ANALYSIS OF PATTERNS IN ALGAL COMMUNITY STRUCTURE IN THE NORTH ALOUETTE RIVER WATERSHED, BRITISH COLUMBIA
by

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ABSTRACT

Patterns in algal community structure and physiochemical characteristics of streams and one impounded subalpine lake in the mountainous North Alouette River watershed, British Columbia, were described for one year from June 1977 to June 1978. In this period, 266 algal taxa were recognized, of which 59 were previously unrecorded in the province. The streams were characterized by an epilithic flora consisting predominantly of unbranched Chlorophyta and secondarily by both branched and unbranched Cyanophyta. Bacillariophyta (diatoms) were species rich (over 100 taxa), but were at all times relatively unimportant in the streams, although frequently dominant in the epipelon of Jacob's Lake. Species of Rhodophyta were locally abundant only in shaded habitats. Many epilithic and epiphytic species were "host" specific in their substrate preferences.

Stream water in the North Alouette was slightly acid ( $\mathrm{pH} 6-7$ ) and nutrient poor, the relative order of anions being $\mathrm{SO}_{4}^{2-}>\mathrm{SiO}_{2}>\mathrm{Cl}^{-}>\mathrm{NO}_{3}^{-}$ $>\mathrm{PO}_{4}^{3-}$ and cations $\mathrm{Ca}^{2+} \simeq \mathrm{Na}^{+}>\mathrm{Mg}^{2+}>\mathrm{K}^{+}>\mathrm{NH}_{4}^{+} \cdot \mathrm{Fe}^{2+/ 3+}, \mathrm{Mn}^{2+}$, and $\mathrm{Al}^{3+}$ were not detected in the dissolved fraction. Other variables indicated this to be a rapidly flowing (often $>\mathrm{lm} \mathrm{sec}{ }^{-1}$ ), cool ( $2-18^{\circ} \mathrm{C}$ seasonally), poorly buffered $\left(\mathrm{HCO}_{3}^{-}=.06-.40 \mathrm{meq} 1^{-1}\right)$, and highly heterogeneous environment. Stations along the stream gradient differed in conditions of slope, current velocity, degree of shading, and substrate size, but not in temperature, pH , and possibly nutrient chemistry.

A principle coordinates analysis ( $\mathrm{P}-\mathrm{Co}-\mathrm{A}$ ) of seasonal succession at one station (Station 1) revealed a cyclic pattern characterized by sequences of gradual and abrupt changes in species composition. Temporal extinction of dominant species did not occur, as has been shown for phytoplankton
populations in lakes. Current velocity, depth, temperature, $\mathrm{Cl}^{-}$, and $\mathrm{SO}_{4}^{2-}$ were significantly correlated ( $\mathrm{P}<0.05$ ) with most of the seasonal variability in the algal community. A smaller amount of the seasonal change was correlated with the flux of dissolved cations. P-Co-A also exposed similarities between six stations within the watershed which were not consistent seasonally, and gave no evidence of distinct zones. Distribution of algal species within Station 1 in May shown by cluster analysis, occurred roughly in two groups, corresponding to near-shore and midstream habitats. The general heterogeneity of algal distribution and the occasional disturbance by flooding gave rise to periodic peaks in diversity, although many common species never became abundant. Hence, no clear-cut relation was realized between the physiochemical environment and species diversity. Hypotheses are generated, suggesting that (1) distribution of red algae was shade limited; (2) diatom dominance was limited by nutrient chemistry; (3) the even pattern of seasonal succession was interrupted by periodic events, such as nutrient pulses and floods; and (4) a large degree of species coexistence was provided by these periodic disturbances.

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## I. INTRODUCTION

Studies of algal communties in flowing waters have followed two general approaches, one concerning metabolic or functional mechanisms, and a second examining structural aspects. The descriptions of pattern in community structure have been useful in recognizing how different ecosystems generally are organized (May, 1976), and have specifically provided insight into the complexities of stream communities (Patrick, 1975). Such works for algal communities in streams have dealt with seasonality (e.g., Blum, 1957; Moore, 1977a, b), patterns of distribution (e.g., Kawecka, 1971; Squires et al. 1973), and species diversity (Patrick, 1967; 1970; Archibald, 1972). The very few works on algal communities of streams in British Columbia (Stockner and Shortreed, 1976, 1978) have dealt largely with functional relations (nutrients and production), whereas studies using the second approach, community structure, are unknown for the province.

Spatial and temporal structure in terrestrial plant communities have often been studies through the use of multivariate statistical techniques (Dale, 1975 ) and these techniques have been applied to problems in lake phytoplankton (Levandowsky, 1972; Allen and Koonce, 1973; Bartell et al., 1978), and both estuarine (McIntire, 1973) and stream (Hufford and Collins, 1976, Fabri, 1977; Leclercq, 1977) diatoms. No studies are known, however, which assess the entire (diatom and non-diatom) community of algal species in streams, using such methods.

The objectives of this study are to provide preliminary information on the taxonomy and community ecology of the algae in a British Columbia stream ecosystem, from a typical coastal mountain watershed. Community structure (Whittaker, 1970) is described here in terms of growth habits of the species
the spatial distribution and diversity of communities in different reaches of the watershed, the spatial and seasonal variation within one community, and the relation between these patterns and the physiochemical environment. Multivariate methods and other ecological criteria are used to produce meaningful patterns from complex variations in the biotic and abiotic environment. These data are used to produce hypotheses as to how the structure of one algal community might differ from planktonic and other stream systems.

## II. THE ENVIRONMENT

## A. LOCATION

The North Alouette River is located in southwestern British Columbia (Fig. 1A) along the southern slopes of the Coast Mountains, approximately 50 km east of Vancouver. It is a broad mountain stream situated in a coastal coniferous forest, typified by many fast stretches over rugged terrain. The stream's origin ( $49^{\circ} 22^{\prime} \mathrm{N} ; 122^{\circ} 30^{\prime} \mathrm{W}$ ) lies at an altitude of ca. 1500 m near the peak of Mt. Blanshard and from there runs in a southwesterly direction. At its completion ( $49^{\circ} 16^{\prime} \mathrm{N}$; $122^{\circ} 43^{\prime} \mathrm{W}$ ) it is near sea level, where it joins the south fork of the Alouette River. These flow into the Pitt River at a point 6 km upstream from a junction with the Fraser River. The catchment area of the combined north and south forks of the Alouette River has been estimated at $208 \mathrm{~km}^{2}$ (Benedict et al., 1973).

The upper reaches ( 8.7 km ) of the stream are within Golden Ears Provincial Park (see Fig. 1B) which then continues through the University of British Columbia Research Forest ( 4.9 km ). The lowest portion (10.0 km) is within the municipality of Maple Ridge. Another segment of the watershed is Jacob's Creek, a length of about 6 km , excluding all of its minor tributaries. This secondary system in large part is within the Research Forest and includes a number of small subalpine lakes. One of these, Jacob's Lake (often as Marion Lake) is considered in this study. This and the remainder of the collecting stations shown (Fig. 1B) will be discussed later.


Figure 1. The southern portion of British Columbia, showing the general location of the North Alouette River watershed (A), and a detailed map of the positions of the sampling stations within the watershed (B).
B. TOPOGRAPHY AND GEOLOGY

The mountainous slopes of the river basin run rather steeply, averaging $63.5 \%$, but varying widely from about $180^{\circ} \%$ to $7 \%$. Along much of the segment studied, the stream lies within a narrow ( $\sim .5 \mathrm{~km}$ ) V-shaped canyon. The streambed is rather wide, averaging about 15 m . Due to extreme flow, anchored substrate consists of boulders frequently greater than one meter in diameter. The tributary Jacob's Creek system is less severe, with an average slope of $23.8 \%$ and mean width of 9 m . The extreme physiography of the study area is considered typical of streams and small rivers in the Coast Mountains (McKee, 1972).

The geology and glacial history of the region have been summarized thoroughly by Roddick (1965) and Armstrong (1957, 1961) so that only a brief description is given here. During the Pleistocene, the area experienced probably three major glaciations. The ice sheet (by most estimations) covered the region as recently as 11,000 years B.P. (Armstrong, 1957). Deposits indicate that when the land was depressed, only the lowest reaches of the North Alouette were under sea water. Mathewes (1973) has shown that marine deposits occur up to present-day elevations of 107 m . This presumably would include the lowest two sampling stations (see Fig. 1B).

The rocks in the streambed are acid granitic and consist largely of quartzdiorite, diorite, and gabbro (Roddick, 1965). These materials are recognized as poorly soluble and lend little in the way of dissolved minerals to the water (Northcote and Larkin, 1963; Golterman, 1975). Through humic substances of the parent material and large numbers of boggy areas, the waters of the catchment have a characteristically yellow-brown color.

## C. CLIMATE AND VEGETATION

C1imate in the area has been classified (Köppen, 1936) as Cfb; a warm maritime-mesothermal, which is humid to rainy. Conditions are characterized by mild temperatures with frequent cloudiness. Mean annual rainfall is in excess of 220 cm . Summers are cool and relatively dry, whereas most of the precipitation occurs during the winter. The driest month, however, may have up to 16.5 cm of rainfall (Krajina, 1969). Snow is infrequent at lower elevations, and may contribute less than $1 \%$ of the total annual precipitation (Krajina, 1969), although at elevations over 350 m it may accumulate for a number of months.

All portions of the watershed studied are located within the Coastal Western Hemlock biogeoclimatic zone (Krajina, 1965, 1969). The stream source and some upper elevational reaches not considered here lie within subalpine and alpine tundra zones. The forest consists primarily of Tsuga heterophylla (Raf.) Sarg., Pseudotsuga menziesii (Mirbel) Franco., and Thuja plicata Donn. The understory is diverse, and the shrubs include Rubus spectabilis Pursh, Gaultheria shallon Pursh, and Vaccinium parvifolium Smith. The ferns Polystichum munitum (Kaulf.) Pres1. and Blechnum spicant (L.) Roth are also common, as well as many mosses. The riparian vegetation differs somewhat, and Alnus rubra Bong., Acer circinatum Pursh, A. macrophyllum Pursh, Populus trichocarpa T. \& G., and Oplopanax horridum (Smith) Miq. occur. For further details on the vegetation in this area, Orloci (1965), Klinka (1976), and Krajina (1965, 1969) should be consulted.

## D. HISTORY OF USE AND RESEARCH

The study area lies within forests which have burned periodically over the past 400 years and logged in some portions by a number of private logging companies between 1924 and 1931 (Cochrane, 1972). Logging (clearcutting) and planting operations are still being carried out by the U.B.C. Forestry classes for training and funding purposes. The watershed nonetheless contains many old growth stands commonly 200 to 300 years in age, and some as much as 800 years (Klinka, 1976). Secondary growth in the vicinity of the stream varies in age from relatively young 20 year, to 130 year old trees, largely of planted Douglas fir. The area within and adjacent to the Research Forest includes many roads for access in logging and research. Public usage is restricted to hiking trails, and further uses (e.g., hunting, fishing) have been prohibited. Although the lowest 10 km of the North Alouette River lie within the municipality of Maple Ridge, it is not subject to any apparent effects of pollution. The North Alouette River has been proposed for use as a supplementary water supply for Maple Ridge (G.V.W.D., 1961; cited in Cochrane, 1972). The proposals of dam construction and reservoir management for this system at present have not been undertaken.

Research in biological and forestry related fields in the immediate area have been extensive, owing in large part to the establishment of the forest for research purposes in 1949. A few works are of relevance to the present study. Klinka (1976) considered terrestrial vegetation and plant synecology, including surficial geology and soils. Other significant studies included the palynology (Mathewes, 1973), road and bridge construction (Pasicnyk, 1976), and water use (Cochrane, 1972) in the North Alouette watershed, as well as nutrient chemistry of streams in an adjacent
(Spring-East Creek system) watershed (Feller, 1977).
The majority of published work on aquatic biota resulted from the IBP studies of Jacob's (Marion) Lake, whose objective was to determine the factors which control energy transfer in the lake ecosystem. The work was summarized by Efford (1967) and a more complete literature assembled by Ha11 and Hyatt (1974). Accounts of algal communities within the program (Dickman, 1969; Gruendling, 1971) and separate from it (Stein and Gerrath, 1968; Kristiensen, 1975) have been restricted to lakes and ponds.

## E. DESCRIPTION OF SAMPLING STATIONS

In this study the North Alouette will be regarded as a stream, contrary to its name. This is owing to its conditions of slope, current velocity, large substrates, and other characters (see Ricker, 1934; Illies, 1961). The stations were selected as representative of the range of conditions present over the length of the stream. These were based on the following criteria:
(1) reasonable access so that necessary equipment and materials were brought into the field;
(2) lack of influence from human disturbance; and
(3) a diversity and overlap of obvious physical characteristics, particularly current velocity, shading, and substrate.

The seven stations are distributed along the watercourse as shown in Fig. 1B. Station 1 is the site of most intensive investigation and is given a more thorough description than the other six stations. A length of ca. 50 m was used for sampling at these stations and nearly a 100 m segment at Station 1. The use of stream orders follow Strahler (1964) and for flow
classes, Bishop (1973). In the latter: cascades are defined as extremely rapid, turbulent ("white") water; riffles are moderately agitated or laminar; and pools are recognized to have little or no flow, and are often deep.

Station 1 represents the lowest segment of the stream ( 130 m elev.) which is rapidly flowing. It is a third ( $3^{\circ}$ ) order tributary with current frequently averaging $1 \mathrm{~m} \cdot \mathrm{sec}^{-1}$. Substrate consists of large and small boulders with few small stones. The mean size is between $75-100 \mathrm{~cm}$ in diameter. Riffles are most common, although cascades are also present. Pools are less frequent, being restricted to the shoreline and leeward sides of large boulders. Depth is variable, both within the basin and seasonally with the mean depth ca .30 cm .

Station 1 shows a pronounced difference in physical conditions with respect to nearness to the shore. The basin is wide, nearly 18 m , hence only about $25 \%$ of the stream is covered by canopy. Midstream is characterized by greater flow and sunlight availability, with extreme algal growth. Algae are primarily attached in encrusting and filamentous forms. The moss, B1india acuta (Hedw.) B.S.G., is the predominant bryophyte in this portion, particularly in areas of extreme flow. Along the shore, the waters are pooled and shaded, and the algal growth forms are largely upright tufts and mucilaginous films. The leafy liverwort, Jungermania obovata Ness is the common bryophyte in this shore habitat. Local accumulation of detritus is present during low flow periods.

Of the other stations, five lie upstream from the main Station and one downstream (Fig. 1B). The downstream Station 7 occupies an area of reduced slope and current, consisting of riffles and pools with few cascading reaches. By this stage, the North Alouette is a fourth order ( $4^{\circ}$ ) tributary occupying land ( 15 m elev.) which is largely Fraser River floodplain (Armstrong, 1957), unlike any of the other stations.

Station 6, the uppermost ( 330 m elev.) site, is an unnamed second order ( $2^{\circ}$ ) creek of the Jacob's Creek system. It will be referred to as "Tributary $B^{\prime \prime}$. The station is a steep series of cascades and pools in a narrow ( 4 m ) streambed and has extensive overstory shading. Depth is highly heterogeneous and pools may be greater than 1 m deep.

Less than 500 m downstream from Station 6, Tributary $B$ flows into the upper arm of Jacob's Creek, also a $2^{\circ}$ tributary. This is the location of Station 5. Below the junction, the stream order is increased to $3^{\circ}$ and is near the bottom of the Jacob's Creek valley ( 305 m elev .) where the current slackens considerably. The substrate consists of small stones and few large rocks. Flow patterns are predominantly pools with riffles very widely spaced. The stream is alternately shaded and open. An emergent vascular plant, Juncus ensifolius Wikst. is found in the pools during the summer.

Jacob's Lake is Station 4 (ca. 302 m elev.) and receives inputs primarily from Tributary $B$ and Jacob's Creek. It is a small bog lake with a mean depth of only 2.4 m (Efford, 1967). The bottom consists of soft mud and ooze. This in conjunction with the rapid flushing rate of less than three days during high flow has resulted in the benthic components being of greater importance than the planktonic (Efford, 1967; Hargrave, 1970). Recently, however, construction of beaver dams near the lake outlet has resulted in a rise in the lake level as well as reduced outflow. Littoral development by a number of macrophytes include Nuphar polysepala Engelm., Potamogeton natans L., P. epihydrus Raf., Menyanthes trifoliata L., and Isoetes occidentalis Henders (Gruendling, 1971). The recent invasion of Utricularia intermedia Hayne has been observed, but was not reported previously.

Below the lake, ca. 0.5 km downstream on Jacob's Creek is Station 3 (elev. 300 m ). The water runs smoothly until reaching a series of jagged rock outcrops where riffles form. Cascades are infrequent and some deep pools form. Jacob's Lake tends to exert a regulating effect on flow so that extremes are not as pronounced as in other stations. Shading is moderate and much of the stream receives nearly full sunlight. The growth of Utricularia extends to this point. The sponge Spongilla lacustris L. is common throughout much of the year.

Jacob's Creek, which joins the North Alouette River 1 km below Station 3 , is a $2^{\circ}$ tributary before the junction. Station 2 is located at this junction and is 4.1 km upstream from the main Station (1). Station 2 is at an elevation of 208 m and is much like Station 1 in flow regime, substrate, and shading.
III. MATERIALS AND METHODS

## A. THEORETICAL AND PRACTICAL CONSIDERATIONS

The array of species in the stream is organized (sensu Hutchinson, 1953) as a scattering of clusters or patches which appear in some instances to be random and at other times, ordered in some more definite way. Ideally then, these individual clumps should be examined individually, rather than assuming homogeneity and assessing the association(s) only as a whole. The physical and chemical environment is also in some ways heterogeneous, with respect to changes both in space and time. Some compromise should be made which will adequately portray these subtleties, but restrict the number of samples and measurements to a workable size. Only Station 1 is considered in detail for within-habitat variations in the algal community and finer grained measurements of abiotic factors.

The diversity in morphology of the algal species in this system individually and collectively also presents some problems with respect to methodology. In planktonic systems, a basic unit for species enumeration is the cell (e.g., Vollenweider, 1969). In terrestrial environments or with macroalgae, 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 found in the lotic system, where microphytes and macrophytes may each become dominant. If mixed stands and epiphytes are also considered, the traditional phytoplankton techniques become entirely inappropriate. In this study, the relative proportions of the species are quantified without recognition of absolute amount. These values
could, if desired, be related to estimates of total algal biomass measured by chlorophyll or carbon (Marker, 1976; Bott et al., 1978; Tett et al., 1978) .

A further consideration is that of inputs of algal inocula from lake sources, primarily Jacob's Lake. The means of distinguishing "accidental" species from opportunistic or merely ubiquitous ones is not clear. However, some lake species may be "aggressive" colonizers and represent something more than transient components from the drift. For this, a classification of growth forms (see Section III-D) is proposed, and this is used in conjunction with differences in relative abundance to answer this problem.

