A COMPARATIVE STUDY OF BENTHIC ALGAL PRIMARY PRODUCTIVITY IN THE AOSERP STUDY AREA

by

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for

ALBERTA OIL SANDS ENVIRONMENTAL
RESEARCH PROGRAM

AOSERP Report 128

February 1983

The Hon. F. Bradley
Minister of the Environment
222 Legislative Building
Edmonton, Alberta

Sir:

Enclosed is the report "A Comparative Study of Benthic Algal Primary Productivity in the AOSERP Study Area".

This report was prepared for the Research Management Division through the Alberta Oil Sands Environmental Research Program.

Respectfully,

W. Solodzuk, P.Eng.
Deputy Minister, Alberta Environment

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ABSTRACT

Studies concentrating upon the epilithic algal community were conducted in five tributary rivers flowing into the Athabasca river: the Muskeg, Steepbank, Hangingstone, MacKay, and Ells rivers. Numerically, cyanophycean algae (*Lyngbya aerugineo-caerulea, Phormidium* sp., *Calothris braunii, Nostoc* spp., and *Anabaena affinis*) dominated, followed by diatoms (*Synedra ulna, Synedra rumpens* , *Gomphonema olivaceum, Gomphonema acuminatum* , *Gomphonema longiceps* v. *subclavata, Nitzschia fonticola, Nitzschia palea, Achanthes lanceolata, Epithemia sorex, Epithemia turgida, Cocconeis placentula* and *Cocconeis pediculus*). One exception was the Hangingstone River where chlorophycean algae (*Stigeoclonium pachydermum* and *Cladophora glomerata*) were next in importance to the Cyanophyta. Seasonal fluctuations in algal species and numbers were influenced by a myriad of interacting factors as were standing crop fluctuations. However, physically disruptive forces, current velocity and discharge, appeared more important than dissolved nutrients. They also affected the chemical composition of the water itself. The mean algal standing crops ranged from 7.94 to 43.23 mg m^{-2}chlorophyll *a* in the MacKay and Ells rivers, respectively, with mean values of 30.46, 22.9, and 22.35 mg•m^{-2} chlorophyll *a* occurring in the Muskeg, Steepbank, and Hangingstone rivers, respectively. Epilithic algal primary productivity was more closely related to standing crop size than irradiance. The annual production averaged 36.2, 54.4, 71.4, 101.6, and 110.0 gm C m^{-2} in the MacKay, Hangingstone, Steepbank, Ells, and Muskeg rivers, respectively.

ACKNOWLEDGEMENTS

This research project WS 1.3.4 was funded by the Alberta Oil Sands Environmental Research Program, a research program established to fund, direct and coordinate environmental research in the Athabasca Oil Sands area of northeastern Alberta. Further funding was provided by a National Science and Engineering Research Council grant to Dr. M. Hickman (NSERC A-6384). The authors acknowledge with utmost appreciation of the work of Marianne Klemka. Special thanks are extended to D. Hadler and the crews of Liftair, particularly Jack Le Roux, and Michael Jeffery and Eva Romaniszyn for their assistance in the field.

1. INTRODUCTION

Algae, whether benthic or planktonic, are affected by a complex myriad of interacting factors, physical, chemical, and biotic. These result in both spatial and temporal changes in species composition, succession, standing crop, and primary productivity. In the lotic system, plants, such as attached algae, can be of considerable trophic importance producing energy for other components of the food chain, both directly and indirectly, as well as providing niches for other organisms.

Difficulties surrounding investigations of attached communities found in lakes, rivers, and oceans have been reviewed by Wetzel (1964), and Round and Hickman (1971). Artificial substrata have been employed but results so obtained can be controversial (Tippett 1970; Hansmann and Phinney 1973). Approaches which deal with the natural community have been developed (Eaton and Moss 1966; Hickman 1969, 1971a, 1971b,1974,1978; Moss and Round 1967; Hickman and Round 1970; Round and Hickman 1971; Backhaus 1967; Marker 1976a, 1976b), but no generalized approaches to these communities have been developed, and information pertaining to many benthic algal communities, particularly the epilithon, is scarce compared with the enormous amount originating from work upon the far more easily studied phytoplankton. However, studies have illustrated the importance of attached algal communities (Westlake 1971; Hickman 1971b, 1978, Marker 1976a, 1976b; Moore 1977). Studies of phytobenthic communities, such as the epilithon, have many problems, including those of quantitative sampling and actual removal of the algae from the rocks. Benthic algal communities are characteristically heterogeneous (Eaton and Moss 1966; Moss and Round 1967; Hickman 1969, 1971b). Species composition and standing crop size, for example, in the epilithic algal community, are not uniform across a river or stream because of flow rate variation associated with increasing depth toward mid-stream (Golowin 1968). Moreover, the chemical nature, size, and morphology of the rocks themselves play an important role.

Investigations of actual primary productivity of attached algae in flowing systems have been accomplished in several ways. Modification of the upstream-downstream oxygen change method originally introduced by Odum (1956) has been used (Stockner 1968;

Flemer 1970; Kelly et al. 1974). However, such a method reveals nothing about individual, defined algal communities. Other techniques have utilized some kind of vessel into which the algae are placed and the incubations performed in situ (Thomas and O'Connell 1966; Hickman 1971b, 1974; Marker 1976b). Many times chambers possessing no mechanism for internal water circulation have been used, and some work has shown that these can underestimate primary productivity (McConnell and Sigler 1959; Rodgers and Harvey 1976). Marker (1976b) devised a chamber for in situ measurements of epilithic algal primary productivity in a small river. However, this particular design proved inadequate for our study because the propeller creating the circulation was electrically powered and these small motors proved totally unreliable in the field. Moreover, heavy batteries were required to power them. Therefore, a small simple circulating chamber was designed, built, and used in this study.

Within the Alberta Oil Sands Environmental Research Program (AOSERP) study area are a chamber of tributary rivers feeding the Athabasca River which are considered important to the overall fisheries of the region. Representative of these tributaries are the Muskeg, Steepbank, Hangingstone, Ells, and MacKay rivers (Figure 1). These rivers lie close to areas which have a potential to be disrupted by removal of oil sands. Consequently, this study was initiated to determine the baseline status of production and populations of epilithic algae in these key tributaries and to provide an estimate of their significance.

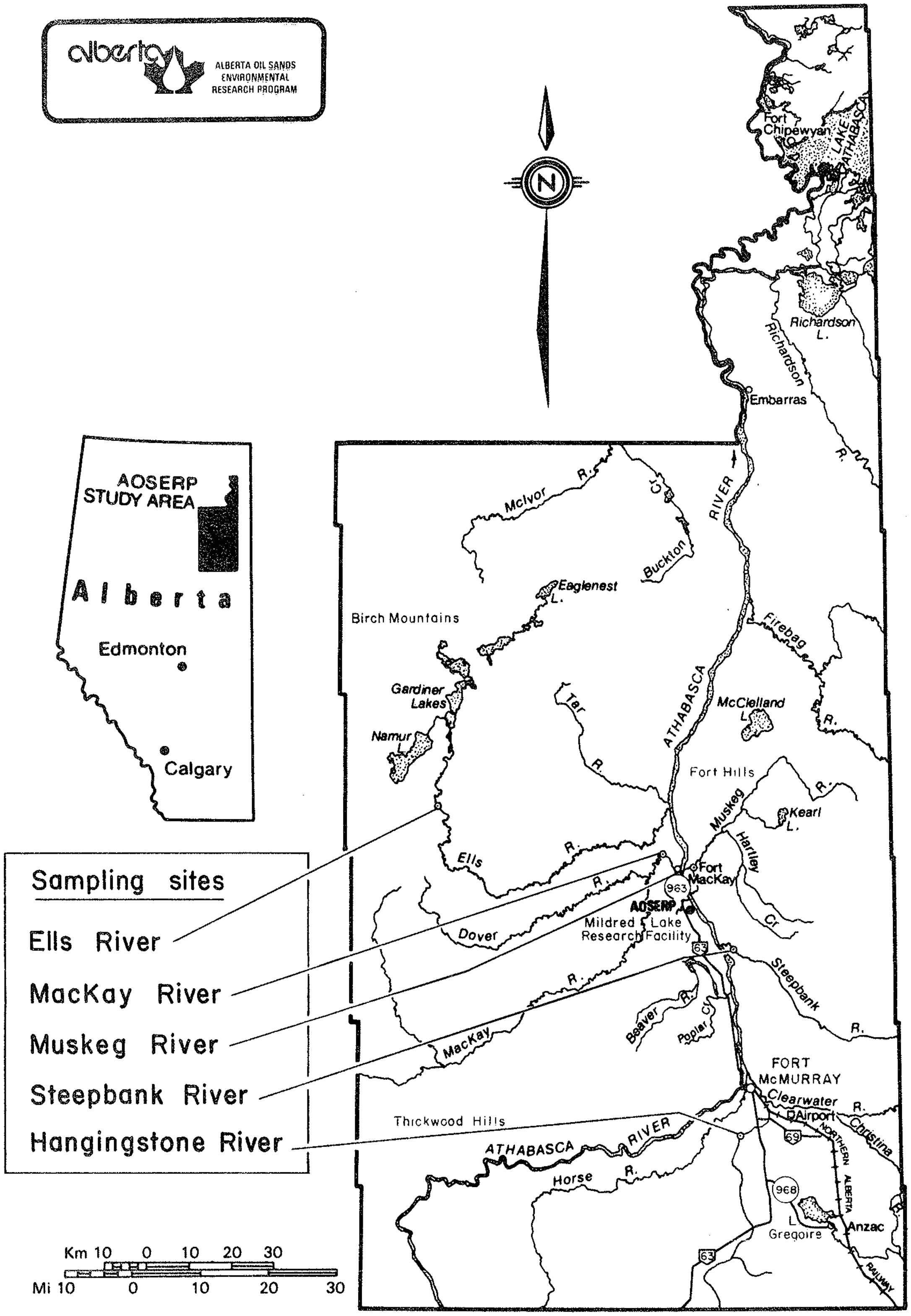

Figure 1. Map of the study area.

2. SITE DESCRIPTION

The Muskeg River is a brown water river originating in the Muskeg Mountains meandering through the Clearwater Lowland to the Athabasca River. In its upper reaches, it flows through clay, silty till, and muskeg, and through outwash sands and muskeg in its lower reaches. The slope varies from 0.003 to 0.004 in the upper and lower reaches, respectively. Sampling was conducted on this river approximately 10 km upstream from the Athabasca River where the predominant bed material is some sand and limestone rocks (Latitude 57°11'N; Longitude 111°34'W).

The Steepbank River is also a brown water tributary draining some 1425 km^2 of surficial deposits of outwash sands and gravels derived from glacial drift and muskeg. The lower reaches flow through the Clearwater Lowland, while about 15 km from the Athabasca River, it flows through exposed bitumen deposits of either McMurray or Athabasca Oil Sands (Cretaceous sandstones). Consequently, the river substrata vary from organic sediment in the uppermost reaches to boulders, small stones, and gravels and lower down, along with oil sands. Samples were collected from a site 1 km upstream from the Athabasca River, (Latitude 57°02'N; Longitude 111°25'W).

The Hangingstone River originates in the Stoney Mountains south of Fort McMurray. It meanders across the Algar Plain and Methy Portage Plain, which are comprised of lower Cretaceous shales and sandstones with an overburden of sand and gravel, and finally the Clearwater Lowland to the Athabasca River at Fort McMurray. It drains clay and silty till as well as muskeg and has a mean slope of 0.003 draining and area of 914 km^2. Samples were collected at a site immediately west of Waterways, 1.5 km from the Athabasca River, and upstream of the effluent discharges associated with the town of Fort McMurray (Latitude 56°40'N; Longitude 111°20'W). The river bed material ranged from organic sediment in the uppermost reaches to sands, gravels, stones, and boulders lower down.

The MacKay River originates in the Birch Mountains and flows east before crossing the Algar Plain and the Clearwater Lowland. It drains hummocky moraine, driftsands, gravels, and silts in the upper reaches, and muskeg, silty till, and lacustrine deposits in the lower reaches. The catchment area comprises 5 232 km^2 and the river has an average slope of 0.002. Samples were collected from a site, located 11 km from the Athabasca River (Latitude $57^{\circ}12'$N; Longitude $111^{\circ}40'$W).

The Ells River flows south from the Birch Mountains, then east across the Algar Plain and Clearwater Lowland, draining an area of 2 700 km^2. It drains hummocky morain, till, sands, gravels, and muskeg in the upper reaches, and clay, silty till (alluvial lacustrine materials), and muskeg in the lower reaches. The average slope is 0.002. Samples were collected from a site in the upper reaches (Latitude $57^{\circ}22'$N; Longitude $112^{\circ}31'$W) where the bed materials ranged from gravel and small stones to boulders. Numerous lakes in the headwater region of the river have an attenuating action upon the discharge rates of this river resulting in no excessive flooding.

3. MATERIALS AND METHODS

3.1 EPILITHIC ALGAL SAMPLING

Artificial substrata have frequently been used in investigations of attached algal communities to obtain both qualitative (i.e., floristic) and quantitative (i.e., standing crop and primary productivity) data (Hynes 1970; Sladeckova 1962; Hohn and Hellerman 1963; Hufford and Collins 1976). Both cell numbers and chlorophyll *a* content have been used as standing crop measures. However, artificial substrata tend to be selective and, consequently, are generaly considered inadequate for studies of natural attached algal communities because this natural community is often not accurately represented upon artificial substrata, both floristically and quantitatively (Wetzel and Westlake 1969; Tippett 1970; Brown 1976). Therefore, throughout this study, only the natural rock substrata which dominated the river beds were investigated.

3.2 DETERMINATION OF ALGAL NUMBERS AND SPECIES COMPOSITION

Two 4 cm^2 areas of rock were delineated by a template and the area within scraped with a sharp scalpel and brushed to remove the epilithic algae. These scrapings were placed in sterile 30 mL vials together with 10 mL filtered river water and several drops of Lugol's iodine solution as preservative. Wherever possible, unpreserved samples were also examined immediately following collection to aid accurate identification of the algae.

Species composition and algal numbers were determined using the inverted microscopic (Wild M-40) and sedimentation technique (Lund et al. 1958). Continuous transects were examined under 40x and 100x magnification and the algae identified and counted. A minimum of 200, but more frequently 800 to 2 000 algae were enumerated. To enable diatoms to be identified, subsamples were treated with a mixture of concentrated sulphuric acid, potassium dichromate, and hydrogen peroxide to remove organic matter, followed by repeated washings in distilled water to remove all traces of acid before slowly drying the cleared diatom frustules onto coverglasses and mounting in Hyrax. Algae were identified according to Bourrelly

(1966, 1968, 1970), Prescott (1961), Patrick and Reimer (1966, 1975), Cleve-Euler 1951-1955), and Hustedt (1930a, 1930b, 1959, 1961-1966).

3.3 DETERMINATION OF CHLOROPHYLL *a* CONTENT

Standing crop size, as measured by the chlorophyll *a* content, was determined in two ways. First, 4 cm^2 scrapes of rocks were made, and second, entire rock surfaces were brushed and cleaned of algae. This technique was employed in connection with the primary productivity measurements, and the results for chlorophyll *a* appearing in this report are derived using this latter method. At the termination of the primary productivity incubation period, the individual rocks were removed from the incubation chambers and immediately brushed and scraped clean of the epilithic algae. A known volume (depending upon observed population size) of this material was filtered onto a Whatman GF/C glass fibre filter, covered with anhydrous magnesium carbonate, carefully wrapped in aluminum foil, and then stored in a freezer until analysed.

Pigments were extracted in 90% acetone at 4°C for 24 h in the dark after homogenizing, using a Polytron-PCU-2-110 homogenizer to ensure complete extraction. The spectrophotometric method and equations of Moss (1967a, 1967b), where correction is made for naturally occurring phaeophytin *a*, were used. Normality of the hydrochloric acid did not exceed that indicated by Riemann (1978).

Several workers have suggested that algae suspended within the water column contribute significantly to river productivity (Patrick 1961; Cairns et al. 1970; Swale 1964; Whitford and Schumacher 1963). Therefore, 1 L water samples were collected from mid-stream 15 cm below the water surface, and filtered for pigment content determinations.

3.4 PRIMARY PRODUCTIVITY

Primary productivity was measured utilizing the carbon-14 technique. Individual rocks, together with their attached epilithic algae, were carefully transferred to 500 mL glass incubation jars. These were filled with river waters (previously filtered through Whatman GF/A glass fibre filter paper to remove organisms and detritus) and inoculated with 10 µCi $NaH^{14}CO_3$ at 1 000 h. Each incubation jar lid was fitted with a shaft which had propellers attached at both ends. The water current rotated the outer propeller which in turn rotated the inner one. This then simulated river flow. The chamber was simple and lightweight which was an essential feature for field studies of this nature where transport to sites is via a helicopter. Rock samples were taken from near the edge and mid-stream and between 10 and 20 replicates were used. Both light and darkened chambers were used and the incubation period lasted until 1 400 h. Jars were always filled to the top (Ilmavirta and Jones 1977). At the end of the incubation period, the algae were removed from the rocks as described earlier. Subsamples were taken for chlorophyll *a* analysis before the remainder was preserved with formalin. Each rock was labelled and retained for area determination which was accomplished planimetrically.

Hydrochloric acid was used to acidify 20 mL subsamples to pH 2.0. These were then aerated for 30 min to remove unincoporated inorganic carbon-14 (Schindler et al. 1972). Afterwards, 2 mL subsamples were placed in Aquasol fluor and the incorporated carbon-14 determined using a Nuclear-Chicago Scintillation Computer, Model 6800. Corrections for quanching were also made.

3.5 WATER CHEMISTRY

Water was collected and immediately filtered through GF/A glass fibre filters to remove detritus and organisms (cf. Happey 1970). Two litres were frozen for metal analysis. Sodium and potassium concentrations were determined using an IL Flame Photometer, Model 148, while those of magnesium, iron, calcium, and manganese were determined by atomic absorption spectrophotometry.

Dissolved silica, chloride, phosphate-phosphorus, nitrate-nitrogen, and alkalinity were determined following MacKereth (1963) and sulphate according to APHA (1976). Phosphate-phosphorus extractions, using n-hexanol and ammonium molybdate, were performed as soon as feasible after collection in the Mildred Lake Research Facility. Similary, 100 mL samples utilized for nitrate-nitrogen determinations were evaporated to dryness in flat-bottomed conical flasks in the same laboratory. Subsequent analysis took place at the University of Alberta. All results were expressed as $mg \cdot L^{-1}$.

Conductivity was measured with a YSI conductivity/temperature meter (Yellow Springs Instrument Co.) YSI Model 33, S-C-1 meter and pH with a Radiometer pH meter.

3.6 PHYSICAL FACTORS

Water depth and temperature were measured. The latter was determined with the conductivity/temperature meter. Irradiance on the river bed was measured using a quantum sensor, measuring quanta in Ph.A.R. (photosynthetically available radiation; 400 to 700 nm) (LI-185, Lambda Instrument Co.). Daily records of total irradiance were determined at the Mildred Lake Research Facility. Hourly summations were utilized in connection with the primary productivity measurements. Discharge and current velocity data were supplied by Water Survey of Canada, Calgary, Alberta.

4. RESULTS

A summary showing the ranges and mean values is presented in Table 1.

4.1 PHYSICAL FACTORS

4.1.1 Water Temperature

Water temperatures were similar in each river (Figure 2). Maximum temperatures occurred each July and thereafter declined. Only in 1977, in the Steepbank and Muskeg rivers, did any marked fluctuations occur.

4.1.2 Discharge

Discharge patterns were similar in each river (Figure 3). In the MacKay, Ells, and Steepbank rivers, maxima occurred in September 1978 and May 1979, with the latter being greater. In contrast, these maxima were of comparable size in the Hangingstone and Muskeg rivers. Interestingly, in both the Muskeg and Steepbank rivers, discharge during 1977 were much lower than in 1978 and 1979.

4.1.3 Irradiance

The seasonal pattern is shown in Figure 4. Variation from river to river occurs because the total irradiance on the day of sampling is presented. In general, maximum values occurred between mid-June and September each year.

4.2 WATER CHEMISTRY

4.2.1 Conductance

Conductance remained essentially constant in the Ells River, ranging from 100 to 125 μmhos$\cdot$cm^{-2} (mean 109.4 ± 8.6), shown in Figure 5. Values were also lowest in this river compared to the other four. In contrast to this river, a distinct seasonal pattern in conductance occurred in the others (Figure 5). All displayed a summer peak which decreased to a minimum during the autumn; then, under ice-cover, conductance increased and maximum values occurred.

Table 1. The mean and range for various physical and chemical factors for the five rivers.

	Units	Rivers				
		Muskeg	Steepbank	Hangingstone	MacKay	Ells
Temperature	°C	0.4 - 21.2 $\bar{x}$ = 10.8	0 - 20.1 $\bar{x}$ = 7.72	0 - 19.0 $\bar{x}$ = 7.65	0 - 23.0 $\bar{x}$ = 9.60	0 - 19.3 $\bar{x}$ = 7.38
Conductance	μmhos cm^{-2}	120 - 400 $\bar{x}$ = 233.6	75 - 420 $\bar{x}$ = 210.0	90 - 425 $\bar{x}$ = 237.4	134 - 580 $\bar{x}$ = 206.8	90 - 125 $\bar{x}$ = 109.4
Calcium	mg·L^{-1}	11.0 - 44.8 $\bar{x}$ = 21.9	8.0 - 43.0 $\bar{x}$ = 19.1	4.5 - 33.8 $\bar{x}$ = 18.2	10.0 - 49.5 $\bar{x}$ = 22.9	7.8 - 16.9 $\bar{x}$ = 12.6
Sodium	mg·L^{-1}	5.6 - 33.2 $\bar{x}$ = 18.1	3.9 - 48.7 $\bar{x}$ = 20.0	7.4 - 56.3 $\bar{x}$ = 27.3	7.9 - 57.5 $\bar{x}$ = 33.1	3.2 - 4.8 $\bar{x}$ = 3.9
Potassium	mg·L^{-1}	0.1 - 5.7 $\bar{x}$ = 1.30	0.1 - 2.4 $\bar{x}$ = 0.70	0.1 - 3.6 $\bar{x}$ = 1.47	0.1 - 3.2 $\bar{x}$ = 1.44	0.1 - 2.4 $\bar{x}$ = 0.89
Magnesium	mg·L^{-1}	2.9 - 16.8 $\bar{x}$ = 7.8	1.1 - 16.2 $\bar{x}$ = 7.9	0.81 - 14.1 $\bar{x}$ = 7.1	2.12 - 21.4 $\bar{x}$ = 9.2	1.6 - 4.9 $\bar{x}$ = 3.6
Iron	mg·L^{-1}	0.03 - 0.99 $\bar{x}$ = 0.18	0.04 - 0.22 $\bar{x}$ = 0.12	0.05 - 0.48 $\bar{x}$ = 0.16	0.02 - 0.36 $\bar{x}$ = 0.16	0.04 - 0.13 $\bar{x}$ = 0.08
Manganese	mg·L^{-1}	0.004 - 0.063 $\bar{x}$ = 0.014	0.002 - 0.053 $\bar{x}$ = 0.013	0.004 - 0.095 $\bar{x}$ = 0.021	0.002 - 0.051 $\bar{x}$ = 0.009	0.004 - 0.018 $\bar{x}$ = 0.010
Sulphate	mg·L^{-1}	0 - 3.75 $\bar{x}$ = 1.09	0.1 - 14.0 $\bar{x}$ = 6.60	3.5 - 28.3 $\bar{x}$ = 15.7	10.5 - 53.0 $\bar{x}$ = 27.3	4.4 - 9.0 $\bar{x}$ = 6.39

continued ...

Table 1. Concluded.

	Units	Rivers				
		Muskeg	Steepbank	Hangingstone	MacKay	Ells
Chloride	mg·L^{-1}	0 - 35.6 $\bar{x}$ = 10.3	0 - 8.0 $\bar{x}$ = 1.75	1.0 - 30.0 $\bar{x}$ = 11.5	0 - 20.0 $\bar{x}$ = 7.58	0 $\bar{x}$ = 0
Nitrate-nitrogen	mg·L^{-1}	0.104 - 0.298 $\bar{x}$ = 0.196	0.150 - 0.345 $\bar{x}$ = 0.224	0.166 - 0.425 $\bar{x}$ = 0.237	0.135 - 0.515 $\bar{x}$ = 0.290	0.081 - 0.161 $\bar{x}$ = 0.122
Phosphate-phosphorus	mg·L^{-1}	0.006 - 0.352 $\bar{x}$ = 0.030	0.013 - 0.232 $\bar{x}$ = 0.049	0.006 - 0.600 $\bar{x}$ = 0.104	0.008 - 0.157 $\bar{x}$ = 0.050	0.012 - 0.285 $\bar{x}$ = 0.069
Dissolved Silica	mg·L^{-1}	0.80 - 9.90 $\bar{x}$ = 5.33	1.20 - 10.65 $\bar{x}$ = 4.54	2.70 - 9.75 $\bar{x}$ = 5.54	0.45 - 9.15 $\bar{x}$ = 3.07	0.32 - 2.20 $\bar{x}$ = 1.17
pH		6.20 - 8.40 $\bar{x}$ = 7.39	6.40 - 8.25 $\bar{x}$ = 7.32	6.50 - 8.50 $\bar{x}$ = 7.59	6.30 - 8.65 $\bar{x}$ = 7.64	6.00 - 9.00 $\bar{x}$ = 7.54
Total Alkalinity	meq·HCO$_3^-$·L^{-1}	1.9 - 4.26 $\bar{x}$ = 2.48	0.82 - 5.30 $\bar{x}$ = 2.42	0.99 - 3.95 $\bar{x}$ = 2.14	0.99 - 4.98 $\bar{x}$ = 2.52	0.80 - 1.50 $\bar{x}$ = 0.97
Discharge	m^3·s^{-1}	0.48 - 22.4 $\bar{x}$ = 4.78	0.33 - 61.5 $\bar{x}$ = 10.06	0.21 - 19.1 $\bar{x}$ = 4.94	0.5 - 86.1 $\bar{x}$ = 12.25	1.6 - 44.6 $\bar{x}$ = 10.6

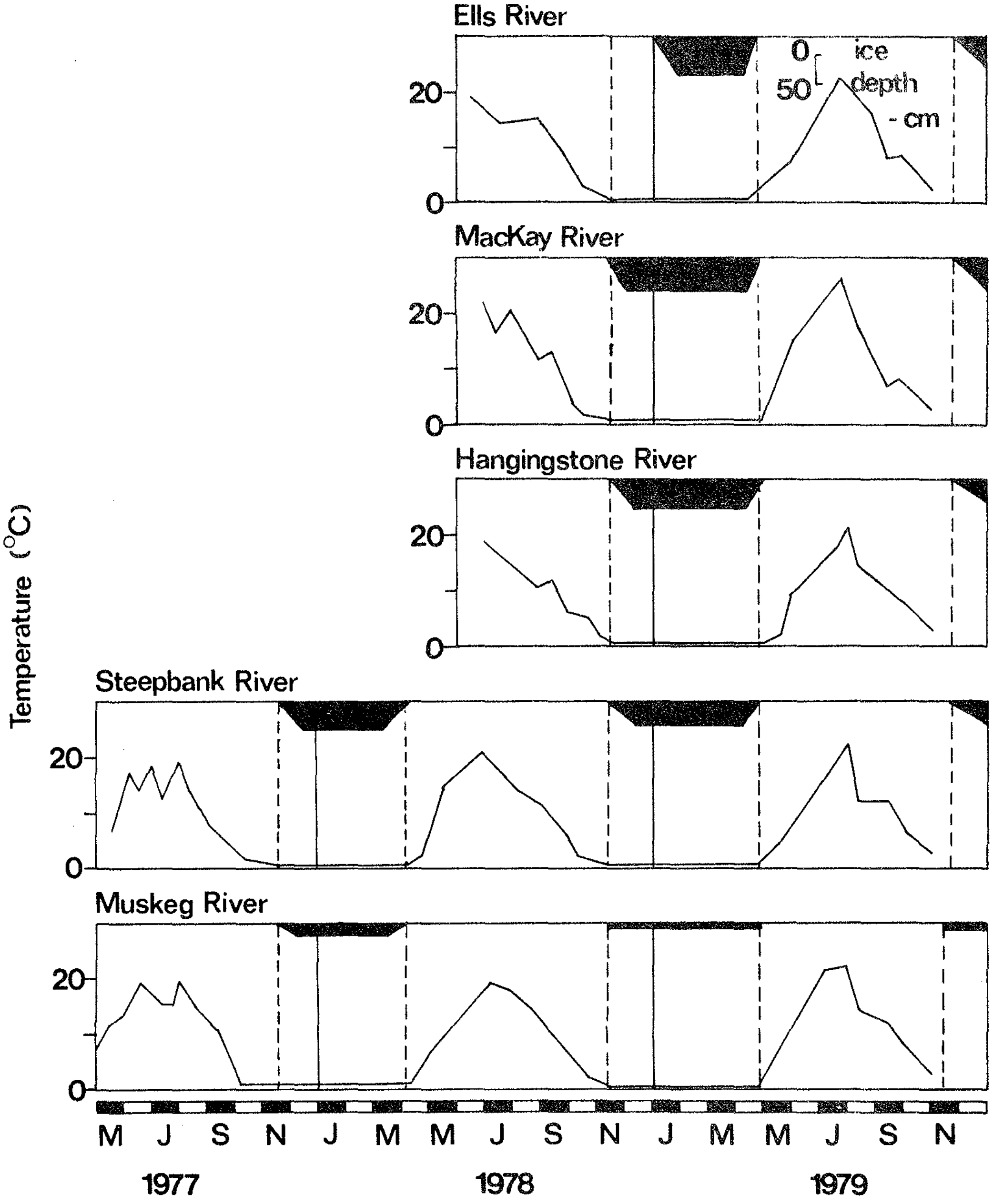

Figure 2. Water temperatures in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

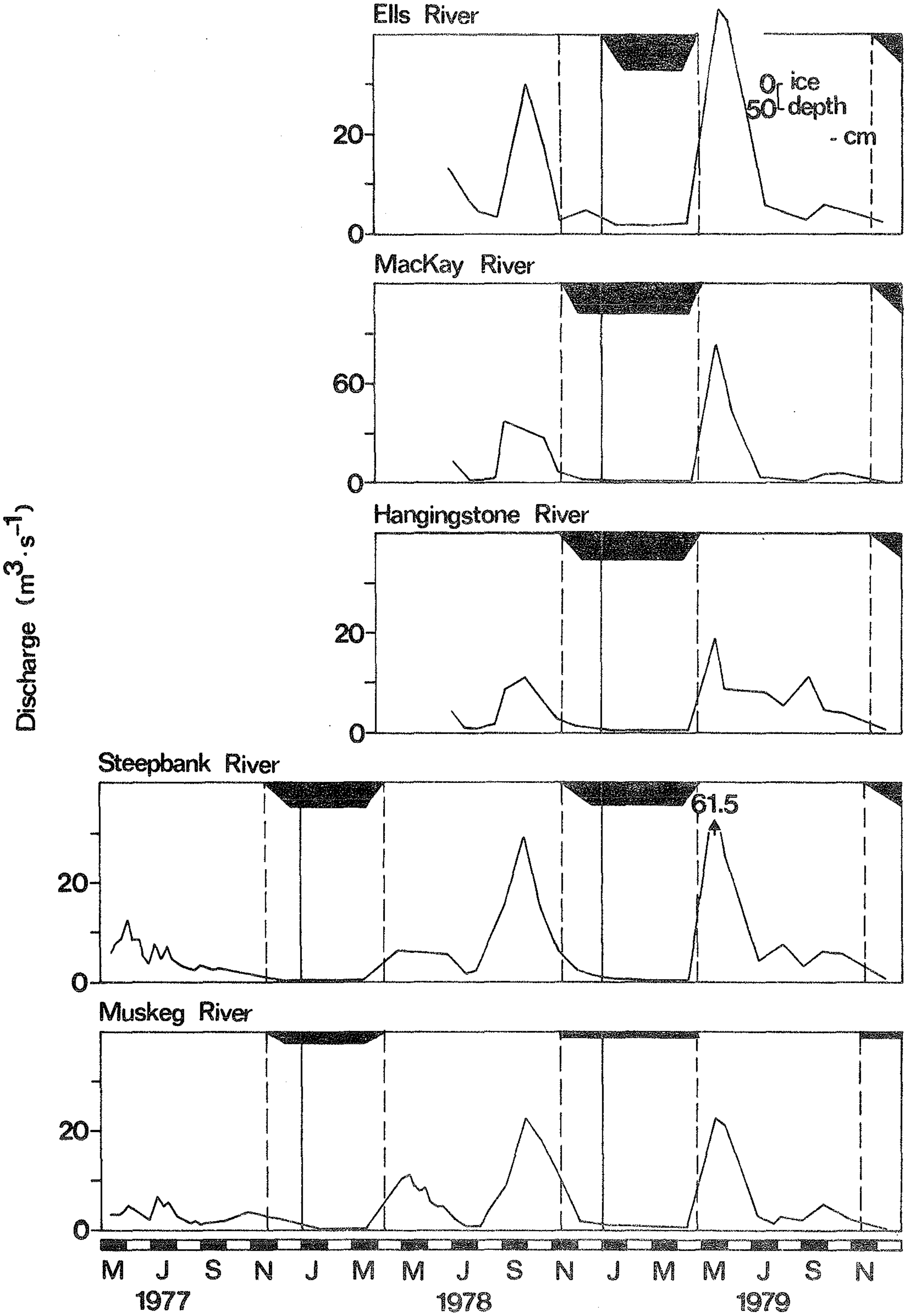

Figure 3. Discharge $(m^3 \cdot s^{-1})$ in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

