot \text{s}^{-1}$ . Reisen and Spencer (1970) demonstrated an inverse relationship between overall diatom density and current velocity up to  $66.3 \text{ cm} \cdot \text{s}^{-1}$  over the short term, but a strongly positive association over the full 6 wk term of a field experiment.

Previous findings suggest that increases in current velocity to  $\sim 50 \text{ cm} \cdot \text{s}^{-1}$  assist the growth of periphytic organisms. With further increases, scoured attached communities represent a reduced base for reproduction, although the rates of various biological processes may increase.

### Materials and Methods

A series of experiments was conducted at 12 sites on six streams in the Seattle, Washington, area during the summer of 1977. The streams ranged from first to fourth order. Site selection and scheduling were intended largely to eliminate light, temperature, turbidity and limitation by inorganic carbon as growth determinants, permitting concentration on the roles of current velocity, phosphorus, nitrogen, and organic carbon. To document differences in shading among stations, light intensity surveys were conducted over a full photoperiod on clear days at each sampling site using a Photo Research Corporation Spectra Lumicon light meter held above the water surface. Light differences over time were gauged by consulting solar radiation records obtained from the University of Washington Department of Atmospheric Sciences, located about equidistant from the northernmost and southernmost stream sites and within 40 km of all sites. Solar radiation was measured with an Eppley  $180^\circ$  pyranometer and recorded by a Lintronic integrating recorder.

To permit quantitative sampling of periphyton, substrates were prepared by cutting basaltic rocks, gathered from a

single site in one of the streams, with a diamond saw provide flat, smooth surfaces. These substrates were placed 20–50 cm of water in a vertical position, parallel to the flow in well-lighted zones. We collected periphyton weekly biweekly for 11 wk by carefully scraping and brushing the growth from designated areas into a jar containing distilled water. Areas sampled were traced on paper for later measurement by planimeter. Fast-drying paint was then spread on the scraped surfaces to avoid future sampling of newly colonized growth, a procedure which caused no noticeable edge effect. The substrates were then returned to the spots in streams from which they had been removed.

In the laboratory the periphyton was prepared for analysis of chlorophyll *a* and adenosine triphosphate (ATP) on the day of collection. The latter quantity was selected as an index of total (autotrophic plus heterotrophic) community development, while the former represented the algal component. Following dispersion of clumps by vigorous shaking, measured subsamples were drawn for the chl *a* and ATP analyses. Chl *a* concentration was determined fluorometrically in 90% acetone extracts, as outlined in Strickland and Parsons (1972), by a Turner fluorometer and expressed in  $\text{mg} \cdot \text{m}^{-2}$  on the basis of the area sampled. Subsamples for ATP analysis were extracted in boiling Tris buffer according to the procedure of Holm-Hansen and Booth (1966). The extract was analyzed in a JRB, Inc., ATP photometer and expressed in  $\text{mg ATP} \cdot \text{m}^{-2}$  of surface sampled.

To judge the relative sizes of the autotrophic and heterotrophic periphytic communities, a Heterotrophic Index (HI) was defined as follows:

$$\text{HI} = \frac{(\text{mg ATP} \cdot \text{m}^{-2}) (250 \text{ mg carbon/mg ATP})}{\text{mg chl } a \cdot \text{m}^{-2}}$$

The conversion factor transforming ATP to total living carbon biomass was based on the recommendation of Holm-Hansen (1973).

A propeller-type current meter, designed and built at the Harris Laboratory of the University of Washington, was used to measure velocity on each periphyton sampling occasion as close as possible to the flat face of the substrate. U.S. Geological Survey stream gauging stations near sampling sites on four of the six streams provided daily discharge records. For these sites velocities measured at each substrate were graphed with respect to discharges on the days velocities were measured. In most cases, particularly those where collectors rested on uniform gravel stream beds, relationships were nearly linear, permitting derivations of linear regression equations, or the graphs where necessary, were used to estimate average velocities on each day of the experimental period.

Water samples were collected biweekly at each periphyton sampling site. On-site analyses were performed for temperature, pH (Porto-matic model 175 meter), specific conductivity (Lab-Line model MC-1, Mark IV meter), and total alkalinity (American Public Health Association, 1975). The remainder of each sample was transported to the laboratory in an ice chest for additional analyses.

Turbidity was measured on a relative Formazin Turbidity Unit (FTU) scale with a Hach Chemical Company model 2100A nephelometric turbidimeter. Total soluble and

TABLE 1. Ranges, mean, and standard deviations for all measurements of physical and chemical variables.

