

Analysis of seasonal succession of attached algae in a mountain stream, the North Alouette River, British Columbia¹

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Seasonal succession of attached algae in the North Alouette River over 1 year is described and analyzed in relation to physicochemical characteristics. An attempt is made to consider quantitatively both diatom and nondiatom species using a multivariate method, principal coordinates analysis (P-Co-A).

Stream water was slightly acidic and nutrient poor, the order of dominance in anions being $\text{SO}_4^{2-} > \text{SiO}_2 > \text{Cl}^- > \text{NO}_3^- > \text{PO}_4^{3-}$ and metals plus ammonium $\text{Ca}^{2+} \approx \text{Na}^+ > \text{Mg}^{2+} > \text{K}^+ > \text{NH}_4^+$. P-Co-A of seasonal succession revealed a cyclic pattern with sequences of gradual and abrupt changes in species composition. Flow, temperature, Cl^- , and SO_4^{2-} , which fluctuated abruptly, were significantly correlated with most of the seasonal change in species summarized by P-Co-A. A smaller amount of the variation, which was more smoothly patterned, correlated with fluxes in dissolved cations. Methods of enumeration and analysis used, although not sensitive to differences in absolute abundance of algal populations, were useful in describing successional patterns in species composition, where both macrophyte and microphyte forms were encountered.

Major species tended to wax and wane seasonally, but exhibited long periods of overlap. Such a pattern supports one idea from the "river continuum concept," that generally species are merely shifting along temporal and spatial axes, while the total exclusion or absence of a population is indeed rare. It is suggested that this form of community structure differs from that typically understood for plant succession.

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La succession saisonnière des algues fixées dans la rivière North Alouette (Colombie-Britannique) est décrite pour une période de 1 an et analysée en relation avec les caractéristiques physico-chimiques. On tente de considérer quantitativement aussi bien les espèces de diatomées que les autres espèces, à l'aide d'une méthode multivariée, l'analyse en coordonnées principales.

L'eau de la rivière est légèrement acide et pauvre en éléments nutritifs. L'ordre de dominance des anions est $\text{SO}_4^{2-} > \text{SiO}_2 > \text{Cl}^- > \text{NO}_3^- > \text{PO}_4^{3-}$ et celui des métaux plus l'ammonium est $\text{Ca}^{2+} \approx \text{Na}^+ > \text{Mg}^{2+} > \text{K}^+ > \text{NH}_4^+$. L'analyse en coordonnées principales de la succession saisonnière montre un patron cyclique avec des suites de changements graduels et abrupts de la composition spécifique. Le flux, la température, la concentration de Cl^- et la concentration de SO_4^{2-} , qui fluctuent brusquement, sont significativement corrélés avec la grande partie des changements saisonniers des espèces qui sont résumés par l'analyse en coordonnées principales. Une plus petite partie de la variation, plus graduelle, est corrélée avec les fluctuations des cations dissous. Les méthodes d'énumération et d'analyse utilisées, bien qu'elles ne soient pas sensibles aux différences dans l'abondance absolue des populations d'algues, sont utiles pour décrire les modes de succession dans la composition spécifique, là où l'on rencontre aussi bien des formes macrophytiques que microphytiques.

L'abondance des principales espèces a tendance à croître et décroître selon la saison, mais les espèces montrent de longues périodes de chevauchement. Une telle situation appuie une des idées du "concept de continuum fluvial," à savoir que généralement les espèces ne font que se déplacer le long des axes temporel et spatiaux, tandis que l'exclusion totale ou l'absence d'une population reste très rare. Cette sorte de structure de communauté diffère de celle typiquement associée à la succession végétale.

[Traduit par le journal]

Introduction

Ecological studies of algal communities in flowing waters have followed two general approaches, one concerning metabolic or functional mechanisms and a

second examining structural aspects. Studies of community structure have been useful in recognizing how different ecosystems are organized (May 1976) and have specifically provided insight into the complexities of stream communities (Patrick 1970). Such works for algal communities have dealt with seasonality (Moore 1977a), patterns of distribution (Squires *et al.* 1973), and species diversity (Archibald 1972). In British Columbia streams, Stockner and Shortreed (1976, 1978) have examined functional relations between

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nutrient levels and algal production. Studies using the second approach, community structure, are however unknown for the province.

The analysis of spatial and temporal structure in plant communities has often been accomplished through the use of multivariate statistical techniques. Such methods have been applied to problems in lake phytoplankton (Levandowsky 1972; Bartell *et al.* 1978), and both estuarine (McIntire 1973) and stream (Hufford and Collins 1976; Descy 1976) diatoms. No studies are yet known which assess the entire (diatom and nondiatom) community of algal species in streams, using such methods.

