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Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia¹

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Abstract

Measurements of photosynthetic pigments have been used to estimate the biomass of benthic microalgae on soft and hard substrates in a small river in the Virginia Piedmont. The irregular distribution of periphyton was partially related to substrate distribution and is explained as a result of spatial variations in the current regime in the river. High flow due to unpredictable and heavy rainfall is shown to be the main factor controlling algal biomass. Deterministic predictions of algal crop are therefore not possible in rivers of this type.

The factors that control the growth and biomass of periphyton (using the term to include all microalgae living on or close to any submerged surface) in a river include temperature, light intensity, current and scour, substrate, grazing, and nutrients (Hynes 1970). Little is known about seasonal changes in periphyton biomass (as opposed to species composition) because few rivers have been sampled quantitatively for a sufficient time. With a few exceptions (e.g. Douglas 1958), direct estimation of the numbers of one or more species has proved too slow for use in extensive surveys, and the use of artificial substrates to facilitate sampling is open to criticism (Tippett 1970). Photosynthetic pigments can be determined more quickly and, despite variability in chlorophyll:organic biomass ratios, can be used as rough measures of plant biomass.

We used estimates of pigment densities in the Mechums, a small river in the Virginia Piedmont, to investigate the hypothesis that periphyton biomass is ultimately controlled more by river flow than by any other factor. In our hypothesis,

variations in flow, acting through changes in the rates of scour, washout, and sedimentation, determine the spatial pattern of, and the time course of changes in, the biomass of periphyton. Spatial variations in river flow are reflected in substrate distribution. Thus periphyton density should relate to substrate as well as flow. In the Mechums as in many rivers, short periods of greatly increased flow result from heavy rainstorms. We suppose that periphyton biomass is very sensitive to these floods. If periphyton otherwise grow steadily, then biomass ought to be proportional to time elapsed since the last flood.

If our hypothesis is correct, and if the rainstorms that produce high river flows are random events, then deterministic predictions of algal productivity will not be possible for rivers like the Mechums.

We thank S. Shoup for some of the velocity data, the Virginia State Water Control Board for the Rivanna North Fork discharge data, and NOAA for the Charlottesville-Albemarle Airport rainfall data.

Methods

The Mechums River drains a forested and farmed basin in Albemarle County, Virginia, on the eastern slopes of the Blue Ridge Mountains. Details of the river and accounts of productivity and respiration measurements are given by Kelly et al. (1974).

The river is not gauged, so continuous

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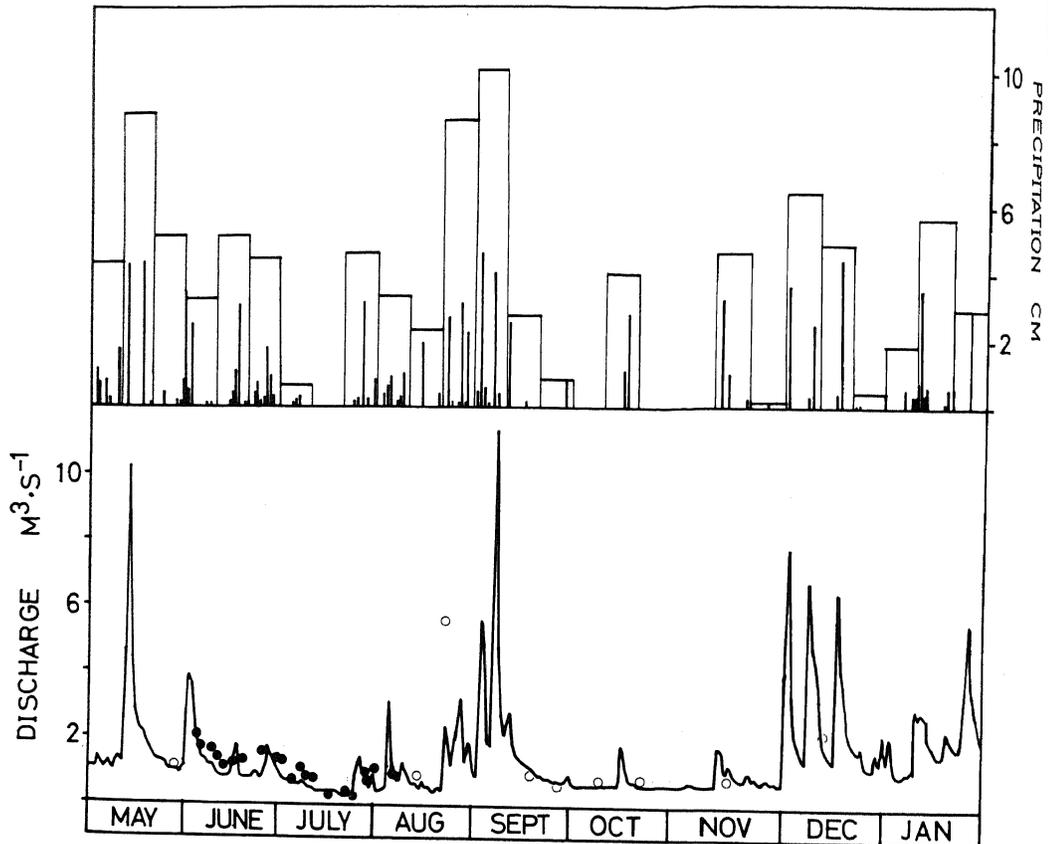