Variable	Unit	No. of observations	Minimum	Maximum	Mean	Standard deviation
Current velocity	cm · s <sup>-1</sup>	212	0.3	137.2	57.6	40.2
Depth	cm	176	8	66	35	13
Temperature	°C	47	11.5	18.0	14.5	1.6
Daily light reception <sup>a</sup>	J · cm <sup>-2</sup>	11	473	1030	492	155
pH	—	47	6.6	7.6	7.2	0.2
Specific conductivity	μs · m <sup>-1</sup>	47	66	198	117	38
Total alkalinity	mg · L <sup>-1</sup> as CaCO <sub>3</sub>	47	24	66	43	14
Turbidity	FTU	47	0.4	64 <sup>b</sup>	9.1	15.4
Orthophosphate—phosphorus	μg · L <sup>-1</sup>	40	2.6	91.3	29.3	20.6
Total soluble phosphorus	μg · L <sup>-1</sup>	32	8.9	118	40.9	25.9
Nitrate-plus-nitrite—nitrogen	μg · L <sup>-1</sup>	40	Trace	1029	283	303
Ammonia—nitrogen	μg · L <sup>-1</sup>	40	9.0	100	30.3	22.1
Dissolved organic carbon	μg · L <sup>-1</sup>	32	0.8	12.3	4.5	3.5
Particulate organic carbon	μg · L <sup>-1</sup>	32	28.7	1003	259	233

<sup>a</sup>Daily total with cloudless conditions as estimated at each sampling site by a light meter survey during 1st week of September, 1977.

<sup>b</sup>All measurements were less than 6.5 FTU, except 10 made during heavy storm runoff.

orthophosphate—phosphorus were analyzed according to the molybdenum blue colorimetric methods of Murphy and Riley (1962), with absorbance read at 885 nm on a Beckman model DK-2A spectrophotometer. Nitrate-plus-nitrite- and ammonia—nitrogen were determined on a Technicon Auto-Analyzer II, the former by a cadmium reduction procedure and the latter with a phenolhypochlorite technique. DOC and POC were analyzed by combusting organics in a LECO model 507-200 induction furnace and measuring the resulting carbon dioxide gas on a Beckman model 865 infrared analyzer.

A variety of procedures was used to establish the nutrient most limiting to algal growth, most prominently algal growth potential bioassays, and the results of correlation exercises performed on the data. The laboratory bioassays were performed according to the method outlined by the National Eutrophication Research Program of the U.S. Environmental Protection Agency (1971).

Data analyses were conducted with reference to average velocities and water quality conditions existing over the respective growth periods. Averages were estimated by computing the means of readings taken over the various periods.

To compare periphyton accrual between sampling stations, chl *a* and heterotrophic index were plotted with respect to time for each stream. The same graphs contained plots of velocity versus time over the same periods. To elucidate further the response of periphytic algae to stream conditions and as a guide to a more formal analysis of the full data set, chl *a* accrual rates were ranked from high to low and associated with the magnitudes of average and peak velocities and average nutrient concentrations existing during the growth periods.

Because of the apparent role of several independent variables in influencing periphyton accumulation and a desire to investigate general tendencies in the data, the combined

results from all streams were also analyzed by stepwise multiple-linear regression. Chl *a* accrual measurements were transformed to the natural logarithm, and regression equations were derived to express the transformed variable in terms of time, average orthophosphate-phosphorus concentration, and average velocity. Such equations were derived for the mid-summer and late-summer experimental periods and for current velocities in the ranges <20, 20–50, and 50–80 cm · s<sup>-1</sup>.

## Results

### PHYSICAL AND CHEMICAL CONDITIONS

Table 1 statistically profiles the 14 physical and chemical characteristics which were monitored during the study. Velocity and concentrations of phosphorus, nitrogen, and organic carbon exhibited considerable variation, with standard deviations ranging from 63 to 107% of the respective means. Depth, temperature, pH, specific conductivity, and total alkalinity were much more closely confined over space and time, with standard deviations ranging from 2.8 to 37% of the respective means. Daily light reception, based on the late summer light survey, did not differ substantially overall among sampling sites, although greater shading at one site did reduce light reception well below the mean. It may thus be inferred that measured differences in periphyton accrual were due largely to variations in velocity, P, N, and organic carbon, rather than in temperature, light availability, or inorganic carbon.

With regard to light variation over time, the total daily solar radiation recorded on the University of Washington campus indicated two periods of distinctly different weather (July 7–August 25 and August 25–September 21), pro-

ducing daily mean values of 1888 and 1298  $J \cdot cm^{-2}$ , respectively. These means show a highly significant difference ( $P < 0.001$ ). Additionally, spot readings taken on July 7 showed maximum midday intensity  $\sim 33\%$  higher than during the 1st week of September. The literature on light inhibition (Talling 1957, 1971; Steeman Neilsen and Hansen 1959; Steeman Neilsen et al. 1962; Steeman Neilsen and Jorgensen 1968) indicates that the elevated midday intensities which existed for an extended period during July and August exceeded the level generally shown to inhibit algal photosynthesis. Measured chlorophyll *a* and ATP accumulations were overall substantially smaller in midsummer compared to the late-summer period. Because moderate temperatures were maintained throughout the summer by mountain runoff and cool groundwater infusion, retarded periphyton accrual was probably the result of light inhibition. Accordingly, when we analyzed the periphyton data, we treated the two periods separately.