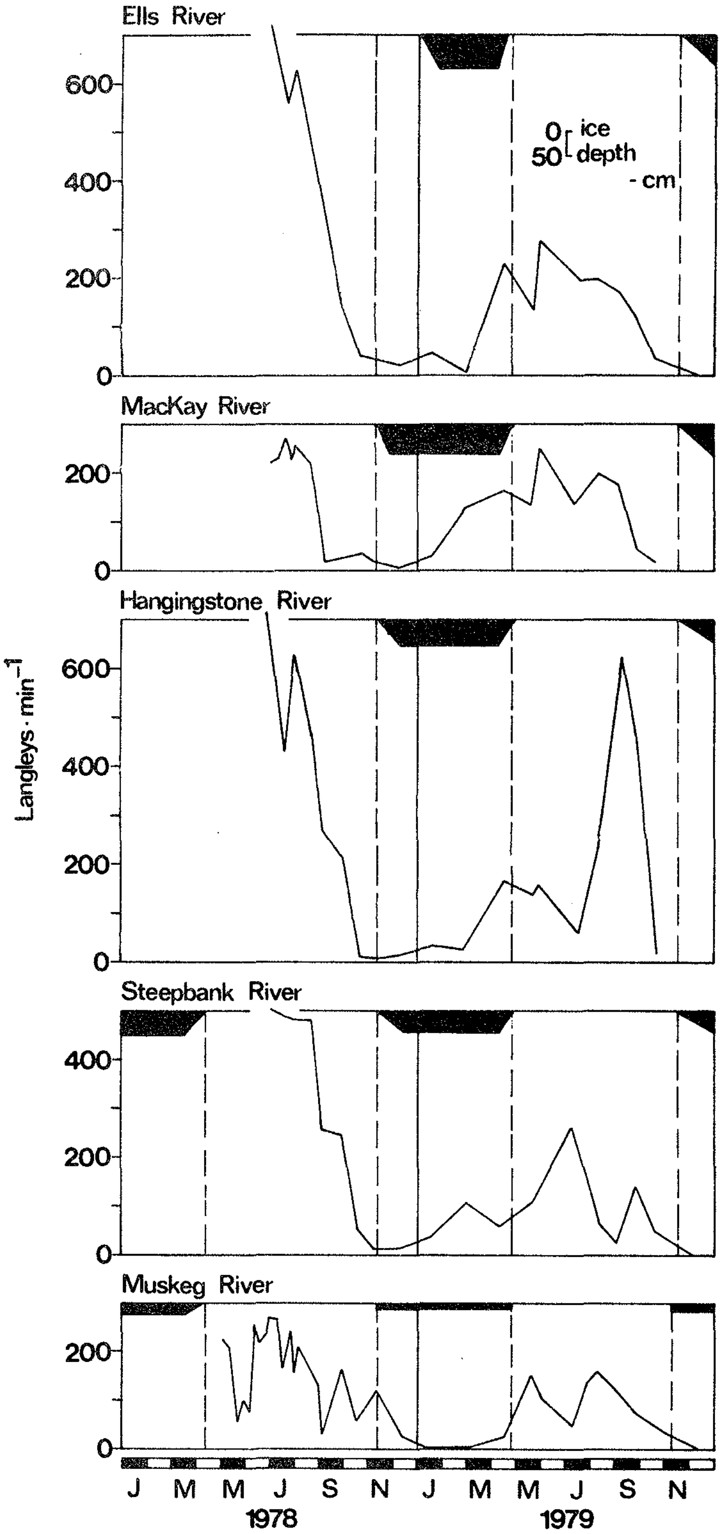

Figure 4. Daily irradiance (Langleys·min^{-1}) on the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

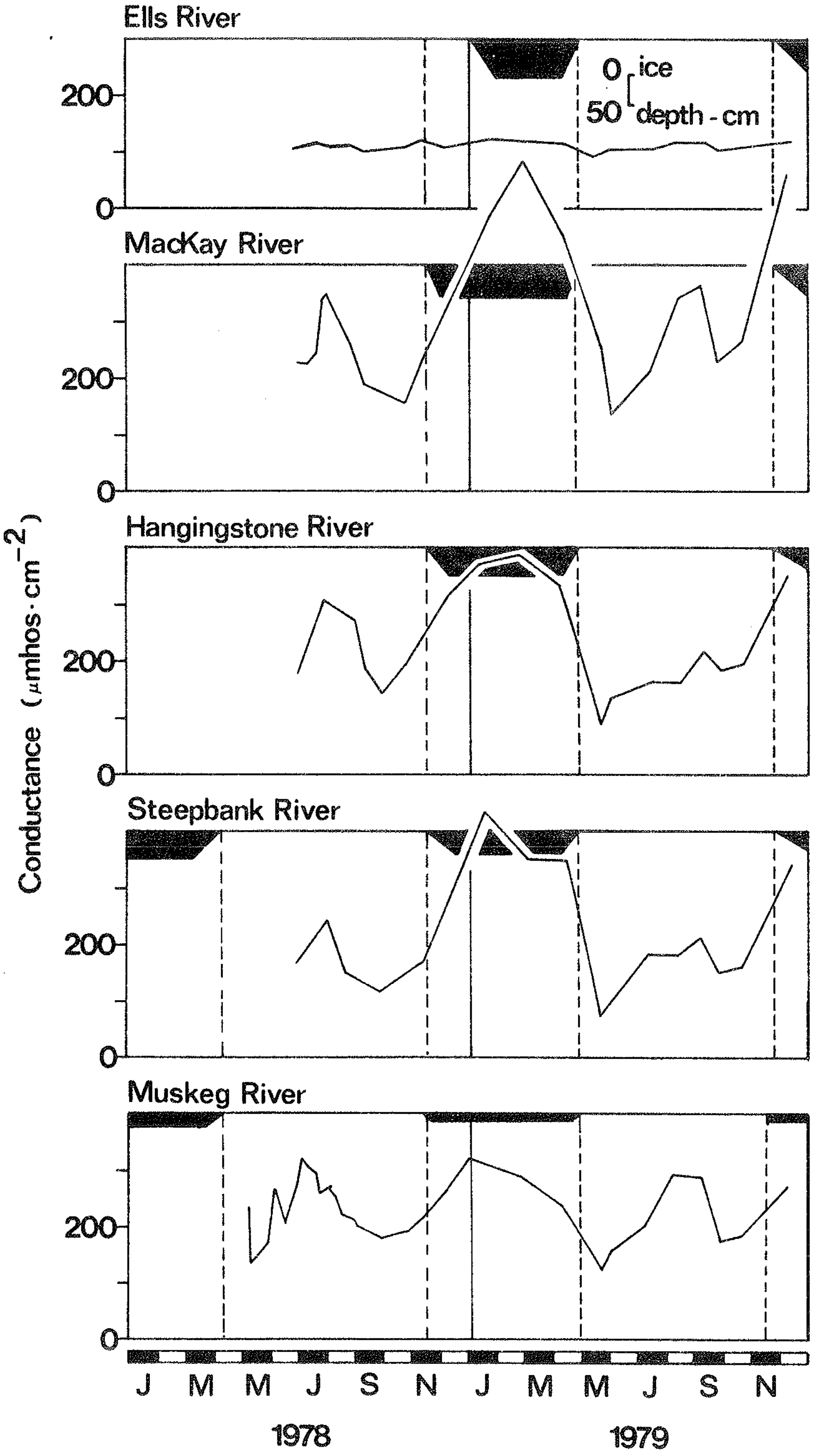

Figure 5. Conductance (μmhos·cm^{-2}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

Following ice break-up, conductance rapidly fell to minima in early May before increasing again to the summer maxima.

4.2.2 Calcium

Calcium levels fluctuated least in the Ells River with a small increase occurring during the winter (Figure 6). Again in marked contrast, large winter peaks occurred in all the other rivers (49.5, 33.1, 43.0, and 44.8 mg L^{-1} in the MacKay, Hangingstone, Steepbank, and Muskeg rivers, respectively) (Figure 6). During the summer of 1978, calcium levels in the Muskeg River fluctuated, displaying several distinct peaks (Figure 6). In the MacKay, Steepbank, and Hangingstone rivers, summer peaks were evident but always smaller than the winter ones. Distinct minima occurred in all rivers during the autumn and spring (Figure 6).

4.2.3 Sodium

Sodium concentrations in the Ells River were lowest on average (Table 1), and fluctuated least (Figure 7). As ice formed, levels decreased and remained uniform and low all winter, not increasing until after ice-breakup in May. Seasonal patterns of sodium concentrations in the other rivers were more variable (Figure 7). A series of distinct peaks punctuated the pattern in the MacKay River. These occurred in August 1978 (52.4 mg L^{-1}), March 1979 (57.5 mg L^{-1}), September 1979 (51.8 mg L^{-1}), and December 1979 (55.1 mg L^{-1}). These peaks originated and disappeared quickly. In between, values fell to minima ranging from 7.9 to 19.5 mg L^{-1} (Figure 7). A decreasing step-wise series of peaks from early August 1978 until a minimum in May 1979 occurred in the Hangingstone River. After May 1979, levels increased steadily peaking again in early December. In the early August peak, the sodium level was 39.5 mg L^{-1}; in early December, 31.2 mg L^{-1}; and in late February, 56.3 mg L^{-1}. The minimum in May 1979 was 7.36 mg L^{-1}, but by early December, it had risen to 38.6 mg L^{-1}. Sodium levels in the Steepbank River fluctuated similarly to those in the Hangingstone River but the winter peak (48.7 mg L^{-1}) was larger than the autumn one (16.4 L^{-1}). The minimum in May 1979 was also lower than in the Hangingstone River (3.9 mg L^{-1}).

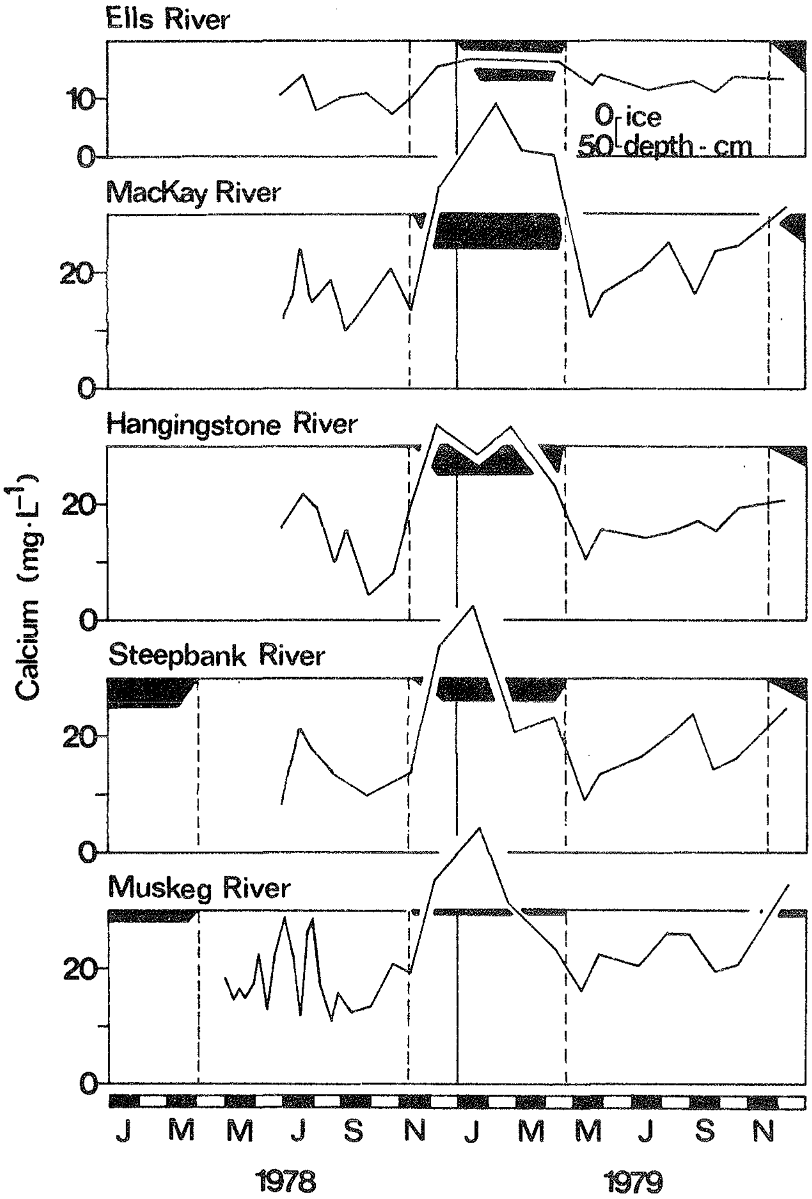

Figure 6. Calcium (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

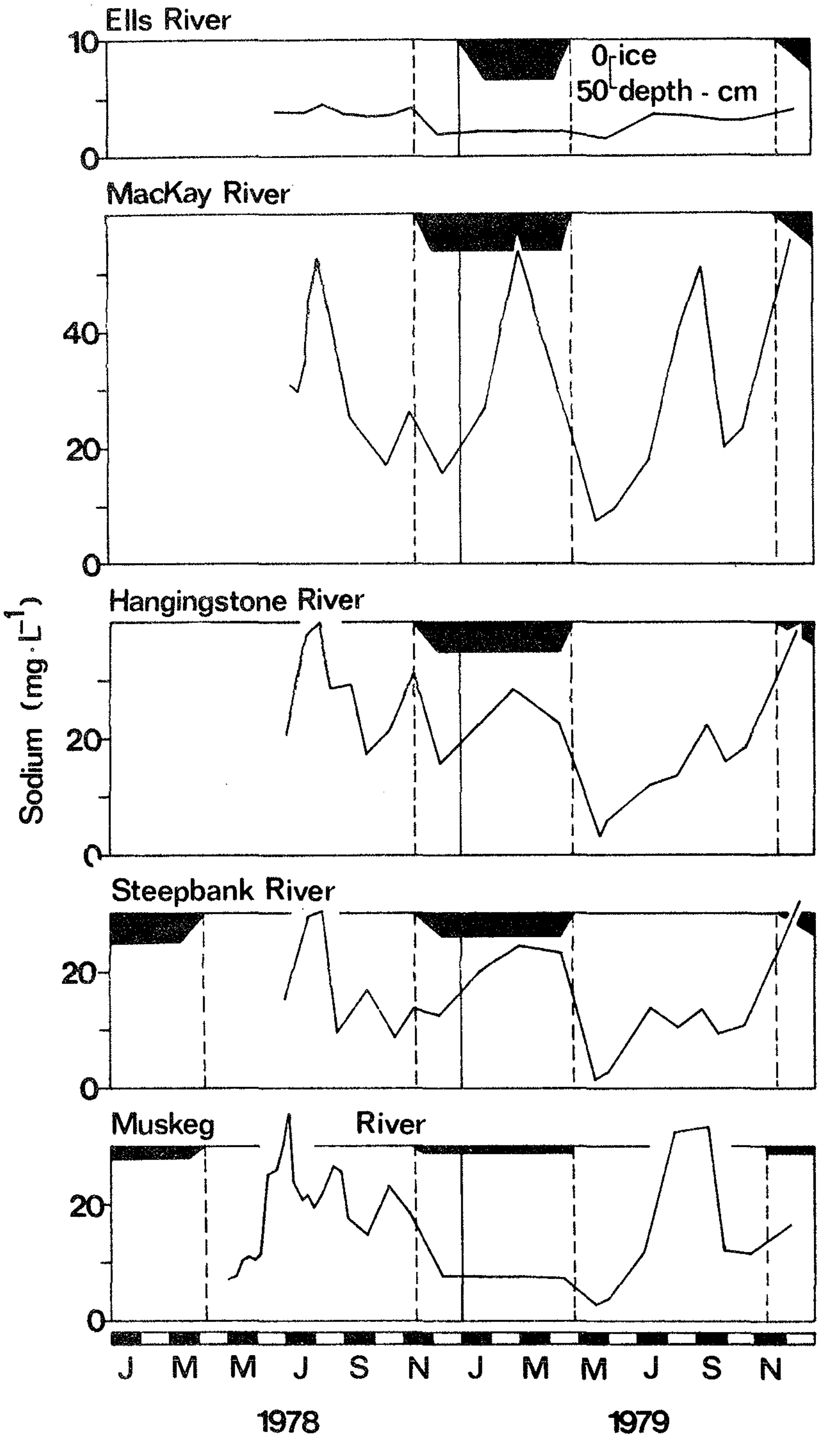

Figure 7. Sodium (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

Afterwards, levels rose quickly but then remained similar during the summer and autumn (9.8 to 13.7 mg L^{-1}) until a sharp increase in early December to 32.0 mg L^{-1} (Figure 7). The decreasing stepwise pattern of peaks was also evident in the Muskeg River with the first peak occurring in early July (35.6 mg L^{-1}), the second in late August (26.50 mg L^{-1}), and the third in mid-October (18.70 mg L^{-1}). Unlike the MacKay, Hangingstone, and Steepbank rivers, but like the Ells River, sodium levels after mid-October 1979 fell and remained low all winter with a May minimum occurring (5.7 mg L^{-1}). Afterwards, sodium levels quickly increased to a peak in early September (33.2 mg L^{-1}) as shown in Figure 7.

4.2.4 Potassium

Seasonal potassium level patterns were quite similar among the five rivers (Figure 8). Varying sized peaks occurred during the summer and late autumn/early winter in each river. Two distinct peaks occurred in the Ells and Hangingstone rivers, in August and November (1.94 and 2.40 mg L^{-1}; 3.60 and 2.88 mg L^{-1}, respectively). One main peak occurred in July/August in the Steepbank River whereas the potassium levels fluctuated more irregularly in the MacKay and Muskeg rivers (Figure 8). Four peaks were discernable in the MacKay River --July (2.4 mg L^{-1}), August (1.94 mg L^{-1}), September (2.3 mg L^{-1}), and November (1.44 mg L^{-1}); five occurred in the Muskeg River--May (3.12 mg L^{-1}), June (2.40 mg L^{-1}), mid-July (5.74 mg L^{-1}), and late August (2.40 mg L^{-1}). Levels were low in each river during the winter but rose again from early May minima to summer peaks, and then the late summer- early autumn maxima. During 1980, in both the Muskeg and MacKay rivers, fluctuations were less variable than in 1979 (Figure 8) and, other than the MacKay River, summer peaks were less than during 1979 (1.50, 1.50, 0.80, and 1.50 mg L^{-1} in the Ells, Hangingstone, Steepbank, and Muskeg rivers, respectively).

4.2.5 Magnesium

Magnesium levels in the Ells River fluctuated little, ranging from 1.6 to 4.9 mg L^{-1} (Table 1). Small minima occurred just

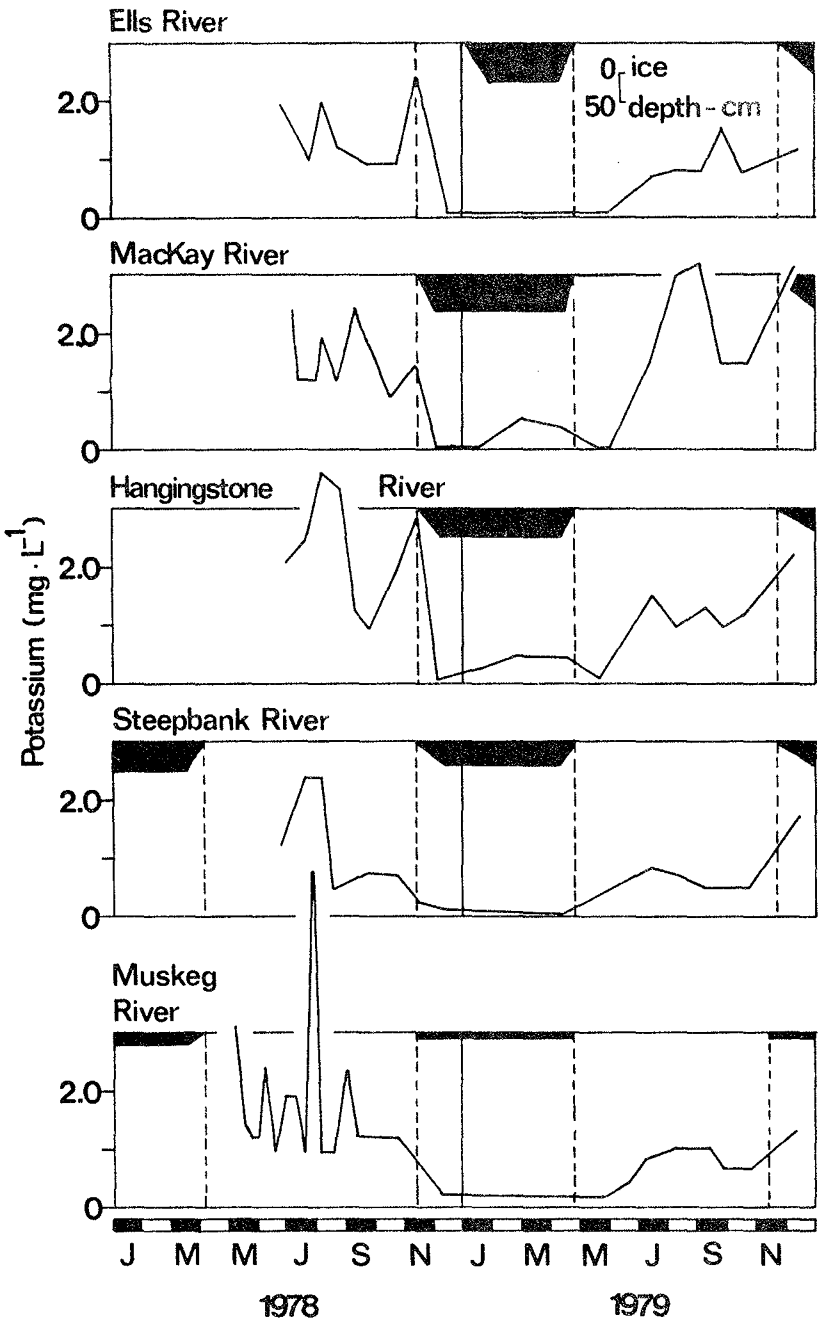

Figure 8. Potassium (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

prior to ice formation and immediately after ice break-up. Seasonal patterns in the other rivers were more pronounced, with small summer peaks and very large winter maxima (17.9, 14.1, 15.8, and 14.9 mg L^{-1} in the MacKay, Hangingstone, Steepbank, and Muskeg rivers, respectively). Magnesium levels decreased rapidly after ice break-up in early May. From these, minima levels rose throughout the summer and autumn, with summer maxima occurring again. Levels were similar to 1979 (6.40 and 8.2, 10.6 and 7.2, 8.7 and 8.8, and 8.9, and 10.3 mg L^{-1} for 1978 and 1979 in the MacKay, Hangingstone, Steepbank, and Muskeg rivers respectively). Most irregularity occurred during 1978 in the Muskeg River (Figure 9).

4.2.6 Iron

Season fluctuations in iron concentrations were most similar in the MacKay, Hangingstone, and Steepbank rivers (Figure 10). Large early winter, late winter/early spring, and autumn (1979) maxima occurred (MacKay--0.36, 0.31, and 0.23 mg L^{-1}; Hangingstone--0.48, 0.26, and 0.25 mg L^{-1}; and Steepbank--0.21, 0.22, and 0.18 mg L^{-1}). Two large peaks occurred in the Muskeg River, in early May and early December 1979 (0.73 and 0.99 mg L^{-1}, respectively) otherwise; values, fluctuated little. Iron levels, although most consistent in the Ells River, fluctuated similarly to the MacKay, Hangingstone, and Steepbank rivers, but the amplitude of the maxima was small (Figure 10) (0.09, 0.10, and 0.13 mg L^{-1} in October 1978 and May and September 1979, respectively).

4.2.7 Manganese

Manganese levels fluctuated most irregularly in the Muskeg River, particularly during 1978 (Figure 11). In this river, two winter maxima (0.04 and 0.05 mg L^{-1}) occurred; after ice break-up, levels rapidly fell and then fluctuated irregularly, although less than during 1978. One large winter maximum occurred in the Steepbank River (0.05 mg L^{-1}) while a minimum appeared during late winter. In contrast to the Muskeg River, levels increased quickly after ice break-up, with two small peaks occurring in May and early August (0.022 and 0.021 mg L^{-1}, respectively). Manganese levels fluctuated

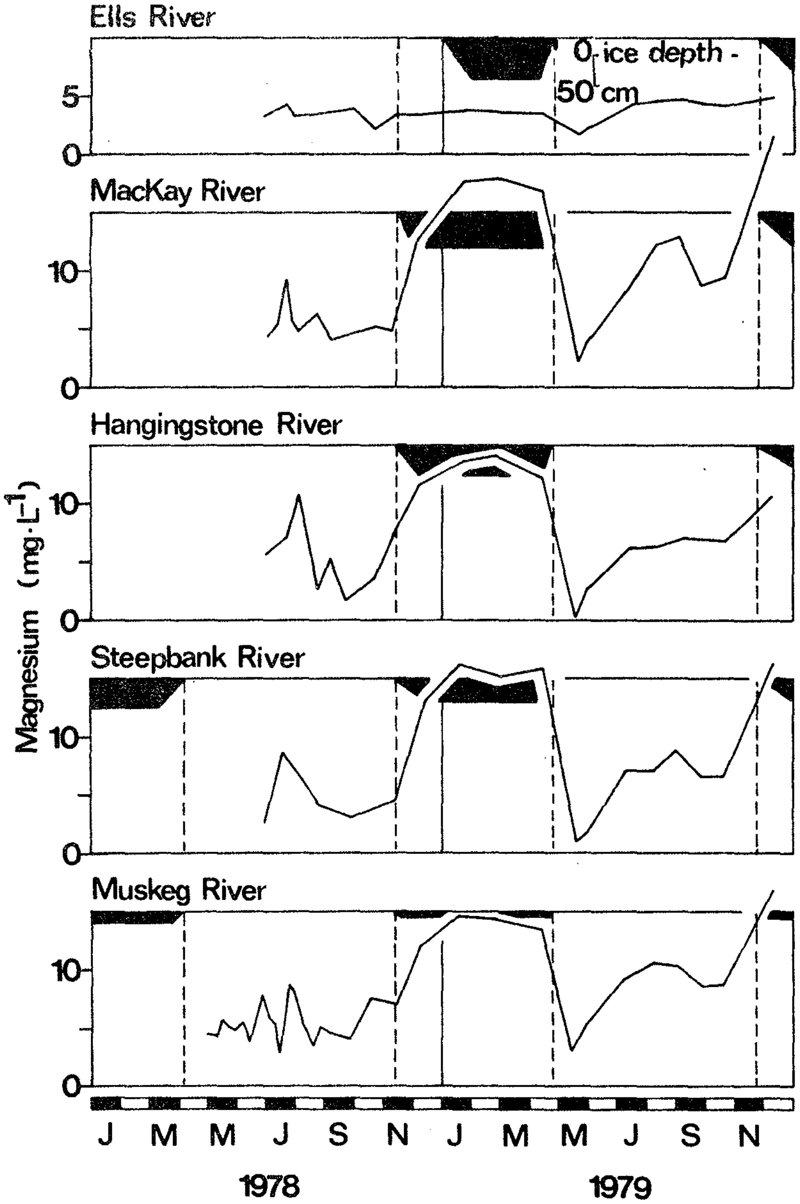

Figure 9. Magnesium (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

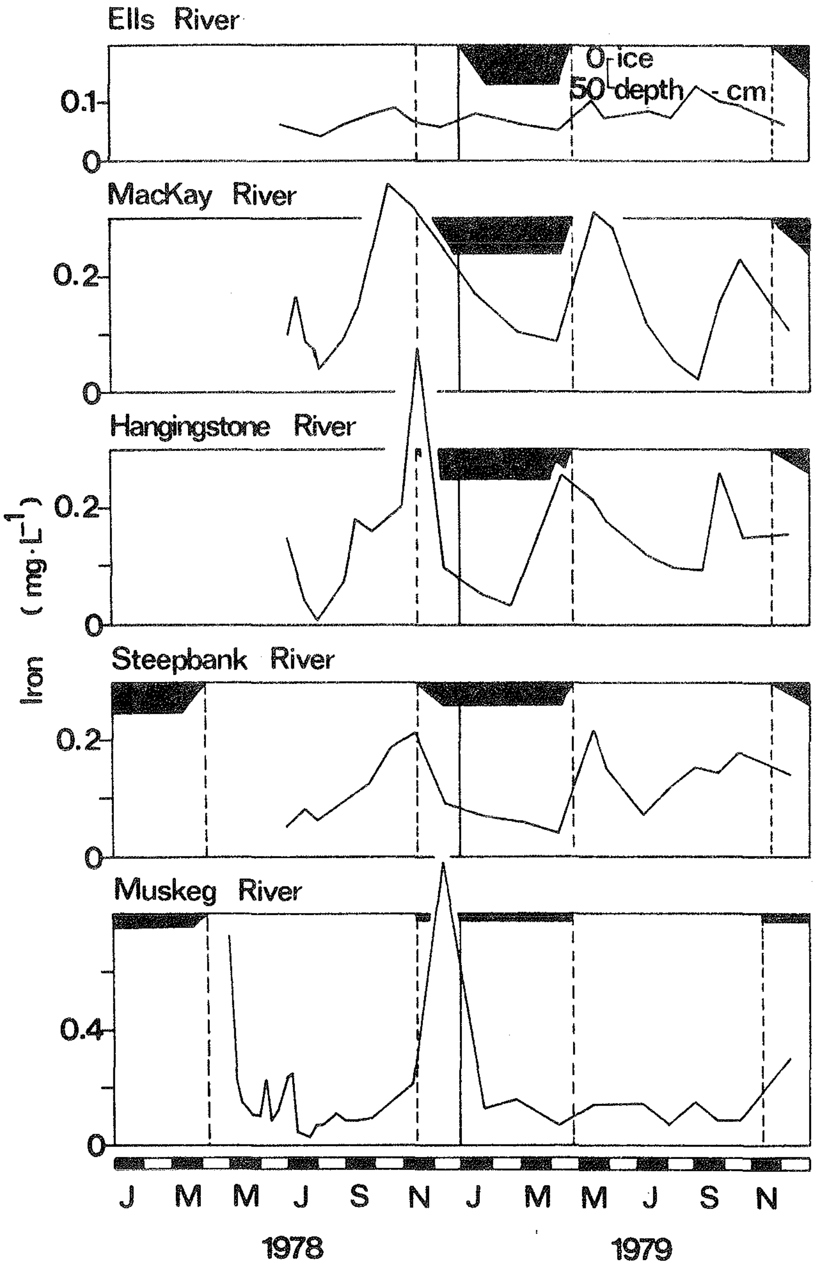

Figure 10. Iron $(mg \cdot L^{-1})$ in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