Fig. 1. Precipitation (daily and 10-day totals) observed at Charlottesville-Albemarle Airport, and Mechums hydrograph, derived mainly from discharge data for North Fork of Rivanna. ●—Discharge measurements made in Mechums; ○—estimates of Mechums discharge from measurements of cross-sectional area.

records from the North Fork of the Rivanna River were used to estimate daily mean discharge in the Mechums. The basins of the rivers are close and have similar drainage characteristics. Mechums discharge was directly determined from velocity profiles for a number of days in June and July, and the discharge from the North Fork was consistently 2.8 times that in the Mechums. Estimates of Mechums flow made later in the year from cross-sectional data generally agreed well with predictions from North Fork records (Fig. 1). Some obvious discrepancies were the result of intense local thunderstorms centered in only one of the drainage basins. Rainfall data were obtained from the Charlottesville-Albemarle Airport, close to the North Fork gauging station but about 20 km NW of the Mechums.

Substrate and periphyton abundance were investigated in a 100-m stretch of river of mean width 15 m. On two occasions, depth contours and substrate distributions were mapped in detail. Two typical transverse transects, separated by 50 m, were sampled at nearly weekly intervals during June, July, and August, and less frequently during autumn and winter.

Soft sediments were sampled at regular intervals along the transects by pushing into the bottom a small petri dish (area about 18 cm² and depth about 1 cm) and sliding an aluminum plate beneath it. To

avoid repetitive sampling of the same points, the start of each transect was on each occasion moved a few decimeters at random. Rocks were picked up randomly from appropriate regions of the transects and placed in thick polyethylene bags with care to lose as little as possible of the periphyton. Orientation and exposure of rocks were noted before removal, so that pigment density could be calculated using the projected area of the rock. Rocks taken ranged from 0.1–5 kg in weight and from 10–30 cm in mean diameter. No correlation was found between chlorophyll density and rock weight and thus we feel that pigment densities on sampled rocks were typical of those too large to be removed.

The nature of the substrate was recorded at 1-m intervals along the transects as mud (up to 0.25-mm particle diameter), sand (0.25–4-mm particle diameter), muddy-sandy gravel (a heterogeneous mixture, probably the result of silt deposition over various sand-gravel mixtures, and 0.07–25-mm particle diameter), gravel (2–25-mm particle diameter, often with sand intermixed), and rock (from 4 cm upward).

Samples were returned in an icebox to the laboratory and immediately frozen. Densities of photosynthetic pigments (in $\text{mg}\cdot\text{m}^{-2}$) were determined using several extractions with methanol as described by Tett et al. (1975). Initially we calculated extract pigment concentrations using

$$C = G(O - A) \quad (1)$$

and

$$P = G(HA - O). \quad (2)$$

O and A refer to pre- and postacidification corrected optical densities at 666 nm. C and P are extract chlorophyll a and pheophytin a concentrations. G and H are defined in Tett et al. (1975).

These equations, however, implicitly assume that the extinction coefficient of pheophytin a at 666 nm in methanol is unaffected by pH. Finding this assumption to be incorrect (Marker 1972, 1977),

we attempted to use the following modified equations.

$$C = G[(O - A) - PJ] \quad (3)$$

and

$$P = G(HA - O)/(1 - GJ). \quad (4)$$

J is a correction factor and is explained by Tett et al. (1977). This procedure, however, sometimes led to the calculation of negative chlorophyll concentrations. As Marker (1977) pointed out, and as we discussed in Tett et al. (1977), the presence of chlorophyll degradation products other than pheophytin, or indeed of any pigment whose extinction properties at 666 nm are not affected by acidification, will introduce errors into estimates of chlorophyll a and pheophytin a . We derived the following modification to Eq. 4 to investigate the errors that might result.

$$P = G[(HA - O) + BE_b(1 - H)]/(1 - GJ). \quad (5)$$

B refers to the concentration in the extract of a third pigment, whose extinction coefficient E_b is supposed to be unaffected by acidification. Neglect of the term $BE_b(1 - H)$ results in overestimation of pheophytin, and hence, through Eq. 3, in underestimation of chlorophyll. The problem was that we had no information concerning E_b and no way of estimating B . It is likely that interfering pigments were present in relatively large amounts in Mechums River extracts, and we therefore decided to use Eq. 1 and 2 on the grounds that with such extracts results were probably no more in error than those obtained from Eq. 3 and 4, and, additionally, included no negative chlorophyll concentrations.

The following reservations therefore apply to our pigment results. Chlorophyll a concentrations calculated by Eq. 1 are corrupted by pheophytin a but are not affected by other pigments. Our determinations of G and J (Tett et al. 1977) show each microgram of pheophytin adds $0.38 \mu\text{g}$ to calculated chlorophyll concentrations. Pheophytin concentrations com-

puted by Eq. 2 are possibly heavily corrupted by other pigments, and hence are useful neither for correcting chlorophyll values obtained from Eq. 1 nor for discussion except in a qualitative fashion. We hereafter refer to "pheopigments" to emphasize the mixed nature of what was estimated.

The problem of pheopigment corruption of our chlorophyll estimates is not so important as it seems. We are concerned mainly with relative changes in pigment density, and our estimates of these changes are in error only if the extent of pheopigment corruption changes. Our results (with some allowance for overestimation of chlorophyll) and those of Marker (1976), Moss and Round (1967), and Hickman and Round (1970) show that the ratio pheophytin *a*:chlorophyll *a* varies from <0.2 in periphyton from clean rock and gravel to 1.8 in mud. By assuming the following mean ratios for our substrate types, and by making some allowance for within-substrate variability in relative amount of pheopigment, we were able to calculate worst-case additions to our variance estimates. A detailed examination of our results, combined with numerical simulation of the effects of interfering pigments, suggests that the true variances are less than these worst-case estimates. The ratios are: mud, 1.8; sand, 1.3; muddy-sandy gravel, 1.3; gravel, 0.7; rock, 0.4.