All streams normally carried very low suspended solid loads, as indicated by the generally low turbidity measurements. On two occasions (August 25–26 and September 18–21), however, substantial rainstorms and attendant erosion greatly increased turbidities. At these times periphyton standing crops were drastically reduced by the frictional scour of particulates transported by elevated velocities. Consequently, it was necessary to terminate studies of normally growing periphyton communities. The earlier storm fortuitously corresponded to the change in the light regime from the inhibiting intensities of mid-summer to the growth-supportive but more muted intensities of late summer. Thus, the total data set could be subdivided to recognize light intensity and scour effects simultaneously. Observation of severe erosion of the substrates also provided an opportunity to generalize on the effects of heavy storm runoff on the sessile community.

All laboratory algal bioassays showed that phosphorus fertilization increased both the rate of growth and the ultimate biomass of the test alga (*Selenastrum capricornutum*) much more effectively than did nitrogen addition. Additional evidence of phosphorus limitation was provided by examining the results of statistical correlation exercises performed with the full data set. Orthophosphate and total soluble phosphorus concentrations demonstrated a highly significant ( $P < 0.001$ ) positive association with  $\ln$  chl *a*. Nitrate-nitrogen concentration was also positively correlated with  $\ln$  chl *a* but at a lower significance level ( $P < 0.05$ ). While it is thus quite apparent that phosphorus was generally more limiting to the periphyton communities examined,  $NO_3-N$  was depleted to trace levels in the water on several occasions during periods of exceptionally heavy algal growth. In these instances nitrogen certainly served, at least momentarily, as a limiting factor.

#### AUTOTROPHIC ACCRUAL

Algae growing on the flattened rock substrates consisted almost entirely of diatoms. Their rate of accumulation was represented by measurements of chl *a* at intervals over the periods of exposure. Figures 1–3 present typical variations of chl *a* with time. The curves were smoothed to express the growth pattern shown between sampling dates. The storm beginning on the 24th day of the experiment was repre-

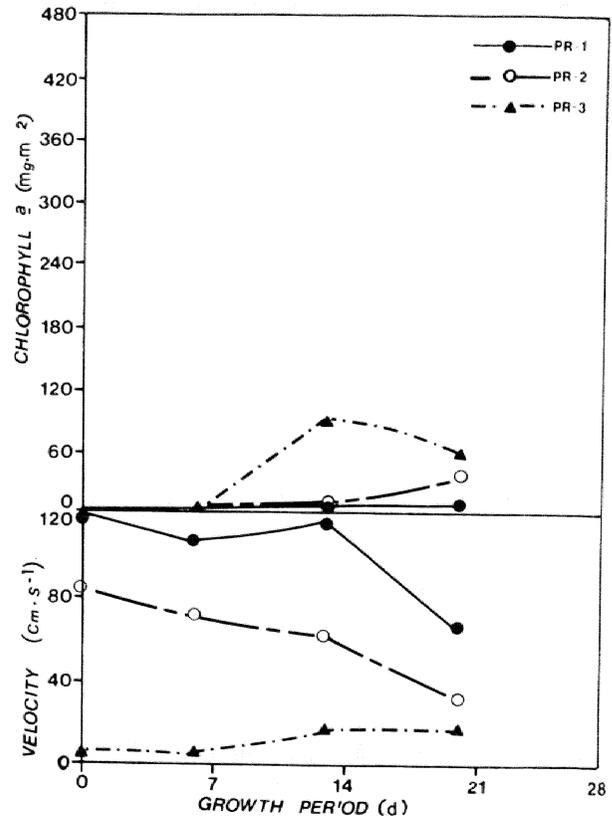


FIG. 1. Chlorophyll *a* ( $mg \cdot m^{-2}$ ) and velocity versus time for three stations; Pilchuck River; August 25–September 14, 1977.

sented by a slope change on that date for Swamp Creek (SC) and Juanita Creek (JC). High water following the storm made recovery of substrates from the Pilchuck River (PR) impossible.

Figures 1–3 indicate several tendencies in the relationships among chl *a* accrual, current velocity, and the limiting nutrient, which were commonly observed in the data. The most basic point demonstrated by the data is that current velocity is a critical determinant of the rate at which attached autotrophs develop in streams. Two sites on Juanita Creek with similar nutrient levels had amounts of chl *a* which differed by 30-fold after 20 d of growth.