The diversity in morphology of algae in many streams presents some problems with respect to statistical methods. In planktonic systems of lakes, the basic unit for enumeration is the cell (Vollenweider 1969). In terrestrial or intertidal communities, plants or plant weight can be used for this purpose (Mueller-Dombois and Ellenberg 1974; Holme and McIntyre 1971, respectively). The qualities of both are often found in lotic systems, where macrophytes and microphytes may each become dominant. If mixed stands and epiphytes are also considered, traditional techniques become entirely inappropriate.

The overall objective of this study, then, is to produce a meaningful description of complex patterns in community structure of an algal community in the North Alouette River, British Columbia. Community structure here is evaluated in terms of its seasonal variation and the relation between this and temporal patterns in the physicochemical environment. Further, an assessment will be made as to the utility of multivariate statistics to stream algae.

The study area

The North Alouette River watershed is located in southwest British Columbia along the slopes of the rugged Coast Mountains, 50 km east of Vancouver (Fig. 1A). All portions of the watershed studied are within the Coastal Western Hemlock Biogeoclimatic zone (Krajina 1969). Here, a maritime climate predominates, with frequent cloudiness, and the mean annual precipitation in excess of 220 cm, occurring mostly as rain. Coniferous trees of *Tsuga heterophylla*, *Thuja plicata*, and *Pseudotsuga menziesii* make up most of the surrounding forest. Major components of the riparian vegetation include *Acer circinatum*, *A. macrophyllum*, *Alnus rubra*, and *Rubus spectabilis*.

Seven collecting stations chosen for an earlier study (Wehr 1979) are distributed along the watercourse (Fig. 1B). In this work, a single station (NA2) was examined in greater detail. This site is located on the North Alouette and is a rapidly flowing fourth-order tributary with an average width along this reach of about 17 m.

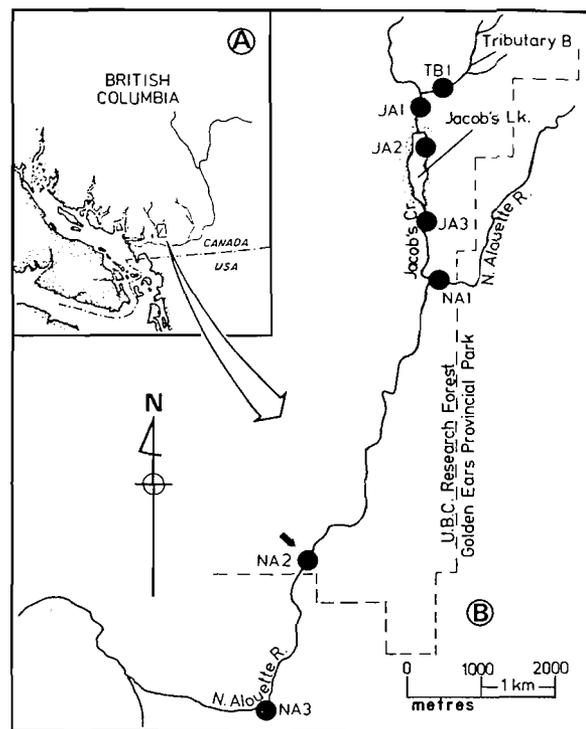


FIG. 1. The southern portion of British Columbia, showing the general location of the North Alouette River watershed (A) and a detailed map of the sampling stations, including the principal station investigated in this study, NA2, shown by the small arrow (B).

The stream bed consists of large and small granitic boulders, with few small stones and no sand or silt. The mean size of these rocks is between 75 and 100 cm in diameter. Annual mean depth was ca. 30 cm. Humic substances from surrounding boggy areas impart a slight yellow colour to the water, but generally the water is highly transparent. About a third of the stream is directly covered by canopy. Algae are attached primarily to boulders and stones, but are also epiphytic on aquatic bryophytes and other algae. Midstream is characterized by greater flow and sunlight with the moss *Blindia acuta* (Hedw.) B.S.G. the predominant bryophyte. The leafy liverwort, *Jungermania obovata* Ness is the common bryophyte closer to shore, where the waters are often pooled and shaded.

Methods

Field collections and measurements

The predominantly epilithic algal communities were collected from rocks using a modification of the half bottle of Douglas (1958). A rubber and foam fitting around the neck provided a seal against submerged rocks to isolate water plus algae from the current. This was also employed for sampling epiphytic associations on aquatic bryophytes. Material was then siphoned off with a large-bore pipette attached to rubber

tubing. Occasionally, for awkward angles, a U-shaped spatula was employed by hand.

The stream was crossed by a series of transect lines using 0.5 cm diameter nylon rope. The transects were placed perpendicular to the flow at ca. 25-m intervals. The lines were marked in decimetre points along their length. Sampling points were selected from a regular, stratified series along these points (Cummins 1962). Below a given point the nearest 10 boulders perpendicular to the transect with algal patches were selected for sampling. These were combined to form an aggregate sample representative of a particular locality in the stream. Initially, 12 of these aggregates (120 points) were sampled until time restrictions reduced this to an average of 8. Biweekly collections were made throughout the year, from 7 June 1977 to 29 June 1978, except when floods prevented access to the river during part of the winter.