## B. COLLECTION OF ALGAL SAMPLES

Many technical problems in sampling lotic algae are considered by Sanders and Eaton (1976), and some of their recommendations are incorporated here. Artificial substrates were not used in the bulk of this study in that, (1) a number of authors (Sladeckova, 1962; Tippet, 1970; Siver, 1977; Kann, 1978; Munteanu and Maly, 1978) found their use to be selective or unrepresentative, and, (2) the complexities mentioned previously (III-A) which may be fundamental to understanding aspects of community structure, are eliminated by creating a uniform microenvironment.

All descriptions and methodology in this section will refer to Station 1 unless otherwise mentioned. The stream was crossed with a series of transect lines using 0.5 cm diam. nylon rope. The transects were placed perpendicular to stream flow at ca. 25 m.intervals. The lines were marked in decimeter points along their. length (after Blum, 1957). Sampling points were selected from a stratified series for routine collections, following

Cummins (1962). Below a given point the nearest ten boulders perpendicular to the transect with algal patches were selected for sampling. These were generally within a one meter length and were combined in one sample representative of a particular locality in the stream. Initially, 12 of these combined samples ( $=120$ points) were taken, until time restrictions reduced this to an average of 8 . Methods for more detailed comparisons are discussed in Section III-E.

The apparatus used for removing the algae and bryophytes at all stations was a modification of the half-bottle designed by Douglas (1958). In the streams studied, substrates with algal assemblages were frequently larger than could be easily removed. Two 1-1iter polypropylene bottles were fused together and fitted with a strip of 8 mm thick foam rubber around the neck, extending 3 mm beyond the rim. This was fastened with a 1 cm diam. rubber vacuum hose, which had a heavy wire inside to secure it. This allowed for a reasonable seal against a submersed rock so that water plus algae were isolated from the current. The scraper follows the original design of Douglas (1958). The loosened material was sịphoned off using a large bore pipette attached to rubber tubing. For awkward angles and in calm waters, a sharpened, U-shaped spatula was employed by hand. Most conditions allowed these procedures to be made in hip-length boots, but wet suits were worn during winter and for peak flow periods.

At Jacob's Lake (Station 4), a series of five horizontal plankton tows were made using a \#25 mesh Wisconsin net. Epiphytic collections were made from scrapes of at least five macrophytes and/or floating logs. Bottom samples were collected using a plastic tube ( 5 mm I.D.) for ten sediment cores, after Round (1953).

Seventeen collections were made through the year at Station 1, from 7 June 1977 to 29 June 1978. The sampling frequency followed biweek1y to monthly periods, largely dependent on flow conditions. During the period mid-November through December, however, sampling was curtailed due to floods. For the other stations, four sampling periods were made over the year, although Station 7 was not initiated until 15 February 1978. All the flowing water stations $(2,3,5-7)$ were collected similarly to that at Station 1, but using only 2 to 4 composite samples, each collected from ten separate rocks. In all, samples were returned to the laboratory in an ice chest live and observed upon arrival. They were kept in 3, 5, 10, or $15^{\circ} \mathrm{C}$ culture chambers, depending on field temperatures.

## C. QUANTIFICATION

As mentioned, absolute values of algal biomass of each species were not estimated. Levandowsky (1972) has indicated that in phytoplankton counts, significant differences between numbers lie primarily in orders of magnitude. The scales of cover used by Braun-Blanquet (1965) and Daubenmire (1968) for terrestrial vegetation and in streams by Backhaus (1967) are adaptable to this lognormal measure. A series of ranks (1-5) used by Holmes and Whitton (1977) were employed in this study, representing the relative amounts of biomass contributed by each species. They are: $0=$ absent $; 1=<0.1 \% ; 2=0.1-1.0 \% ; 3=1.0-5.0 \% ; 4=5.0-10.0 \%$; and $5=>10 \%$. The method was designed for estimation of macrophytes and so was modified for both macro- and microphytes.

Samples in the laboratory were partially shredded with forceps and mixed in a 350 ml observation dish. Four 5 ml subsamples were taken from
each and the combination preserved in Lugol's iodine. Portions of fresh material were prepared for observation and scanned under 300X using a Leitz-Wetzar microscope. Five strips across the field constituted "microtransects" whose width ( $330 \mu \mathrm{~m}$ ) was determined by the width of the ocular grid on the microscope. Cover estimates for the series of strips resulted in an average value for all species encountered in the subsample. This procedure was repeated eight times for a total of forty 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 cover class.

Diatoms were never high1y abundant (rank of 5) in the streams and thus for more than $95 \%$ of all species no enumeration was necessary. The few numerous diatom species were assigned their average cover estimate, and further counts and identification of rare cells were made of frustules cleaned as follows. Six 10 ml subsamples were removed from each sample and placed in a 150 ml beaker. Cleaning and mounting followed Patrick and Reimer (1966), using Hyrax ( $\underline{n}=1.71$ ) and made in duplicate. These were examined in the same routine as with fresh material, but observed with a Zeiss standard UPL phase microscope (ocular grid 290 mmide). In Station 4 diatoms often predominated, so counts of live cells were made before detailed observation of cleaned frustules.

## D. TAXONOMIC AND ECOLOGICAL CLASSIFICATION

The general classification of algal groups follows Stein (1975), with the exception of the diatoms, where Silva (1962) is recognized. The Cyanophyta (=Cyanobacteria of Stanier et al., 1978) were identified using

Geitler (1932) and Desikachary (1959). In specific instances, Kann (1972, 1973) was used for Chamaesiphon, Kann and Komárek (1970) and Komárek (1972) for Phormidium, Komárek and Kann (1973) for Homeothrix, and for Tolypothrix, Golubić and Kann (1967) were used.

Preliminary identification of Chlorophyta followed Prescott (1962) and Bourrelly (1966). Specifically, the Ulotrichales and Chaetophorales followed Printz (1964); for the Zygnematales Transeau (1951) and Randhawa (1959) were used in the Zygnemataceae, with West and West (1904, 1905, 1909, 1912), West et al. (1923), Smith (1924), and Stein and Gerrath (1968) used for the Mesotaeniaceae and Desmidiaceae. Ch1orella species were identified using Prescott (1962) and Fott and Nováková (1969), although symbionts in distinctly different associations were regarded as ecologically separate in this study.

The Chrysophyta (Chrysophyceae) were identified using Bourrelly (1957) and Huber-Pestalozzi (1941), whereas the Prymnesiophyceae followed Parke et a.1. (1962). Bacillariophyta taxonomy follows Patrick and Reimer (1966, 1975), Cleve-Euler (1951, 1952, 1953a,b, 1955), Hustedt (1927, 1930a,b, 1961, 1964), Huber-Pestalozzi (1942), and Hohn and Hellerman (1963). For specific problems, Koppen (1975) was consulted for Tabellaria, Belcher and Swale (1977) for Thalassiosira, and Lange-Bertalot (1976) for some species of Nitzschia. The nomenclatural revisions of Van Landingham (1967-1975) were followed, except where superseded by more recent accounts.

Euglenophyta were identified using Prescott (1962) and Huber-Pestalozzi (1955). The Cryptophyta and Pyrrophyta follow Bourrelly (1970) and HuberPestalozzi (1950). The general taxonomy of the Rhodophyta agrees with Bourrelly (1970), but specific identification followed the papers of Skuja
(1935), Israelson (1942), Whitford and Schumacher (1969), Haraguchi and Kobayasi (1969), and Mori (1975).

When observed, all species were given a three letter, two number species code and classified according to growth habit(s) when possible. The categories are after Round (1964) and reflect substrate preferences. These are: (a) epiphytic -- attached to plants or other algae; (b) epilithic -- attached to rocks; (c) epipelic -- associated with sediments; (d) metaphytonic -associated with plants or other substrates but not attached and often from drift; and, (e) planktonic -- freely floating in the water column.

## E. HABITAT VARIATIONS

Experiments were designed to examine differences in the algal community temporally and spatially. Spatial heterogeneity and substrate selectivity were examined at Station 1.

Colonization of bare substrates was followed during August 1977. Three granite boulders (ca. 0.5 cm diam.) chosen were similar in weight and texture and scrubbed clean with nylon brushes and surface sterilized with $95 \%$ ethyl alcohol. They were placed in a riffle adjacent to each other, where current, depth, and shading were measured to be nearly equivalent for the three. Next to these, three Plexiglas sheets ( $35 \times 22 \times 1 \mathrm{~cm}$ ) were bolted to concrete blocks, after Stockner and Shortreed (1976). One substrate of both types was removed successively after 1, 2 , and 4 weeks, following Patrick et al. (1954), Weber and Raschke (1970), Wihlm et al. (1977), and others cited in these. Because replicates were not made, this design was used only to assess differences between substrates and colonization time, not conditions of the stream overall.

In May 1978, a more detailed analysis was made of the variations in the array of species spatially along an apparent gradient of current from one margin of the stream to the other (see Fig. 2). In this, the transect points were located at eight intervals 2 m apart. Samples were taken along perpendicular lines as in routine work (section III-B), but 7 algal patches, rather than 10 , were removed along each perpendicular, and these were kept in separate vials. Thus, 56 distinct samples were compared with each other in this matrix. Factors of temperature, dissolved $\mathrm{O}_{2}, \mathrm{pH}$, current velocity, and light availability were also examined along this transect.

## F. PHYSIOCHEMICAL METHODS

Field: Temperature was measured using an Etco field mercury thermometer and pH with a Markson (model 85) portable pH meter, accurate to $\pm 0.05 \mathrm{pH}$ units. Both pH and temperature were measured at five points along a given transect and taken at five, two-hour intervals during the sampling day. The variance of these are expressed as a standard deviation from the mean of the 25 measurements. Depth profiles were measured to the nearest cm , and the mean then calculated.

Incident light was determined by means of a Belfort Instruments recording pyrheliometer placed on a rock outcrop which received an average amount of shading as determined by a series of individual measurements. Damage to the instrument, however, prevented continuous data collection. Shading effects due to canopy for this and the gradient analysis were estimated using a Licor (model LI-185A) quantum meter taken at 2.0 m intervals along the transects. Current velocity was measured with a General Oceanics (model 2030) digital flowmeter, taken at 10 points along. two transects.
 location of transects and sampling grid for gradient analysis.

Triplicate measurements were made at each point and then averaged.
All of the above measurements in situ were at Station 1 on the dates of algal sampling plus one day (29 October 1977) when floods prevented algal collections. At the other stations, only current velocity, pH , and temperature were estimated. Station 1 water samples were also taken for further analysis. Samples for nutrient determinations were collected in 1 liter polypropylene bottles in duplicate, rinsing these with stream water three times, filled, and capped underwater (after Stainton et al., 1974). Most regions of the stream were well mixed and thus spatial variations in dissolved minerals were not considered. A 500 ml water sample was taken each date for alkalinity ( as $\mathrm{HCO}_{3}^{-}$) determinations. Five 300 ml water samples were collected at different points at Station 1 in glass BOD bottles held underwater. The first two $\mathrm{O}_{2}$ reagents were added in the field to prevent losses during storage. All samples were transported to the laboratory in an ice chest.

Laboratory: The two nutrient samples were separated and 1 liter was filtered (Whatman GF/C glass fiber). Both samples were rapidly frozen $\left(-15^{\circ} \mathrm{C}\right)$ for future analysis. The filtering precaution to remove particulate fractions (Strickland and Parsons, 1972) was later found to have a negligible effect. At the time of analysis, the frozen samples thawed for 24 hours at room temperature and were well mixed to redissolve any ions precipitated during freezing (Golterman, 1969).

All anion $\left(\mathrm{PO}_{4}^{3-}, \mathrm{NO}_{3}^{-}, \mathrm{Cl}^{-}, \mathrm{SO}_{4}^{2-}\right)$, dissolved $\mathrm{SiO}_{2}$, and $\mathrm{NH}_{4}^{+}$concentrations were determined using a Technicon Autoanalyzer II, following standard methods outlined by the manufacturer (Technicon Industrial Systems, 1971a-d, 1973). Cations $\left(\mathrm{Ca}^{2+}, \mathrm{Na}^{+}, \mathrm{K}^{+}, \mathrm{Mg}^{2+}, \mathrm{Fe}^{3+/ 2+}, \mathrm{Mn}^{2+}, \mathrm{Al}^{3+}\right)$ were determined
using atomic absorption spectrophotometry (Varian-Techtron, Ltd.; model AA-5).

Samples for alkalinity ( $\mathrm{HCO}_{3}^{-}$) determinations were not frozen but were analyzed within 8 hours of collection. For this, titrations were done using standardized $0.02 \mathrm{NH}_{2} \mathrm{SO}_{4}$ (A.P.H.A., 1965) with a pH meter rather than color indicators. Dissolved $\mathrm{O}_{2}$ levels were determined within 12 hours after acidification via the azide modification of the Winkler techinque (A.P.H.A., 1965). Percent saturation was calculated after Lind (1974).

## G. STATISTICAL METHODS

For statistical analysis, the abundance ranks were converted to their median values. This allowed calculation of the mean abundance for each species on a given date and place, but preserving differences in the orders of magnitude. In presenting results of species composition between stations or dates (where total cover values may differ), species importance was used (Whittaker, 1970). The importance ( $\underline{\mathrm{I}}_{\mathrm{a}}$ ) of species a would be:

$$
\begin{equation*}
I_{a}=\frac{\text { Mean Abundance of One Species }}{\text { Mean Abundances of All Species }}=\frac{\bar{A}_{x_{a}}}{\sum_{x=1}^{n} \bar{A}_{x}} \tag{1}
\end{equation*}
$$

where $\overline{\mathbb{A}}_{\underline{x}}$ is the mean abundance of species $\underline{x}$ and $\underline{n}$ is the total number of species. This is comparable to relative dominance (Mueller-Dombois and Ellenberg, 1974). The values range between 1, for absolute dominance (i.e., the only species) and 0 , if absent. Diversity of species was expressed in two ways. These were simple species number ( $\underline{S}$ ) and species diversity ( $\underline{H}^{\prime}$ ), using the Shannon-Weiner index:

$$
\begin{equation*}
\mathrm{H}^{\prime}=-\Sigma \mathrm{p}_{\mathrm{i}} \cdot \ln \mathrm{p}_{\mathrm{i}}, \tag{2}
\end{equation*}
$$

where $\underline{p}_{\underline{i}}$ is the relative importance value of the $\underline{i} t h$ species (Shannon and Weaver, 1949).

For multivariate analyses of affinities between dates and stations, an ordination similar to Principle Components Analysis (Orloci, 1966) was used. This method, Principle Coordinates Analysis (P-Co-A), or Gower ordination (Gower, 1966), is more efficient for data in which the number of variables (species) is much greater than cases (dates or stations). The specific program used here is that of Bradfield (1977). The similarity index for this is based on the cosine of the angle between each vector summarizing the abundance of each species. In data with more than two variables, the cosine function takes the form:

where $\underline{x}_{i j}$ is the value of the $\underline{j}$ th species in case $\underline{i}, \underline{x}_{k j}$ is the value of the $j$ th species in case $\underline{k}$, and $\underline{m}$ is the total number of species. When these similarities are computed, a geometric representation of all similarities between all cases is produced, reflected in the distances between their plotted positions. Generally, each component axis contributes successively less of the total variability expressed by all the date-place units. Thus, the first two axes are of greatest importance in any ordination, although the third axis is also given. The nearness of all points
will reveal similarities but does not necessarily classify the cases into groups, emphasizing the continuum nature of species distribution (MuellerDombois and Ellenberg, 1974).

A simple linear correlation (Anderson, 1958) was used to compare the seasonal behavior of physiochemical 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 a1. (1978).

For purposes of describing variations within Station 1, additional statistics were employed. Similarity between two assemblages colonizing bare substrates was judged using the Sфrensen similarity coefficient:

$$
\begin{equation*}
I S=\frac{2 M W}{M A+M B}, \tag{4}
\end{equation*}
$$

where MW $=$ the sum of the smaller of the species abundances of all species in common to both substrates, $\underline{M A}$ and $\underline{M B}$ are the values for all species present on substrate $\underline{A}$ and $\underline{B}$, respectively (Sфrensen, 1948). The comparison of species associations along a transect for gradient analysis was made to recognize groups of difference, rather than the continuous nature of the species themselves. For this, a cluster analysis of samples was used (Orloci, 1975). The algorithm was that of Ward (1963).

## IV. BIOLOGICAL RESULTS

## A. GENERAL TAXONOMIC AND ECOLOGICAL FEATURES

From June 1977 through June 1978, 266 algal taxa were identified from the seven stations (Table 1). 59 taxa are new records for British Columbia (Stein and Borden, 1978) as indicated (*) in the table. The enumeration of species by date for Station 1 and by station for four dates at the other six stations are listed in Appendix $A$ and $B$, respectively. Although diatoms were extremely rich in species, the streams were typified by stands of green and bluegreen algae.

A few major species exhibited extremes in morphological variability. Phormidium autumnale was common in many stations but within a given stand on any one date many differences were encountered: i) the trichome apex varied from bluntly rounded to tapered-capitate and curved; ii) ceil dimensions were not constant $[(4.0)-4.5-5.5-(6.8) \cdot \mu \mathrm{m}$ diam. $]$ within a single filament, and varied from shortened disks to quadrate cylinders; iii) macroscopic color ranged from yellow-brown to dark brown and deep blue-green.

Another common species, Klebsormidium rivulare, was extremely plastic with respect to cell diameter $[(5.5)-6.5-10.0-(11.5) \mu \mathrm{m}]$ and chloroplast form. The plastid was a flattened plate in $2-8$ celled "germlings" but in larger filaments, was a parietal band which extended between half and nearly the entire cell length. This band sometimes was wrapped around the cell interior from one-quarter to one-half the diameter of the filament.

Batrachospermum moniliforme occurred as clumps in pools at all lotic stations except Station 2. Generally, it was of typical morphology and reproduction, with a broad color range of reddish brown to grey-green. It
was observed to perennate in grey or brownish crusts. Sometimes the plumose thallus would originate from these crusts, and at other times the simply branched "chantransia" stage would arise from the same. No difference in the appearance of the crustose growth was observed during the year. Efforts to maintain crude cultures were not successful.

Table 1 gives information pertaining to the high degree of selectivity among many species as to growth habit and substrate. $30 \%$ ( 81 taxa) were exclusive to one of the five defined ecological regimes. Slightly more than half of these ( 46 taxa) were encountered in the metaphyton and likely represent a drift component from an upstream source.