More specifically, the graphs for the Pilchuck River and Juanita Creek indicate that chl *a* accrual was inversely related to velocity. In contrast, the Swamp Creek data show that the higher algal standing crop developed at the site with the faster flow. It is notable that  $PO_4-P$  concentration, averaging  $52 \mu g \cdot L^{-1}$  for the period, was substantially higher in Swamp Creek (SC) than the Pilchuck River (PR) ( $8 \mu g \cdot L^{-1}$ ) or Juanita Creek (JC) ( $38 \mu g \cdot L^{-1}$ ). It is also noteworthy that velocity at station SC-2 was usually in the moderate  $50-60 cm \cdot s^{-1}$  range, while that at stations PR-1, PR-2, and JC-2, which were characterized by higher currents than the other streams, generally exceeded  $60 cm \cdot s^{-1}$ . As in the work of Ball et al. (1969), very small quantities of chl *a* were measured where velocity approached or exceeded  $1 m \cdot s^{-1}$ .

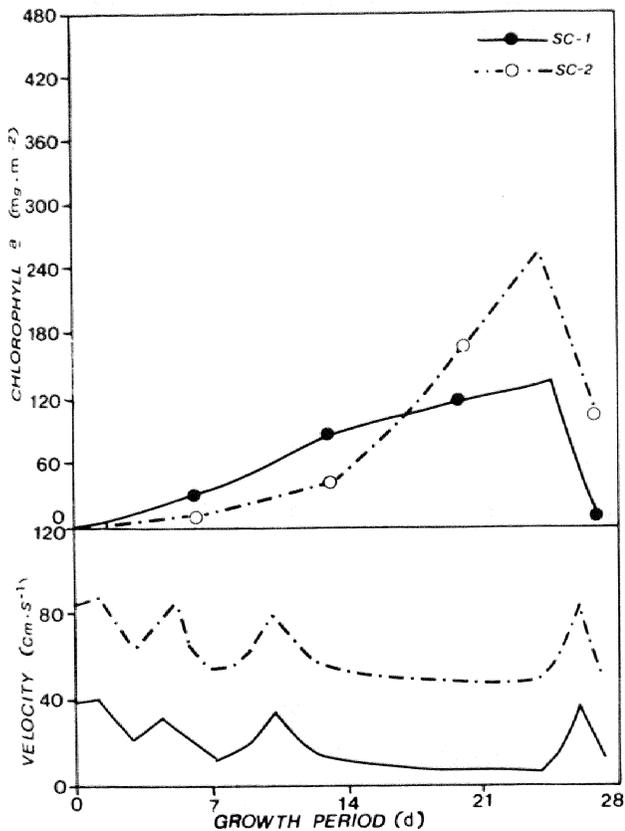


FIG. 2. Chlorophyll *a* ( $\text{mg} \cdot \text{m}^{-2}$ ) and velocity versus time for two stations; Swamp Creek; August 25–September 21, 1977.

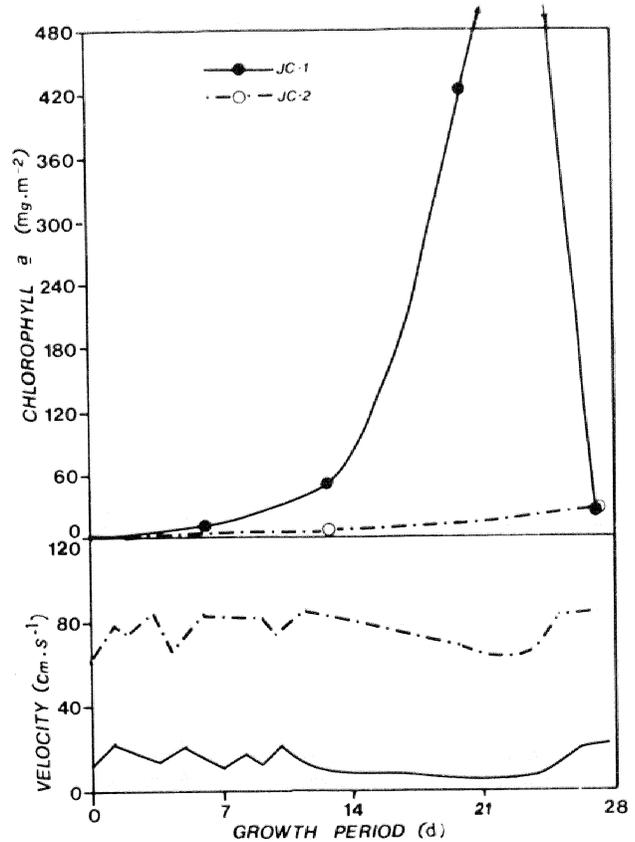


FIG. 3. Chlorophyll *a* ( $\text{mg} \cdot \text{m}^{-2}$ ) and velocity versus time for two stations; Juanita Creek; August 25–September 21, 1977.

