COMMUNITY DYNAMICS OF DESMIDS (CHLOROPHYTA) IN PEATLAND POOLS OF THE NORTH HARBOUR PENINSULA: THE SIGNIFICANCE OF HABITAT VARIATION

E. TODD HOWELL

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Community Dynamics of Desmids (Chlorophyta) in Peatland Pools of The North Harbour Peninsula: The significance of Habitat Variation

by

© E. Todd Howell, B.Sc. (Hons.)

A thesis submitted in partial fulfillment
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ABSTRACT

Three primary gradients of pool habitat variation have been identified for twelve pools within adjacent slope fen and basin bog environments on the North Harbour Peninsula, Newfoundland. These gradients correspond to: 1) a minerotrophic gradient 2) a permanency gradient and 3) a surface water flow gradient. The dynamics of desmid communities associated with the Sphagnum fringes of these pools have been examined and are strongly modified by the gradients.

Fifty-eight of the desmid species observed were distributed with the minerotrophic gradient and range from those endemic to minerotrophic pools (43%) to those endemic to ombrotrophic pools (16%). Pool dominants were heterogeneously distributed and comprised associations with few shared species at extremes of the gradient. The determining factor in relation to minerotrophy appears to be changes in water chemistry. Positive correlations were found with pH, Ca, Mg, Fe, NO_3^- and silicate and negative correlations with tannins + lignins COD and PO_4^{3-} ($P > .01$).

Thirty-eight of the desmid species were restricted to permanent pools. The less-species-rich temporary pools shared most all dominant species with permanent pools but lacked many of the permanent pool dominants. Dominant species of temporary pools showed a greater unevenness of abundance than in permanent pools. The determining factor

with respect to pool permanency appears to be differential desiccation tolerance by vegetative cells in desmid species.

Pool water flow lowered total desmid population densities and induced a high degree of temporal variability, apparently by washing away portions of the loosely adhering desmid growths.

No systematic temporal variation, other than seasonal total population changes, was observed in the desmid communities over the study period. Pools not subject to water flow or temporary drying showed persistance in the importance of dominant species groups. The high degree of temporal consistency in the desmid communities was in contrast to a high degree of temporal variation in pool water quality.

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INTRODUCTION

The desmid (Chlorophyta, Desmidiaceae) flora of peatlands is diverse and highly heterogeneous (Strom, 1926; Flensburg, 1967; Flensburg & Malmer, 1970; Peterfi, 1974; Woelkerling, 1976), and this heterogeneity is paralleled by a strong variation in the biotic and abiotic conditions which prevail on a small scale and over time, even within a single peatland site. An important question, which is addressed in this study, is: to what degree does the peatland habitat variation contribute to the dynamics of the desmid communities, and what are the factors which are causative of this variation?

The Island of Newfoundland, with more than 200,000 ha of peatlands (Wells & Pollett, 1983), offers an ideal situation in which to address this question. By selecting a site with marked gradients of conditions, and by the employment of quantitative sampling techniques combined with measurement of biotic and abiotic variables, it is possible to render such a potentially unwieldy investigation somewhat manageable in scope. The study concerns a series of twelve peatland pools situated in a single site at North Harbour, on the Avalon Peninsula, Newfoundland, these pools selected to provide as wide a range as possible of the biological and ecological conditions likely to be encountered on a bog site typical of much of the Avalon Peninsula.

Of the seven published works on Newfoundland desmids all but one consist of taxonomic lists from a range

of habitats, including peatlands. The works of Taylor (1934, 1935) provide a valuable taxonomic basis for desmid study, consisting of the description and illustration of a large number of taxa. The sole ecological peatland work is that of Howell & South (1981), and although posing general questions on desmid population changes it is limited in application, dealing with only a single small genus, Tetmemorus.

Quantitative ecological studies of desmids in the peat habitat are limited (Duthie, 1965; Woelkerling, 1976; Woelkerling & Gough, 1976; Howell & South, 1981; Hooper, 1981). The most suitable technique available is that of Gough & Woelkerling (1976a) which is designed for sampling the "aufwuchs" (Sladeckova, 1962) component of aquatic macrophytes. In this study the aquatic Sphagnum of peatland pool fringes was used as the sampling substrate; the method had been employed with a measure of success by Howell & South (1981) and Hooper (1981), based on the Gough & Woelkerling (1976a) methodology. This study appears, however, to be the first in which such a quantitative technique has been employed to examine the relation between desmid communities with respect to a variety of habitats and over time, within a single peatland site.

Newfoundland peatlands have been extensively studied (see Wells & Pollett (1983) for a review) and are well characterized. Gradients of habitat are well documented, and are concerned with site topography and

variables associated with development of the peat layer. In general terms, changes in the origin of moisture supply to peatland pools, either strictly atmospheric (ombrotrophic condition) or atmospheric plus from mineral soil water (minerotrophic condition), correspond to a main gradient of variation paralleled by changes in water chemistry and biological characteristics. Further factors important with respect to the peatland pool environment include the permanency of the water body (Malmer, 1962b; Hosiaisluoma, 1975) and the degree of water movement (Sparling, 1966; Ingram, 1967), both with consequential changes in physical, chemical, and biological variables.

Previous studies suggest that desmid communities are affected by changes associated with these gradients (Flensburg, 1967; Flensburg & Malmer, 1970; Flensburg & Sparling, 1973; Hosiaisluoma, 1975; Jensen et al., 1979; Coesel, 1981, 1982). By combining quantitative desmid sampling with measurement of these gradients over time at the North Harbour site, it was hoped to be able to assess the degree and the way in which the variation associated with these gradients contributes to desmid community dynamics.

Water quality changes associated with the minerotrophic gradient have been speculated as causal in the changes in desmid composition in peat pools (Du Rietz, 1954; Péterfi, 1974). The understanding of chemical factors important in desmid growth is however limited. Laboratory culture experiments indicate that pH, Ca, and CO_2: HCO_3^-:

CO_3^{2-} balance individually or in concert may affect desmid growth (Van Der Ben, 1970; Moss, 1972, 1973a, Tassigny, 1971a; Hosiaisluoma, 1976; Gough, 1977). Interpretation of the results of these works in relation to minerotrophic gradient is limited by the number of species tested and the difficulty in relating experimental conditions to those in nature.

The permanency of peatland pools has been reported as important in determining the richness and composition of desmid communities (Grönblad, 1935; Croasdale, 1973; Hosiaisluoma, 1975). Most desmid species are considered intolerant of even limited desiccation (Evans, 1958, 1959) with non-permanent water bodies characterized by the few tolerant species. The effect of what must be a differential level of desmid die-off along the permanency gradient on community structure has not been determined. Evapo-concentration of the water mass of small temporary pools during warm weather has a strong effect on water chemistry (Malmer, 1962b; Tolonen & Hosiaisluoma, 1978). It is unknown what consequence this differential change between permanent and temporary pools has on observed desmid spatial patterns.

Surface water movements in peatland pool systems act in transporting organisms and material, and are erosive and abrasive forces. Moving waters are less stagnant, better oxygenated and with chemical character differing from standing water (Sparling, 1966). Bland & Brook (1974) found

water circulation to be destructive to desmid communities of the macrophyte aufwuchs in the littoral regions of ponds and lakes, resulting in fewer species and lower total populations. No information relating to the consequence of water movement on desmids could be found in the peatland context.

Temporal succession in desmid species composition and dominance are reported in fen waters (Duthie, 1965; Howell & South, 1981). Other workers have reported consistency, at least over a seasonal cycle (Coesel, 1982; Hooper, 1981). Temporal changes in the peat environment are pronounced over a seasonal cycle as a result of changing weather conditions and biological activity. Of general importance to pool biota are changes in water temperature, illumination and water chemical composition. Seasonal differences are reported by Malmer (1962b), Duthie (1965), Grolière & Njine (1973), McLachlan & McLachlan (1975), and Howell & South (1981). Conceivable differences in temporal change in water quality exist between ombrotrophic and minerotrophic waters due to differences in gross biological activity and may explain differences in temporal change in desmid communities.

Qualitative field study of desmids in the peatland habitat have produced much speculation on causes and consequences of habitat variation on the dynamics of the desmid community, yet no one has accurately documented community dynamics using quantitative methods over the

supposed gradient ranges. A quantitative estimation of the dynamics over peatland habitat gradients will allow a more rigorous testing of the distributional hypothesis generated by qualitative methods, will allow a more refined examination of causal agents in desmid dynamics, and will allow an examination of the nature of community ecology in desmids.

MATERIALS AND METHODS

STUDY SITES

A fen site and bog site situated on the North Harbour Peninsula, St. Mary's Bay (Figure 1) were selected for study on the basis of their having a wide range of pool types in close proximity. From this peat complex, 12 pools, judged to have the widest variation in degree of minerotrophic influence and size, were selected for detailed study. The initial evaluation of minerotrophic status of the pools was based on vegetational composition of the pool area and field pH measurements of pool water.

Peat depth contour maps were made for both sites and a surface elevation (relative) map for the fen site. The elevation map was made to evaluate direction and potential for surface flow between sample pools. Since the bog site was mostly flat, with no inter-flow between pools, such a map was unnecessary.

The positions of peat depth determinations were based on a grid divided into squares of 20 x 20 paces. The depth was determined using a Russian-type peat corer. An aerial photograph (No. A19760-85; Dept. Energy, Mines and Resources, Canada) was used to determine the site perimeters. The map placement of the site pools and depth contours was based on compass triangulation. The elevation contours for the fen site were determined from readings from positions on a grid with 5 m squares. Relative elevation was determined using a Wild level and a stadia rod.

Elevations are given relative to the lowest point on the site.

Prior to sampling, marker pegs of lengths of wooden dowel rods were driven into the pool sediment in the deepest part of the pool. These rods were marked at water level to provide a reference point to allow fluctuations in pool water level to be recorded.

Peat water level measurments began in March 1981. Perforated PVC tubing with an inside bore diameter of 4 cm, length of ca. 150 cm, and plugged at the base was used to measure peat water level. Two such tubes were placed on each site, being driven into the peat as far as possible with the pipe top remaining above the peat surface. Water levels in the pipes were measured with a dip stick.

Qualitative vegetational surveys were carried out throughout the study period (Sept. 1980 - Aug. 1981).

A Ryan thermograph was placed at the water surface in the largest permanent pool of the study site (PB1, Figure 2) in March 1981 and ran continuously to the end of the study period.

STUDY POOLS (NAMING SYSTEM)

All study pools were designated by a name consisting of two letters a number. The first letter is either P or T and is descriptive of the degree of permanency of the water body over time. This attribute is variable between all pools, but two broad classes are apparent. A subjective boundary was defined to separate pools that would

be expected to dry up over a growing season from those which would not be expected to dry up. A pool in which the aquatic Sphagnum fringe was fully exposed to the atmosphere due to recession of the pool water level at any point during the study period was classed as a temporary pool and designated by a T. A pool in which this did not occur at any point during the study was classed as permanent and designated by a P. A more critical relative evaluation of pool permanency is given in the evaluation of the pool permanency gradient.

The second letter in the name is either B (bog) or F (fen), but with designations not intended to be interpreted in terms of pool minerotrophic status. It identifies which of the two study sites the pool was located on. The number in the name is used to separate individual pools of the same two letter designations.

SAMPLING PROCEDURE

Quantitative Sampling of Desmids

On nine occasions from September 1980 to August 1981 quantitative samples of desmids in the aquatic Sphagnum fringes were taken from each of 12 sampling pools of the two sites (see Table 1 for dates). Samples for all pools in any given month were taken within a 4-day period. Sampling procedures were based on Gough & Woelkerling (1976a) and Howell & South (1981). Sphagnum shoots of the pool fringes, fully submerged and at surface level were sampled. Samples were removed by hand by gently separating a clump of shoots

Table 1: SAMPLE DATES AND NUMBERS OF SPHAGNUM SAMPLES IN SAMPLE SETS

Pool	Number of Sphagnum samples in set	'80 Sep	80 Nov	80 Dec	81 Mar	81 Apr	81 May	81 Jun	81 Jul	81 Aug
					Day					
TB1	2-3 (1)	3	8	16	7	22	21	23	23	25
TB2	2 (1)	3	10	16	7	22	21	23	23	25
PB1	6-8 (3)	3	8	16	7	22	21	23	23	25
PB2	6-8 (3)	3	10	16	7	22	21	23	23	25
PB3	5 (3)	2	7	17	6	21	20	22	22	25
TF1	3 (1)	4	8	16	8	21	20	22	22	24
TF2	3 (1)	2	7	17	8	21	20	22	22	24
TF3	3 (2)	2	7	17	6	21	20	22	22	24
TF4	3-4 (1)	2	7	17	6	21	20	22	22	24
PF1	4-5 (2)	4	8	17	8	21	20	22	22	24
PF2	5-6 (2)	4	8	18	8	21	20	22	22	24
PF3	8-10(3)	4	8	17	8	21	21	22	22	24

Note: Values in brackets give the number of samples taken in December 1980 when pools were ice and snow covered.

and placing them in plastic bags (Whirlpac; 21 x 14 cm). The amount removed was estimated in proportion to the sample bag to maintain a roughly comparable sample mass. The procedure was completed quickly and without squeezing. A sampling container as used by Howell & South (1981) was not suitable for this study, due to large variations in absolute amounts and tightness of packing of the fringe Sphagnum. Sampling positions along the pool fringe were randomly located; at each sample position the nearest portion of Sphagnum fringe was removed.

The number of samples taken from individual pools varied (Table 1) and was subjectively assigned on the basis of pool size and availability of removable Sphagnum fringe. There is a positive correlation between pool size and numbers of samples taken, but it is not strictly related to perimeter length. The number of samples taken was reduced during the period when the pools were snow and ice covered, and samples were difficult to obtain without damage to the pool.

Water chemistry

For every set of algal samples taken during the study, two water samples were taken from specific points in each sample pool. One litre and 0.25 l polyethylene bottles were submerged below the pool surface and completely filled. In the temporary pools, when water levels were too low for this procedure, water was removed using a hand operated

suction pump. This allowed a minimum of disturbance to the sediment. At the same point, bottom and surface oxygen levels and temperature were measured using a portable YSI oxygen meter.

For one or two dates from July-August 1981 profiles from water surface to sediment for pH were determined using a combination pH probe. Sediment depth and layering of the pool were also determined on these data.

Physical Measurements

On each sample date the water level of the pools relative to marker pegs was determined. Peat water level in the four measuring tubes was also determined.

A general summation of the physical condition of the pool and surrounding peat was made on each sample date. This included observations on sediment colour and texture, water surface scums, water flow and vegetational changes (mainly new growth and decay changes).

SAMPLE ANALYSIS

Preparation of Desmid Samples

All Sphagnum samples taken for algal analysis were immediately fixed with 50 ml of FAA (26:10:3:1; water:95% ethanol:formalin:glacial acetic acid). The removal of the aufwuchs material from the Sphagnum was based on a procedure given by Gough & Woelkerling (1976a).

Samples from the same pool for each sample date were combined to produce one final sample. Replicated sets of samples were taken for a representative set of four pools during the August 1981 sample dates.

Each sample in a pool set was treated similarly. The preserved sample was first agitated by squeezing within the Whirlpac bag for ca. 1 min. The liquid portion of the sample was poured through cotton gauze into a clean volumetric flask. The sample then had another 50 ml of FAA added, was similarly agitated and poured into the same volumetric flask. The sequence was repeated for a third time. All samples in the pooled set were similarly treated with washings being poured into the same initial volumetric flask. Sizes of flasks used ranged from a 500 ml flask for 2 samples up to a 2000 flask for 8 samples. Following addition of all sample washings to the flask, distilled water was added to fill the flask to the exact volume. The flask was then capped and shaken well. A total of five subsamples of 10 ml volume were removed from the flask using a volumetric pipette and placed in capped 15 ml centrifuge tubes. These were the quantitative desmid samples.

The efficiency of the algal extraction procedure can be inferred from Howell & South (1981) in which a similar procedure extracted between 86-93% of the desmid material based on a total from six washings. Gough & Woelkerling (1976a) also evaluated a procedure similar to that used in this study and predicted an 88% removal of

algal material from Sphagnum shoots given a washing effort comparable with that used in this work.

The remaining moss portions of the samples were placed on preweighed filter paper and dried in an oven at 75-85°C for 48 h and then weighed to ± .005 g.

Idehtification and Qualitative Analysis of Desmid Samples

From the initial September and November 1980 samples a detailed list of all observed desmid taxa was made. Each identification was accompanied by a scaled drawing made with the aid of an Abbe drawing tube. Photomicrographs were taken for many taxa. These results are not presented but are available for confirmation of identifications. Identifications follow a number of authors and are presented in Appendix I. Identification was aided by the use of an Iconograph of desmids compiled and owned by Dr. H.C. Croasdale (Dartmouth College, New Hampshire). Interpretations and groupings of taxa result from observations of field material from which only distinct and separable taxa were recognized and used.

The qualitative analysis was made on Sphagnum - extracted quantitative samples. For each pool sample, a list of taxa was made. The procedure in this project used a total of 8 slides (3 qualitative and 5 quantitative). The qualitative slides were made from a drop of concentrated desmid sample covered with a 22 x 22 mm coverslip; they were completely scanned. The number of qualitative slides

required to record most taxa in a sample was determined from trials where further slides were examined until no or very few new taxa were observed.

Quantitative Analysis of Desmid Samples

Sedgwick-Rafter counting chambers (1 cm^3 volume, 1000 mm^2 surface area) were used to count desmids in terms of volume of sample, and counts were then used to calculate numbers of desmids in relation to Sphagnum dry weights. This was done by counting desmids in 20 random fields (0.96 mm^2) from a Whipple grid in the microscope ocular, from each of five slides (chambers), at a magnification of 100X. The initial desmid samples were variably concentrated (0-100%), depending on the density of particulate material in the sample, prior to use. Before addition of the sample to the chamber, the sample was mixed thoroughly. The chamber was filled using a procedure recommended by McAlice (1971). A large bore pipette was used to fill the chamber at one of two open corners remaining when a coverslip was slid across the slide chamber at a 45° angle. The slide was allowed to settle for a minimum of 10 minutes before examination as recommended by Woelkerling et al. (1976) for FAA preserved material.

The reproducibility of the counts were determined from replicates. The desmid totals from 2 replicates were within 10% of the mean; of a total of 9 taxa with cell

counts of 10 or more, 8 were within 15% of the mean, the other was within 20% of the mean.

The calculation of desmid quantities was made using the formula:

Cells/g of dry *Sphagnum* = A/B x C/D x E/F x G/H

where

A = total bottom area of counting chamber

B = area of whipple grid

C = number of cells observed in total count

D = number of fields counted

E = volume of washings (Volumetric Flask size)

F = weight of dry *Sphagnum*

G = volume of concentrated desmid sample

H = volume of initial sample

For preparation of results, estimates were treated in one of three ways depending on the total number of cells observed. Taxa on which the estimate is based on nine cells or more are given as a real number. Taxa based on 4-8 cells are noted as present in low relative amounts. Taxa totalling less than four cells were not reported individually, but combined to give a value for undetermined (undet.) taxa. Only living cells (with chloroplasts) were used in the quantitative enumeration. For filamentous taxa, individual sections of filament were considered a single individual.

Water Sample Chemical Analysis

The North Harbour sites are within walking distance of a cabin which was used as a field laboratory.

The 1 l water samples were filtered through a glass fiber filter (Gelman type A-E) using a suction apparatus, within an hour of collection. At the same time colour was determined for 20 ml of the filtered water by visual comparison with a series of Pt/Co standards. The remaining portion of the sample was then frozen until further analysis. The 250 ml water samples were first used to determine pH, this being done with a Corning 610A expanded scale pH meter. A pH - reference combination electrode was allowed to sit in the unagitated sample until equilibrium was reached. The water sample was then placed in an Erlenmeyer flask and heated in a water bath to 25°C. Conductivity was determined using a Barnstead BM 70-CB conductivity meter and a YSI cell with a constant of 0.1 ± 1%. It was observed that conductivity readings wandered and would not stabilize in some cases after periods of more than 15 minutes. It was suggested that this resulted from adsorption of material in the water onto the platinum plates of the probe (M. Hooper, pers. comm.). It was decided to use a 10 sec immersion period of the probe for readings. The measurement was repeated 3-5 times until a consistent reading was obtained. Such results were reproducable and are considered valid. The field determined oxygen levels in

sample pools were converted to percentage oxygen saturation using the nomographic method of Mortimer (1981).

Further chemical analyses of water samples were performed by the Water Analysis Facility of the Chemistry Department, Memorial University of Newfoundland. Parameters measured and methods used are given in Table 2. Samples were frozen for periods up to 3 months prior to analysis.

Macrophyte Vegetation Analysis

Vegetation analysis consisted of visual estimates of abundance of macrophytes, mainly those in and around the sample pools. Collected samples were preserved by pressing or air drying and were then identified. Sphagnum identifications follow Nyholm (1969), except S. flavicomans which is after Crum & Anderson (1981). Due to an inability to separate S. nemoreum and S. subnitens, specimens of these taxa are grouped and referred to as S. nemoreum/subnitens. Other bryophytes follow Crum (1976). The liverwort Gymnocolea inflata is after Arnell (1971). The vascular plants are after Ryan (1978) for the trees and shrubs and Marie-Victorin (1964) for all others.

Quantitative Data Analysis

The qualitative desmid data and percentages from quantitative desmid data were arranged in an ordered two-way table by classification of taxa and samples using the program TWINSPAN (Hill, 1979b). TWINSPAN is a polythetic

Table 2 : WATER CHEMISTRY PARAMETERS MEASURED BY THE WATER ANALYSIS FACILITY, MUN, AND METHODS USED

PARAMETER	UNITS OF MEASUREMENT	METHOD USED
Ca	mg/l Ca	A.A.S. with N_2O / acetelyene flame
Mg	mg/l Mg	A.A.S. with air / acetelyene flame
Fe	mg/l Fe	A.A.S. with air / acetelyene flame
Na	mg/l Na	A.A.S. with air / acetelyene flame
silicate	mg/l Si	T.A., Anonymous(1980) no. 14105
nitrate	mg/l N	T.A., Anonymous(1980) no. 07110
ammonia	mg/l N	T.A., Anonymous(1980) no. 07505
phosphate	mg/l PO_4	T.A., Anonymous(1980) no. 15256
total P	mg/l PO_4	T.A., Anonymous(1980) no. 15406
chloride	mg/l Cl	Anonymous(1975), method 408 A
sulfate	mg/l SO_4	Anonymous(1975), method 427 C
tannins+lignins	mg/l	Anonymous(1975), method 513
COD	mg/l	Anonymous(1975), method 508
Kjeldahl N	mg/l N	Strickland & Parsons(1972)

notes : A.A.S. = Atomic Absorption Spectrophotometer, Varian Techtron 5.

T.A. = Technicon Autoanalyser II

devisive method and is a development of the method of Indicator Species Analysis of Hill et al. (1975). A series of ordinations by Reciprocal Averaging of Hill (1973) are used to identify directions of variation in data groups which are dichotomously split to produce a hierarchy. Samples are first classified and then preferences of species in samples are used to define a classification of species. TWINSPAN was not used in this study to define groupings of samples and species.

An ordination technique called detrended correspondence analysis (DCA) (Hill, 1979a; Hill & Gauch, 1980) and a computer program DECORANA (Hill, 1979a) was used to ordinate qualitative and quantitative desmid data. Qualitative compositional data were changed to a quantitative form prior to ordinations by summing the number of times a specific taxon occurred in a pool out of the nine sample dates. Thus one value, an integer between 1-9, was obtained for each taxon for each pool. The quantitative dominant species data were used in raw form, cells/g dry Sphagnum for ordination. All taxa were used in the qualitative ordination, whereas for quantitative data ordinations, trial ordinations were used to identify outliers. These taxa were removed in subsequent trials and are noted in the results. In all ordinations rare species were not down weighted and program default options for rescaling of axes, numbers of segments used and the rescaling threshold were used. An overview of DCA, its use

with DECORANA, and its interpretation are given in Appendix II.

Sample scores on extracted axes obtained in the quantitative desmid ordinations were analyzed with respect to sample water composition using correlation analysis with the Pearson correlation coefficient (Sokal & Rohlf, 1981). The significance levels of the correlations were also determined.

RESULTS

STUDY AREA

The North Harbour Peninsula has abundant peat deposits (Figure 1). A medially situated plateau rising to an elevation of ca. 80 m is covered with an extensive blanket bog. The sloping sides of the peninsula are composed of a mosaic of Picea mariana (Mill) B.S.P. forest and sloping fens.

The bog site lies at the north end of the plateau; morphologically it fits the domed bog of Wells (1981). The peat surface is mostly flat, but slopes slightly along the east edge, with a Picea mariana forest margin. The study pools are above this sloping area. Maximum peat depth of the site is 3.5 m, this being in a central depression. The domed nature of the bedrock bottom and the decrease in peat depth at the margins are apparent from Figure 2. Pools and wet hollows are abundant on the site. Five pools were considered permanent and did not dry up on any date during the study. No water flow was observed from any point on the site, with impermeable boundaries of peat separating the pools.

The west margin of the area is composed of two forested hills, drainage from which reaches the bog edge. No apparent surface flow onto the bog was observed. The surface vegetation of the site is a combination of dry low hummocks dominated by Sphagnum and sedges, and hollows which may be dry and similar in vegetation to the hummocks, or may

Figure 1: Location of the North Harbour study sites.

legend: A = bog site

B = fen site

(:::) = peat deposits

50 ------ 50 = surface elevation contours (in feet)

note: This Figure was based on the following:

1) aerial photograph no. A19760-85, Department of Energy, Mines and Resources, Canada.

2) 1: 50,000 topographic map no. 1 N/4, Department of Energy Mines and Resources.