Generally the stream system was dominated by epilithic forms, consisting predominantly of Zygnema insigne, Klebsormidium mucosum, as well as Phormidium autumnale and $\underline{K}$. rivulare, mentioned earlier. In some reaches, the epilithon was also characterized by Stigonema mamillosum, Bulbochaete pygmaea, and Audouinella hermanni. One bluegreen alga, Homeothrix varians, was an encrusting species exclusively restricted to cascading segments directly under the strike of rapid water. Mougeotia $s p$. (sterile) was the only major species that frequently occupied an epiphytic habit. Desmids and diatoms were ecological "generalists", occupying commonly more than one habit.

In some instances, growth habits were, as in epiphytic forms, "host" specific. In particular, the members of the Chamaesiphonales were restricted to one or two particular substrates. Chamaesiphon confervicola (Cyanophyta) was the most common of these, and was found attached only to Zygnema insigne (Chlorophyta). During periods when the host was uncommon, the epiphyte did not grow on other dominant filamentous species. Clastidium
setigerum was present throughout the year in the North Alouette (Station 1) and nearly all observations were as attached to the moss Blindia acuta and never on associated algae or the rock to which the moss was anchored.

Planktonic species were uncommon, even in Jacob's Lake. Those encountered in lotic stations were amongst filamentous or mucilaginous forms as metaphyton. A comparison of all species from the lake was made with all downstream stations to determine the importance of the lake as an inoculum source (Appendix C). A large proportion of the lake taxa (82\%) were transported to the stream (Table 2). Only $27 \%$ of all lake species were capable of colonization in an attached habit. Many of these characteristically were dominants in the flowing stations but uncommon in Jacob's Lake, such as Z. insigne or K. rivulare. Epipelic species, predominantly diatoms, reached significant proportions in the lake and were successful colonizers of the streams, although never abundant (rank of 5).

Table 1. List of species identified from all stations of the watershed, with their assigned species codes and dominant growth habit(s) ( * = taxon previously unrecorded in British Columbia; XX = common growth habit; $\mathrm{X}=$ growth habit observed but uncommon; -- = not observed in particular growth habit).


HABIT
Epiphyton Epilithon Epipelon Metaphyton Phytoplankton

## CYANOPHYTA - Stigonemales

| HPLO1 | Hapalosiphon sp. A |
| :---: | :---: |
| STG01 | Stigonema mamillosum (Lyngb.) C.A. Ag. CHLOROPHYTA - Volvocales |
| CDYO1 | Chlamydomonas sp. A |
| EøD01 | Eudorina cf. elegans Ehr. Tetrasporales |
| SHCOI | Schizochlamys gelatinosa.A. Br. ex Kut |
| TTRO1 |  |

TTR02 T. Zubrica (Roth) C.A. Ag.
Ulotrichales
UKL01 Klebsormidium mucosum (Boye-Petersen) Silva et al. *
UKL03 K. mivulare (Kutz.) Silva et al. *
MCP01 Microspora-pachyderma (Wille) Lag.
Chaetophorales
CET01 Chaetospaeridium gZobosum (Nordst.) Kleb.
DPRO1 Draparnaldia plumosa (Vauch.) C.A. Ag.
SGCO1 Stigeoclonium subsecundum Kutz. *
Chlorococcales
AKDO1 Ankistrodesmus faloatus (Corda) Ralfs.
AECO1 Asterococcus superbus (Cienk.) Scherff.
CRA02 Characium cf. ambiguum Herm.
CRAOL C. falcatum schroed.
cøv01 Chlorella vulgaris Beif. (zooxanthellae in Spongilla lacustris L.)
Cøv02 C. vulgaris Beif. (zooxanthellae in Ophrydium sp.)
CML01 Coelastrum cambricum Arch.
ØST01 Oocystis borgei Snow
PDIO1 Pediastrum boryanum (Turp.) Meneg.
SCD01 Scenedesmus quadricauda (Turp.) Bréb.
Oedogoniales
BUL01 Bulbochaete pygmaea Pring.

| -- | -- | -- | XX | -- | -10 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| x | xx | -- | -- | -- | $\stackrel{\sim}{0}$ |
| -- | -- | -- | X | XX |  |
| -- | -- | -- | -- | XX | O |
| -- | XX | -- | -- | -- | 考 |
| -- | XX | -- | -- | -- | $\stackrel{\square}{\square}$ |
| -- | XX | -- | -- | -- |  |
| -- | xx | -- | X | -- |  |
| x | Xx | -- | x | -- |  |
| x | XX | -- | -- | -- |  |
| x | -- | -- | x | xx |  |
| -- | Xx | -- | -- | -- |  |
| -- | XX | -- | -- | -- |  |
| -- | -- | -- | xx | x |  |
| -- | -- | -- | -- | XX |  |
| XX | - | -- | x | -- |  |
| x x | -- | -- | x | -- |  |
| -- | XX | -- | -- | -- |  |
| -- | XX | x | -- | -- |  |
| -- | -- | -- | -- | xx |  |
| -- | -- | -- | x | Xx |  |
| -- | -- | x | -- | Xx |  |
| -- | -- | -- | x | XX |  |
| X | XX | -- | -- | -- |  |

SPECIES

CHLOROPHYTA - Oedogoniales (Cont.)
ØED01
ØED02 0 . sp. B (reproduction unk.; 6-7 )
Zygnematales
Mesotaeniaceae
DSM46 Gonatozygon monotaenium de Bary
DSM03 Netrium digitus (Ehr.) I. \& R.
DSM12 N. digitas v. naegelii (Breb.) Krieg.
DSM43 Spirotaenia condensata Bréb.
Desmidiaceae
DSM23 Bambusina borreri (Ralfs.) c1.
DSMO2 Closterium abruptum W .
DSM08 C. abruptum v. brevius W. \& W.
DSM26 C. sp. A ( $370 \mu \mathrm{~m}$, lunate)
DSM35 C. dionae Ehr.
DSM28 C. gracile Bréb.
DSM38 C. intermedium Ralfs
dSm32 C. jenneri Ralfs
DSM18 C. juncidum v. elongatum Roy \& Biss.
DSM13 C. parvulum Naeg.
DSM14 C. pritchadianum Arch.
DSM22 C. setaceum Ehr.
DSM04 Cosmarium sp. A (semicells $10 \times 12.5 \mu \mathrm{~m}$; granulate)
DSMO1 C. blyttii wille
DSM56 C. spp. B ( $\sim 20 \mu \mathrm{~m}$ )
DSM15 C. caelatum Ralfs
dSM05 C. monomazum v. polymazum Nordst.
DSM51 C. obtusatum Schmid.
DSM27 C. ornatum Ralfs
DSM25 C. cf. pachydermum Lund

HABIT


| -- | -- | -- | x | Xx |
| :---: | :---: | :---: | :---: | :---: |
| -- | -- | -- | xx | x |
| -- | -- | -- | xx | -- |
| -- | -- | -- | xx | -- |
| -- | -- | -- | xX | -- |
| -- | -- | -- | XX | Xx |
| -- | -- | -- | XX | XX |
| -- | -- | -- | xx | -- |
| -- | -- | -- | xX | XX |
| -- | - | -- | XX | -- |
| -- | -- | -- | Xx | X |
| -- | -- | -- | xx | -- |
| -- | -- | -- | xX | -- |
| - | -- | x | xx | -- |
| -- | -- | -- | XX | -- |
| -- | -- | -- | xx | -- |
| -- | -- | -- | XX | -- |
| -- | -- | -- | XX | -- |
| -- | -- | x | Xx | -- |
| -- | -- | -- | xx | -. |

Epiphyton Epilithon Epipelon Metaphyton Phytoplankton

| CHLOROP | $\begin{aligned} & \text { YTA - Zygnematales } \\ & \text { Desmidiaceae (Cont.) } \end{aligned}$ |
| :---: | :---: |
| DSM57 | Cosmarium praegrande Lund |
| DSM07 | C. reniforme (Ralfs) Arch. |
| DSM29 | C. simii Roy \& B1ss. * |
| DSM19 | C. subcucumis Schmid. |
| DSM47 | Desmidium baileyi (Ralfs) Nordst. |
| DSM24 | Euastrum bidentatum Naeg. |
| DSM50 | $E$. didelta (Turp.) Ralfs |
| DSM10 | E. inerme (Ralfs) Lund. |
| DSM42 | Hyalotheca dissiliens (Sm.) Bréb. |
| DSM31 | H. mucosa (Dillw.) Ehr. |
| DSM44 | Micrasterias radiata Hass. |
| DSM37 | M. sol (Ehr.). Kitz. |
| DSM34 | Peniwn minutum v. crassum W. West |
| DSM11 | P. polymorphum Perty |
| DSM45 | Pleurotaenium maximum (Reinsch) Lund |
| DSM09 | SpondyZosium planum (Wolle) W. \& W. |
| DSM54 | S. pulchrum (Bail.) Arch. |
| DSM48 | Staurastrum aretiscon (Ehr.) Lund. |
| DSM53 | S. sp. A |
| DSM49 | S. gladiosum Turn. |
| DSM40 | S. gracile Ralfs |
| DSM16 | S. muticum Brêb. |
| DSM20 | S. ophiura Lund. |
| DSM36 | S. polymorphum Bréb. |
| DSM06 | S. punctulatum Brêb. |
| DSM30 | S. teliferum Ralfs |
| DSM39 | Staurodesmus dejectus (Bréb.) Teil. |
| DSM41 | Triploceras verticillatum Bail. |
| DSM21 | Xonthidium antilopaeum (Bréb.) Kütz. |
| DSM52 | $X$. armatum v. fissum Nordst. |

HABIT
Epiphyton Epilithon Epipelon Metaphyton Phytoplankton
CHLOROPHYTA - Zygnematales $\underset{\text { Desmidiaceae (Cont.) }}{ }$

| DSM55 | Xanthidium cristatum Brêb. | -- | -- | -- | X | XX |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Zygnemataceae |  |  |  |  |  | O |
| MøU01 | Mougeotia sp. A ( diam. $=12-34 \mu \mathrm{~m})$ | XX | XX | XX | X | X | $\stackrel{+}{+}$ |
| SPI01 | Spirogyra sp. A ( diam: $\simeq 27 \mu \mathrm{~m}$ ) | X | XX | -- | X | XX | $\stackrel{\rightharpoonup}{\square}$ |
| ZYG01 | Zygnema insigne (Hass.) Kutz. | X | XX | -- | X | -- | $\stackrel{\sim}{\circ}$ |
| ZYG02 | 2. sp. B ( diam. = $20 \mu \mathrm{~m}$ ) | XX | -- | -- | X | -- |  |
|  | CHRYSOPHYTA - Chromulinales |  |  |  |  |  |  |
| CIP01 | Chromulina parvula Conr. * | -- | -- | -- | X | XX |  |
| CXP01 | Chysopyxis bipes Stein | XX | -- | -- | -- | -- |  |
|  | Ochromonadales |  |  |  |  |  |  |
| DNB02 | Dinobryon bavaricum Imh. | -- | -- | -- | -- | XX |  |
| DNBO1 | D. divergens Imh. | -- | - | -- | X | XX |  |
| MAL01 | Mallomonas caudata Iwan. | -- | -- | -- | XX | X |  |
| MAL02 | M. doignonii Bourr. * | -- | -- | -- | XX | X |  |
| $\emptyset \mathrm{CRO1}$ | Ochromonas cf. mutabilis Klebs * | -- | -- | X | XX | XX |  |
| SRN01 | Synura sphagnicola Korsch. | -- | -- | X | -- | XX |  |
|  | Prymnesiales |  |  |  |  |  |  |
| CRYO1 | Chrysochromulina parva Lack. * | X | -- | XX | XX | XX |  |
|  | BACILLARIOPHYTA - Eupodiscales |  |  |  |  |  |  |
| CbS01 | Actinoptychus cf. undulatus Ehr.* | -- | -- | -- | XX | -- |  |
| CYC02 | cyclotella meneghiniana Kutz. | X | -- | -- | XX | -- |  |
| CYCO1 | C. stelligera cl. \& Grun. | -- | -- | X | XX | XX |  |
| MEL02 | Melosira distans (Ehr.) Kiutz. | -- | XX | XX | XX | X |  |
| MELO1 | M. granulata (Ehr.) Ralfs | -- | -- | X | X | XX |  |
| SDC01 | Stephanodiscus astrea (Ehr.) Grun. | X | -- | -- | XX | X |  |
| COS02 | cf. Stephanopyxis broschii Grun. * | -- | -- | -- | XX | -- |  |
| THA01 | Thalassiosira fluviatilis Hust. * | -- | -- | -- | XX | -- |  |

Table 1. Continued.

| Epiphyton | HABIT |  |  | Phytoplankton |
| :---: | :---: | :---: | :---: | :---: |
|  | Epilithon | Epipelon | Metaphyton |  |
| -- | -- | X | XX | x |
| xX | -- | -- | XX | X |
| xX | xX | -- | -- | -- |
| -- | -- | XX | XX | -- |
| -- | -- | -- | XX | XX |
| -- | -- | -- | -- | XX |
| -- | -- | -- | XX | XX |
| -- | -- | -- | XX | -- |
| XX | XX | -- | -- | -- |
| XX | XX | -- | X | -- |
| xX | Xx | -- | -- | -- |
| XX | XX | -- | x | -- |
| -- | -- | XX | XX | X |
| -- | -- | -- | XX | -- |
| XX | -- | -- | XX | -- |
| XX | -- | -- | XX | -- |
| XX | XX | -- | -- | -- |
| XX | - | -- | XX | x |
| Xx | XX | X | x | -- |
| X | -- | XX | X | XX |
| XX | XX | x | Xx | X |
| -- | -- | -- | XX | XX |
| -- | -- | XX | XX | XX |
| -- | -- | -- | XX | -- |
| -- | -- | XX | X | X |
| XX | -- | -- | -- | -- |
| X | -- | Xx | XX | X |
| -- | -- | XX | XX | X |
| X | -- | XX | XX | XX |



SPECIES

BACILLARIOPHYTA - Eunotiales (Cont.)
EUN07 Eunotia flexuosa Bréb. ex Kutz.
EUNO2 $E$. cf. hexaglyphis Ehr. *
EUN19 E. naeglii Migula *
EUN04 E. parallela Ehr. *
EUNO1 E. pectinalis (Dillw.) Rabh.
EUN05 E. perpusizla Grun. *
EUN14 E. septrionalis østr.
EUN20 E. serra Ehr.
EUN06 E. serra v. diadema (Ehr.) Patr.
EUN16 E. soleirolii (Kütz.) Rabh. *
EUN17 E. sueica A. C1.
EUN03 E. tenella (Grun.) Hust.
EUN15 E. vanheurckii Patr.
EUN18 E. vanheurckii v. intermedia (Krasske ex Hust.) Patr.
PEROI Peronia fibula (Breb. ex Kütz.) Ross.* Achnanthales

ACN05 Achnanthes Zanceolata (Breb.) Grun.
ACN04 A. Zanceolata v. dubia Grun. *
ACNO1 A. minutissima Kütz.
ACN03 A. stewartii Patr.
CNS01 Cocconeis placentula v. euglypta (Ehr.) Grun. * Naviculales
APH02 Amphora ovalis v. libyca (Ehr.) Cl.*
APH01 A. coffeaeformis (Ag.) Kütz.
NVA15 Anomoemeis follis (Ehr.) Cl.
NVA29 A. serians (Bréb. ex Kutz.) C1.
NVA04 $A$. serains v. brachysira (Bréb. ex Kuitz.) Hust.
NVA08 A. vitrea (Grun.) Ross
CYM03 Cymbelza sp. A (Both margins convex, $\sim 41 \mu \mathrm{~m}$ )
CYM06 C. sp. B (strongly arched, $36 \mu \mathrm{~m}$ )

| Epiphyton | Epilithon | Epipelon | Metaphyton | Phytoplankton | - |
| :---: | :---: | :---: | :---: | :---: | :---: |
| XX | -- | X | XX | X | D |
| -- | -- | XX | XX | -- | $\square$ |
| -- | -- | XX | X | -- | $\bigcirc$ |
| xX | -- | x X | X | x | 9 |
| xx | xx | x | xx | x |  |
| -- | -- | X | XX | XX | $\stackrel{\square}{\square}$ |
| -- | -- | xx | x | -- | $\bigcirc$ |

habit


| CYM08 CYM02 | Cymbella cf. cistula (Hempr.) Kirchn. C. cesatii (Rabh.) Grun. ex A.s. |
| :---: | :---: |
| CYM05 | C. gracilis (Ehr.) Kutz. |
| CYM13 | C. hauckii V.H. * |
| Cymio | C. heteropleura v. subrostrata C1. * |
| CYM04 | C. minuta Hilse ex Rabh. * |
| CYM07 | C. minuta f. latens (Krasske) Reim. * |
| СYм09 | C. muelleri Hust. * |
| CYM12 | C. naviculiformis Auersw. ex Heib. |
| Crml 1 | C. cf. proxima Reim. * |
| DPN01 | Diploneis oblongella (Naeg. ex Kitz.) Ross |
| DPN02 | D. finnica (Ehr.) C1. |
| EPM02 | Epithemia smithii Carruth. |
| EPMO1 | E. sorex Kütz. |
| FRU03 | Frustulia rhomboides (Ehr.) DeT. |
| FRU01 | F. rhomboides v. capitata (A. Mayer) Patr. |
| FRU02 | $F$. rhomboides v. saxomica (Rabh.) DeT. |
| GPN06 | Gomphoneis herculeana (Ehr.) C1. |
| GPN07 | Gomphonema acuminatum Ehr. |
| GPNO1 | G. angustatum (Kutz.) Rabh. |
| GPN05 | G. apicatum Ehr. * |
| GPN02 | G. sp. A (ends'not set off, $\sim 23 \mu \mathrm{~m}$ ) |
| GPN08 | G. sp. B (two isolated punctae, $\sim_{\text {naviculoid) }}$ |
| GPN03 | G. montanum v. media Grun.* |
| GPN04 | G. parvulum (Kütz.) Kutz . |
| NVA01 | Navicula sp. A (ends $\pm$ capitate, $48 \mu \mathrm{~m}$ ) |
| NVA32 | N. cocconeiformis Greg. ex Grev. |
| NVA11 | N. cuspidata (Kütz.) Kütz. * |
| NVA05 | N. sp. D (ellipsoid-rhombic $\sim 16 \mu \mathrm{~m}$ ) |
| NVA24 | N. explanata Hust |


|  | BACILLARIOPHYTA - Naviculales |
| :---: | :---: |
| NVA13 | Navicula sp. E (Ends capitate, striae indistinct, $\sim 27 \mu \mathrm{~m}$ ) |
| NVA36 | N. Levanderi Hust. |
| NVA27 | N. minima Grun. |
| NVA10 | N. cf. monmouthiana-stodderi Yerm. * |
| NVA35 | N. placenta Ehr. * |
| NVA26 | N. polystoma v. pantocsekii Wisl. \& Kolbe * |
| NVA16 | N. pseudoscutiformis Hust. |
| NVA19 | N. pupula kutz. |
| NVA30 | N. pupula v. elliptica Hust. * |
| NVA25 | N. pupula v. rectangulamis (Greg.) Cl. \& Grun. |
| NVA09 | N. radiosa kitz. |
| NVA22 | N. rhynchocephala v. elongata Grun. * |
| NVA07. | N. cf. scutiformis Grun ex A.S. * |
| NVA31 | N. subtilissima Cl. |
| NVA28 | N. cf. validicostata Cl.-Eul.* |
| NVA21 ${ }^{\text {a }}$ | N. vanheurckii Patr. * |
| NVA20 | N. vinidula (Kütz.) Ehr. |
| NEIO1 | Neiditom affine (Ehr.) Pfitz. |
| NEIO2 | N. iridis v. amphigomphus (Ehr.) A. Mayer |
| NEIO3 | N. tromescens (Grun.) Cl. * |
| Nva34 | Pinnulamia biceps Greg. |
| nva06 | P. hilseana Jan. * |
| NVA33 | P. maior (Kiitz.) Rabh. |
| NVA18 | P. parvula (Ralfs) Cl.-Eul. |
| NVA12 | P. microstouron Ehr. C1. |
| NVA14 | P. viridis (Nitz.) Ehr. |
| SNSO2 | Stauroneis anceps f. gracilis Rabh. |
| NVA23 | S. ignorata Hust. |
| NVA17 | S. phoenicenteron (Nitz.) Ehr. |
| SNSO1 | S. phoenicenteron f. gracilis (Ehr.) Hust. |