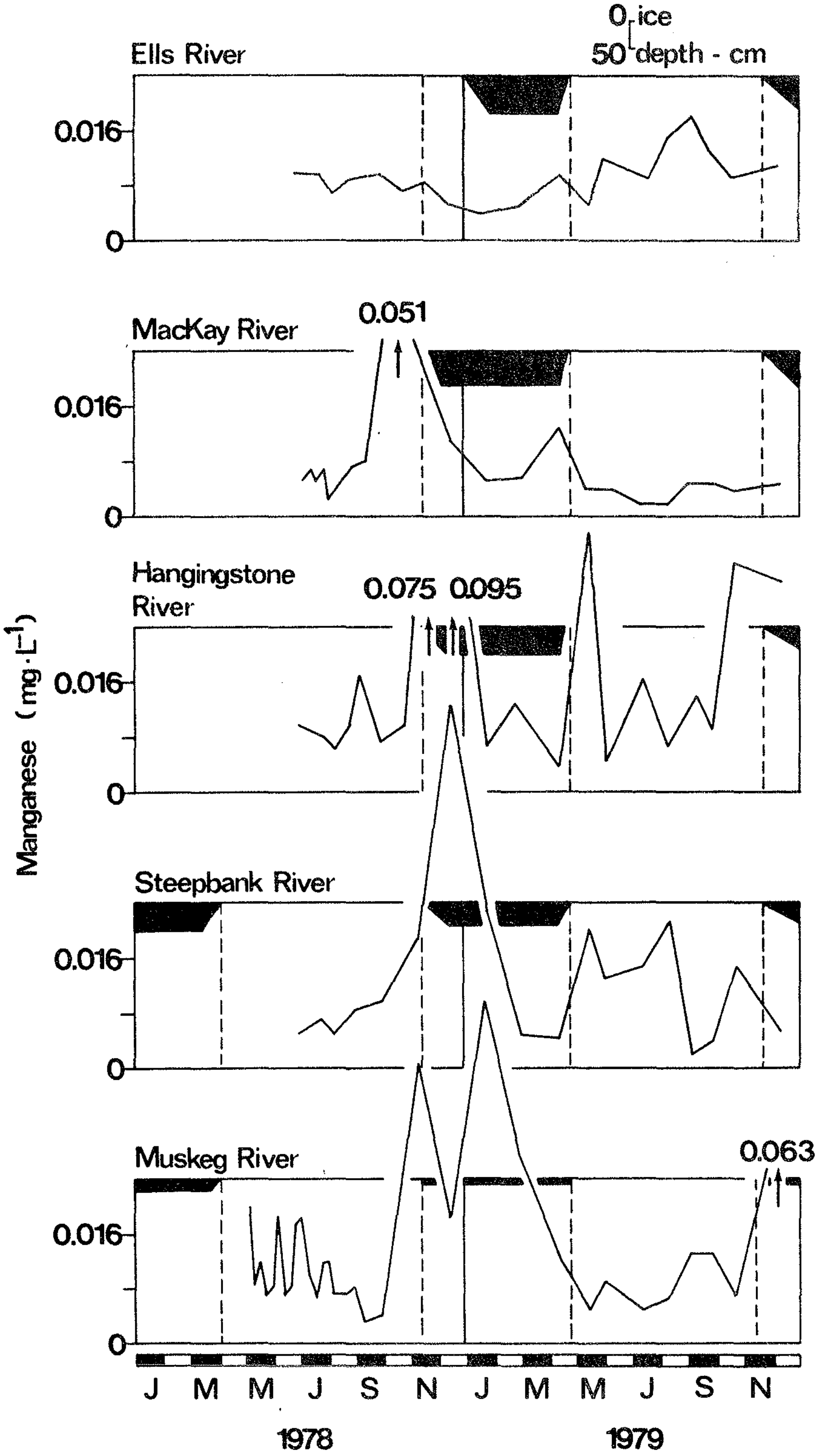

Figure 11. Manganese ($mg \cdot L^{-1}$) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

irregularly in the Hangingstone River with peaks of 0.075 and 0.095 mg L^{-1} occurring during the early winter (Figure 11). Also, as with the Steepbank River, a peak occurred in early May (0.04 mg L^{-1}). Fewer rapid and irregular fluctuations occurred in the MacKay River (Figure 11). Here, the seasonal pattern was dominated by a large autumn and a smaller winter maximum (0.051 and 0.013 mg L^{-1}, respectively); otherwise little fluctuation occurred. Finally, in the Ells River, manganese levels decreased slowly from June 1978 (0.01 mg L^{-1}) to a minimum in November (0.007 mg L^{-1}), after which they rose irregularly to a peak in September 1979 (0.010 mg L^{-1}), shown in Figure 11.

4.2.8 Sulphate

The most similar seasonal sulphate patterns occurred in the MacKay, Hangingstone, and Steepbank rivers (Figure 12). Small summer peaks occurred each year and the largest concentrations occurred during the winter (53.0, 23.5, and 13.4 mg L^{-1} in the MacKay, Hangingstone, and Steepbank rivers, respectively). The Ells River followed the general pattern but the peaks were far less pronounced. In fact, sulphate levels only fluctuated between 4.4. and 9.0 mg L^{-1} (Figure 12; Table 1). The most irregular seasonal pattern was found in the Muskeg River where levels fluctuated widely during 1978, particularly from May to August. Two winter peaks occurred, one in November (3.3 mg L^{-1}) and the other in February (3.75 mg L^{-1}) shown in Figure 12. After May 1979, sulphate levels increased slightly and, in complete contrast to 1978, hardly fluctuated.

4.2.9 Chloride

Chloride was undetectable in the Ells River (Table 1). Seasonal patterns were similar in the MacKay, Hangingstone, and Steepbank rivers with a large winter maximum and a smaller summer one (Figure 13). Values of 20.0, 30.0, and 8.0 mg L^{-1} were found during the winter in these three rivers, respectively. The seasonal pattern was similar in the Muskeg River but the winter maximum was much smaller than the summer. Levels fluctuated far more in 1978 than in 1979 (Figure 13). Two large peaks occurred during the summer of 1978

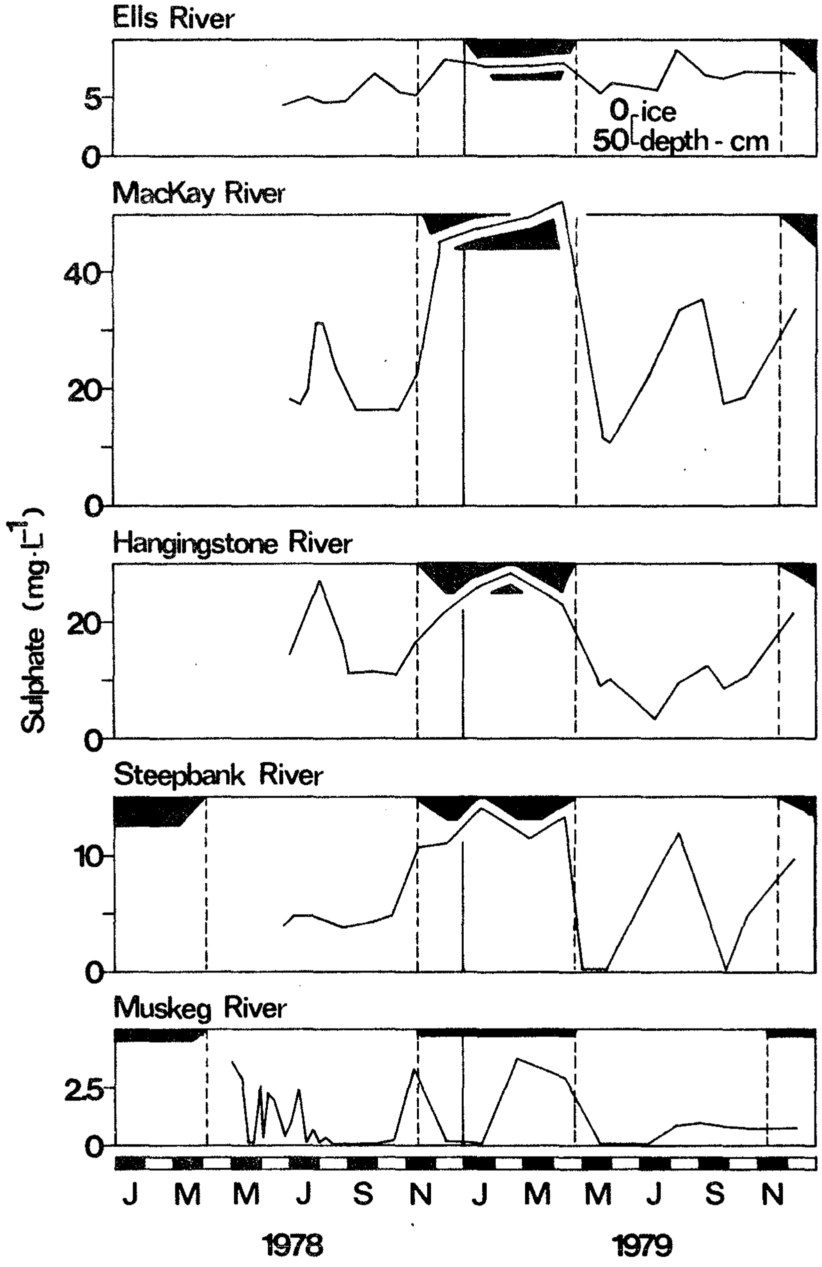

Figure 12. Sulphate (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

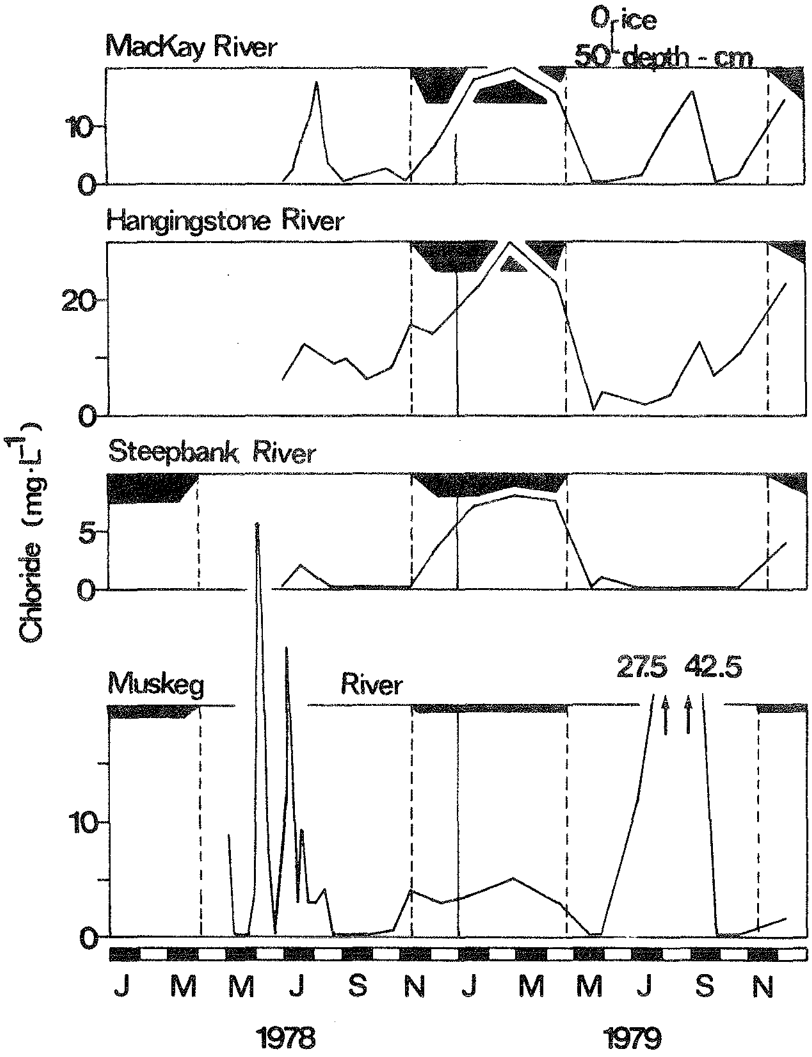

Figure 13. Chloride (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

(35.6 and 25.0 mg L^{-1} in early June and early July, respectively). Similarly, two peaks occurred during summer 1979 but in early August and September (27.5 and 42.5 mg L^{-1}, respectively) (Figure 13). Winter levels only reached 5.0 mg L^{-1} (late February 1979).

4.2.10 Nitrate-Nitrogen

No distinct seasonal nitrate-nitrogen fluctuations occurred in the Ells River (Figure 14). Only small peaks in early November 1978 (0.155 mg L^{-1}) and March (0.161 mg L^{-1}), May (0.124 mg L^{-1}), and September 1979 (0.146 mg L^{-1}). More distinctive patterns occurred in the other four rivers (Figure 14). Basically, all four rivers displayed the same pattern. Nitrate-nitrogen levels were low during mid-summer, but rose to autumn/early winter peaks. Then, as ice formed, concentrations first decreased and then, in all but the Muskeg River, increased again in late February/early March only to fall as the ice thawed. Maximum levels found were 0.515, 0.425, 0.115, and 0.298 mg L^{-1} in the MacKay, Hangingstone, Steepbank, and Muskeg rivers, respectively. Again, most variability occurred during 1978 in the Muskeg River (Figure 14).

4.2.11 Phosphate-Phosphorus

Unlike the majority of other chemical parameters, phosphate-phosphorus fluctuated widely and irregularly in the Ells River with four major peaks occurring--late August (0.15 mg L^{-1}), early December (0.24 mg L^{-1}), mid-January 1979 (0.26 mg L^{-1}), and mid-May (0.29 mg L^{-1}) in Figure 15. The seasonal pattern in the MacKay River was simpler with the low phosphate-phosphorus values of the summer preceding an increase which culminated in mid-winter maximum (0.094 mg L^{-1}). A small peak occurred in May (0.065 mg L^{-1}) but in general, values decreased to another summer minimum (Figure 15). Large winter maxima occurred in both the Hangingstone and Steepbank rivers (0.25 and 0.60 mg L^{-1}; 0.12, 0.21, and 0.23 mg L^{-1}, respectively). In both, a minimum occurred in May. Afterwards values increased particularly in the Hangingstone River where a mid-July peak of 0.084 mg L^{-1} occurred. An even larger maximum occured in September of the previous year (0.46 mg L^{-1}) shown in Figure 15. A more

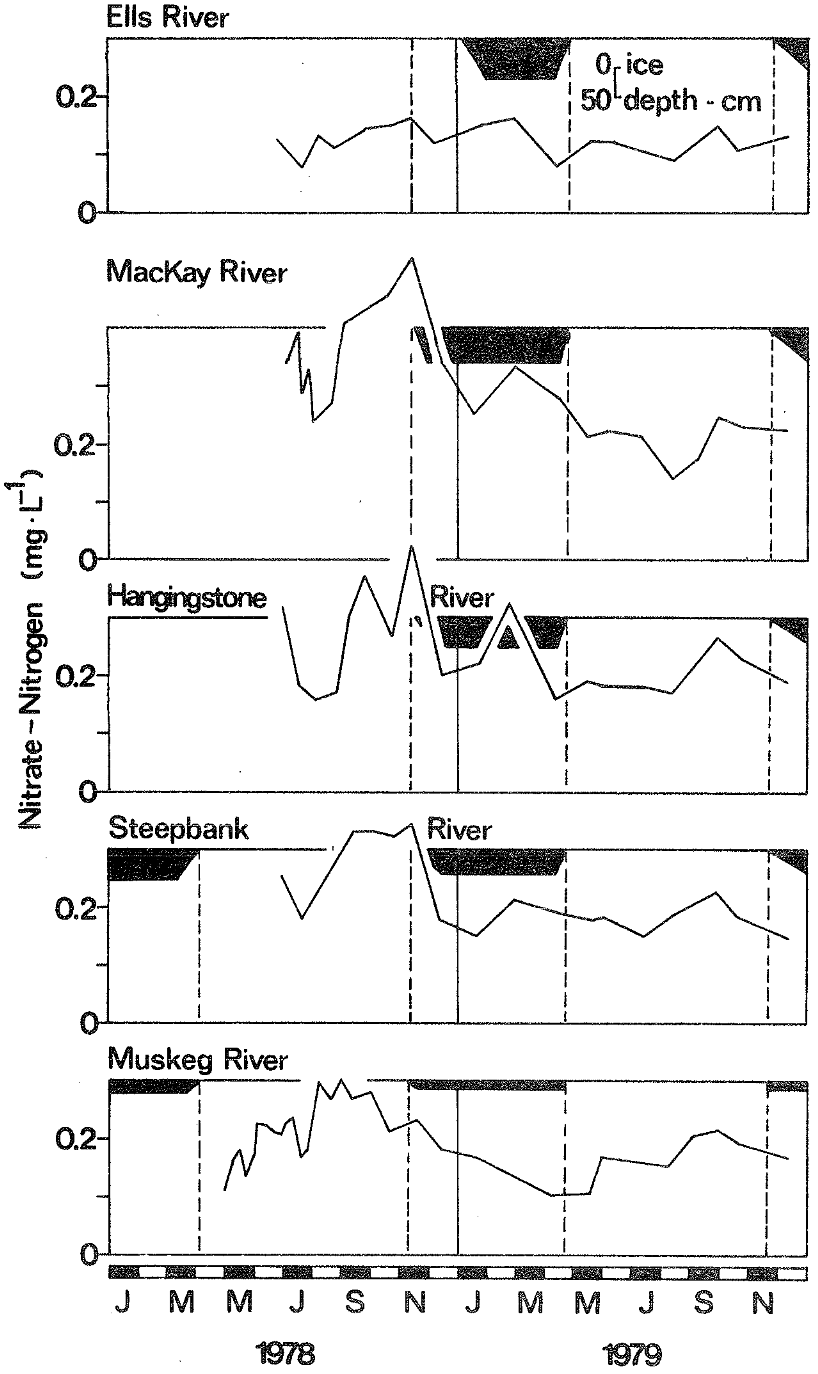

Figure 14. Nitrate-Nitrogen ($mg \cdot L^{-1}$) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

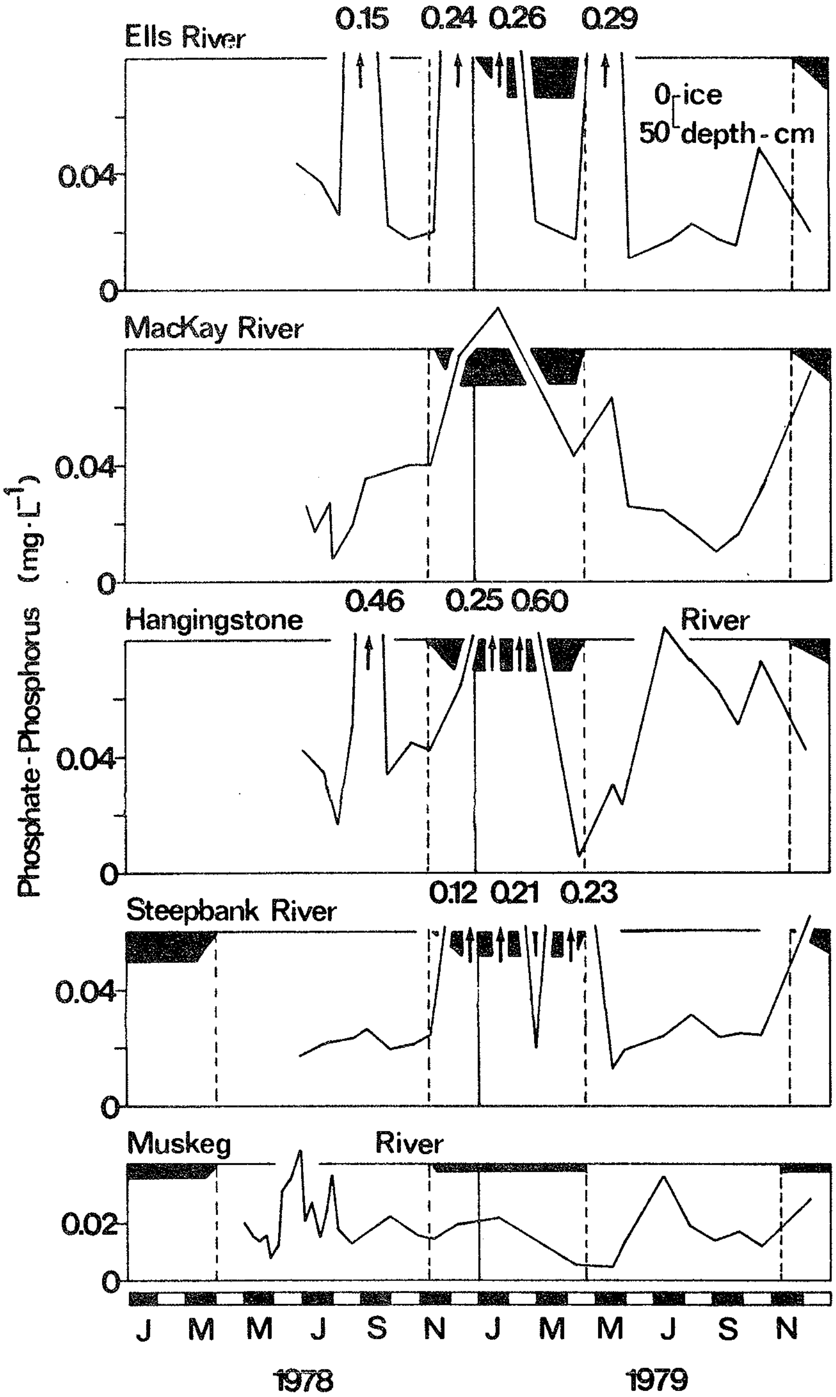

Figure 15. Phosphate-Phorphorus (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

irregular pattern but with smaller maxima occured in the Muskeg River (e.g., 0.045 and 0.037 mg L^{-1} in late June and late August, respectively). No dramatic increases occurred during the winter; after January 1979, values decreased until a minimum was reached in May. Phosphate-phosphorus levels then rose reaching a peak in early July (0.036 mg L^{-1}).

4.2.12 Dissolved Silica

Dissolved silica fluctuations were quite similar in all but the Ells River (Figure 16). Here levels fluctuated least. In the other rivers, the increases to a winter maximum and its demise were the dominant features (Figure 16). Values were similar in these rivers (Table 1) with lowest levels being in the MacKay River. However, even the mean value for this river was three times that of the Ells River.

4.2.13 pH and Alkalinity

pH and alkalinity fluctuations are presented in Figures 17 and 18. In all rivers, pH varied from acidic to basic, with maximum and minimum values occurring during the summer and winter months, respectively. Generally, in these five rivers, pH decreased from a summer maximum, reached an autumn minimum, after which an early winter peak occurred in November. Following this, values fell, rising again during the spring.

Total alkalinity in all but the Ells River peaked during August, decreased during the autumn, and increased greatly during the winter months, only to decrease during the spring. Little fluctuation occurred in the Ells River.

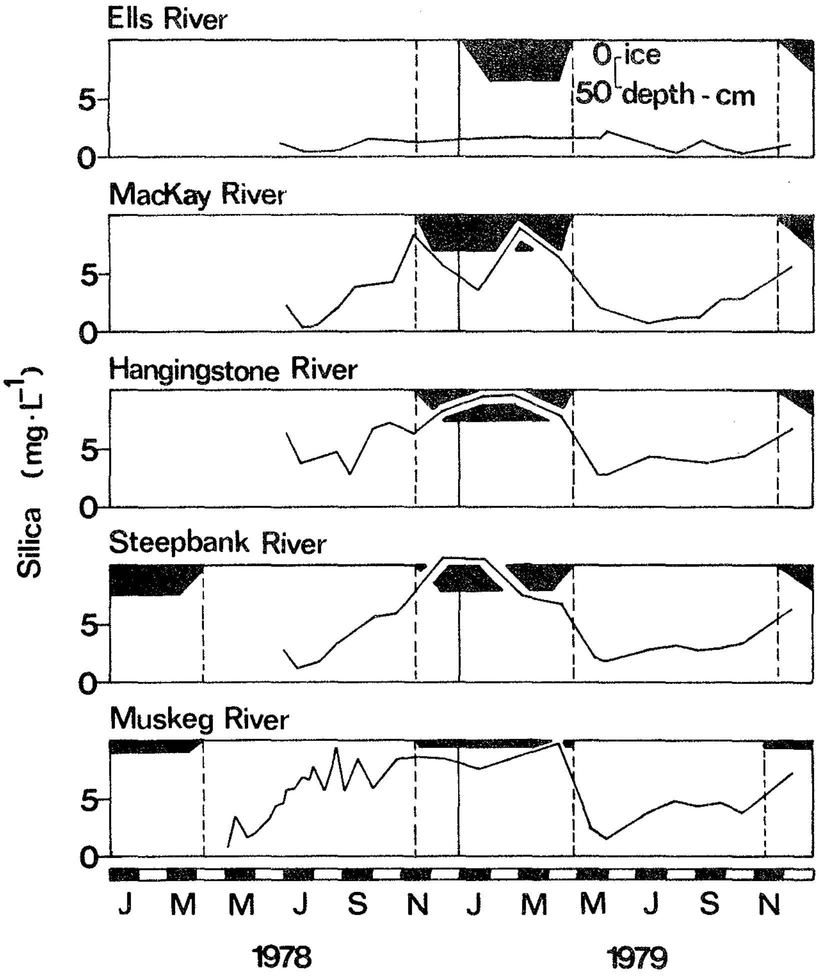

Figure 16. Dissolved Silica (mg·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

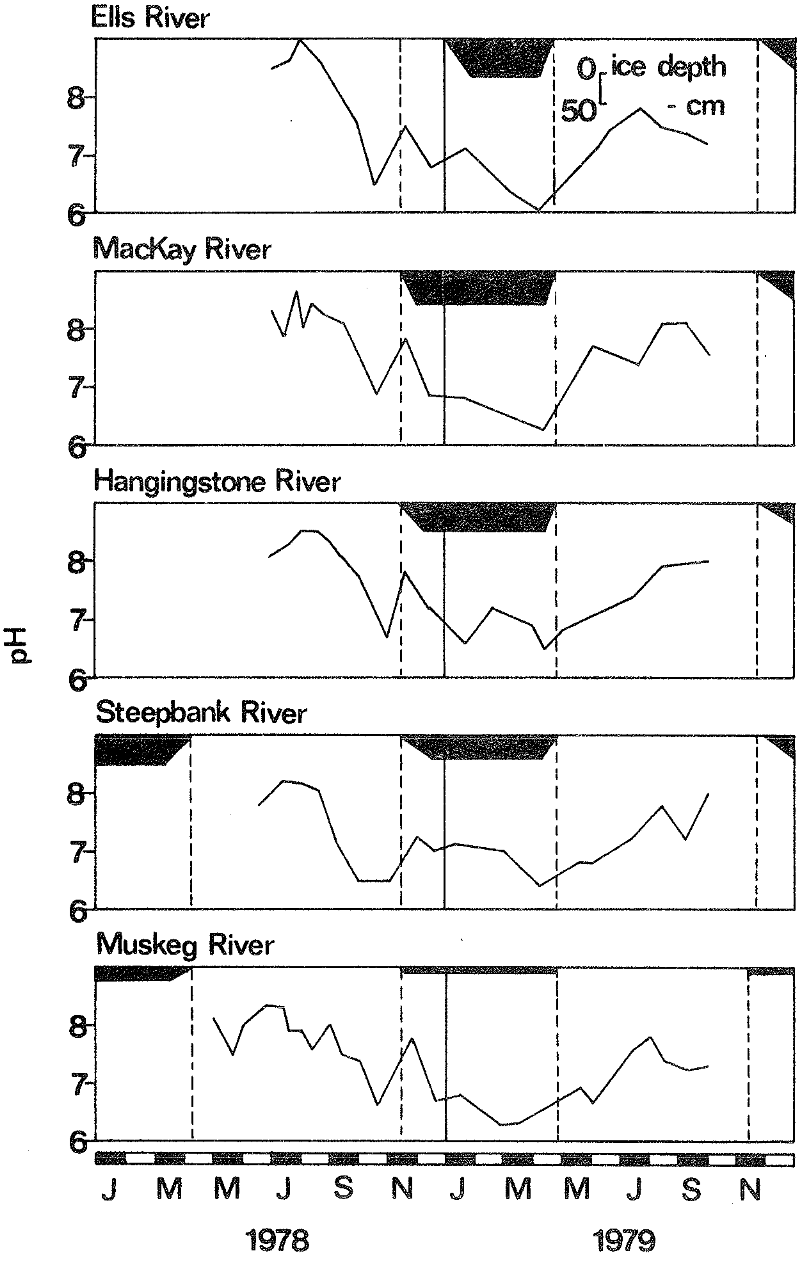

Figure 17. pH in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

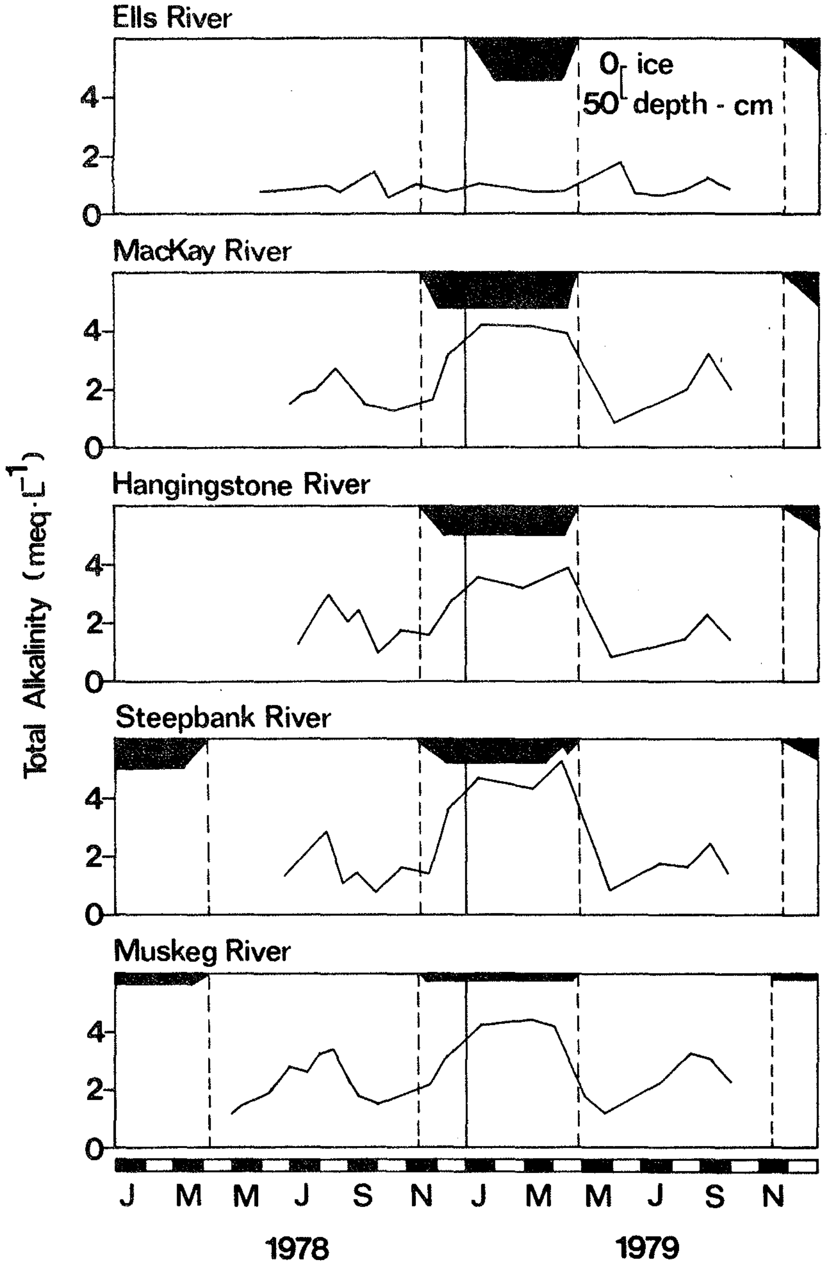

Figure 18. Total alkalinity (meq·L^{-1}) in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

4.3 SPECIES COMPOSITION

Algae from four divisions dominated the epilithon in all five rivers. These were the Cyanophyta (blue-green algae), Chlorophyta (green algae), Bacillariophyta (diatoms), and Rhodophyta (red algae). A list of all the species encountered is presented in Table 2.