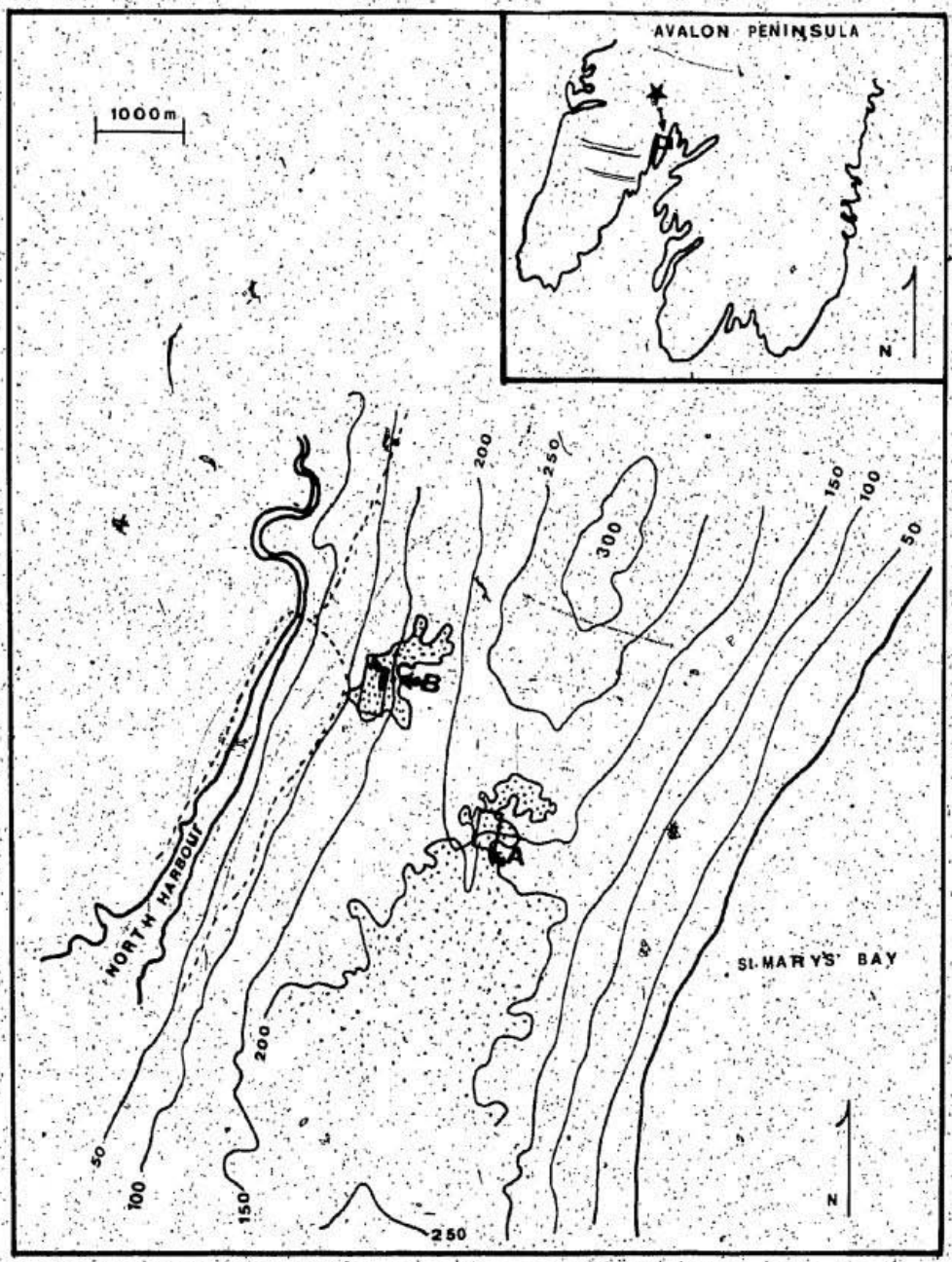

AVALON PENINSULA
N
1000m
200
250
300
150
100
50
NORTH HARBOUR
ST. MARY'S BAY
N
50
100
150
200
250

Figure 2: Bog site map with peat depth contours.

legend:

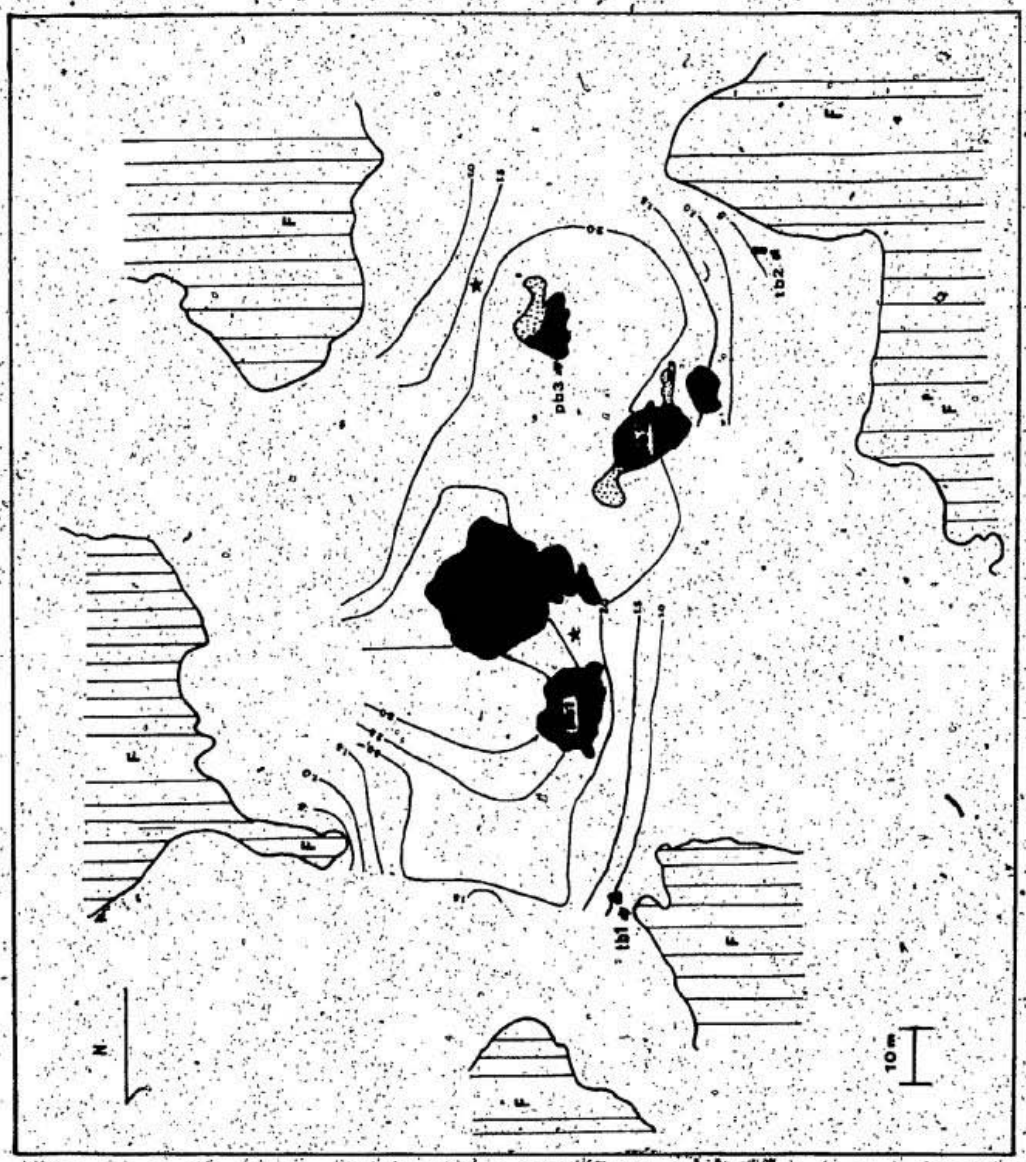
pb1 = sample pool

★ = location of peat water level measurement pipe

1.0 ——— 1.0 = peat depth contours (in meters)

F = forested areas

= wet flats


F
F
F
F
F
F
F
tb2
pb3
tb1
N
10m

be wet and dominated by Sphagnum. There are also large areas of wet flats dominated by Sphagnum. See Figure 3 for a general view of the bog site.

The fen site is situated near the bottom of the west slope of the peninsula (Figure 1). The surface morphology of the area is heterogeneous and characteristic of a slope fen (Wells, 1981).

The south end is an area of relatively heavy peat deposition with a maximum depth of 3 m (Figure 4). Proceeding north, this area is bordered by a sloping, funnel-shaped drainage area characterized by large amounts of water and loose waterlogged peat. At the north fringes of this area the peat surface rises to a flat to slightly sloping area of shallow minerotrophic peat with a depth of less than 1 m. There are small drainage paths in this region (Figure 5). The margins of the site are forested, with Picea mariana being the dominant tree species. See Figure 6 for a general view of the fen site.

Detailed descriptions of sample pool morphometrics, Sphagnum fringe characteristics, bottom construction and vegetation are given in Appendix III. Photographs of representative bog and fen site pools are given in Figures 7 and 8 respectively.

Figure 3: General view of the bog site.

Figure 4: Fen site map with peat depth contours.

legend:

PF1 = sample pool

★ = location of peat water level measurement pipes

1 ——— 1 = peat depth contours (in meters)

≡ = forested areas

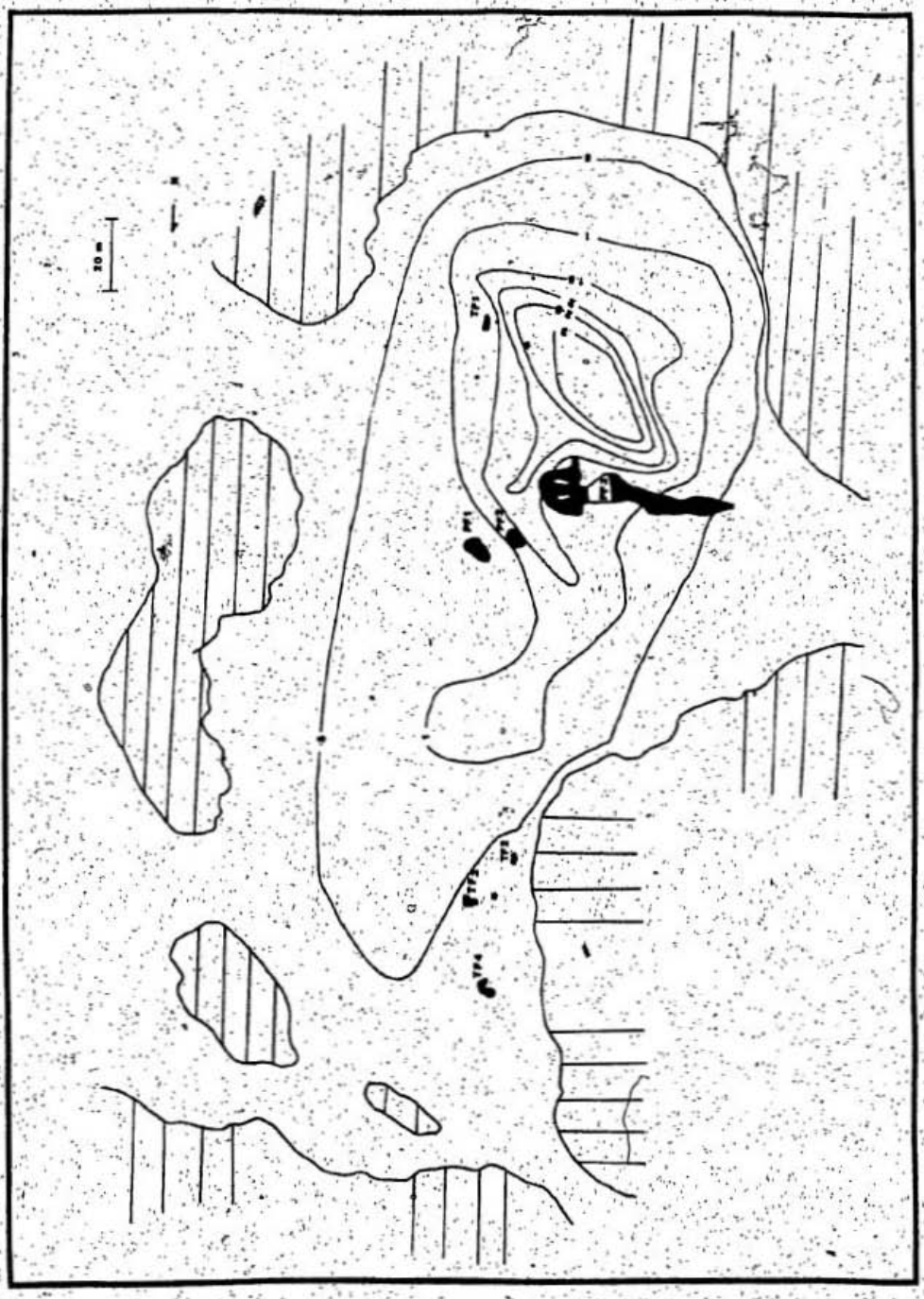

20 m

Figure 5: Fen site map with relative surface elevation contours.

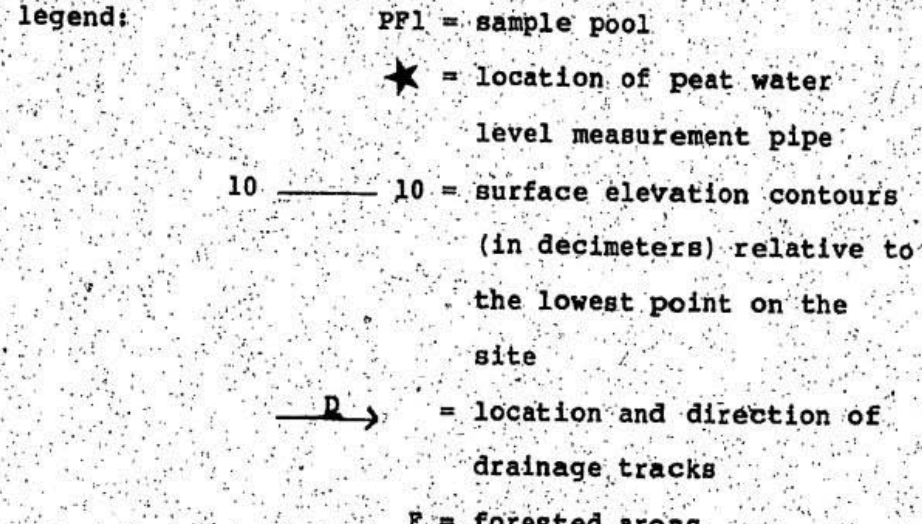


Figure 6: General view of the fen site.

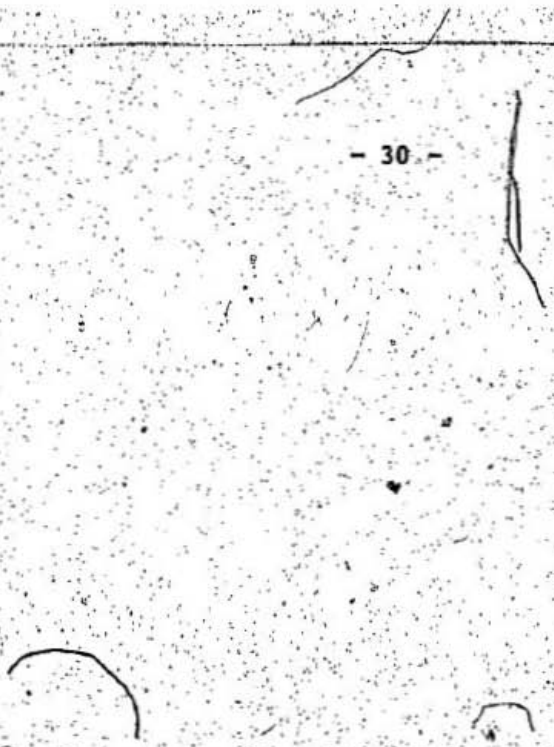
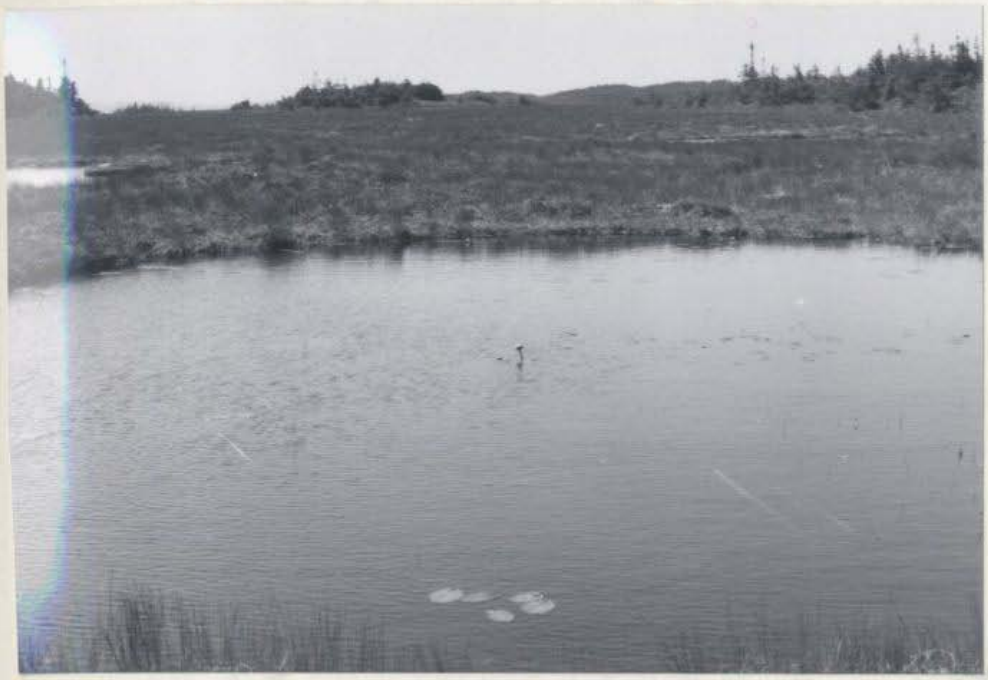


Figure 7: Representative examples of the bog site sample pools.



POOL
PB1

POOL
TB2

Figure 8: Representative examples of the fen site sample pools.

POOL
PF3

POOL
TF3

RELATIVE PLACEMENT OF STUDY POOLS ON PRIMARY GRADIENTS OF SPATIAL HABITAT VARIATION

Rationale

The critical evaluation of physical, chemical and biological parameters of habitat variation concurrent with the location and time of desmid sampling was a prerequisite for this study. Given an accurate documentation of the spatial dynamics of the desmid community, interpretation of habitat relations would be limited by the detail of habitat examination.

From the suite of physical/chemical variables of habitat condition examined, it was possible to identify three primary gradients of spatial variation relevent to pools. Described will be a minerotrophic gradient, a permanency gradient and a surface water flow gradient. These gradients incorporate groups of variables which have both direct and indirect relations with the primary gradient. These gradients were used as the basis for evaluation of habitat variation with desmid spatial patterns. The gradients were defined on the basis of a composite of specific physical/chemical variables. The validity of the variables used in assessing the pool placement on gradients is considered in Appendix IV.

Spatial variation in biological variables (macrophyte flora) was not used in defining pool placement on primary gradients because such variables were only

qualitatively examined. The correlation is however strong for variation in components of the macrophyte flora with primary gradients, and can be inferred from Appendix III.

Minerotrophic Gradient

The twelve sample pools selected for study form a gradient on the basis of degree of input of mineral soil water or minerotrophic influence. Two pools, PB1 and PB2, receive the smallest inputs and are interpreted as nearest to the ombrotrophic condition. PB3 is close to PB1 and PB2 on the gradient but is suspected to receive a very slight input of mineral soil water. Five of the six fen site pools are interpreted as highly minerotrophic and lie at the other extreme of the gradient. In PF1, PF2, PF3, TF4, TF2 and TF3 there are heavy inputs of mineral soil water; however, there is variation in the degree to which pool bottom sediment impedes mineral soil water seepage. Three further pools, TB1, TB2 and TF1, are intermediate on the gradient. Pool TB1 is interpreted as receiving a slight input of mineral soil water but lies at the ombrotrophic end of the gradient, whereas TF1 receives a moderate input and lies at the minerotrophic end. TB2 is intermediate to TB1 and TF1.

Initial evaluation of pool placement on the minerotrophic gradient was made on the basis of the character and depth of the pool peat basement, details of which are given in Appendix III. Pools PB1, PB2 and PB3 had the deepest peat bottoms with maximum depths ranging from

200-245 cm. Of note is that PF3 had areas of bottom greater than 200 cm in depth but unlike PB1, PB2 and PB3, in which the pool bottoms were compacted and complete, the bottom was loosely compacted, waterlogged and completely eroded away in places. Thus the peat basement of PF3 does not act as an effective barrier to mineral soil water seepage as in the former permanent bog site pools. Pool PB3 had the minimum depth of peat basement of the three pools (PB1, PB2 and PB3) nearest the pure ombrotrophic condition, that being 110 cm, 40 cm less than PB1 and PB2. This may contribute to a possibly higher degree of mineral soil water seepage in PB3.

Pool TF1 had a slightly lower depth of peat basement than the above group, 80-140 cm, and the bottom was complete and well compacted. This pool lies in a slight depression on a drainage slope (Figure 5) with possibly an increased amount of subsurface water movement.

Pools TB1 and PF2 were comparable in depth of peat basement, 50-80 cm, but differed in bottom character. TB1 had a complete and compacted bottom whereas PF2 had a bottom loose in construction, waterlogged and broken in places. TB1 lies in a mostly level plain whereas PF2 lies in a strong drainage slope (Figure 5). Pools TB2 and PF1 had depths of peat bottom which are comparable and slightly less than those of TB1 and PF2. They differ in character as do TB1 and PF2, with TB2 resembling TB1 and PF1 resembling PF2. Comparable depths of peat basement are thought to be more

effective barriers to mineral soil water seepage in TB1 and TB2 than in PF1 and PF2.

The remaining fen site pools TF2, TF3 and TF4 lacked a peat basement and had the pool water mass in contact with the mineral soil. These pools are highly minerotrophic.

The water chemistry of peatland pools can be used to interpret relative degrees of minerotrophic influence. The composition of atmospheric precipitation and mineral soil water differ strongly and in a predictable way. Given that a pool water mass will be a variable combination of water derived from precipitation (plus organic soil runoff) and mineral soil water, key parameters of water quality can be identified which vary strongly with combinations of water type.

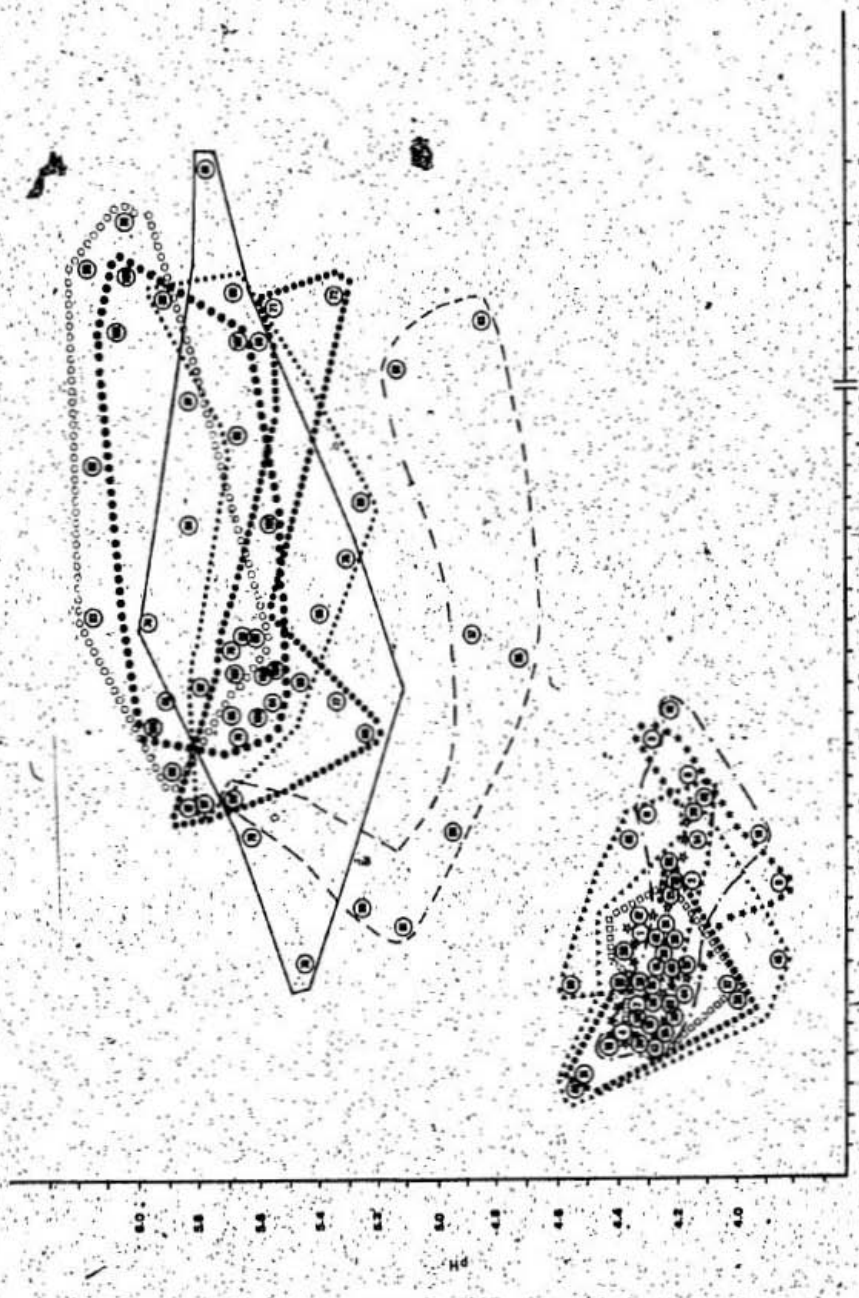
Parameters of water quality interpreted to be most variable with degree of minerotrophic influence (Ca + Mg, pH, Ca:Mg, Fe, COD:tannins + lignins) were used to place sample pools on a minerotrophic gradient.

A scatter plot of all sample values of Ca + Mg against pH (Figure 9) shows two main groupings of samples. The groups are distinct on the basis of pH but overlap in the range of Ca + Mg values. Samples from pools PB1, PB2, PB3, TB1, TB2 and TF1 fall in the low scoring group and samples from TF2, TF3, TF4, PF1, PF2 and PF3 fall in the high scoring group. Pools of the high scoring group were distinctly enriched with mineral soil water. Pools of the

Figure 9: Scatter plot of Ca + Mg against pH using all samples from all pools.

legend:

pool TB1 =	☆ ☆ ☆ ☆	; numbers 1 to 9
pool TB2 =	— · — ·	; numbers 10 to 18
pool PB1 =	□ □ □ □	; numbers 19 to 27
pool PB2 =	■ ■ ■ ■	; numbers 28 to 36
pool PB3 =	△ △ △ △	; numbers 37 to 45
pool TF1 =	▲ ▲ ▲ ▲	; numbers 46 to 54
pool TF2 =	— — —	; numbers 55 to 63
pool TF3 =	● ● ● ●	; numbers 64 to 72
pool TF4 =	———	; numbers 73 to 81
pool PF1 =	O O O O	; numbers 82 to 90
pool PF2 =	* * * *	; numbers 91 to 99
pool PF3 =	✪ ✪ ✪	; numbers 100 to 108


Ca + Mg mg/l
pH

low scoring group were not, or were relatively less enriched with mineral soil water.

The low scoring pool group consists of two subgroups variable in Ca + Mg values. Pools TB1, TB2 and TF1 had maximum values exceeding those of PB1, PB2 and PB3. Interpretation of this result is difficult in that TB1, TB2 and TF1 are shallow, small water volume, temporary pools compared with PB1, PB2 and PB3 which are larger and permanent. The higher Ca + Mg values in the temporary pools need not relate to a greater degree of minerotrophic influence. A greater evapo-concentration of water mass during dry periods and a greater sediment surface area to water volume in the temporary pools may result in higher Ca + Mg values compared with similar permanent pools.

In comparison of the Ca + Mg values of TF1, TB1, TB2 it can be seen that TB1 and TF1 have values mostly higher than TB2 but with strong overlap.

The Ca + Mg values for pools in the high scoring group do not differ greatly and are mostly of a comparable range. An obvious difference, however, is that pH values of pool TF2 are lower than other pool samples in this group. This is not related to the degree of minerotrophic influence since the pool sits directly on bedrocks, but is thought to reflect differences in degree of flushing. TF2 is more structurally isolated by peat margins and more removed from drainage paths (Figure 5). The lower pH values in TF2 are

thought to result from a higher degree of stagnancy of the water mass compared with other pools of the group.

The Ca:Mg ratios for all samples for all pools are given in Table 3. Good separation of the sample pools is apparent. All samples from pools PB1, PB2 and PB3 show a consistent mass dominance of Mg with maximum values being 0.63, 0.72, 0.73 in PB1, PB2, PB3 repectively. This is considered indicative of the ombrotrophic nature of these pools. Magnesium is typically in a greater concentration in coastal precipitation whereas calcium is typically in a greater concentration in mineral soil water (see Mattson et al., 1944). Thus in ombrotrophic pools, fed exclusively or predominately with precipitation, Mg will be in greater concentrations than Ca.

The Ca:Mg ratios for samples of TB1 showed increases over PB1, PB2, PB3; the maximum value was 1.0 with two further values above 0.8. These values were, however, lower than those of the highly minerotrophic pools TF3, TF4, PF1, PF2 and PP3 in which there was an almost consistent mass dominance of Ca. An example is PF2 which had Ca:Mg values ranging from 1.1 to 1.5.