Finally there is the problem of the statistical properties of the pigment data. Theory suggests that the biomass of growing periphyton increases exponentially and thus that pigment densities should have an approximately log-normal distribution. The need for logarithmic transformation of our data was confirmed by the existence, in most cases, of a significant correlation between pigment density variance and means when these were calculated for untransformed data (see Sokal and Rohlf 1969). No such relationship was found for gravel samples, presumably because mean values were low and errors that were independent of the mean were dominant. In view however of the a priori reasoning and the

Table 1. Best estimates of standard deviations of chlorophyll densities on each substrate type, following logarithmic transformation of data. A—Substrate type; B—logarithmic standard deviation; C—total number of samples; D—number of occasions substrate sampled; E—degrees of freedom (C-D). Mud (1)—4 June through 6 August, and from 12 December; mud (2)—14 August through 15 November; Msg—muddy-sandy gravel.

A	B	C	D	E
Mud (1)	0.34	50	11	39
Mud (2)	0.14	24	8	16
Sand	0.32	100	19	81
Msg	0.42	24	11	13
Gravel	0.21	22	10	12
Rock	0.23	65	17	48

need for a uniform approach, data from all substrates were logarithmically transformed before further statistical treatment.

Results

Chlorophyll distribution—Figure 2 illustrates the variation in chlorophyll density across the river. Much of the variability can be related to substrate differences which in turn derive from differences in current velocities. For example on 11 June (Fig. 2A) pigment densities were highest close to the banks, where a mixture of silt and fine sand was deposited in low current velocities. Coarse sand was found in the highest velocities in the middle of the river and had the lowest pigment densities.

A significant correlation ($r = 0.76$, reducing to 0.72 if corrections are made for variation in the extent of pheopigment corruption between substrates) was found between logarithmically transformed chlorophyll densities and current velocities for 76 soft sediment samples taken between 4 June and 6 August. However, periphyton biomass recorded at a particular location is not a direct result of the velocity at that moment but is the cumulative outcome of the flow regime over some prior period. As the nature of the substrate is probably the best indicator of the flow regime, the soft sediment pigment data were divided into four groups corresponding to the substrate types described above. This resulted in reduced

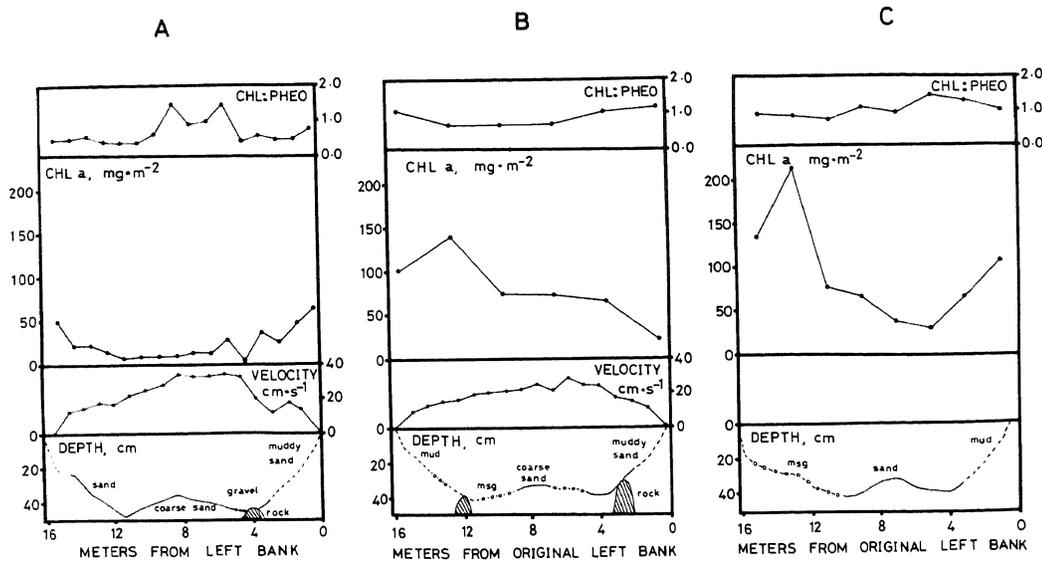


Fig. 2. Cross section of Mechums River, 1974. A—11 June (discharge = $1.3 \text{ m}^3 \cdot \text{s}^{-1}$); B—30 July ($0.9 \text{ m}^3 \cdot \text{s}^{-1}$); C—15 November ($0.8 \text{ m}^3 \cdot \text{s}^{-1}$). Preceding "major floods" terminated on 3 June and 4 September.

correlations between velocity and log-transformed chlorophyll (mud, $n = 27$, $r = 0.33$; gravel, $n = 6$, $r = 0.22$; muddy-sandy gravel, $n = 10$, $r = 0.44$). Only in the case of sand was the correlation significant ($n = 33$, $r = 0.41$).