Epiphyton Epilithon Epipelon Metaphyton Phytoplankton

| XX | -- | xX | x | XX |
| :---: | :---: | :---: | :---: | :---: |
| -- | -- | -- | Xx | -- |
| Xx | XX | XX | xX | X |
| xX | -- | -- | X | xx |
| -- | -- | XX | -- | -- |
| -- | -- | XX | x | -- |
| xx | -- | x | xX | -- |
| xx | -- | -- | x | -- |
| -- | -- | -- | xX | -- |
| -- | -- | xx | X | X |
| xx | x | Xx | xx | x |
| -- | -- | xX | x | X |
| -- | -- | - | -- | XX |
| -- | -- | x ${ }^{\text {x }}$ | Xx | -- |
| -- | -- | -- | x x | XX |
| x | -- | -- | XX | -- |
| -- | -- | -- | x ${ }^{\text {x }}$ | x |
| x | -- | x $x$ | x | x |
| X | -- | x | x | x |
| -- | -- | xx | -- | -- |
| x | -- | xX | -- | -- |
| x | x | xx | xx | Xx |
| -- | -- | xx | -- | x |
| -- | -- | xx | x | - |
| -- | -- | Xx | x | xX |
| -- | -- | XX | x | x |
| -- | -- | -- | xx | X |
| -- | -- | xx | X | -- |
| XX | -- | Xx | x | x |
| X | -- | xX | x | X |

HABIT

| Epiphyton | Epilithon | Epipelon | Metaphyton | Phytoplankton | - |
| :---: | :---: | :---: | :---: | :---: | :---: |
| -- | -- | -- | xx | XX | $\bigcirc$ |
| -- | -- | -- | XX | -- | $\stackrel{H}{+}$ |
| -- | -- | -- | xx | x | C |
| -- | -- | -- | x | x x | $\stackrel{\sim}{\sim}$ |
| xx | -- | x | x x | x |  |
| xx | xX | x | xX | -- |  |
| x | -- | xx | xx | x |  |
| -- | -- | x x | x | xx |  |
| xx | -- | X | x | X |  |
| -- | -- | -- | xX | xX |  |
| -- | -- | x | -- | xx |  |
| -- | -- | -- | -- | xx |  |
| x | -- | x | x | Xx |  |
| x | -- | x | Xx | x |  |
| xX | xx | -- | -- | -- |  |
| XX | xx | -- | -- | -- |  |
| -- | xx | -- | -- | -- |  |
| -- | XX | -- | -- | -- | . |

Table 2. Proportions of algal taxa, by group, from Jacob's Lake present downstream (drift or attached) and in attached habits, expressed in numbers ( $n$ ) and decimal fraction ( P ) of the original number ( $N$ ) of taxa (based on data of Appendix $C$ ).

| ALGAL GROUP | $\begin{aligned} & \text { TAXA IN } \\ & \frac{\text { JACOB'S L. }}{N} \end{aligned}$ | PRESENCE DOWNSTREAM |  | COLONIZED IN ATTACHED HABITS |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | n | P | n | P |
| Cyanophyta | 16 | 13 | . 81 | 5 | . 31 |
| Ch1orophyta | 57 | 43 | . 75 | 12 | . 21 |
| Chrysophyta | 9 | 6 | . 67 | 1 | . 11 |
| Bacillariophyta | 101 | 90 | . 89 | 33 | . 33 |
| Euglenophyta | 1 | 0 | . 00 | 0 | . 00 |
| Pyrrophyta | 2 | 1 | . 50 | 0 | . 00 |
| Cryptophyta | 1 | 1 | 1.00 | 0 | . 00 |

## B. LONGITUDINAL PATTERNS OF THE ALGAL COMMUNITIES

In comparing species assemblages at all stations, there are a few recurrent associations in the stream (summarized in Table 3). Most flowing stations were typified by the presence of filamentous greens and bluegreens. The warmer months (June, August) are largely dominated by Zygnema insigne and Phormidium autumnale, whereas Klebsormidium rivulare showed a predominance in the February period. In this winter collection, Station 1 was sampled on 27 January 1978 and Station 2 on 3 March 1978, due to floods (see also Section IV-C).

Stations 1, 2, and 7 of the North Alouette were Zygnema dominated much of the year, although $P$. autumnale was abundant in early fall (9 August 1977). Due to the larger size of the stream at these stations, streamside pools were often deep, and contained associations differing from the main. Here, Batrachospermum moniliforme, Stigonema mamillosum, and Tolypothrix penicillata were abundänt. Station 7 also exhibited many tufts of Audouine1la hermanni.

Stations 5 and 6 were somewhat similar to the North Alouette stations, but more often were colonized by $\underline{K}$. mucosum, which unlike $\underline{Z}$. insigne or most other filamentous species, had few algal epiphytes. It was not apparent from light microscope observations whether mucilage or other mechanisms were involved. The winter maximum of $\underline{K}$. rivulare occurred only at the upper (Station 6) of these stations, although propagules were present and available to Station 5, in that these were no more than 500 m apart.

As noted, few plankton taxa occurred at Jacob!s Lake (Station 4), which was primarily characterized by attached forms, mainly a sterile

Mougeotia sp. and Frustulia rhomboides (2 varieties). This station was the only region of the watershed where diatoms were present in dominant (rank of 5) proportions. These attached forms contributed nearly all the "resident" stream flora (see Appendix A).

The outflow (Station 3) of Jacob's Creek had a unique quality in the presence of associations of Chlorella vulgaris as endosymbionts in two different sessile animals (Spongilla lacustris and Ophrydium sp.). The associations differed also in their seasonal maxima. The dominant algae were Stigonema mamillosum year round, while others, such as Bulbochaete pygmaea and $\underline{K}$. rivulare were more seasonal. Accumulation of diatom epiphytes were more common than at all other stations.

The species data do not provide immediately recognizable distinctions between stations, although a few generalizations can be made: i) most flowing stations (1, 2, 5-7) were characterized by a number of unbranched filamentous green and bluegreen algae, which are epilithic; ii) the lake outflow (Station 3) was mostly comprised of branched greens and bluegreens which were epilithic, and two symbiotic associations of Ch1orella; and iii) Jacob's Lake (Station 4) was generally a non-planktonic system where those species found in the water column are often more abundant in the sediments or attached to submersed plants, and diatoms were most frequently encountered.

The algal communities at each station when summarized in terms of species number and diversity show that generally, there was no strong relation between species number and diversity expressed as $H^{\prime}$ (Table 4). Thus 'H' only will be referred to as diversity here. Further, the seasonal trends for each station are not altogether similar. The stations downstream
from the lake (1, 2, 7), excluding the outflow, exhibited the lowest diversity during the winter (15 February 1978). On the other hand, the two upstream stations (5, 6) were less diverse during early fall (9 August 1977). Peaks of diversity occurred at all stations during spring (18 May 1978), but the other months did not pattern similarly. In summary, patterns of species diversity ( $H^{\prime}$ ) indicate the stations may be grouped into three segments: i) a downstream reach can be identified which is beyond the immediate effects of lake outflow (Stations 1, 2, 7) which showed reduced diversity in winter and greatest in late spring (May/June); ii) an upstream area near the lake (Stations 5, 6, and perhaps 3) is distinguished by lowest diversity in early fall (9 August 1977), secondarily in the winter (15 February 1978), and species rich conditions during May and June; iii) a lake zone (Station 4) where species diversity was reduced slightly during the winter, but generally high all four sampling periods.

A comparison of the entire species assemblage at each station along the stream for each of the dates has been made by multivariate analysis. Each sampling period is considered separately and a summary of the ordination results are at the end of this section. Ordination of the August data set for Stations 2-6 is shown in Fig. 3. These data were summarized so that more than $99 \%$ of the total variance was accounted for in the first three axes. Of this, nearly $55 \%$ was described by the first axis (Fig. 3A). The plot indicates that Stations 5 and 6 are nearly identical in species composition in August, differing only slightly along the third coordinate axis. Site 2 also bears strong resemblance to these stations, although it separated along the third axis (Fig. 3B). Overall, the stations above Jacob's Lake are furthest from the point representing Station 4, measured
along the first axis. The outflow Station (3) on the other hand, is more similar to the lake than the other flowing station (2, 5, 6). Station 2 , which is further downstream, is considerably more similar to the upstream stations than to the nearest station at Jacob's Creek (3). Stations 5 and 6 were characterized by the dominance of Klebsormidium mucosum, and at Station 2 it was codominant with Zygnema insigne. This can be interpreted that the stations differ from each other along the first axis as determined by the presence of $K$. mucosum. It appears that the first and possibly the second axes are related to proximity to the lake. The specific influences of Jacob's Lake, whether from species loading or through some physical factors, will be considered after the abiotic data (Section VI-A).

The ordination using February data produced axes where the first three dimensions described a total of more than $83 \%$ of the variance. The first and second individually contained nearly 36 and $30 \%$, respectively, of the variance. The plot (Fig. 4) includes Station 7 , the lowest collecting station on the North Alouette. Generally, there is a cluster of the uppermost (6) and lowermost (7) stations rather strongly on all three axes, but the outflow (3) bears resemblance to these along the first and second axes as well. The other upstream Station (5) appears similar to these along the second axis.

The point swarm for the February data exposes a less distinct separation of flowing stations from Jacob's Lake (4). The lake was covered by a translucent ice layer (ca. 3 cm thick) which may have affected absolute levels of standing crop (not measured). Station 2 is relatively distinct along the first and third axes. The later sampling date of this station (3 March) will be considered later (Sections VI-A,B). The variable most
important in discriminating between stations is $\underline{K}$. rivulare, which was not abundant at Station 2. Aside from Station 2, the February period appears to show less longitudinal patterning of species assemblages than did the August period.

In the ordination of species data for Stations $2-7$ during May (Fig. 5), the first three axes cumulatively represented nearly $86 \%$ of the total variance, with the first axis individually, 41\%. At this time, the lake (4) is positioned as most dissimilar to all other stations, with the outflow (3) bearing resemblance to it only along the first axis. The downstream Stations 2 and 7 cluster strongly away from these, and would appear to diverge more than the upstream Stations, 5 and 6.

The spread along the second axis is not easily understood if considered strictly from the standpoint of the stream gradient. During this time all flowing stations except the outflow (3) had a dominance of $\underline{Z}$. insigne, and one other alga. Stations 5 and 6 were joined by an abundance of $\underline{K}$. mucosum, whereas Stations 2 and 7 had very little of this. Codominant in these downstream stations was $\underline{P}$. autumnale. The nearness of these two along the second axis is at present uninterpretable. The third coordinate axis adds little further information as to the similarity of the stations, and differs mostly in reversing the positions of the $2 / 7$ and $5 / 6$ clusters, rather than revealing new affinities (Fig. 5B). It appears the relative differences in the importance of $\underline{Z}$. insigne and secondary dominants were characteristics of comparison for this period.

By June, the species data of alternate Stations 2-7 are more efficiently summarized than earlier, where $93 \%$ of the total variance is expressed by the first three axes and nearly half by the first axis alone. The gradient
downstream from the lake is more clearly expressed along the first axis (Fig. 6), where the outflow of Jacob's Creek (3) is in an intermediate position of similarity and longitudinal position. The flowing Stations 2, 5, 6, and 7 are also more definitely clustered along all three axes than in February and May. The spatial pattern of the affinities between stations expressed in the first two dimensions of the ordination is similar to that in August, although the lake (4) and its outflow (3) are reversed along the second axis. The third axis in the June plot exposed one major difference at the outflow, likely due to the occurrence of Stigonema mamillosum, which at this time is poorly represented elsewhere. It would appear that the algal community at this Station (3) is less like that at Jacob's Lake (4) than in August of the previous year. All stream stations were continued to be characterized by an abundance of Zygnema, and increasingly so for the Jacob's Creek outflow Station.
A.consideration of the species abundance, diversity, and ordination results between stations produces a number of generalizations. These are:

1. For much of the year, there are distinct differences in species composition along the stream-watershed, which appear to be related to the stream gradient, although not for the winter (February/March).
2. Jacob's Lake differs most strongly from all the stream stations, but is not entirely without species common to them.
3. Although many stations are species rich, only the lake has an even proportion of species and hence high diversity ( $H^{\prime}$ ) at all four times of the year sampled.

Conversely, the stream stations exhibited periodic low and high diversity over the year.
4. At certain times, particularly June, the stations appreciably downstream from the lake $(2,7)$ bear strong resemblance to lotic stations above the lake $(5,6)$.

Table 3. Abundance of major species at seven sampling stations, expressed as species importance (Ia, see III-G) on four dates (see Table 1 for species codes, * = Station 2 data on 9 . October 1977, ** = Station 1 data on 3 March 1978, . -- = not observed; ND = no data available).


Table 4. Comparison of species diversity at seven sampling stations at four dates, expressed as species number (S) and ecological diversity ( $H^{\prime}$ ) ( $*=$ Station 2 data on 9 October 1977, ** = Station 1 data on 3 March, 1978, ND = no data).

STATION



Figure 3. A plot of the similarities between five alternate collecting stations (2-6) for 9 August 1977, expressed by P-Co-A in the first and second (A) and first and third (B) coordinate axes (see Fig. 1 for station locations).


Figure 4. A plot of the similarities between six alternate collecting stations (2-7) for 15 February 1978, expressed by P-Co-A in the first and second (A) and first and third (B) coordinate axes (see Fig. 1 for station locations).


## A



## B

Figure 5. A plot of the similarities between six alternate collecting stations (2-7) for 18 May 1978, expressed by $P-C o-A$ in the first and second (A) and first and third (B) coordinate axes (see Fig. 1 for station locations).


Figure 6. A plot of the similarities between six alternate collecting stations (2-7) for 23 June 1978, expressed by P-Co-A in the first and second (A) and first and third (B) coordinate axes (see Fig. 1 for station locations).

## C. WITHIN-HABITAT VARIATIONS IN THE ALGAL COMMUNITY

OF STATION 1

The temporal variation in the abundance of seven dominant species is compared in Fig. 7 and expressed as importance values (Ia). As the observations are for 13 months, they are sufficient to generalize for only one year. These data indicate a gradual progression from one dominant species to the next. None of these, however, was absent or in significantly low quantities to have been missed in the enumeration process. Most species were readily observable at all times of the year and did not "disappear" or alternate between resting stages (e.g., zygospores in the Zygnemataceae) and the vegetative condition.

The major species can be separated into classes of occurrences, which are reasonably distinct from each other. $\underline{Z}$. insigne and $\underline{K}$. mucosum predominate in the late spring-summer until $\underline{P}$. autumnale and Oedogonium sp. A expand in importance in the early autumn. The large burst of $\underline{K}$. rivulare is marked by゙ a low abundance of other species during the winter months, where both bluegreen and diatom epiphyte growth is also reduced. During later winter and early spring, Tolypothrix penicillata peaked, while spring and summer forms began their increase again. The temporal variation in abundance of Stigonema mamillosum was not predictable, as it had periodic peaks and lows throughout the year.

The temporary periods between peaks are times of relatively even species coexistence. This is supported by the seasonal changes in species diversity (Fig. 8). The pulse of greatest diversity ( $H^{\prime}$ ) was in early September, before $\underline{K}$. rivulare had reached large proportions with a second,
less extreme peak occurring the following May. Here again, changes in species number (S) does not mimic the pattern of diversity ( $H^{\prime}$ ), particularly during the increase to its highest levels ( $H^{\prime}=2.33$ ) in August-September. Community diversity appears to follow a pattern outlined for dominant species, where the late-spring is separate from autumn-winter. These are likely distinct from a group of late winter-spring months.

The temporal pattern was also considered through ordination methods. In this, the comparison was between sampling dates. The 17 sampling dates with 203 variables (species) produced vectors where the first coordinate axis accounted for nearly $50 \%$, and cumulatively the first three axes, $87 \%$ of the total variance (Fig. 9). The similarity between sampling dates reveals a cyclic pattern from June 1977 to June 1978, considered by the first two axes (Fig. 9A). This model can be envisioned as a disk, where the seasonal succession of species follows the course around the edge and completes the cycle in one year. The third axis is less obvious, and only contributes another $7 \%$ of the information content to the total picture (Fig. 9B). The three dimensions together would appear as a disk which exhibits some "wobble", rather than as a flat plate. Nonetheless, the analysis shows the succession proceeded in a cyciic 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 roughly proportional to the rate of change in species composition between dates. The long period from mid-October to January did not show a significant change in the community. The two dates (9 October 1977, 27 January 1978) were both characterized by
a predominance of $K$. rivulare. The most dramatic change in composition occurred two sampling dates earlier, between late January and early March. This response can be correlated with a large drop in importance of $\underline{K}$. rivulare and the succeeding increase in $\underline{Z}$. insigne.

When observing the mosaic of algal species in the field at Station 1 , it appeared that there was not an even or random distribution along the streambed. Some species were found only on a specific position on a rock or only on rocks in some places. The colonization experiment, to a degree, supports these observations (Table 5). As indicated by the large change in species composition (small similarity value) of both substrate types with time, a difference in species composition was shown for different exposure periods. In this short-term succession, the two substrates had low similarity to each other in the initial and final stages of the experiment. A period of convergence did occur after the second week, but it was shortlived. By week 4, smaller forms (diatoms) were selected for on the artificial substrate, in contrast to the natural substrate, which then had an assemblage of filamentous greens. This latter association was also true for the stream overall at this time of year (Fig. 7; Appendix A).