The remaining two pools, TB2 and TF1 had Ca:Mg values mostly higher than the ombrotrophic pools (PB1, PB2, PB3) and mostly less than the highly minerotrophic pools. Pool TB2 has a maximum value of 1.2 slightly higher than the TB1 maximum but otherwise most values were comparable. Similarly, TF1 had a maximum value of 1.18 but had five

Table 3: RATIOS OF CALCIUM OVER MAGNESIUM (MASS ABUNDANCE) FOR POOL WATER SAMPLES

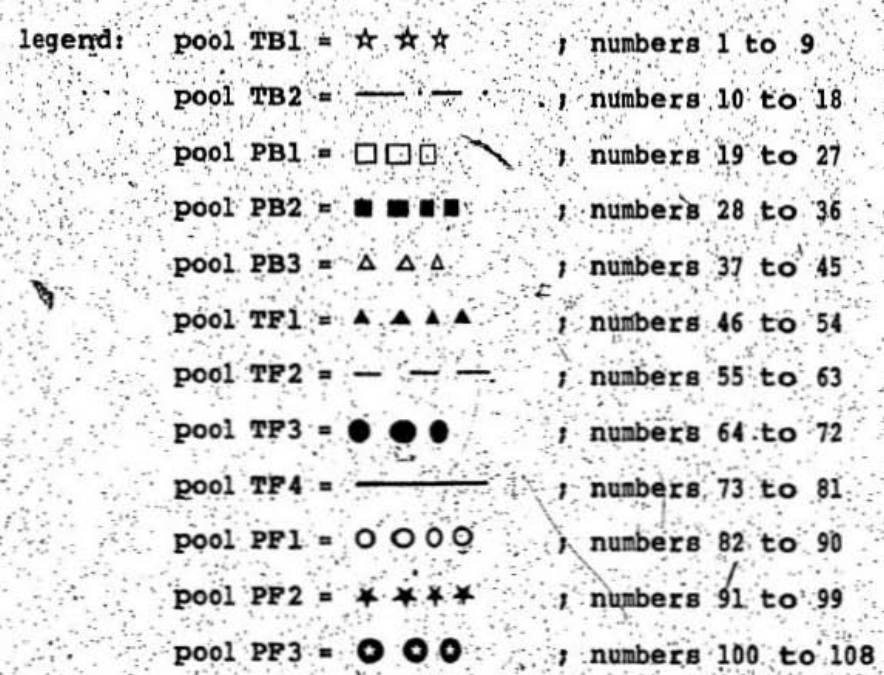
	POOLS			
	PB1	PB2	PB3	TB1
Sept. 80	0.70	0.67	-	1.00
Nov. 80	0.62	0.56	0.57	0.60
Dec. 80	0.62	0.58	0.63	0.82
Mar. 81	0.55	0.73	0.61	0.51
Apr. 81	0.53	0.47	0.47	0.43
May 81	0.52	0.47	0.51	-
Jun. 81	0.67	0.62	0.30	0.64
Jul. 81	0.57	0.60	0.40	0.88
Aug. 81	0.72	0.62	0.47	0.68
	TB2	TF1	TF2	TF3
Sept. 80	0.83	1.18	0.95	-
Nov. 80	0.53	0.86	0.72	1.00
Dec. 80	1.22	0.67	1.02	0.92
Mar. 81	0.54	0.70	1.30	1.05
Apr. 81	0.52	0.44	0.79	1.07
May 81	-	0.58	-	1.04
Jun. 81	0.61	0.85	1.02	1.20
Jul. 81	-	0.96	0.96	1.29
Aug. 81	1.01	0.81	0.69	1.40
	TF4	PF1	PF2	PF3
Sept. 80	-	1.34	-	1.15
Nov. 80	1.33	1.26	1.17	1.20
Dec. 80	1.29	1.18	1.24	1.22
Mar. 81	0.73	1.26	1.26	1.25
Apr. 81	1.40	1.28	1.30	1.25
May 81	1.67	1.46	1.44	1.44
Jun. 81	1.41	1.16	1.24	1.21
Jul. 81	1.50	1.50	1.46	1.35
Aug. 81	1.86	1.38	1.42	1.54

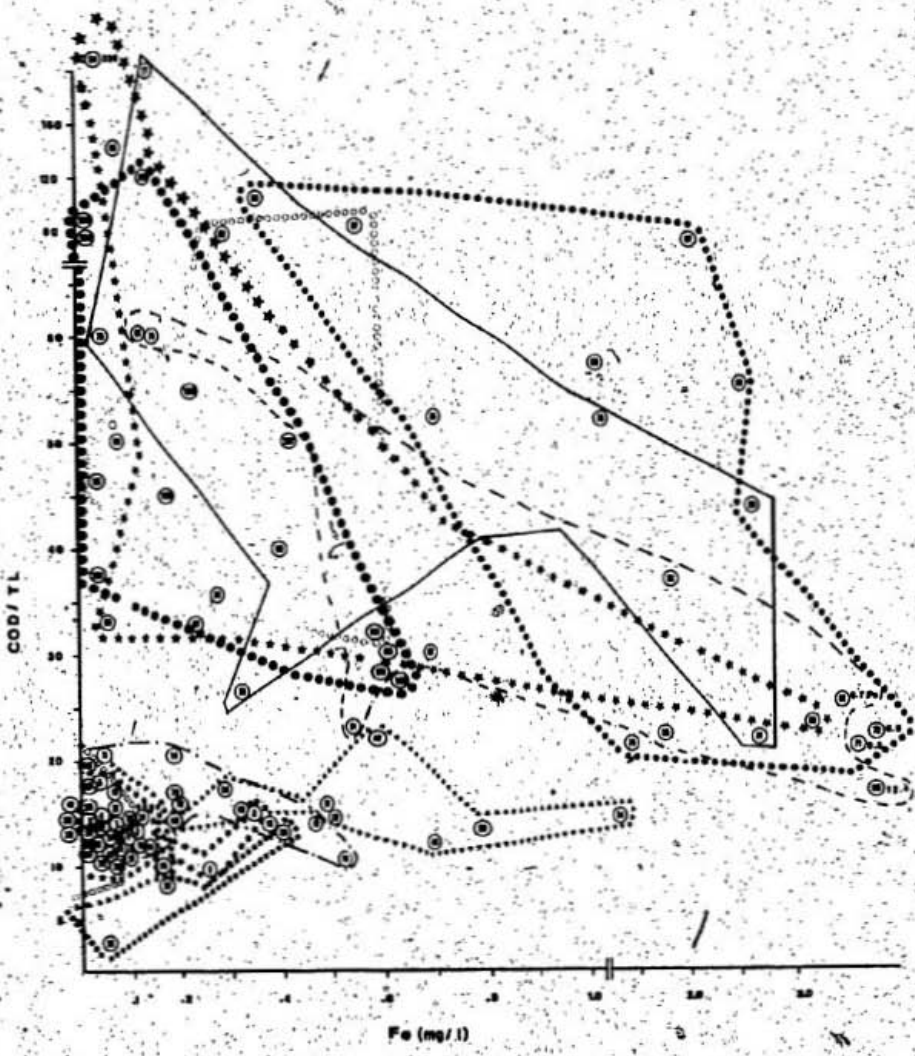
values above 0.8. It is interpreted that TB1, TB2 and TF1 receive a degree of input of mineral soil water, it being greater than that of bog pools PB1, PB2 and PB3, but much less than that of fen pools TF2, TF3, TF4, PF1, PF2, PF3. Pool TF1 appears to have a greater degree of minerotrophic influence than TB1 or TB2.

A scatter plot of Fe against COD:tannins + lignins is presented in Figure 10. The figure demonstrates the relative minerotrophic influence of the three temporary pools TB1, TB2 and TF1 but as well it corroborates the interpretations previously given. Iron is in a greater concentration in mineral soil water compared with precipitation and consequently is found in greatest concentrations in minerotrophic waters (Malmer, 1962a; Tolonen and Hosiaisluoma, 1978). Iron in peat waters studied underwent a strong seasonal cycle (see Appendix VI) which resulted in overlap in values between ombrotrophic and minerotrophic waters during low Fe solubility periods. Thus it is the maximum values of Fe which are most useful in interpreting differences in minerotrophic influence.

The Fe values from TB1 lie in the low range of values, comparable with PB1, PB2 and PB3 with the exception of two higher values, and have a maximum of only 0.34 mg/l. TB2 samples have three values outside the range of TB1 samples with a maximum value of 0.50 mg/l. The maximum value of Fe in TF1 exceeds that of TB2 by 0.8 mg/l and is 1.2 mg/l with an additional three values exceeding the

Figure 10. Scatter plot of Fe against COD:tannins + lignins using all samples from all pools.




COD / TL
Fe (mg/l)

maximum of TB2. Thus it appears that the degree of minerotrophic influence was greatest in TF1 and least in TB1.

Of note are the maximum Fe values in PF1, PF3 and TF1. Pools PF1 and PF3 were of distinctly greater minerotrophic influence than TF1 yet have lower maximum Fe values. The anomolous Fe values can be explained by a differential solubility of Fe and Fe-containing compounds between pools. Low pH, low dissolved oxygen and the presence of reducing organic compounds tend to increase the solubility of iron by favouring the ferrous state (Koenings, 1976). Water pH was lower (Figure 9) and there was a greater buildup of refractory organic materials (Figure 10) in TF1 compared with PF1 and PF2. The saturation of the water mass with iron compounds in PF1 and PF3 was verified by the presence of a heavy iron and organic floc which was absent in TF1.

A slight input of mineral soil water in PB3 compared with PB1 and PB2 has been suggested, but no evidence based on water chemistry is apparent. The basis of the speculation is a difference in the upper sediment layer of PB3 compared with PB1 and PB2. The upper layers of PB3 had a reddish brown colour compared with grey-green in PB1 and PB2 (see Appendix III). The red-brown colour is thought to originate from inputs of iron from mineral soil water.

Permanency Gradient

Peatland pools vary in the extent of evaporation of the water mass during periods of dry weather. Over time, a gradient of pool permanency can be identified which distinguishes pools which are least likely to have major drops in water level from those which are likely to dry up frequently. The degree of pool permanency was evaluated on the basis of pool morphology, site topography, observations of pool water level fluctuations during sample dates, and pool vegetation.

Pools in which the water level did not drop below the Sphagnum fringe during the study period have been subjectively identified as permanent pools and as a group have a higher degree of permanency than the temporary pools where such a major reduction in water level was observed. Within the group of permanent pools, the degree of permanency is variable and given a longer period of examination, major reductions in water level in some pools would be predicted. A relative ranking of the sample pools in relation to predicted degree of permanency is given in Table 4.

Pool PB1 is the deepest pool (50-70 cm depth) and has the largest surface area (Figure 2). It lies close to the center of a depression in the bedrock in an area of heavy peat deposition (Figure 2). It is expected to have the highest degree of permanency and probably has gone the longest time period with the Sphagnum fringes submerged. Of

Table 4: A Relative Ranking of the Sample Pools on the Permanency Gradient.

Pool	Rank (increasing values indicate higher degrees of permanency)
TB2	1
TB1	2
TF2	3
TF1	4
TF3	5
TF4	5
PF1	6
PB3	6
PB2	7
PF2	7
PF3	8
PB1	9

the remaining permanent pools the depth of open water is comparable (maximum < 40 cm), however placement in drainage networks and perimeter distances (surface area) do vary. Pool PF3 has the largest perimeter distance and lies at the base of the major drainage network of the fen site (Figure 5). It is considered to have the greatest degree of permanency of the fen site pools. The other permanent pools of the fen site, PF2 and PF1, have roughly comparable surface areas and volumes (Appendix III), however PF1 lies higher on a drainage slope (Figure 5) and is better drained than PF2. This is supported by the flow through of water observed in PF1. Pool PF1 lacked a population of the aquatic macrophyte Nuphar variegatum Engelm. in contrast with PF2. It is interpreted that PF2 has a higher degree of permanency than PF1. The remaining permanent bog pools, PB2 and PB3, cannot be placed relative to the permanent fen pools. Pool PB2 has a larger volume than PB3 (Appendix III) and lies in an area of slightly greater peat deposition (Figure 2). PB2 has a large population of the aquatic macrophyte Eriocaulon septangulare With. whereas truly aquatic plants are lacking in PB3. Thus PB2 likely has a higher degree of permanency than PB3.

Of the six temporary pools in which the water level dropped below the Sphagnum fringe, TB2 has the least degree of permanency, having completely dried up on two dates during the study (Figure 11). The pool lies in an area of shallow peat on a relatively high bedrock slope of

Figure 11: Water level fluctuations in temporary pools..

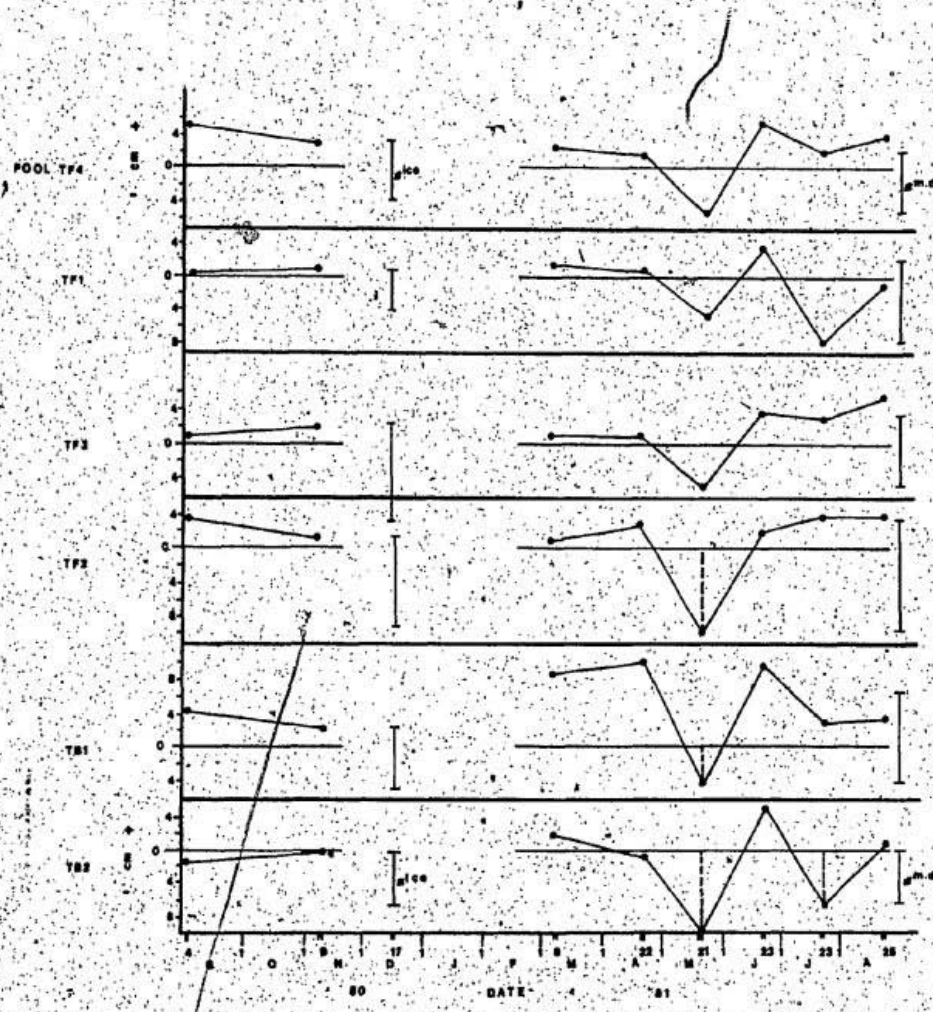
legend:  = a date on which the pool water mass was completely evaporated

ice = depth of ice in pool during the December sample date

m.d. = maximum depth of open water measured in the pool

notes: 1) the zero mark corresponds to the reference point on the water level measurement peg.

2) fluctuations of water levels may exceed maximum depth of open water. This is accounted for by the observation that depth of bottom sediment varies over time.


POOL TF4
TF1
TF3
TF2
TB1
TB2
DATE
80
81

the bog site (Figure 2). It is well drained as supported by the continuously dry nature of the surrounding peat and by the observation that even in times of heavy rain the pool fringes did not flood as did other temporary pools.

Pool TB1 is interpreted as having the next least degree of permanency of the set, having had Sphagnum fringes exposed to the atmosphere on two dates (May, July 1981) and having dried completely once (May 1981). It has a small water volume with a perimeter of 6.5 m and maximum depth of 11 cm. See Figure 12 for views of TB1 in wet and dry conditions.

The remaining temporary pools showed reduction in water level below the Sphagnum fringes on only one date (May 1981). Pool TF2 is considered to have the least degree of permanency of these pools, having completely dried up on that date. TF2, in contrast to TF1, TF3, and TF4, is isolated from drainage inflows (Figure 5). The remaining pools, TF1, TF3, and TF4, are difficult to define as to the degree of permanency. TF1, although having the greatest perimeter length, 16.7 m compared with 10.8 and 4.3 for TF4 and TF3 respectively (depths are comparable), had a substantial drop in water level during the July sample (not observed in TF3 and small in TF4 (Figure 11)). Thus TF1 may be placed slightly lower on the permanency gradient than TF3 and TF4.

Figure 12: A representative temporary pool showing variation in water level.

POOL
TB1
May 1981

POOL
TB1
June
1981

Surface Water Flow Gradient

Study pools were placed on a gradient of surface water flow based on the degree and frequency of water movement in the pool. Placement on the gradient was evaluated using observations of surface flow during sample dates and on interpretation of site topography.

A relative ranking of sample pools in relation to the degree of surface water flow is given in Table 5. Only three of the sample pools (PF1, PF3, TF4) were observed to have surface flow at any time during the study. The remaining nine pools are considered to have equally low placement on the flow gradient.

Throughout the study period the water table was at or near the peat surface (Table 6), thus surface water flows were strongly related to rainfall events. Water flows in pools were not measured, only noted, because it was thought the large variations in flow observed over short periods of time would make instantaneous sample date measurements of little value.

Pool PF3 had a continuous flow through of water during the study. The rate was highly variable, increasing rapidly with rainfall but dropping off sharply shortly after rain stoppage. The pool lies perpendicular to the fen site elevation contours (Figure 5) forming a drainage channel in a low lying trench. It has the highest degree of flow of all sample pools. Next highest on the gradient is PF1, in which a slow flow through (relative to PF3) was observed on

Table 5: A Relative Ranking of the Sample Pools on the Surface Water Flow Gradient.

Pool	Rank (Values increase with greater degree of water movement.)
TB1	1
TB2	1
PB1	1
PB2	1
PB3	1
TF1	1
TF2	1
TF3	1
PF1	1
TF4	2
PF2	3
PF3	4

Table 6 : FLUCTUATIONS OF PEAT WATER LEVELS IN BOG AND FEN SITES

Distance from peat surface to water level in peat water level measurement pipes (in cm)

	Bog site		Fen site	
Date	Pipe A	Pipe B	Pipe A	Pipe B
April 81	26	20	1	24
May 81	15	20	3	27
June 81	7	16	1	17
July 81	23	4	8	24
August 81	15	-	7	27

4 of 9 sample dates. The flow was observed during periods of moderate to heavy rainfall. PF1 is located near PF3 but higher on a drainage slope. Pool PF2 receives drainage from PF1 via a wet soak but surface flows into or out of PF2 were not observed. The remaining pool TF4 places intermediate to PF1, and the pools with no surface flow, on the flow gradient. The pool is linearly shaped running parallel to a surface slope (Figure 5). On 2 of 9 sample dates a slight flow into and out of TF4 was observed, this during periods of heavy rain.

SPATIAL VARIATIONS IN THE DESMID COMMUNITIES

Desmid Community Composition

The desmid communities of the Sphagnum aufwuchs were taxonomically rich, with a total of 135 taxa representing 20 genera observed from a composite of all samples. The number of taxa observed from individual sample pools ranged from 24 to 94 (Table 7). The number of taxa occurring in each sample pool on each sample date is given in Figure 13.

The composition of the desmid communities of the 12 sampling pools varied strongly. Examination of Table 5 shows that species vary in occurrence in pools of differing placement on the minerotrophic gradient and on the permanency gradient. Table 8 gives an approximate percentage breakdown of the total study site flora in terms of pool type. It is apparent that many species were

Table 7: DESMID SPECIES COMPOSITION IN INDIVIDUAL SAMPLE POOLS

	Pools	TPPPTTTPPPTT FFFFFFFBBBBB 412332112312
Cl. juncidum		.66.....
Cl. angustatum		.99.....
C. debaryi		.1.....
C. caelatum		.13.....
C. isthmium		..2.....
St. pyramidatum		..1.....
M. tetrapreta		.22.....
Pl. rectum		.99.....
Cl. baillyanum		.596.....
Cl. intermedium		..26.....
Cl. costatum		..12.....
Cl. ulna		.981.....
Cl. archerianum		.977.....
Cl. moniliferum var. concavum		...7.....
C. angulosum		.312.....
C. ornatum		..21.....
C. margaritiferum		.884.....
C. eloiseanum		...4.....
E. pectinatum		.998.....
M. papillifera		.152.....
Pl. ehrenbergii		.795.....
Pl. coronatum		.2.6.....
St. orbiculare		.984.....
Gt. brebissonii		.6.1.....
Cl. venus		1323.....
Cl. cynthia		5646.....
Cl. toxon		2795.....
C. reniforme		6755.....
E. boldtii		4685.....
E.oblongum		231.....
St. monticulosum		6.12.....
C. subcrenatum		3.....
C. quadratum var. nepalense		.34.2.....
E. pinnatum		.45.1.....
C. octhodes		.1.1.4.....
Cl. dianae		88982.....
Cl. gracile		29942.....
Cl. kuetzingii		99982.....
Cl. rostratum		99851.....
C. pseudopyramidatum		29333.....
E. bidentatum		7998..2.....
E. humerosum		313.1.....
Cl. closterioides		599459.....
Cl. striolatum		999999.....
C. tumidum		39955.1.....
C. pyramidatum		6999.11.....
E. ansatum		1966.11.....
Cl. ralfsii		.88611.....
St. lapponicum		.2252.7.....
M. oscitans		..4.1.....
C. ralfsii var. taylorii		5221562.....
St. crenulatum		4272211.....
St. brebissonii		1217881.....
C. nymannianum		...2..6.....
C. difficile		91.1961.....
C. quadratum		23..21.....
A. cucurbitinum		.....1.....
C. venustum		6.2.975.....
E. intermedium		.....1.....
E. giganteum		.2.26.91....
E. cuneatum		...31121....
E. ampullaceum		7.14866....3
E. montanum		5697759..1..
E. insinge		2.4138956...
E. crassum		3745478.8..4
E. ventricosum		39986632...1
E. didelta		9895892...13
E. allenii		..22...1...,

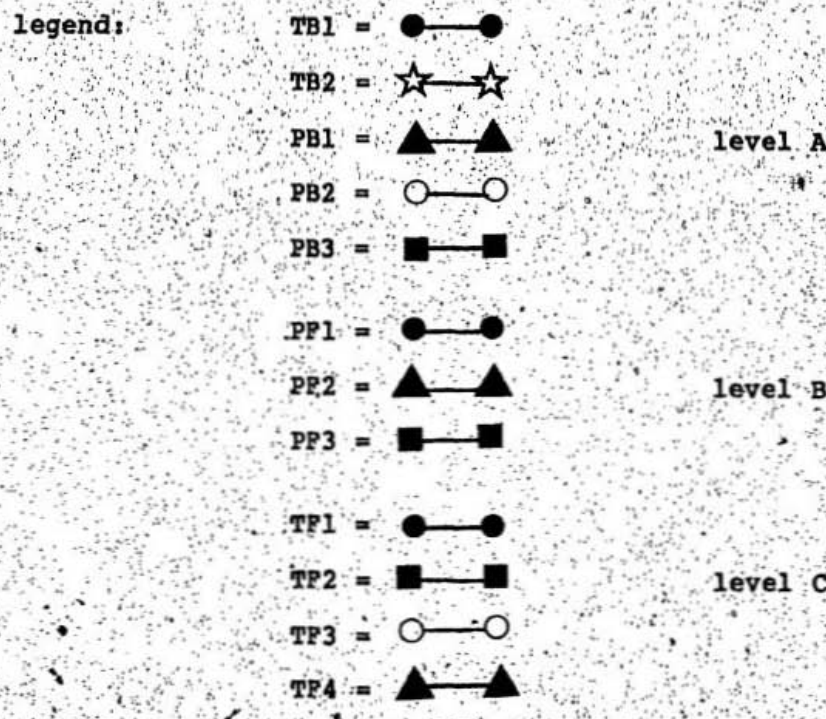
	Pools	TPPPTTTPPPTT FFFFFFFBBBBB 412332112312
M. denticulata		.341....1...
M. triangularis		1..3...1....
P. cylindrus		2343.....45
C. anoenum		28577..74.1.
C. sp.		7846..1211..
C. obliquum		112.1.....21
T. brebissonii var.brebissonii		999899933..6
T. granulatus		9999999571.4
Cl. acutum		23344..44831
E. binale		8777..49998.
A. cucurbita		966989999998
Cy. brebissonii		799899999999
M. jenneri		13.5.4724193
N. digitus		899929699995
P. silvae-nigrae		744777889899
St. margaritaceum		455631698893
T. laevis		298927999944
M. truncata		89872.59962.
X. armatum		75661.58687.
B. borreri		.996.199999.
E.insulare		.222.121381.
T.brebissonii var. minor		.2.7197677.5
M.arcuata		.....6.2...
M. novae-terrae		.221..18976.
H. dissiliens		.872...64...
H. laevicincta		.163...2.6..
D. swartzii		.87....34...
D. gracilicaps		...3....1...
St. brachiatum		.195...986..
Sd. extensus		.896...633..
E. denticulatum		.3451..799..
Tl. granulata		.364..1452..
E. validum		2.13..2456..
St. anatinum		1.61...999..
P. spirostriolatum		.65.1..215..
St. anatinum var. simplicius		.756...9982.
X. antilopaeum		214....8974.
C. subtumidum		1.31...9995.
T.brebissonii var. brebissonii		2997...99913
Sd. phimus		..11..376723
Pl. minutum		...7..999999
Sd. sellatus		..1..389952
D. quadratum		.11....596..
E. pingue		.....412...
Pl. tridentulum		.....49889.
St. quadrispinatum		.....19999.
Sd. omearii		243542
C. subcucumis		.....99999.
C. quinarium		.....18..9
St. simonyii		78995
St. furcatum		.....9898.
G. neglecta var. A		.....99...
Do. undulatum		.....81...
M. arcuata var. expansa		.....59...
Tr. gracile		.....87...
X. torreyi		.....692..
C.contractum		.....999..
G. neglecta		.....999..
Pl. minutum var. latum		.....994..
St. elongatum		.....999..
St. inconspicuum		.....113..
Cl. sp. B		.....9..
C. pseudotaxichondrum		.2....899..
X. cristatum		..9....459..
E. elegans		..2....889..
Cl. sp. A		.....1526..
Ar. octocornis		...1...79...
Total species observed		589843466532 554842853114

Note: The results from all samples from a given pool have been combined. The numbers given indicate occurrences out of a total of nine samples.

The table was structured with the aid of the computer program TWINSPAN, (see materials and methods).

Genus abreviations used are given in Appendix I.

Figure 13: Numbers of desmid taxa occurring in individual pool samples.