Although, because of the small number of samples taken from each substrate type, different variances were calculated for each occasion of sampling, the differences between occasions were not significant. We therefore calculated a best estimate of the variance for each substrate type by totalling, for all occasions, sums of squares from each occasion that the substrate was sampled and dividing by the total degrees of freedom (Table 1). The hypothesis implicit in this statistical treatment is that, except in the case of mud data, the nature and extent of within-substrate patchiness remained more or less constant during the whole period of observation. In the case of mud samples it was necessary to divide the data into two periods, between which there were significant differences in mean variance.

Table 1 shows that 95% confidence intervals for individual samples were very wide. For example, on any particular

date, the chlorophyll density of sand samples ranged from about 0.21 to about 4.8 times the mean value for sand on that date. Tett et al. (1975) found extraction errors for sand-derived chlorophyll to be on the order of $\pm 25\%$. This does not take into account possible variation in corruption of chlorophyll values by pheophytin, but even so it is evident that most of the range in sample values was due to patchiness. These conclusions apply to all other samples except those taken from mud between 14 August and 15 November. For these, 95% limits were from about 0.5 to 2.0 times the relevant mean. Much of this range can be explained by extraction error alone, implying that mud pigment densities were more homogeneous than those on other substrates.

Figure 3 shows, for each substrate type, the variation with time in logarithmic mean chlorophyll *a* densities. The bars ($\pm 1 \text{ SE}$) were obtained by dividing the standard deviations in Table 1 by the square root of the number of samples taken from the substrate on that occasion of sampling. The values in Table 1 take account of possible variation in degree of corruption within sediments and dates,

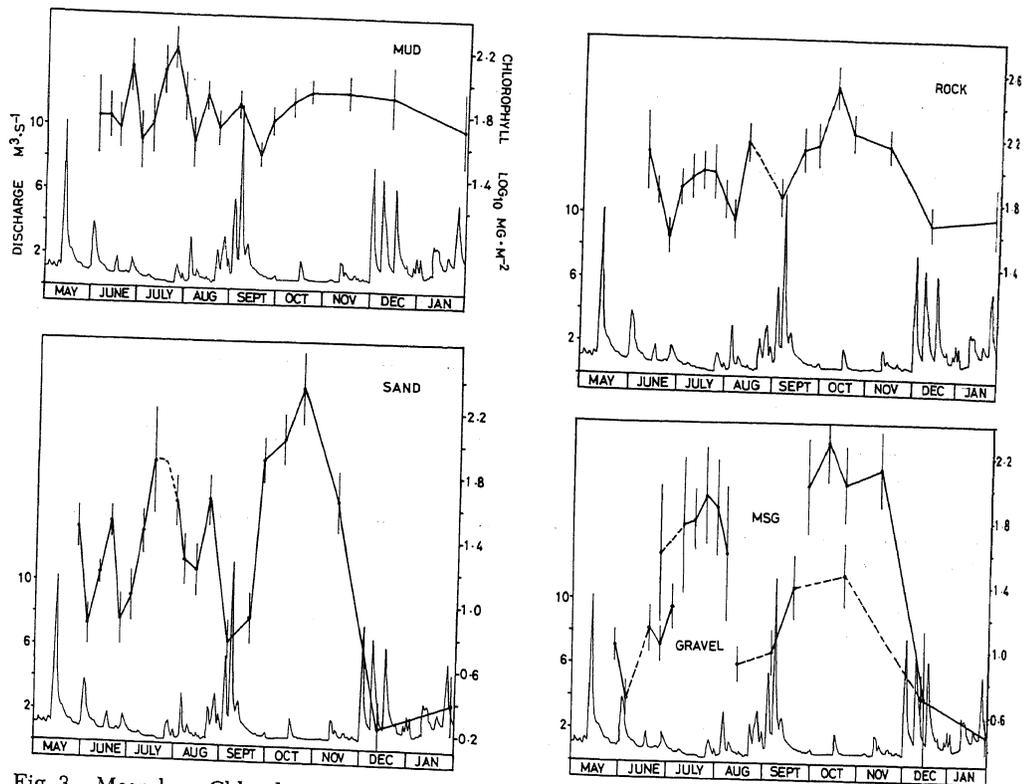


Fig. 3. Mean \log_{10} Chl *a* density on various substrates. Vertical bars show ± 1 SE but take no account of possible variations in degree of corruption by pheopigments. Points connected by broken lines indicate that whereas river was sampled during that period, no samples were taken from that particular substrate. Widely separate parts of graphs for gravel and muddy-sandy gravel (MSG) are however not connected. Hydrograph shows occurrence of high flow periods.

but not of those between dates. They should possibly be increased by up to 0.03 for the smallest values.

Pheopigments—Extracts from rock and, to a lesser extent, gravel, consistently showed a lower pheopigment content than extracts from mud, sand, and muddy-sandy gravel. Chlorophyll:pheopigment ratios for mud and rock are shown in Fig. 4. Allowance can be made for worst-case effects of pheophytin corruption of mud chlorophyll values, relative to rock values, by decreasing all logarithmic mud ratios by 0.19.

Macrophytes—The riverweed *Podostemum ceratophyllum* was the only macrophyte present. Plants appeared vigorous during May and June but declined during July and August. In late September old plants began to grow again and

new plants were seen. The riverweed disappeared at the end of the year. During its periods of abundance, *P. ceratophyllum* was found on 25–30% of rocks and thus on about 8% of the riverbed, although with quite variable density. Occasional samples of rocks bearing the riverweed were taken and estimates made of the pigment density of associated epiphytic and epilithic algae. This was not significantly different from that of periphyton on stones without the riverweed, and thus we did not distinguish between periphyton densities on the two types of rock. The chlorophyll density of riverweed, estimated at less than an average of $10 \text{ mg} \cdot \text{m}^{-2}$ over the 100-m reach, was insignificant compared to periphyton chlorophyll densities of 50–150 $\text{mg} \cdot \text{m}^{-2}$ in June and July and 200 in October.