The spatial patterning of algal species across the stream was analyzed by cluster analysis (Fig. 10). The major result is the production of two large clusters which differ largely in nearness to the shore. The righthand group are those low and high numbered samples from the extremes of the transect. The bulk of the left-hand cluster is made up of samples from midstream. Choice of the number of clusters is in part arbitrary, but the analysis also produced a step-wise listing of the error associated with each successive grouping. Thus, within a range of $4-12$ clusters desired
(for the eight perpendiculars), the clustering associated with the lowest error jump is at the 10 -cluster level. This is considered the most "natural" grouping of the data. Beyond the two major clusters, the other eight fall nearer to one or the other.

The clusters can be superimposed on the sample map (Fig. 11). The matrix of 56 samples can be placed on the grid which indicates their relative position to the transect and order along the perpendicular. The clustered groups are identified by contour lines (not drawn to scale). The pattern reveals a very large, distinct group of assemblages that occur near midstream and for much of the northwest margin. The other large group does not follow strictly with nearness to the shore, although this and most anomalous groups have no representatives in the midstream region. Some of the margin samples from each side have been clustered together. Thus, algal species and associations encountered at Station 1 exhibited a number of structural aspects which vary in space and time. They can be summarized by these two aspects.

Temporal: i) The dominant species at Station 1 fluctuated over the period of one year, but at no time were any of the species locally extinct.
ii) Species diversity was greatest during early autumn (August/September) and spring (April/ May) and depressed during winter (January/ February).
iii) A cyclic pattern was recognized in the seasonal change of species (succession), although two drastic changes in community composition were
revealed (September and January/March) and occurred in a short span of time.

Spatial: i) A complex of species assemblages exists in the stream which are not evenly or randomly distributed.
ii) A short-term succession was found to differ in structure between the two substrate types.
iii) Many species show affinities to particular substrates and localities within the stream, and do so in a recognizable pattern.

Figure 7. Seasonal changes in the abundance of the major algal species at Station 1 of the North Alouette River, . expressed as importance ( $I_{a}$ ) values. Species are presented in order of their first peak from the beginning of the study (see Table 1 for species codes).

IMPORTANCE (Ia) OF io iv in MAJOR SPECIES



Figure 8. Seasonal changes in species diversity of the algal community at Station 1 of the North Alouette River. Diversity is expressed as species number (S) and ecological diversity ( $\mathrm{H}^{\prime}$ ).


Figure 9. A plot of the similarities between algal communities on 17 sampling dates at Station 1 of the North Alouette River, expressed by P-Co-A in the first and second (A) and first and third (B) coordinate axes. The chronological trajectory of points are connected by lines whose length correspond to the relative amount of change in species composition $(\bullet=1977,0=1978)$.

Table 5. Comparison of species assemblages at three successional stages for two substrate types, expressed as similarity ( $I_{s}$ of Sфrensen, 1948); where $1=$ complete and $0=$ no similárity (refer to Table 1 for species codes).

| TEMPORAL DIFFERENCES | COMPARISON |  | WEEKS |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  | 1 vs. 2 | 2 vs. 4 | 1 vs. 4 |
|  | Within the Plexiglas assemblage | .16 | . 11 | . 23 |
|  | Within the granite assemblage | . 02 | . 64 | . 13 |
| SUBSTRATE DIFFERENCES |  | Week 1 | Week 2 | Week 4 |
|  | Major species on | SPIO1 | ZYG01 | GPN01 |
|  | Plexiglas | SYNO1 | SYN01 | ACN01 |
|  |  | ACN01 | UKL03 | SYNO1 |
|  | Major species on | STG01 | ZYG01 | ZYG01 |
|  | granite | TXP01 | SPI01 | STG01 |
|  |  | ACNO1 | TAB01 | SPI01 |
|  | Similarity ( $I_{s}$ ) <br> between substrates | . 06 | . 61 | . 11 |

Figure 10. Cluster analysis of algal associations on separate stones collected along a cross-stream gradient, Station 1 of the North Alouette River, 4 May 1978.



Figure 11. Map of algal associations along a cross-stream gradient on 4 May 1978 (groups identified through cluster analysis, see Fig. 10; figure not drawn to scale).

## V. PHYSIOCHEMICAL RESULTS

## A. COMPARISON OF STATIONS ALONG THE STREAM

The abiotic data collected on dates of algal sampling for alternate Stations (2-7) include only temperature, pH , and current velocity (Table 6). Characteristics of altitude, stream width (and hence relative shade), slope, substrate size, and position relative to the lake are considered for comparison.

The temperature trends were similar between stations seasonally. February was the coldest and August the warmest month of the four dates in all stations. Interestingly, the Jacob's Lake epilimnion was in February the coldest station, whereas during the other periods, it was warmer than all others. Evidently, surface water temperature of the lake changes more rapidly than in any of the shallower streams. This indicates that some stratification likely occurs, even though the lake is regarded as nearly constantly mixed (Efford, 1967). Overall however, it can be assumed that all stations behave similarly with respect to seasonal temperatures.

The pH appears less regular both between stations and dates. All stations were largely circumneutral, although there were a majority of values recorded between pH 6 and 7. Feller (1977) found that the soils of this area have a good deal of mineral leaching, which results in a reduction in the concentration of hydrogen ions from the rainwater through to the stream. Patterns in pH , although not particularly strong, can be outlined. Downstream, Stations 1, 2, and 7, as well as the upper Station 6, had high values during February and low values in May. The outflow (Station 3) was
most erratic, but did not follow patterns in Jacob's Lake to any degree. Little change occurred for Station 5 , varying $\pm 0.15 \mathrm{pH}$ units from a mean of 6.25. The three near-lake/lake Stations (3, 4, 5) apparently were independent of each other with respect to pH characteristics.

Current velocity generally was rapid at all stream stations with the exception of Station 5, which is characterized by large pools and infrequent, small riffles. In flow conditions, Station 5 was most dissimilar to all other stations, excluding Jacob's. Lake. The main stem reaches of the North Alouette, particularly Stations 1 and 2 , were most rapid, sometimes averaging over $1 \mathrm{~m} \mathrm{sec}{ }^{-1}$. The lowest station on the North Alouette did exhibit a reduced current, where slope is much less than upstream stations. Average values can be ranked more or less in the order Stations $1>2>3=$ $6>7>5>4$. Although the average values for Station 6 were similar to that of Station 3, they were quite dissimilar. Station 6 consisted of many extreme cascades alternating with large pools, and Station 3 was primarily riffles. The temporal pattern is similar for all stations, which may be expected. The stations all are interconnected and occur within a length of ca. 12 km , and hence, experience roughly similar climatic conditions.

These variables of temperature, pH , and current velocity can be summarized further in their relative value in comparing dates and stations. Current velocity exposed differences between stations regardless of time of year. Temperature was similar between stations, but highly seasonal. The values recorded for pH , however, did not easily define categories or temporal responses for these locations. Those characteristics which remained effectively constant, such as slope: and stream width, will also be regarded as factors of comparison between stations.

Table 6. Temperature ( ${ }^{\circ} \mathrm{C}$ ), pH , and current velocity ( $\mathrm{cm} \mathrm{sec}{ }^{-1}$ ) measured at single times at seven collecting stations on four sampling dates $(*=S t a t i o n 1$ on 3 March 1978 , $* *=$ Station 2 on 9 October 1977, $N D=$ no data available, $--=$ assumed negligible).

|  | 9 AUGUST $1977^{* *}$ |  |  | 15. FEBRUARY $19.78{ }^{*}$ |  |  | 18 MAY 1978 |  |  | 23 JUNE 1978 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| STATION | TEMP | pH | CURR | TEMP | pH | CURR | TEMP | pH | CURR | TEMP | pH | CURR |
| 1: Main station, North Alouette River | 18.3 | 7.20 | 58 | 3.1 | 7.15 | 95 | 8.1 | 6.50 | 119 | 13.4 | 6.80 | 61 |
| 2: Stream junction, North Alouette River | 8.0 | 6.70 | 64 | 2.1 | 7.35 | 104 | 9.2 | 6.35 | 106 | 11.0 | 6.55 | 67 |
| 3: Jacob's Creek at lake outflow | 19.0 | 7.00 | 53 | 3.0 | 5.85 | 87 | 10.2 | 6.40 | 89 | 17.0 | 6.85 | 56 |
| 4: Jacob's Lake | 19.2 | 6.15 | -- | 2.0 | 6.15 | -- | 12.2 | 6.30 | -- | 18.2 | 6.65 | -- |
| 5: Upper Jacob's Creek | 17.0 | 6.10 | 15 | 2.4 | 6.25 | 25 | 9.4 | 6.15 | 25 | 11.2 | 6.40 | 16 |
| 6: Tributary B | 15.0 | 6.55 | 52 | 2.2 | 7.40 | 86 | 6.8 | 6.45 | 88 | 10.2 | 6.90 | 55 |
| 7: Lower North Alouette River | ND | ND | ND | 4.0 | 7.00 | 73 | 11.8 | 6.45 | 73 | 13.8 | 6.25 | 47 |

B. TEMPORAL PATTERNS IN PHYSIOCHEMICAL PARAMETERS

## WITHIN STATION 1

The water chemistry and other abiotic parameters were measured in detail at Station 1. As duplicate samples for the nutrient chemistry were all that were taken (assuming well-mixed), no error bars are shown for the cation and anion concentrations. The low overall values for dissolved substances are within the range found for other Pacific coastal watersheds in British Columbia (Scrivener, 1975; Feller, 1977) and Washington (Triska and Sedell, 1976).

The patterns of the four dissolved anions plus ammonia are not entirely similar (Fig. 12). Trends in $\mathrm{NO}_{3}^{-}$and $\mathrm{NH}_{4}^{+}$appear to show an inverse relation. $\mathrm{SO}_{4}^{2-}$ and $\mathrm{Cl}^{-}$ions exhibit very little change over the year, although a slight increase occurred over winter. $\mathrm{SO}_{4}^{2-}$ and $\mathrm{Cl}^{-}$were the most abundant anions on the average. $\mathrm{PO}_{4}^{3-}$ was somewhat erratic, but the mean value was less than that measured in an adjacent watershed (Feller, 1977) and the least concentrated of the group: The anions were generally highest during late summer and autumn. The order of their relative average concentrations plus $\mathrm{SiO}_{2}$ (Fig. 14) were: $\mathrm{SO}_{4}^{2-}>\mathrm{SiO}_{2}>\mathrm{Cl}^{-}>\mathrm{NO}_{3}^{-}>\mathrm{PO}_{4}^{3-}$.

Of the seven cations measured, the concentrations of only four were within detectable limits (Fig. 13). $\mathrm{Fe}^{2+/ 3+}, \mathrm{Mn}^{2+}$, and $\mathrm{A} 1^{3+}$ ions were never found in the dissolved fraction. This is similar to that recorded by Wali et al. (1972), where these minerals were not detectable in Jacob's Lake water, but appreciable concentrations occurred in the sediments. In contrast to the anions, the cations showed a remarkably high degree of similarity in temporal pattern. All showed their greatest level in mid-

August and generally so over much of the late summer/early fall. Low levels were also synchronized in a number of periods during the spring and assumedly through the winter. Generally, the order of concentrations was: $\mathrm{Ca}^{2+} \simeq \mathrm{Na}^{+}>\mathrm{Mg}^{2+}>\mathrm{K}^{+}>\mathrm{NH}_{4}^{+} \gg \mathrm{Fe}^{2+/ 3+} \stackrel{?}{=} \mathrm{Mn}^{2+} \stackrel{?}{=} \mathrm{Al}^{3+}$.

The seasonal levels of alkalinity, $\mathrm{pH}, \mathrm{SiO}_{2}$, and $\mathrm{O}_{2}$ are presented in Fig. 14. The low alkalinity (as $\mathrm{HCO}_{3}^{-}$) levels measured in the stream water follow the general conditions outlined earlier for most areas in the Coast Mountains (Northcote and Larkin, 1963). With this low buffering capacity it is perhaps surprising the pH values did not vary greatly both within the day (standard deviation) and seasonally. The slightly higher values during June 1977 were not repeated the following June. The widest variations in pH occurred when alkalinity was at its lowest, during winter. Dissolved $\mathrm{SiO}_{2}$ was relatively abundant, averaging more than any other ion except $\mathrm{SO}_{4}^{2-}$. The seasonal pattern of $\mathrm{SiO}_{2}$ was similar to the cations. A strong peak occurred during mid-August and subsequently in early March. Dissolved oxygen was always at or above saturation levels all times of the year. Absolute values varied, largely responding to seasonal temperature changes, the major factor influencing concentration (Golterman, 1975; Wetzel, 1975).

Although light energy was measured, equipment failures did not allow a complete picture. Generally, data for average daily radiation showed a gradual increase from early June ( $27 \mathrm{gm} \cdot \mathrm{cal} \mathrm{cm}{ }^{-2} \mathrm{~d}^{-1}$ ) to a maximum in early and mid-August ( $32-36 \mathrm{gm} \cdot \mathrm{cal} \mathrm{cm}^{-2} \mathrm{~d}^{-1}$ ), and then reducing to half the maximum by November. The following spring this pattern appears similar (data incomplete). The measurements for any week were marked by at least a few cloudy days so that the annual picture varies only by a factor of about two ( $17-40 \mathrm{gm} \cdot \mathrm{cal} \mathrm{cm}^{-2} \mathrm{~d}^{-1}$ ). More continuous data of water temperatures do reflect the seasonal character of sunlight available to the system.

The stream temperatures indicate a degree of diurnal flux by maximum and minimum values (Fig. 15). The water temperatures appear to follow a seasonal pattern much related to daylength, where August was the warmest month. During this period, the algal populations experienced a daytime flux of as much as $4^{\circ} \mathrm{C}$. Whether the complete diurnal flux is any greater is unknown, but due to the canyon effect in this area, measurements were made over the time during which the direct effects of sunlight were present. The temperatures ranged nearly 5-fold over the year, although complete freezing never occurred.

Flow conditions, which are reflected in stream depth and current velocity, were highly varied seasonally and within Station 1 on any one date (Fig. 15). Both depth and current followed similar patterns and are considered here as two expressions of one phenomenon. Stream width might also be considered a function of flow, but varied less than $10 \%$ from the mean ( 17.5 m ), hence provides little information concerning changes in stream levels. Stream flow was greatest in late autumn-winter. The decline after October may not be as immediate as shown (interpolated), as floods made sampling impossible during this period. Spring also exhibited a pulse in current velocity, although of less intensity. The time from late spring until the beginning of autumn (March-August) was one of calmer flow, but these dates were at times interrupted by brief spates.

When considered as a whole, the physiochemical environment of the stream may be reduced to a number of distinguishable patterns. Because differences in scale of the graphs may misrepresent similarities in pattern, a simple linear correlation between all variables was made (Table 7). The first group which can be identified may be regarded as the "cation group." $\mathrm{K}^{+}$is
least strongly (positively) correlated among these, but in addition to $\mathrm{Ca}^{2+}, \mathrm{Na}^{+}$, and $\mathrm{Mg}^{2+}, \mathrm{NO}_{3}^{-}$is also strongly and positively correlated. $\mathrm{NH}_{4}^{+}$ did not produce a significant negative correlation as was assumed simply by observing Fig. 13. Although one cation, $\mathrm{Na}^{+}$, did correlate reasonably well with the changes: in stream depth, this will not be considered part of the assigned group, but will be mentioned later.

A second group changed gradually over the year, largely reflecting differences in daylength. This "daylength group" includes a strong correlation between temperature, dissolved $\mathrm{O}_{2}$, and presumably light. A third associated group of variables includes $\mathrm{Cl}^{-}, \mathrm{SO}_{4}^{2-}, \mathrm{NH}_{4}^{+}$, current, depth and $\mathrm{SiO}_{2}$. In this "streamflow group", a strongly significant ( $\mathrm{P}<0.001$ ) correlation between current velocity and depth supports the earlier assumption that these behave similarly. All members of this group are positively correlated, with the exception of $\mathrm{SiO}_{2}$. Whether pH is allied to this group (a very strong correlation with depth) or the cation groups (two lesser correlations out of five) is not clear. Two outliers, $\mathrm{PO}_{4}^{3-}$ and $\mathrm{HCO}_{3}^{-}$, surprisingly had no strong correlations to any variables measured, and were for the most part, sporadic.

The inability to place all the physiochemical variables into separate classes is not surprising. The correlation between some members of the cation group with the streamflow group may reflect effects due to a phenomenon not directly measured, such as rainfall, which may alter the amounts of some dissolved minerals. The intercorrelations undoubtedly reflect the artificiality of the grouping process to some extent as well. Golterman (1975) states that temporal changes in stream-water chemistry frequently vary inversely with flow. The large number of negative correla-
tions with current velocity and depth follow this observation (Table 7). The cations $\mathrm{Ca}^{2+}$ and $\mathrm{K}^{+}$also correlate strongly with the daylength group, but possible biological interrelations cannot be assumed with any certainty. The lack of any strong correlation between alkalinity, $\mathrm{PO}_{4}^{3-}$, and all other variables, although unexplained at present, does not indicate a lack of importance, as these correlations merely point out the significance of coincident phenomena. For example, $\mathrm{PO}_{4}^{3-}$ concentrations found in this study are within or below levels found to be limiting growth of a number of freshwater algal species (Miller, 1972; Rhee, 1973; Titman, 1976).


Figure 12. Temporal variability of anions $\left(\mathrm{Cl}^{-}, \mathrm{PO}_{4}{ }^{3-}, \mathrm{SO}_{4}{ }^{2-}, \mathrm{NO}_{3}{ }^{-}\right.$) and $\mathrm{NH}_{4}^{+}$at Station 1 .


Figure 13. Temporal variability of cations ( $\mathrm{Ca}^{2+}, \mathrm{Mg}^{2+}, \mathrm{Na}^{+}, \mathrm{K}^{+}$) at Station 1.


Figure 14. Temporal variability of alkalinity $\left(\mathrm{HCO}_{3}{ }^{-}\right), \mathrm{SiO}_{2}, \mathrm{pH}$, and dissolved $\mathrm{O}_{2}$ at Station 1.
$\begin{array}{cc}\text { MEAN STREAM DEPTH MAX/MIN WATER MEAN CURRENT VELOCITY } \\ (\mathrm{cm}) & \text { TEMP. }\left({ }^{\circ} \mathrm{C}\right)\end{array}$ ( $\mathrm{cm} \mathrm{sec}-1$ )


Table 7. Linear correlation between all physiochemical variables for three levels of significance $(*=P<0.05, * *=P<0.01, * * *=P<0.001)$.