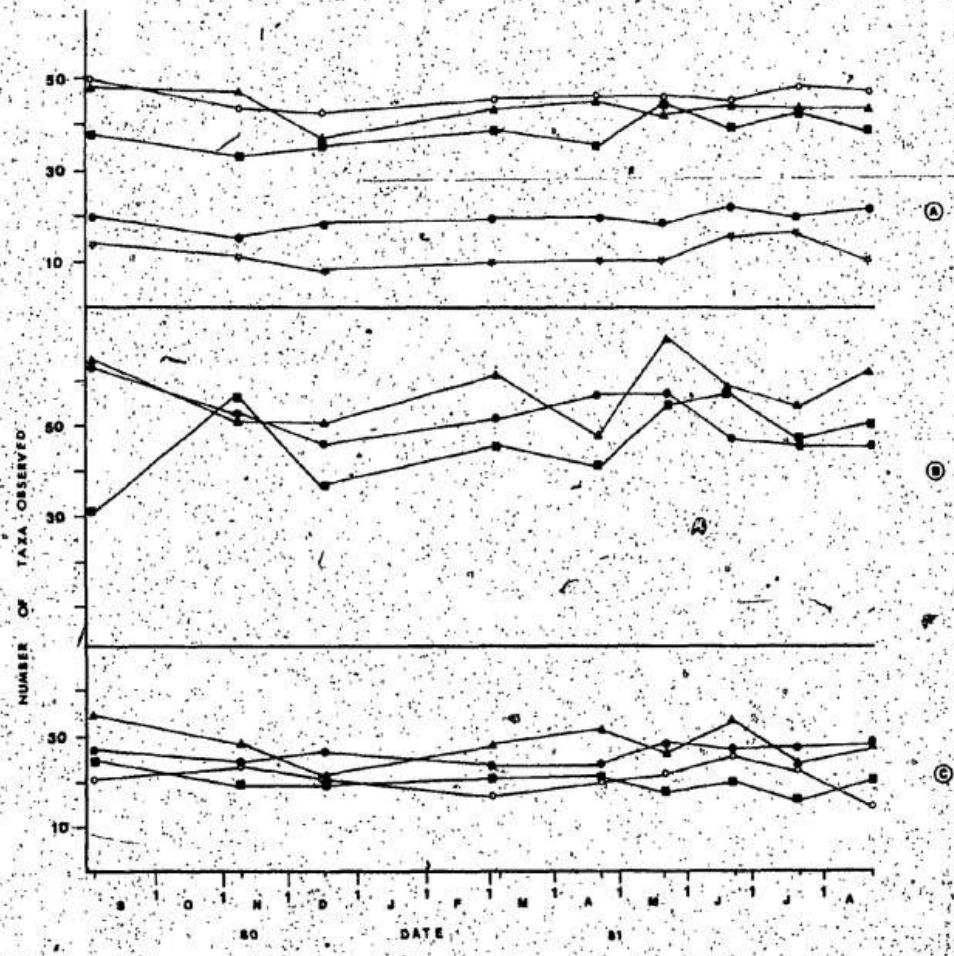

NUMBER OF TAXA OBSERVED
50
30
10
A
50
30
B
30
10
C
S
O
N
D
J
F
M
A
M
J
J
A
80
DATE
81

Table 8: DISTRIBUTION OF DESMID SPECIES BY POOL TYPE

	permanent pools only	temporary pools only	both types
highly minerotrophic pools only	24 (18)	2 (1.50)	31 (23.0)
ombrotrohic pools only (TF1 excluded)	14 (10.4)	0 (0.00)	7 (5.2)
both types	13 (9.6)	0 (0.00)	42 (31.1)

Note: x(y) ; x is the number of species occuring in the given combination of pool types, y is the percentage of the total desmid flora represented.

ubiquitous, or at least have a potential for being so, and occurred in all pool types. The majority of species showed affinity for specific pool types. The largest number of species was restricted to permanent pools and highly minerotrophic pools. Only a very few species were restricted to ombrotrophic pools and even fewer to temporary pools. It is of note that eight taxa (6% of the total flora) were endemic to a single pool.

The main species distribution gradients were further examined by ordination analysis using Detrended Correspondence Analysis (DCA). The first two sample and species axes of the ordination of qualitative desmid occurrences are given in Figure 14.

The pool minerotrophic status was the main determining factor in desmid community species composition. The first sample axis has a gradient length of 237 and an eigenvalue of 0.52 (see Appendix II for interpretation of DCA axes). The gradient of axis 1 separates samples from pools of contrasting minerotrophic influence. All fen site pool samples excepting TF1 score low on axis 1. These pools (PF1, PF2, PF3, TF2, TF3 and TF4) were strongly influenced by mineral soil water and were placed highest on the physically/chemically defined minerotrophic gradient. At the high extreme of axis 1, are samples from PB1, PB2 and PB3 with samples from TB1 scoring marginally lower. PB1, PB2 and PB3 were judged nearest the ombrotrophic condition, with TB1 being slightly enriched with mineral soil water.

Figure 14 : DCA ordination axis 1 plotted against axis 2 for qualitative desmid data.

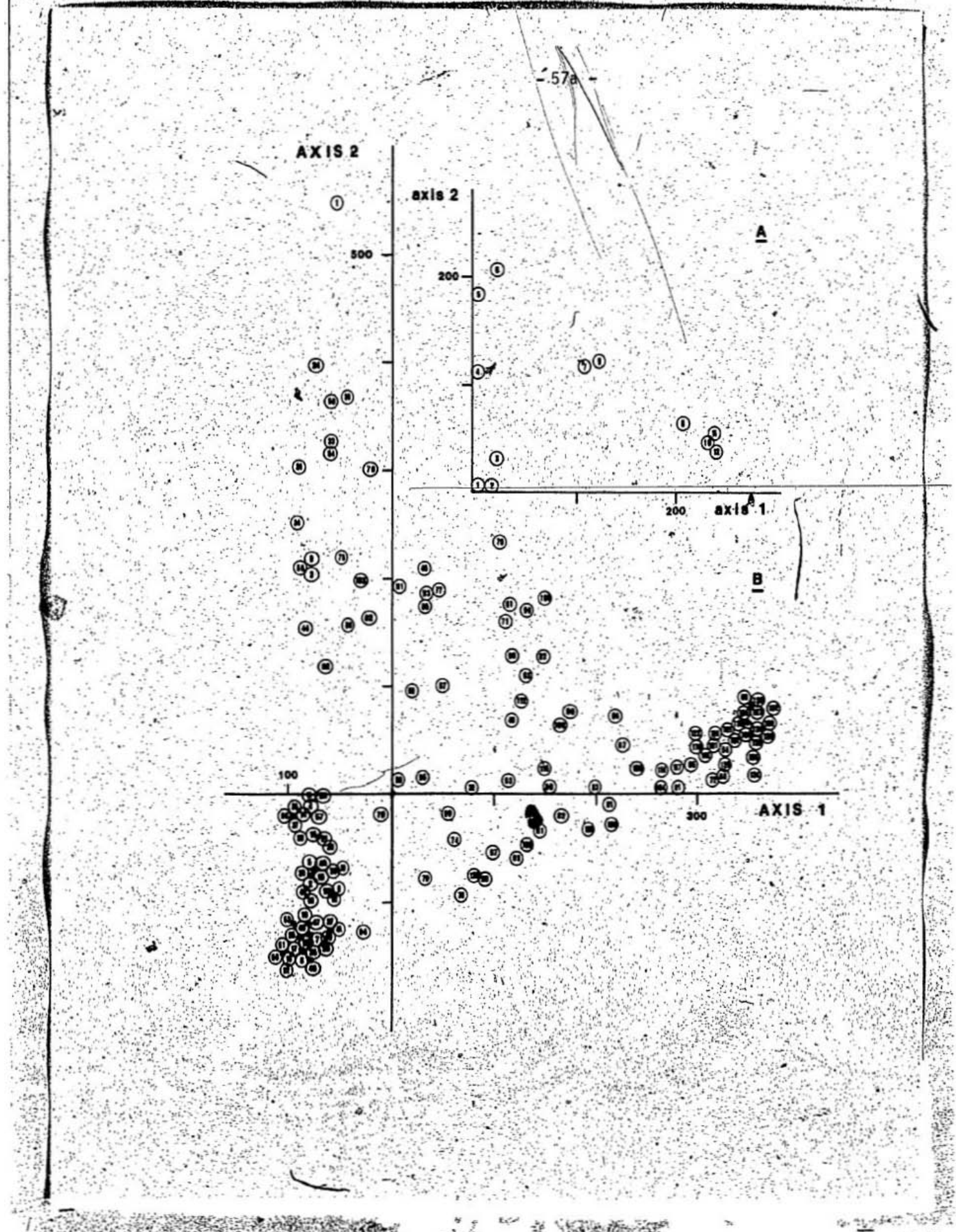
legend :

plot A = samples

1 = PF1 3 = PF3 5 = TF3 7 = TF1 9 = TB2 11 = PB2
2 = PF2 4 = TF4 6 = TF2 8 = TB1 10 = PB1 12 = PB3

plot B = species

1 = A.cucurbitinum
2 = Cl.venus
3 = Cl.crostarioides
4 = Cl.dianae
5 = Cl.gracile
6 = Cl.junciduum
7 = Cl.baillyanum
8 = Cl.intermedium
9 = Cl.striolatum
10 = Cl.ralfsii
11 = Cl.keutzingii
12 = Cl.costatum
13 = Cl.angustatum
14 = Cl.rostratum
15 = Cl.cynthia
16 = Cl.toxon
17 = Cl.ulna
18 = Cl.archerianum
19 = Cl.moniliferum var.concavum
20 = C.tumidum
21 = C.pyramidatum
22 = C.debaryi
23 = C.angulosum
24 = C.difficile
25 = C.caelatum
26 = C.isthmium
27 = G.ornatum
28 = C.margaritiferum
29 = C.reniforme
30 = C.eloiseanum
31 = C.subcrenatum
32 = C.nymannianum
33 = C.ralfsii var.taylorii
34 = C.quadratum
35 = C.quadratum var.nepalense
36 = C.venustum
37 = E.oblongum
38 = E.ansatum
39 = E.bidentatum
40 = St.pyramidatum
41 = E.pectinatum
42 = E.pinnatum
43 = E.boldtii
44 = E.humerosum
45 = E.giganteum
46 = E.intermedium
47 = M.papillifera
48 = M.tetrapreta
49 = Pl.ehrenbergii
50 = Pl.coronatum
51 = Pl.rectum
52 = St.inconspicuum
53 = St.orbiculare
54 = St.brebissonii
55 = St.monticulosum
56 = Gt.brebissonii
57 = M.oscitans
58 = C.ochtodes
59 = St.lapponicum
60 = X.torreyi
61 = A.cucurbita
62 = B.borreri
63 = Cl.acutum
64 = Cl.sp.A
65 = C.subtumidum
66 = C.pseudopyramidatum
67 = C.obliquum
68 = C.pseudotaxichondrum
69 = C.amoenum
70 = C.sp.
71 = Cy.brebissonii
72 = D.quadratum
73 = D.swartzii
74 = D.graciliceps
75 = E.didelta
76 = E.ampullaceum
77 = E.cuneatum
78 = E.insigne
79 = E.allenii
80 = E.binale
81 = E.denticulatum
82 = E.montanum
83 = E.insulare
84 = E.pingue
85 = E.crassum
86 = E.ventricosum
87 = E.validum
88 = H.dissiliens
89 = H.laevicincta
90 = M.arcuata
91 = M.novae-terrae
92 = M.jenneri
93 = M.truncata
94 = M.denticulata
95 = M.triangularis
96 = M.digitus
97 = P.spirostriolatum
98 = P.silvae-nigrae
99 = P.cylindrus
100 = Pl.minutum
101 = Pl.tridentulum
102 = St.furcatum
103 = St.brachiatum
104 = St.anatinum
105 = St.anatinum var.simplicius
106 = St.margaritaceum
107 = St.quadrispinatum
108 = Te.granulata
109 = T.brebissonii var.minor
110 = T.brebissonii var.intermedius
111 = T.brebissonii
112 = T.laevis
113 = T.granulatus
114 = X.antilopaeum
115 = X.armatum
116 = X.cristatum
117 = Sd.phimus
118 = Sd.sellatus
119 = Sd.omearii
120 = Sd.extensus
121 = Ar.octocornis
122 = C.subcucnis
123 = C.contractum
124 = C.quinarium
125 = E.elegans
126 = G.neglecta
127 = G.neglecta var. A
128 = Do.undulatum
129 = M.arcuata var.expansa
130 = Pl.minutum var.latum
131 = St.simonyi
132 = Tr.gracile
133 = St.elongatum
134 = Cl. sp. B
135 = St.crenulatum


AXIS 2
500
100
100
300
AXIS 1
axis 2
200
200
axis 1
A
B

Samples from pools TF1 and TB2 score medially on axis 1. This further supports the interpretation of axis 1 as a minerotrophic gradient, in that these two pools were detectably enriched with mineral soil water but only moderately so relative to the highly minerotrophic pools.

The means of a subset of water chemistry variables relevent to the minerotrophic gradient for each pool over the study period are given in Table 9. Comparison with pool sample placement on axis 1 shows negative relation of pH, Fe, Ca, Mg and silicate means with increasing scores, and a positive relation with tannins + lignins and COD.

The greatest variation in distribution of desmid species over the study site was in relation to species axis 1 and correlated with changes in sample pool minerotrophic status. Species vary strongly in position on the axis, with the largest number scoring low at the minerotrophic end. Many species occur throughout the intermediate ranges of axis 1, these having no or relatively less relationship to the minerotrophic status of the pool. Species scoring high on axis 1 are fewer in number than those scoring low or intermediately, and are those found mainly or solely in ombrotrophic pools.

The characteristics of compositional change along the minerotrophic gradient were two-fold: species had differing ranges of occurrence on the gradient, with many species restricted to pools of extremes of minerotrophic influence; species richness increased with an increased

Table 9: MEANS AND RANGES OF SELECTED WATER CHEMISTRY PARAMETERS BY POOL OVER THE STUDY PERIOD

Pool	Mean	Range
	pH	
PF1	5.92	5.58 - 6.17
PF3	5.75	5.56 - 6.07
PF2	5.65	5.23 - 5.92
TF4	5.61	5.31 - 5.97
TF3	5.55	5.22 - 5.82
TF2	5.06	4.72 - 5.68
TF1	4.27	4.10 - 4.55
PB2	4.22	3.81 - 4.51
PB1	4.19	3.77 - 4.37
PB3	4.16	3.85 - 4.53
TB1	4.10	3.40 - 4.38
TB2	4.09	3.38 - 4.39
	Fe mg/l	
TF2	3.06	0.12 - 12.40
TF3	2.48	0.35 - 6.60
TF4	0.90	0.04 - 2.71
PF2	0.68	0.02 - 3.15
TF1	0.55	0.18 - 1.23
TB2	0.27	0.05 - 0.52
PF1	0.25	< 0.02 - 0.58
PF3	0.18	< 0.02 - 0.62
TB1	0.11	< 0.02 - 0.34
PB2	0.09	< 0.02 - 0.40
PB3	0.05	< 0.02 - 0.16
PB1	0.03	< 0.02 - 0.07
	Ca mg/l	
PF1	1.44	0.73 - 3.01
TF4	1.33	0.30 - 3.80
PF2	1.30	0.61 - 2.22
PF3	1.29	0.81 - 2.51
TF3	1.09	0.61 - 2.17
TF2	0.80	0.38 - 1.43
TB2	0.40	0.17 - 0.83
TF1	0.39	0.19 - 0.59
TB1	0.37	0.16 - 0.64
PB1	0.24	0.19 - 0.35
PB3	0.24	0.11 - 0.46
PB2	0.21	0.14 - 0.35
	NO_3 mg/l N	
PF2	0.027	< 0.005 - 0.076
PF1	0.023	< 0.005 - 0.092
PF3	0.015	< 0.005 - 0.067
TB3	0.008	< 0.005 - 0.031
TF4	0.005	< 0.005 - 0.024
TF2	0.004	< 0.005 - 0.035
PB2	0.003	< 0.005 - 0.018
TF1	0.002	< 0.005 - 0.009
PB3	0.001	< 0.005 - 0.012
TB2	0.001	< 0.005 - 0.006
TB1	-	< 0.005 - <0.005
PB1	-	< 0.005 - <0.005
	COD mg/l	
TB2	54	25 - 77
TB1	53	22 - 112
TF2	51	12 - 127
TF1	48	23 - 71
PB3	43	23 - 60
PB1	41	18 - 62
TF3	34	10 - 71
PB2	33	9 - 58
TF4	27	8 - 58
PF2	26	10 - 44
PF3	23	9 - 36
PF1	17	3 - 32

Pool	Mean	Range
	Conductivity Scm	
PF1	52.4	30.2 - 90.6
TB1	46.9	33.9 - 68.3
TB2	46.5	36.5 - 61.6
PB3	46.2	30.5 - 67.9
PF2	45.6	33.0 - 67.8
PF3	45.5	34.3 - 66.9
TF4	45.3	30.6 - 69.7
TF3	43.1	32.2 - 54.1
TF2	42.4	27.0 - 61.4
PB1	42.1	29.4 - 63.7
TF1	39.7	34.0 - 52.0
PB2	39.1	30.5 - 57.4
	Silicate mg/l Si	
TF3	0.421	< 0.005 - 1.190
PF1	0.335	< 0.005 - 0.744
TF2	0.324	< 0.005 - 0.943
PF3	0.314	< 0.005 - 0.871
TF4	0.263	< 0.005 - 1.080
PF2	0.187	< 0.005 - 0.924
TF1	0.121	< 0.005 - 0.252
TB1	0.085	< 0.005 - 0.324
TB2	0.076	< 0.005 - 0.228
PB3	0.020	< 0.005 - 0.060
PB1	0.018	< 0.005 - 0.060
PB2	0.017	< 0.005 - 0.072
	Mg mg/l	
PF1	1.06	0.61 - 2.00
PF3	0.98	0.65 - 1.62
PF2	0.96	0.54 - 1.54
TF3	0.93	0.58 - 1.57
TF2	0.90	0.40 - 2.05
TF4	0.88	0.41 - 2.08
TB2	0.52	0.31 - 0.76
TB1	0.51	0.31 - 0.78
TF1	0.49	0.34 - 0.73
PB3	0.44	0.18 - 0.72
PB1	0.40	0.30 - 0.56
PB2	0.37	0.19 - 0.60
	Tannins + Lignins mg/l	
TB1	4.0	1.5 - 7.4
PB3	3.8	1.9 - 6.0
TB2	3.7	1.9 - 6.7
TF1	3.5	1.5 - 6.4
PB1	3.0	1.5 - 4.3
PB2	2.9	1.3 - 4.7
TF2	2.2	0.2 - 6.4
TF3	1.2	< 0.1 - 3.2
TF4	0.7	< 0.1 - 1.9
PF2	0.7	< 0.1 - 1.7
PF3	0.5	< 0.1 - 1.3
PF1	0.3	< 0.1 - 0.9
	PO_4 mg/l	
TB2	0.026	0.014 - 0.054
TB1	0.024	< 0.005 - 0.079
TF1	0.015	< 0.005 - 0.033
PB3	0.013	< 0.005 - 0.031
PB1	0.008	< 0.005 - 0.026
PB2	0.005	< 0.005 - 0.016
TF4	0.004	< 0.005 - 0.022
TF2	0.003	< 0.005 - 0.015
PF1	-	< 0.005 - 0.008
PF3	-	< 0.005 - <0.005
PF4	-	< 0.005 - <0.005
TF3	-	< 0.005 - <0.005

degree of minerotrophic influence. The composition of pools of intermediate degrees of minerotrophic influence, TF1, TB2 and TB1, show compositional change to be gradual between extremes of minerotrophic influence. These pools contain mixes of species, some with ranges otherwise restricted to pools of extremes of minerotrophic influence. Pool TF1 was the most median on the minerotrophic gradient and had the greatest mix of such species: 13 species restricted to highly minerotrophic pools, 7 species otherwise restricted to ombrotrophic pools.

It was not possible to elucidate which components of the changing pool minerotrophic status were responsible for determining species ranges on the gradient. The suites of water chemistry parameters correlating with the species composition of axis 1 suggest that either singly or in combination, changes in pH, mineral levels, and type or amount of organic materials affect species distribution. In the intermediate gradient pools, TF1, TB1 and TB2, pH and the organic components (COD, tannins + lignins and colour) do not differ from those of other more ombrotrophic pools (Table 9, Appendix VI). In these pools increased minerals (Ca, Mg and Fe) correlate with the occurrence of more minerotrophic species. The occurrence of restricted ombrotrophic species in TF1 then correlates with lower pH and higher organics (COD and tannins + lignins). From the widely differing ranges of species occurrence it is likely

that individual species may be affected by different variables of water quality.

The degree of permanency of a peatland water mass strongly affects the composition and richness of the desmid community. The second sample axis of the composition ordination has a gradient length of 208 and an eigenvalue of 0.22. The placement of samples on this axis is not strictly related to any pool characteristic, but does have a degree of relation with pool permanency. Samples from permanent pools, both with a high and low degree of minerotrophic influence, score low on axis 2. All temporary pools with the exception of TB1 score intermediate to high on axis 2. The variation in sample scores from the highly minerotrophic temporary pools (TF2, TF3 and TF4) corresponds negatively with relative placement on the physically defined permanency gradient. TF2, the pool with the least degree of permanency, scores highest on axis 2. The sequence of axis 2 scores for this group also correlates negatively with the total number of species observed in the pools (Table 7).

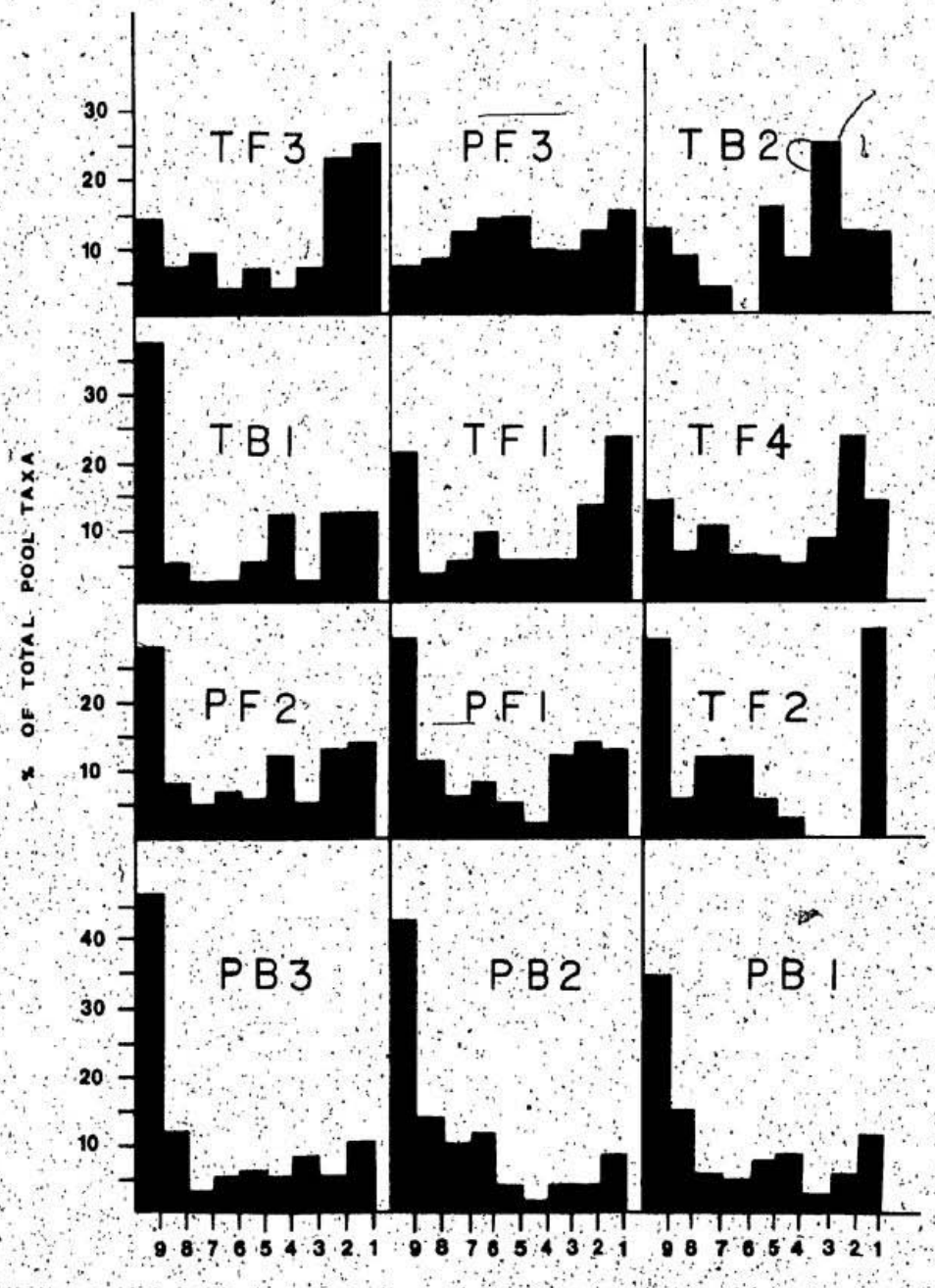
If axis 2 is interpreted as a gradient of permanent to temporary pool types then the placement of samples from TB1 and TB2 on this axis is anomolous. Samples from TB2 and TB1 score medially yet their temporary nature would suggest they should score highly on axis 2. A possible explanation for this observation may be that a greater amount of variation in the data occurred in minerotrophic pools in relation to pool permanency compared

with ombrotrophic pools. Since different species were found in minerotrophic and ombrotrophic pools, the gradient could be more strongly shaped by minerotrophic pool samples. This can be substantiated by examining the number of species showing preferences for permanency between ombrotrophic and minerotrophic pools. The minerotrophic pools do have a greater number of such species, as is evident from Table 8 and examination of the spread of species on species ordination axes 1 and 2 (Figure 14).

The second species axis separates species that occur in only permanent pools from those which occur in both temporary and permanent pools. Species that occurred only in temporary pools score highest on the axis but are very few in number and are probably not important in the gradient relative to the previous two species groups. Species separation on axis 2 is greatest for minerotrophic species and only marginal for ombrotrophic species.

Change along the permanency gradient was characterized by the permanent pools being more species rich than temporary pools. Many species occurring in permanent pools did not occur in temporary pools (Table 7) and were apparently intolerant of even limited desiccation. Indirect evidence for a greater die-off rate of species in temporary compared with permanent pools was obtained in the present study. The percentages of the species of individual pool communities occurring with a given frequency in the sample set are presented in Figure 15. With some exceptions,

Figure 15: Percentages of pool desmid taxa occurring with given frequencies.


TF3
PF3
TB2
TB1
TF1
TF4
PF2
PF1
TF2
PB3
PB2
PB1
% OF TOTAL POOL TAXA
NUMBER OF SAMPLE OCCURRENCES (TOTAL SAMPLES=9)

temporary pools, compared with permanent pools, have a lower proportion of the community common to all repetitive samples and have a higher proportion of the community that occurred only rarely (1 or 2 samples).

Very few species were restricted to temporary pools. Examination of the numbers of species in individual samples (Figure 13) and total numbers of species in pools (Table 7) shows the relation between greater species richness and a greater degree of pool permanency. Samples from TB2, the least permanent pool, have the fewest species. Differences in species richness between the groups TB1, TF2 and TF1, TF3, TF4 relate to differences in degree of permanency, the latter group with a relatively greater degree of permanency and being more species rich. The permanent pool samples were more species rich than those of similar temporary pools.

Further ordination axes had much lower eigenvalues (0.06: axis 3), were not interpretable and are not presented or discussed.

The interpretation of compositional differences between pools requires some understanding of the degree to which the physical separation of sample pools blocks dispersal. In this study dispersal differences do not appear to shape compositional patterns greatly. Two temporary pools (TF1, TB2) have very close sample scores on axis 1 and 2 of the species composition ordination. The two pools however occur on different study sites. The pools do

vary in number of species yet both have the property of sharing taxa not found elsewhere on their respective sites (Table 7). The degree of endemism of taxa to single pools was low (6% of total flora) with these species being mostly rare.

Surface movement of water in the peatlant pools studied had no apparent effect on desmid species composition of the Sphagnum aufwuchs. Species composition was comparable in the three highly minerotrophic permanent pools which have variable amounts of water movement (PF3, regular flow varying from slow to strong; PF1, occasional slow flow; PF2, no surface flow). The number of species occurring in samples (Figure 13) and the total number of species occurring over the study period (Table 7) varied only slightly between these three pools. The overall compositional similarity between these pools can be inferred from Table 7 and the results of the ordination of qualitative desmid species data (Figure 14). Samples from PF1, PF2 and PF3 score closely on axis 1 and axis 2.

The species composition of TF4, the only remaining pool with surface water flow, was slightly divergent from that of TF3, a pool of comparable degree of minerotrophic influence and permanency. Samples from TF4 were more species rich than those of TF3 with most TF3 species occurring in TF4 samples (Table 7). It is noteworthy that no species of TF4 absent in TF3 were restricted otherwise to pools with surface water movement.

The degree of water movement in peatland pools was positively correlated with the size of the drainage area of the pool and the extent of drainage input. Surface drainage inflows may be an important factor in short distance dispersal of desmids on peat sites. Pools with inflows may be richer in species. The increased richness of TF4 samples compared with TF3 samples may be explained by this.