The occurrence of a different pattern of periphyton growth in relatively phosphate-rich Swamp Creek versus streams having lower phosphorus concentration suggests an interaction between current velocity and the limiting nutrient. These results imply that velocity increase, up to a point, enhances the ultimate accumulation of periphytic algae when the limiting nutrient concentration is sufficient. On the other hand, all plots demonstrate that initial colonization is favored by lower velocities.

Runoff associated with the storm of September 18–20

(days 24–26) accounts for scouring of periphyton growth exhibited by the curves in Fig. 2 and 3. Results for stations SC-1 and JC-1 illustrate that communities adapted to higher average velocity declined to a lesser degree than did those inhabiting sites having slower currents ordinarily. The considerable loss of chl *a* at site JC-1 in connection with a peak velocity not substantially higher than normal suggests that erosion may be due more to elevated turbidity than current.

Ranking of chl *a* accrual rates, along with the coincident

TABLE 2. Multiple linear regression equations for  $\ln$  chl *a* within various current velocity ranges for two experimental periods.

Equation <sup>a</sup>	$R^2$	$n$	Expt. period <sup>b</sup>	Velocity range ( $\text{cm} \cdot \text{s}^{-1}$ )
$\ln \text{chl } a = 0.638 + 0.0161T + 0.1051V + 0.0226P$	0.374	24	1	<20
$= -1.473 - 0.0712T + 0.0725V + 0.0627P$	0.459	13	1	20–50
$= 1.736 + 0.0231T - 0.0341V + 0.0556P$	0.546	8	1	50–80
$= 1.107 + 0.1918T - 0.0902V + 0.0349P$	0.779	7	2	<20
$= -6.871 + 0.3576T + 0.0806V + 0.0997P$	0.531	7	2	20–50
$= 0.084 + 0.1636T - 0.0270V + 0.0362P$	0.699	15	2	50–80

<sup>a</sup>Symbols: Chl *a* = chlorophyll *a* ( $\text{mg} \cdot \text{m}^{-2}$ ),  $T$  = time (days),  $V$  = current velocity ( $\text{cm} \cdot \text{s}^{-1}$ ),  $P$  = orthophosphate-phosphorus concentration ( $\mu\text{g} \cdot \text{L}^{-1}$ ),  $n$  = number of data points,  $R^2$  = coefficient of determination.

<sup>b</sup>Period 1, July 7–August 25, 1977, period 2, August 25–September 21, 1977.

velocities and nutrient concentrations, revealed several conclusive patterns of association, as follows:

Relative chl <i>a</i> accrual rate	Relative independent variable magnitude
High	Moderate average velocity Moderate peak velocity Moderate-high PO <sub>4</sub> -P concentration Moderate-high total soluble phosphorus concentration
Low	High average velocity High peak velocity Low PO <sub>4</sub> -P concentration Low total soluble phosphorus concentration Low NO <sub>3</sub> -N concentration

These observations suggest that rapid accrual of algal biomass, as represented by chl *a*, required moderate velocity over the growth period. High-ranking chl *a* accumulation rates almost never occurred at the highest (near 100 cm · s<sup>-1</sup>) or lowest (near zero) velocities. Observing a large chl *a* standing crop at the conclusion of the growth period also depended on the peak velocity not exceeding the range of moderate velocities. The associations between chl *a* accrual and nutrient concentrations indicated above are consistent with those denoted earlier for individual sites.

Stepwise multiple linear regression was applied to investigate statistically the combined data, in light of the dependence of chl *a* accrual on several variables and the apparent existence of an interaction between velocity and the limiting nutrient. These equations are in the general form:

$$\ln \text{chl } a = a_0 + a_1T + a_2P + a_3V.$$

Table 2 presents the equations derived.

The multiple regression equations show several trends. Algal growth in both experimental periods responded positively to velocity in the range 20–50 cm · s<sup>-1</sup>. On the other hand, response was negative in both periods in the 50–80 cm · s<sup>-1</sup> range. At the lowest velocities the relationship of growth to velocity was inconclusive, being negative in one case and positive in the other. Thus, the equations state that velocity increase beyond 50 cm · s<sup>-1</sup> decreased the accumulation of periphytic algae, while increases in the range terminating at 50 cm · s<sup>-1</sup> generally enhanced algal growth.