## C. GRADIENT ANALYSIS OF PHYSIOCHEMICAL VARIABILITY <br> AT STATION 1

In conjunction with the algal distribution analysis, within Station 1 , a number of factors were measured along the first transect at regular intervals. These were pH , temperature, dissolved $\mathrm{O}_{2}$, current velocity, depth, and incident light. Measurements on the micro-scale were made in weeks before ( 31 March, 17 April) and after (26 May, 8 June, 29 June) the date of algal sampling, as well as on that date (4 May). Although absolute values changed temporally, the patterns along the transect did not vary over this time. Mean values of the six dates are given (Fig. 16). The first two variables, pH and temperature, did not change significantly, and so were measured only at three intervals. The equality of both of these on any of the six dates (little standard deviation) supports this. Dissolved $0_{2}$ varied slightly but produced no evidence of a gradient.

Current velocity did vary across the stream. Midstream was the region of greatest flow, but apparently the resistance offered by either stream bank was not equal. This segment of the stream was at a bend, and as indicated by Hynes (1970), tended to displace the idealized flow pattern. Depth was also not uniform, where shallows were recorded at edge and midstream. The availability of light also varied across the transect, but apparently less irregularly than did current velocity. The orientation of this segment of the stream was generally southwesterly, so that the southeast bank was more strongly affected by shading. Further, as the sun moved across the sky, different localities of the midstream were under full irradiance. Hence, large standard deviations were observed at these positions, and less so in the shaded parts.

In general, three factors were measured, depth, current velocity, and irradiance, which changed significantly along the transect. The experiment, however, was not designed to test between these variables. Nonetheless, the measurements do expose a degree of spatial heterogeneity within one locality, even though at present, similarly varying factors cannot be separated with any certainty.


Figure 16. Cross-stream variability of pH , temperature, dissolved $\mathrm{O}_{2}$, current velocity, depth, and irradiance at Station 1 on for six weeks during spring of 1978 .

## VI. DISCUSSION

## A. SYNTHESIS OF BIOLOGICAL AND PHYSIOCHEMICAL RESULTS

Temperature distinguished between times of year for any given station, whereas variations in current velocity revealed differences between the stations themselves (Section V-A). These results suggest that flow characteristics may have been effectual in the production of different species composition along the stream gradient. Further consideration of the analyses indicates that this may not be entirely true. For example, neighboring Stations 5 and 6 were shown to have highly similar algal communities at all times of the year (Figs. 3-6), yet their flow regimes were not all alike (Table 6).

The picture of longitudinal differences along the stream is most likely characterized both by changes attributable to seasonal fluctuations and those features, like current velocity, are "fixed" in their relative differences between stations. The communities found at each station during the winter (February) are least clearly separable from each other, after considering dominant species (Table 3), species diversity (Table 4), and ordination of the complete assemblages (Fig. 5). The exception of a rather distinct Station 2 on the North Alouette can now be explained in that on this later collecting date (3 March), Zygnema insigne had taken an abrupt increase in importance (shown in Station 1, Figs. 8, 10). However, using these same criteria of dominant species, diversity, and the $\mathrm{P}-\mathrm{Co}-\mathrm{A}$, the strongest clustering of stations occurred during June 1978 (Tables 3, 4, Fig. 6) and August (Tables 3, 4, Fig. 3). Here, four of five lotic stations were highly similar, but differed from the outflow stream, all of which diverged from

Jacob's Lake. An interpretation of this difference in patterning would suggest an overriding influence of the cold temperatures during winter, while at other times of the year species composition was largely influenced by current velocity.

The difficulty in explaining the causes of highly similar species composition at Station 5 and Station 6, however, has not been removed. Superficially, the algal vegetation and habitats of the two appear quite dissimilar. The slower flowing upper arm of Jacob's Creek (5) was very poorly colonized all year, except at the infrequently spaced riffles. Less than 500 m upstream, the fast flowing Tributary B (6) was heavily carpeted with algae and bryophytes. Owing to the proximity of the two stations, it may be assumed that the species pool from this cascading region served to colonize Station 5. Hence, it is not surprising that the two stations have many species in common. Accumulation of algae in the slower flowing station (5) was restricted primarily to the riffles, suggesting the upstream propagules had some specificity for a rheophilic habit. The lack of difference expressed by ordination, then, is a reflection of the enumeration method as well, in that only the proportion of each species was recorded, and not biomass.

The complex of physiochemical factors examined at Station 1 to describe temporal variation was simplified by identifying groups of factors that responded similarly over the year. The daylength group varied gradually, whereas the cation and streamflow groups, as well as the few erratically changing factors all had sudden peaks and lows in time. The seasonal progression of major species (Fig. 7) and the pattern from ordination results for the algal community (Fig. 9) exhibited periods that at times
changed smoothly and at other times, rapidly. Some of these accelerated changes were during early to late September, late January to early March, and early to mid-August. In general, these were times when the abundance of Klebsormidium rivulare, Zygnema insigne, and Phormidium autumnale either greatly increased or decreased. A more precise measure of the rate of change, based on the measured distances from the $\mathrm{P}-\mathrm{Co}-\mathrm{A}$ plot between points versus the number of days spanned, provides the following order: September (. 36 $\mathrm{cm} /$ day $) ~>$ August (. $32 \mathrm{~cm} /$ day) $>$ January-March (. $24 \mathrm{~cm} /$ day) .

When compared with the major fluxes in the physiochemical environment, the large-scale species replacement of September corresponds with a time of increasing current velocity and depth (Fig. 15), but not with the other member of this group, dissolved $\mathrm{SiO}_{2}$ (Fig. 14). The August species flux was a period where all cations increased ( Fig .13 ) , plus $\mathrm{NO}_{3}^{-}$and $\mathrm{SiO}_{2}$ (Figs. 12, 14). Finally, the January to March succession was marked by increases again in dissolved $\mathrm{SiO}_{2}$, as well as pH (Fig. 14), and slightly in the cations. Current velocity here dropped.

The consideration of all species data made by correlating the coordinates of the first three axes of the seasonal ordination (Fig. 10) with the temporal flux of all physiochemical variables (Figs. 13-16) can be compared in one unit (Table 8). The differences in species composition described by the first coordinate axis correlates significantly with the anions $\mathrm{Cl}^{-}$ and $\mathrm{SO}_{4}^{2-}$, also current velocity and depth, all positively. This axis correlates negatively with temperature. The first axis is associated largely with the changes in importance between an association dominated by K. rivulare and a $\underline{Z}$. insigne/P. autumnale association. The $\underline{K}$. rivulare association thus was found at times of low temperature, high current velocity,
and. greater concentrations of $\mathrm{Cl}^{-}$and $\mathrm{SO}_{4}^{2-}$. The $\underline{Z}$. insigne/으 autumnale association was more of a spring-summer occurrence, where greater temperatures were joined by reduced current, and $\mathrm{Cl}^{-}$and $\mathrm{SO}_{4}^{2-}$ concentrations. This was also a period of greater plankton accumulation amongst the filamentous species.from the drift, mostly of desmids.

The second coordinate axis correlated significantly and this time positively with temperature, and all members of the cation group, as well as negatively with $\mathrm{O}_{2}$. The behavior of the second axis represented a distinction between a large number of minor species. One extreme was an association variously composed of Oedogonium sp . A, K. mucosum, Batrachospermum moniliforme, and $\underline{P}$. autumnale. This is contrasted with an association of Tolypothrix penicillata, Stigonema mamillosum, Audouinella hermanni and again, $\underline{K}$. rivulare. This less distinct axis is further complicated in that moderate levels of $\underline{Z}$. insigne were present on dates plotted on either ends of this vector. When compared with Fig. 9, however, species diversity was greatest on dates corresponding to the largest (positive) values on the second axis. Hence, species diversity was highest during periods of higher cation and $\mathrm{NO}_{3}^{-}$concentrations, greater temperatures, and low dissolved $\mathrm{O}_{2}$. The third axis did not correlate significantly with any of the variables measured. In all, flow conditions and temperature flux were significantly correlated with, and may be influential in the patterning of species associations seasonally as well as between segments of the stream. Concentrations of dissolved substances, particularly $\mathrm{SO}_{4}^{2-}$ and $\mathrm{Cl}^{-}$, may be factors affecting the presence of some dominant species over the year. The increased levels of cations, $\mathrm{NO}_{3}^{-}$, and temperature were associated with periods of greater diversity at Station 1.

Synthesis of data collected for a cross-stream gradient at Station 1 provides finer details of the relation between algal distribution and abiotic factors. The midstream association was at this time dominated by Z. insigne, and to a lesser degree, $\underline{K}$. rivulare. The marginal, or streamedge habitat was characterized by an accumulation of $T$. penicillata, K. mucosum, and S. mamillosum. Shading caused by the streamside canopy differed for these two associations, as did flow regime. This suggests both may elicit some response in the algal distribution. Un1ike the seasonal or longitudinal patterning, there was no evidence suggesting temperature was a factor in the microdistribution within Station 1. Further, both current and irradiance were more appreciably reduced toward the one margin where the bulk of the representatives of the stream-edge group were found.

The separation of these hypothesized causal factors cannot be easily accomplished from the data at hand. However, some evidence from betweenstation results (Section IV-B) may be of use in this respect. Tributary B is a narrow and well-shaded, but rapidly flowing stream. Upper Jacob's Creek is more openly lighted and slowly flowing. If current regime were most effectual in the Station 1 microdistribution, the species composition at Tributary B in May would be more similar to the midstream association, with Upper Jacob's Creek more similar to the stream-edge association. If light were more important, the reverse would be true. As mentioned, little difference in species composition was found between these two stations. During May, the principal representatives at both were $\underline{K}$. mucosum, $\underline{Z}$. insigne, and $\underline{S}$. mamillosum, which at Station 1 , occurred in distinct groups. It appears that instead of discriminating between two possible effects, these
two have remained intertwined. In any event, the results thus far suggest that light availability and current velocity were affecting the microdistribution of algal species at a wide reach of the North Alouette River on at least one date. It is presumed these factors were acting independently, but present methods were unable to discern between them.

Table 8. Correlation between environmental factors and scores of the first three coordinate axes of the date ordination, given for three levels of significance ( $*=P<0.05$, ** $=P<$ 0.01 , *** $=\mathrm{P}<0.001$; data from Figs. 9, 12-15) .

CORRELATION WITH COORDINATE SCORES
FACTORS
$\mathrm{PO}_{4}{ }^{3-}$
$\mathrm{HCO}_{3}{ }^{-}$
$\mathrm{C1}^{-}$
$\mathrm{SO}_{4}{ }^{2-}$

| AXIS 1 | AXIS 2 | AXIS 3 |
| :---: | :---: | :---: |
| .1123 NS | -.1093 NS | -.1293 NS |
| .0496 NS | .1334 NS | .0987 NS |
| $.6448 * *$ | .0006 NS | -.0997 NS |
| $.6433 * *$ | .0875 NS | .0469 NS |
| $.5614 *$ | -.1274 NS | .2342 NS |
| $.6280 * *$ | -.3778 NS | .1164 NS |
| -.1969 NS | $.7263 * * *$ | -.0412 NS |
| -.2653 NS | $.6478 * *$ | -.3479 NS |
| -.0337 NS | $.6570 * *$ | -.3711 NS |
| -.1901 NS | $.5131 *$ | .0552 NS |
| -.4298 NS | .0050 NS | -.2008 NS |
| .3336 NS | $.6873 * *$ | -.2536 NS |
| .3970 NS | -.0211 NS | -.1674 NS |
| $-.4715 *$ | $.6548 * *$ | .2270 NS |
| -.4135 NS | $-.7171 * * *$ | -.2701 NS |
| -.1229 NS | .3586 NS | -.1724 NS |

B. IMPORTANCE OF MAJOR SPECIES AND THEIR LONGITUDINAL DISTRIBUTION

By and large, the two most widespread and abundant species of algae in the North Alouette stream system during this study were the filamentous greens, Zygnema insigne and Klebsormidium rivulare. These species have not been reported widely in North American streams (B1um, 1956; Whitton, 1975), nor specifically in nearby areas of Washington (Cushing, 1967), Oregon (Sherman and Phinney, 1971; Hansmann and Phinney, 1973), Montana (Gumtow, 1955; Parker et al., 1973), Alberta (McCart et a1., 1977), the Yukon (Bryan et al., 1973), or Northwest Territories (Moore, 1977c). This is probably as much a reflection of the scarcity of studies on British Columbia streams (Stein, 1975; Stockner and Shortreed, 1976), as it is of the differences that such systems have from more alkaline, continental systems. The lack of Cladophora- or diatom-dominated communities (reported by the preceding authors) in the North Alouette supports to a degree the generalizations of Margalef (1960), for nutrient-poor mountain streams, which however, were not discussed in any detail.

The major species of the North Alouette system are comparable with floral types identified in Scandanavia (Israelson, 1949). In oligotrophic regions these streams were regarded as the "Zygnema type", where in addition to a number of sterile and a few reproductive species as dominants, further parallels were present. Israelson noted the coexistence of Batrachospermum moniliforme, Stigonema mamillosum, Mougeotia sp., Spirogyra sp. and Bulbochaete sp. (the last three sterile). All were abundant in various segments of the North Alouette watershed. The Scandanavian flora was also
characterized by a "subtype", in heavily shaded and pooled streams, with the accumulation of humic substances. These were typified by large stands of Batrachospermaceae, as found in segments of Upper Jacob's Creek and other similar streams of the U.B.C. Research Forest not included in this study. Observations of crustose growths of Batrachospermum in less shaded reaches of Jacob's Creek, especially Station 5, may likely be due to light inhibition.

Klebsormidium, or related genera were not reported by Israelson (1949). However, a number of species, including $\underline{K}$. rivulare (as Hormidium rivulare), have been reported in streams of lower pH in England (Say et al., 1977) and Germany (Backhaus, 1968). Alpine streams in Austria with comparable nutrient chemistry, flow, and substrate type also exhibit a similar community composition, including K. rivulare, Phormidium autumnale, Tolypothrix penicillata, B. moniliforme, and a number of other species (Kann, 1978).

The probable causes for such a green and bluegreen dominated system in the North Alouette are no more evident from this work than from the literature. A very large species pool of diatoms from Jacob's Lake was available to the stream (Table 2). These were:successful colonizers in number (33 taxa), as compared with other algal groups, yet none were able to reach dominant proportions (rank of 5) in flowing water any time of the year. Douglas (1958) reported a reduction of diatom growth in streams of peaty areas as compared with calcareous regions nearby. The same pH levels (Table 6) and geology (Roddick, 1965) occur throughout the watershed, yet diatoms did flourish in Jacob's.Lake. This does not support Doug1as' theory based on alkalinity. Patrick and coworkers (1969) were able to demonstrate a selection of bluegreen algae in manganese-poor water and diatoms where levels were greater than $0.04 \mathrm{mg} / 1$. Manganese was not measurable in the
stream water of this study, but concentrations were found to exceed $5 \mathrm{mg} / 1$ in the sediments of Jacob's Lake (Wali et al., 1972), where diatoms predominated (rank of 5 in a majority of samples). Although this is highly suggestive, the stream studied by Patrick was of considerably greater pH , alkalinity, and nutrient levels, and their communities did not produce large amounts of green algae, the principal group at the North Alouette.

The streams of the North Alouette system may possibly be considered a less stable environment than lake sediment for diatom colonization, due to scouring from the current: However, a number of species commonly regarded as rheophilic, including Hannaea arcus, Cocconeis placentula, and Gomphonema parvulum (Hustedt, 1937-1938; Patrick and Reimer, 1966; Lowe, 1974) were common, but never dominant in the streams. In any event, the results for the North Alouette River do not agree with previous findings (Patrick, 1967) that the available species pool (e.g., diatoms from Jacob's Lake) and an adequate "invasion rate" (via flushing from the lake epipelon) will necessarily induce a diversified community. As there are few records in the literature of algal communities in similar streams to the North Alouette, an explanation of this discrepancy must await further study.

The comparisons between stations within the watershed indicate a degree of similarity between Stations $1,2,5,6$, and 7 for each of the four times of the year sampled. The concept of longitudinal zonation expressed for many animals (Hynes, 1970) and less frequently for algae (Scheele, 1952; Kawecka, 1971) in streams appears questionable for algal communities in the North Alouette system. It may be that all stations lie within what Illies and Botosaneanu (1963) regard as a single zone, the rhithron. Their classification recognizes high flow rate, a lack of extremely warm tempera-
tures, and rocky substrates are important. Because these characteristics pertained to the distribution of attached fauna, this category may not adequately portray those limits to which algal species respond. Further, it seems that rather than entire communities occurring in distinct zones, the results indicate that many species were responding independently to changing environmental constraints along the stream gradient, as observed by Backhaus (1968). For example, although. a Zygnema or Klebsormidium association was found in most instances at the lotic stations, Audouinella hermanni was present only at the lower three stations, and attained dominant proportions (rank of 5) in samples only from the lowest station (7).

Trends in species diversity longitudinally were also not distinct. Mack (1953) found that in one Austrian stream system, algal communities were increasingly diverse further downstream. In the present study (Table 4), the greatest levels of diversity among the streams were at times upstream, and in other instances, downstream. In either condition, no evidence was found for patterns of increase or decrease longitudinally. The fact that Jacob's Lake was more diverse than all other stations indicates that species diversity, again, was not simply a matter of species loading to downstream stations. Further, the above-1ake Station 6 showed greater diversity for three of the four periods than did the North Alouette at Station 2 , which was about 1.2 km below the lake outflow.

The ordination results. (Figs. 3-7) indicate there were gradual differences in species composition between stations along the stream, but did not clearly demonstrate a simple progression. For August, Jacob's Creek at the lake outflow (3) was highly distinct from either of its nearest neighbors among the flowing water stations (5, 2). Instead, the above-lake (6, 5)
and lowest ( 1,2 ) stations sampled at this time were highly similar. This points out that the impoundment of Jacob's Creek precludes any possibility of a strictly altitudinal basis for zonation. The changes in species composition with time were such that the pattern of similarities between stations during February (Fig. 5) had little resemblance to that of August (Fig. 3). This flux of affinities between communities at different stations was true for May and June as well. These observations indicate that algal populations were sufficiently modified by either seasonal (e.g., temperature) or periodic (e.g., flow regime) events, so that no consistent zonal pattern occurred over the year.

## C. TEMPORAL VARIABILITY AND SEASONAL.SUCCESSION

AT STATION 1

Seasonal succession of algal species at Station 1 over one year did not follow the general model where species build up and disappear in a "tree-by-tree replacement process", as generalized by Horn (1976), and which follows for most freshwater phytoplankton communities of lakes (Hutchinson, 1967; Round, 1971). In the North Alouette River there was a persistence of the entire assemblage within which the wax and wane of certain species occurred. Round (1972) found that epipelic algae in two pools had broader seasonal peaks, resulting in longer periods of coexistence between species than in phytoplankton. These species did not extend over the entire year, as did epilithic algae in the North Alouette River. Figure 17 compares hypothetical growth curves for phytoplankton and epipelon of lakes (Fig. 17A, B) with the pattern of epilithic algae from the stream in this study (Fig. 17C). The growth of species 1 in the lotic system is similar to that of Klebsormidium rivulare, species 2 as Zygnema insigne, species 3 as Phormidium autumnale, and species 4 comparable to Oedogonium sp. A.