Considering the composition of samples from all pools, six taxa (4.4% of the total flora) were restricted to pools with some degree of water movement. Of these, two were endemic to PP3, one was endemic to TF4 and no species occurred in all three pools with water movement. Specific adaptation to water movement does not appear important in determining the distribution of species; distribution of taxa observed may equally result from random dispersal.

Desmid Community Dominants

Strong spatial variation in the suites of dominant species (i.e., those most numerically abundant) in the sampled desmid communities was observed. Examination of Table 10, a TWINSPAN arranged table of percentage abundance of the suites of dominant species in individual samples, reveals several trends of variation. The highly minerotrophic pool samples and the most purely ombrotrophic pool samples share very few dominant species. Samples from pool TF1 and TF2 are somewhat transitional between the two groups, but few species are involved in the transition

Table 10: PERCENTAGE ABUNDANCE OF DOMINANT DESMID SPECIES IN INDIVIDUAL SAMPLES

Pool	: PTTTTTTTTTTTTTTTTTTTPPPPPPPPPPPPPPPPPPPPPPPPPPPPPPTTTTPPTTTTTTTTTTTTTTTTTTTTTPTTTTTTTTTTTTTPPPPPPPPPPPPPPPPPPPPPPP
	: FFFBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBBFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFFF
	: 33311111111111222222111111111112222222222333333333444332222222223111111111112432344443333311111111122332222222233
Date Sequence	53512345678992567891234567899123456789123456789145723123456781123456789912998368912679123456789344812567899978
Ar. octocornis	..........................1........2..
P. cylindrus	................3...
P. silvae-nigrae	....4.23633.236.445...2..12.223333322.2.222222...4..........1...2....4.3.4..
Pl. tridentulum	.................1..
Pl. minutum var. latum	..........................1.21.......2..
C. subcucumis	...2322322333......1...................1..
C. subtumidum	.................3444544344223333222232223321..
C. contractum	.................1........1....1..
C. quinarium	..........................2....1.12...
C. pseudotaxichondrum	...................................1....2211...
C. difficile	.46...
Cl. acutum	...................................2..
Cl. spy 8	...................................2..2..12..
Sd. aristiferus	..........................1........2....11..
Sd. omearii	...........23..............1.........11...
Sd. phimus	.....................................1..
St. quadrispinatum	...7644143444.............212.....33432221134..
St. simonyii	...2..............1.....1...
St. furcatum	.................1.....22.....222211.....1221..
St. anatinum	....................2222.21....22.133.2.21...
St. margaritaceum	.................2...................2.....1...
St. elongatum	....2..
E. binale	.................22.2233222233223332334324333...
E. insigne	..........................1...
E. denticulatum	..................................11...1.11..1................
E. elegans	......................................1...
E. insulare	.................................2.32.2222..
G. neglecta	..........................23.2.21...
X. torreyi	..........................2...
G. neglecta var. A	.................333222.12242322..2..
A. cucurbita	......2...23....4.44544454443443444434435444435653547777666677.22233322225538.......................................
A. cucurbitinum	....2...
Pl. minutum	...32222.222.......22.221222212..2.1.213.222223.............478766687774..
E. montanum	....1..22..
St. brebissonii	....51...
C. sp.	....3..3..2.....................
Cy. brebissonii	55423656365547666464.444344334.4433324.353433...3.433444.3.2123344333.4.......4.34.23.333442.3.3223332222.
T. laevis	..........................1...2122...1...11..................2..................25..................................
Cl. venus	..4...4...
B. borreri	...2.2222.22..................1.......2...21.......................................2..222...32...2.121...1..
Pl. rectum	....22.3.2.23.2...2...112..
Pl. ehrenbergii	....1....
Cl. dianae	3..4..........................212...112.
Cl. striolatum	....4.........2...........3335.4464754642333232.3233321212214.
Cl. kuetzingii	....................................2.......................0.4...............2..2.22..2..........
Cl. gracile	....22..233434.2...1..22333..
Cl. juncidum	....2............................
C. tumidum	....2....1.11......
Sd. extensus	....2.............2.11....
St. orbiculare	....1...........................
St. brachiatum	........................21..35545444..
E. ansatum	....1...........................
E. pectinatum	....1..
Cl. closterioides	....2..........2...11...
Cl. ralfsii	....1...........................
Cl. toxon	....12.22..............1..1..
Cl. ulna	....42343422332...33.22222..
Cl. baillyanum	....1..
C. pyramidatum	....3....6..3..............3..............2.3.22.23323233222222223
C. amoenum	....3.........................
C. margaritiferum	....112..
Te. granulata	....1..3332223
E. ventricosum	....1...
E. boldtii	........1...11122..
X. cristatum	........1..........................1..1..1.1.1..
H. dissiliens	....1...........................
T. granulatus	....44.5..............2...22222.3.2.66534.3.3223223233.....32.212222..
T. brebissonii	...................2.....1...12...22.11.......11......1..............................3..3..2..2434.3332222..
N. digitus	...........................21222.....2.2.....1.......2.1...23.2..................3...........3...2.2...2..2222222..

notes.: 1) date sequence : 1 = Sept. 80; 2 = Nov. 80; 3 = Dec. 80; 4 = Mar. 81; 5 = Apr. 81; 6 = May 81; 7 = Jun. 81; 8 = Jul. 81; 9 = Aug. 81.

2) table entries refer to percentage classes: 1 = 0 – 3 % of the total sample cell count ; 2 = 3.1 – 8 % ; 3 = 8.1 – 16 %; 4 = 16.1 – 30 %; 5 = 30.1 – 42 %; 6 = 42.1 – 68 %; 7 = 68.1 – 88% ; 8 = 88.1 – 100 %.

3) The table was structured with the aid of the computer program THINSPAN.

relative to the total species in all samples. Only one species, Cylindrocytis brebissonii, occurred abundantly in all pools, being present as a dominant in 82 of the total of 109 samples. The number of species in the suites of dominants decreases sharply from permanent to temporary pool samples. Concurrently, the percentage abundances were greater by individual taxa in temporary pools compared with permanent pool samples, suggesting a more even spread of abundance in permanent pools.

Variation in the suites of dominant desmid species was further examined using ordination analysis by DCA. The results from individual samples from each pool for the complete sample period were ordinated to allow an assessment of variation in individual communities over time, compared with variation between sample pools. Weightings used for species were densities as cells/g dry weight Sphagnum. Ordination trials using percentage abundance weightings produced results roughly similar to raw density data, but had the disadvantage of overweighting species from samples with relatively few dominant species. Outliers, those species taking extreme and anomolous scores as determined by preliminary ordination trials, were dropped from the final data set as recommended by Gauch (1977). Eight of the initial 69 taxa used in the ordination were so dropped. Such species occurred in only one or two samples with these samples having few other dominant taxa.

An ordination plot of sample and species axes 1 and 2 is given in Figure 16. The first sample axis has a gradient length of 431 and an eigenvalue of 0.79. Samples from pools of differing minerotrophic status are separated on axis 1, with ombrotrophic pool samples scoring low and minerotrophic pool samples scoring mostly high. The most purely ombrotrophic pool samples, PB1, PB2 and PB3, and TB1, a pool of slight minerotrophic influence, score at the low end of axis 1 in an overlapping range. Samples from TB2, a pool of low to moderate minerotrophic influence, score slightly higher on axis 1. Samples from TF2, TF3, TF4, PF1, PF2 and PF3, highly minerotrophic pools, score moderate to high on axis 1. The first sample axis correlates positively with pH, Ca, Mg and silicate, and negatively with COD and tannins + lignins at the 99% significance level (Table 11). Thus the gradient of axis 1 is interpreted as relating to the degree of minerotropic influence.

The placement of samples from TF1 on axis 1 is anomolous with the interpretation of the axis but may be explained by the character of TF1 samples and the operation of DCA. Samples from TF1 score lowest on axis 1 yet were expected to score medially if the degree of pool minerotrophic influence is the underlying variable in creation of axis 1. Pool TF1 receives a moderate input of mineral soil water. Samples were highly dominated by Pl. minutum (Appendix V). This species was a characteristic ombrotrophic pool species (Table 10), found in all

Figure 16 : DCA ordination axis 1 plotted against axis 2 for quantitative desmid data (all samples).

legend : plot A = samples

TB1 = 65 - 74; ✲ ✲ ✲ , TB2 = 94 - 100; — · — , PB1 = 75 - 84; □□□

PB2 = 85 - 93; ■■■■ , PB3 = 101 - 109; △△△ , TF1 = 38 - 47; ▲▲▲

TF2 = 48 - 56; — — — , TF3 = 57 - 64; ●●●● , TF4 = 1 - 9; ———

PF1 = 10 - 18; · · · · , PF2 = 19 - 28; ✱ ✱ ✱ , PF3 = 29 - 37;

plot B = species

1 = A.cucurbita	*24 = Cl.venus	47 = E.pectinatum
2 = Ar.octocornis	25 = Cl.juncidum	48 = E.insulare
*3 = A.cucurbitinum	26 = C.tumidum	49 = Cl.closteriodes
*4 = P.cylindrus	27 = B.borreri	50 = Cl.ralfsii
5 = P.silvae-nigrae	28 = Cy.brebissonii	51 = Cl.toxon
6 = Pl.minutum	29 = Sd.extensus	52 = Cl.ulna
7 = Pl.tridentulum	30 = Sd.sellatus	53 = Cl.baillyanum
8 = Pl.minutum var.latum	31 = Sd.omearii	54 = C.pyramidatum
9 = Pl.rectum	32 = Sd.phimus	55 = C.amoenum
10 = Pl.ehrenbergii	33 = St.orbiculare	56 = C.margaritiferum
11 = C.subcucmis	34 = St.quadrispinatum	57 = T.granulatus
12 = C.subtumidum	35 = St.simonyii	58 = T.laevis
13 = C.contractum	36 = St.furcatum	59 = T.brebissonii
14 = C.quinarium	37 = St.braciatum	60 = Te.granulata
15 = C.pseudotaxichondrum	38 = St.anatinum	*61 = St.brebissonii
*16 = C. sp.	39 = St.margaritaceum	62 = E.ventricosum
*17 = C.difficile	40 = St.elongatum	*63 = E.boldtii
*18 = Cl.acutum	41 = E.binale	64 = G.neglecta
19 = Cl. sp. A	42 = E.insigne	65 = X.torreyi
20 = Cl.dianae	43 = E.denticulatum	66 = X.cristatum
21 = Cl.striolatum	44 = E.elegans	67 = G.neglecta var. A
22 = Cl.keutzingii	*45 = E.montanum	68 = H.dissiliens
23 = Cl.gracile	46 = E.ansatum	69 = N.digitus

notes :

1) the sample numbers run in sequence of sampling date, starting with the earliest date.
2) the last two sample numbers for pools TB1, TF1, PF2, & PB1 are replicates.
3) the December and March samples are not included for TB2; no species were quantified.
4) the March sample is not included for TF3; no species were quantified.
5) species marked with an asterick were deleted from the analysis; they were identified as outliers.

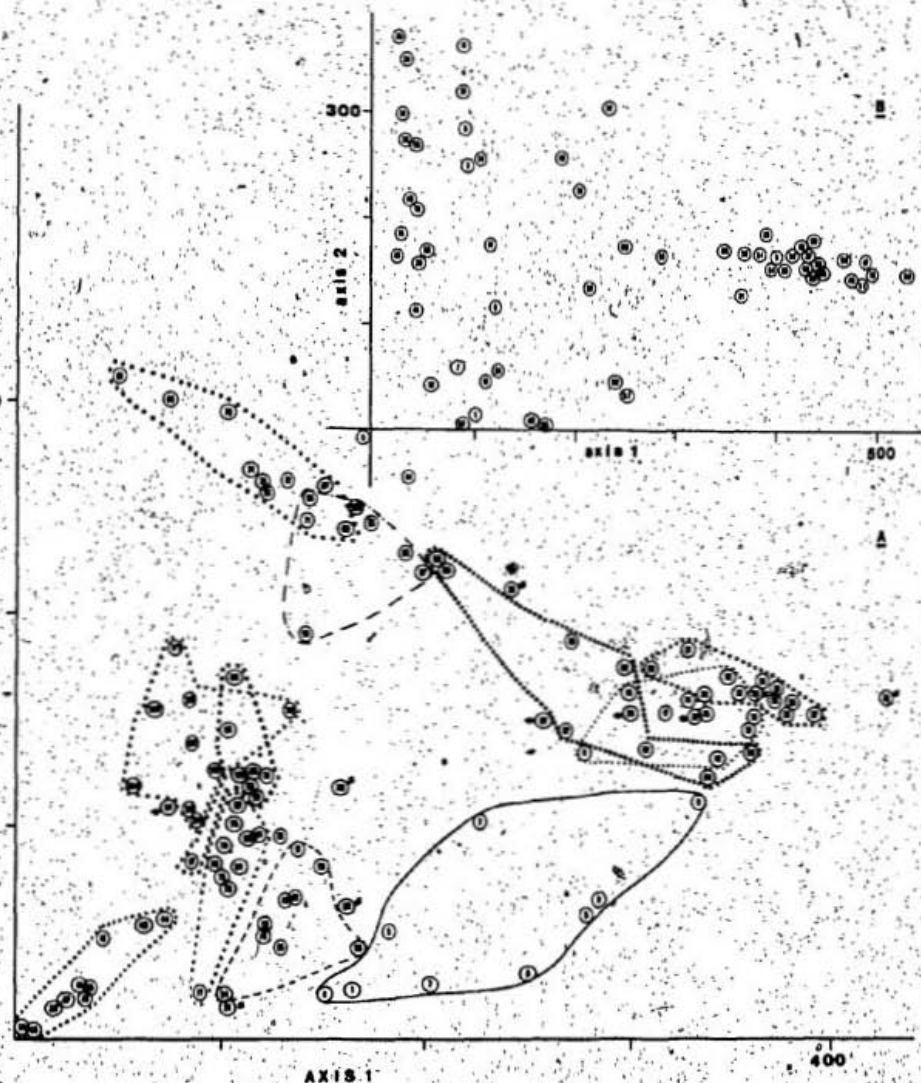

300
axis 2
B
axis 1
500
300
A
AXIS 2
AXIS 1
400

Table 11: PEARSON CORRELATION COEFFICIENTS OF ORDINATION SAMPLE AXES SCORES AGAINST WATER CHEMISTRY VARIABLES FOR THE THREE QUANTITATIVE DESMID DATA ORDINATIONS

	Complete sample set ordination				Ombrotrophic pool sample subset				Minerotrophic pool sample subset			
Axis	1	2	3	4	1	2	3	4	1	2	3	4
pH	0.80	-	-	-	-	-	-	-	-.56	-	-	-
conductivity	-	-	-	-	-	-	-	-	-	-	-	-
oxygen(sat.)	-	-	-	-	-	-.51	-	-	-	-	-	-
oxygen(conc.)	-	-	-	-	-	-.42	-	-	-	-	-	-
nitrate	-.36	-	-	-	-	-	-	-	-	-	-	-
ammonium	-	-	-	-	-	-	-	-	-	-	-	-
kjeldahl N	-	-	-	-	-	-	-	-	-	-	-	-
phosphate	0.33	-	-	0.26	-	0.39	-	-.37	-	-	-	-
total P	-	-	-	-	-	-	-	-	-	-	-	-
calcium	0.67	-	-	-	-	0.44	-	-	-.39	-	-	-
magnesium	0.57	-	-	-	-	-	-	-	-	-	-	-
iron	-	-	-	-	0.75	-	-	-	-	-	-	-
silicate	0.41	-	-	-	0.42	0.37	-	-	-	-	-	-
tannins+lignins	-.56	-	-	-	-	-	-	-	-	-	-	-
COD	-.32	-	-	-	-	0.38	-	-	-	-	-	-
colour	-	-	-	-	-	0.45	-	-	-	-	-	-

Note: All coefficients given are significant at $Pr \leq .01$

ombrotrophic and slightly minerotrophic pools but absent elsewhere. The nature of the gradient of axis 1 results in the low scoring of Pl. minutum on species axis 1. The extremely high abundance in TF1 samples causes a high weighting of Pl. minutum. Since the sample scores are the average of species scores, TF1 samples score low. Other species of more minerotrophic affinity in TF1 samples which score higher on axis 1 and would otherwise result in a higher placement of TF1 samples on axis 1 were not significant in the sample average score due to low relative weighting.

Variation in scoring of samples from the highly minerotrophic pools (TF2, TF3, TF4, PF1, PF2, PF3) on sample axis 1 cannot be related to the degree of pool minerotrophic influence, in that these pools were roughly equally placed on the physical minerotrophic gradient. Sample placement in this group on axis 1 correlates positively with pool placement on the physical permanency gradient. Samples from TF2, the pool of least degree of permanency scoring relatively lowest, and samples from PF1, PF2, pools with a high degree of permanency, scoring highest. Samples from TF3, TF4 score relatively intermediate, being in agreement with their placement on the permanency gradient. The samples from PF3 score irregularly throughout the range of minerotrophic pools and this is attributed to anomolous, relatively large variation in composition and relative

abundance of dominant species in PF3 samples over the study period (see Appendix V).

The gradient of sample axis 1 is thus complex, being as a whole descriptive of a minerotrophic gradient but also incorporating a permanency gradient at its median to high ranges. The permanency gradient relates only to highly minerotrophic pool samples.

Species axis 1 separates species of differing ecological affinities along the minerotrophic gradient. Species scoring low were mostly restricted to ombrotrophic pools and those with a slight degree of minerotrophic influence, whereas those scoring high were restricted to highly minerotrophic pools. Those species wide ranging in pools of the minerotrophic gradient score intermediately on axis 1. Examination of the plot of species axis 1 shows that there is a moderate polarization of species at the extremes of the axis with few species scoring medially. This describes an important feature of spatial change in dominant species along the minerotrophic gradient, that being that few species were shared in samples from pools of extremes of gradient placement. The sample gradient length of axis 1 was 450 = 4.3 SD units and indicates very few shared species in samples at opposing ends of the axis (see Appendix II).

The second sample axis of the ordination (Figure 16) has a gradient length of 313 and an eigenvalue of 0.36. Separation of samples from ombrotrophic permanent pools PB1,

PB2 and PB3 from those of temporary pools TB1 and TB2 is apparent and suggests a gradient related to pool permanency. However, samples from highly minerotrophic pools (plus TF1) show only a moderate degree of separation. Examination of species axis 2 shows that separation is great in those species scoring low to median on axis 1 (i.e. those species restricted to ombrotrophic pools or wide ranging on the minerotrophic gradient) whereas there is little separation of species scoring high on axis 1 (i.e. species with affinity for highly minerotrophic pools). This suggests that the direction of variation in the data responsible for the creation of axis 2 relates to ombrotrophic pool samples. This result is to be expected given the strong differences in dominant species in relation to axis 1 (minerotrophic gradient).

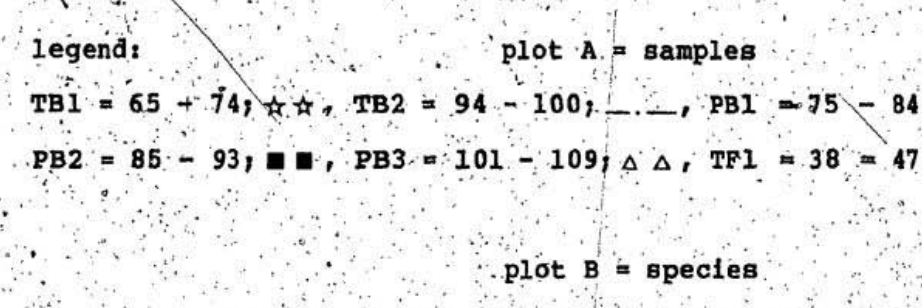
A greater degree of resolution of compositional relationships between the suites of dominant species from the various sample pools was achieved by splitting samples into two more homogenous groups (lower Beta diversity: Whittaker, 1972) and further ordinating (DCA) the groups separately. Gauch (1977) states that individual ordination of disjunct submatrices of a data set, these being sample subsets with no or very few species in common, may give much better results than the ordination of the complete data set. The main disjunction in suites of dominant species was in relation to axis 1, relating to the minerotrophic status of the sample pools. TF1 and TF2 shared species with both

extremes of the gradient and separation of the data set required arbitrary placement of TF1 and TF2 samples with the contrasting groups. TF1 shared four species with ombrotrophic pools that were otherwise restricted as dominants to ombrotrophic pools and shared only one such species with minerotrophic pools. Thus TF1 samples were ordinated with the ombrotrophic group. TF2 shared three species each with ombrotrophic and highly minerotrophic pools that were otherwise restricted to that pool type. TF2 qualitative species composition strongly resembled the highly minerotrophic pool group (Table 7) so it was decided to place TF2 samples with that group.

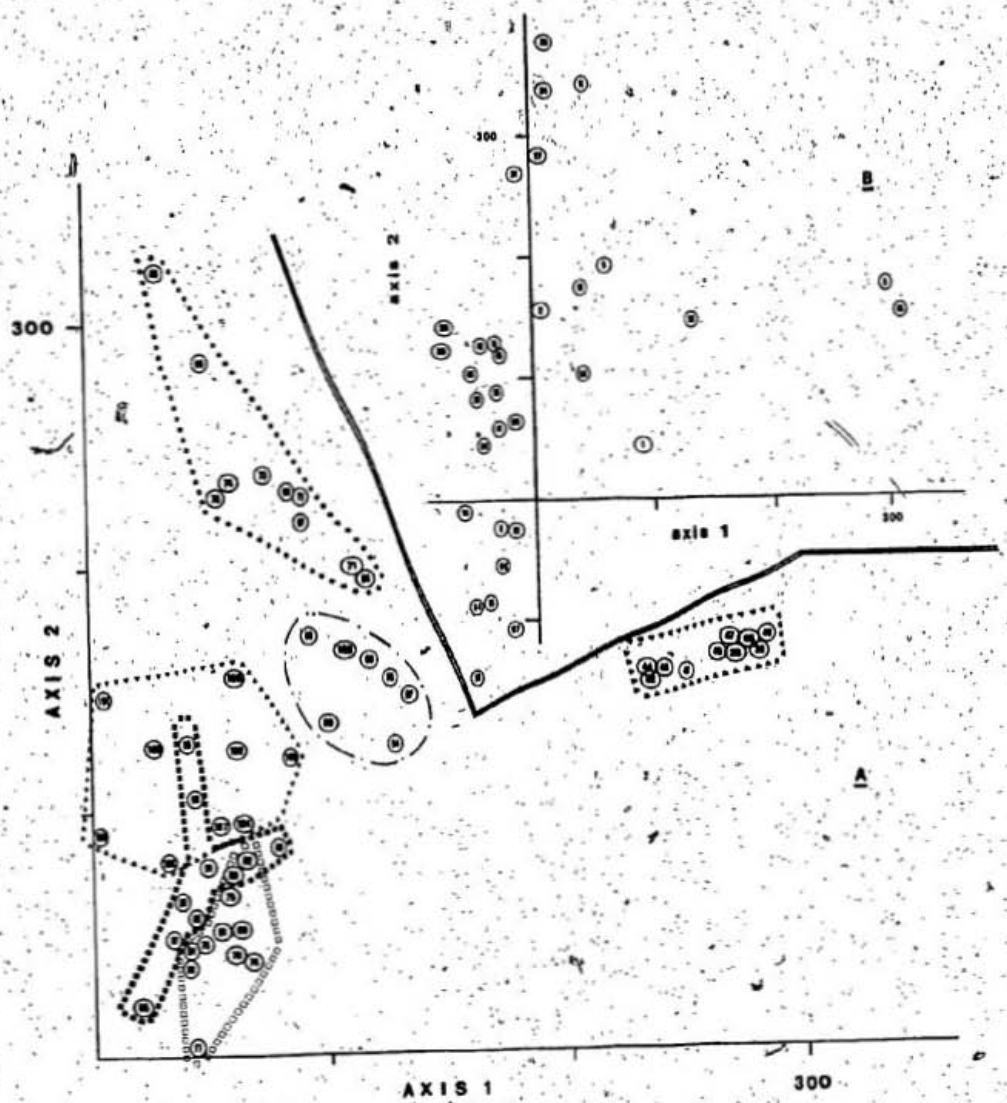
The first two sample and species ordination axes (DCA) of the suites of most abundant species in the ombrotrophic pool subset of samples is given in Figure 17. Included in this group are samples from PB1, PB2, PB3, TB1, TB2 and TF1. The group will be referred to as the ombrotrophic subgroup, but it should be noted that it includes pools of slight to moderate minerotrophic influence.

The first sample axis has a gradient length of only 280 and an eigenvalue of 0.61. There is little separation of samples on axis 1 except for the high scoring of TF1 samples, away from the remaining low scoring samples. The relative positioning of samples is comparable with the results of the first axis of the ordination of the complete data set (Figure 16), except that the position of TF1

Figure 17: DCA ordination axis 1 plotted against axis 2 for quantitative desmid data (ombrotrophic subgroup of samples).



Notes:
1) the sample numbers run in sequence of sampling data starting with the earliest date.
2) the last two sample numbers for pools TB1, PF1, and TF1 are replicates.
3) The December and March samples are not included for TB2. No species were quantified.


300
AXIS 2
AXIS 1
300
C
B
A
axis 2
axis 1
300

samples is reversed and more extreme. The placement of samples correlates positively with the degree of sample pool minerotrophic influence. The sample axis also correlates positively with Fe and silicate levels in sample pools at the 99% significance level (Table 11). Change in sample composition along axis 1 is characterized by subtle differences in the mix of species and relative abundance of these species. There is considerable sharing of species in samples at the extremes of the axis.

Species axis 1 separates species having affinity for pools of moderate minerotrophic influence from those with affinity for ombrotrophic pools. There is little separation of species, with a few scoring medial or high and most scoring low. This can be explained partially by the fact that the ombrotrophic pools sampled were permanent whereas the pools with a degree of minerotrophic influence were temporary; the number of species in suites of dominant species was sharply reduced in temporary pools compared with permanent pools.

The second sample axis of the ordination of the ombrotrophic samples has a gradient length of 322 and an eigenvalue of 0.34. The gradient of axis 2 is interpreted as relating to the degree of pool permanency. Samples from PB1, the pool with the greatest degree of permanency, score lowest on axis 2. Samples from two remaining permanent pools PB2 and PB3, score slightly higher on axis 2. All temporary pool samples score higher but with some overlap

with PB3 samples. The positioning of TB1 samples higher than those of TB2 samples on axis 2 is anomolous. TB2 had a distinctly lower degree of permanency than PB1.

Species axis 2 of the ombrotrophic pool group oridination separates species on the basis of affinities for degree of pool permanency. Those species scoring lowest were restricted to permanent pools, or at least show greatest abundance in this pool type. The smaller number of species scoring highest on axis 2 showed greatest relative abundance in temporary pools, but were not restricted as dominants to this pool type. The intermediate range species are more difficult to interpret, some being wide ranging on the permanency gradient, others being in greatest relative abundance in PB3 compared with PB1 or PB2 samples, and being unimportant in temporary pool samples.

Changes in the suites of dominant species along the gradient of axis 2 are characterized by the absence of many species in temporary pools occurring as dominants in permanent pools. The dominants of temporary pools were mostly wide ranging with respect to permanency and show no greater abundance in temporary pools.

The first two ordination axes (DCA) of the suites of dominant species in the highly minerotrophic pool subset of samples are given in Figure 18. The group includes samples from PF1, PF2, PF3, TF2, TF3 and TF4, and will be referred to as the minerotrophic subgroup of samples.

Figure 18: DCA ordination axis 1 plotted against axis 2 for quantitative desmid data (minerotrophic subgroup of samples).

legend: plot A = samples

TF2 = 48 - 56; _ _ , TF3 = 57 - 64; ● ● , TF4 = 1 - 9; ____

PF1 = 10 - 18; . . . . , PF2 = 19 - 28; * * , PF3 = 29 - 37.