It may also be noted in Table 2 that both equations developed for the 20–50 cm · s<sup>-1</sup> velocity range have negative initial coefficients (*a*<sub>0</sub>), although these coefficients are positive in every other case. This occurrence is coupled with sharp increases in the phosphorus coefficients (*a*<sub>2</sub>) in both cases compared to the respective equations for <20 cm · s<sup>-1</sup>. This aspect of the regression equations indicates mathematically that a velocity increase from the low to the medium range hindered chl *a* accumulation where phosphorus concentration was relatively low but enhanced accrual at higher P concentrations.

This relationship is illustrated in Fig. 4 using equations derived for the late summer period, in which chl *a* is graphed with respect to PO<sub>4</sub>-P concentration for the three velocity

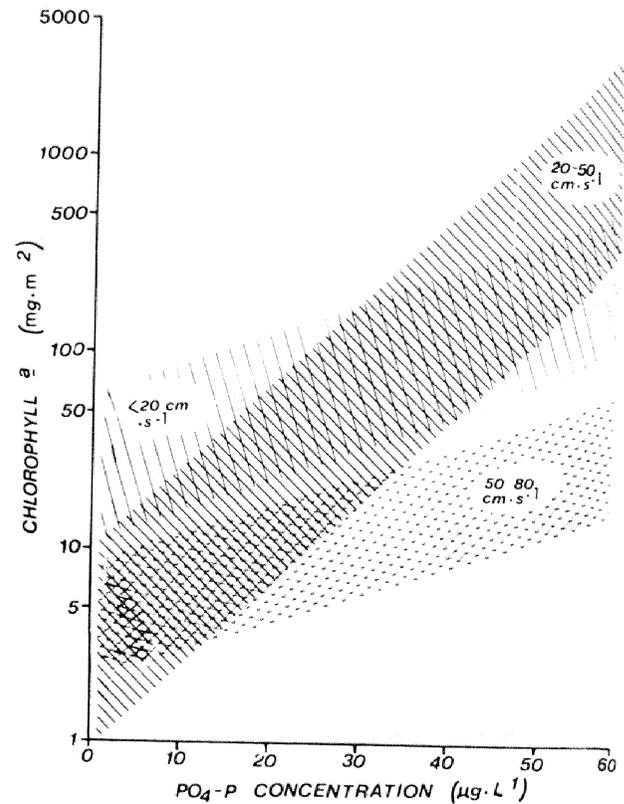


FIG. 4. Chlorophyll *a* accumulation in 14 d according to multiple linear regression equations derived from data collected August 25–September 21, 1977.

ranges and a 14-d growth period. The regression analysis thus predicts that 2 wk of periphytic algal accumulation in the 20–50 cm · s<sup>-1</sup> velocity range would surpass that in the <20 cm · s<sup>-1</sup> range under most velocity conditions only when the PO<sub>4</sub>-P concentration is greater than ~45 µg · L<sup>-1</sup>. The lowest levels of chl *a* accumulation are forecast in the 50–80 cm · s<sup>-1</sup> range generally and the 20–50 cm · s<sup>-1</sup> when limiting nutrient concentration is very low.

#### HETEROTROPHIC ACTIVITY

Development of the attached heterotrophic community was investigated primarily with the aid of the Heterotrophic Index. As illustrated by Fig. 5–7, a higher index (more heterotrophs relative to autotrophs) nearly always developed at the higher velocity in a given stream. It tended to increase when severe erosion of the community resulted from a storm, as occurred at stations SC-1 and JC-1. The association between HI and velocity was further investigated by a statistical correlation analysis performed on the total data set. The index was positively correlated with average velocity at a significance level of *P* < 0.001. Thus, high ordinary velocities and elevated peaks following storms apparently favored the attached consumers and decomposers relative to the primary producers.

As a further observation concerning the periphyton community as a whole, statistical analysis showed ln ATP to