Temperature was measured with a mercury thermometer and pH with a Markson pH meter, model 85. Both pH and temperature were measured at five points along one transect taken at five, 2-h intervals during the sampling day. The daytime variances of these measurements are expressed as a standard deviation from the mean of 25 values. Depth profiles were also measured along the transects to the nearest centimetre. Seasonal variation in incident light was determined using a Belforts Instruments recording pyreheliometer placed on a rock outcrop, which received an average amount of shading based on a series of individual measurements. Damage to the instrument, however, prevented continuous data collection. Current velocity was measured with a General Oceanics model 2030 digital flow meter, taken at 10 points along the transects.

Water samples for nutrient analyses were collected in acid-washed (10% HCl) 1-L polypropylene bottles in duplicate. These were rinsed three times in stream water and capped underwater. A 500-mL sample was also taken for alkalinity determinations. Five 300-mL water samples were collected at different points in glass BOD bottles. The first two O₂ reagents were added in the field to prevent losses during storage. All samples were transported back to the laboratory in an ice chest.

Laboratory analyses

The two nutrient samples were separated and 1 L was filtered within 24 h (Whatman GF/C glass fiber). Both were rapidly frozen (-15°C) for future analysis. The filtering precaution was later found to have a negligible effect on the elements and nutrients measured. At the time of analysis, the frozen samples thawed for 24 h at room temperature and were well mixed. All anion (PO₄³⁻, NO₃⁻, Cl⁻, SO₄²⁻) dissolved SiO₂, and NH₄⁺ levels were determined using a Technicon autoanalyzer II, following standard methods outlined by the manufacturer (Technicon Industrial Systems 1971a, 1971b, 1971c, 1971d, 1973). Metals (Ca²⁺, Na⁺, K⁺, Mg²⁺, Fe^{2+/3+}, Mn²⁺, Al³⁺) were determined via atomic absorption spectrophotometry (Varian-techtron Ltd., model AA-5).

Alkalinity samples were left unfrozen and analyzed within 8 h of collection. Titrations were made against standardized 0.02 N H₂SO₄ (American Public Health Association 1965) using a pH meter. Dissolved O₂ was determined within 12 h via the azide modification of the Winkler technique (American Public Health Association 1965).

Quantification and statistics

Absolute values of algal biomass were not estimated, but relative abundance ranks which approximate a logarithmic scale, were employed (Holmes and Whitton 1977). They are 0, absent; 1, <0.1%; 2, >0.1 - 1.0%; 3, >1.0 - 5.0%; 4, >5.0 - 10.0%; and 5, >10%. Each rank, as it is used here, represents an estimate of the relative amount of the total biomass contributed by each species for a given sampling time, but does not consider per unit area or volume. In any collection, the assemblage was often composed of complex macrophytic algae, such as *Stigonema* or *Batrachospermum*, filamentous forms, such as *Zygnema* or *Audouinella*, as well as various unicells such as *Achnanthes*. As such, neither cell numbers nor numbers of plants could be counted, thus requiring a more general visual estimate derived as follows.

In the laboratory, samples were homogenized and slide preparations made for microscopic analysis, using either a Leitz-Wetzlar (general) or a Zeiss UPL phase (diatoms) microscope. Five strips across the field constituted "microtransects" whose width (330 μm) was determined by the ocular grid. This procedure was repeated on eight preparations, for a total of 40 microtransects per sample. Errors due to randomness were possible but not likely to exceed the broad range (one-half to one order of magnitude) of an assigned abundance class.

To apply this scale to statistical analysis, the abundance ranks were converted to their median values (e.g., rank of 4, 5 - 10% = 7.5%), allowing calculation of a mean abundance for all samples on a given date. In presenting results of species abundances between dates, species importance is used (Whittaker 1970). The importance of species *a* would be

$$[1] I_a = \frac{\text{Mean abundance of one species}}{\text{Mean abundances of all species}}$$

$$= \frac{\bar{A}_a}{\sum_{x=1}^n \bar{A}_x}$$

where \bar{A}_x is the mean abundance of each species *x* and *n* is the total number of species. Hence, the values range between 1, for absolute dominance (i.e., the only species) and 0, if absent.

Patterns of affinities between communities on the various dates are analyzed using principal coordinates analysis (P-Co-A) or Gower ordination (Gower 1966). In this method, the original set of *n* axes used to describe the total variation in the data matrix is reduced to a smaller, significant set of coordinate axes (as in principal components analysis (PCA)) which preserve the distances between the original set of points (Poole 1974). It has many advantages over principal components as it is not limited to the use of Euclidean distance and allows considerable scope for choice of a distance function (Gower 1966). Such characteristics are valuable particularly when there are greater numbers of variables (in this study, 203 species) than cases (17 sampling dates) to be analyzed. Further advantages are discussed at length in Sneath and Sokal (1973). The specific program used here is that of Bradfield (1977), and Wahlstedt and Davis (1968) may be consulted for a complete program using a form of PCA equivalent to principal coordinates.