Macrophyte chlorophyll was not included in whole river pigment estimates because it seemed dubious to equate macrophyte and periphyton chlorophyll densities as indices either of photosynthetic potential or of biomass.

Overall chlorophyll density—We did not calculate the mean chlorophyll density for the 100-m reach directly (by summing sample values) as this would have required too large a number of random samples. Instead we took samples “stratified” by substrate type and computed the overall density indirectly from the means for each substrate (C_t) weighted according to the proportion (S_t) of riverbed occupied by that substrate (subscript t indicates substrate type). Because the errors of neither the chlorophyll estimates nor the substrate proportions were normally distributed, a Monte Carlo method was used to give best estimates of overall density and of the confidence intervals for these estimates.

The procedure is illustrated in Table 2. The proportion of various substrate types having been estimated from the maps of the 100-m reach, observations of substrate along the two standard transects were used to correct for variations

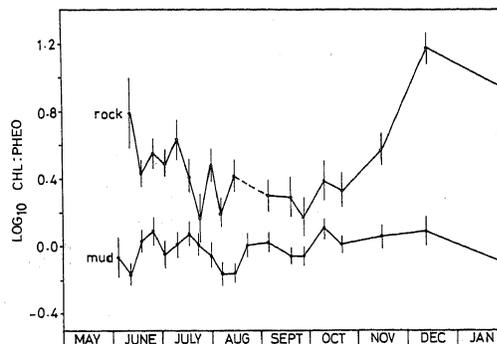


Fig. 4. Temporal variation in \log_{10} Chl a :pheopigment ratios for mud and rock samples. Bars give ± 1 SE, but do not allow for possible variations in degree of chlorophyll corruption by pheophytin or in pheopigment composition. Dashed line indicates that no rock samples were taken on 22 August.

present on each occasion of sampling. The values of S_t thus obtained (Fig. 5) were randomly corrupted using errors initially normally distributed but then modified so that $\sum_t S_t'$, the sum of the corrupted proportions, was equal to the sum of observed proportions $\sum_t S_t = 1$. The errors used were such that 95% of the S_t' values fell within $\pm 1/3$ of the uncorrupted values. This error is less than that indi-

Table 2. Example of computation of overall chlorophyll density from data of 25 June 1974. (See text for method of simulating corrupted values.)

Data	Mud	Sand	Msg	Gravel	Rock										
Proportion of bottom covered (S_t)	0.19	0.30	0.04	0.20	0.27										
\log_{10} Chl a $\text{mg} \cdot \text{m}^{-2}$ (C_t)	2.08	0.86	1.58	1.02	1.56										
No. samples (N_t)	4	4	1	3	5										
Simulated data set															
Chl a $\text{mg} \cdot \text{m}^{-2}$	202	3	40	8	23										
(simulated sample values)	341	38		5	70										
	89	4		25	56										
	105	14			41										
					35										
Mean Chl a $\text{mg} \cdot \text{m}^{-2}$ (C_t')	184	14.8	40.0	12.7	45.0										
Proportion of bottom covered (S_t')	0.158	0.411	0.043	0.172	0.216										
Product of C_t' and S_t' ($\text{mg} \cdot \text{m}^{-2}$)	29.1	6.1	1.7	2.2	9.7										
Sum of products = overall Chl a density (D) = $48.8 \text{ mg} \cdot \text{m}^{-2}$															
Distribution of 200 values of D															
Rank	1	3	5	11	31	51	71	median	131	151	171	191	196	198	200
D	93.8	86.0	81.9	72.9	63.4	56.3	52.0	46.7	42.2	39.4	34.6	28.5	27.3	24.6	19.5
Logarithmic mean = $1.67 \log_{10} \text{mg} \cdot \text{m}^{-2}$ (SD = $0.12 \log_{10} \text{mg} \cdot \text{m}^{-2}$)															

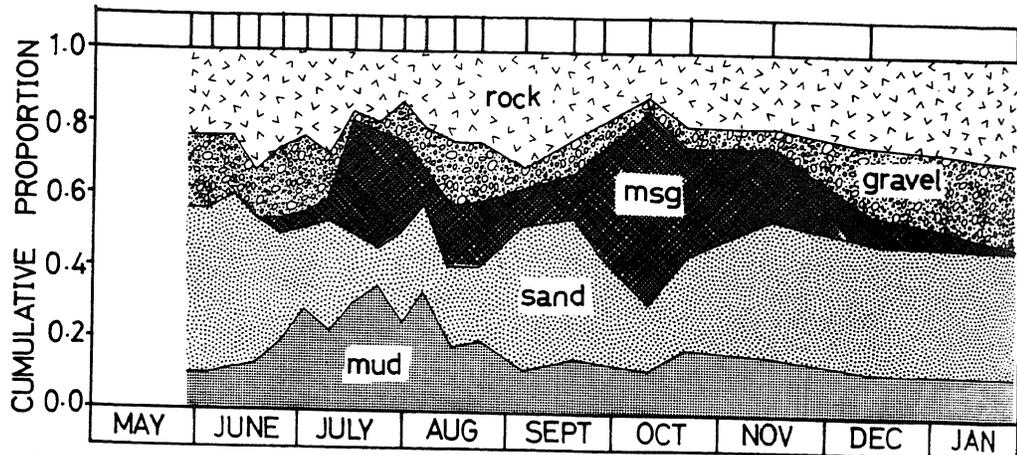


Fig. 5. Cumulative proportion of river bottom occupied by various substrates on different occasions of sampling, corrected to represent 100-m stretch of Mechums River. Sampling dates at top of diagram. Whole stretch mapped on 18 June and 19 September.