A greater degree of species coexistence in communities generally is thought to be provided by greater niche space (Hutchinson, 1961). Lake sediment may provide microhabitats for algal species (Round, 1972) and certainly the results of the cross-stream gradient analysis suggest this is true at Station 1 (Section VI-A). Some means of preventing species exclusion would be acting, in that temporal separation is not a factor (MacArthur, 1970) for this system.

The cycling pattern of succession (see Fig. 9) may not be a complete picture if the year to year variation is extreme. There is no reason to assume that pulses in current velocity and low temperatures will always coincide, as they did during the year of this study (1977-1978). If a spate were to occur during August on a following year, the seasonal pattern may be quite different from that presently outlined. The drastic changes in community composition over short periods (e.g., early to late September; early to mid-August) may be regarded as caused by catastrophic events, that is, floods and large nutrient pulses. In summary, the degree of environmental unpredictability (from an alga's viewpoint) reduces the evenness of seasonal patterning (Figs. 9, 17), and may affect the ability of invading species to colonize the system (Slobodkin and Sanders, 1969).

## LENTIC PHYTOPLANKTON <br> A



B


C

Figure 17A, B, C. Hypothetical gowth curves of major algal species for three freshwater environments, based on Round (1972: A,B) and the present study (C).

## D. GENERAL PROBLEMS OF ENVIRONMENTAL HETEROGENEITY

The major thrust of argument has been that the stream environment of the North Alouette watershed is sufficiently varied that few species are excluded temporally (distinct seasonal communities) or spatially (longitudinal zones). This raises the question of whether such conditions should lead to high species diversity (Whittaker, 1969). In the year studied, large numbers of species coexisted within a localized region (Fig. 8), but much of the time the great majority of species were rare. Hence, there were few species of high importance. Periods of higher diversity did occur, particularly after abrupt changes in environmental conditions, and especially, current velocity. Thus, great changes in the composition (preceding section) and diversity peaks tended to coincide.

The incidence of disturbance has been suggested by Levin and Paine (1974) to bring about greater environmental heterogeneity by providing opportunity for random colonization and interrupting the normal succession process. Preliminary results in this study show that the otherwise gradual process of seasonal succession was drastically altered in August-September, corresponding to periods of high diversity (Fig. 9). This however, was not true for the large reshuffling of species between late January and early March, when diversity was much lower (Figs. 8, 9). Connell (1978) and Huston (1979) have recently reemphasized the importance of disturbance, but suggested that conditions of "intermediate disturbance" (frequency or intensity) will maintain high diversity rather than catastrophic events, which could eliminate all but a few highly adapted species.

The most diverse locality studied within the watershed, Jacob's Lake,
may have been subject to a more moderate disturbance (i.e., lake flushing; Efford, 1967) than the streams. Paine (1966) found that in space-limited communities (most sessile organisms), an absence of disturbance allowed competitive dominants to outcompete other species, hence reducing species diversity. The less dynamic conditions of June-July at Station 1 (Figs. 1316) were periods when one species, Zygnema insigne, was highly abundant. The data at present are not complete enough to produce convincing explanations as to the causes of local diversity patterns in this system. Nonetheless, the properties of such a highly fluctuating and heterogeneous environment suggest this system is worth further study. Possible approaches are considered in the following section. A fundamental problem is quantifying what level of current velocity, or any other abiotic factors, constitute a severe or catastrophic condition (Slobodkin and Sanders, 1969), and at what leve1s these become an "intermediate disturbance" (Conne11, 1978). That is, when does a high flow condition become a flood? Further, if diversity of stream algae in.the North Alouette is affected by a combination of variables, and not predictable from one element alone (shown in laboratory microcosms of phytoplankton; Reed, 1978), then the recognition of this is further complicated.

## E. CONCLUSIONS AS TESTABLE HYPOTHESES

The objectives of this study were largely descriptive, as there is a paucity of basic information relating to the ecology of algal species and communities in coastal streams of British Columbia. In following with the "hypothetico-deductive philosophy" (Fretwe11, 1972), experience is best summarized in the form of an explanation. Owing to the rather tentative understanding the data provide, the explanations must be approached with caution. The explanations from any descriptive study should then be formalized into hypotheses which can be tested ( $H_{1}$ to $H_{4}$, following).

The preliminary problem concerned causes of differences in species composition and their distribution. Given that a large pool of green, bluegreen, diatom, and red algal species exist within the stream-watershed (Table 1, Appendix A) and that these species are freely transported between stations (Table 2), a complex of factors may be suggested in causing the presence of any particular species.

Heavily shaded segments of Jacob's Creek and shaded near-shore habitats were regions of greatest accumulation of species of Rhodophyta. It is assumed that

$$
\begin{aligned}
& \text { distribution of red algae within this system is most } \\
& \text { strongly limited by availability of shade, and only } \\
& \text { secondarily by the absence of extreme current velocity. }
\end{aligned}
$$

The adverse effects of light have been supported to a degree by Rider and Wagner (1972) in laboratory experiments. One test of this in the field would involve the removal of a segment of stream-bank vegetation and the construction of artificial shading within an openly lighted stream (after Mundie, 1974). A second test of light as well as current would be provided
by transplant experiments of stones colonized by Audouinella or Batrachospermum to nearby localities of the stream where current or irradiance would be the only factors altered. A similar experiment was done by Parker et al. (1973) with Hydrurus, Monostroma and Batrachospermum. Both tests could be used to discriminate between causes of microdistribution that was exposed along the transect within Station 1.

Determinants of community dominants may also be predicted. Based on the preliminary results and literature discussed earlier,
the occurrence of a. green/bluegreen versus diatom dominated community appears to be a result of some chemical factor(s) (possibly manganese), rather than current velocity or some other physical factor.

A test for this would involve the use of "header boxes" (Stockner and Shortreed, 1978) in the stream with a series of troughs in which are placed a random collection of stones with their associated algal assemblages. Some troughs would have continually added to them a flow of cations or other chemicals in order to reach the levels found in Jacob's Lake sediment, where diatoms were predominant. In a second test, a sample of the epipelic community from Jacob's Lake would be reinoculated into acid-washed, steri1ized lake sediment and placed in membrane-filter chambers (Sch1ichting, 1976) suspended immediately above the lake bottom. This would allow only the dissolved nutrients from the lake water to affect algai growth. If richer nutrients of the sediments were causal, a switch in species composition in each manipulation would be expected. A lack of species change suggests physical factors may be more influential.

The pattern of seasonal succession observed over one year was a combination of gradual and abrupt changes in the community. It was marked by a
greater degree of temporal coexistence than generally observed for lake phytoplankton (Round, 1972; Fig. 17). A lack of temporal or local extinction has been suggested to be a result of environmental heterogeneity (Hutchinson, 1957) and periodic disturbance (Paine, 1966). Hence, the seasonal changes in species composition of this stream are likely due to factors with a regular, cyclic pattern (e.g., daylength, temperature, irradiance); whereas abrupt or discontinuous events (e.g., nutrient pulses, floods) give rise to large-scale changes in the community.

This aspect leads into the general problem of heterogeneity and diversity.
The gradually varying environmental conditions in the stream lead to success of a few dominant species, whereas periodic disasters (or minor disasters?) prevent local extinction and result in higher diversity.

A test of these two problems would be considered from the same experimental design. Side channels of the stream could be constructed, after Warren et al. (1964), which would allow different major manipulations. Through the use of weirs or flow diversion, the current velocity could be more or less constant, allowing the gradually varying factors to exert a greater effect than periodic ones. Other channels could be artificially disturbed or provided with additional structural heterogeneity (Reed, 1978).

If $H_{3}$ were true, the ordination of species succession in the flowcontrolled channel would be less erratic than shown by these preliminary results (Fig. 9) or by controls. If $H_{4}$ were true, the more predictable environment should lead to reduced species diversity. Also, there should be greater temporal exclusion of species, approaching the situation for lake
phytoplankton. Other immediate stresses, such as nutrient pulses, can be tested in the same manner. The systems of enhanced heterogeneity (e.g., a diversity of substrate sizes) are predicted to do the opposite. If predictions are not met, the perturbation chosen may be (as a single causal element) excluded from consideration. Finally, the severity or frequency of an "intermediate disturbance" (Connell, 1978) can be considered in a step-wise comparison with species diversity directly.

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Appendix A. Abundance of all algal taxa at Station 1 for 17 sampling dates, where abundance values range from 0 - 1 (see Table 1 for species codes).


## DATE (DAY/MONTH/YEAR)

| SPEECIES | 070677 | 210677 | 050777 | 190777 | 020877 | 160877 | 060977 | 270977 | 091077 | 270178 | 030378 | 310378 | 170478 | 040578 | 260578 | 080578 | 290678 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |


| Bulo 1 |  |  |  |  | 0.0002 | 0.0001 | 0.0001 |  |  |  |  | 0.0002 | 0.0002 |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 2 YGO 1 | 0.5157 | 0.6522 | 0.8493 | 0.6798 | 0.5478 | 0.1914 | 0.2229 | 0.0053 | 0.2042 | 0.1432 | 0.6670 | 0.5019 | 0.6446 | 0.6593 | 0.6896 | 0.8586 | 0.8335 |
| zYg02 |  |  |  |  |  |  | 0.0055 |  |  |  |  |  |  |  |  |  |  |
| SPIO1 | 0.0140 | 0.0222 | 0.1029 | 0.2785 | 0.5230 | 0.1353 | 0.1395 | 0.0053 | 0.0022 | 0.0002 | 0.0005 | 0.0094 | 0.0039 | 0.0200 | 0.1899 | 0.0265 | 0.0881 |
| Mov0 1 | 0.0001 | 0.0001 | 0.0006 | 0.0067 | 0.0003 | 0.0002 | 0.0003 | 0.0005 | 0.2000 | 0.0003 | 0.0007 | 0.0020 | 0.0018 | 0.0021 | 0.0040 | 0.0047 | 0.0129 |
| DSH01 |  | 0.0001 | 0.0002 | 0.0004 | 0.0004 | 0.0003 | 0.0001 |  |  |  |  |  |  | 0.0002 |  |  |  |
| DSM02 | 0.0001 | 0.0007 | 0.0005 | 0.0015 | 0.0005 | 0.0004 |  |  |  |  |  | 0.0002 | 0.0002 | 0.0004 | 0.0002 | 0.0004 | 0.0020 |
| DSM03 | 0.0002 | 0.0003 |  | 0.0001 | 0.0002 | 0.0003 | 0.0001 | 0.0005 |  | 0.0002 |  | 0.0002 | 0.0002 | 0.0003 |  |  |  |
| DSM04 | 0.0001 |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |
| DS405 |  | 0.0001 |  | 0.0001 |  | 0.0002 | 0.0002 | 0.0003 |  |  |  |  |  |  |  |  |  |
| DSM06 |  | 0.0004 | 0.0001 | 0.0005 | 0.0006 | 0.0007 | 0.0003 | 0.0003 | 0.0002 |  | 0.0002 | 0.0002 | 0.0005 | 0.0006 | 0.0002 | 0.0002 | 0.0002 |
| DS:07 |  | 0.0005 | 0.0005 | 0.0004 | 0.0004 | 0.0004 | 0.0003 | 0.0003 |  |  | 0.0002 |  | 0.0003 | 0.0007 | 0.0002 | 0.0003 | 0.0002 |
| DSM08 |  | 0.0001 |  |  |  |  | 0.0003 |  |  |  |  |  | 0.0002 | 0.0004 |  |  |  |
| dSm09 |  | 0.0001 | 0.0003 | 0.0004 | 0.0003 | 0.0002 | 0.0002 |  |  |  |  |  | 0.0002 |  |  |  |  |
| DSH 10 |  | 0.0001 |  |  | 0.0001 |  |  |  |  |  |  |  | 0.0002 | 0.0003 | 0.0002 |  |  |
| DSM11 |  | 0.0001 |  | 0.0001 |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |
| DSE 12 |  | 0.0001 | 0.0003 | 0.0004 | 0.0001 |  | 0.0001 |  | 0.0004 |  | 0.0002 |  |  | 0.0004 | 0.0002 | 0.0002 |  |
| DSM 13 |  | 0.0002 | 0.0002 | 0.0003 | 0.0001 | 0.0002 | 0.0003 | 0.0005 | 0.0002 |  |  |  |  |  |  | 0.0002 |  |
| DSA14 |  | 0.0001 | 0.0001 |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |
| DSM15 |  |  | 0.0001 | 0.0003 | 0.0001 |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |
| DSA 16 |  |  | 0.0006 |  |  | 0.0001 |  | 0.0003 |  |  |  |  |  |  | 0.0002 |  |  |
| DSM 18 |  |  |  | 0.0002 |  |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  |  |
| DSM19 | 0.0001 |  |  | 0.0001 | 0.0003 |  |  | 0.0005 | 0.0004 | 0.0002 | 0.0002 |  | 0.0002 | 0.0004 | 0.0004 |  | 0.0002 |
| DSM20 |  |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM21 |  |  |  | 0.0001 | 0.0003 |  |  |  |  |  |  |  | 0.0002 | 0.0003 |  |  |  |
| DSH22 |  |  |  | 0.0001 | 0.0001 |  |  |  |  | 0.0002 |  |  |  |  |  |  |  |
| DSM23 |  |  |  | 0.0001 |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  |  |  |
| DSA24 |  |  |  |  | 0.0002 | 0.0003 |  |  |  |  |  | 0.0002 | 0.0002 | 0.0004 | 0.0004 |  |  |
| DSM25 |  |  |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM26 |  |  |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM27 |  |  |  |  |  | 0.0001 |  | 0.0003 |  |  |  |  |  |  |  |  |  |
| DSM28 |  |  |  |  |  |  |  | 0.0003 | 0.0002 |  |  |  | 0.0002 |  |  |  |  |
| DSM29 |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |  |  |  |  |
| DSM30 |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |  |  |  |  |
| DSM 31 |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |
| DSM 32 |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |  |
| DSM34 |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |  |
| DSM35 |  |  |  |  |  |  |  |  |  |  |  |  | 0.0003 |  |  |  |  |
| DSM 36 |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |
| DSM37 |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |
| DSM38 |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  |  |
| DSM39 |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  |  |
| DSM 40 |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  |  |
| DSM4 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |
| DSM42 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM43 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM44 |  |  |  |  |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |
| DSM45 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM46 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM47 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM 48 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM49 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM50 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM51 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |
| DSM52 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |



| DSH53 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| DSA44 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSA55 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSA56 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DSM57 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| EGL01 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| CIP01 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| OCR01 0.00020 .00050 .00050 .0006 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| MAL01 0.00020 .0002 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| MALO2 0.0002 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SEN01 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| cxpol |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| DN801 |  |  |  |  |  | 0.0001 | 0.0002 |  | 0.0002 |  |  |  |  |  |  |  |  |
| DHB02 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| CBY01 0.0005 0.0005 0.0004 0.0002 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SDC01 | 0.0004 | 0.0010 | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| cycol | 0.0001 | 0.0002 | 0.0001 | 0.0001 | 0.0002 |  | 0.0006 | 0.0003 |  |  | 0.0002 | 0.0002 | 0.0003 | 0.0007 | 0.0005 | 0.0003 | 0.0004 |
| cyco2 | 0.0006 | 0.0002 | 0.0001 |  |  |  |  |  | 0.0006 |  |  |  |  |  |  |  |  |
| MELO1 | 0.0006 | 0.0004 | 0.0002 | 0.0001 |  | 0.0001 |  |  |  | 0.0002 |  |  |  |  |  |  |  |
| MEL 02 |  |  |  |  |  | 0.0003 | 0.0001 | 0.0005 | 0.0004 | 0.0002 |  | 0.0002 | 0.0004 | 0.0010 | 0.0007 | 0.0033 | 0.0002 |
| $\cos 01$ |  | 0.0002 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| $\cos 02$ |  |  | 0.0001 | 0.0001 |  |  |  |  | 0.0006 |  | 0.0002 |  |  |  |  |  | 0.0002 |
| that 1 |  |  | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| tab01 | 0.0127 | 0.0124 | 0.0122 | 0.0070 | 0.0085 | 0.0115 | 0.0100 | 0.0212 | 0.0100 | 0.0088 | 0.0293 | 0.0085 | 0.0100 | 0.0100 | 0.0100 | 0.0151 | 0.0085 |
| tab02 | 0.0001 | 0.0005 | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| datol | 0.0006 | 0.0004 | 0.0007 | 0.0005 | 0.0006 | 0.0005 | 0.0009 | 0.0007 | 0.0010 | 0.0008 | 0.0007 | 0.0007 | 0.0010 | 0.0090 | 0.0008 | 0.0008 | 0.0004 |
| dato 2 | 0.0001 |  |  |  |  |  | 0.0001 |  |  |  |  |  |  | 0.0002 |  |  |  |
| MDNO? | 0.0002 | 0.0005 | 0.0002 | 0.0004 | 0.0004 | 0.0003 | 0.0004 | 0.0005 |  |  | 0.0004 | 0.0004 | 0.0004 | 0.0010 | 0.0004 | 0.0002 | 0.0002 |
| tcyol |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PGLO1 | 0.0003 | 0.0005 | 0.0002 | 0.0003 | 0.0002 | 0.0004 | 0.0002 |  |  | 0.0002 |  |  |  |  |  |  |  |
| FGL02 |  |  |  |  |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |  |
| PGL03 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PGLO4 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| PGL05 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ASt01 |  | 0.0001 | 0.0004 | 0.0003 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SYNO1 | 0.0028 | 0.0050 | 0.0032 | 0.0040 | 0.0024 | 0.0032 | 0.0027 | 0.0055 | 0.0064 | 0.0062 | 0.0055 | 0.0023 | 0.0065 | 0.0066 | 0.0085 | 0.0060 | 0.0010 |
| SYN02 | 0.0005 | 0.0005 | 0.0004 | 0.0004 | 0.0004 | 0.0005 | 0.0014 | 0.0035 | 0.0008 | 0.0007 | 0.0007 | 0.0005 | 0.0010 | 0.0010 | 0.0007 | 0.0010 | 0.0004 |
| SyN03 |  | 0.0005 |  |  | 0.0001 |  |  |  |  |  | 0.0002 |  |  |  |  |  |  |
| SYN04 | 0.0002 |  |  | 0.0001 | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |
| SYN05 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SYN06 |  |  | 0.0010 | 0.0013 | 0.0024 | 0.0001 |  |  |  |  | 0.0002 | 0.0002 |  |  |  | 0.0002 |  |
| SYN07 |  |  | 0.0001 | 0.0001 | 0.0002 |  |  |  |  |  |  |  |  | 0.0003 | 0.0002 |  |  |
| PER01 | 0.0001 |  |  |  |  |  |  |  |  |  |  |  | 0.0002 | 0.0002 |  | 0.0002 |  |
| han 01 | 0.0004 | 0.0003 | 0.0001 | 0.0003 | 0.0005 | 0.0009 | 0.0004 | 0.0005 | 0.0006 |  |  | 0.0002 | 0.0004 | 0.0010 | 0.0002 | 0.0007 | 0.0022 |
| Hano2 |  |  | 0.0001 |  | 0.0002 |  |  |  |  |  |  |  |  | 0.0003 |  |  | 0.0002 |
| SAB01 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Eunot | 0.0037 | 0.0124 | 0.0017 | 0.0025 | 0.0040 | 0.0032 | 0.0046 | 0.0032 | 0.0028 | 0.0033 | 0.0144 | 0.0097 | 0.0007 | 0.0021 | 0.0038 | 0.0021 | 0.0114 |
| Euno2 | 0.0001 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Eunos | 0.0010 | 0.0043 | 0.0055 | 0.0047 | 0.0025 | 0.0032 | 0.0016 | 0.0030 | 0.0026 | 0.0033 | 0.0005 | 0.0022 | 0.0055 | 0.0044 | 0.0010 | 0.0010 | 0.0008 |
| EUNO4 | 0.0004 | 0.0005 | 0.0005 | 0.0013 | 0.0004 | 0.0004 | 0.0002 | 0.0005 | 0.0006 |  | 0.0004 | 0.0007 | 0.0010 | 0.0010 | 0,0007 | 0.0006 |  |
| EUNO5 | 0.0005 | 0.0007 | 0.0006 | 0.0008 | 0.0005 | 0.0005 | 0.0008 | 0.0007 | 0.0008 | 0.0008 | 0.0007 | 0.0008 | 0.0007 | 0.0008 | 0.0008 | 0.0010 | 0.0007 |
| EuN06 |  |  |  |  | 0.0001 |  |  |  |  |  |  |  | 0.0002 |  |  |  |  |
| Eunot | 0.0003 |  | 0.0001 |  |  | 0.0002 | 0.0001 |  | 0.0004 | 0.0002 |  | 0.0002 | 0.0002 | 0.0002 |  | 0.0002 | 0.0002 |
| EUNOB | 0.0001 | 0.0005 | 0.0002 | 0.0001 |  |  |  | 0.0005 | 0.0006 | 0.0002 | 0.0004 | 0.0004 |  | 0.0008 | 0.0004 | 0.0003 | 0.0004 |
| EUN10 |  |  | 0.0002 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