The similarity index or distance function for this is based on the cosine of the angle between each vector summarizing the abundance of each species. As species abundances are always nonnegative, the greatest dissimilarity between two cases with only two species would be represented by vectors in an angle of 90° , producing a cosine = 0. Conversely, two such communities with complete equality would lie along equal vectors, producing an angle of 0° , and a cosine = 1. Hence values always range from 0 to 1. In data with more than two variables, the cosine function takes the form

$$[2] \quad S_{ik} = \frac{\sum_{j=1}^m X_{ij} \cdot X_{kj}}{\left[\left(\sum_{j=1}^m X_{ij}^2 \right) \left(\sum_{j=1}^m X_{kj}^2 \right) \right]^{1/2}}$$

where S_{ik} is the similarity between cases i and k , X_{ij} is the importance value of the j th species in case i , X_{kj} is the importance value of the j th species in case k , and m is the total number of species (Sneath and Sokal 1973). When these similarities are computed, a geometric representation of the similarities between all cases is generated, reflected in the distances between their plotted positions. A simple linear correlation was used to compare the seasonal behavior of physicochemical factors with the seasonal succession of species over the year. The coordinate scores provided by P-Co-A were used in defining the temporal variation of the algal community, after Bartell *et al.* (1978).

Results

Physicochemical parameters

Seasonal patterns of dissolved ions are given in Fig. 2. The low overall values for these dissolved substances are within the range found for other Pacific coastal watersheds in British Columbia (Stockner and Shortreed 1976; Feller 1977). SO_4^{2-} and SiO_2 were the most abundant ions on the average. The patterns of the four anions plus SiO_2 are not seasonally similar (Fig. 2). PO_4^{3-} was somewhat erratic and the least abundant member of this group. The anions were generally in highest concentration during summer and autumn. The order of their relative average concentrations was $\text{SO}_4^{2-} > \text{SiO}_2 > \text{Cl}^- > \text{NO}_3^- > \text{PO}_4^{3-}$.

Of the seven metals measured, only four were within detectable limits. $\text{Fe}^{2+/3+}$, Mn^{2+} , and Al^{3+} were never found in the dissolved fraction. In contrast to the anions and silica, metals showed an apparently high degree of similarity in seasonal patterning (Fig. 3). All exhibited their maxima in mid-August and on through late summer and early autumn. Low levels also appeared to be synchronized. The order of their concentrations plus NH_4^+ was $\text{Ca}^{2+} \cong \text{Na}^+ > \text{Mg}^{2+} > \text{K}^+ > \text{NH}_4^+$. These relative differences are similar to that found in an adjacent watershed (Feller 1977).

Seasonal levels of pH, O_2 , alkalinity, current velocity, depth, and temperature are presented in Fig. 4. The low alkalinity (as HCO_3^-) measured for the stream

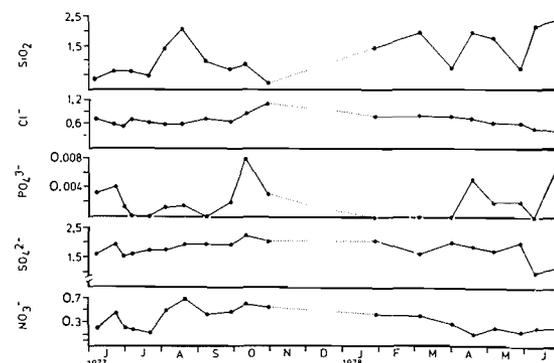


FIG. 2. Seasonal variation in dissolved anions and silica, expressed in milligrams per litre.

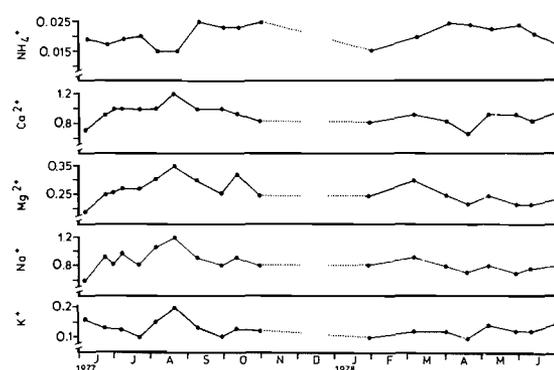


FIG. 3. Seasonal variation in dissolved metals and ammonia, expressed in milligrams per litre.

water is in agreement with general conditions outlined for most areas of the Coast Mountains (Northcote and Larkin 1963), being poorly buffered. However, pH values did not vary greatly within the day (standard deviations) or seasonally. Greatest pH shifts during the day occurred when alkalinity was lowest, during winter.