cated in Greig-Smith (1957) for 30 observations, the number made on the two standard transects, but can be justified on the grounds that we estimated changes in

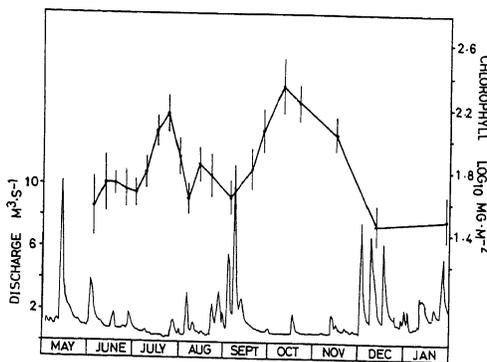


Fig. 6. Overall \log_{10} Chl *a* density for 100-m stretch of Mechums River, computed by Monte Carlo method (see text and Table 2). Usual interpretation applies to \pm SE bars in this figure: if estimates of *D* were made by repeatedly sampling at random, then 68% of individual *D* estimates would be within error bars. If two points are sufficiently far apart so that SE bars do not overlap, they may be considered to be significantly different with a probability ≤ 0.05 of error in this conclusion (large-sample case applied, since errors used to corrupt simulated values were mostly based on more than 30 df). SE bars take no account of possible variations in pheopigment corruption resulting from changes in pattern of chlorophyll:pheopigment ratios associated with changes in proportions of various substrates. These effects are, however, likely to be submerged in other variation.

sediment proportions relative to the detailed maps and used systematic rather than random sampling.

To obtain mean pigment densities for each substrate the logarithmic means shown in Fig. 3 were perturbed N_t times with a normally distributed random variable and an appropriate standard deviation from Table 1. N_t refers to the number of samples taken from a substrate on any one occasion. The N_t perturbed values were exponentiated, summed, and divided by N_t to give C'_i —an indirect estimate of the arithmetic mean for the substrate. The C'_i values were not necessarily the same as arithmetic means computed directly from untransformed sample values, the latter means being biased estimates of the former.

Two hundred sets of S'_i and C'_i were computed and used to obtain 200 estimates of overall chlorophyll density, $D = \sum S'_i C'_i$, for each occasion of sampling. These estimates showed a skewed distribution that was corrected by logarithmic transformation. Logarithmic means and standard errors calculated from the 200 estimated values and plotted in Fig. 6 are therefore the best estimates of the mean chlorophyll density and its standard error over the 100-m reach. "Best" is used here in the sense of least biased: the chlorophyll estimates

Table 3. Floods and chlorophyll density. "Major" flood is an increase in discharge of $2 \text{ m}^3 \cdot \text{s}^{-1}$ or more; "minor" flood, increase of between 1 and $2 \text{ m}^3 \cdot \text{s}^{-1}$. A—Flood-free period; B—dates of flood; C—length of flood-free period; D—interval from beginning of flood-free period until date given in E; E—date of observation of maximum chlorophyll density during flood-free periods or of minimum chlorophyll density immediately after floods; F—chlorophyll *a* density, $\log_{10} \text{ mg} \cdot \text{m}^{-2}$.

A	B	C	D	E	F
Flood-free period					
13 Sep–15 Oct		33	28	10 Oct	2.34
30 Jun–24 Jul		25	24	23 Jul	2.15
6–21 Aug		16	9	14 Aug	1.83
4–15 Jun		12	8	11 Jun	1.71
19–25 Jun		7	7	25 Jun	1.67
During or immediately after minor flood					
	16–18 Jun		0	18 Jun	1.71
	12–13 Nov		2	15 Nov	2.03
	26–29 Jun		3	2 Jul	1.65
	25–27 Jul		3	30 Jul	1.88
	16–17 Oct		4	21 Oct	2.23
During or immediately after major flood					
	22–27 Aug		0	22 Aug	1.76
	8–12 Dec		0	12 Dec	1.45
	31 May–3 Jun		1	4 Jun	1.56
	5 Aug		1	6 Aug	1.61
	2–4 Sep		1	5 Sep	1.62
	25–27 Jan		1	28 Jan	1.49

are of course corrupted by pheophytin. Our Monte Carlo method took no account of possible variations in corruption between substrates, and thus the error estimates might be slightly low. Because most observed variation resulted from patchiness it is unlikely that there was appreciable underestimation.

Rainfall, discharge, and chlorophyll density—Figure 1 shows a series of river spates associated with heavy rainstorms, and Fig. 3 and 6 indicate a relationship between pigment density and flow. Table 3 shows a relationship between "major" and "minor" floods and maxima or minima in observed chlorophyll densities.

Between 15 May 1974 and 31 January 1975 there were 11 periods of 7 days or longer free of floods. The longest lasted 33 days and the median length was 12 days. The river was in a state of flood on 61 out of 261 days, and 31 days fell into periods when there were <7 days between floods. There were five periods (totalling 211 days) of >7 days between

major floods, of which the longest lasted 82 days and the median length was 36 days.