In the Muskeg River, cyanophycean algae dominated with *Lyngbya Aerugineo-caerulea* and *Phormidium* sp. being most important (Figures 19 and 20). In late July 1978, cyanophycean algae accounted for more than 90% of the total epilithic algal community, but by late August, this had decreased to 53%. Two other cyanophycean algae, *Calothrix breviarticulata* and *C. Braunii* , contributed significantly at times (Figure 20). However, they showed more definite growth patterns, and therefore more stringent growth requirements than either *Lyngbya* or *Phormidium*, which were present in large numbers all the time. Diatoms were most prevalent May and August to October 1978, with *Synedra ulna* and *Nitzschia fonticola* important in May. These, together with *Gomphonema olivaceum* and *Synedra rumpens* , were important during the latter period. During 1978, chlorophycean algae were less important than these two groups but during September they accounted for 15.3% when *Draparnaldia glomerata* was present. Rhodophycean algae, *Batrachospermum vagum* and *Audouinella violacea*, were also present contributing significantly only in May, July, and November 1978. The former species was most prevalent in May and November, and the latter during July.

From December 1978 until April 1979, only cyanophycean and bacillariophycean algae were found. The two species of *Calothrix* began growth in early December and slowly increased in numbers during the winter to peak during May and early June 1979. Also, both *Lyngbya aerugineo-caerulea* and *Phormidium* sp. were present and these, too, began increasing in numbers under ice-cover during March. The winter diatom population comprised mainly *Synedra ulna*, *Gomphonema olivaceum* (after January 1979), *Synedra rumpens* and, again after January, as well as for the first time, *Gomphonema acuminatum* (Figure 20). From May 1979, cyanophycean algae decreased in importance from 75% to 59.7% by late July. After an increase during August and early September,

Table 2. The complete list of algal species encountered in the Five rivers.[a]

Species	M	SB	HS	MK	E[a]
CYANOPHYTA					
Anabaena affinis Lemm.	+	+	+	+	+
A. inaequalis Borge	-	+	-	-	-
A. variabilis Kütz.	+	+	+	+	+
A. wisconsinense Prescott	+	-	-	-	-
Aphanizomenon flos-aquae (L.) Ralfs.	+✓	-	-	-	-
Calothrix braunii Bornet & Flahault	+	+	+	+	+
C. breviarticulata West & West	+	+	-	-	-
C. fusca (Kütz.) Bornet & Flahault	+	-	-	-	-
Chamaesiphon incrustans Grunn.	+	+	-	-	-
Chroococcus limneticus Lemm.	+✓	+✓	-	+✓	-
Fischerella musicola (Borzi) Gomont	-	+	-	-	-
Gomphosphaeria aponina Kütz.	-	-	-	+✓	-
G. lacustris v. *compacta* Lemm.	+✓	-	-	-	-
Lyngbya aerugineo-caerulea (Kütz.) Gomont	+	+	+	+	+
L. aestuarii (Mert.) Lieb.	-	+	-	-	-
L. epiphytica Hieronymus	+	+	-	-	-
L. nordgaardii Wille	+	+	-	-	-
L. taylorii Drouet & Stickland	+	+	-	-	-
L. versicolor (Watt.) Gomont	+	+	-	-	-
Merismopedia elegans A. Braun	+	-	-	-	-
M. glauca (Ehr.) Naegeli	+	-	-	+	-
Microcoleus vaginatus (Vauch.) Gomont	-	+	-	-	-
Microcystis aeruginosa Kütz.emend Elenkin	+	+	-	-	-
Nostoc sp.	+	+	+	+	+
N. commune Vaucher	+	+	+	+	+
N. microscopicum Carmichael	+	+	+	+	+

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
N. verrusosum Vaucher	+	+	+	+	+
Oscillatoria sp.	+	+	-	-	+
O. amphibia C.A. Agardh.	-	-	-	+	-
O. lacustris (Kleb.) Geitler	+	+	-	-	-
O. tenuis C.A. Agardh.	+	+	-	-	-
Phormidium favosum (Bory) Gomont	+	+	-	-	-
P. tenue (Menegh.) Gomont	+	+	-	-	-
Rhaphidiopsis sp.	-	-	-	-	+✓
Rivularia haematities (D.C.) C.A. Agardh.	+	+	-	-	-
Schizothrix inctoria Gomont	+	+	-	-	-
Tolypothrix distorta Kütz.	-	+	-	-	-
CHLOROPHYTA					
Ankistrodesmus falcatus (Corda) Ralfs.	+✓	+✓	+✓	+✓	+✓
A. spiralis (Turner) Lemm.	+✓	-	-	-	-
Chaetophora incrassata (Hud.) Hazen	+	+	-	-	-
Chlamydomonas sp.	+	+	+	+	+
C. globosa Snow	-	-	-	+	-
Cladophora glomerata (L.) Kütz.	+	+	+	+	+
Chlorella ellipsoidea Gerneck	-	-	-	+	-
C. vulgaris Beyer	+	+	+	+	+
Closterium sp.	+✓	+✓	+✓	+✓	+✓
Coelastrum scabrum Reinsch	+	-	-	+	-
Coleochaete divergens Pringsheim	+	-	-	-	-
Cosmarium sp.	+✓	+✓	-	+✓	-
Crucigenia quadrata Morren	+	-	-	-	-
C. tetrapedia (Kirch.) West & West	-	+✓	-	-	-
Dictyosphaerium ehrenbergianum Naegeli	+✓	+✓	-	-	-
D. pulchellum Wood	+✓	+✓	-	-	+✓

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
Draparnaldia acuta (C.A.✓Ag.) Kütz.	+	-	-	-	-
D. glomerata (Vauch.) C.A. Ag.	+	+	-	-	-
Elkatothrix sp.	-	+	-	-	-
Gloeocystis gigas (Kütz.) Lager	-	-	-	+	-
Hyalotheca sp.	-	+	-	-	-
Mougeotia sp.	+	+	-	-	+
Microspora loefgrenii (Nordst.) Lager	-	+	-	+	-
M. pachyderma (Wille) Lager	-	-	-	-	+
Oedogonium sp.	+	+	+	-	+
Pediastrum biradiatum Meyer	-	+✓	-	-	-
P. biradiatum v. *emarginatum* (f. *convexum* Prescott)	-	-	-	+	-
P. boryanum (Turp.) Meneghini	-	-	-	-	+✓
Pithophora varia Wille	+	+	-	-	-
Pleurotaenium spp.	-	-	+	-	-
Rhizoclonium hierglyphicum (C.A. Ag.) Kütz.	+	+	-	-	-
Scenedesmus acutiformis Schroeder	-	-	-	+✓	-
S. biruga (Turp.) Lager	+✓	-	-	+✓	-
S. dimorphus (Turp.) Kütz.	-	-	-	-	+
S. obliquus (Turp.) Kütz.	+	+	-	-	+
S. quadricauda (Turp.) de Bréb.	-	-	-	+✓	-
Sorastrum spinulosum Naegeli	-	-	-	+	-
Sphaerocystis schroeteri Chodat	-	-	-	+	-
Sphaeroplea annulina (Roth.) C.A. Agardh.	-	-	-	+	-
Spirogyra sp.	+	+	-	+	-
Stigeoclonium sp.	+	+	+	+	+
S. pachyderm Prescott	+	+	-	-	-
Staurastrum sp.	-	+✓	+✓	-	-
Tetraëdron asymmetricum Prescott	-	+✓	-	-	-

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
Ulothrix sp.	+	+	+	+	+
U. subconstricta G.S. West	+	+	-	-	-
U. subtilissima Rabenhorst	+	+	-	-	-
U. zonata (Weber & Mohr) Kütz.	+	+	-	-	-
Zygnema sp.	+	-	-	-	-
RHODOPHYTA					
Batrachospermum vagum (Roth.) C.A. Agardh.	+	+	-	-	-
Audouinella violacea (Kütz.) Hamel	+	+	-	-	-
A. Pygmaea Kütz.	+	+	-	-	-
EUGLENOPHYTA					
Phacus sp.	-	+	-	-	-
CHRYSOPHYTA					
Dinobryon sertularia Ehr.	-	-	-	+ ✓	-
Mallomonas caudata Iwanoff	+	+	+	+	+
CRYPTOPHYTA					
Cryptomonas erosa Ehr.	+	+	-	-	-
C. ovata Ehr.	+	+	-	-	-
BACILLARIOPHYTA					
Achnanthes lanceolata Bréb.	+	+	+	+	+
A. lanceolata v. *rostrata* Hust.	+	+	+	+	+
A. minutissima Kütz.	+	+	+	+	+

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
A. peragallii Brun & Herbaud	-	-	-	+	+
Amphipleura lindheimeri Grun.	-	-	-	+	+
A. pellucida Kütz.	+	+	+	+	+
Amphora ovalis Kütz.	+	+	-	-	+
A. perpusilla Grun.	-	-	-	-	+
Asterionella formosa Hass.	+✓	+✓	-	-	+✓
Caloneis alpestris (Grun.) Cl.	+	-	-	-	-
Cocconeis pediculus Ehr.	+	+	+	+	+
C. placentula Ehr.	+	+	+	+	+
C. placentula v. *euglypta* (Ehr.) Cl.	+	+	-	-	-
Cyclotella catenata Brun.	-	-	+	-	-
C. comta (Ehr.) Kütz.	-	+	-	+	+
C. kützingiana Thwaites	-	-	+	-	-
C. meneghiniana Kütz.	+	+	+	+	+
Cymatopleura solea (Breb.) W. Sm.	+	-	+	-	+
Cymbella amphioxys (Kütz.) Grun.	-	-	-	-	+
C. cistula (Hemprich) Grun.	+	+	+	-	+
C. lanceolata (Ehr.) V.H.	-	-	-	+	-
C. naviculiformis Auerswald	+	-	-	-	+
C. prostrata (Berkeley) Cl.	+	+	+	-	+
C. sinuata Greg.	+	+	+	-	+
C. tumida (Bréb.) V.H.	-	-	+	-	+
C. turgida (Greg.) Cl.	+	-	-	-	-
C. ventricosa Kütz.	+	+	+	+	+
Diatoma elongatum Agardh.	+	+	+	+	+
D. anceps (Ehr.) Grunn.	+	-	-	-	-
D. vulgare Bory	+	+	+	+	+
D. vulgare v. *grandis* (Smith) Grun.	+	+	+	+	+
D. vulgare v. *ovalis* (Fricke) Hust.	-	-	-	-	+

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
D. vulgare v. *producta* Grun.	-	-	-	+	+
Epithemia argus Kütz.	+	-	-	-	-
E. sorex Kütz.	+	+	+	+	+
E. turgida (Ehr.) Kütz.	+	+	-	-	-
E. turgida v. *granulata* (Ehr.) Grun.	+	+	+	+	+
E. zebra (Ehr.) Kütz.	-	+	-	-	-
Eunotia lunaris (Ehr.) Grun.	+	-	-	-	-
E. pectinalis v. *minor* (Kütz.) Rabh.	-	-	-	+	-
E. valida Hust.	-	-	-	+	-
Fragilaria capucina Desm.	+	+	+	-	+
F. capucina v. *acuta* Grun.	-	-	-	-	+
F. capucina v. *lanceolata* Grun.	-	-	-	-	+
F. construens (Ehr.) Grun.	+	+	+	-	+
F. construens v. *venter* (Ehr.) Grun.	+	+	+	+	+
F. crotonensis Kitton	-	+✓	+✓	-	-
F. leptostauron (Ehr.) Hust.	-	-	-	-	+
F. pinnata Ehr.	-	-	+	-	+
F. vaucheriae (Kütz.) BoyePet.	-	+	+	-	+
F. virescens v. *capitata* Krasske	-	+	-	+	-
Frustulia rhomboides v. *amphipleuroides* Grun.	-	+	-	-	+
Gomphonema acuminatum Ehr.	+	+	-	-	-
G. acuminatum v. *coronata* (Ehr.) W. Sm.	-	-	+	-	-
G. abbreviatum (Agardh.) Kütz.	+	-	+	-	+
G. angustatum v. *producta* Grun.	-	-	-	-	+
G. bohemicum Reichelt & Fricke	+	+	+	+	+
G. constrictum Ehr.	+	-	-	-	-
G. gracile Ehr.	-	+	-	-	-
G. lanceolatum Ehr.	+	+	+	+	+
G. longipes v. *subclavata* Grun.	-	+	+	-	+

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
G. olivaceum (Lyngb.) Kütz.	+	+	+	+	+
G. olivaceum v. *calcarea* Cl.	-	-	-	-	+
G. parvulum Kütz.	+	+	+	+	+
G. parvulum v. *exilis* Grun.	+	+	+	+	+
G. ventricosum Greg.	+	-	-	-	-
Gyrosigma acuminatum Kütz.	+	+	+	-	+
Hantzschia amphioxys f. *capitata* O. Mull.	-	-	-	+	+
Melosira granulata (Ehr.) Ralfs.	-	-	-	-	+
M. islandica O. Mull.	+	+	+	+	+
M. varians C.A. Agardh.	+	+	+	+	-
Meridion circulare Agardh.	+	+	+	-	+
Navicula bacilliformis Grun.	-	-	-	-	+
N. cryptocephala Kütz.	+	+	+	+	+
N. cuspidata Kütz.	+	+	-	-	+
N. dicephala (Ehr.) W.Sm.	-	-	-	+	-
N. gracilis Ehr.	+	+	-	+	+
N. graciloides A. Meyer	+	+	+	-	+
N. hungarica v. *capitata* (Ehr.) Cl.	-	-	-	-	+
N. lapidosa Krasske	-	-	+	-	-
N. minima v. *atomoides* (Grun.) Cl.	-	-	-	-	+
N. placentula (Ehr.) Grun.	-	+	-	+	+
N. placentula v. *rostrata* A. Meyer	-	-	+	+	+
N. pupula Grun.	+	+	-	-	-
N. pupula v. *rectangularis* (Greg.) Grun.	-	-	+	-	-
N. radiosa Kütz.	+	+	+	+	+
N. rhynchocephala Kütz.	+	+	-	+	-
N. scoliopleuroides Quint	-	-	-	-	+
Neidium affine (Ehr.) Cl.	-	-	-	+	+
N. affine v. *amphirhynchus* (Ehr.) Cl.	-	-	-	+	-

continued ...

Table 2. Continued.

Species	M	SB	HS	MK	E
Nitzschia acicularis W.S.M.	+	-	-	-	-
N. acuta Hantzsh.	-	-	+	-	-
N. amphibia Grun.	+	+	-	-	-
N. clausii Hantzsch.	-	-	-	+	-
N. commutata Grun.	-	+	-	-	-
N. dissipata (Kütz.) Grun.	+	+	+	+	+
N. fonticola Grun.	+	+	-	-	+
N. gracilis Hantzsch.	+	+	+	+	+
N. hantzschiana Rabh.	-	+	-	-	-
N. heurfleriana Grun.	-	-	-	-	+
N. ignorata	-	-	-	-	+
N. palea (Kütz.) W.Sm.	-	+	+	+	+
N. paleacea Grun.	-	-	-	-	+
N. recta Hantzsch.	-	-	+	-	-
N. romana Grun.	-	-	-	-	+
N. sublinearis Hust.	+	-	-	+	-
Opephora martyi Héribaud	-	-	-	-	+
Pinnularia gibba Ehr.	+	-	+	+	-
P. mesolepta (Ehr.) W. Sm.	+	+	+	-	-
P. molaris Grun.	-	-	+	-	-
P. nodosa v. *constricta* Mayer	-	-	-	-	+
P. viridis v. *sudetica* (Hilse) Hust.	-	-	-	+	-
Rhoicosphenia curvata (Kütz.) Grun.	+	+	+	+	+
Rhopalodia gibba (Ehr.) O. Müll.	+	+	+	+	-
R. gibberula (Ehr.) O. Müll.	+	+	+	+	-
R. parallela (Grun.) O. Müll.	-	+	+	+	-
Stauroneis anceps Ehr.	-	-	-	+	-
S. phoenicenteron Ehr.	-	-	-	-	+
S. legumen Ehr.	+	-	-	-	-
Stephanodiscus astraea (Ehr.) Grun.	-	-	+✓	+✓	+✓

continued ...

Table 2. Concluded.

Species	M	SB	HS	MK	E
S. hantzschii Grun.	+✓	+✓	+✓	+	-
Surirella angustata Kütz.	-	-	+	+	+
S. didyma Kütz.	-	-	-	+	-
S. delicatissima Lewis	-	-	-	+	-
Surirella linearis v. *helvetica* (Brun.) Meister	+	-	-	-	-
S. ovalis Bréb.	-	-	-	+	-
S. robusta v. *splendida* (Ehr.) V.H.	-	-	-	+	+
S. tenera Greg.	-	-	-	-	+
Synedra cyclopum Brutschii	-	-	-	-	+
S. capitata Ehr.	+	-	-	-	-
S. pulchella Kütz.	+	+	-	-	-
S. rumpens Kütz.	+	+	-	-	+
S. rumpens v. *familiaris*(Kütz.) Grun.	+	+	-	-	+
S. ulna (Nitzsch.) Ehr.	+	+	+	+	+
Tabellaria fenestrata (Lyngby.) Kütz.	+	+	+	+	+
T. flocculosa (Roth.) Kütz.	+	-	-	-	-

[a] M = Muskeg River
SB = Steepbank River
HS = Hangingstone River
MK = Mackay River
E = Ells River
\+ = present
\- = absent
✓ = phytoplankton

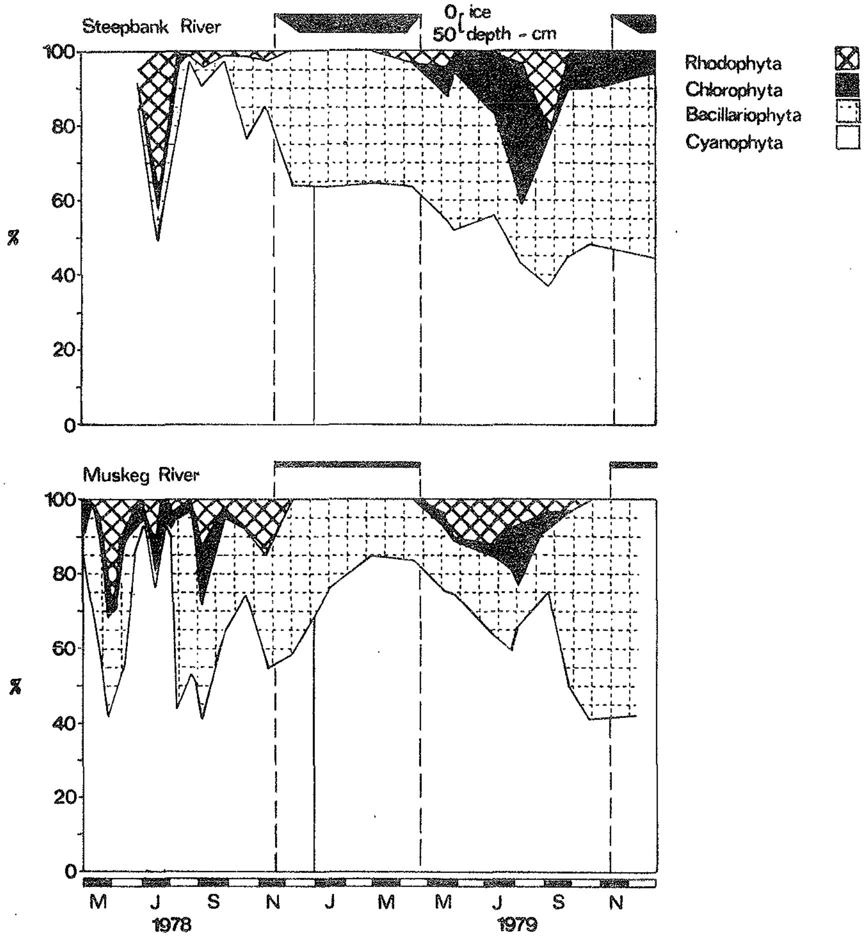

Figure 19. Seasonal changes in the percentage composition of the epilithon in the Steepbank and Muskeg rivers.

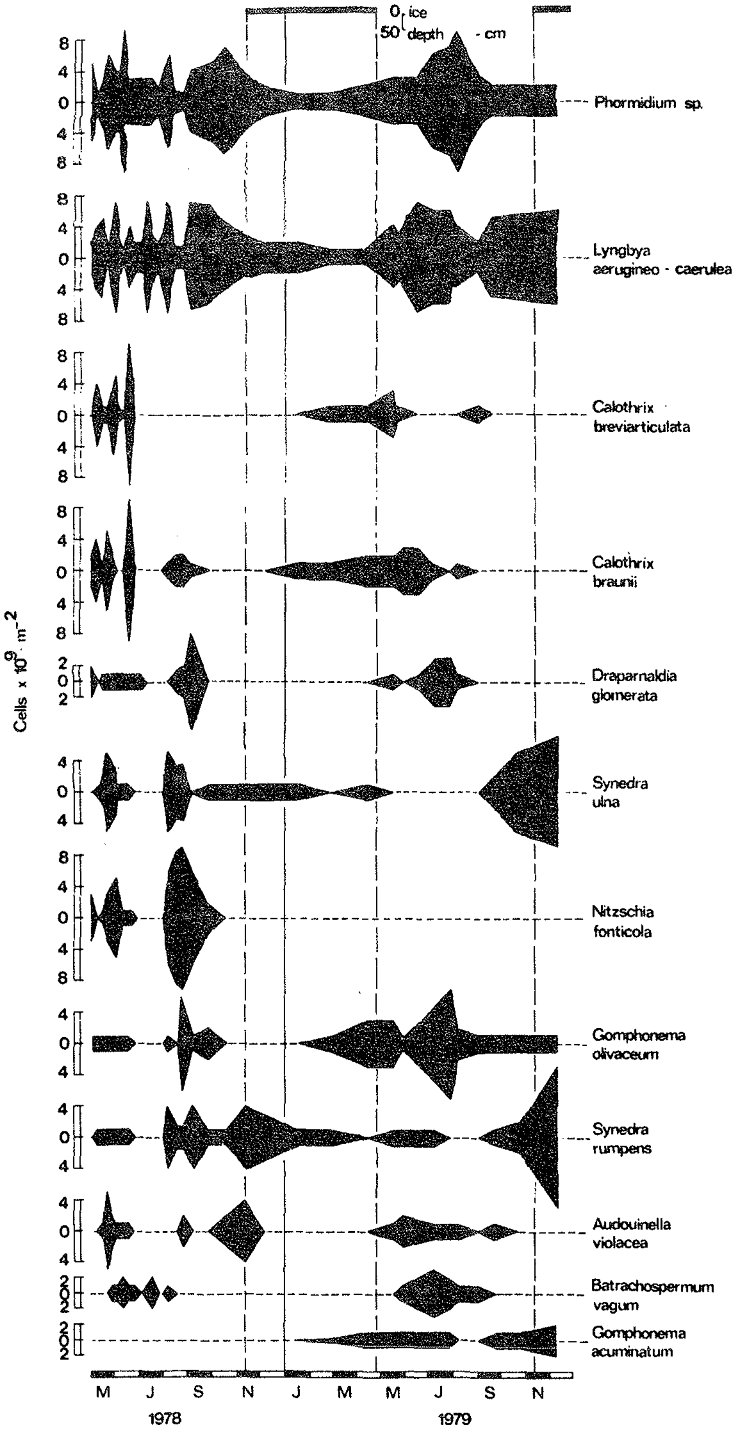

Figure 20. Seasonal succession of the dominant epilithic algae in the Muskeg River.

corresponding to large *Phormidium* and *Lyngbya* populations, further decreases to 41% occurred by mid-October. Diatoms continued to constitute the second major algal group from May to late July 1979 and again from early September until early December when they accounted for 56%. *Gomphonema olivaceum* . particularly, was important from May to late July, while *Synedra ulna* and *Synedra rumpens* dominated from early September onwards. Rhodophycean algae were again present during 1979. *Audouinella violacea* peaked in late May and *Batrachospermum vagum* in mid-July. From May to early July, rhodophycean algae accounted for 10 to 12% of the total populations. Chlorophycean algae were less conspicuous with *Draparnaldia glomerata* the most important species (Figures 19 and 20).

Cyanophycean algae were again dominant in the Steepbank River (Figures 19 and 21) but only from early November 1978 when they accounted for 85% of the total population. They declined in importance during the remainder of 1978 and also in 1979. *Lyngbya aerugineo-caerulea* and *Phormidium* sp. were again the most important cyanophycean algae (Figure 22). However, a large population of *Calothrix braunii* developed during the autumn and early winter of 1978. During 1979, the populations of these three algae never reached the 1978 levels. From a low of 49.5% in mid-July of 1978, the cyanophycean algae attained a peak contribution of 98% by mid-August. In contrast, levels never exceeded 64.7% (March) during 1979, and by early December, they had fallen to 44.5%. During 1978, the rhodophycean algae *Audouinella violacea* and *Batrachospermum vagum* were important, peaking in mid-July (39.3%). Both were present during 1979, contributing slightly less and later in the year (August to September). Diatoms were again important and steadily increased in importance as the cyanophycean algae decreased. *Epithemia sores* was most prevalent during July and late autumn-early winter 1978. *Achnanthes lanceolata* peaked along with *Epithemia* during this latter period. Then, as ice formed, *Nitzschia fonticola* and *Gomphonema olivaceum* peaked. However, all these populations decreased before March when numbers of *Synedra rumpens* increased. Peak diatom contributions during 1978 occurred during October to December averaging 24.3%. Levels were much higher during 1979 reaching 49.8% by early

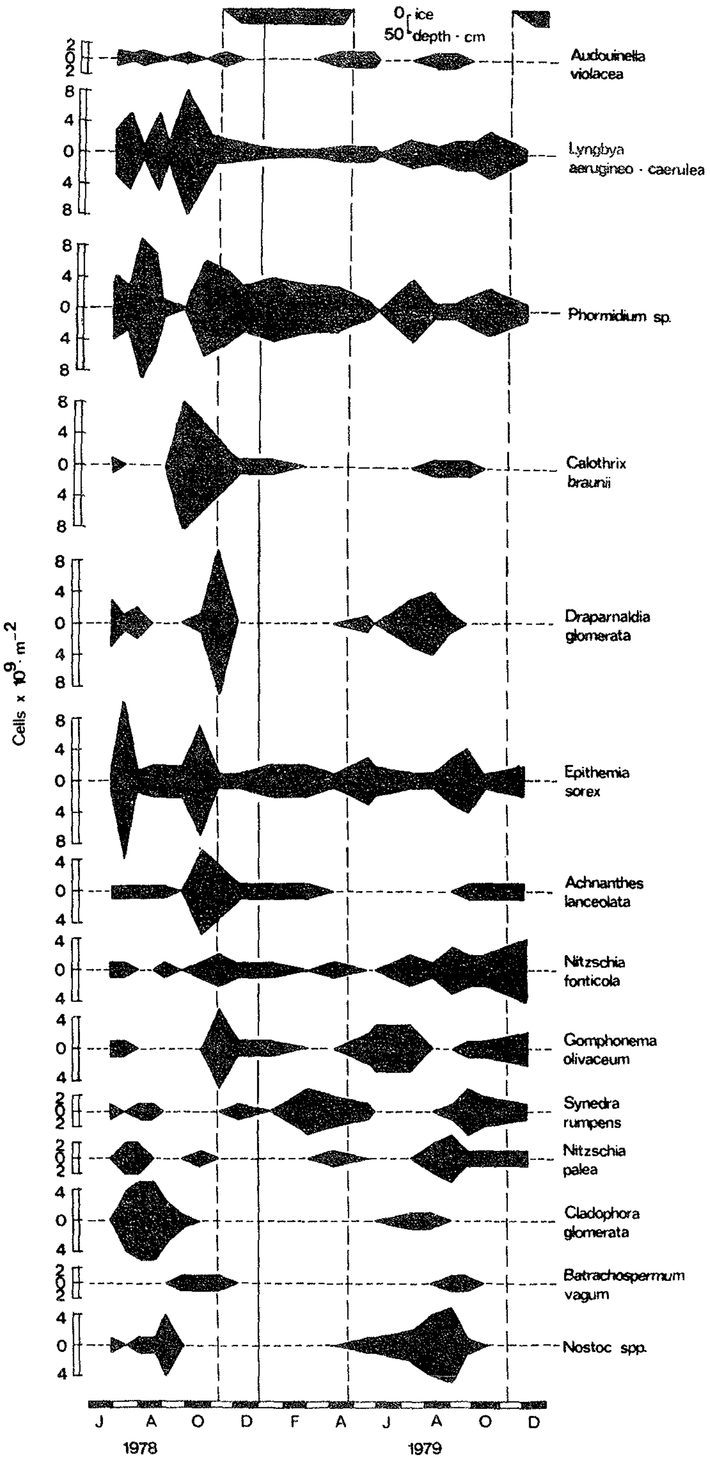

Figure 21. Seasonal succession of the dominant epilithic algae in the Steepbank River.

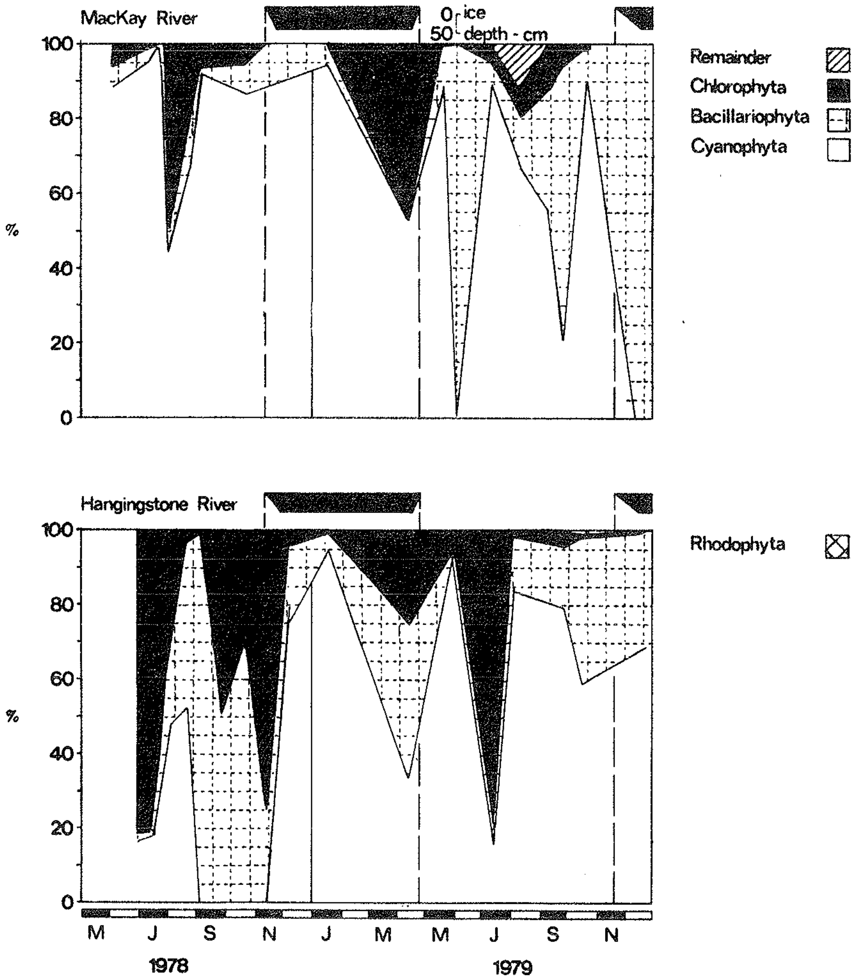

Figure 22. Seasonal changes in percentage composition of the epilithon in the MacKay and Hangingstone rivers.