DATE (DAY/MONTH/YEAR)



DATE (DAY/MONTH/YEAR)

| SPECIES | 070677 | 210677 | 050777 | 190777 | 020877 | 160877 | 060977 | 270977 | 091077 | 270178 | 030378 | 310378 | 170478 | 040578 | 260578 | 080678 | 290678 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| nva06 | 0.0001 | 0.0005 | 0.0001 | 0.0003 | 0.0003 | 0.0001 | 0.0001 | 0.0003 | 0.0004 | 0.0002 | 0.0002 | 0.0004 | 0.0004 | 0.0007 | 0.0008 | 0.0002 | 0.0002 |
| nval2 |  | 0.0001 |  | 0.0001 |  |  | 0.0001 |  |  |  |  |  | 0.0002 | 0.0002 |  |  | 0.0002 |
| dVal4 |  |  |  |  | 0.0001 |  |  |  | * |  |  |  | 0.0002 | 0.0002 |  |  |  |
| aval 18 |  |  |  |  |  | 0.0001 |  | 0.0003 |  |  |  | 0.0002 | 0.0002 | 0.0004 | 0.0004 | 0.0002 |  |

Appendix B. Abundance of all algal taxa at alternate collecting stations (2-7) for four dates (day/month/year), where values range from 0-1 (see Table 1 for species codes).


DATES POB STATION 2 DATES FOR STATTON 3







| species | $1080977$ | FS FOR 021578 | STATION 051878 | $\begin{gathered} 6 \\ 062378 \\ \hline \end{gathered}$ | $\begin{gathered} \text { Dates } \\ 021578 \\ \hline \end{gathered}$ | $\begin{array}{r} \text { POR STA } \\ 051878 \\ \hline \end{array}$ | $\begin{gathered} \text { Tron } 7 \\ 062378 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| BULO1 |  | 0.0050 | 0.0005 | 0.0005 | 0.0182 |  | 0.0005 |
| 2YG01 | 0.0100 | 0.0273 | 0.5050 | 0.5273 | 0.0034 | 0.5050 | 0.5000 |
| ZYG02 |  |  |  |  |  |  |  |
| SPI01 | 0.0010 |  | 0.0323 | 0.5273 |  | 0.5273 | 0.5050 |
| Movol |  | 0.0546 | 0.0273 | 0.0055 | 0.0034 | 0.0005 | 0.0005 |
| DSM01 |  |  |  |  | 0.0004 |  |  |
| DSM02 | 0.0010 |  | 0.0005 | 0.0005 |  | 0.0005 | 0.0005 |
| DSM03 | 0.0010 |  |  | 0.0005 |  |  |  |
| DSM04 |  |  |  |  |  |  |  |
| DSM05 |  |  |  |  |  |  |  |
| DSM06 | 0.0010 |  |  | 0.0005 |  |  |  |
| DSM07 | 0.0010 |  |  | 0.0005 |  | 0.0005 |  |
| DSM08 |  |  |  |  |  |  |  |
| DSM09 |  |  |  |  |  |  |  |
| DSM 10 |  |  |  |  |  |  |  |
| DSM 12 |  |  |  |  |  |  |  |
| DSM 13 | 0.0010 |  |  |  |  |  |  |
| DSM 14 |  |  |  |  |  |  |  |
| DSA 15 |  |  |  |  |  |  |  |
| DSM 16 |  |  |  |  |  |  |  |
| DSE18 |  |  |  |  |  |  |  |
| DSM 19 |  |  |  | 0.0005 |  |  |  |
| DSM 20 |  |  |  |  |  |  |  |
| DSM21 |  |  |  |  |  |  |  |
| DSM 22 |  |  |  |  |  |  |  |
| DSM23 |  |  |  |  |  |  |  |
| $\begin{aligned} & \text { DSM } 24 \\ & \text { DSM } 25 \end{aligned}$ |  |  |  |  |  |  |  |
| DSM26 |  |  |  |  |  |  |  |
| DSM27 |  |  |  |  |  |  |  |
| DSM 28 | . |  |  |  |  |  |  |
| DSM29 |  |  |  |  |  |  |  |
| DSM 30 |  |  |  |  |  |  |  |
| DSM31 |  |  |  |  |  |  |  |
| DSM 32 |  |  |  |  |  |  | 0.0005 |
| DSM 34 |  |  |  |  |  |  |  |
| DSM 35 |  |  |  | 0.0010 |  |  | 0.0005 |
| DSM36 |  |  |  |  |  |  |  |
| DSM37 |  |  |  |  |  |  |  |
| DSM 38 |  |  |  |  |  |  |  |
| DSE39 |  |  |  |  |  |  |  |
| $\begin{aligned} & \text { DSM40 } \\ & \text { DSM4 } 1 \end{aligned}$ |  |  |  |  |  |  |  |
| DSM42 |  |  |  |  |  |  |  |
| DSM43 |  |  |  |  |  |  |  |
| DSM44 |  |  |  |  |  |  |  |
| DSM45 |  |  |  |  |  |  |  |
| DSM46 |  |  |  |  |  |  |  |
| DSM47 |  |  |  |  |  |  |  |
| DSM48 |  |  |  |  |  |  |  |
| DSM49 |  |  |  |  |  |  |  |
| DSM50 DSM5 1 |  |  |  |  |  |  |  |
| DSM51 DSM52 |  |  |  |  |  |  |  |
| DSM52 |  |  |  |  |  |  |  |




DATES FOR STATION 6 DATES POR STATION 7


APPENDIX C. Presence of all algal taxa from Jacob's Lake (Station 4) in drift and attached habits to downstream stations (see Table 1 for species codes; PPL = phytoplankton, EPE = epipelic, EPH = epiphytic, EPL = epilithic, MET = metaphytonic).

| SPECIES <br> CODE | PREDOMINANT LAKE HABIT | PRESENCE IN STREAM (+) | COLONIZED ( + ) OR DRIFT ONLY (-) | DOMINANT STREAM HABIT IF ATTACHED |
| :---: | :---: | :---: | :---: | :---: |
| CCø01 | PPL |  |  |  |
| XEN01 | PPL | + | - |  |
| GøC01 | EPH |  |  |  |
| MPD01 | PPL | + | - |  |
| MIC01 | PPL | + | - |  |
| ANB01 | PPL |  |  |  |
| CALO2 | EPH | + | $+$ | EPH |
| CAL01 | EPH | + | + | EPH |
| LYG01 | MET | + | - |  |
| LYG04 | MET | + | - |  |
| ¢SC01 | MET | + | - |  |
| PHRO2 | EPH | + | + | EPH |
| CSP01 | MET | + | - |  |
| TXP01 | EPH | + | $+$ | EPL |
| STG01 | EPH | + | + | EPL |
| CDY01 | PPL | + | - |  |
| EøD01 | PPL |  |  |  |
| UKLO1 | MET | + | + | EPL |
| UKL03 | EPH | + | + | EPL |
| MCP01 | EPH | + | + | EPL |
| CET01 | PPL | + | + | EPH |
| AKD01 | PPL | + | - |  |
| AEC01 | PPL |  |  |  |
| CøV02 | EPE | + | + | EPL |
| CML01 | PPL |  |  |  |
| ¢ST01 | PPL |  |  |  |
| PDI01 | PPL |  |  |  |
| SCD01 | PPL | + | - |  |
| BUL01 | EPH | + | + | EPL |
| ¢ED01 | EPH | + | + | EPL |
| ¢ED02 | EPH | + | + | EPL |
| DSM46 | PPL |  |  |  |
| DSM03 | MET | + | - |  |
| DSM12 | MET | + | - |  |
| DSM23 | PPL | + | - |  |
| DSM02 | PPL | + | - |  |
| DSM28 | PPL | + | - |  |
| DSM38 | PPL | + | - |  |
| DSM32 | MET | + | - |  |

APPENDIX C. Continued.

| SPECIES CODE | PREDOMINANT LAKE HABIT | PRESENCE IN STREAM (+) | COLONIZED (+) OR DRIFT ONLY (-) | DOMINANT STREAM HABIT IF ATTACHED |
| :---: | :---: | :---: | :---: | :---: |
| DSM18 | PPL | + | - |  |
| DSM14 | PPL | + | - |  |
| DSM22 | MET | + | - |  |
| DSM01 | EPE | + | - |  |
| DSM56 | MET |  |  |  |
| DSM05 | MET | + | - |  |
| DSM27 | MET | + | - |  |
| DSM5 7. | PPL | + | - |  |
| DSM07 | PPL | + | + | EPH |
| DSM19 | MET | $+$ | - |  |
| DSM47 | PPL |  |  |  |
| DSM24 | EPH | + | - |  |
| DSM50 | EPH |  |  |  |
| DSM10 | MET | + | - |  |
| DSM42 | PPL | + | - |  |
| DSM44 | PPL | + | - |  |
| DSM37 | PPL | + | - |  |
| DSM45 | PPL |  |  |  |
| DSM54 | PPL |  |  |  |
| DSM48 | PPL |  |  |  |
| DSm53 | PPL | + | - |  |
| DSM49 | EPH |  |  |  |
| DSM40 | MET | + | - |  |
| DSM06 | PPL | + | - |  |
| DSM39 | EPE | + | - |  |
| DSM41 | PPL | + | - |  |
| DSM21 | PPL | $+$ | - |  |
| DSM52 | PPL |  |  |  |
| DSM55 | PPL | + | - |  |
| MøU01 | EPH | + | $+$ | EPL |
| SPIO1 | EPH | + | + | EPL |
| ZYG01 | MET | + | + | EPL |
| ZYG02 | EPH | + | - |  |
| CIPO1 | PPL | + | - |  |
| CXP01 | EPH |  |  |  |
| DNB01 | PPL | + | - |  |
| DNB02 | PPL |  |  |  |
| MAL01 | PPL | + | - |  |
| MALO2 | PPL | + | - |  |
| $\emptyset \mathrm{CRO1}$ | PPL | $+$ | - |  |
| SRNO1 | PPL |  |  |  |
| CRYO1 | PPL | + | + | EPH |
| CYC02 | MET | + | - |  |
| CYCOI | PPL | $+$ | - |  |
| MEL02 | EPH | + | - |  |
| MEL01 | PPL | + | - |  |
| SDC01. | PPL | + | - |  |

APPENDIX C. Continued.

| $\begin{aligned} & \text { SPECIES } \\ & \text { CODE } \end{aligned}$ | PREDOMINANT <br> LAKE HABIT | PRESENCE IN STREAM (+) | $\begin{aligned} & \text { COLONIZED (+) OR } \\ & \text { DRIFT ONLY (-) } \end{aligned}$ | DOMINANT STREAM HABIT IF ATTACHED |
| :---: | :---: | :---: | :---: | :---: |
| AST01 | PPL | $+$ | - |  |
| DAT02 | PPL | + | + | EPH |
| FGL02 | EPE | + | - |  |
| FGL03 | PPL | + | - |  |
| FGL05 | PPL |  |  |  |
| FGL01 | PPL | + | - |  |
| SMB01 | EPE | + | - |  |
| SYN03 | PPL | + | + | EPH |
| SYN01 | EPE | + | + | EPL |
| TAB02 | PPL | + | - |  |
| TAB01 | PPL | $+$ | + | EPH |
| ATN01 | EPE | + | - |  |
| EUN21 | EPE | + | - |  |
| EUN08 | EPE | + | + | EPH |
| EUN12 | EPE |  |  |  |
| EUN13 | EPE | + | + | EPH |
| EUN07 | EPH | + | + | EPH |
| EUNO2 | MET | + | - |  |
| EUN19 | EPE | + | - |  |
| EUN04 | EPH | + | + | EPH |
| EUN01 | EPH | $+$ | + | EPH |
| EUN05 | EPE | + | + | EPH |
| EUN14 | EPE | + | - |  |
| EUN20 | EPE |  |  |  |
| EUN06 | EPE | + | - |  |
| EUN16 | MET | + | $+$ | EPH |
| EUN17 | EPE | + | - |  |
| EUNO3 | MET | + | + | EPH |
| EUN15 | MET | + | - |  |
| PERO1 | EPE | + | - |  |
| ACNO1 | MET | + | + | EPL |
| ACN03 | PPL | + | - |  |
| NVA15 | EPE | + | - |  |
| NVA29 | EPE | + | - |  |
| NVA04 | EPE | + | + | EPH |
| NVA08 | EPE | + | + | EPH |
| CYM03 | EPE | + | - |  |
| CYMO2 | EPE | + | + | EPH |
| СYM05 | EPH | + | + | EPH |
| CYMl 3 | EPH |  |  |  |
| DAT01 | PPL | + | + | EPL |
| CYM10 | EPE | + | - |  |
| CYM04 | MET | + | + | EPL |
| CYM09 | MET | + | - |  |
| CYM12 | EPE | + | - |  |
| DPN01 | EPE | + | - |  |
| DPN02 | EPE | + | - |  |

APPENDIX C. Continued.

| SPECIES CODE | PREDOMINANT <br> LAKE HABIT | PRESENCE IN STREAM (+) | $\begin{aligned} & \text { COLONIZED (+) OR } \\ & \text { DRIFT ONLY } \end{aligned}$ | DOMINANT STREAM HABIT IF ATTACHED |
| :---: | :---: | :---: | :---: | :---: |
| EPM02 | EPE |  |  |  |
| EPM01 | PPL | $+$ | - |  |
| FRU03 | EPE | + | $+$ | EPH |
| FRU01 | EPH | + | + | EPH |
| FRU02 | EPE | + | - |  |
| GPN06 | EPH | + | + | EPL |
| GPN07 | EPE |  |  |  |
| GPNO1 | MET | + | $+$ | EPL |
| GPN03 | EPH | $+$ | + | EPH |
| GPN04 | MET | + | + | EPL |
| NVA01 | EPH | $+$ | - |  |
| NVA32 | EPE | + | - |  |
| NVA 13 | PPL | $+$ | - |  |
| NVA27 | EPH | $+$ | + | EPH |
| NVA10 | EPH | + | - |  |
| NVA35 | EPE |  |  |  |
| NVA26 | EPE | + | - |  |
| NVA16 | MET | $+$ | - |  |
| NVA19 | EPH | + | - |  |
| NVA25 | EPE | + | - |  |
| NVA09 | EPE | $+$ | + | EPH |
| NVA22 | EPE | $+$ | - |  |
| NVA07 | PPL |  |  |  |
| NVA37 | EPE | $+$ | - |  |
| NVA21 | EPH | + | - |  |
| NVA20 | PPL | $+$ | - |  |
| NEIO1 | EPE | + | - |  |
| NEIO2 | EPE | + | - |  |
| NEIO3 | EPE |  |  |  |
| NVA34 | EPE |  |  |  |
| NVA06 | MET | $+$ | $+$ | EPH |
| NVA33 | EPE |  |  |  |
| NVA18 | EPE | + | + | EPH |
| NVA12 | EPE | $+$ | - |  |
| NVA14 | EPE | $+$ | - |  |
| SNS02 | MET | + | - |  |
| NVA23 | EPE | + | - |  |
| NVA17 | EPE | $+$ | - |  |
| SNS01 | EPE | + | - |  |
| NZA02 | PPL | + | - |  |
| NZA05 | PPL | + | - |  |
| NZA07 | PPL | $+$ | - |  |
| NZA04 | EPE | + | + | EPH |
| NZA06 | EPE | + | + | EPH |
| NZA01 | EPE | + | $+$ | EPH |

APPENDIX C. Continued.

| SPECIES CODE | PREDOMINANT <br> LAKE HABIT | PRESENCE IN STREAM (+) | COLONIZED (+) OR DRIFT ONLY | DOMINANT STREAM HABIT IF ATTACHED |
| :---: | :---: | :---: | :---: | :---: |
| SUR01 | EPE | $+$ | - |  |
| SUR03 | EPH | + | - |  |
| SUR02 | PPL | + | - |  |
| EGL01 | PPL |  |  |  |
| GLD01 | PPL | $+$ | - |  |
| PDN01 | PPL |  |  |  |
| CPT01 | PPL | + | - |  |