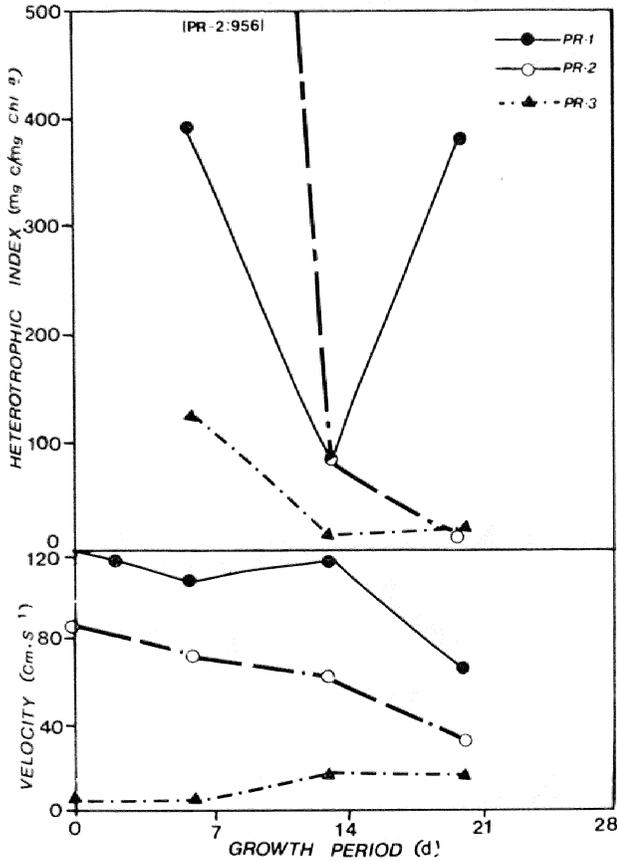


FIG. 5. Heterotrophic index and velocity versus time; Pilchuck River: August 25–September 14, 1977.

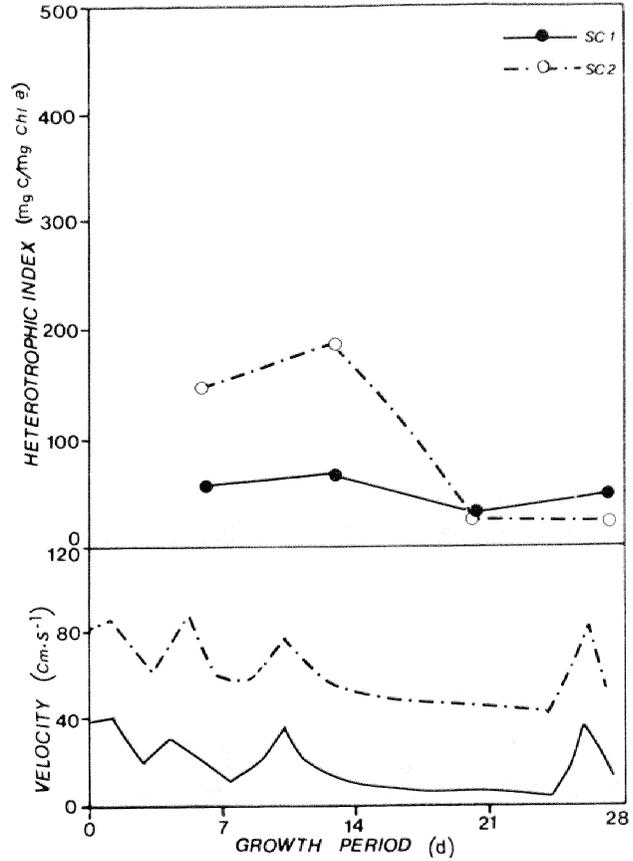


FIG. 6. Heterotrophic index and velocity versus time; Swamp Creek: August 25–September 21, 1977.

correlate positively and significantly with both dissolved organic carbon concentration ( $P < 0.001$ ) and  $\text{PO}_4\text{-P}$  concentration ( $P < 0.01$ ). There was, however, no significant correlation with particulate organic carbon. The periphyton in the streams studied, therefore, must have consisted primarily of algae and decomposing organisms, subsisting on dissolved materials, with forms capable of handling particulate organics, such as protozoa and rotifers, of secondary importance.

### Discussion

A consistent pattern appeared in the analysis of relative chl *a* accrual rates for the individual streams and in the statistical treatment of the combined data set. Relationships of accrual rate with time for the respective streams generally showed chl *a* accumulation to be inversely related to velocity, except when orthophosphate-phosphorus concentration continuously surpassed  $45 \mu\text{g} \cdot \text{L}^{-1}$ . In these instances, which occurred mostly in Swamp Creek, growth at the station having a velocity of  $\sim 50 \text{ cm} \cdot \text{s}^{-1}$  exceeded that at  $10\text{--}20 \text{ cm} \cdot \text{s}^{-1}$  after about 2 wk of growth. Multiple regression equations derived from the full data set for both the earlier and later experimental periods demonstrated the same trend: chl *a* accumulation was favored by velocity increase as long as  $\text{PO}_4\text{-P}$  concentration exceeded a minimum value, which depended

on the two velocities being compared. Otherwise, accrual was more rapid at relatively low velocity. Graphs of individual stream results and multiple regression predictions also agreed where high velocities were concerned: the lowest standing crops were observed in analyses of the individual cases as well as the general data in that region.

It should be noted that these results are in general agreement with results from other work (McIntire 1966; Phaup and Gannon 1967; Ball et al. 1969; Sperling and Hale 1973; Rodgers and Harvey 1967). Specific confirmation of the interaction between velocity and nutrients noted here does not appear, however, because previous studies did not encompass the wide ranges of both velocity and limiting nutrient concentration investigated in this work.