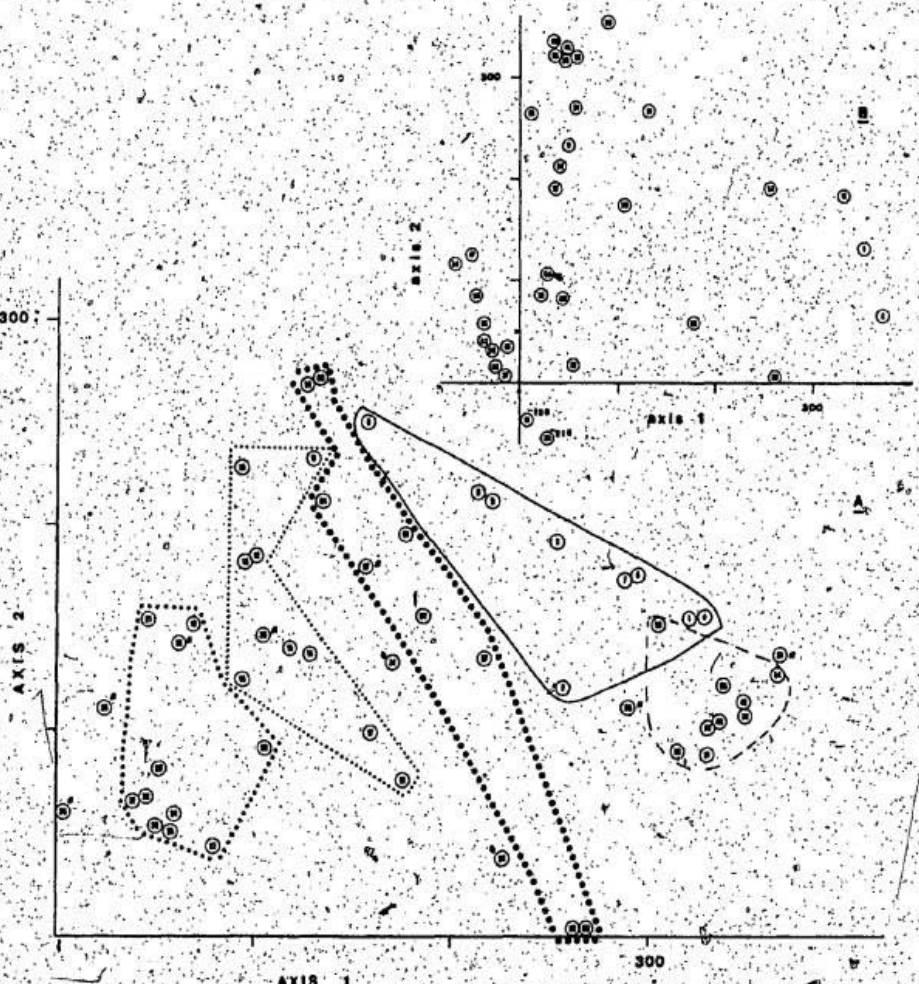
plot B = species

1 = A. cucurbita	47 = E. pectinatum
3 = A. cucurbitinum	49 = Cl. closteriodes
9 = Pl. rectum	50 = Cl. ralfsii
10 = Pl. ehrenbergii	51 = Cl. toxon
16 = C. sp.	52 = Cl. ulna
20 = Cl. dianae	53 = Cl. baillyanum
21 = Cl. striolatum	54 = C. pyramidatum
22 = Cl. keutzingii	56 = C. margaritiferum
23 = Cl. gracile	57 = T. granulatus
25 = Cl. juncidum	58 = T. laevis
26 = C. tumidum	59 = T. brebissonii
27 = B. borreri	60 = Te. granulata
28 = Cy. brebissonii	62 = E. ventricosum
29 = Sd. extensus	63 = E. boldtii
33 = St. orbiculare	66 = X. cristatum
37 = St. braciatum	68 = H. dissiliens
46 = E. ansatum	69 = N. digitus

notes: 1) the sample numbers run in sequence of sampling date starting with the earliest date.

2) the last two sample numbers for pool PF2 are replicates.

3) the March sample is not included for TF3. No species were quantified.


300
AXIS 2
AXIS 1
300
B
axis 2
axis 1
300
A

The first sample axis has a gradient length of 3.67 and and eigenvalue of 0.74. The axis separates samples from permanent pools from those of temporary pools. Samples from TF2 score highest on axis 1, overlapping with those of TF3. TF2 had the least degree of permanency in this group with TF3 being as well distinctly temporary in character but with a slightly higher degree of permanency. PF1 and PF2 samples score low on axis 1. These pools have a high degree of permanency. With the exception of PF3, conformity between sample placement on the axis and pool permanency is strong. PF3 samples are spread throughout the range of axis 1. The explanation is the same as given for the similar result observed with axis 1 placement of PF3 samples in the ordination of the complete data set.

Species axis 1 shows a good spread of scores, with a large number of species clumped at the low end. Species scoring low were restricted to or showed greatest abundance in permanent pool samples. The few high scoring species were more abundant in temporary pools. Species showing no affinity to degree of pool permanency scored intermediately.

Changes in the suites of dominant species in samples along the gradient of axis 1 is comparable in character with that observed for the permanency gradient (axis 2) of the ombrotrophic sample subgroup ordination. Many of the permanent pool dominants were absent in temporary pools but the temporary pool dominants were also dominants in permanent pools. In the minerotrophic subgroup

there were slightly more species that showed a greater abundance in temporary pools.

The second sample axis has a gradient length of 268 with an eigenvalue of 0.21. There is no separation of samples from differing sample pools, all of which overlap completely. The ranges of sample scores differ, and are smallest in TF2 and largest in TF3. The sample placement on axis 2 corresponds loosely with a time series in samples from PF2 and PF1, with early samples scoring relatively higher than latter samples. For the remaining pool sample there is no apparent interpretation of its placement on axis 2.

Examination of species axis 2 shows a good spread of species scores. The species scoring above 300 were of infrequent, irregular occurrence. A distinction between the species scoring above and below 200 can be made that accounts for the time series observed in PF1 and PF2 sample placement on axis 1. The higher (above 200) scoring species had a greater abundance in early samples of PF1 and PF2 compared with a greater abundance of the lower scoring species in the later samples. The majority of species scoring under 200 and above 50 however showed no marked and regular temporal variation.

Variation in the suites of dominant species in desmid samples have been linked to identifiable gradients of variation; the minerotrophic gradient considering the complete data set, the minerotrophic gradient in the

ombrotrophic pool subset, and the permanency gradient in both ombrotrophic and minerotrophic pool subsets. However, much of the variation contained in the data has not been identified by ordination analysis in a manner which can be interpreted. Some characteristics of the remaining variation are apparent nonetheless. The suites of dominant species in the groups of samples from individual pools have characteristics which make them unique from all other pools. An examination of the ordination axis plots of the ombrotrophic and minerotrophic subgroups of samples (Figure 17, 18) shows that in all cases, excepting PF3, pool samples form a cloud which, although overlapping to an extent with other pool sample clouds, is distinct. The closeness of sample clouds cannot be interpreted as indicative of the degree of similarity, in that samples of different composition and different relative abundance of shared species can score similarly. A difference in scoring does indicate, however, that sample composition or relative abundance of shared species is different.

Samples from pools of similar character have the highest number of shared, abundant species. However, distinctions occur even between very similar pools. Those species shared by similar pools typically vary widely in relative abundance. This characteristic can be observed from Table 10, which gives the composition and percentage abundance of species in all samples from all pools. Comparison of the dominants of TF2 and TF3 samples for

example shows a sharing of two important species yet these species differ strongly in relative abundance between these two physically comparable pools. Many other examples of this nature can be interpreted from Table 10 based on previously given descriptions of pool characteristics.

These results suggest the importance of factors other than those related to minerotrophic gradient or permanency gradient in the creation of dominance patterns in desmid communities.

It is apparent that variables related to the degree of pool minerotrophic influence and degree of pool permanency were responsible for strong selection pressures for groups of desmid species. With the large number of variables implicit within a natural system, concise statements of cause and effect are impossible. However, some inferences based on correlational evidence are possible.

Minerotrophy is a main factor determining both species composition and species dominance. The nature of changes in dominant species along the minerotorphic gradient suggests that factors related to pool minerotrophic status determine which group of species may become abundant. Other possibly independent factors determine which species of that group will be dominant.

The causal factors in determining species abundance that are correlating or resulting from changes in minerotrophy are thought to be aspects of water chemistry.

The highest correlation of water chemistry parameters with the minerotrophic gradient, sample axis 1 of the ordination of all pool samples, was with pH (Table 11). The suites of dominant desmid species of TF2 are of note in relation to pH changes. Although the pool is highly minerotrophic, it had consistently lower pH (6 of 8 samples) than all other highly minerotrophic pools (Figure 9). The water pH ranged from 4.72 - 5.68, with a mean of 5.06. Samples of TF2 lie lower on axis 1 than other highly minerotrophic pool samples (Figure 16) and are directly adjacent to samples from ombrotrophic pools. TF2 samples exhibited a marked difference from other highly minerotrophic temporary pool samples in that species wider-ranging on the minerotrophic gradient were most abundant. Restricted minerotrophic species were most abundant in the other highly minerotrophic temporary pools TF3 and TF4 but were of little importance in TF2.

Changes in dominant species along the minerotrophic gradient may also be related to changing mineral levels. Calcium, Mg and silicate correlated positively with sample axis 1 (increasing degree of minerotrophic influence) of the ordination of the suites of dominants from all sample pools, whereas Fe and silicate correlated positively with sample axis 1 (increasing degree of minerotrophic influence) of the ordination of the suites of dominants from the ombrotrophic pool subgroup of samples

(Table 11). In the latter ordination, axis 1 was independent of pH and organic materials.

The composition of dominants in samples of TF1 is of note when considering the importance of mineral levels in determining dominants. TF1 had slightly increased Fe levels compared with ombrotrophic pools but lower levels than in highly minerotrophic pools. In TF1 samples an ombrotrophic species was most abundant. Another dominant, T. granulatus was of distinctly minerotrophic affinity. The remaining dominants were wide-ranging on the minerotrophic gradient or were endemic to TF1. These results suggest both inhibitive and limiting effects in operation in TF1.

The levels of organic materials in the peat pools were in general correlated negatively with an increasing degree of minerotrophic influence (Table 9). Tannins + lignins and COD both correlated negatively with sample axis 1 (increasing degree of minerotrophic influence) of the ordination of the suites of dominants of all sample pools (Table 11). A specific case where organic materials may be related to dominance patterns is from pool TF2. The pool had a higher build-up of refractory organic materials compared with other highly minerotrophic pools (see COD: tannin + lignin ratio, Figure 10). This may be related to the distinct group of dominants in this pool previously described. However, marked seasonal changes in COD, tannins + lignins, and colour observed in TF2 and all other pools were not correlated with changes in dominant species.

Differences in N and P availability along peatland minerotrophic gradients have not been reported in relation to algal growth, but may be significant. Nitrate levels correlated positively and PO_4^{3-} levels negatively with sample axis 1 (increasing degree of minerotrophic influence) of the ordination of the suites of dominants from all pool samples (Table 11). Examination of Table 9, giving the mean levels of chemical parameters in sample pools, shows permanent higly minerotrophic pools to have highest NO_3^- levels and temporary ombrotrophic - slightly minerotrophic pools to have highest mean PO_4^{3-} levels. The mean values of both parameters were comparable between all other pools. The high number of estimations in which PO_4^{3-} and NO_3^- levels were below the detectable limits of the analysis method reduce the significance of the means (see appendix VI for number of undetectable readings).

As with the relationship of desmid community composition and the minerotrophic gradient, the permanency gradient relates to variables which select for both desmid species composition and dominance patterns. The nature of the selection for species groups in consequence to varying degrees of pool permanency appears related to the ability of desmid species to withstand desiccation. Most desmid species appear unable to tolerate even limited desiccation and were absent from temporary pools. Those species dominating temporary pools appear most adapted to desiccation. The causal factors determining which specific

species dominate temporary pools out of the suites of species capable of surviving degrees of desiccation is uncertain. The collected data are too limited to determine if differences in degrees of permanency within temporary pool groups have a selecting effect, such that the most desiccation-tolerant species will dominant the pools with the least degree of permanency.

In addition to selection for desiccation - tolerant desmid species in temporary pools, other aspects of the physical character of such pools may be important in determining dominant species. The sample ordination axes interpreted as relating to the permanency gradient given, when correlated with water chemistry data, produced significant correlations (Table 11). Sample axis 1 of the minerotrophic pool subgroup of samples (axis goes from a high to low degree of permanency) correlated negatively with pH and Ca. Since all pools were highly influenced by mineral soil water this was not a factor. It was observed that as pool size decreased so did the degree of stagnation increase. The smaller pools appear less flushed with a resulting greater build-up of organic acids from decomposition processes and more concentrated effect of acidification by cation exchange by fringe Sphagnum. This is most apparent in TF2 but all of the temporary pools of this group have a reduced pH. The explanation for the lower Ca levels in the highly minerotrophic temporary pools compared with permanent pools is not apparent. The increased pH in TF2 has previously been suggested as

contributing to the distinct suite of dominant species observed in this pool. Otherwise, pH differences between permanent and temporary pools were small and irregular and not thought important. Similarly no strong relation between changing Ca levels and dominant desmid species was observed with respect to the permanency gradient of the minerotrophic subgroup.

The second sample axis of the ordination of the ombrotrophic subgroup of samples was interpreted as correlating negatively with the degree of permanency. The axis also correlated positively with colour, Ca, silicate, COD, PO_4^{3-} and negatively with O_2 content and O_2 percent saturation (Table 11). The temporary pools have varying degrees but slightly greater percolation of mineral soil water than permanent pools, in addition to the differences in degree of permanency. This may partially account for greater levels of Ca and silicate in the temporary pools of this subgroup. Also, the temporary pools have a higher sediment surface area to water volume ratio than permanent pools. The effects of sediment mineralization will be more concentrated in temporary pools. There will be increased oxygen utilization for decomposition processes and increased inputs of minerals, organic compounds and other inorganic nutrients per volume of water. Also contributory to the observed correlations is the fact that temporary pools with smaller water volumes were subject to greater evapo-concentration of the water mass during warm periods than were permanent pools.

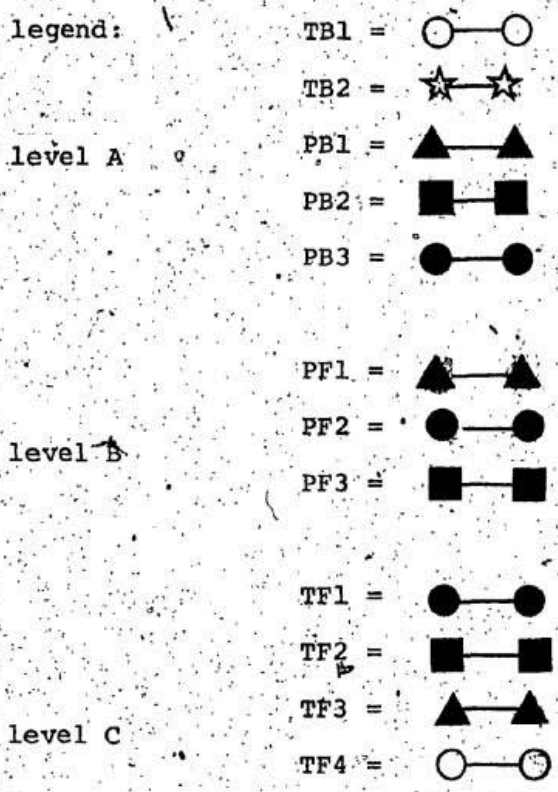
Desmid Community Structure

Abundance histograms for the suites of dominant taxa for each pool over time are given in Appendix V. Three community types are recognizable based on the spread of abundance between species, the total community population density, and the temporal variation in suites of dominants.

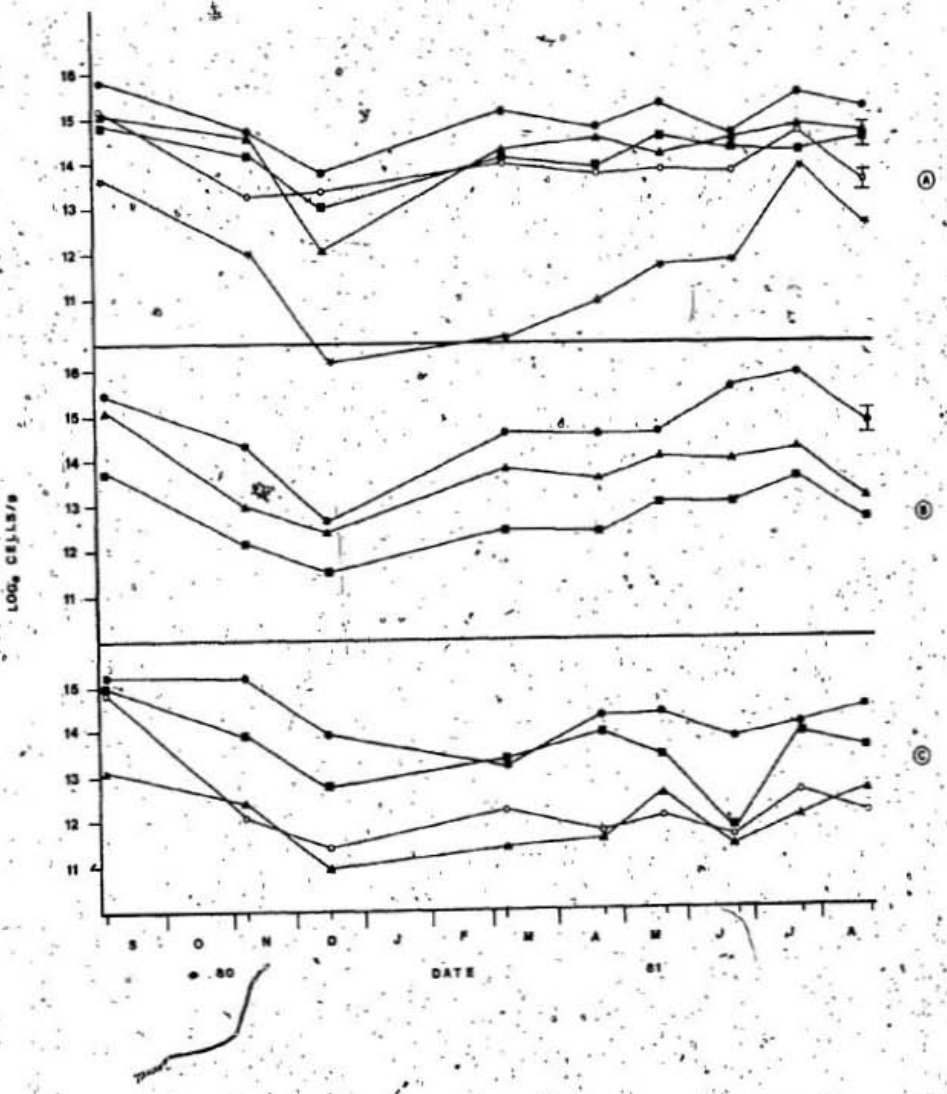
The first community type characterized by samples from all permanent pools, excepting PF3, is marked by a distinct spread of species abundances. A group of 2-5 species, in roughly equal numbers, was of highest relative abundance. There was also a gradation of species of lower abundance. These permanent pools had higher numbers of quantifiable species (given the counting procedure used) than the other community types. Total population densities of desmids in permanent pools, excepting PF3, ranged from 1.6×10^5 ($\log_e = 12$) to 6.6×10^6 ($\log_e = 15.7$) cells/g Sphagnum (Figure 19). No consistent differences in total desmid densities between permanent pools as a group and temporary pools as a group were detectable. Within the group of permanent pools there were no consistent differences attributable to pool type; ombrotrophic and minerotrophic pools had comparable total densities. A further characteristic of the permanent pool community type is that such pools maintain a degree of consistency in composition and structure over time.

From the remaining temporary pools and PF3 samples the two other community types could be identified. In

Figure 19: Total desmid population densities in individual samples.



note: extended lines give the values of two replicates with the data point being the mean.


LOG10 CELLS/g
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variance with the first community type, the remaining types can be characterized by an extreme domination by one or two species in most samples. This, in addition to the reduction in the numbers of species in the suites of dominants in temporary pools, given a uniform procedure for enumeration and of selecting dominants, allows a separation of permanent and temporary pool types. This latter difference may now be significant when total desmid populations vary between compared pools.

The two temporary pool community types are distinguished by differences in total population density and temporal stability. The first type, characteristic of TB1, TF1 and TB2 samples, is distinguishable by a moderate consistency in composition and relative abundance of species over time and by total population densities comparable with the permanent pool type.

The second temporary pool community type was shown by samples from TF3, TF4 and TB2. PF3, although of permanent nature, is included with this group. This community type is identified by strong variation in composition and relative abundance of dominant species over time. The total population densities in this group of samples were lower than observed in the other community types. Compared with other pools of this group, PF3 samples had a more even spread of abundance between component species but otherwise compared well and was strongly divergent from other permanent pool samples.

All of the desmid samples examined could be described as having a relatively small number of abundant species, with more moderately abundant species, and large numbers of rare species. The evenness (equitability of abundances in the community (Alatalo, 1981)) in samples from different pools was strongly variable. Domination of numbers by single species was greatest in TF1 and TF2 samples and least in PF2, PB1, PB2, PB3, PF1 and PF3. A more critical graphical procedure for defining species-abundance distributions of the general type shown by the desmid communities is given by Whittaker (1972). For all species independently, an abundance measure transformed to a log scale is plotted on the ordinate with the species rank in decreasing order plotted on the abscissa. An index of equitability (Ec), which gives the mean number of species per log cycle of the sampled species-abundance sequence, may be used in association with this graphical method (Whittaker, 1972).

Desmid sample plots and Ec values of these plots for each pool for the July sample, a period of maximal or near maximal development of the desmid communities, are given in Figure 20. The numbers of cells observed in the 100 field counting regime was used as a measure of abundance. All species observed were included.

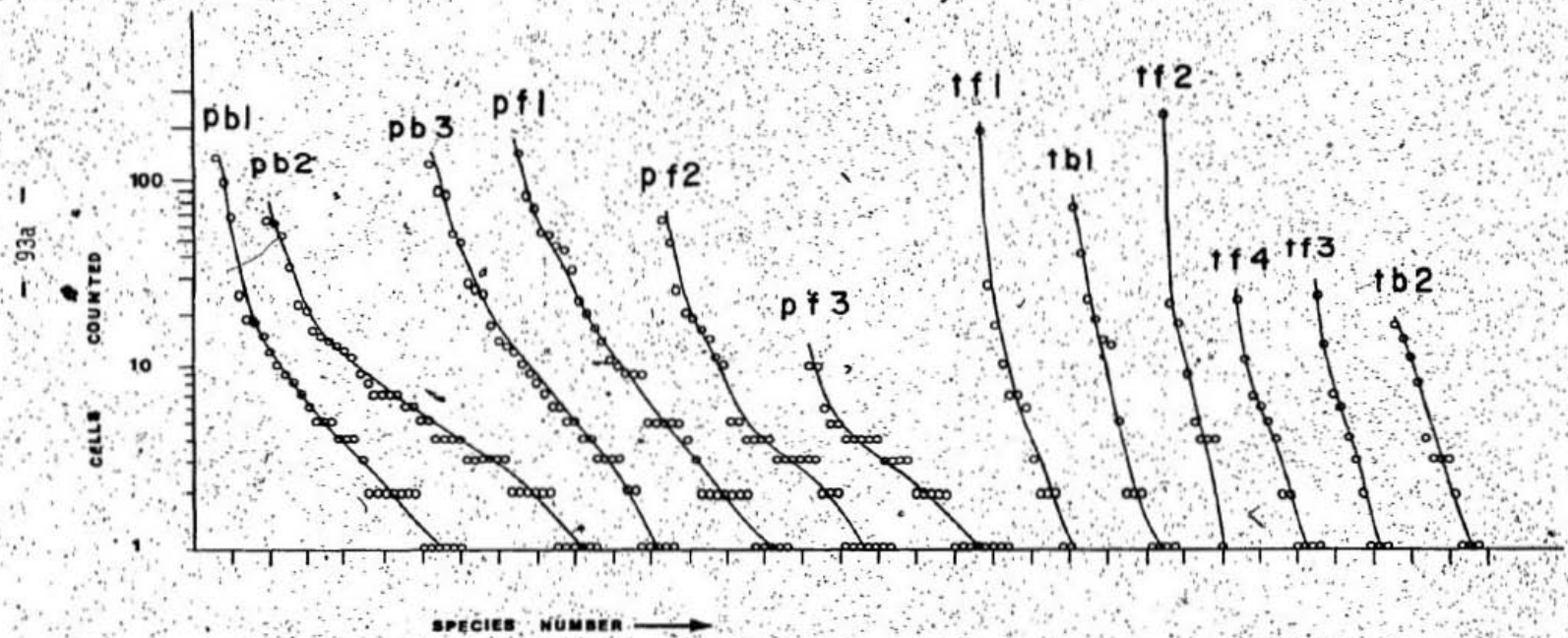
Two groups of pools with differing evenness of species abundance may be inferred from Figure 20. The permanent pool samples (PF1, PF2, PF3, PB1, PB2 and PB3) had

Figure 20: Species-abundance distribution plots of the desmid communities of each sample pool for the July 1981 samples.

notes: 1) E_e = an index of equitability. See text for details.

2) cell counted axis gives the total number of cells of an individual species counted in the standard enumeration procedure.

3) species number gives the species rank in descending order of abundance. Each species represents an individual taxon.



93a

E_c = 15·4 21·6 15·6 16·4 15·9 20·8 5·7 7·3 3·6 8·6 7·0 9·2

a more even spread of species abundance than the temporary pool samples (TB1, TB2, TF1, TF2, TF3 and TF4). The species abundance curves of the permanent pools approach lognormal whereas those of the temporary pools were more linear, approaching a geometric series. The Ec values of the permanent pool samples were higher than those of the temporary pool samples, ranging from 15.4 to 21.6 compared with 3.6 to 9.2 in the temporary pools. Increasing values of Ec represent a greater evenness of abundance.

One possible explanation for the major difference in evenness of abundance between temporary and permanent pools may relate to the destruction (die off) of portions of the Sphagnum fringe desmid communities when exposed to the atmosphere. In temporary pools, possibly few species survive desiccation events with sizable populations. These species would conceivably be able to produce still larger relative populations than the more desiccation sensitive species following rewetting of the pools, assuming equal utilization of available resources. These few desiccation tolerant species may thus become highly numerically dominant over time resulting in an overall uneven distribution of species abundance. No separation of samples from ombrotrophic and minerotrophic pools based on evenness of abundance could be detected.

TEMPORAL HABITAT VARIATIONS

This study was conducted over a one year period, September 1980 - September 1981, and thus describes changes

associated with a full seasonal cycle. The study period would be described as having a mild winter season with low amounts and duration of snow cover (Figure 21). The fall, spring and summer periods were wet with frequent periods of precipitation. The period of warm summer weather was short with only few occasions of persistent high temperatures.

Water and air temperatures show strong trends of variation indicative of seasonal changes (Figure 21). Ice cover in the sample pools was not monitored except during sample dates, but its duration can be inferred from air temperatures and depth of snow covering readings taken daily at nearby Colinet (Figure 21). Ice cover probably lasted from late December 1980 to early March 1981.