Discussion

The results indicate a complex relationship between current velocity, prior flow regime, substrate type, and pigment density. We will first consider how these factors interact with regard to periphyton patchiness, and then how the unpredictable occurrence of floods influences the average chlorophyll density of the river.

Velocity, substrate, chlorophyll density, and patchiness—Water movement sorts particles by size, but the process is complex and the earlier current regime can result in a substrate and periphyton distribution that only roughly reflects velocities at the time of sampling. Lateral variation in current speed arranges sediments across a river section (Fig. 2). Rifles, pools, curves, and other irregularities produce longitudinal variation. The different substrates support different pig-

ment densities, each differently influenced by sedimentation, bedload movement, and scouring.

There was a significant but irregular relationship between chlorophyll density and velocity at the time of sampling. Because biomass develops over a period of time, the irregularities seem likely to be related to prior currents and the way these have affected the substrates. There were differences between substrates both in mean pigment densities and in mean extent of periphyton patchiness. The latter is shown by the variance differences in Table 1. Figure 3 shows densities to be more variable with time on some substrates than on others. Thus chlorophyll densities on mud were least susceptible to varying flow, those on sand most susceptible. This is probably because mud was deposited in low velocity regions where there was slight bed movement, whereas sand, in regions of higher current, was more sensitive to changes in flow. During long periods of base flow, however, sand developed high chlorophyll densities, probably because little sedimentation occurred to smother the periphyton. The complexity of the situation is also demonstrated by gravel, which normally bore low periphyton biomasses. During low flow periods, however, silt deposition on areas of coarse sand and gravel led to the occurrence of muddy-sandy gravel (Fig. 6) with high pigment densities. During October this sediment covered a large part of the riverbed and had a very patchy coating of diatom filaments (probably *Melosira* sp.). The patchiness in periphyton distribution might have been due to the sensitivity of muddy-sandy gravel to small differences in flow. By contrast, the relative homogeneity of pigment densities in muddy areas during the low flow period of August through November can be explained by the mud at the river edge being undisturbed and biomass reaching nearly an equilibrium level.

Chlorophyll density on rocks (Fig. 3) is controlled by factors additional to those so far mentioned. Although the presence of a large amount of rock usually results

in a riffle, rocks are not always in regions of greatest flow. Major floods overturn small rocks; after a half-bankful flood ($8 \text{ m}^3 \cdot \text{s}^{-1}$) in December we found some stones with algae on their undersides. The lack of correlation between rock weight and chlorophyll density can however be explained, because there were few floods that large.

During base flow periods silt, containing diatoms and blue-green algae, coated rocks in low current areas. Small increases in flow washed much of this away, and sand scouring probably occurred at higher flows. Following such increases in flow, we noticed that the algae remaining on rocks were mainly encrusting greens and blue-greens. In this paper we have treated the periphyton as a unit, but it is clear that in some instances species composition and habit are important in determining the relationship between flow and chlorophyll density.

Pheopigments and the fate of periphyton—The natural breakdown of chlorophyll, via what we call here pheopigments, is poorly understood. Although it may be slower than is usually supposed (see Vallentyne 1957; Hickman and Round 1970), we assume that the degradation of chlorophyll does not take place until, but then follows rapidly upon, cell death. Observations of large amounts of pheopigments in periphyton extracts have been reported by Marker (1972), as well as ourselves, and imply the presence in the sediments of many dead algae. We found that both absolute and relative amounts of pheopigments varied between substrates and with time, and, as in the case of chlorophyll, the density of these pigments is likely to have resulted from complex interactions between current, substrate, bedload movement, and sedimentation. The changes in the chlorophyll:pheopigment ratio on rocks (Fig. 4) provide a relatively simple example. During periods of high flow, rocks were clean of sediment and dead cells were probably washed away, accounting for the high ratios observed during June and from November onward. During periods of low flow, silt was de-

posited on many rocks, presumably both killing existing epilithic populations and developing a periphyton similar to that of soft sediments, thus causing a decrease in the ratio. Correction for pheopigment corruption emphasizes the main features of Fig. 4.

The main cause of periphyton loss in the Mechums is probably burial and washout. Algae can be swept away to form a pseudophytoplankton (*see* Butcher 1932) that might later be redeposited alive in slow current areas. The fate of buried periphyton is unclear. Pennate diatoms and some other algae are phototactic (Halldal 1962; Eaton and Moss 1966) and might be able to migrate back to the surface (*see also* Round and Happey 1965). However, cores taken from marine or freshwater sediments commonly contain chlorophyll as well as pheopigments at depths of several centimeters (e.g. Hickman 1974; Hickman and Round 1970; Pamatmat 1968), implying that significant numbers of live algae are buried. The vertical distribution of pigments in Mechums sediment was not investigated and thus it seems likely that, except for that on rock, algal biomass was underestimated. On the other hand, only the algae within a few millimeters of the sediment surface are exposed to light and able to photosynthesize.