Dissolved O_2 was always at or above saturation levels all times of the year (Fig. 4). Absolute concentrations varied inversely with changes in water temperature. Seasonal pattern in temperatures appear to follow differences in day length, where August was the warmest month. During this period, algal populations experienced a daytime flux of as much as 4°C . The entire diurnal flux was not measured. Although light energy was measured, equipment damage prevented a complete picture. Data available indicate a pattern similar to temperature, with an increase from June 1977 ($27 \text{ cal}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$; $1 \text{ cal} = 4.1868 \text{ J}$) to a maximum in mid-August ($32\text{--}36 \text{ cal}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$). By November the level was half the maximum. Measurements for any week were marked by at least a few cloudy days, so that the annual flux varied by only a factor of about two. The more continuous data of water temperatures nonetheless

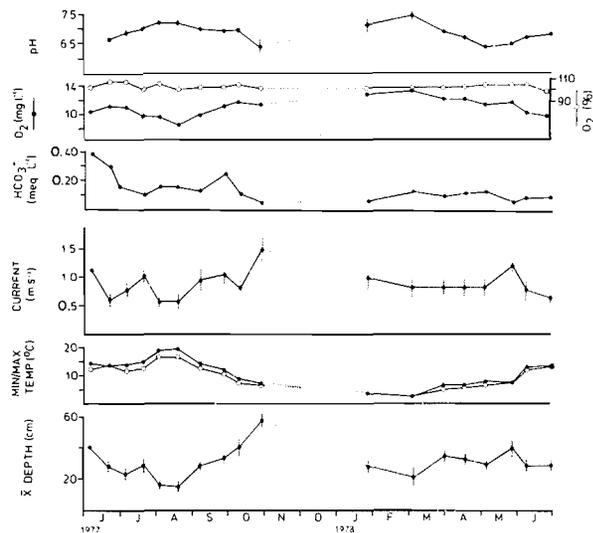


FIG. 4. Seasonal variation in pH, dissolved O_2 ($mg\ L^{-1}$ and % saturation), alkalinity ($meq\ L^{-1}$), current velocity ($m\ sec^{-1}$), temperature ($^{\circ}C$), and mean depth (cm).

likely reflect the seasonal character of sunlight available to the stream.

Flow, which is described in stream depth and current velocity (Fig. 4), was highly varied seasonally, being greatest in late autumn to winter. The decline after October may not be as immediate as shown (interpolated), as floods made sampling impossible during this period. Times of calmer flow during the year were also interrupted by brief spates.

The algal flora

Generally the stream was dominated by epilithic forms, consisting of predominantly filamentous green algae from the Zygnematales and Ulotrichales, as well as a number of branched and unbranched filamentous blue-green algae. Epiphytic forms were encountered in lesser amounts. In particular, species of blue-green algae from the Chamaesiphonales and many diatom species, such as *Gomphonema angustatum*, *Cymbella minuta*, and *Hannaea arcus*, were attached to both the larger algal species and aquatic bryophytes. Nearly half of the 203 taxa identified were diatoms, yet these rarely ever reached levels in the stream great enough to be coded greater than 2 ($>0.1 - 1.0\%$).

Another nonabundant group of algae represented by many species over the year were the desmids. These were frequently found loosely attached to the bryophytes and macrophytic algae, such as within the mucilage of *Batrachospermum moniliforme*. By and large, the nonepilithic species were quite diverse and widespread amongst a variety of microhabitats. A few, however, were highly specific as to their habitat preferences. For example *Clastidium setigerum* (Cyanophy-

ceae) was present throughout the year and nearly always attached to the moss *Blindia acuta* in areas of greatest flow, but never on associated algae or the rock to which the "host" was anchored. A more complete discussion of the floristics and distributional patterns is presented elsewhere (Wehr 1979).

Seasonal succession of the algae

The temporal variation in the abundance of seven major species for the 13-month period is compared in Fig. 5, expressed as importance values. These indicate a gradual progression from the dominance of one species to the next. *Zygnema insigne* and *Klebsormidium mucosum* were found to predominate in late spring to the summer, until *Phormidium autumnale* and *Oedogonium* sp. A expand in importance in early autumn.

Later, a large burst of *Klebsormidium rivulare* in September was marked by the reduction in the growth of blue-green algae and diatoms epiphytic on the dominant filamentous algae found in warmer months. During late winter and early spring, the blue-green alga *Tolypothrix penicillata* reached its peak, while the spring forms began their increase again. One abundant alga, *Stigonema mamillosum*, was not seasonally predictable, as it had periodic peaks and lows throughout the year.