December. The spring diatom population was dominated by *Epithemia sorex* and *Gomphonema olivaceum*. Then from a low of 15.3% in August, diatom contribution steadily increased as populations of *Epithemia sorex* , *Nitzschia fonticola* , *Gomphonema olivaceum* , *Synedra rumpens* , and *Nitzschia palea* increased in size. Chlorophycean algae were also more prevalent during 1979, particularly from July to August, when large populations of *Draparnaldia glomerata* and *Cladophora glomerata* developed (Figures 19 and 21) contributing 28 to 38%.

The epilithon of the MacKay River was dominated by far fewer algae than the other four rivers (Figure 23). In general, cyanophycean algae were the most important algal group, particularly during 1978. Whereas, during the following year, diatoms assumed far more importance, accounting for 100% on 2 June and 9 December (Figure 22). *Lyngbya aerugineo-caerulea, Calothrix braunii,* and *Anabaena affinis* were the dominant cyanophycean algae (Figure 23); *Cladophora glomerata* and *Chlamydomonas* spp., the dominant chlorophycean algae; and *Epithemia sorex* the dominant diatom. In 1978, the peaks of *Lyngbya* and *Calothrix* coincided in mid-July when cynophycean algae accounted for 99.3% of the total epilithic algal population; whereas, during 1979, only the spring peaks coincided. The summer peak of *Calothrix* occurred in mid-July, while that of *Lyngbya* did not occur until 5 September. At each time, cyanophycean algae accounted for 92.9 and 55.6% of the total population. Chlorophycean algae constituted 47.3% of the total population in early August 1978, corresponding to populations of *Chlamydomonas* spp. and *Cladophora glomerata* . The only other major contribution occurred under ice-cover in April (*Cladophora glomerata*, 47.4%). From here, no one particular chlorophycean algae dominated and as a group they remained small. Diatoms accounted for a far greater proportion of the epilithon during 1979, particularly because of *Epithemia sorex* which had a restricted distribution during 1978. In contrast, it was present in far greater numbers during 1979 on all but one sampling date.

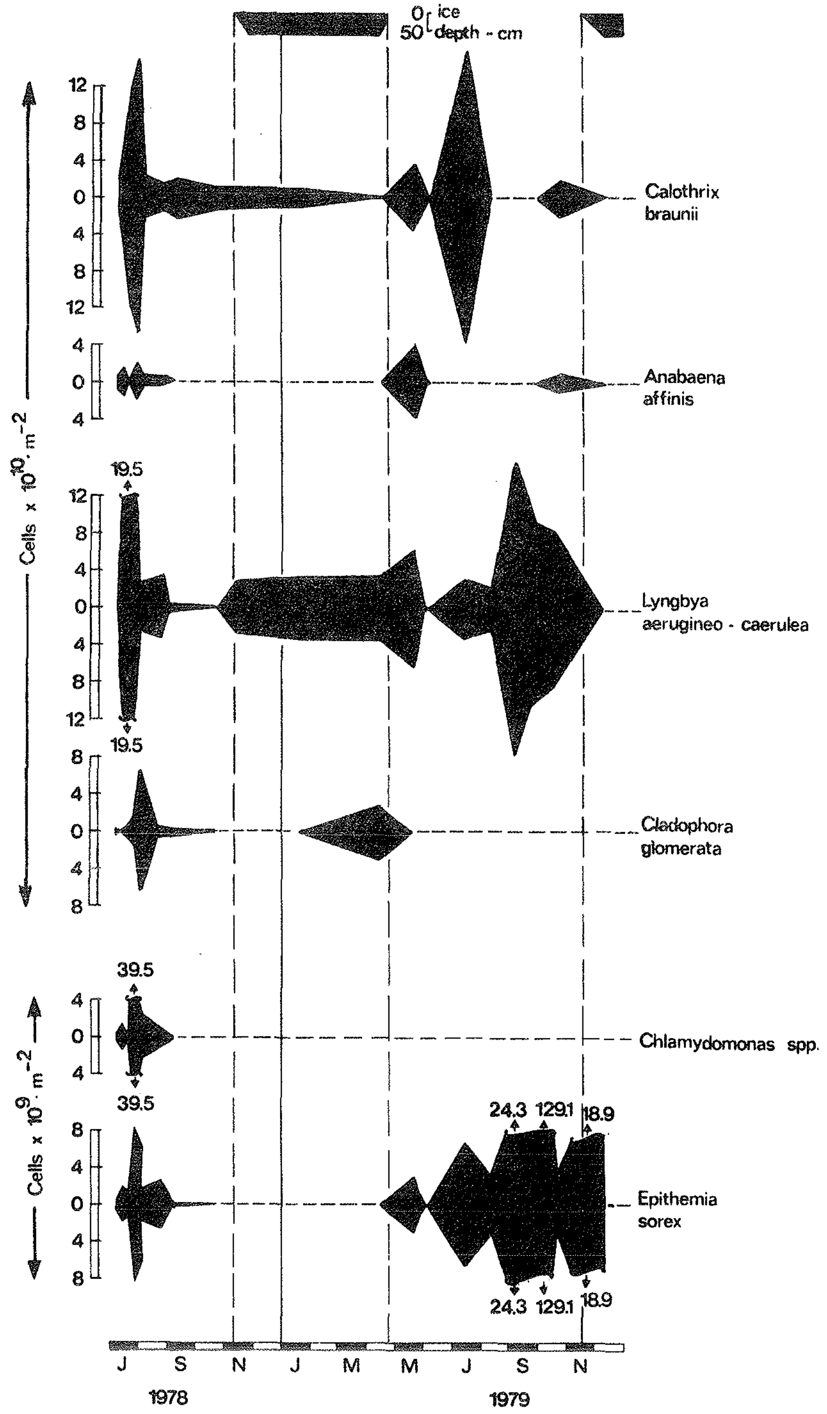

Figure 23. Seasonal succession of the dominant epilithic algae in the MacKay River.

In Hangingstone River, cyanophycean algae were not as important as in the other four rivers during 1978 (Figure 22). Initially, chlorophycean algae accounted for 81% of the total population with *Stigeoclonium pachydermum* being most important (Figure 24). However, after mid-July, this algae was never encountered again. By early August, cyanophycean algae had increased to 47.9% and reached the 1978 maximum of 52.3% at the end of this month. *Anabaena affinis* , *Calothris braunii,* and *Lyngya aerugineo - caerulea* were the dominant cyanophycean algae. From late-August until November, no cyanophycean algae were found. Instead, by early September, diatoms accounted for 98.8% of the total population (mainly *Epithemia turgida*). Thereafter, diatom contribution decreased reaching a low of 4.3% in mid-January. Concomitant with this decrease, chlorophycean algae (mainly *Cladophora glomerata*) increased in importance, and also all cyanophycean algae (from November 1978) when *Anabaena affinis* and *Calothris braunii* reappeared. By mid-April, diatoms were most important (40.3%--mainly *Gomphonema olivaceum* followed by cyanophycean and chlorophycean algae; 33.2 and 26.5%, respectively. However, by the end of May, the cyanophycean algae accounted for 93.9% of the total population when *Lyngbya aerugineo-caerulea* dominated. Chlorophycean algae dominated during July (77.3%--mainly *Chlorella vulgaris*). Thereafter, they were quite insignificant with cyanophycean algae (mainly *Calothrix*) and diatoms (mainly *Epithemia turgida*) dominating.

Cyanophycean algae in the Ells River dominated on all but two occasions (Figures 25 and 26). *Lyngbya aerugineo - caerulea, Calothrix braunii,* and *Anabaena affinis* were the dominant cyanophycean algae. *Lyngbya* was always present, producing its largest populations during autumn 1978 and July 1979; *Calothrix braunii* peaked in April and July 1979, although, like *Anabaena affinis,* smaller populations were present during 1978 with a small peak occurring in September; and *Anabaena* peaked in July and late September 1979.

On those two occasions that cyanophycean algae did not dominate, late June 1978 and early August in 1978 and 1979, respectively, diatoms and chlorophycean algae dominated. In late June 1978, *Synedra ulna, Synedra rumpens, Cocconeis placentula, Cocconeis pediculus, Gomphonema olivaceum,* and *Gomphonema longipes* v. *subclavata*

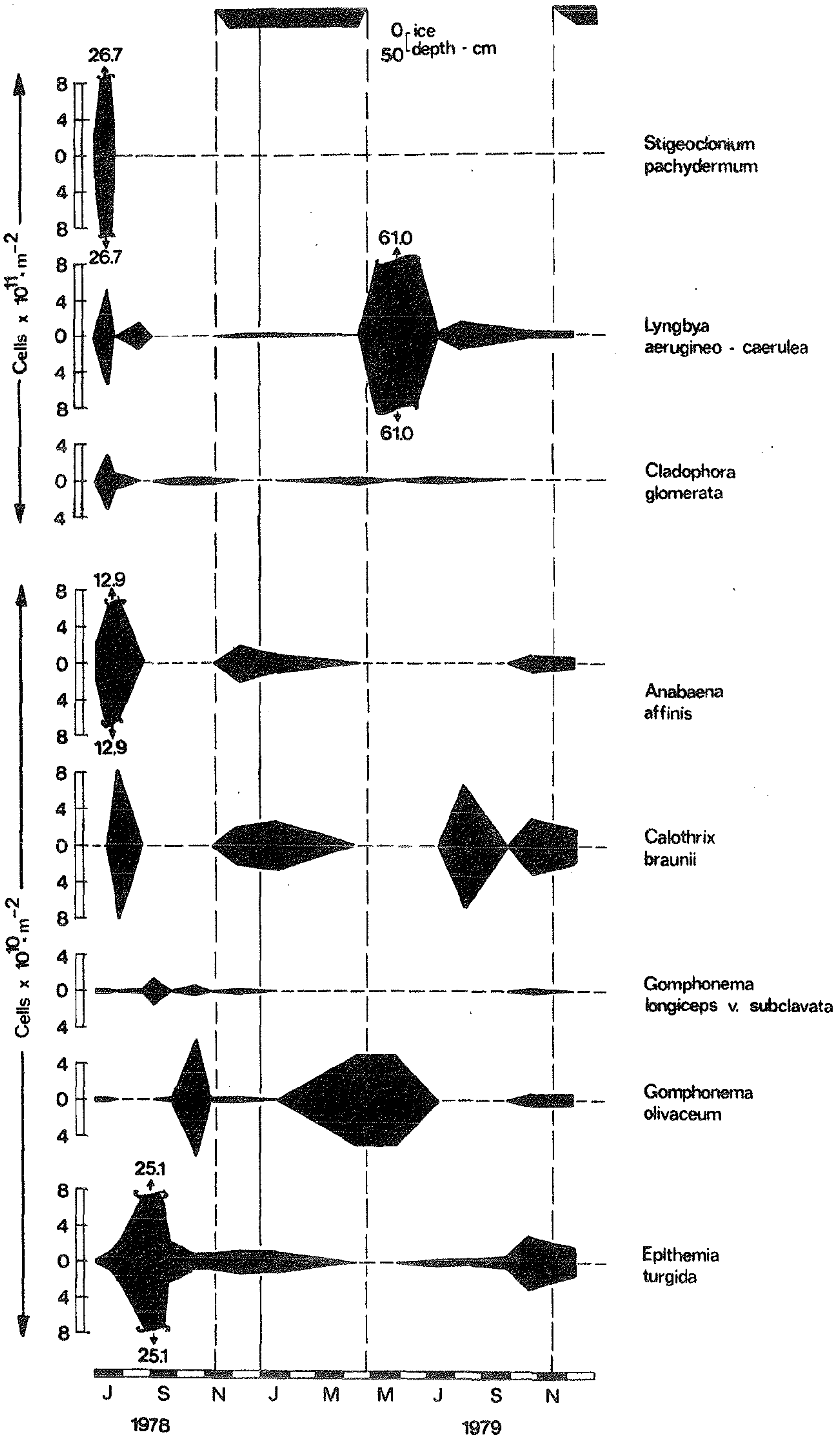

Figure 24. Seasonal succession of the dominant epilithic algae in the Hangingstone River.

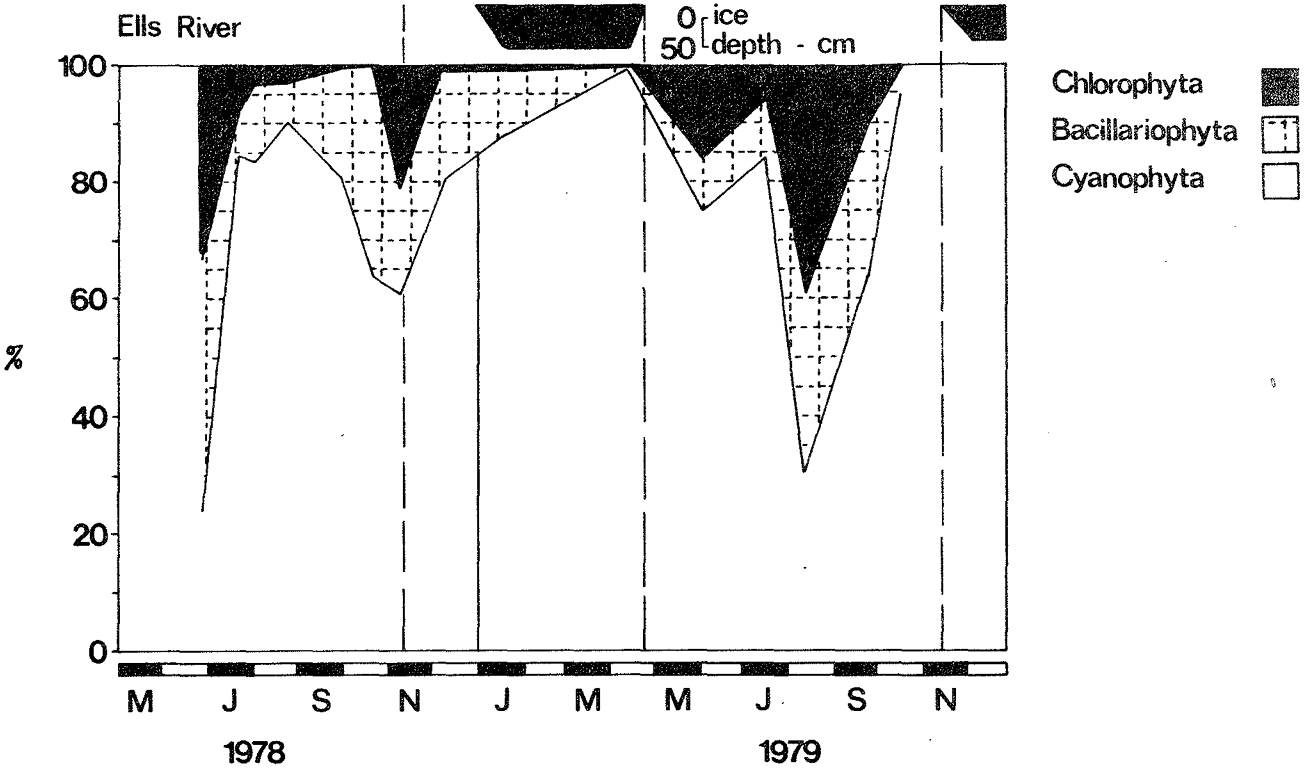

Figure 25. Seasonal changes in the percentage composition of the epilithon in the Ells River.

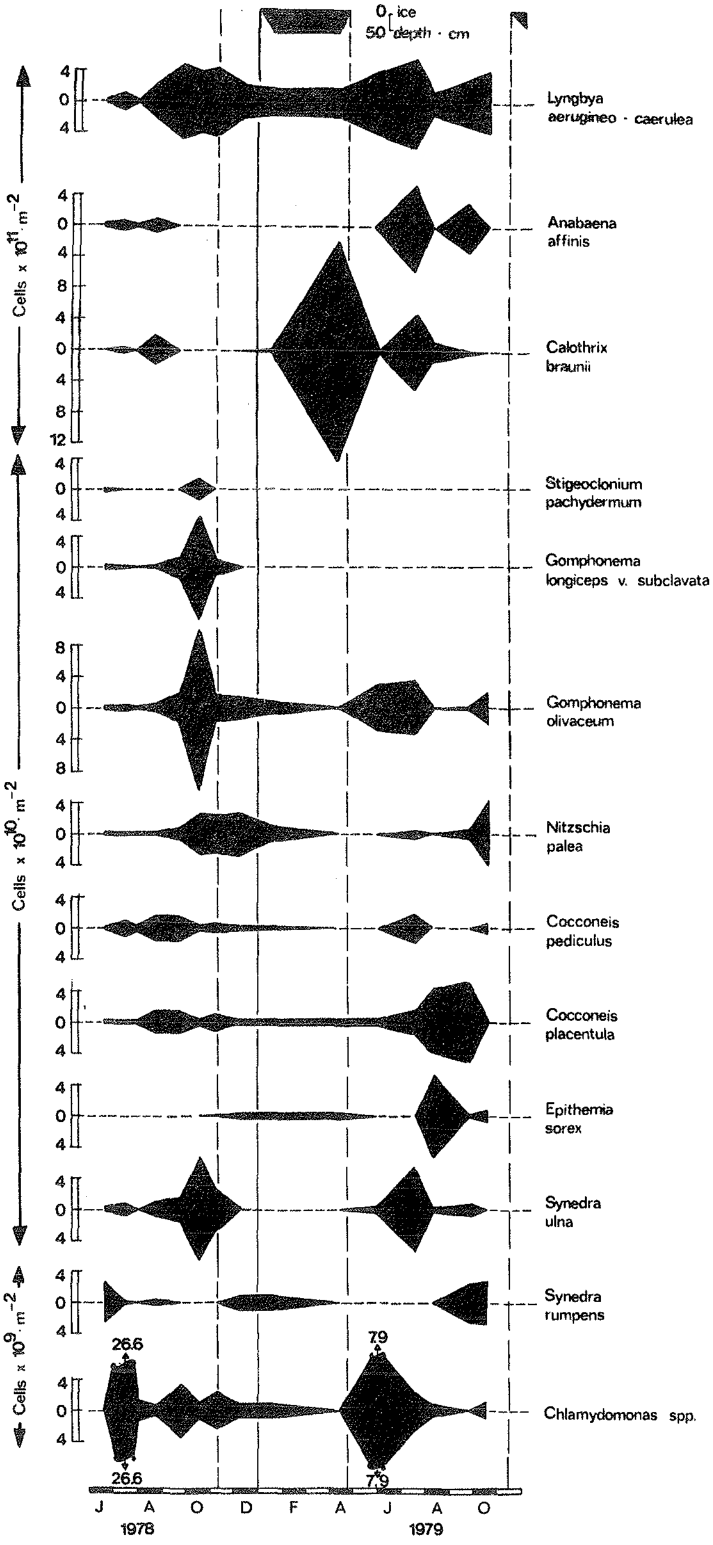

Figure 26. Seasonal succession of the dominant epilithic algae in the Ells River.

were all present (Figure 26); in August 1979, *Epithemia sorex* and *Cocconeis placentula* were the dominant diatoms. In both instances, the dominant chlorophycean algae were *Chlamydomonas* spp.

4.4 CELL NUMBERS

In the Muskeg River, total cells peaked in the spring and autumn of 1978, but in 1979, a summer peak in July occurred between a much smaller spring and larger autumn peaks (Figure 27). The dominant species during these peaks are shown in Table 3. The species composition was very similar in the spring and autumn maxima of both years. However, *Nitzschia fonticola* and *Synedra ulna* were not present in the 1979 spring peak, and *Batrachospermum vagum* and *Gomphonema olivaceum*, present in spring 1979, were not in 1978. Similarly, *Draparnaldia glomerata*, *Nitzschia fonticola*, and *Gomphonema olivaceum*, present in the 1978 autumn peak, were not in 1979. Instead, both *Draparnaldia glomerata* and *Gomphonema olivaceum* were present during the summer maximum of 1979. *Gomphonema acuminatum* contributed significantly only in autumn 1979. Cyanophycean algae were almost always most numerous (Figure 27). Exceptions occurred during the autumn each year. Diatoms comprised the next most numerous group followed by chlorophycean and rhodophycean algae for the Muskeg River are present in Table 4.

During 1978, in the Steepbank River, a small summer peak followed by a late autumn peak occurred (Figure 28). Populations remained high during the winter, decreasing only slightly in early March 1979. This winter population was dominated by *Phormidium* sp., *Epithemia sorex*, and *Synedra rumpens* (Table 5). A small spring peak was apparent in 1979 followed by larger summer and winter peaks. Again, species composition was very similar at the maxima each year, although in spring 1979, *Phormidium* sp. was not as prevalent as in 1978 and the two diatoms *Gomphonema olivaceum* and *Synedra rumpens* were important only in 1979. Also, four species not found in the 1978 summer peak occurred in 1979, along with the four species, found in 1978, namely *Draparnaldia glomerata*, *Nitzschia palea*, *Nostoc* spp. and *Gomphonema olivaceum*. *Draparnaldia glomerata* also occurred during the autumn peak in 1978. Only this species and *Calothrix braunii* were absent from the 1979 autumn peak.

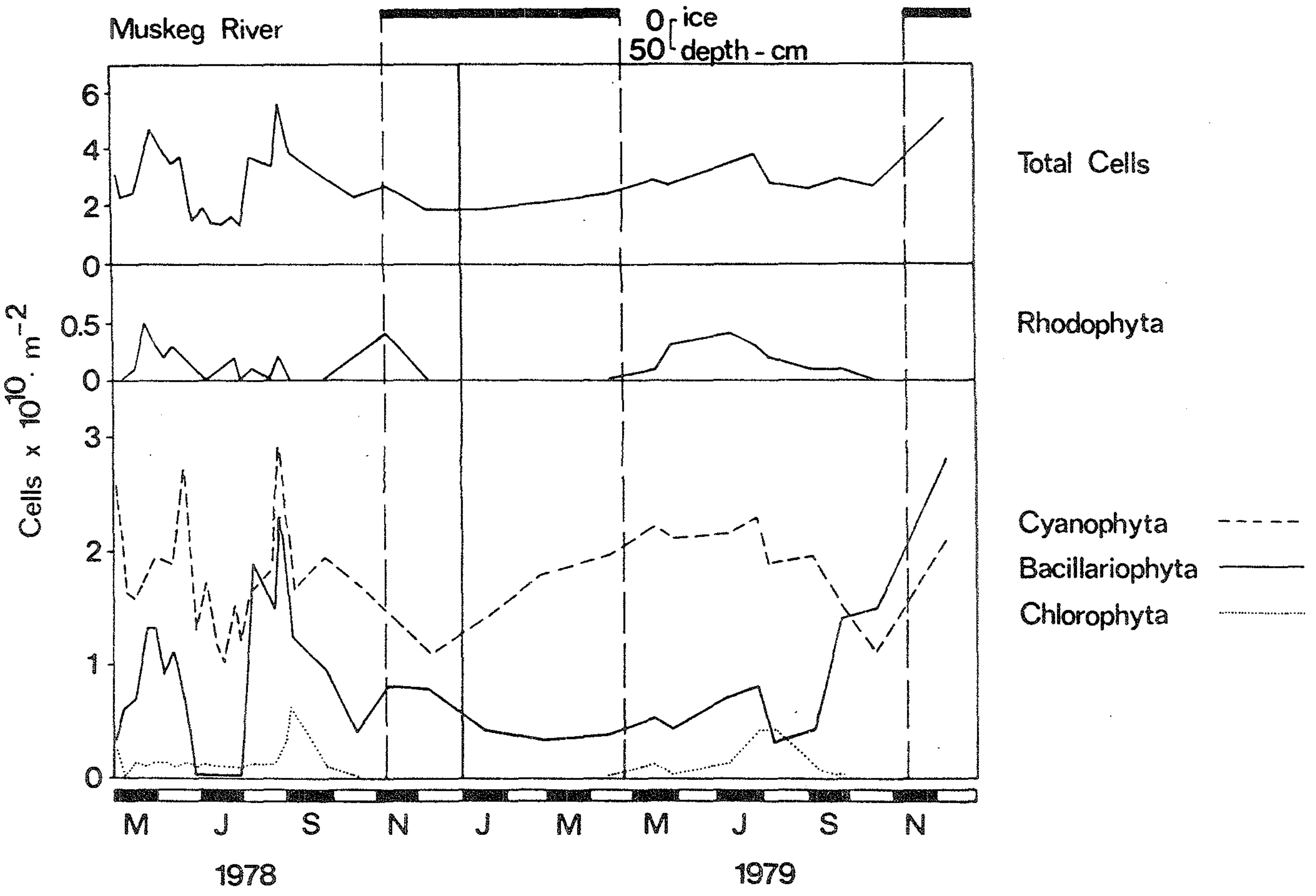

Figure 27. Seasonal changes in total cells, Cyanophyta, Bacillariophyta, Chlorophyta, and Rhodophyta in the Muskeg River.

Table 3. The algae dominant during the spring, summer, and autumn cell number peaks in the Muskeg River.

Year	Maximum		
	Spring	Summer	Autumn
1978	*Phormidium* sp.	no maximum	*Phormidium* sp.
	Lyngbya aerugineo-caerulea		*Lyngbya aerugineo-caerulea*
	Calothrix breviarticulata		*Calothrix braunii*
	Calothrix braunii		*Draparnaldia glomerata*
	Synedra ulna		*Synedra ulna*
	Nitzschia fonticola		*Nitzschia fonticola*
	Audouinella violacea		*Gomphonema olivaceum*
1979	*Phormidium* sp.	*Phormidium* sp.	*Lyngbya aerugineo-caerulea*
	Lyngbya aerugineo-caerulea	*Lyngbya aerugineo-caerulea*	*Synedra ulna*
	Calothrix breviarticulata	*Draparnaldia glomerata*	*Synedra rumpens*
	Calothrix braunii	*Gomphonema olivaceum*	*Gomphonema acuminatum*
	Gomphonema olivaceum	*Batrachospermum vagum*	*Phormidium* sp.
	Audouinella violacea		
	Batrachospermum vagum		

Table 4. Mean and range of the total cells, diatoms, and cyanophycean, chlorophycean, and rhodophycean algae in the Muskeg River for the study period.

	Range (cells x 10^{10} m^{-2})	Mean (cells x 10^{10} m^{-2})
Total cells	1.30 to 5.63	2.90
Cyanophyta	1.02 to 2.90	1.78
Bacillariophyta	0.01 to 2.30	0.79
Chlorophyta	0 to 0.61	0.12
Rhodophyta	0 to 0.50	0.13

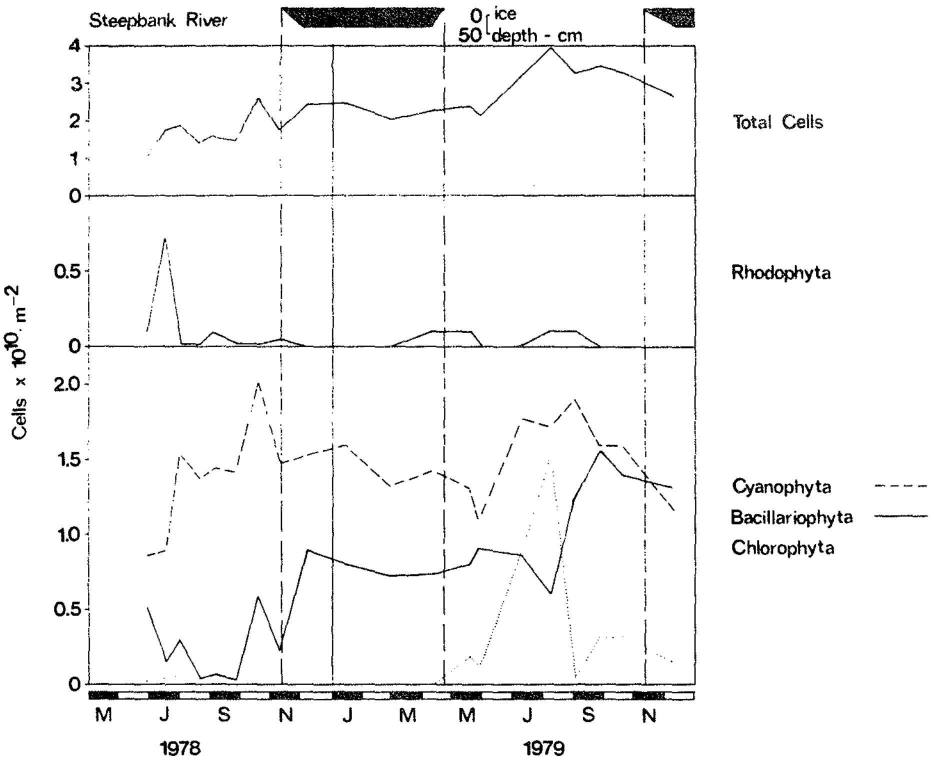

Figure 28. Seasonal changes in total cells, Cyanophyta, Bacillariophyta, Chlorophyta, and Rhodophyta in the Steepbank River.

Table 5. The algae dominant during the spring, summer, and autumn cell number peaks in the Steepbank River.

Year	Maximum		
	Spring	Summer	Autumn
1978	*Lyngbya aerugineo-caerulea*	*Lyngbya aerugineo-caerulea*	*Lyngbya aerugineo-caerulea*
	Epithemia sorex	*Phormidium* sp.	*Phormidium* sp.
	Phormidium sp.	*Cladophora glomerata*	*Calothrix braunii*
		Epithemia sorex	*Draparnaldia glomerata*
		Draparnaldia glomerata	*Epithemia sorex*
			Achnanthes lanceolata
			Gomphonema olivaceum
			Nitzschia fonticola
1979	*Epithemia sorex*	*Lyngbya aerugineo-caerulea*	*Lyngbya aerugineo-caerulea*
	Lyngbya aerugineo-caerulea	*Draparnaldia glomerata*	*Phormidium* sp.
	Gomphonema olivaceum	*Epithemia sorex*	*Epithemia sorex*
	Synedra rumpens	*Nitzschia palea*	*Nitzschia fonticola*
		Nostoc spp.	*Synedra rumpens*
		Gomphonema olivaceum	*Achnanthes lanceolata*
		Cladophora glomerata	*Gomphonema olivaceum*

Cyanophycean algae were always most numerous except in early December 1979 (Figure 28; Table 6), followed by diatoms. Only during mid-summer 1979 did very large chlorophycean populations develop. The largest rhodophycean population occurred in July 1978 when *Audouinella violacea* was present.

Quantitative sampling on the MacKay River did not commence until after the spring peak in 1978. However, a large summer maximum occurred (Figure 29) comprising cyanophycean algae (Table 7) along with smaller populations of chlorophycean algae and diatoms. Cyanophycean algae were invariably the most numerous group followed by diatoms and then chlorophycean algae. No autumn maximum occurred during 1978 but in 1979, spring, summer, and autumn peaks appeared, slightly larger than the former. However, none approached the size of the 1978 summer peak. Little change occurred in the dominant of these peaks (Table 8) and diatoms along with cyanophycean algae became very important during autumn 1979 with massive populations of *Epithemia sorex* developing.