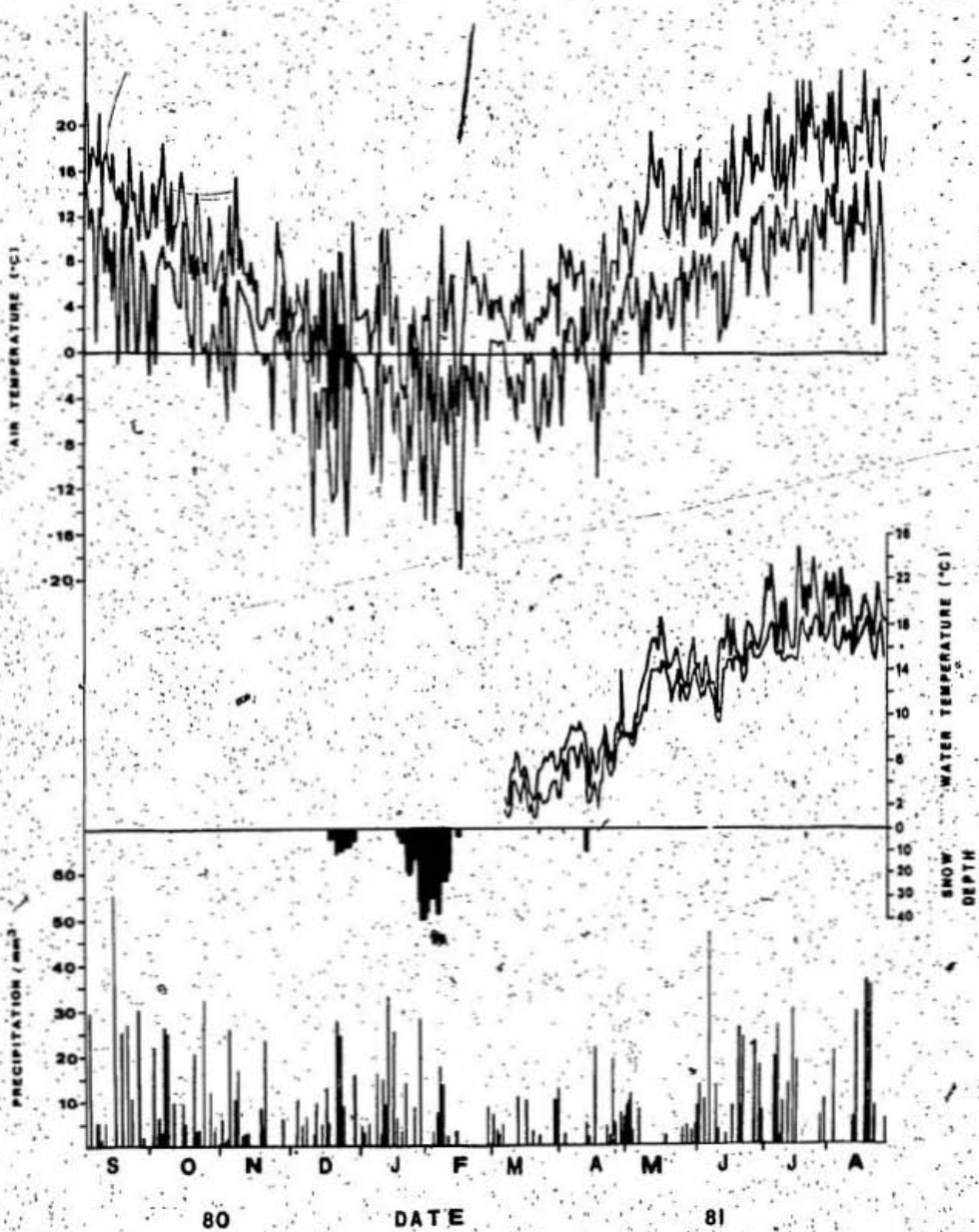
Although not assessed, the duration and frequency of periods of fog were an important component of the weather in this coastal location. Periods of fog were frequent and common in all seasons.

Strong temporal changes in pool water chemistry were observed in all sample pools. Line graphs of measured chemical parameters over time for each sample pool are given in Appendix VI and allow a critical evaluation of temporal changes in water quality. Only general features of these changes will be considered here.

Although only a single seasonal cycle was examined in this study, with interpretations of seasonality difficult on such a basis, a main component in water quality variation seems related to a seasonal cycle. These changes were

Figure 21: Precipitation, maximum and minimum air temperatures and snow cover for the study period as recorded at Colinet plus water temperatures in PB1.

note: all data excluding water temperatures were taken from Anonymous (1980-1981).


AIR TEMPERATURE (°C)
WATER TEMPERATURE (°C)
SNOW DEPTH (CM)
PRECIPITATION / mm³
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largely common to all pools except where modified by other factors such as degree of minerotrophic influence and pool water volume. Changes in water colour in sample pools over the study period gives a rough timing of most seasonal changes in water quality.

Water colour was lowest in early spring and highest in late summer. Commencing in early spring, water colour showed a progressive increase until reaching maximal levels in July or August. Water colour showed a progressive decline following this period, reaching low values in late fall. The December samples from some pools showed an increased colour whereas others did not.

The components of water composition reflected in water colour changes are uncertain. In ombrotrophic pools colour was correlated positively with the indicators of organic materials, COD and tannins + lignins, whereas in highly minerotrophic pools it was strongly positively related to Fe levels. What is significant about water colour is that it appears to indicate general changes in water quality.

During early spring 1981, the water masses in sample pools were clear and levels of dissolved organic materials were lowest. The levels of Fe, silicate, Ca and Mg were also low, and in pools showing temporal variation in oxygen saturation, oxygen levels were highest. Air and water temperatures were low (Figure 21), and macrophytes had

not yet commenced active growth. It appeared that the pools had been recently flushed, conceivably by snow melt.

With the coming of early summer the water masses were at a higher temperature for longer priods of time and there were large increases in macrophyte growth. The levels of organic materials increased slightly in this period, resulting either from greater breakdown of materials or losses from actively growing plants.

In mid to late summer pronounced changes in water quality and pool character were apparent. The water masses were highly coloured. In the highly minerotrophic pools excepting PF3, the water surfaces were covered with oily scums, thought to be an iron precipitate. In these same pools the levels of Fe, silicate, Ca and Mg had increased markedly. In the bog site pools the increases in minerals were absent in the most ombrotrophic and small in pools with a slight degree of minerotrophic influence. The levels of tannins + lignins and COD had increased markedly in all pools. Variable decreases in oxygen saturation were observed in some highly minerotrophic pools.

Since sampling ceased in September 1981 it is not possible to follow the progression into the fall, however samples were taken in November of the previous year and may be pertinent. The study site was sampled qualitatively during the summer of 1980 with much the same pattern of change being observed as in summer 1981. The frequency of

precipitation was greater in summer 1980 with a lower degree of stagnation in pools observed compared with 1981.

The fall 1980 samples show what appears to be a clearing of the water mass. The levels of tannins + lighins were moderate but decreased from those of September 1980 samples.

Winter changes in water quality are to be expected, with ice cover being an important variable in such changes. However, little can be said about the winter component of the cycle. The December samples from below ice in some ombrotrophic pools showed increases in Ca, Mg and NH_4^+, possibly related to anaerobic conditions. The ice cover in the fen site pools was minimal during this period, and water masses were clear, low in organic material and minerals, and well oxygenated.

The positive correlation of water temperature (air temperature for the first portion of the study) with the level of dissolved organic materials, as indicated by COD, tannins + lignins and colour, suggests that there was a seasonal variation in the rate of mineralization of accumulated organic material in pools. The variation in dissolved organic materials may also be a result of macrophyte growth and/or senescence releases, but this possible contribution is thought to be secondary to the breakdown of accumulated detrital material. This interpretation is based on the better timing of gradual temperature-related decompositon influxes of organic

materials, compared to the major shifts in macrophyte growth and senesense, with observed patterns of change in dissolved organic materials.

The increased levels of minerals in highly minerotrophic and, to a lesser extent, slightly minerotrophic pools in later summer are striking. Increased solubility, desorption from sorption complexes or input from macrophytes may conceivably be related to the increased mineral levels. In several highly minerotrophic pools oxygen supply was lower than utilization during late summer, with major drops in saturation observed. A likely lowering of the redox potential of the water mass in such pools may conceivably be related to the increased mineral levels.

Other components of water quality measured showed temporal variations of a pattern either different from that given, such as total phosphorus (a wide winter-spring peak), or else showed more complex and erratic change, such as pH. All pools showed temporal variations distinct from other pools. Many variables can be identified which contribute to temporal changes in water quality. The sequence of weather patterns, the degree of water movement in the sample pools, pool morphometrics, and the amount and character of the biota have all been observed to contribute what is a complex set of variations but will not be described here. The seasonal cycle in water quality previously given is thought to represent a main direction of variation which has some degree of applicability to all pools and is in a general way predictable.

TEMPORAL VARIATIONS IN THE DESMID COMMUNITIES

Desmid Community Composition

Over the study period no regular pattern of increase or decrease in species richness was observed in the desmid communities studied. The numbers of taxa occurring in samples over time from individual pools was unexpectedly consistent (Figure 13). The greatest fluctuations were in the most species-rich fen pools, but they did not follow a pattern.

The specific composition of the pool communities showed no apparent cyclic or successional temporal variations. Variations in the occurrence of individual species appeared at random with the degrees of variation related to the species abundance. Relatively abundant species were consistently present over time, whereas low abundance species varied to a greater extent. Arranged tables of species composition over time were used to assess variations, but are not presented.

Survival of desmid species over the potentially physically stressing winter period was high. The winter period was short-lived and mild. Examination of Figure 21 shows that snow cover was not extreme, maximum of 40 cm at Colinet, and air temperatures were not excessively low. Whether a greater loss of desmid species could be predicted given a longer and more harsh winter period is of interest. Personal observations of the summer/winter desmid

communities of a variety of Western Newfoundland peat sites over three previous winter periods suggests that reduction in species can be large.

Winter survival by desmids at the North Harbour sites was predominantly by vegetative cells. Only a few species (4 of 135) produced sexual resting bodies over the study period. The infrequency of zygospore production and the lack of timing with environmental stresses (ie. ice cover and pool drying) suggest that such resting stages were not an overall strategy for survival in the desmid communities.

Desmid Community Dominants

Only a small degree of seasonal or successional change was observed in the suites of dominant species in the desmid communities over the one year study period. A survey of Appendix V reveals that although temporal changes in absolute and relative abundance of dominants does occur, the overall regularity observed in most pools is striking given the difficulty in accurate quantification. Ordination analysis of dominant species did not detect any general trends in temporal variation. Given the differences in dominant species between pools, overall trends should perhaps not be expected. However, examination of the sequences of samples from individual pools would reveal temporal changes if occurring.

Such changes have been found. The spring and summer samples of TF1 are separated on axis 1 of the dominant species ordination of ombrotrophic and slightly minerotrophic pool samples (Figure 17). A slight seasonal change in PB3 was detected on axis 2 of the same ordination. The ordination of the minerotrophic subgroup of samples (Figure 18) revealed what appeared to be a degree of temporal succession in dominants of PF1 and PF2 on the 2nd axis.

Three types of temporal changes in dominant species have been detected. The first type is of a possibly cyclic nature, being related to season. The second is successional in nature, consisting of regular and progressive changes in relative abundance of species. The last type of change is erratic, characterized by strong irregular changes in relative abundance over periods as short as a single sampling interval.

Some taxa in specific pools showed apparently seasonal changes in relative abundance. A small group of species showed a strong relative reduction in abundance during the winter-spring period. The most distinct were St. quadrispinatum in ombrotrophic pools, T. granulatus in TF1, and St. brachiatum plus Te. granulata in PF2. No species appeared more abundant in this period but some species were less reduced in abundance than others. The decrease in relative abundance of these species may be related to

decreasing temperature and or decreasing length and intensity of daily illumination.

The second type of temporal change in dominant species observed was successional, being gradual and persisting for a period of time. Such changes were shown by only a small proportion of the communities studied and are difficult to interpret given the inherent variability in species population density estimates. The strongest example of such change is the limited succession of dominants observed in PF1 and to a lesser extent in PF2. The September-April samples of PF1 were characterized by roughly comparable densities of T. granulatus, Cl. ulna, Cl. striolatum, Cy. brebissonii and Cl. gracile. In the May-July samples the relative abundance of Cy. brebissonii and Cl. gracile increased markedly. In general however there were few such gradual successions of sufficient magnitude to be apparent.

The third and most conspicuous type of temporal changes in relative abundance were those of irregular occurrence and short duration. The extent of such changes was highly variable. Major changes of this type in dominant species were characteristic of pools TF3, TF4, TB2 and PF3. The dominant species in samples of this group of pools changed erratically in relative abundance. In all cases, however, a group of species of more frequent occurrence and in relatively high amounts, was identifiable.

The strong variations in the suites of dominant species observed in PP3, TF3, TF4 and TB2 are thought indicative of real change as opposed to an artifact of sampling or enumeration error. Pools TP1, TF2, TB1 of similar size and sampling characteristics with the above group of pools showed high degrees of temporal consistency in dominant species.

The pools showing erratic variation in dominant species share two further characteristics: the total desmid population densities were reduced compared with other pools (Figure 19); the percentages of the species that occur qualitatively in all samples is reduced and the percentage occurring only rarely is increased compared with other pools (Figure 15). This, in agreement with and in addition to the observed variability in composition of dominants, suggests community instability resulting from some environmental stress.

This may be accounted for in TB2 by the more extreme level of desiccation to which the Sphagnum fringe was subjected compared with other temporary pools. The pool was assessed to have the least degree of permanency. It lacks bottom vegetation and has a sediment microflora depauperate in species and quantity, both features indicative of extreme drying. This explanation does not account for the variation observed in TF3 and TF4. TB1 and TB2, pools with a lower degree of permanency than TF3 and TF4, show consistency in composition and have total

populations comparable with permanent pools. Stresses accounting for the variability in TF3 and TF4 were not apparent.

The variability in dominant species in PF3 may be explained by a continuous flow of surface water in this pool. The water movement may have resulted in the destruction and movement of portions of the aufwuchs community along the flow course, and in the elimination and addition of dominant desmid species to the aufwuchs, thus creating a high degree of temporal and spatial variability.

The total desmid densities from all sample pools show what appears to be a seasonal change related to temperature. In most pools there was a drop in total densities in the December samples, to the lowest observed levels. This coincides with the beginning of the ice cover period (Figure 21). In general, total densities were reduced in the November-March period, the period of coldest water temperature. Maximum total densities occurred in the periods of warmer water temperature, April-September, but not necessarily the period of warmest water. All pools except TF3, PB2 and TF1 had maximum summer densities in the July samples, with variable reductions in the August samples. The remaining pools had August maxima. All pools showed a late summer maximum, but in many pools the difference between the maximum and other samples of the April-August period was slight.

It is striking that, given the extent of what is interpreted as a cyclic change in pool water quality (see Appendix VI), no overall seasonal changes in the suites of dominant desmid species were observed to correlate with these changes in water chemistry. Perhaps finer changes in relative abundance of species may be related to the water quality changes, but, the accuracy of the biological data does not justify detailed analysis.

DISCUSSION

The examination of desmid community spatial patterns over characteristic gradients of peatland habitat represents the main thrust of this thesis. It was also thought important to include a temporal gradient of variation in this study so that the way in which spatial patterns changed over seasonal cycles could be examined. A key objective was to make inferences on the causal factors in desmid community dynamics in this habitat. The level to which evaluation of causal factors can be taken, given the nature of the study, is admittedly limited, yet interpretations do yield an invaluable framework for the design of experiments aimed at defining these causal factors.

It has been demonstrated that the dynamics of desmid communities of the Sphagnum aufwuchs of pools from the North Harbour peat sites were, to a high degree, related to abiotic/biotic variables of the habitat. The groupings of dominant species, as well as species composition, were clearly related to two factors: the degree of pool minerotrophic influence, and the degree of pool permanency.

A total of 59.3% of all species observed showed distributional affinities related to the minerotrophic gradient, with the floras of ombrotrophic pools distinct from minerotrophic pools.

For many species the range of tolerance along the minerotrophic gradient was narrow; many ombrotrophic species

did not occur in minerotrophic pools and even more minerotrophic species were absent from ombrotrophic pools. The net result was that minerotrophic pools were richer in species than ombrotrophic pools. These results are in accord with the frequently reported and generally accepted relationship of desmid composition with the minerotrophic gradient in peatlands. Péterfi (1974) studied desmid distribution in a set of 60 Rumanian bogs and reported three distribution types in relation to a minerotrophic gradient. As observed in the present study, the highest number of species was those with affinity for minerotrophic pools and the lowest number those with affinity for ombrotrophic pools. The wide ranging group of species was intermediate in number. Similarly, Flensburg & Malmer (1970), studying the micro-flora of Akult Mire (Sweden), a large bog-fen complex, interpreted a main gradient of floral distribution as coincidental with the minerotrophic gradient. Of the 157 observed desmid species, the highest number of taxa was restricted to the fen sites and many of these showed a limit corresponding with the hydrologic mineral soil water limit. A difference from the present study is that no desmid species were restricted to the ombrotrophic sites. Further studies in which peatland distributions of desmids related to pool minerotrophic status are given are those of Du Rietz (1954), Flensburg (1967) and Hosiaisluoma (1975).

The groupings of dominant desmid species observed between pools showed strong relation with the minerotrophic

gradient. Extremely few species occurred as dominants in both ombrotrophic and minerotrophic pools. An interesting observation is that most species wide ranging on the minerotrophic gradient show strong affinity to specific conditions when examined quantitatively. This suggests that the level of minerotrophic influence has a strong regulating effect on the abundance of most desmid species. The degree of minerotrophic influence appeared to select for suites of species. The relative abundance within the suites was dependent on other variables, however, with the result that pools of a similar degree of minerotrophic influence contained, to an extent, different dominants.

The factors causing variations in desmid occurrence and abundance along the minerotrophic gradient are uncertain, although aspects of the water quality are thought to be responsible. Correlation of ordination sample axes related to the minerotrophic gradient with variables of water chemistry suggests that acidity levels, mineral content or organic content may be determinant of desmid growth and survival. pH was most highly correlated followed by Ca, Mg and tannins + lignins with the minerotrophic gradient axis of the complete data set, whereas Fe was highly correlated with a sample subset representing the ombrotrophic end of this gradient. Based on comparisons of species abundance in specific pools, it appears that species show different relations with the levels of pH, Ca, Mg and Fe.

Certain species may be limited by low mineral levels in ombrotrophic waters. The occurrence and abundance of select minerotrophic species in high acidity and highly coloured pools enriched with Ca, Mg or Fe supports this. Why ombrotrophic species are so limited in minerotrophic waters, in some cases in occurrence and in most cases in abundance, is a perplexing question. More than simple availability of minerals is involved in selection along the gradient, and there may be inhibitive factors, conceivably those of pH tolerance or mineral toxicity. Given the highly species-diverse nature of desmid communities in this habitat, competitive exclusion does not seem a probable cause of the suppression of ombrotrophic species in minerotrophic waters. Growth regulating variables associated with nutrition or physical tolerance are more suspect.

PH appeared to be a major variable in desmid occurrence and abundance along the minerotrophic gradient of the present study. This is in agreement with a general relation of the pH of water bodies and desmid distributions (see Prescott 1948; Brook 1981). Specific studies can be cited which show variation in desmid occurrence in relation to pH over ranges comparable with the minerotrophic gradient. Kovask (1971) studying desmids of a large number of Russian water bodies of a wide pH range described five groups of algae on the basis of the pH of the water bodies where the species occurred, the first two groups relevant to

the minerotrophic gradient. A total of 9% of his flora of 410 taxa occurred at pH < 5 whereas 34% occurred in the pH range of 5 to 7. Hirano (1960) working on a range of Japanese water bodies described two groups of desmids in relation to pH ranges of occurrence comparable with those of the minerotrophic gradient. A larger group of species were found in the pH 4.5 - 6.8 range compared with the pH 4.1 to 4.4 range. The works of Coesel on the distribution of desmids in a range of habitats in the Netherlands (Coesel 1975, 1981, 1982; Coesel et al., 1978) also give examples which illustrate the relation of pH with distribution patterns.

The pattern of correlation of desmid occurrence and abundance with pH in the present study suggested that different species may have different tolerance ranges, with both high and low pH inhibition occurring over the range of pH 3.8 to 6.0. Laboratory culture studies on desmid growth in relation to pH verify that there is some basis for this speculation. Moss. (1973a) observed that desmid species examined in culture had different minimum pH tolerances, with most not growing at levels below pH 4.5 - 5.1. Gough (1977) cultured three desmid species, two from a hardwater lake and the other from an acid lake and found significant differences in growth with pH. The acid water species grew better at pH 6 whereas the hardwater species grew better at pH 8.5.

The distribution of desmids over broad pH ranges characteristic of oligotrophic-eutrophic gradients has been explained in relation to availability of differing inorganic carbon sources (CO_2: HCO_3^-: $CO_3^=$) for photosynthesis (Moss, 1972, 1973a). Low pH adapted species may only be able to utilize free CO_2 whereas high pH adapted species may as well utilize HCO_3^- in the absence of free CO_2 at high pH. This hypothesis does not predict the variation in desmid community dynamics observed along the minerotrophic gradient. Free CO_2 which is energetically a better carbon source the HCO_3- (Hutchinson, 1975) will be the predominant form in the pH range of the gradient. At pH 6, the highest observed in this study, a dilute solution at 15°C would contain 72% of the inorganic carbon as free CO_2 (Hutchinson, 1957). Free CO_2 would not be expected to be limiting at any point along the minerotrophic gradient.

Mineral levels, particularly that of Ca, have been thought important in desmid distribution (Prescott, 1948) and this is supported by the distribution of desmid species in relation to the minerotrophic gradient of the present study. The pattern of correlation of desmid abundance and simple occurrence with Ca and Mg levels along the gradient suggest that species may be limited at low levels (ombrotrophic pools) and be inhibited at high levels (highly minerotrophic pools). Kovask (1973) and Coesel (1981) noted strong differences in ranges of desmid species occurrence in relation to mineral levels in a range of water types and

observed maximum numbers of species at moderate ranges (conductivity = 300 - 500 uS cm^{-1}: Coesel; HCO_3^- = 60 - 150 mg/l: Kovask). Kovask (1973) gives Ca levels of 2 - 3 mg/l as the maximum tolerated by bog species, but does not define what a bog species is. Of the species listed by Kovask (1973) that were found in the present study, five occurred in the 0 - 10 mg/l HCO_3^- range, 15 occurred in the 10 - 60 mg/l range, 19 in the 60 - 150 mg/l range, and seven in the 150 - 240 mg/l range. No ombrotrophic species in the present study were given by Kovask, thus it is not possible to infer whether high mineral levels could be inhibitive to such species as suggested. What is apparent, however, is that fen species may be absent in ombrotrophic waters due to low mineral levels.

Moss (1972) examined the effect of Ca on some oligotrophic algae in culture. Oligotrophic desmids were not affected by Ca and Mg levels comparable with hard waters, and there was no difference in growth between Ca levels of 10 - 100 mg/l. The interpretation of these results in relation to species distribution on the minerotrophic gradient of the present study is limited. No ombrotrophic species were tested. Of those minerotrophic species examined a minimum of 0.1 mg/l Ca was sufficient for growth, except for Desmidium swartzi which required 1 mg/l Ca. The results of Moss (1972) are in contradiction to those of Gough (1977) in which the growth of soft water Triploceras was reduced at high Ca levels and conversely a

hard water Cosmarium had a reduced growth rate in soft water. A Closterium species tested was not affected by Ca levels.

Experimental determinations of the nutritional mineral requirements in a range of peatland desmids, as well as some understanding of factors likely occurring in nature that may affect mineral uptake and utilization is required. The combined efforts of a chemist, characterizing mineral cycling and sorbtion complexes, and a physiologist, evaluating effects of the likely mineral environments on desmid species, may go a long way towards explaining the behaviour of desmids along the minerotrophic gradient.

The levels and quality of organic materials may be important in desmid distribution and abundance along the minerotrophic gradient, but little evidence was obtained to support this. Instances where organic materials showed strong temporal variation were not paralleled by changes in desmid composition or dominance.

Speculations have been made that organic materials play a role in desmid distribution (Brook, 1981), but little experimental investigation has been attempted. There is as yet no evidence of heterotrophic potential in desmids. The occurrence of vitamins may affect the distribution of certain desmid species (Tassigny, 1971b; Moss, 1973b) but there is at present no evaluation of this possibility in relation to distribution of peat algae.

The relationship of the availability of the macronutrients N and P with the minerotrophic gradient is not well understood. The results of the present study were disappointing in that most estimations of NO_3^-, PO_4^{3-} and NH_4^+ were below the detectable limits of the methods used. It was noted, however, that NO_3^- levels were distinctly higher in permanent fen pools. Based on the mode of nitrogen supply to a peatland site it is possible to predict a nitrogen gradient relating to the minerotrophic gradient. Rosswall & Granhall (1980), studying the nitrogen budget of an ombrotrophic bog, found nitrate production in the peat to be negligible, with all nitrate being of atmospheric origin. The main inorganic N form was NH_4^+, which originated from the slow microbial mineralization of plant material. A total of 95% of the N in the system was in dead organic material, and was released at a rate of 0.8% per year. A similar situation probably exists in the ombrotrophic pools, but with a slight increase in mineralization release, given the higher pH of pool water compared with the surrounding peat. Given equal atmospheric inputs between ombrotrophic and minerotrophic pools and the significance of the mineralization rate in the regeneration of nitrogen, the minerotrophic pools will have a greater supply of inorganic nitrogen. The mineralization rate is more rapid in minerotrophic peat compared with ombrotrophic peat due to the lower acidity of minerotrophic peat (Wells & Pollett, 1983). A comparable situation is likely for the pools.

In addition, blue-green algae associated with aquatic Sphagnum have a high nitrogen fixing capacity (Basilier et al., 1978; Basilier, 1980) but with the amount of fixation substantially greater in minerotrophic pools compared with ombrotrophic pools (Basilier et al., 1978). This again is due to the lower pH of ombrotrophic waters.

Although a greater N supply seems probable in minerotrophic pools, any potential significance of this in determining differential competitive abilities within desmid communities may be difficult to assess. Yet this is an unexplored and conceivably significant question in understanding the minerotrophic gradient.

The second major gradient of variation in both desmid species occurrence and abundance in the peat pools studied was the pool permanency gradient. It differs in nature from the minerotrophic gradient by being more related to physical stresses as opposed to nutritional and/or toxicity effects.

The degree of pool permanency had a significant effect on desmid species composition. Pools which dried out or showed major reduction in water level during the study had reduced numbers of species compared with permanent pools of comparable degree of minerotrophic influence. Many desmid species appeared intolerant of desiccation for even limited periods, and were selected against in temporary pools. Those tolerant species appeared to be variably so, with the most frequently dried pools containing the fewest

species. The mechanism of survival by such species appeared to be by physiological adaptation, as no evidence of other survival strategies was observed.

The importance of pool permanency in determining species richness in desmid communities has been reported by other workers. Croasdale (1973), studying the algae of Ellesmere island, found desmid species richness to be lowest in temporary pools, highest in permanent pools and intermediate in semipermanent pools. Hosiaisluoma (1975) observed an increase in algal species with greater wetness of the habitat in mud bottomed peatland pools. Similarly, Hooper (1981) found the diversity of algal species to increase with greater wetness in a Sphagnum mat. Coesel (1981) detected a positive relation between numbers of desmid species with increased moisture in Sphagnum tussocks of a quivering bog.

Desiccation experiments on desmids were conducted by Evans (1959). Of 23 desmid species tested, most could not survive desiccation in the vegetative state. Four species were capable of withstanding desiccation for periods ranging from 12 to 69 days.

Distinct hemi-atmophytic (sub-aerial) associations of desmid species were reported by Grönblad (1935) and further support a vegetative state tolerance of desiccation in certain desmid species. Similarly, characteristic sub-aerial desmids were reported by Coesel (1981). Of these desiccation-resistant species several were common in

temporary pools of the present study, these being C. subcucumis, N. digitus, Cy. brebissonii, E. oblongum, T. granulatus and T. laevis. Several of the common temporary muddy peat desmid species reported by Hosiaisluoma (1975) for Finnish peats were also common in temporary pools in the present study, these being Pl. minutum, P. silvae-nigrae, C. obliquum, A. cucurbita and Cy. brebissonii.