Throughout this succession, however, none of the major species was absent or in significantly low quantities to have been missed in the enumeration process. Most were readily observable at all times of the year in macroscopic patches or colonies and did not "disappear" or alternate between resting stages (e.g., Zygospores in the Zygnemataceae) and the vegetative condition. The major species progressed seasonally in a succession of broad peaks, where the various populations exhibited a fair degree of temporal overlap.

Further patterns in the seasonal succession are exposed through P-Co-A of the entire species assemblage (Fig. 6). This method efficiently summarized a matrix of

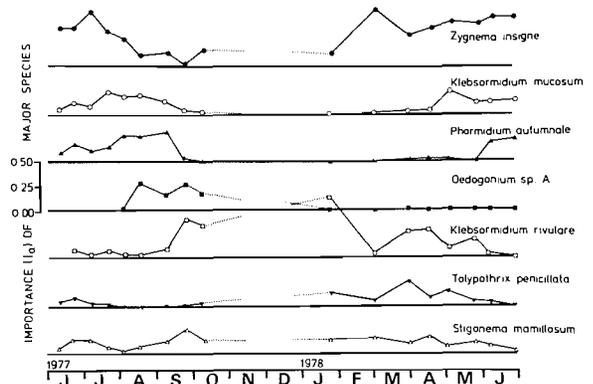


FIG. 5. Seasonal changes in the abundance of seven major algal species expressed as importance values (I_a ; see Methods).

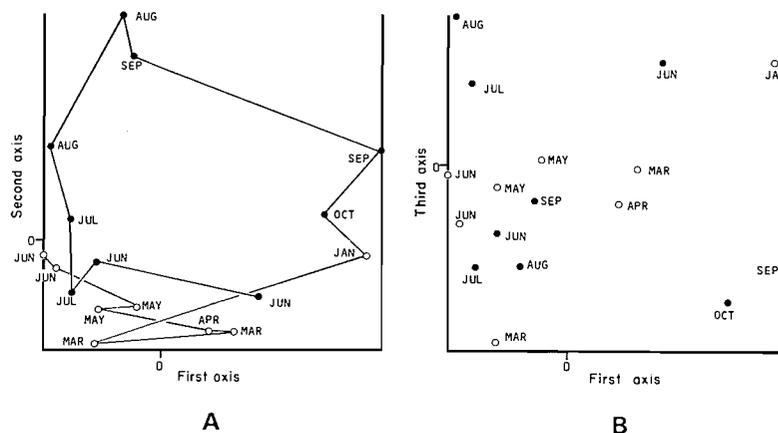


FIG. 6. A plot of similarities between algal communities on 17 sampling dates, expressed through principal coordinates analysis for the first and second (A) and first and third (B) coordinate axes. In the first two dimensions, the chronological trajectory of points are connected by lines whose length correspond to the relative amount of change in species composition (●, 1977; ○, 1978).

17 sampling dates and 203 variables (species), where the first coordinate axis accounted for nearly 50%, and cumulatively the first three axes, 87% of the total variance in the data. The geometric representation of the affinities between communities on various dates is given as a dispersion of points, where the most similar are plotted nearest together.

In general, the similarity of sampling dates reveals a cyclic pattern from June 1977 to June 1978, considered by the first two axes (Fig. 6A). This pattern may be envisioned as a disk, where the succession of species follows the course around its edge and completes the cycle in 1 year. The third axis (Fig. 5B) is less obvious, but only contributed another 7% of the total variance in the data. The three dimensions together would appear as a disk that exhibits some "wobble," rather than as a flat plate. The succession nonetheless is portrayed as having proceeded in a cyclic manner, where the beginning and end meet.

The ordination also reveals a few properties of the date units individually. Bartell *et al.* (1978) indicate that the length of the lines between successive points in such a plot are proportional to the rate of change in species composition between dates. The long gap in sampling between mid-October and January (due to floods) did not show a great change in the community. Both dates were characterized by a predominance of *Klebsormidium rivulare*. One of the most extreme changes in composition occurred two sampling periods earlier, during September, in a period of 21 days. Here the community changed from a *Zygnema insigne* + *Phormidium autumnale* dominated to a *K. rivulare* + *Oedogonium* sp. A dominated association.

Synthesis of biological and physicochemical results

The relation between the seasonal patterns of the

TABLE 1. Correlation between the seasonal behavior of the physicochemical environment and the succession of algal species. Physicochemical variables are correlated with the loadings of the first three coordinate axes in the P-Co-A, showing levels of significance (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant)