Again, quantitative sampling on the Hangingstone River in 1978 did not commence until after the spring peak and, as in the MacKay River, a large summer peak was present followed by a much smaller autumn one. The spring and summer peaks merged in 1979 and the autumn one was very tiny (Figure 30). Species composition during the peaks was again similar from year to year. However, *Stigeoclonium pachyderma* was found only during July 1978, and *Gomphonema olivaceum*, dominant during autumn 1978 as well as during the merged spring/summer maximum of 1979, formed only a small population during autumn 1979 (Table 9; Figure 30). Cyanophycean algae were again numerically dominant but, unlike the other four rivers, the second most numerous group were chlorophycean algae followed by diatoms (Table 10).

The 1978 summer peak and the 1979 maximum in the Ells River were small compared to the other rivers. However, the autumn maxima were of comparable size (Figure 31). Cyanophycean algae were predominant with *Lynbya aerugineo-caerulea* dominant all the time (Table 11). In this river, more diatom species contributed significantly than in the other four (Table 12). *Lyngbya* was the

Table 6. Mean and range of the total cells, diatoms, and cyanophycean, chlorophycean, and rhodophycean algae in the Steepbank River for the study period.

	Range	Mean
	(cells x 10^{10} m^{-2})	
Total cells	1.02 to 3.93	2.36
Cyanophyta	0.86 to 2.00	1.45
Bacillariophyta	0.03 to 1.55	0.66
Chlorophyta	0 to 1.51	0.18
Rhodophyta	0 to 0.70	0.07

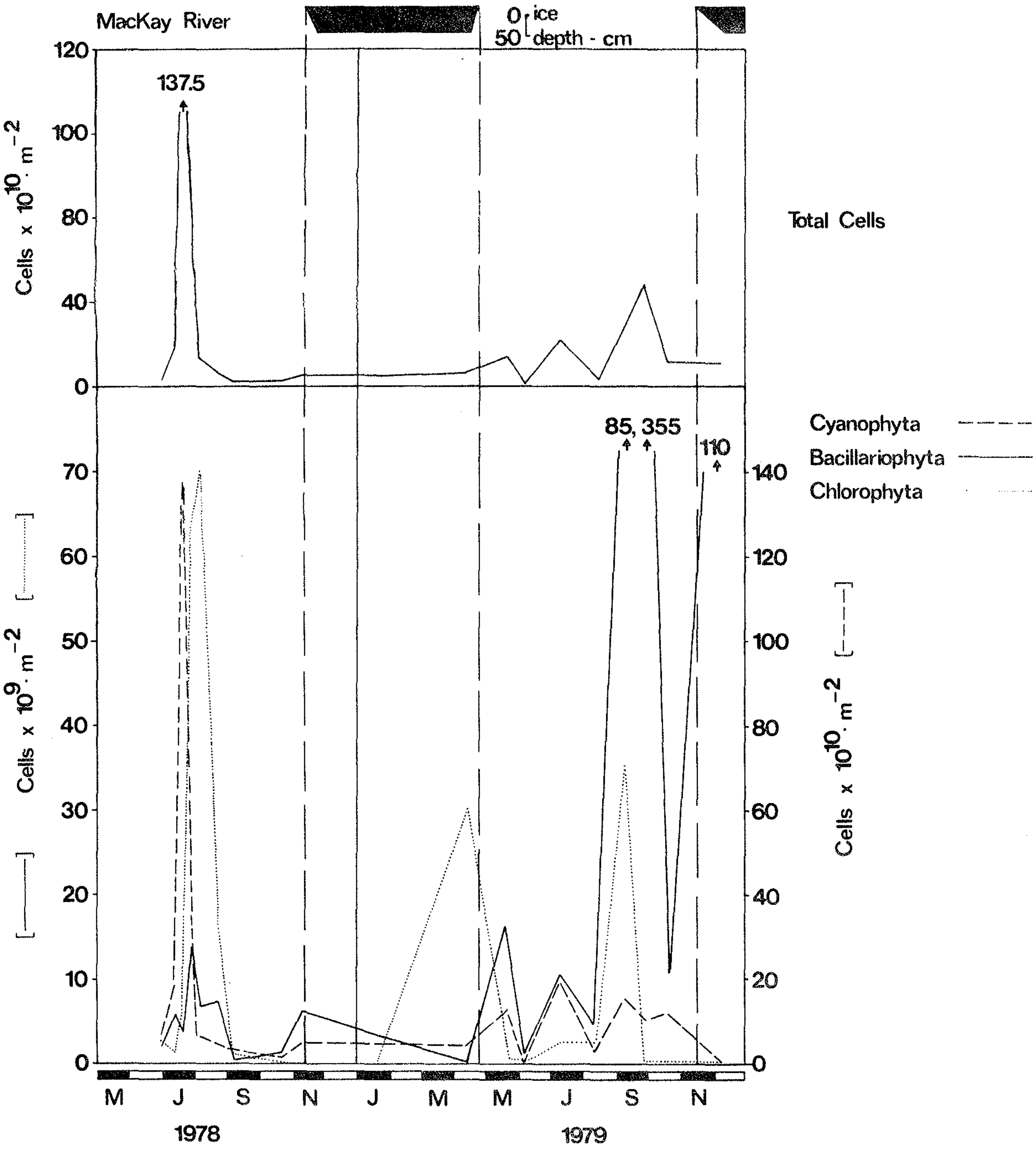

Figure 29. Seasonal changes in total cells, Cyanophyta, Bacillariophyta, and Chlorophyta in the MacKay River.

Table 7. Mean and range of the total cells, diatoms, and cyanophycean and chlorophycean algae in the MacKay River.

	Range	Mean
	(cells x 10^{10} m^{-2})	
Total cells	0.10 to 137.50	20.30
Cyanophyta	0 to 136.50	15.40
Bacillariophyta	0 to 35.50	3.39
Chlorophyta	0 to 7.05	1.38

Table 8. The algae dominant during the spring, summer, and autumn cell number peaks in the MacKay River.

Year	Maximum		
	Spring	Summer	Autumn
1978	Not sampled	*Calothrix braunii* *Lyngbya aerugineo-caerulea* *Cladophora glomerata* *Chlamydomonas* spp. *Epithemia sorex*	No maximum
1979	*Calothrix braunii* *Anabaena affinis* *Lyngbya aerugineo-caerulea* *Epithemia sorex*	*Lyngbya aerugineo-caerulea* *Calothrix braunii* *Epithemia sorex*	*Lyngbya aerugineo-caerulea* *Epithemia sorex*

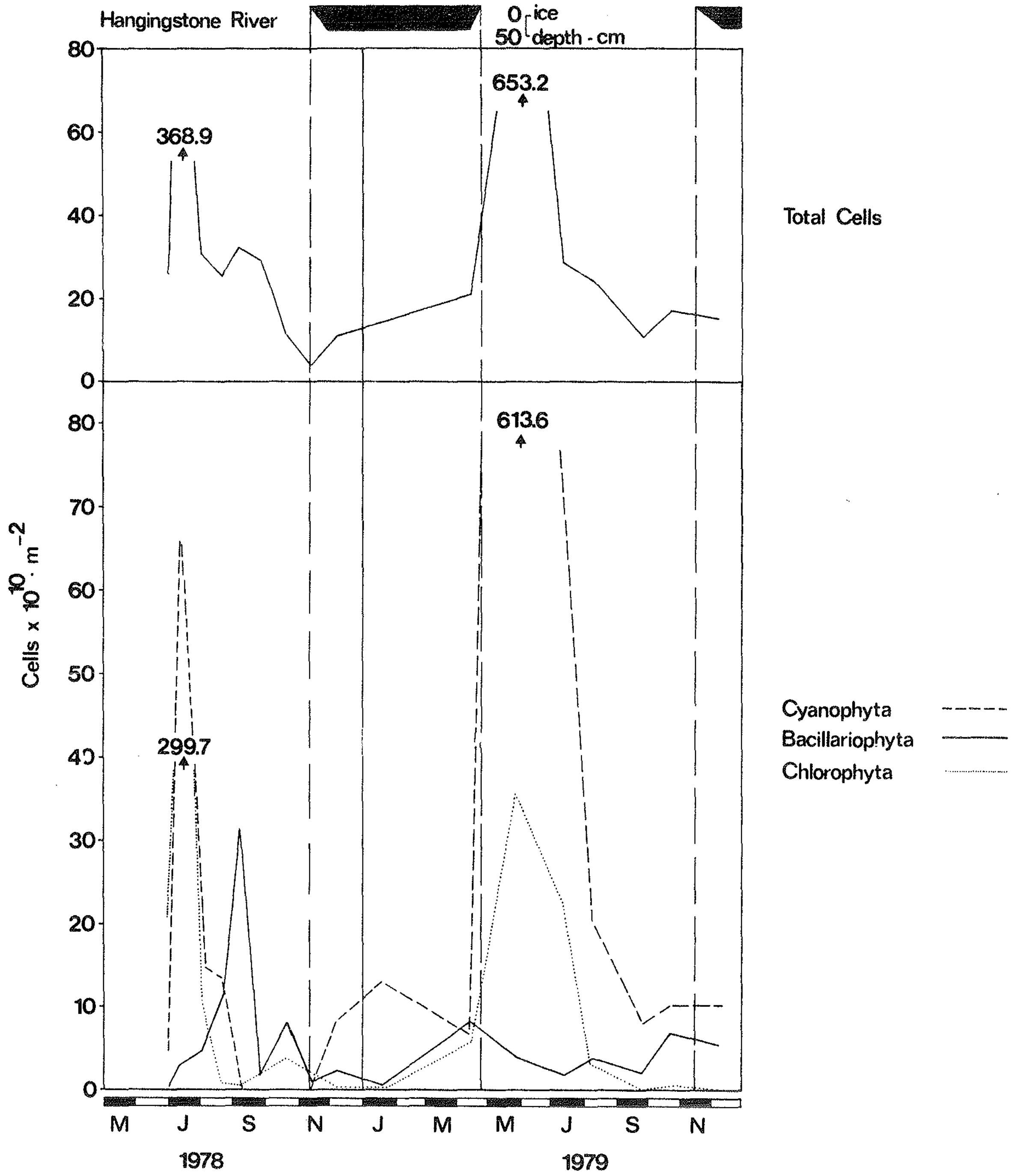

Figure 30. Seasonal changes in total cells, Cyanophyta, Bacillariophyta, and Chlorophyta in the Hangingstone River.

Table 9. The algae dominant during the spring, summer, and autumn cell number peaks in the Hangingstone River.

Year	Maximum		
	Spring	Summer	Autumn
1978	Not sampled	*Stigeoclonium pachydermum*	*Epithemia turgida*
		Lyngbya aerugineo-caerulea	*Gomphonema olivaceum*
		Cladophora glomerata	
		Anabaena affinis	
		Calothrix braunii	
1979	Spring and summer		
	Lyngbya aerugineo-caerulea		*Calothrix braunii*
	Calothrix braunii		*Epithemia turgida*
	Gomphonema olivaceum		

Table 10. Mean and range of the total cells, diatoms, and cyanophycean and chlorophycean algae in the Hangingstone River.

	Range	Mean
	(cells x 10^{10} m^{-2})	
Total cells	29.00 to 653.16	75.80
Cyanophyta	0 to 613.57	46.70
Bacillariophyta	0.30 to 31.50	5.64
Chlorophyta	0 to 299.70	23.80

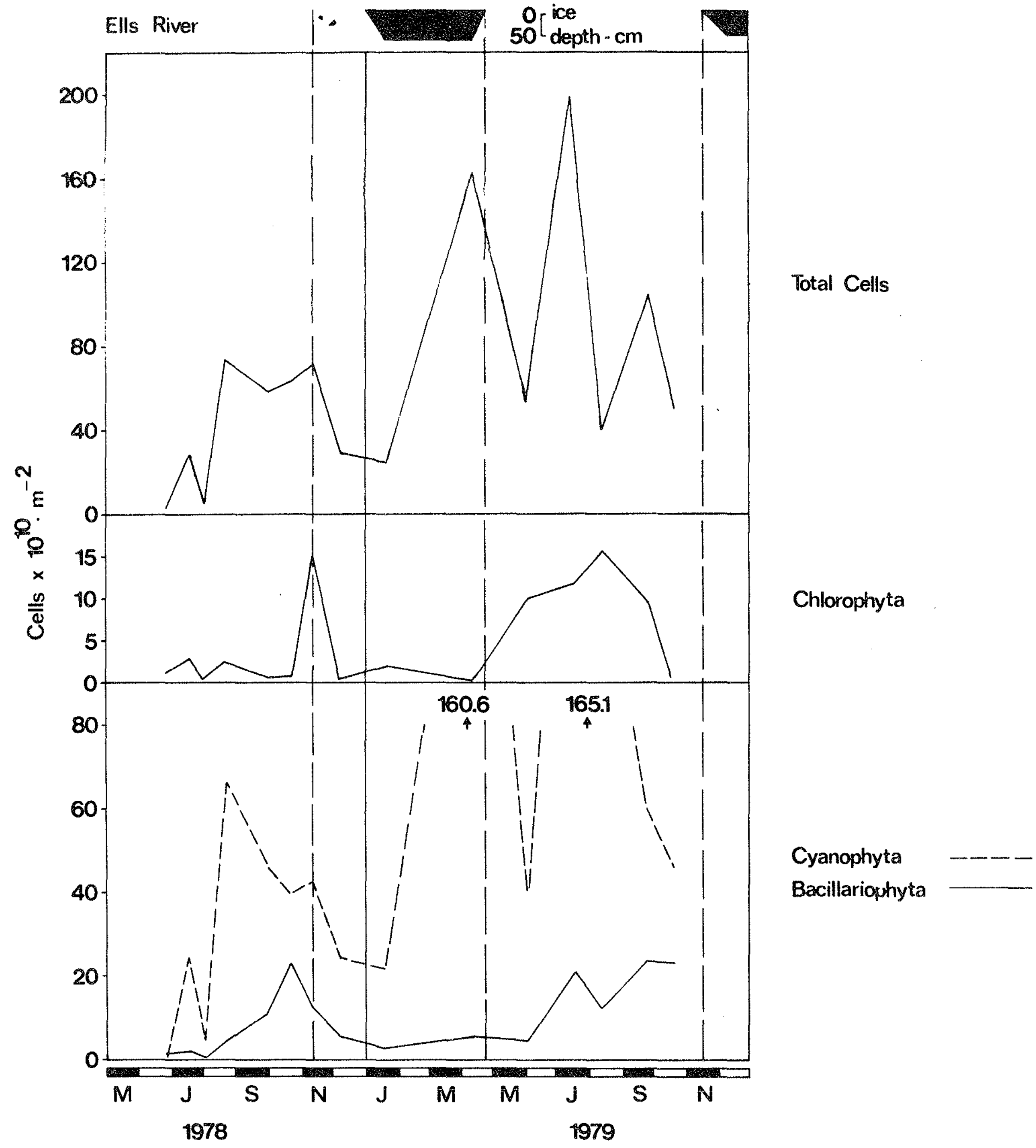

Figure 31. Seasonal changes in the total cells, Cyanophyta, Bacillariophyta, and Chlorophyta in the Ells River.

Table 11. The algae dominant during the spring, summer, and autumn cell number peaks in the Ells River.

Year	Maximum		
	Spring	Summer	Autumn
1978	Not sampled	*Lyngbya aerugineo-caerulea* *Anabaena affinis* *Cocconeis pediculus* *Synedra rumpens* *Chlamydomonas* spp.	*Lyngbya aerugineo-caerulea* *Stigeoclonium pachydermum* *Gomphonema longiceps* v. *subclavata* *Gomphonema olivaceum* *Cocconeis pediculus* *Cocconeis placentula* *Synedra ulna* *Chlamydomonas* spp.
1979	*Lyngbya aerugineo-caerulea* *Calothrix braunii* *Gomphonema olivaceum*	*Lyngbya aerugineo-caerulea* *Anabaena affinis* *Calothrix braunii* *Gomphonema olivaceum* *Synedra ulna*	*Lyngbya aerugineo-caerulea* *Gomphonema olivaceum* *Nitzschia palea* *Cocconeis placentula* *Epithemia sorex* *Synedra rumpens*

Table 12. Mean and range of the total cells, diatoms, and cyanophycean and chlorophycean algae in the Ells River.

	Range (cells x 10^{10} m^{-2})	Mean
Total cells	3.70 to 197.70	63.8
Cyanophyta	0.90 to 165.12	50.7
Bacillariophyta	0.51 to 23.98	8.50
Chlorophyta	0 to 15.49	4.60

dominant cyanophycean algae in the summer of 1978; whereas it, along with *Anabaena affinis* and *Calothris braunii*, were the dominants in 1979. Two diatoms, *Gomphonema olivaceum* and *Synedra ulna*, were also present in 1979 whereas *Synedra rumpens* had been in 1978. The autumn peaks comprised many diatom species some of which occurred both years (Table 11). However, only in 1978 was *Stigeoclonium pachyderma* found. Cyanophycean algae on average dominated followed by diatoms and chlorophycean algae (Figure 31).

On average, therefore, cyanophycean algae were numerically the dominant algal group in all five rivers followed by diatoms, except in the Hangingstone River, where they were superseded by chlorophycean algae (Table 13). Largest mean populations occurred in the Hangingstone and Ells rivers and the smallest in the Muskeg and Steepbank rivers.

4.5 CHLOROPHYLL *a*

Seasonal fluctuations in the epilithic standing crop as measured by chlorophyll *a* content are shown in Figure 32. They basically follow the cell count data from the spring, summer and autumn peaks. However, the timing and size did not always correspond. In the Muskeg River during 1978, chlorophyll *a* concentrations fluctuated more than during 1979, showing both spring and autumn maxima, but unlike cell counts, a summer one as well. The spring peak, like cell counts, was small in 1979 with the standing crop rising to a maximum in early December (Figure 32). A summer/autumn chlorophyll peak was evident in the Steepbank River while a massive peak (229.8 mg m^{-2} chlorophyll *a*) occurred in early December 1978. Then, during 1979, no spring peak was evident. However, small summer and autumn maxima did occur (Figure 32). Standing crop values in the MacKay River were lower than the other four rivers again showing a summer peak and, like cell counts, no autumn one in 1978. However, as in the Muskeg, Steepbank, and Hangingstone rivers, a peak occurred in early December 1978 under ice-cover. Then, in 1979, only an autumn chlorophyll maximum, although very small occurred. The standing crop in the Hangingstone River was identical to the Steepbank

Table 13. Mean cell numbers for each algal group in the five rivers.

	Rivers				
Cells x 10^{10} m^{-2}	Muskeg	Steepbank	MacKay	Hangingstone	Ells
Cyanophyta	1.78	1.45	15.40	46.70	50.7
Bacillariophyta	0.79	0.66	3.39	5.64	8.50
Chlorophyta	0.12	0.18	1.38	23.80	4.60
Rhodophyta	0.13	0.07	-	-	-
Total Cells	2.90	2.36	20.30	75.80	63.8

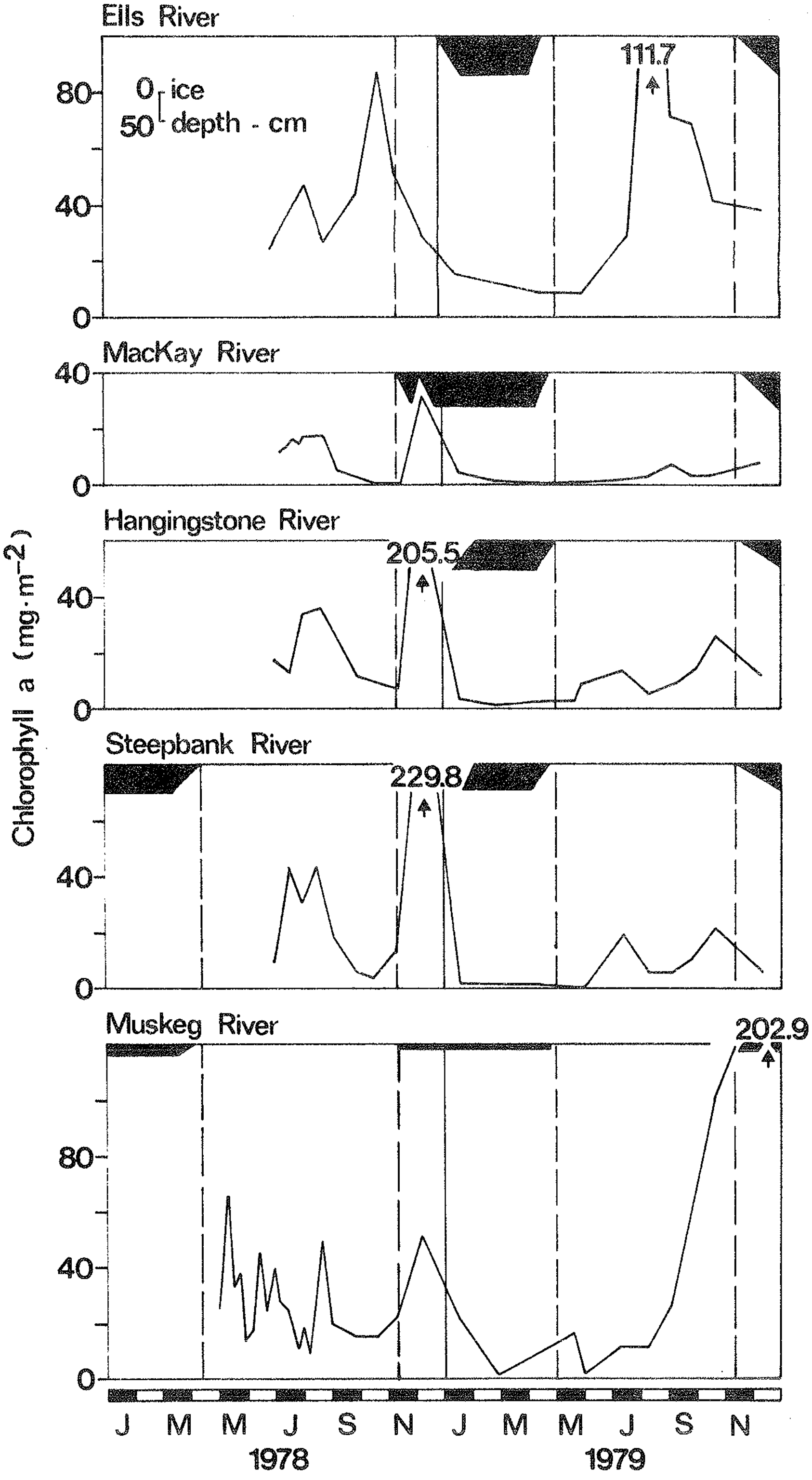

Figure 32. Seasonal fluctuations in epilithic algal standing crop, as measured by chlorophyll *a* content, in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

River while that in the Ells River showed a small summer and larger autumn peak, paralleling cell numbers, but no early spring maximum. Instead, growth culminated in a large summer maximum in August 1979.

The mean and range of the epilithic algal standing crop as measured by chlorophyll *a* content are presented in Table 14. The largest mean standing crop occurred in the Ells River followed by the Muskeg River, with those of the Steepbank and Hangingstone rivers next, while the smallest mean standing crop occurred in the MacKay River. This is a different sequence than found with cell numbers but reflects the two different measures of estimating standing crop size.

The plankton of these rivers was dominated by a mixture of non-epilithic and senescing epilithic algae. Standing crop fluctuations were more irregular than those of the epilithon but still showed spring, summer, and autumn peaks as well as some winter ones (e.g., Ells, MacKay, and Hangingstone rivers) shown in Figure 33. The range and mean values are presented in Table 15.

4.6 PRIMARY PRODUCTIVITY

Seasonal primary productivity fluctuations are illustrated in Figure 34. They are more variable than those for standing crop. However, summer maxima occurred in all rivers but spring and autumn maxima did not occur consistently except in the Muskeg River. Interestingly, winter peaks occurred under ice and snow cover in January 1979 in the Hangingstone and MacKay rivers, in March in the Muskeg and Stepbank rivers, and in late April in the Ells and MacKay rivers. Generally, maximum productivity occurred during the summer months. Again, an exception was the Muskeg River in 1978.

Since a section of the Muskeg River bed was artificially shaded, simultaneous experiments were performed underneath as well as in situ. On average, the shading resulted in an approximate halving of the primary productivity, thus illustrating the importance of irradiance in controlling primary productivity (Table 16). A comparison between algal primary productivity at the edge and at a mid-stream site revealed no overall difference when mean values were examined. The results were variable with significant differences favouring the edge station occurring only on four occasions in the Muskeg River

Table 14. Range and mean standing crop of the epilithon as measured by chlorophyll *a* content.

River	Chlorophyll *a* ($mg \cdot m^{-2}$) Range	Mean
Muskeg	1.33 to 202.95	30.46
Steepbank	0 to 229.84	22.99
MacKay	0.11 to 30.66	7.94
Hangingstone	1.42 to 205.46	22.35
Ells	8.38 to 111.72	43.23

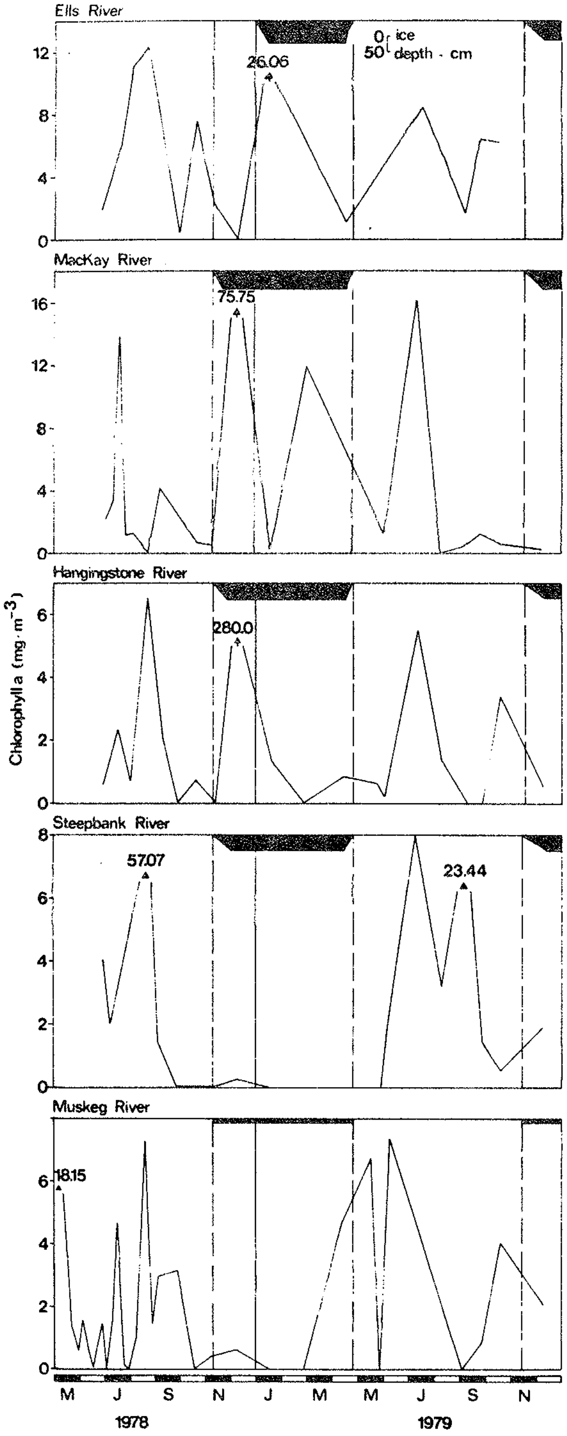

Figure 33. Standing crop, as measured by chlorophyll *a* content, of the planktonic algae in the Ells, MacKay, Steepbank, and Muskeg rivers.

Table 15. Range and mean standing crop of the plankton as measured by chlorophyll *a* content.

River	Chlorophyll *a* ($mg \cdot m^{-3}$) Range	Mean
Muskeg	0 to 18.15	2.93
Steepbank	0 to 57.07	5.42
MacKay	0 to 75.75	7.12
Hangingstone	0 to 280.00	15.11
Ells	0.01 to 26.06	6.44

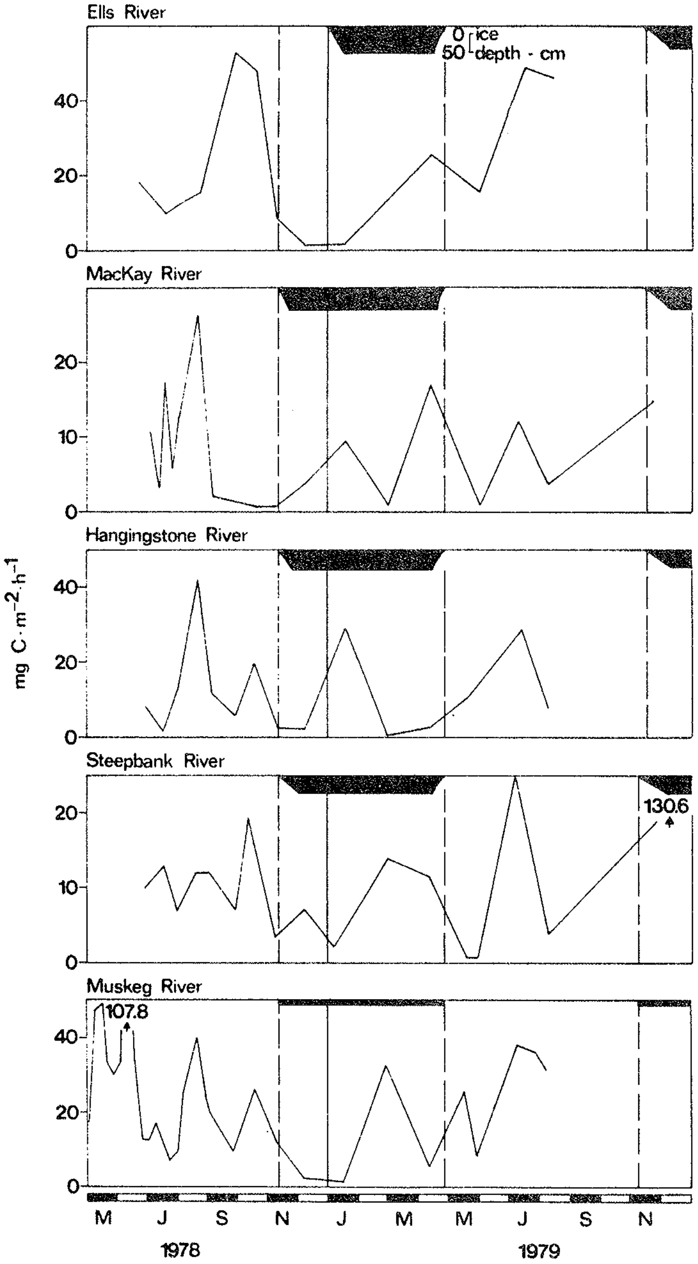

Figure 34. Epilithic algal primary productivity in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

Table 16. The mean and ranges of the primary productivity of the epilithic algae in artificial shade and in situ.

	$mg\ C \cdot m^{-2} \cdot h^{-1}$	
	Range	Mean
Shade	0.4 to 56.7	12.8
In Situ	6.9 to 107.8	26.5

(Table 17). These results were not unexpected because of the shallowness of the river and the horizontal variability in standing crop size (shore and mid-stream overall mean standing crops were 25.3 and 22.2 mg m^{-2} chlorophyll *a*, respectively).

The range and mean primary productivity values are presented in Table 18. On average, epilithic algal primary productivity was highest in the Muskeg and Ells rivers, the Steepbank and Hangingstone rivers formed the next pair, and the least productive epilithic algal community was that found in the MacKay River. Interestingly, the mean standing crop, as measured by chlorophyll *a* content, and mean primary productivity of the epilithic algae in these five rivers were positively correlated ($r = 0.869$, $p < 0.10$).

4.7 CORRELATIONS

Correlations between standing crop, growth of major algal groups, and primary productivity with various physical and chemical factors over the entire study period and the open water periods of 1978 and 1979 were examined to provide possible information about any potential controlling factors.

During the open water period of 1978, no one nutrient was limiting to standing crop size. In the Muskeg River, nutrient supply was more than adequate to support the standing crop; whereas, in the Steepbank, Hangingstone, and MacKay rivers, dissolved silica and nitrate-nitrogen were important (Table 19). Iron also gave a significant negative correlation in the Hangingstone River, while all major nutrients, together with iron and manganese, did in the MacKay River. Only manganese appeared important in the Ells River.