In explanation of the tendencies described, it is hypothesized that offsetting mechanisms, both functions of velocity, are involved. Velocity increase apparently assists productivity by improving turbulent diffusion. Whitford (1960) has hypothesized that the effect of greater turbulence is to increase the diffusion gradient and improve the exchange of materials between water and living cells. In contrast, any increase adds to the frictional shear force of the passing flow tending to tear a progressively greater proportion of the produced material from the surface of attachment. The latter effect must predominate unless nutrient concentration is sufficient to establish an

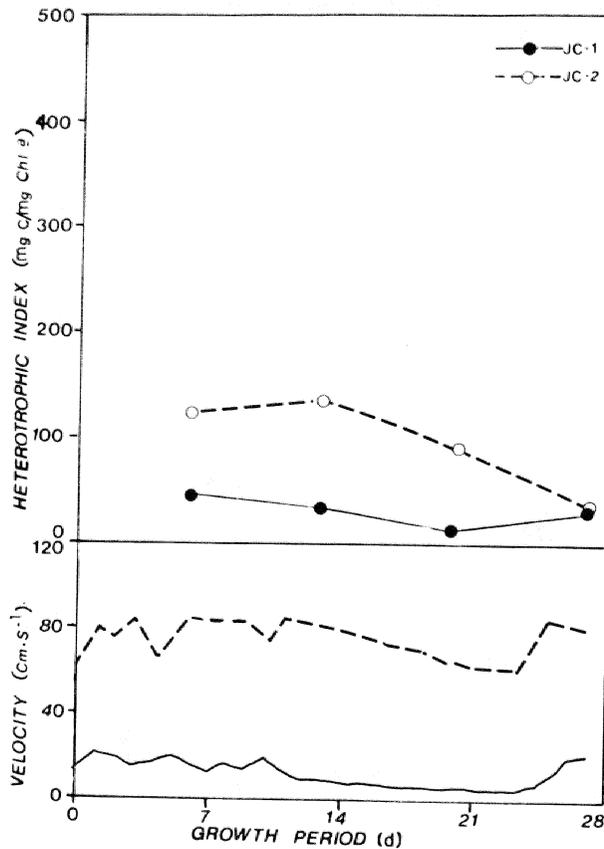


FIG. 7. Heterotrophic index and velocity versus time; Juanita Creek; August 25–September 21, 1977.

efficient delivery system. Velocity increase to a level well above  $50 \text{ cm} \cdot \text{s}^{-1}$  increases friction to the point that the advantage of improved nutrient delivery is overcome.

Representing gross production, periphyton growth rate at a given nutrient concentration would be expected to increase with increasing velocity and consequent improved diffusion. Velocity would thus improve the efficiency with which periphyton absorbs nutrients. Biomass accrual rate and ultimate standing crop, measures which omit exported production, appear to react to velocity fluctuations in the more complex fashion previously described as a result of the interplay of the effects of diffusion and erosion.

Concerning the heterotrophic members of the periphyton, consideration of both the plots of Heterotrophic Index for the individual streams and correlations using the aggregated data again showed consistency. The strong tendency for the accrual of heterotrophs to be favored relative to that of autotrophs by velocity increases and high poststorm peak velocities may have several explanations. First, the animal members of the periphyton may have a greater ability to cling to the substrate than the algae and thus exist in relatively greater abundance in fast currents. If this is true, they would also better survive erosive stresses. A second conceivable reason is that sudden velocity increases detach much of the algae, making more food available to the decomposers residing

downstream. A related effect may be the entrainment and transport of organic materials formerly sequestered in the stream bed. Also, decomposers may colonize the newly cleaned substrate more readily than producers.

The insights into the responses of the autotrophic and heterotrophic lotic periphyton to wide ranges of current velocity and nutrients gained from this research have some management implications. Flow regimes and nutrient concentrations are subject to modification by such human impacts as stream channel reconstruction, storm runoff drainage, point source effluents, and water diversions for irrigation or other purposes. It is clear that the lotic primary producers and associated sessile organisms are strongly affected by alterations of their physical and chemical environments of the magnitudes that can be expected as a result of such alterations. These effects may include increased productivity, perhaps culminating in dominance by nuisance algal forms or filamentous heterotrophs or, conversely, severe reduction of the attached community by erosive stress. To the extent that periphytic organisms interact trophically with other stream biota, which is often considerable, especially in shallow, well-lighted streams (McConnell and Sigler 1959; Cummins et al. 1966; Southworth and Hooper 1974; Elwood and Nelson 1972; Eichenberger 1975; Lyford and Gregory 1975), such negative or positive impacts on the periphyton can be expected to reverberate throughout the flowing water food web.

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