Factors	Correlation with coordinate scores		
	Axis 1	Axis 2	Axis 3
PO ₄ ³⁻	0.112 NS	-0.109 NS	-0.130 NS
HCO ₃ ⁻	0.050 NS	0.133 NS	0.099 NS
Cl ⁻	0.645**	0.001 NS	-0.100 NS
SO ₄ ²⁻	0.643**	0.080 NS	0.047 NS
Current	0.561*	-0.127 NS	0.234 NS
Depth	0.628**	-0.378 NS	0.116 NS
Ca ²⁺	-0.197 NS	0.726***	-0.041 NS
Na ⁺	-0.265 NS	0.648**	-0.348 NS
Mg ²⁺	-0.034 NS	0.657**	-0.371 NS
K ⁺	-0.190 NS	0.513*	0.055 NS
SiO ₂	-0.430 NS	0.005 NS	-0.201 NS
NO ₃ ⁻	0.334 NS	0.687**	-0.254 NS
NH ₄ ⁺	0.397 NS	-0.021 NS	-0.167 NS
Temperature	-0.472*	0.655**	0.227 NS
Dissolved O ₂	0.414 NS	-0.717***	0.270 NS
pH	-0.123 NS	0.359 NS	0.172 NS

physicochemical environment and species succession is shown by correlation of the coordinates of the first three axes of the seasonal ordination with the temporal flux of all measured abiotic variables (Table 1). The differences in species composition described by the first coordinate axis correlates significantly with the anions Cl⁻ and SO₄²⁻, as well as current velocity and depth, all positively. This axis also correlates negatively with temperature. The first axis is associated with the changes in importance between an association dominated by *K.*

rivulare and one by *Zygnema insigne* and *Phormidium autumnale*. The *K. rivulare* association thus was found at times of low temperature, high current velocity, and greater concentrations of Cl^- and SO_4^{2-} . The *Zygnema* + *Phormidium* association was a spring–summer occurrence where greater temperatures were joined by reduced current, Cl^- , and SO_4^{2-} concentrations. This was also a period of greater accumulation of drifting desmids and epiphytism by blue-green algae (Chamaesiphonales) and diatoms among the filamentous dominants.

The second coordinate axis correlates significantly (positively) with temperature, and all measurable metals and NO_3^- , as well as negatively with O_2 . The second axis represented a distinction between a large number of minor species and some other major species. The positive extreme was an association variously composed of *Oedogonium* sp. A, *Klebsormidium mucosum*, *Batrachospermum moniliforme*, and *Phormidium autumnale*. This is contrasted with an association of *Tolypothrix penicillata*, *Stigonema mammosum*, *Audouinella hermanni*, and again, *K. rivulare* on the negative range of this axis. The third axis did not correlate significantly with any of the variables measured.

Discussion

The succession of major species (Fig. 5) over 1 year did not follow the general model where species abruptly build up and disappear in a “tree-by-tree replacement process,” as generalized by Horn (1976), and which is believed to follow for most freshwater phytoplankton communities of lakes (Hutchinson 1967; Round 1971). In the North Alouette River there was a persistence of the entire epilithic assemblage, within which the wax and wane of certain species occurred. Vannote and co-workers (1980) have surmised that the traditional concept of biological succession, with its sequence of discrete successional stages, may be obsolete for rivers. Rather, they suggest a “continuous heritage” of species exists, where the total absence of a population is rare, and overlapping species abundances merely shift along a temporal or spatial axis. Such a theory is supported by the present data. A comparison with previous examples of algal succession should explain this point.

In studying the epipelton of two pools, Round (1972) found the major algal species had broader seasonal peaks than do phytoplankton, resulting in longer periods of coexistence. Figure 7 compares the hypothetical growth curves described by Round (1972) for phytoplankton and epipelton of lakes, with the pattern of the major epilithic algae of the North Alouette. The more complex picture in this study reveals a greater degree of seasonal overlap among the major species. The growth of species 1 in the present study is similar to that of *Klebsormidium rivulare*, species 2 to *Zygnema insigne*,

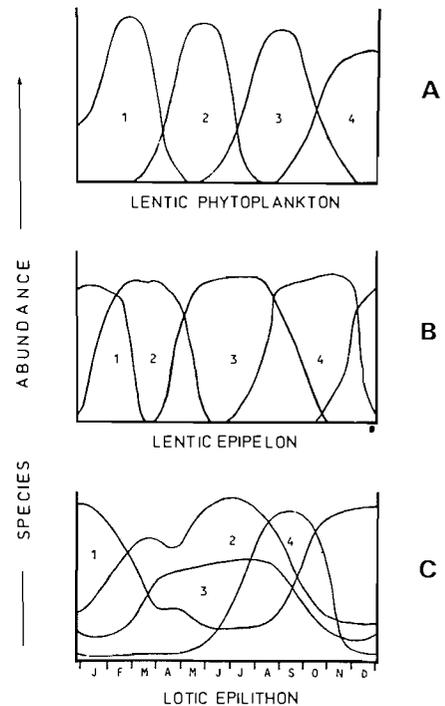


FIG. 7. Hypothetical growth curves of major algal species for three freshwater environments, based on Round (1972) (A and B) and the present study (C).

species 3 to *Phormidium autumnale*, and species 4 to *Oedogonium* sp. A.