Chlorophyll density changes with time—Few extended time series observations have been made of river periphyton abundance. Marker (1976) has reported 2 years of observations of the chlorophyll density on gravel and small stones in an English chalk stream fed from springs and hence not likely to suffer from severe floods. There were chlorophyll peaks in the spring of each year. He suggested that the March increase in biomass might have resulted from increasing light; however, he could not explain the decrease at the end of April. Hickman (1974) and Waters (1960) measured chlorophyll *a* densities over periods of 13–15 months, the former in epilithon from the canals of a power station in Alberta, the latter on small concrete cylinders in a Minnesota stream. Both

found the greatest chlorophyll densities in spring, but neither attempted a detailed explanation of this pattern. Tominaga and Ichimura (1966) measured pigment densities on stones in a mountain river in Japan. During a 1-year study they found that standing crop was greatest in winter and explained this as a result of more frequent flooding in summer. Perhaps the most thorough observations have been those of Douglas (1958) who for 4 years made frequent cell density estimates of the diatom *Achnanthes* on rock faces, stones, and moss in a mountain brook in the English Lake District. She, like us, concluded that neither light nor temperature had much effect and that the main regulating factor was flow. Butcher (1932), although using artificial substrates, also found current and floods important in controlling biomass.

Mean chlorophyll density showed a clear relationship to flow in the Mechums River (Fig. 6), increasing during low flow and decreasing abruptly after floods (Table 3). These changes were due mainly to changes in density on certain substrates (Fig. 3) and to a lesser extent to changes in the relative proportions of substrates (Fig. 5). Periphyton increased on all substrates during low flow. Floods, particularly major ones, had a catastrophic effect, removing or burying a large part of the periphyton. Recovery appeared to begin as soon as the river subsided. The major factor controlling periphyton biomass is thus the length of periods free of floods. Growth may be slower in winter due to reduced light and temperature, as was found by Tominaga and Ichimura (1966) using artificial substrates, but in the Mechums high flow and more frequent wintertime floods obscure any decrease in growth rate.

Many of the fluctuations in biomass, as well as the relationship between substrate, flow, and biomass, could be an indirect result of human activities in the drainage basin. Under natural conditions the Mechums would probably be a clear mountain stream with a fairly constant, moderate periphyton biomass growing mainly on rocks. Due to deforestation,

soil erosion, and nutrient input from farm, industrial, and domestic effluents, the nutrient and silt levels in the Mechums and similar rivers are relatively high. During low flow, silt and sand support large periphyton crops, which would probably not develop without sediment input or high nutrient levels. These large crops are sensitive to changes in flow (more likely to follow rainfall now than in the natural state of the land) and so, due to land-use practices in the basin, the overall biomass is now subject to wide fluctuations. Similar fluctuations in productivity in the Mechums and other rivers with man-influenced basins are reported by Kelly et al. (1975).

Implications of the fluctuating biomass—Although the probable frequency of precipitation is known and the frequency distribution and most probable duration of flood-free periods can be calculated for the Mechums, it is impossible to predict the dates of rainstorms and hence the duration of individual flood-free periods. Because this is the most important factor controlling algal crop, it is thus not possible to construct a deterministic model to predict periphyton biomass. Studies that imply or construct such a model for rivers like the Mechums are likely to be misleading.

The stochastic biomass fluctuations have practical as well as theoretical implications. Periphyton are important in studies of pollution, but most workers have used artificial substrates (see Tippet 1970). It does, however, seem unlikely that periphyton on glass or Plexiglas slides will respond to the dominant factors of velocity, sedimentation, and bedload movement in the same way as do algae on natural, particularly soft, substrates. We have shown that the diverse substrates of a riverbed carry different biomasses; it is quite likely that species composition also varies. Many rivers that suffer from pollution also receive an increased sediment load, and it is just these rivers that are likely to show the greatest heterogeneity in substrate and periphyton biomass, and the greatest variability with time. It is thus hard to believe that

the periphyton collected on slides in such rivers represents any kind of typical biomass or diversity.

Conclusions

The evidence we have discussed supports our hypothesis that flow is the most important regulator of periphyton biomass in the Mechums River. Although nutrient levels probably control maximum biomass in rivers like the Mechums (see Kelly et al. 1975), the amount of variation in the chlorophyll density of samples from the same part of the river shows that nutrients do not play a major part in determining biomass at any particular point. This is the result of the flow regime, which also determines the type of sediment. Again, whereas light and water temperature must influence periphyton growth rate, the effects of winter-summer differences in these factors are likely to be hidden by the catastrophic effects of floods, which are more frequent in winter due to the reduced capacity of the soil to absorb precipitation.

Spatial variation in the periphyton crop is thus the result of point-to-point differences in the flow regime in the river. Such differences are, at least in theory, predictable from a knowledge of the shape of the streambed and the overall flow. Temporal variation results from periphyton growth and washout, and the effects of scour and sedimentation. The effects of washout and scour become crucial during the short periods of high flow that we have called floods, and which, resulting from heavy rainstorms, are unpredictable.

We therefore infer that it is not possible to make deterministic predictions of periphyton biomass in rivers like the Mechums. But how far are our conclusions applicable to rivers in general? There is little biological evidence to answer this question. The results of Douglas (1958) demonstrate the importance of flow in regulating periphyton biomass in a mountain stream. Tominaga and Ichimura (1966) reached the same conclusion and felt that as a result of the irregularity

of floods it was difficult to detect a general trend of seasonal change in a sessile algal community. Conversely Marker (1976) found a pronounced seasonal pattern in a spring-fed stream in which the flow was, presumably, more constant.

Many streams and small rivers in hill country are liable to floods, especially where human activity has affected the drainage characteristics of the basin. Larger rivers, particularly where regulated by lakes or reservoirs and spring-fed streams, have less variable flow. Notwithstanding this, many rivers naturally overflow their banks every year (Blom 1969). We conclude that floods can be an important factor in the ecology of river periphyton.

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