Only in the Ells and MacKay rivers was temperature correlated with standing crop. It correlated negatively in the Ells River and positively in the MacKay River (Table 20). Irradiance was important in all rivers except the Muskeg River. Current velocity was more important than discharge in general being most significant in the

Table 17. A comparison of primary productivity of epilithic algae at a shallow edge site and in mid-stream in the Muskeg River.

Month	Mid-stream (mg C·m^{-2}·h^{-1})		Shallow Edge (mg C·m^{-2}·h^{-1})
May	27.9	<	30.9
June	41.9	>	22.3
	82.9	<	132.6[a]
	33.7	>	33.5
	11.8	<	13.8
July	10.7	<	14.8
	18.2	>	15.5
	11.8	=	11.8
	4.7	<	9.1[a]
	10.4	>	8.8
August	12.6	<	42.3
	50.3	>	18.7
	17.1	<	31.0[a]
September	31.2	>	8.9
October	32.2	>	23.8
November	4.7	<	19.5[a]
December	1.9	<	2.6
Mean	23.8		25.9

[a] Significantly different according to "t" test.

Table 18. Range and mean epilithic algal primary productivity.

River	$Mg\ C \cdot m^{-2} \cdot h^{-1}$	
	Range	Mean
Muskeg	1.08 to 107.76	25.32
Steepbank	0.56 to 130.6	16.29
MacKay	0.54 to 26.01	8.26
Hangingstone	0.06 to 41.94	12.42
Ells	1.11 to 52.51	23.20

Table 19. Correlations between epilithic algal standing crop and potentially limiting nutrients for the entire study period and for the open water periods of 1978 and 1979.

Nutrient	Entire Study Period				
	Muskeg	Steepbank	Hangingstone	Ells	MacKay
SiO_2	N.S.[a]	$r = 0.385$ $p < 0.10$	N.S.	$r = -0.420$ $p < 0.10$	N.S.
NO_3-N	N.S.	N.S.	N.S.	N.S.	N.S.
PO_4-P	N.S.	N.S.	N.S.	$r = -0.365$ $p < 0.10$	N.S.
Mn	N.S.	$r = 0.747$ $p < 0.005$	$r = 0.687$ $p < 0.005$	$r = 0.447$ $p < 0.05$	N.S.
Ca	N.S.	$r = 0.371$ $p < 0.10$	$r = 0.412$ $p < 0.05$	$r = -0.442$ $p < 0.05$	N.S.
Na	N.S.	N.S.	N.S.	$r = -0.357$ $p < 0.10$	N.S.
	Open Water Period (1978)				
SiO_2	N.S.	$r = -0.726$ $p < 0.10$	$r = -0.590$ $p < 0.10$	N.S.	$r = -0.854$ $p < 0.01$
NO_3-N	N.S.	$r = -0.675$ $p < 0.10$	$r = -0.679$ $p < 0.05$	N.S.	$r = 0.918$ $p < 0.01$
PO_4-P	N.S.	N.S.	N.S.	N.S.	$r = -0.932$ $p < 0.01$
Fe	N.S.	N.S.	$r = -0.591$ $p < 0.10$	N.S.	$r = -0.875$ $p < 0.01$
Mn	N.S.	N.S.	N.S.	$r = -0.610$ $p < 0.10$	$r = -0.774$ $p < 0.05$

continued ...

Table 19. Concluded.

Nutrient	Open Water Period (1979)				
	Muskeg	Steepbank	Hangingstone	Ells	MacKay
SiO_2	N.S.	$r = 7.17$ $p < 0.10$	$r = 0.621$ $p < 0.10$	$r = 0.594$ $p < 0.25$	N.S.
NO_3-N	$r = -0.404$ $p < -0.25$	N.S.	$r = 0.479$ $p < 0.25$	N.S.	$r = -0.605$ $p < 0.25$
PO_4-P	N.S.	$r = 0.385$ $p < 0.25$	$r = 0.464$ $p < 0.25$	N.S.	N.S.
Fe	$r = -0.427$ $p < 0.25$	$r = 0.406$ $p < 0.25$	N.S.	N.S.	$r = -0.679$ $p < 0.10$
Ca	N.S.	N.S.	$r = 0.828$ $p < 0.05$	N.S.	N.S.
Na	N.S.	N.S.	$r = 0.538$ $p < 0.25$	N.S.	$r = 0.862$ $p < 0.05$
Mn	N.S.	N.S.	N.S.	$r = 0.627$ $p < 0.25$	N.S.

[a] N.S. = Not significant.

Table 20. Correlations between epilithic algal standing crop and physical factors for the entire study period and for the open water periods of 1978 and 1979.

Physical Factors	Muskeg	Steepbank	Hangingstone	Ells	MacKay
	Entire Study Period				
Temperature	r = -0.265 p < 0.10	N.S.	r = -0.191 p < 0.25	N.S.	N.S.
Irradiance	N.S.	N.S.	N.S.	r = -0.197 p < 0.25	N.S.
Current Velocity	r = -0.146 p < 0.25	r = -0.236 p < 0.25	r = -0.231 p < 0.25	N.S.	r = -0.287 p < 0.25
Discharge	r = -0.168 p < 0.25	r = -0.202 p < 0.25	r = -0.217 p < 0.25	N.S.	r = - 306 p < 0.10
	Open Water Period (1978)				
Temperature	N.S.	N.S.	N.S.	r = -0.746 p < 0.05	r = 0.893 p < 0.01
Irradiance	N.S.	r = 0.637 p < 0.10	r = 0.637 p < 0.05	r = -0.695 p < 0.10	r = 0.958 p < 0.01
Current Velocity	r = -0.385 p < 0.10	r = -0.629 p < 0.10	r = -0.447 p < 0.25	r = 0.416 p < 0.25	r = -0.720 p < 0.05
Discharge	N.S.	r = -0.596 p < 0.25	r = -0.413 p < 0.25	r = - .354 p < 0.25	r = -0.909 p < 0.01
	Open Water Period (1979)				
Temperature	r = -0.625 p < 0.10	N.S.	r = -0.421 p < 0.25	N.S.	r = -0.592 p < 0.25
Irradiance	r = -0.516 p < 0.25	N.S.	r = -0.488 p < 0.25	N.S.	N.S.
Current Velocity	N.S.	r = -0.651 p < 0.10	r = -0.664 p < 0.10	r = 0.671 p < 0.25	r = -0.764 p < 0.10
Discharge	N.S.	r = -0.628 p < 0.10	r = -0.517 p < 0.25	r = 0.639 p < 0.25	r = -0.635 p < 0.25

MacKay River, (where also discharge was even more significant than velocity), and next in the Muskeg and Steepbank rivers (Table 20). Significance levels were low in the Ells and Hangingstone rivers. The autumn decrease in standing crop size undoubtedly resulted from the increased discharge and current velocity rates during this period.

Similarly, no one overriding nutrient or physical factor was responsible for controlling fluctuations and population sizes of the major algal groups. Only dissolved silica appeared to be limiting to diatom growth in two rivers, the Hangingstone and MacKay; no other nutrient correlated with diatom growth in any river (Table 21). Irradiance was correlated with diatom growth in the Mackay and Ells rivers (Table 22) along with temperature in the latter. Both temperature and irradiance were negatively correlated with diatom growth. Current velocity was correlated with diatom growth in only the Muskeg, MacKay, and Ells rivers and discharge in only the latter two while irradiance was correlated in only the MacKay River (Table 22). Nutrient correlations were less clear with the Chlorophyta (Table 21). Calcium was implicated in the Muskeg River, dissolved silica in the Steepbank River, and nitrate-nitrogen and iron in the MacKay River; none were limiting in either the Hangingstone or Ells rivers. Neither irradiance nor temperature was correlated with the Chlorophyta (Table 22). However, current velocity and discharge were negatively correlated with Chlorophyta growth in the Steepbank, Hangingstone, MacKay, and Ells rivers. Thus, physically disruptive forces were most important in controlling chlorophycean algal populations during the open water period of 1978. Only nitrate-nitrogen correlated with the Cyanophyta and that was in the Hangingstone River (Table 21). Of the physical factors, only current velocity and discharge were important, particularly in the Hangingstone and MacKay rivers (Table 22). In the Muskeg and Steepbank rivers, although correlations existed, they were positive. Members of the Rhodophyta correlated with irradiance only in the Muskeg River, and nitrate-nitrogen, current velocity, and discharge in the Steepbank River (Tables 21 and 22).

Table 21. Correlations between the major epilithic algal groups and potentially limiting nutrients for the entire study period and for the open water periods of 1978 and 1979.

Nutrient	Entire Study Period			
	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
MUSKEG RIVER				
PO_4-P	N.S.	N.S.	N.S.	N.S.
SiO_2	N.S.	N.S.	$r = -0.356$ $p < 0.05$	$r = -0.414$ $p < 0.05$
NO_3-N	$r = 0.352$ $p < 0.05$	N.S.	N.S.	N.S.
Ca	N.S.	N.S.	N.S.	$r = -0.268$ $p < 0.10$
Mg	N.S.	$r = 0.344$ $p < 0.05$	N.S.	$r = -0.234$
Mn	N.S.	N.S.	N.S.	$r = -0.221$ $p < 0.10$
STEEPBANK RIVER				
PO_4-P	$r = 0.914$ $p < 0.005$	N.S.	N.S.	N.S.
SiO_2	N.S.	$r = -0.264$ $p < 0.25$	N.S.	$r = -0.348$ $p < 0.10$
NO_3-N	$r = -0.492$ $p < 0.05$	$r = -0.361$ $p < 0.10$	N.S.	N.S.
HANGINGSTONE RIVER				
PO_4-P	$r = 0.728$ $p < 0.005$	N.S.	N.S.	-
SiO_2	$r = -0.359$ $p < 0.10$	$r = -0.301$ $p < 0.25$	$r = -0.393$ $p < 0.10$	-
NO_3-N	N.S.	N.S.	$r = -0.222$ $p < 0.25$	-
Fe	N.S.	$r = -0.322$ $p < 0.25$	N.S.	-
Cl	N.S.	N.S.	$r = -0.260$ $p < 0.25$	-
K	N.S.	N.S.	$r = -0.343$ $p < 0.25$	

continued ...

Table 21. Continued.

Nutrient	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
MacKAY RIVER				
PO_4P	$r = 0.774$ $p < 0.005$	N.S.	$r = -0.202$ $p < 0.25$	-
SiO_2	N.S.	$r = -0.302$ $p < 0.25$	$r = -0.380$ $p < 0.10$	-
NO_3-N	$r = -0.223$ $p < 0.25$	$r = -0.187$ $p < 0.25$	N.S.	-
ELLS RIVER				
PO_4-P	$r = -0.316$ $p < 0.25$	$r = -0.393$ $p < 0.10$	$r = -0.230$ $p < 0.25$	-
SiO_2	N.S.	N.S.	N.S.	-
NO_3-N	$r = 0.357$ $p < 0.10$	N.S.	$r = -0.373$ $p < 0.10$	-
Ca	$r = -0.434$ $p < 0.05$	N.S.	N.S.	-
Na	$r = -0.521$ $p < 0.025$	$r = -0.284$ $p < 0.25$	N.S.	-
		Open Water Period (1978)		
MUSKEG RIVER				
PO_4-P	N.S.	N.S.	N.S.	N.S.
SiO_2	N.S.	N.S.	N.S.	N.S.
NO_3-N	N.S.	N.S.	N.S.	N.S.
Ca	N.S.	$r = -0.523$ $p < 0.10$	N.S.	N.S.
STEEPBANK RIVER				
PO_4-P	N.S.	N.S.	N.S.	N.S.
SiO_2	N.S.	$r = -0.753$ $p < 0.05$	N.S.	N.S.
NO_3-N	N.S.	N.S.	N.S.	$r = -0.723$ $p < 0.05$

continued ...

Table 21. Continued.

Nutrient	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
HANGINGSTONE RIVER				
PO_4-P	N.S.	N.S.	N.S.	-
SiO_2	$r = -0.614$ $p < 0.10$	N.S.	N.S.	-
NO_3-N	N.S.	N.S.	$r = -0.581$ $p < 0.10$	-
MacKAY RIVER				
PO_4-P	N.S.	N.S.	N.S.	-
SiO_2	$r = -0.558$ $p < 0.10$	N.S.	N.S.	-
Fe	N.S.	$r = -0.609$ $p < 0.10$	N.S.	-
ELLS RIVER				
PO_4-P	N.S.	N.S.	N.S.	-
NO_3-N	N.S.	N.S.	N.S.	-
SiO_2	N.S.	N.S.	N.S.	-
		Open Water Period (1979)		
MUSKEG RIVER				
PO_4-P	N.S.	N.S.	N.S.	$r = 0.707$ $p < 0.05$
NO_3-N	$r = 0.476$ $p < 0.25$	$r = -0.600$ $p < 0.10$	$r = -0.715$ $p < 0.05$	$r = -0.403$ $p < 0.25$
SiO_2	N.S.	$r = 0.361$ $p < 0.25$	$r = -0.450$ $p < 0.25$	N.S.
STEEPBANK RIVER				
PO_4-P	N.S.	$r = 0.713$ $p < 0.10$	$r = 0.672$ $p < 0.10$	N.S.
NO_3-N	$r = -0.490$ $p < 0.25$	$r = 0.451$ $p < 0.25$	$r = 0.407$ $p < 0.25$	$r = 0.406$ $p < 0.25$
SiO_2	N.S.	$r = 0.541$ $p < 0.25$	$r = 0.681$ $p < 0.10$	N.S.

continued ...

Table 21. Concluded.

Nutrient	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
Ca	N.S.	N.S.	$r = 0.802$ $p < 0.05$	N.S.
Na	N.S.	N.S.	$r = 0.945$ $p < .005$	N.S.
HANGINGSTONE RIVER				
PO_4-P	N.S.	$r = -0.503$ $p < 0.25$	$r = -0.865$ $p < 0.01$	-
NO_3-N	N.S.	$r = 0.523$ $p < 0.25$	N.S.	-
SiO_2	N.S.	$r = -0.765$ $p < 0.05$	$r = -0.976$ $p < 0.005$	-
Ca	$r = 0.928$ $p < 0.005$	N.S.	N.S.	-
Na	$r = 0.521$ $p < 0.25$	$r = -0.745$ $p < 0.05$	$r = -0.538$ $p < 0.25$	-
MacKAY RIVER				
PO_4-P	$r = 0.889$ $p < 0.01$	$r = 0.386$ $p < 0.25$	N.S.	-
NO_3-N	N.S.	N.S.	N.S.	-
SiO_2	$r = 0.414$ $p < 0.25$	N.S.	N.S.	-
Na	N.S.	$r = 0.571$ $p < 0.25$	N.S.	
ELLS RIVER				
PO_4-P	$r = -0.524$ $p < 0.25$	$r = -0.773$ $p < 0.05$	N.S.	-
NO_3-N	$r = 0.376$ $p < 0.25$	N.S.	N.S.	-
SiO_2	N.S.	N.S.	N.S.	-
Na	N.S.	$r = -0.417$ $p < 0.25$	$r = 0.568$ $p < 0.25$	-
Ca	$r = -0.983$ $p < 0.005$	$r = -0.460$ $p < 0.25$	$r = 0.504$ $p < 0.25$	-

Table 22. Correlations between the major epilithic algal groups and physical factors for the entire study period and for the open water periods of 1978 and 1979.

Physical Factors	Entire Study Period			
	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
MUSKEG RIVER				
Temperature	N.S.	$r = 0.462$ $p < 0.005$	N.S.	$r = 0.305$ $p < 0.10$
Irradiance	$r = -0.352$ $p < 0.05$	N.S.	N.S.	N.S.
Discharge	N.S.	N.S.	$r = -0.288$ $p < 0.10$	N.S.
Current Velocity	N.S.	N.S.	N.S.	$r = 0.227$ $p < 0.10$
STEEPBANK RIVER				
Temperature	$r = -0.382$ $p < 0.10$	$r = 0.229$ $p < 0.25$	N.S.	$r = 0.395$ $p < 0.10$
Irradiance	$r = -0.680$ $p < 0.005$	N.S.	$r = -0.474$ $p < 0.05$	$r = 0.412$ $p < 0.05$
Discharge	N.S.	N.S.	N.S.	N.S.
Current Velocity	$r = 0.181$ $p < 0.25$	N.S.	N.S.	N.S.
HANGINGSTONE RIVER				
Temperature	N.S.	$r = 0.354$ $p < 0.10$	N.S.	-
Irradiance	N.S.	$r = 0.293$ $p < 0.25$	N.S.	-
Discharge	$r = 0.245$ $p < 0.25$	$r = -0.185$ $p < 0.25$	$r = 0.325$ $p < 0.25$	-
Current Velocity	$r = 0.234$ $p < 0.25$	$r = -0.234$ $p < 0.25$	$r = 301$ $p < 0.25$	-
MacKAY RIVER				
Temperature	N.S.	$r = 0.259$ $p < 0.25$	$r = 0.300$ $p < 0.25$	-
Irradiance	$r = -0.305$ $p < 0.25$	$r = 0.397$ $p < 0.10$	$r = 0.386$ $p < 0.10$	-

continued ...

Table 22. Continued.

Physical Factors	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
MacKAY RIVER				
Discharge	N.S.	$r = 0.259$ $p < 0.10$	$r = 0.300$	-
Current Velocity	N.S.	$r = -0.466$ $p < 0.05$	N.S.	-
ELLS RIVER				
Temperature	N.S.	N.S.	N.S.	-
Irradiance	$r = -0.472$ $p < 0.10$	N.S.	$r = -0.231$ $p < 0.25$	-
Discharge	N.S.	N.S.	N.S.	-
Current Velocity	N.S.	N.S.	N.S.	-
	Open Water Period (1978)			
MUSKEG RIVER				
Temperature	N.S.	N.S.	N.S.	N.S.
Irradiance	N.S.	N.S.	N.S.	$r = -0.421$ $p < 0.10$
Discharge	N.S.	N.S.	$r = 0.305$ $p < 0.25$	N.S.
Current Velocity	$r = 0.256$ $p < 0.25$	N.S.	$r = 0.413$ $p < 0.25$	N.S.
STEEPBANK RIVER				
Temperature	N.S.	N.S.	N.S.	N.S.
Irradiance	N.S.	N.S.	N.S.	N.S.
Discharge	N.S.	$r = -0.664$ $p < 0.10$	$r = 0.423$ $p < 0.25$	$r = -0.479$ $p < 0.25$
Current Velocity	N.S.	$r = -0.786$ $p < 0.05$	$r = 0.446$ $p < 0.25$	$r = -0.570$ $p < 0.25$

continued ...

Table 22. Continued.

Physical Factors	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
HANGINGSTONE RIVER				
Temperature	N.S.	N.S.	N.S.	-
Irradiance	N.S.	N.S.	N.S.	-
Discharge	N.S.	$r = -0.452$ $p < 0.25$	$r = -0.627$ $p < 0.10$	-
Current Velocity	N.S.	$r = -0.454$ $p < 0.25$	$r = -0.639$ $p < 0.10$	-
MacKAY RIVER				
Temperature	N.S.	N.S.	N.S.	-
Irradiance	$r = -0.558$ $p < 0.10$	N.S.	N.S.	-
Discharge	$r = -0.739$ $p < 0.05$	$r = -0.557$ $p < 0.10$	$r = -0.371$ $p < 0.25$	-
Current Velocity	$r = -0.645$ $p < 0.10$	$r = -0.722$ $p < 0.05$	N.S.	-
ELLS RIVER				
Temperature	$r = -0.836$ $p < 0.05$	N.S.	N.S.	-
Irradiance	$r = 0.870$ $p < 0.05$	N.S.	N.S.	-
Discharge	$r = 0.599$ $p < 0.25$	$r = -0.521$ $p < 0.25$	N.S.	-
Current Velocity	$r = 0.626$ $p < 0.25$	$r = 0.514$ $p < 0.25$	N.S.	-

continued ...

Table 22. Continued.

Physical Factors	Open Water Period (1979)			
	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
MUSKEG RIVER				
Temperature	$r = -0.440$ $p < 0.25$	$r = 0.562$ $p < 0.10$	$r = 0.571$ $p < 0.10$	$r = 0.899$ $p < 0.005$
Irradiance	$r = -0.696$ $p < 0.10$	$r = 0.657$ $p < 0.10$	$r = 0.504$ $p < 0.10$	N.S.
Discharge	N.S.	$r = -0.405$ $p < 0.25$	$r = 0.335$ $p < 0.25$	N.S.
Current Velocity	N.S.	N.S.	N.S.	N.S.
STEEPBANK RIVER				
Temperature	$r = -0.438$ $p < 0.25$	$r = 0.516$ $p < 0.25$	$r = 0.565$ $p < 0.25$	N.S.
Irradiance	N.S.	N.S.	N.S.	$r = 0.494$ $p < 0.25$
Discharge	$r = -0.390$ $p < 0.25$	N.S.	$r = 0.697$ $p < 0.10$	N.S.
Current Velocity	$r = -0.403$ $p < 0.25$	N.S.	$r = -0.794$ $p < 0.05$	N.S.
HANGINGSTONE RIVER				
Temperature	$r = -0.753$ $p < 0.10$	N.S.	N.S.	-
Irradiance	N.S.	N.S.	N.S.	-
Discharge	$r = -0.351$ $p < 0.25$	$r = 0.976$ < 0.005	$r = 0.696$ $p < 0.10$	-
Current Velocity	$r = -0.465$ $p < 0.25$	$r = 0.938$ $p < 0.005$	$r = 0.647$ $p < 0.10$	-
MacKAY RIVER				
Temperature	N.S.	$r = -0.364$ $p < 0.25$	N.S.	-
Irradiance	$r = 0.477$ $p < 0.25$	N.S.	$r = -0.454$ $p < 0.25$	-

continued ...

Table 22. Concluded.

Physical Factors	Diatoms	Chlorophyta	Cyanophyta	Rhodophyta
Discharge	N.S.	$r = -0.44$ $p < 0.25$	N.S.	-
Current Velocity	N.S.	$r = -0.764$ $p < 0.05$	N.S.	-
ELLS RIVER				
Temperature	$r = 0.540$ $p < 0.25$	$r = 0.832$ $p < 0.025$	$r = 0.444$ $p < 0.25$	-
Irradiance	N.S.	$r = 0.727$ $p < 0.10$	N.S.	-
Discharge	$r = -0.472$ $p < 0.25$	N.S.	N.S.	-
Current Velocity	$r = -0.417$ $p < 0.25$	N.S.	N.S.	-

Factors controlling epilithic algal primary productivity were also variable (Tables 23 and 24). Standing crops were important during the open water period of 1978 in the Muskeg, MacKay, and Hangingstone rivers but not in the Steepbank or Ells rivers. In fact, no factor examined correlated with primary productivity during this period in the Steepbank River and, other than standing crop, no other factor correlated in the Muskeg and Hangingstone rivers. In contrast, in both the Ells and, particularly, the MacKay River, many factors correlated with productivity (Table 24).

Again, during the open water period of 1979, no single factor was responsible for standing crop fluctuation (Tables 19 and 20). Dissolved silica and nitrate-nitrogen appeared limiting in the Ells and MacKay rivers, respectively. Similarly, current velocity and discharge were limiting only in the Steepbank and Hangingstone rivers. Temperature and irradiance were negatively correlated with standing crops only in the Muskeg and Hangingstone rivers (Tables 19 and 20). Iron was the only other ion to give a negative correlation and this happened in the Muskeg, MacKay, and Steepbank rivers. All other nutrient correlations with standing crop were positive (Tables 19 and 20).

Similarly, as in 1978, no one factor or factors was responsible for determining the wax and wane of the major algal groups (Tables 21 and 22). Dissolved silica was never limiting to diatom growth in any river; only phosphate-phosphorus and calcium were negatively correlated with diatoms, and only in the Ells River. Physical factors, particularly current velocity and discharge, played a role in the Hangingstone, Steepbank, and Ells rivers, as did temperature in these and the Muskeg River, and irradiance in the latter river and the MacKay River. Other nutrients where correlated did so positively (Tables 21 and 22). Correlations were yet again less clear with the Chlorophyta with nitrate-nitrogen being implicated in limiting chlorophycean growth in the Muskeg, Steepbank, and Hangingstone rivers; dissolved silica in the latter river, phosphate-phosphorus in this and the Ells river, along with calcium and sodium in the Ells River. Temperature was important in all but the

Table 23. Correlations between epilithic algal standing crop and primary productivity for the entire study period and for the open water periods of 1978 and 1979.

River		Open Water Period	
	Entire Study Period	1978	1978
Muskeg	$r = 0.356$ $p < 0.05$	$r = 0.536$ $p < 0.05$	$r = 0.678$ $p < 0.10$
Steepbank	N.S.	N.S.	$r = 0.989$ $p < 0.005$
Hangingstone	N.S.	$r = 0.668$ $p < 0.10$	$r = 0.921$ $p < 0.10$
MacKay	$r = 0.310$ $p < 0.25$	$r = 0.776$ $p < 0.05$	N.S.
Ells	$r = 0.519$ $p <-0.10$	N.S.	$r = 0.603$ $p < 0.25$

Table 24. Correlations between epilithic algal primary productivity and physical and chemical factors for the entire study period and for the open water periods of 1978 and 1979.

Chemical and Physical Factors	Entire Study Period				
	Muskeg	Steepbank	Hangingstone	MacKay	Ells
Irradiance	N.S.	$r = -0.212$ $p < 0.25$	N.S.	$r = 0.316$ $p < 0.05$	N.S.
Temperature	N.S.	N.S.	$r = -0.222$ $p < 0.25$	N.S.	$r = 0.294$ $p < 0.25$
NO_3-N	N.S.	$r = -0.259$ $p < 0.25$	$r = -0.350$ $p < 0.25$	$r = - 434$ $p < 0.10$	N.S.
PO_4-P	N.S.	N.S.	N.S.	N.S.	$r = -0.565$ $p < 0.05$
SiO_2	$r = -0.339$ $p < 0.05$	N.S.	N.S.	$r = 0.271$ $p < 0.25$	N.S.
Ca	$r = -0.413$ $p < 0.005$	N.S.	$r = -0.334$ $p < 0.25$	N.S.	$r = -0.364$ $p < 0.25$
Mg	$r = -0.289$ $p \quad 0.10$	$r = 0.410$ $p < 0.10$	$r = -0.278$ $p < 0.25$	$r = 0.207$ $p < 0.25$	N.S.
Cl	N.S.	$r = 0.588$ $p < 0.05$	$r = -0.266$ $p < 0.25$	N.S.	N.S.
K	N.S.	$r = 0.363$ $p < 0.10$	$r = 0.241$ $p < 0.25$	N.S.	N.S.

continued ...

Table 24. Continued.

	Open Water Period (1978)				
	Muskeg	Steepbank	Hangingstone	MacKay	Ells
Irradiance	N.S.	N.S.	N.S.	$r = 0.786$ $p < 0.05$	N.S.
Temperature	N.S.	N.S.	N.S.	$r = 0.649$ $p < 0.10$	N.S.
NO_3-N	N.S.	N.S.	N.S.	$r = 0.855$ $p < 0.01$	N.S.
PO_4-P	N.S.	N.S.	N.S.	$r = 0.779$ $p < 0.05$	N.S.
SiO_2	N.S.	N.S.	N.S.	$r = -0.625$ $p < 0.10$	$r = 0.712$ $p < 0.05$
Mg	N.S.	N.S.	N.S.	$r = 0.664$ $p < 0.10$	N.S.
Ca	N.S.	N.S.	N.S.	$r = 0.649$ $p < 0.10$	N.S.
Fe	N.S.	N.S.	N.S.	$r = -0.693$ $p < 0.10$	$r = 0.835$ $p < 0.05$
Mn	N.S.	N.S.	N.S.	$r = 0.613$ $p < 0.10$	$r = 0.701$ $p < 0.05$

continued ...

Table 24. Concluded.

	Open Water Period (1979)				
	Muskeg	Steepbank	Hangingstone	MacKay	Ells
Irradiance	N.S.	$r = 0.935$ $p < 0.10$	N.S.	$r = -0.977$ $p < 0.005$	$r = -0.999$ $p < 0.001$
Temperature	$r = 0.629$ $p < 0.25$	$r = 0.950$ $p < 0.10$	N.S.	$r = 0.999$ $p < 0.001$	$r = 0.996$ $p < 0.001$
NO_3-N	N.S.	$r = -0.982$ $p < 0.05$	N.S.	N.S.	N.S.
PO_4-P	$r = 0.605$ $p < 0.25$	N.S.	N.S.	N.S.	N.S.
SiO_2	$r = 0.746$ $p < 0.10$	N.S.	N.S.	N.S.	N.S.
Mg	$r = 0.686$ $p < 0.10$	N.S.	N.S.	N.S.	N.S.
Mn	$r = -0.822$ $p < 0.05$	N.S.	N.S.	N.S.	N.S.
Cl	$r = 0.517$ $p < 0.25$	N.S.	N.S.	N.S.	N.S.
Na	$r = 0.560$ $p < 0.25$	N.S.	N.S.	N.S.	N.S.
K	$r = 0.755$ $p < 0.10$	N.S.	N.S.	N.S.	N.S.

Hangingstone River but irradiance only in the Ells and Muskeg rivers. Both current velocity and discharge were positively correlated with chlorophycean growth in the Hangingstone River and negatively in the MacKay River. Only discharge correlated in the Muskeg River in a negative manner. Further variation occurred with the Cyanophyta (Tables 21 and 22) with no pattern emerging. Only nitrate-nitrogen appeared limiting to the Rhodophyta and only in the Muskeg River.

Epilithic algal standing crops were correlated with primary productivity in all but the MacKay River during the open water period of 1979 (Table 23). Similarly, both irradiance and temperature were correlated in all but one river, the Hangingstone (Table 24). During this period, standing crops, irradiance, and temperature appeared, in general to be most important. Only in the Muskeg River did any nutrient correlate and, like the Mackay River during 1978, many did (Table 24).

Over the entire study period, no one nutrient was limiting to standing crop size. This was undoubtedly due to physical limitations during the winter months coupled with nutrient increases under ice-cover through decreased flow. No nutrient correlated in the Muskeg and MacKay rivers (Table 19), while those that did in the Steepbank River were positively correlated. Only in the Ells River did significant negative correlations occur (e.g., with SiO_2 and PO_4^{-1}). Thus, in general, nutrient levels are more than adequate to support the algal populations. Of the physical factors, current velocity and discharge were consistently the most important (Table 20), except in the Ells River where irradiance was. Thus, physically disruptive forces appear to be more important during the entire study period than nutrient levels in all but the Ells River (Tables 19 and 20).

Similarly, no one overriding nutrient or physical factor was responsible for controlling fluctuations and populations sizes of the major algal groups. Dissolved silica appeared to be limiting to the diatom group only in the Hangingstone River, while nitrate was implicated in the Steepbank and MacKay rivers and phosphate-phosphorus in the Ells River (Table 21). Temperature was correlated with diatom growth in the Steepbank River, whereas irradiance was correlated in all but the Hangingstone River (Table 22). In all four instances, it was a negative correlation reflecting the spring and autumn diatom growth peaks. Current velocity and discharge were unimportant in general over the entire study period. Overall, no nutrient or physical factor appeared limiting to the growth of the Chlorophyta in the Muskeg River (Tables 21 and 22), while dissolved silica and nitrate-nitrogen were implicated in the Steepbank and MacKay rivers. Phosphate-phosphorus and dissolved silica were implicated in the Ells and Hangingstone rivers (Table 21). Iron and sodium also gave significant correlations in these rivers but these undoubtedly arose from the high winter concentrations and low chlorophycean populations during this period. Temperature was important in all but the Ells River where no physical factor correlated with chlorophycean growth. In the Hangingstone and MacKay rivers, irradiance, discharge, and current velocity were important (Table 22). No nutrient correlated with cyanophycean algal growth in the Steepbank River; irradiance was the only factor which correlated (Table 22). In contrast, phosphate-phosphorus was implicated in the MacKay and Ells rivers along with dissolved silica and nitrate-nitrogen in each, respectively (Table 21). Temperature and irradiance were both positively correlated in the former river but only irradiance (negatively) in the latter (Table 22). Again, in the Hangingstone River, dissolved silica, nitrate-nitrogen, chloride, potassium, discharge, and current velocity were correlated but both the latter positively. Rhodophycean algal growth correlated with temperature and dissolved silica in both the Steepbank and Muskeg rivers but with other different factors in each river (Tables 21 and 22).