It has been suggested (Round 1972) that because epipellic algae of lentic environments do coexist considerably, lake sediments may provide a greater variety of microhabitats than the water column, hence allowing spatial refuge for potentially competing species. Assuming this is true, the stream environment may perhaps possess a greater diversity of microhabitats than in the previous two systems. Whether this can be generalized for stream epilithon as a whole is much less clear. Moore (1977a) found that during fluctuations in absolute abundance, the dominant epilithic diatom, *Achnanthes saxonica*, in one small stream remained the most abundant throughout the year. The author has also reported (Moore 1977b), however, in another stream, drastic differences in the relative abundances of major taxa in the epilithon.

While the abundance peaks of the major algal species in the North Alouette do broadly overlap seasonally, their patterns were not without abrupt fluctuations. Rapid changes in community composition, as revealed through ordination (Fig. 6), for the most part fell along the first coordinate axis. Among other variables, this axis significantly correlated with both increasing current velocity and depth (Table 1). The drastic changes in species composition may here perhaps be caused by catastrophic events, while at other times the progression

was more gradual. Douglas (1958) has also reported irregular variations in the periodicity of major epilithic species in one stony beck, which was found to be mainly dependent upon unpredictable flow conditions.

From the present data, it would appear that spring-summer periods of reduced flow, warmer temperatures and increased SO_4^{2-} and Cl^- levels encourage the growth of Zygnematales and *Phormidium* in this stream. Granitic, nutrient-poor streams in Scandinavia show a similar species composition (Israelson 1949). Fewer systems exhibit a winter dominance of *Klebsormidium rivulare*, although it is widely reported from cold alpine streams in Austria (Kann 1978). Possibly the reduction of algal epiphytes on this species during winter is related to increases in current velocity (significantly correlated). Along the second axis, many additional species vary in abundance. For example, *Batrachospermum moniliforme* was one species more abundant along the positive range of the coordinate axis, a period significantly correlated with warmer temperatures and slightly greater metal and NO_3^- levels. One of its alternates along the second axis, *Audouinella hermanni*, seemed to have a preference for cold temperatures and lower levels of these nutrients. Dillard (1966) found a very similar seasonal pattern for these two genera in North Carolina, although only temperature was considered in their dynamics. As multivariate analysis was found necessary in the present study in discerning patterns amongst the various species combinations and many environmental factors, studies of other river communities which have not used similar analytical techniques cannot be easily compared.

The estimation of species abundances in this study has employed a ranking of relative abundance comparable to the Braun-Blanquet scale (Braun-Blanquet 1965). Such a method gives no estimation of the absolute levels of algal biomass per unit area. Mueller-Dombois and Ellenberg (1974) have explained, however, that estimates in many types of vegetation cannot be made on a more refined level. This is perhaps why so many quantitative studies of stream algae which employ multivariate stratagems have had to consider only diatoms (Descy 1976; Hufford and Collins 1976; Squires *et al.* 1979), as they are simply enumerated, or if nondiatom algae are also considered, only presence-absence data have been used (Kaesler and Cairns 1972). Hence, either a highly precise analysis is made of only one portion of the algal vegetation, which may even be of lesser importance than other taxa (e.g., diatoms in the present study), or a somewhat less exacting estimate is produced for the entire community.

Levandowsky (1972) has explained that in phytoplankton populations significant differences in cell numbers lie primarily in orders of magnitude. Levandowsky converted cell counts to ranks of abundance (each being

10 times greater than the previous (comparable with the ranks employed in this study)) and using a position vectors technique, exposed affinities from a complex data matrix of 70 cases by 90 variables. Such ranks were shown to reduce sampling error and bias due to sample size by weighting more abundant species. In particular, this eliminates overemphasizing the many rare species, as is inherent in the Jaccard index (Mueller-Dombois and Ellenberg 1974), for example. Recently, Maarel (1979) has compared methods for the transformation of various cover-abundance scales, finding a numerical Braun-Blanquet scale to be a useful framework for ordination. Further, he has shown that a logarithmic transformation of scalar data performed most effectively with data from three community types, as compared with various weighting and standardization techniques.

The present analysis has revealed a number of seasonal patterns in community structure. Although no quantitative estimates of seasonality in standing crop were made, if desired, these data could be related to total algal biomass (Tett *et al.* 1978). The methods employed were useful in recognizing how patterns in the entire community compare with the prevailing environmental regime. As the data are for a 13-month period, they are sufficient to generalize for only 1 year. There is no reason to assume, for example, that pulses in current velocity or temperature should necessarily occur in early autumn. Nonetheless, the seasonal succession of species in that time was clearly shown to pattern in a cyclic manner, one in which specific environmental events could be correlated with species change. In addition, the idea of species replacement within this community was found to differ from that understood for phytoplankton, in support of ideas suggested in the river continuum concept (Vannote *et al.* 1980).

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