Factors controlling primary productivity were again variable. Overall standing crops were correlated with primary productivity in three rivers, the Muskeg, MacKay, and Ells (Table 23). The remaining factors were quite variable among the five rivers (Table 24).

Summary tables are presented in Tables 25 through 27. These not only emphasize the variability among the five rivers but also show differences from year to year. They also show the importance of current velocity and discharge to standing crop and the major algal groups (i.e., physically disruptive forces--Tables 25 and 26). Also, standing crop size was important in controlling primary productivity; more so than irradiance levels during this study (Table 27). Complex and interrelated relationships between physical, chemical, and biotic factors and standing crop and primary productivity fluctuations exist and each river reacts similarly and yet differently.

Table 25. Summary of factors potentially influencing epilithic algal standing crops.

Study Period	Factors
Muskeg River	
Entire period	Temperature.
Open water 1978	Current velocity.
Open water 1979	Temperature.
Steepbank River	
Entire period	Current velocity; Discharge.
Open water 1978	SiO_2; NO_3-N; Irradiance; Current velocity; Discharge.
Open water 1979	Current velocity; Discharge; Temperature; Irradiance; Na; Ca; SiO_2; NO_3-N; PO_4-P.
Hangingstone River	
Entire period	Current velocity; Discharge; Temperature.
Open water 1978	NO_3-N; Irradiance; SiO_2; Fe; Current velocity; Discharge.
Open water 1979	Current velocity; Discharge; Temperature; Irradiance; Ca; Na; SiO_2; NO_3-N; PO_4-P.
Ells River	
Entire period	SiO_2; NO_3-N; Ca; Na; Irradiance.
Open water 1978	Temperature; Irradiance; Mn; Current velocity; Discharge.
Open water 1979	Current velocity; Discharge; SiO_2; Mn.
MacKay River	
Entire period	Current velocity; Discharge.
Open water 1978	Irradiance; PO_4-P; NO_3-N; Discharge; Temperature; Fe; SiO_2; Mn; Current velocity.
Open water 1979	Current velocity; Fe; Discharge; NO_3-N; Na.

Table 26. Summary of factors potentially influencing the growth of the major algal groups.

Algal Groups	Factors
DIATOMS	
Muskeg River	
Entire period	Irradiance.
Open water 1978	Current velocity.
Open water 1979	Irradiance; NO_3-N; Temperature.
Steepbank River	
Entire period	Irradiance; Temperature; Current velocity.
Open water 1978	-
Open water 1979	Temperature; Current velocity; Discharge; NO_3-N.
Hangingstone River	
Entire period	SiO_2; Discharge; Current velocity.
Open water 1978	SiO_2
Open water 1979	Temperature; Current velocity; Discharge; Ca; Na.
Ells River	
Entire period	Na; Ca; Irradiance; PO_4-P.
Open water 1978	Temperature; Irradiance; Current velocity; Discharge.
Open water 1979	Ca; Temperature; PO_4-P; Discharge; Current velocity; NO_3-N.
MacKay River	
Entire period	Irradiance; NO_3-N.
Open water 1978	Discharge; Current velocity; SiO_2; Irradiance.
Open water 1979	Irradiance; PO_4-P; SiO_2.

continued ...

Table 26. Continued.

Algal Groups	Factors
CHOROPHYTA	
Muskeg River	
Entire period	Temperature.
Open water 1978	Calcium.
Open water 1979	Irradiance; NO_3-N; Temperature, Discharge; SiO_2.
Steepbank River	
Entire period	NO_3-N; Temperature; SiO_2.
Open water 1978	SiO_2; Current velocity; Discharge.
Open water 1979	Temperature; NO_3-N; PO_4-P; SiO_2.
Hangingstone River	
Entire period	Temperature; Fe; SiO_2; Irradiance; Current velocity; Discharge.
Open water 1978	Current velocity; Discharge.
Open water 1979	SiO_2; Na; NO_3-N; PO_4-P; Current velocity; Discharge.
Ells River	
Entire period	PO_4-P; Na.
Open water 1978	Discharge; Current velocity.
Open water 1979	Temperature; PO_4-P; Irradiance; Na; Ca.
MacKay River	
Entire period	Irradiance; Current velocity; Discharge; Temperature; SiO_2; NO_3-N.
Open water 1978	Current velocity; Discharge; Fe.
Open water 1979	Current velocity; Discharge; Temperature; PO_4-P; Na.

continued ...

Table 26. Continued.

Algal Groups	Factors
CYANOPHYTA	
<u>Muskeg River</u>	
Entire period	SiO_2; Discharge.
Open water 1978	Current velocity; Discharge.
Open water 1979	NO_3-N; Irradiance; Temperature; SiO_2; Discharge.
<u>Steepbank River</u>	
Entire period	Irradiance.
Open water 1978	Current velocity; Discharge.
Open water 1979	Current velocity; Discharge; Temperature; Na; Ca; SiO_2; PO_4-P; NO_3-N.
<u>Hangingstone River</u>	
Entire period	SiO_2; K; Discharge; Current velocity; NO_3-N.
Open water 1978	Current velocity; Discharge; NO_3-N.
Open water 1979	SiO_2; PO_4-P; Na; Discharge; Current velocity.
<u>Ells River</u>	
Entire period	NO_3-N; Irradiance; PO_4-P.
Open water 1978	-
Open water 1979	Ca; Temperature; Na.
<u>MacKay River</u>	
Entire period	Irradiance; SiO_2; Temperature; PO_4-P.
Open water 1978	Discharge
Open water 1979	Irradiance

continued ...

Table 26. Concluded.

Algal Groups	Factors
RHODOPHYTA	
Muskeg River	
Entire period	SiO_2; Temperature; Ca; Mg; Current velocity; Mn.
Open water 1978	Irradiance.
Open water 1979	Irradiance; NO_3-N; PO_4-P.
Steepbank River	
Entire period	Irradiance; Temperature; SiO_2.
Open water 1978	NO_3-N; Current velocity; Discharge.
Open water 1979	Irradiance; NO_3-N.

Table 27. Summary of factors potentially influencing epilithic algal primary productivity.

Muskeg River	
Entire period	Standing crop; Ca; SiO_2; Mg.
Open water 1978	Standing crop.
Open water 1979	Mn; K; SiO_2; Mg; Standing crop; Temperature; PO_4-P; Na; Cl.
Steepbank River	
Entire period	Cl; Mg; K; NO_3-N; Irradiance.
Open water 1978	-
Open water 1979	Standing crop; Irradiance; Temperature; NO_3-N.
Hangingstone River	
Entire period	NO_3-N; Ca; Mg; Cl; K; Temperature.
Open water 1978	Standing crop.
Open water 1979	Standing crop.
Ells River	
Entire period	PO_4-P; Standing cropl Ca; Temperature.
Open water 1978	Fe; SiO_2; Mn.
Open water 1979	Temperature; Irradiance; Standing crop.
MacKay River	
Entire period	NO_3-N; Irradiance; Standing crop; SiO_2; Mg.
Open water 1978	Irradiance; PO_4-P; NO_3-N; Standing crop; Fe; Mg; Ca; Temperature; SiO_2; Mn.
Open water 1979	Temperature; Irradiance.

5. DISCUSSION

Numerically, cyanophycean algae were the most important epilithic algae particularly, *Lyngbya aerugineo-caerulea*, *Phormidium* sp., *Calothrix braunii*, *Nostoc* spp., and *Anabaena affinis*, followed by diatoms, namely, *Synedra ulna*, *Synedra rumpens*, *Gomphonema olivaceum*, *Gomphonema acuminatum*, *Gomphonema longiceps* v. *subclavata*, *Nitzschia fonticola*, *Nitzschia palea*, *Achnanthes lanceolata*, *Epithemia sorex*, *Epithemia turgida*, *Cocconeis placentula*, and *Cocconeis pediculus*. One exception was the Hangingstone River where chlorophycean algae were next in importance to the Cyanophyta with *Stigeoclonium pachydermum* and *Cladophora glomerata* dominant. Other important chlorophycean algae included *Draparnaldia glomerata* and *Chlamydomonas* spp., at the sites studied. Rhodophycean algae occurred only in the Muskeg and Steepbank rivers but at others sites in all but the Ells River the rhodophycean algae, *Batrachospermum vagum* was found (Hickman et al. 1980). The other rhodophycean algae found were *Audouinella violacea* and *Audouinella pygmaea*; both occurred in the Muskeg and Steepbank rivers.

Epilithic algal standing crops and the algal groups fluctuated seasonally. However, they were not controlled by a single factor, but instead by a complex myriad of interacting factors, chemical and physical as well as biotic. The latter were not investigated during this study. Variations were apparent from river to river, season to season, and year to year, particularly when nutrients were examined in relation to standing crop fluctuations. However, during open water periods, as well as overall, physical factors appeared important in controlling standing crop size. This is not surprising since, in these flowing systems, discharge and current velocity can change, substantially and rapidly, sweeping away not only the algae but also the rocks to which they attach. The late summer/ autumn sudden increase in discharge and current velocity in 1978 dramatically reduced population sizes in all but the Ells River. Here, rates fluctuated least because of the buffering capacity of headwater lakes. Several factors, of course, are implicated. The rapid disappearance of algae from rocks depends not only upon standing crop size but also on the mode of attachment, whether the algae are encrusting or filamentous forms or in the case of some diatoms, whether they exist on mucilage stalks, as well as their physiological condition, that is, whether they are actively growing or senescing. As the epilithic algal standing crops increase in size, the increasing thickness of algal growth or increasing length of filaments alter resistance to flow. Therefore, during periods of high standing crops, effects of increased discharge and current velocity become more devastating. Increased resistance is further enhanced through the accumulation of suspended sediments and detritus among the algae themselves. This whole process will be further accentuated as basal cells senesce in dense populations, thus producing weaknesses. Current velocity and discharge rates were not only important in controlling epilithic algal standing crops but also major algal groups, particularly diatoms and the Chlorophyta.

Variations among rivers occurred among the major algal groups and nutrients and physical factors. Dissolved silica concentrations were related to the wax and wane of diatoms populations only in the Hangingstone and MacKay rivers. Even this relationship was inconsistent from year to year in these two rivers. Wang and Evans (1969) and Edwards (1974) also found a similar relationship in their studies, whereas Marker (1976b) did not in shallow chalk streams. Again, physical factors appeared more important than nutrients, a phenomenon not uncommon with diatoms in flowing systems (c.f. Moore 1977). Great river to river variability occurred with respect to the Chlorophyta and Cyanophyta and again physically disruptive forces were important whereas irradiance, in general, appeared most important with the Rhodophyta, but much variation was apparent. In these five rivers, physical forces were more important than nutrient levels in controlling epilithic algal populations, eventhough both negative and positive correlations with nutrients were found. Thus, nutrients, could and probably did, play a role in the wax and wane of epilithic algal standing crops and the individual species.

Physical forces also affected the chemical composition and nutrient status of the water itself in these rivers. This further complicates relationships between the algae and dissolved nutrients but again emphasizes the importance of physical forces in controlling the biota. Conductance, for example, increases as discharge rates fall, particularly during the winter, and is negatively correlated in a logarithmic manner to discharge rates in all but the Ells River (Figure 35). Other ions and nutrients follow this pattern, even dissolved silica and phosphate-phosphorus (Table 28). Potassium did not correlate in the Muskeg and MacKay rivers but did correlate linearly in the other three. Schwartz (1979) reported similar findings in the Muskeg River. He found that potassium as added to the water during the spring snow melt as surface run-off mobilized potassium ions found on the soil surface. In contrast to dissolved silica and phosphate-phosphorus, nitrate-nitrogen was positively correlated in a logarithmic manner with discharge rates in all but the Ells River (Table 28). Thus, much of the nitrogen entering the rivers originates in the catchment area as well as being supplied by the nitrogen fixing capabilities of cyanophycean algae and bacteria.

As the cyanophycean algae dominated the epilithic algal standing crop, and they are important fixers of atmospheric nitrogen this aspect was investigated in an ancillary study using a modified acetylene reduction technique such that in situ epilithic nitrogen fixation could be measured using both light and dark incubation bottles (Charlton and Hickman, in prep.). Briefly, distinct late spring/early summer maxima of nitrogen fixation occurred. Then, as water temperatures fell and ice formed, the rate of fixation fell to undetectable levels (Figures 36 and 37). Throughout the two-year study period, light fixation, on average was consistently greater than dark fixation (Table 29). Values obtained in these rivers are comparable to those found by Horne and Carmiggelt (1975) and Horne (1975) in California streams. Thus, the epilithic cyanophycean algae (and bacteria) are important contributors to the nitrogen budget of these rivers, along with allochthonous input from the catchment areas.

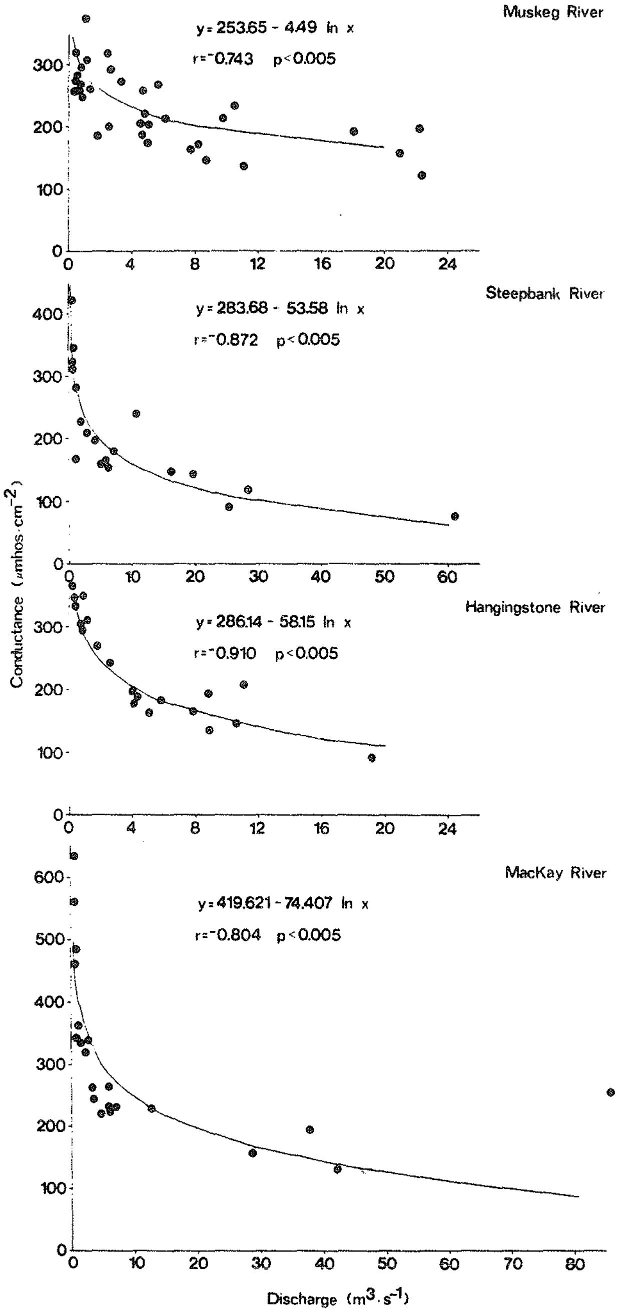

Figure 35. Relationship between conductance and discharge in the Muskeg, Steepbank, Hangingstone, and MacKay rivers.

Table 28. Relationships between various ions and discharge.

Ion	Muskeg	Steepbank	Hangingstone	MacKay	Ells
Na	$y = 21.9 - 2.7\ln x$ $r = -0.368$ $p < 0.025$	$y = 30.5 - 8.0\ln x$ $r = -0.894$ $p < 0.005$	$y = 31.4 - 4.9\ln x$ $r = -0.562$ $p < 0.01$	$y = 54.3 - 12.3\ln x$ $r = -0.834$ $p < 0.005$	$y = 4.4 - 0.3\ln x$ $r = -0.695$ $p < 0.005$
K	N.S.	$y = 0.84 - 0.0\ln x$ $r = -0.273$ $p < 0.25$	$y = 1.9 - 0.0\ln x$ $r = -0.351$ $p < 0.10$	N.S.	$y = 1.0 - 0.1$ $r = -0.271$ $p < 0.25$
Mg	$y = 10.1 - 2.1\ln x$ $r = -0.674$ $p < 0.005$	$y = 12.2 - 3.0\ln x$ $r = -0.894$ $p < 0.005$	$y = 9.6 - 2.6\ln x$ $r = -0.859$ $p < 0.005$	$y = 11.6 - 2.3\ln x$ $r = -0.631$ $p < 0.005$	$y = 4.1 - 0.05$ $r = -0.702$ $p < 0.005$
Ca	$y = 26.6 - 3.9\ln x$ $r = -0.618$ $p < 0.005$	$y = 24.6 - 3.9\ln x$ $r = -0.657$ $p < 0.005$	$y = 22.1 - 4.2\ln x$ $r = -0.753$ $p < 0.005$	$y = 29.96 - 4.8\ln x$ $r = -0.636$ $p < 0.005$	N.S.
Cl^-	N.S.	$y = 4.6 - 1.8\ln x$ $r = -0.754$ $p < -0.005$	$y = 15.9 - 4.8\ln x$ $r = 0.836$ $p < 0.005$	$y = 13.4 - 3.9\ln x$ $r = -0.806$ $p < 0.005$	N.S
$SO_4^=$	N.S.	$y = 9.9 - 2.3\ln x$ $r = -0.780$ $p < 0.005$	$y = 20.2 - 4.8\ln x$ $r = 0.919$ $p < 0.005$	$y = 38.4 - 7.5\ln x$ $r = 0.845$ $p < 0.005$	N.S.
SiO_2	$y = 6.5 - 0.99\ln x$ $r = -0.469$ $p < 0.005$	$y = 6.0 - 1.1\ln x$ $r = -0.536$ $p < 0.01$	$y = 6.7 - 1.1\ln x$ $r = -0.676$ $p < 0.005$	$y = 3.7 - 0.4\ln x$ $r = -0.241$ $p < 0.25$	$y = 7.6 - 0.1\ln x$ $r = -171$ $p < 0.25$
PO_4-P	$y = 0.02 - 0.002\ln x$ $r = -0.295$ $p < 0.05$	$y = 0.09 - 0.03\ln x$ $r = -0.625$ $p < 0.005$	$y = 0.13 - 0.03\ln x$ $r = -0.283$ $p < 0.25$	N.S.	N.S.
NO_3-N	$y = 0.10 + 0.01\ln x$ $r = 0.157$ $p < 0.25$	$y = 0.2 + 0.19\ln x$ $r = 0.431$ $p < 0.05$	$y = 0.2 + 0.03\ln x$ $r = 0.167$ $p < 0.25$	$y = 0.3 + 0.02\ln x$ $r = 0.264$ $p < 0.25$	N.S.

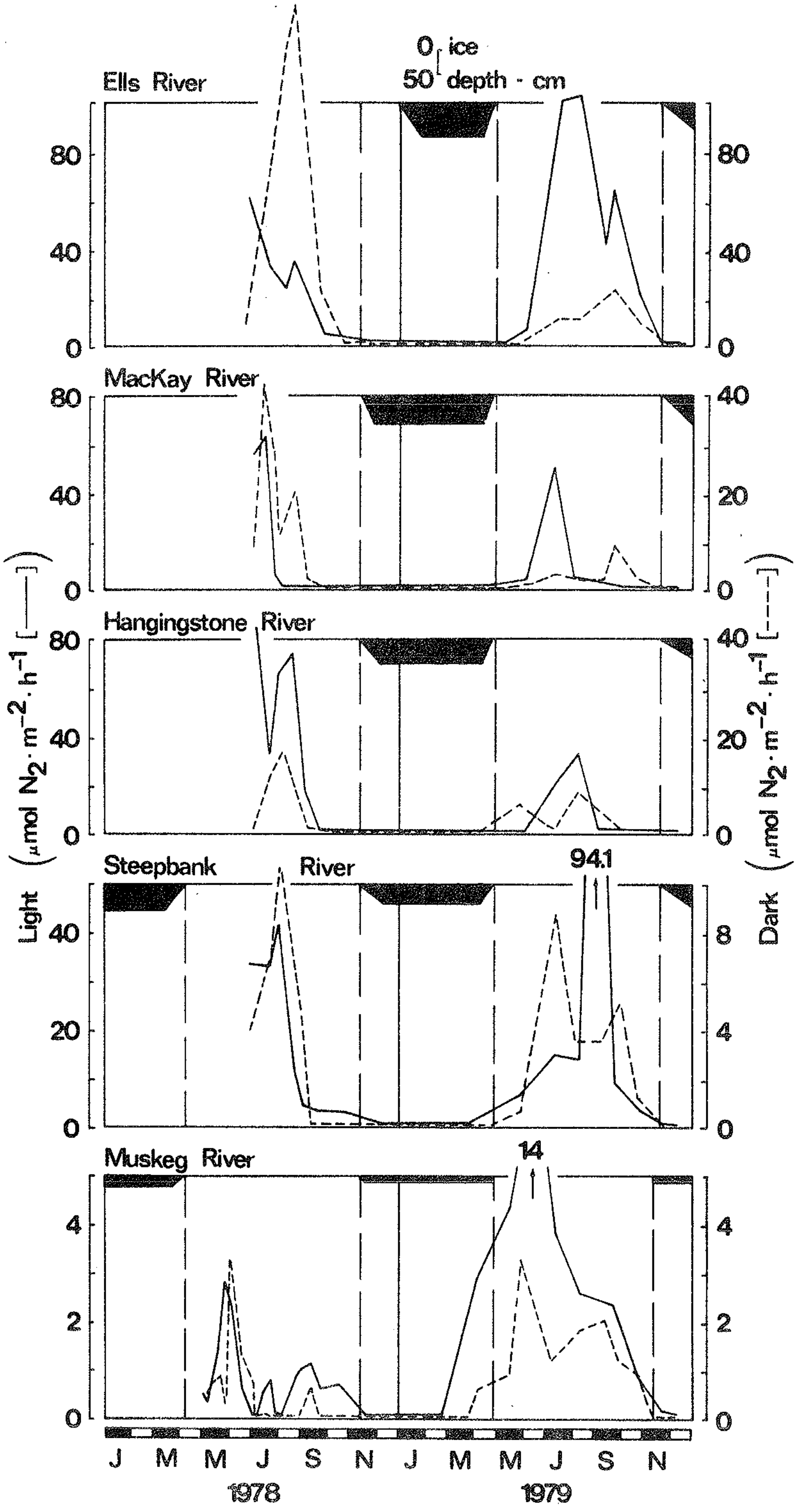

Figure 36. Epilithic nitrogen fixation in the Ells, MacKay, Hangingstone, Steepbank, and Muskeg rivers.

Table 29. Mean and range of epilithic nitrogen fixation (nmol N_2 $h^{-1} \cdot m^{-2}$).

	Nitrogen Fixation					
	Over Entire Period		Open Water 1978		Open Water 1979	
	Light	Dark	Light	Dark	Light	Dark
Muskeg	0 - 14 300 x̄ = 1 423	0 - 3 180 x̄ = 650	10 - 2 830 x̄ = 749.2	10 - 3 300 x̄ 573	20 - 14 300 x̄ = 3 624	40 - 3 180 x̄ 1 330
Steepbank	310 - 94 100 x̄ = 12 264	10 - 16 800 x̄ = 2 862	410 - 41 500 x̄ = 23 832	10 - 16 800 x̄ = 6 676	310 - 94 100 x̄ = 17 930	330 - 8 920 x̄ = 3 410
Hangingstone	0 - 84 000 x̄ = 17 204	0 - 17 000 x̄ = 2 204	0 - 84 000 x̄ = 39 400	100 - 17 000 x̄ = 4 170	590 - 33 400 x̄ = 11 380	110 - 8 820 x̄ = 2 490
MacKay	90 - 64 000 x̄ = 8 722	860 - 42 000 x̄ = 5 985	90 - 64 000 x̄ = 16 430	860 - 4 200 x̄ = 16 430	1 020 - 49 000 x̄ 8 680	440 - 2 960 x̄ = 1 530
Ells	10 - 110 000 x̄ = 27 142	390 - 143 000 x̄ = 23 550	10 - 61 000 x̄ = 21 600	390 - 143 000 x̄ = 49 900	710 - 110 000 x̄ = 56 190	530 - 21 900 x̄ = 12 470

Only in three rivers, the Muskeg, Steepbank, and Hangingstone did the epilithic algal standing crops begin to approach the high values (300 to 600 mg m^{-2} chlorophyll *a*) that have been reported by Tominaga and Ichimura (1966) and Edwards and Owens (1965) in streams; McIntire (1968) in artificial streams; and Felfoldy (1961) on a lake shore. The maxima in these rivers were 202.95, 229.84, and 205.46 mg m^{-2} chlorophyll *a*, respectively. Such maxima are comparable to estimates of the maximum phytoplankton standing crop per unit area of the euphotic zone of eutrophic lakes which may be expected on theoretical grounds (about 200 to 300 mg m^{-2} chlorophyll *a*) (Talling et al. 1973). Actually, as pointed out by Marker (1976a), direct comparisons are difficult because in many studies no corrections were made for the presence of chlorophyll degradation products. The standing crops of these five rivers, though, are comparable to those found by Marker (1976a) in the shallow chalk rivers.

Conversion of the epilithic algal standing crop (mg m^{-2} chlorophyll *a*) to organic dry weight, following Marker (1976a), was made to gain insight into the contribution in organic matter by the epilithic algae realizing that this is but an estimate since chlorophyll *a* as a percentage of the dry weight can vary widely depending not only upon the physiological state of the algae but also the species involved. In a small chalk river, the maximum contribution during a diatom peak was between 12 to 15 gm m^{-2} organic matter (Marker 1976a). Such values were approached in the Steepbank, Hangingstone, and Muskeg rivers (Table 30). Maximum values were much lower in the Ells and MacKay rivers, although the largest mean value occurred in the Ells River where the standing crops experienced less variation. The rivers can be classified as eutrophic following Butcher (1946) who gave cell numbers of benthic algae between 2 to 10 x 10^9 cells m^{-2} for eutrophic waters.

Disparities arose between cell numbers and chlorophyll *a* content. This is not surprising since the epilithic algal community comprises a vast, heterogeneous collection of different algae of different sizes, chloroplast sizes, divisions, and undoubtedly physiological states. Also, cell numbers will over-emphasize the importance of tiny but numerically abundant algae and under-emphasize the large but less abundant forms (Hickman 1973). Chlorophyll *a* is

Table 30. Maximum and mean contribution of the epilithon to the organic matter of the five rivers.

River	Organic Matter ($gm \cdot m^{-2}$)	
	Maximum	Mean
Muskeg	10.15	1.53
Steepbank	11.48	1.15
Hangingstone	10.28	1.13
MacKay	1.53	0.40
Ells	5.58	2.15

a measure of volume (organelle volume) and, in communities comprising such a heterogeneous collection of algae, is usually more closely related to estimates of cell volume (Hickman 1973).

Overall, primary productivity of the epilithic algae was greatest in the Muskeg and Ells rivers followed by the Steepbank, Hangingstone, and MacKay rivers. It was, in general, related to standing crop size; more so than irradiance, with few exceptions occurring. In none of the rivers, during the overall study or during the two open water periods, was it ever correlated with standing crop in all three instances. Mean primary productivity and standing crops were also closely related. The annual epilithic algal production ranged from 36.2 to 110.0 gm C m^{-2} in the MacKay and Muskeg rivers, respectively. Values of 71.4, 54.4, and 101.6 gm C m^{-2} were formed for the Steepbank, Hangingstone, and Ells rivers, respectively.

In flowing systems, the actual passage of water over the rock surfaces and attached algae affects respiration gaseous diffusion, mineral uptake, and photosynthesis rates. As indicated by McConnell and Sigler (1959), Hickman (1974), and Marker (1976b), any chamber in which circulation does not occur is likely to underestimate productivity. The chambers used in this study attempted to circumvent this problem by utilizing natural river current to create circulation inside the chamber. This was first attempted by Bombowna (1972). However, even if current velocities were comparable inside and outside, the actual water movement at the surface or among the attached algae is probably quite different (Marker 1976b). Moreover, the shape and size of the chamber will affect water movements. Only in two rivers did positive correlations result between primary productivity and current velocity (Table 31); the majority of correlations were negative. These data no doubt arise from the relationship between current velocity and standing crop sizes (Table 20) where invariably negative correlations resulted. This again indicates the importance of physically disruptive forces in controlling epilithic algal standing crop size and because of the close relationship between the latter and productivity, epilithic algal primary productivity.

Specific rates of photosynthesis [mg C(mg chlorophyll a $)^{-1} \cdot h^{-1}$] were variable among the rivers (Table 32). These values are

Table 31. Relationship between epilithic algal primary productivity and current velocity.

Rivers	Entire Study Period	Open Water 1978	Open Water 1979
Muskeg	N.S.	$r = 0.165$ $p < 0.25$	$r = -0.825$ $p < 0.10$
Steepbank	$r = -0.284$ $p < 0.25$	N.S.	$r = -0.685$ $p < 0.25$
Hangingstone	N.S.	N.S.	N.S.
MacKay	$r = -0.383$ $p < 0.10$	$r = -0.429$ $p < 0.25$	N.S.
Ells	$r = 0.396$ $p < 0.10$	$r = 0.873$ $p < 0.05$	$r = -0.989$ $p < 0.05$

Table 32. Mean specific rates of photosynthesis [mg C (mg chlorophyll a)$^{-1}$·h^{-1}].

River	Mean
Muskeg	8.64
Steepbank	3.01
Hangingstone	0.82
MacKay	1.16
Ells	3.60

greater than found by McConnell and Sigler (1959), Bombowna (1972), and Marker (1976b) for benthic algae in rivers. The mean value in the MacKay River was similar to that for epiphytic algae in a small pond (Hickman 1971a). Values for the other rivers were similar to values found by Hickman and Klarer (1975) for epiphytes in Lake Wabamun, Alberta [range 5.3 to 20.8 mg C(mg chlorophyll *a*)$^{-1}$$\cdot$h^{-1}] .

Therefore, in summary, this study has described the major epilithic algal groups; the species composition and succession of dominants; standing crops (chlorophyll *a* and cell numbers); primary productivity; and, very briefly, nitrogen-fixation fluctuations in relation to the physico-chemical environment. The factors influencing the algae, their wax and wane, standing crops, and primary productivity have been indicated. No one factor is responsible; instead, interacting factors are responsible. By far, the most important are the physical factors, both disruptive and non-disruptive, and of these, current velocity and discharge are most important. The latter is also related to the chemical makeup of the water itself. Thus, discharge and, to a lesser extent, the biota modify the nutrient status of the water. Current velocity, a physically disruptive force, is important in affecting and controlling population size, standing crops, and primary productivity, the latter through controlling standing crop size. Naturally, some of the epilithic algae grow better in faster flowing water since they are better adapted than others. Their growth is enhanced by increases in current velocity (e.g., Cyanophyta compared to filamentous Chlorophyta). Therefore, any manipulation of discharge rates and current velocity will greatly affect the epilithic algae and the chemical environment of the river. Control to eliminate drastic changes in discharge and current rates will undoubtedly increase standing crop sizes and productivity. However, too much reduction could lead to sedimentation of suspended inorganic and organic matter carried in the water and elimination of the attached flora and fauna, with replacement by organisms preferring inorganic and/or organic sediments.

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