Sexually produced zygospores of desmids are thick walled and are a potential means of surviving unfavourable conditions such as desiccation. However, conjugation in nature by desmids is sporadic or absent in the majority of species (Coesel, 1974; Heimans, 1969; Strom, 1926). Homfeld (1929), studying zygote production in nature, was unable to determine factors responsible for stimulation of conjugation. Zygotes were more frequently found in small water bodies, but pools with abundant desmids and that were observed to dry up both fast and slowly, showed no evidence of zygote production. In the present study, zygote production was infrequent and irregular. Over the study period Cy. brebissonii and B. borreri were most frequently observed to conjugate, and this being in ombrotrophic pools. Actinotaenium cucurbita was observed to conjugate infrequently in the minerotrophic pools. A single pair of T. laevis was observed in conjugation. Zygospore production did not become more frequent in temporary pools during reduction of the water level. Conjugation and zygospore production may explain the irregular persistence in

temporary pools of species otherwise intolerant of desiccation. The infrequency of conjugation, however, suggests that survival by desmids in temporary pools is largely via desiccation-resistant vegetative cells.

Survival in temporary pools during dry periods is potentially via the production of asexual spores or cysts. Brandham (1965) reported the production of four types of asexual resting bodies in desmids grown in culture. None of his resting bodies were observed to germinate. During the course of the present study no evidence of asexual resting bodies was observed.

The dominant desmid species of the pools studied were strongly selected for by the degree of pool permanency. Whether there is a trade-off between the degree of desiccation tolerance and the ability to compete in more permanent situations is unknown. Temporary pool dominants were frequently dominants in permanent pools, but the heterogenous nature of dominants between pools makes it difficult to draw conclusions.

An additional, predominately physical factor which appeared to have significance in the dynamics of desmid populations in a small number of pools was that of water movement. Surface water flow in peatland pools appears to have a destructive effect on the desmid communities of the Sphagnum aufwuchs. Desmids lack specific substrate attachment organs, loosely adhering to the substrate by the production of a sticky mucilaginous sheath. As a result it

is possible that individuals can easily be washed away from the substrate. Bland & Brook (1974) present observations that suggest water movement around shoots of submerged macrophytes removed a portion of the desmid epiphytic community. Studying the desmids of two Minnesota lakes they observed that the desmid populations in the aufwuchs of Potamogeton were reduced in an exposed area with water circulation compared with a sheltered area. As well, the desmid tychoplankton was much more abundant in locations with water circulation compared with sheltered locations. The destructive effect of water movement on the algal periphyton of streams is documented. Horner & Welch (1981) showed that chlorophyll a build-up on rock was negatively corrected with water flow velocity in six Washington streams. An erosive stress from the frictional force of the passing water mass resulted in the tearing off of a portion of the produced algal material. Hynes (1970), in describing the character of periphytic microphyte communities of lotic waters, stated 'Microphytes occur as irregular mosaics on stream and river beds and are subject to great seasonal change ... certain groups of species tend to occur together but because of the instability of the habitat the arrangement is probably due to change ... there are no or few species associations in running waters.' This is in agreement with the character of the sampling pool of the present study in which a consistent flow-through of water was observed. The total desmid population was reduced in

this pool compared with similar pools lacking water flow. As well, the composition and relative abundance of dominant species in this pool were much more temporally variable than in other similar pools with no or little water flow.

A further potential explanation for the variance of the desmid community in this pool compared with those lacking flow may be related to increased competition in this pool by algal species adapted to flow conditions, of which many have been reported (eg. Blum, 1956; Whitford, 1960). However, species of algae having a holdfast and adhering to the Sphagnum were not observed in sufficient quantities in this pool to account for the observed depauperate desmid community.

Evenness of species abundance within a community is an informative parameter of community structure suggestive of the degree of inter-species competition. Notable relations of equitability within the desmid communities were observed between contrasting pool types in this study. Temporary pools had a more uneven spread of abundance than permanent pools. In temporary pools, one to three species were frequently observed to be much more abundant than the remaining species, whereas in permanent pools a larger group of species was frequently observed to be highly abundant. This is in contrast to the comparable equitability patterns observed between ombrotrophic and minerotrophic pool communities.

These results suggest that temporary pool conditions, relative to those of permanent pools, may result in a reduced degree of interspecies competition. This is predictable in that temporary pools have a high degree of physical stress with relatively few adapted species. Following desiccation there is an availability of substrate and probably nutrients, with few species with a significant surviving seed population. Such species presumably can then become highly abundant relative to other species. The greater unevenness of species abundance characteristic of temporary pools was observed to be maintained, over the study period, in three temporary pools which did not completely dry up in this period. This suggests that once the equitability pattern is established it is not easily broken down, at least over the time frame and conditions of the study.

It is significant that equitability patterns were comparable between pools of different placement on the minerotrophic gradient. It suggests that in all permanent pools there may be a comparable and high level of interspecies competition. It may, however, simply result from the fact that permanent pools provide a stable growth environment in which many species are capable of surviving.

The maintenance of the high numbers of species in the permanent pools is perplexing. The qualitative data on the frequency of species occurrence over time reveals that many species of low abundance were maintained in permanent

pools over the study period. There appear to be factors maintaining a low level of competitive exclusion, or else the reintroduction of excluded species is rapid. A possible explanation of this is easily conceived in relation to niche differentiation on the basis of spatial and/or temporal habitat variation, even within units as small as a single pool. A similar observation and interpretation of desmid diversity in water bodies in the Netherlands was made by Coesel (1982).

It is clear that the described gradients of habitat variation do not fully account for the spatial patterns of desmids in the Sphagnum aufwuchs of the pools studied. The likelihood of species occurring together or being a dominant in the aufwuchs is related to these main gradients of variation. It remains questionable as to what determines the specific composition of a community and the relative abundance of species within that community. It may be argued that each sampling pool has its own unique character which encompasses variation in physical, chemical and biological attributes. If the assumption is made that individual desmid taxa have unique conditions of optimal growth then the desmid communities may be uniquely selected for in each pool from the suites of species that are dispersed in it.

If there is a non-random reason for the greater abundance of specific taxa in specific pools, then the explanation will be found by examining the sequence of

likely causal variables. However, partially or wholly random variables may also shape desmid communities and will be even more difficult to assess.

Dispersal may be important in determining the specific composition of a desmid community and may further have implications as to which species become abundant. The presently documented modes of desmid dispersal suggest that variations in the timing and success of dispersal are to be expected. Brown et al. (1964) collected viable cells of Cosmarium sp., Cylindrocystis sp., and Roya sp. from atmospheric samples, showing at least a limited potential for aerial dispersal. Such desiccation-resistant species will be evenly and widely distributed. Otherwise, desmid cells travel by water courses or are physically transported to other water bodies by birds (Irénée-Marie, 1938; Proctor, 1966) or insects (Parsons et al., 1966). In Newfoundland the green frog (Rana clamitans) and the moose (Alces alces) are likely important dispersal agents for desmids in peatlands.

Previous studies in which desmid distributions have been evaluated have noted the significance of dispersal. Heimans (1969) noted that given a number of desmid species strongly preferring a similar water type, it is difficult to determine a fixed group of characteristic species of that water type from comparisons of species lists from such locations. The difficulty was attributed to uneven dispersal of species. Coesel (1981) noted the

problem of random dispersal differences in shaping desmid associations. With regard to a very large number of samples from the Dutch Broads he was unable to define sharp associations of species. Desmid assemblages could be used as indicators of environmental type but the characteristic groupings were not of consistent composition. Thus it may be that the timing of dispersal events may contribute to differential abundances of species with comparable habitat preference and intrinsic growth rates.

The observations of Patrick (1977) on the colonization of glass slides by diatoms in flowing waters demonstrates how the sequence of arrival of algal species to a substrate influences the subsequent composition of the community and the dominance pattern. This example should, however, be compared cautiously with the situation of desmids in the Sphagnum aufwuchs, given the strong differences in substrate and organisms. The number of species occurring on the glass slide increased greatly at first, but varied only slightly after four days. Following the filling of the slide, the species eliminated were those with small populations. Slides colonized at the same time had very similar communities. The species arriving first at the slide became the most abundant. Once the slide was filled, the community maintained its structure.

At present, in the absence of data on the range of factors affecting optimal desmid growth, intrinsic growth rates of a spectrum of species and data on the nature of

community development, it is impossible to explain the reasons for the uniqueness of groupings of dominant species, even between comparable pool types. It is probable that all aspects of the question cited contribute to the final solution, but innovative experimental designs both in the field and in culture will be required to arrive at a more definitive answer.

Temporal changes in the desmid communities over the course of this study period were unexpectedly few. A complete seasonal cycle was examined over which successions in dominant species were expected. Only a small element of such change was observed in two sample pools, PF1 and PF2, and then with only a small proportion of the dominant species involved. All permanent pool communities, excepting PF3, and three temporary pool communities, (TB1, TF1 and TF2) maintained throughout the study period mostly the same suites of dominant species. Although relative abundance varied within the suites of species between sample dates, remarkable consistency was observed.

A striking finding of this study is that the desmid communities showed strong responses in terms of species composition and groupings of dominants to spatial changes in water quality (ie. minerotrophic gradient), but showed little to no over-all relationship with the strong changes in water quality associated with seasonal changes.

There can be two interpretations of this result. The first is that chemical parameters, changing temporally,

were not significant in determining relative growth rates or growth success between desmids. For example, pH is a chemical parameter not predictably or strongly related to the temporal changes in water quality, but is highly correlated with selection of desmid species. It is unlikely that this is the complete explanation in that most all aspects of water quality were to a degree related to the temporal change. Included in this group were parameters also correlating with spatial selection of desmid species, the strongest examples being Ca, Mg and Fe.

The second and more probable explanation is that the desmid communities studied were not highly dynamic, with most species having in this habitat and under the prevailing conditions a slow division rate and slow turnover rate. This may account for a low response to temporal variation in water quality, the duration of changes being too short for the resulting differential growth rates between species to manifest themselves as major changes in relative abundance. The period over which the desmid communities have had to respond to changes in water quality resulting from peat development is relatively large.

The importance of time frame in the realization of changes in the desmid community resulting from differential growth rates in species stemming from habitat variation requires experimental evaluation. Information on species turnover rates in natural conditions would be invaluable. An experimental approach to this question would be to

elevate the levels of limiting growth factors in situ and then compare temporal desmid changes in experimental and control situations. This, however, would firstly require an investigation of factors limiting to desmid growth in this habitat.

Reports of successional change in desmid communities by other researchers are both in agreement and disagreement with the findings of the present study. Coesel (1982) presented data for dominant desmid species in an oligotrophic water body over a seven-year period. During this period electrolyte concentrations remained comparable and the dominant desmid species showed a high degree of consistency. The greatest variability was in the less abundant species. Similarly, Hori & Ito (1959) studied the desmid community of a small lake over an eight-year period. A sequence of desmid associations was correlated with increased organic pollution in the early part of the period, and decreased pollution in the latter. The changes were slow, occurring gradually over a period of 1-2 years. Duthie (1965) and Howell & South (1981), however, described successional sequences of desmids over time frames of less than one year. Duthie (1965), studying the dynamics of sediment desmids in a fen pool, observed a succession of dominant species over a 14-month period. He was unable to relate the sequence of species with measured variables of the habitat. Howell & South (1981) observed a succession in the relative abundance of five taxa of the genus Tetmemorus

over a May-August period in two fen pools. The changes were observed to coincide with a general enrichment in water quality over this period. The changes in water quality reported are partially comparable with the seasonal changes reported in the present study.

Changes in total desmid population densities recorded over the study period show what appears to be a seasonal trend, with lower population totals occurring in fall and winter.

The winter-spring reduction in total desmid densities observed in this study are to be expected, given the temperature growth responses of desmids. Moss (1973b) experimentally determined temperature optima for eight desmid species. Seven showed broad growth peaks between 10-30°C, but most had little growth at 5°C or less.

There are, however, reports in which winter reductions in desmid populations have not been large and instances where minimum levels have not been during the fall-winter. Duthie (1964) reported only a 1/5 quantitative reduction in desmids on the sediment of a fen pool in North Wales after 70 days of snow cover. Duthie (1965) followed the desmids on a fen pool sediment over a two year period and found a spring-early summer minimum in total densities.

Several species in the present study showed relatively greater quantitative reductions during the fall-winter period, presumably related to differential temperature tolerances. Such temperature preference/

tolerance for bog algae was noted by Péterfi (1967) in Salicea peat bogs. He reported the existence of wide temperature-tolerant eurythermic species and stenothermic species, with cold optima.

Overall, the observations of Strom (1926) on the seasonal behaviour of desmids in Norwegian peatlands are in agreement with the present study. The algal flora of peat bogs was described as generally uniform with no marked periodicity. Desmids were common in the late summer with a quantitative maximum in August, which may be maintained for a period into the fall. There was a winter decrease, with a marked reduction of algae with ice conditions.

This study represents an advancement in the understanding of desmids in the peatland environment by virtue of the use of a quantification technique, which allows estimates of population density which are comparable spatially and temporally. It is the first study in which density estimates for populations of dominant desmids at the species level has been obtained over a range of peatland conditions. Such data are a potentially more revealing source of information on aboitic/biotic interrelations than the examination of compositional data. There are, however, serious short-comings in the method used and these must be kept in mind when interpreting the results. The estimates of population densities are rough, with fine differences being of dubious significance. The estimates were made from a group of combined samples and represent a weighted average

of the desmid community continuum of the pool. The combining of samples is necessary due to the high degree spatial heterogeneity of desmids in peatland pools (see Duthie, 1965). The reliability of estimates of desmid populations from peatland pools can to an extent be inferred from Howell and South (1981) in which estimates from replicated pooled samples were mostly comparable, but with a considerable degree of variance.

Only limited replication of estimates were used in the present study. The availability of sampling substrate was a critical problem in this study. More extensive replication of samples and increasing the number of samples in combined units was not possible without excessive destruction of the pool environment. The choice of sample numbers in combined sets is necessarily biased by the availability of substrate in the pool.

Development of a new sampling strategy is imperative for the advancement of field study in this difficult habitat. The method needs to be applicable to the range of peat sites, not so labour intensive as to be impractical for wide-ranging and replicated sampling, must produce results descriptive of natural conditions and estimates with sufficiently low deviations to permit standard analysis of variance. The problem is complicated by sampling scale, which in order to achieve such ideals may have to be very small and consequently of limited applicability to more general problems.

SUMMARY AND CONCLUSIONS

(1) Three primary gradients of spatial habitat variation were identified as important to the peatland pool environment, these gradients being: (1) a minerotrophic gradient, (2) a permanency gradient and (3) a surface water flow gradient.

(2) A high degree of the spatial dynamics of the desmid communities of the pool Sphagnum aufwuchs was related to the primary gradients of spatial habitat variation.

a) Desmid species composition, species richness and species dominance were strongly related to pool minerotrophy. Highly minerotrophic pools were more species rich and had more endemic species than ombrotrophic pools. Very few dominant species were shared between pools of differing minerotrophic status. The causal factor in the variation was thought to be changes in water quality, particularly the levels of acidity, mineral content and organic content.

b) Desmid species composition, species richness and species dominance were strongly related to the degree of pool permanency. A high percentage of desmid species were absent from temporary pools whereas very few temporary pool species were absent from permanent pools. The evenness of species abundance was greater in permanent pools. The causal factor in the variation was thought to be

differential desiccation tolerance and die-off of desmid species in temporary pools.

c) The total population densities and the temporal stability of desmid communities were negatively related to the degree of pool water movement. This was thought to result from the removal of desmid material from the Sphagnum finges by water movement.

(3) A strong temporal pattern of habitat variation relating to the peatland pool environment was identified. Variations encompass seasonal cycles in water quality, in water temperatures and in the form of precipitation.

(4) Few general patterns of temporal desmid community dynamics were interpreted. Total desmid population densities had winter spring minima and summer maxima with the pattern loosely related to temperature.

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APPENDIX I

Desmid Species List

Various works were consulted in making identifications of the desmid taxa reported. The detailed lists and figures of Newfoundland desmids in Taylor (1934, 1935) and of southern Labrador in Croasdale and Grönblad (1964) were referred to in all cases where possible. Other floras consulted included Irénée-Marie (1938), Skuja (1964), Forster (1965) and Croasdale (1973). Specific works have been used for certain groups of genera; Prescott et al. (1972) for saccoderm genera, Teiling (1954) for the genus Actinotaenium, Ružička (1977) and Prescott et al. (1975) for the genera Closterium, Penium, Pleurotaenium, Docidium and Triploceras, Howell and South (1981) for Tetmemorus, Prescott et al. (1977) for the genera Micrasterias and Euastrum, Teiling (1952) and Scott and Grönblad (1957) for the genus Groenbladia, Teiling (1977) for the genus Staurodesmus. The monographs of British desmids by West and West (1904, 1905, 1908, 1912) and West et al. (1923) were referred to for all groups.

The following is a list of desmid species observed in this study, with notes on some identifications. The letters contained within brackets associated with generic names refer to the abbreviations used in this thesis.

(A.) Actinotaenium cucurbita (Bréb.) Teil.

A. cucurbitinum (Biss.) Teil.

(Ar.) Arthrodesmus octocornis Ehr.

(B.) Bambusina borreri (Ralfs) Cleve

(Cl.) Closterium acutum Bréb.

Cl. angustatum Kütz. - combined with Cl. ulna Focke for quantitative enumeration and referred to as Cl. ulna. Treated separately for the qualitative analysis. Differential identification based on cell wall markings which are not always clear with material viewed in Sedgwick- Rafter counting cells.

Cl. archerianum Cleve

Cl. baillyanum (Bréb.) Bréb.

Cl. closterioides (Ralfs) Louis and Peters

Cl. costatum Corda

Cl. cynthia De Not

Cl. dianae Ehr.

Cl. gracile Bréb.

Cl. intermedium Ralfs

Cl. juncidum Ralfs

Cl. keutzingii Bréb. - combined with Cl. rostratum Ehr. for quantitative enumeration and referred to as Cl. keutzingii. Treated separately for the qualitative analysis. Most specimens are distinguishable but with a definite intergrading of forms.

Cl. moniliferum var. concavum Klebs

Cl. ralfsii Bréb.

Cl. rostratum Ehr. - see note under Cl. keutzingii.

Cl. striolatum Ehr.

Cl. toxon West

Cl. ulna Focke

Cl. venus Kütz.

Cl. sp. A - thought to be an undescribed species

Cl. sp. B - thought to be an undescribed species

(C.) Cosmarium amoenum Bréb.

C. angulosum Bréb.

C. caelatum Ralfs

C. contractum Kirchn.

C. debaryi Arch.

C. difficile Lutkem.

C. eloiseanum Wolle

C. isthmium West

C. margaritiferum Menegh.

C. nymannianum Grun.

C. obliquum Nordst.

C. ochtodes Nordst.

C. ornatum Ralfs

C. pseudopyramidatum Bréb.

C. pseudotaxichondrum Nordst.

C. pyramidatum Bréb.

C. quadratum Ralfs.

C. quadratum var. nepalense Förster

C. quinarium Lund.

C. ralfsii var. taylorii Krieger and Gerloff

C. reniforme (Ralfs) Arch.

C. subcrenatum Hantzsch.

C. subcucumis Schm.

C. subtumidum Nordst.

C. tumidum Lund.

C. venustum (Bréb.) Arch.

C. sp. - a small species (< 10 m, maximum dimenstion), near C. bioculatum Bréb, C. tenue Arch., C. tinctum Ralfs and C. inconspicum West and West.

(Cy.) Cylindrocystis brebissonii Menegh. - forms referable to Cy. crassa De Bary were included under this species.

(D.) Desmidium graciliceps (Nordst.) Lagerh.

D. quadratum Nordst.

D. swartzii Ag.

(Do.) Docidium undulatum Bail.

(E.) Euastrum allenii Cushm.

E. ampullaceum Ralfs

E. ansatum Ralfs

E. bidentatum Näg.

E. binale (Turp.) Ehr.

E. boldtii Schm.

E. crassum (Breb.) Kütz.

E. cuneatum Jenner ex Ralfs

E. denticulatum (Kirchn.) Gay

E. didelta (Turp.) Ralfs

E. elegans (Bréb.) Kutz

E. giganteum (Wood) Nordst.

E. humerosum Ralfs

E. insigne Hass.

E. insulare (Wittr.) Roy

E. intermedium Cleve

E. montanum West and West

E. oblongum (Grev.) Ralfs

E. pectinatum Bréb.

E. pingue Elfving.

E. pinnatum Ralfs

E. validum West and West

E. ventricosum Lund.

(Gt.) Gonatozygon brebissonii De Bary

(G.) Groenbladia neglecta (Racib) Teil.

G. neglecta var. A - corresponds with G. taylorii Scott and Grönbl. The observed degree of variation of this form from G. neglecta suggests that it is not a distinct species.

(H.) Hyalotheca dissiliens (Sm.) Bréb.

H. laevicincta Taylor

(M.) Micrasterias arcuata Bail.

M. arcuata var. expansa Nordst. (Bail.)

M. denticulata Bréb. ex. Ralfs

M. jenneri Ralfs

M. novae-terrae (Cushm.) Krieger

M. oscitans Ralfs

M. papillifera Breb. ex Ralfs

M. tetrapreta (Corda) Bréb. ex Ralfs

M. triangularis Wolle

M. truncata (Corda) Bréb.

(N.) Netrium digitus (Ehr.) Itzig. and Rothe

(P.) Penium cylindrus (Ehr.) Bréb.

P. silvae-nigrae Rabanus.

P. spirostriolatum Barker

(Pl.) Pleurotaenium coronatum (Bréb.) Rabenh.

P. ehrenbergii (Bréb.) De Bary

Pl. minutum (Ralfs) Delp.

Pl. minutum var. latum Kaiser

Pl. rectum Delp.

Pl. tridentulum (Wolle) West

(St.) Staurastrum anatinum Cooks and Wills

St. anatinum var. simplicius Croasd.

St. brachiatum Ralfs

St. brebissonii Arch.

St. crenulatum (Näg.) Delp.

St. elongatum Barker

St. furcatum (Ehr.) Breb. - also included under this name were St. pelagicum West and West and St. novae-terrae Taylor. A strong gradation of form was observed between these three taxa, with separation of species being difficult and highly subjective.

St. inconspicuum Nordst.

St. lapponicum (Schm.) Grönbl.

St. margaritaceum (Ehr.) Menegh.

St. monticulosum Bréb.

St. orbiculare Ralfs

St. pyramidatum West

St. quadrispinatum Turn.

St. simonyii Heimerl.

(Sd.) Staurodesmus extensus (Borge) Teil.

Sd. omearii (Arch.) Teil.

Sd. phimus (Turner) Thom.

Sd. sellatus Teil.

(Te.) Teilingia granulata (Roy and Bisset) Bour.

(T.) Tetmemorus brebissonii var. brebissonii (Menegh.) Ralfs – all observed varieties of T. brebissonii were combined for the quantitative enumeration but referred to separately for the qualitative analysis.

T. brebissonii var. intermedius Flensb.

T. brebissonii var. minor De Bary

T. granulatus (Bréb.) Ralfs

T. laevis (Kütz.) Ralfs

(Tr.) Triploceras gracile Bail.

(X.) Xanthidium antilopaeum (Bréb.) Kütz.

X. armatum (Bréb.) Rabenh.

X. cristatum Bréb.

X. torreyi Wolle

APPENDIX II

Detrended Correspondence Analysis (DCA)

DCA is a continuous multivariate ordination technique which uses an eigenvector method of solution. The technique is specifically adapted for indirect gradient analysis of biological community data and requires ony two assumptions, both compatible with raw community data (Hill, 1979a). The data must be either of binary or continuous scores of species in samples, and the samples must occur on gradients such that species occupy only portions of the theoretical ranges of these gradients. DCA has conceptual similarity with reciprocal averaging (RA) of Hill (1973), an ordination method which has been successfully applied to analysis of vegetational data (see Pakarinen and Ruuhijarvi, 1978 ; Happey-Wood , 1980). DCA differs from RA in two major computational points designed to improve the quality and increase the interpretation of ordinations.

Hill (1973) described RA as a method of successive approximations, its basis being an iterative process by which species scores are used to define sample scores and reciprocally, sample scores to define species scores. In this way refined scores of species and samples are obtained, a species score being the average of sample scores in which the species occurs, and sample scores being the average of species in samples. The reciprocal averaging of species and sample scores is continued until the scores converge on a

unique solution, which also has the property of being independent of the initial scores (Hill, 1973). With quantitative data, averages are weighted corresponding to the abundance measure used. The final solution reached is the first axis of the ordination. Subsequent ordination axes are obtained by repeating the reciprocal averaging process of species and sample scores but starting with species scores that have been detrended so as to remove the effect of the first axis gradient. This is accomplished by subtracting multiples of the first axis scores from the starting scores. Since in both RA and DCA, computations are by a method of eigenvector analysis, there is associated with each ordination axis an eigenvalue. The eigenvalue can be used to infer relative amounts of variation incorporated in ordination axes, with higher values usually associated with more meaningful axes.

DCA extraction of first axes is similar in procedure to that of RA in that the algorithm of reciprocal averaging is used to calculate species and sample axis scores, but differs in that an additional scaling of species and sample scores is applied to final scores. The scaling of RA ordination axes have no intrinsic ecological interpretation and have the shortcoming of typically being contracted at the ends and expanded in the middle (Hill, 1979a). Although RA does not operate under the assumption of a linear relation with axis and axis variables as other eiginvector methods such as PCA and FA, the axes are still

to a degree distorted by the curvilinearity encountered in ecological data (Hill, 1979a; Gauch et al. 1981). In DCA initial RA axes are rescaled with the object of producing a more even scaling, with species appearing and disappearing at consistant rates along the sample axes. This is achieved by correcting species scores so that on average, species scores within samples have unit standard deviation (Hill, 1979a; Hill and Gauch, 1980). With the computer program DECORANA, the default case for rescaling axes consists of four interactions of the rescaling process. Rescaled species scores are used to calculate final sample scores. DECORANA allows for the selection of a rescaling threshold which is simply the option of not rescaling axes of less than a specified gradient length. In the present study all axes were rescaled.

The rescaling of DCA axes improves the quality of ordinations when non-linear species abundance profiles are encountered, and allows an ecological interpretation of the sample axes (Hill, 1979a). The scaling is indicative of the rate of appearance and disappearance of species in samples and as such is a measure of beta-diversity. The unit of the sample axis is termed the standard deviation, with axis intervals of 100 equal to 1 S.D. unit. Four S.D. units of a gradient is the range over which a species rises to its maximal level and falls again to its lowest level: samples with greater than 4 S.D. units apart will share few or no species (Hill, 1979a); Hill and Gauch, 1980). In contrast,

the species axis scaling has no such interpretation (Hill and Gauch, 1980).

DCA differs from RA in the calculation of 2nd and higher order axes in that a more stringent method of detrending species scores, to be used in the calculation of subsequent axes, is employed. With RA, subsequent pairs of axes are uncorrelated but may not be mathematically independent (Gauch et al. 1981). Ecologically uninterpretable axes, having typically a quadratic relation with a previous axis, may be extracted before more ecologically meaningful axes with RA (Hill, 1979a). This possibility is eliminated in DCA by using a detrending procedure which ensures that subsequent pairs of axes have no systematic relation. This is achieved by breaking a previous sample axis into segments and readjusting the sample scores in all such segments so that the mean sample score is zero. With DECORANA in the default case, the sample axes are broken into 26 segments. Breakage of the axis and readjustment of scores is carried out three times, with the final sample scores being an average. Sample scores are used to calculate detrended species scores.

The performance of DCA as a method of vegetational ordination has been evaluated in relation to RA and several non-metric ordination techniques by Gauch et al. (1981). They concluded that DCA did give better results than RA, not being as distorted by outliers, better recovering valid axes and having a superior scaling of axes. Compared with four

non-metric methods, DCA generally gave better results and had practical advantages. In a similar way Gauch et al. (1977) have evaluated RA in relation to several variants of PCA, this allowing some indirect comparison of DCA and PCA. RA was found to be preferential over PCA for ecological data in all cases tested and was in general more tolerant of non-linear responses of species along gradients, less sensitive to outliers and better able to handle data with high beta-diversity. Thus at present, DCA appears to be a valid ordination technique for vegetational data.

APPENDIX III

Pool Descriptions

Details of pool morpho-metrics and floristics are presented for each sample pool. The information is given in a telegraphic form, standardized to the following format: pool perimeter length; character of pool fringe and components used for algal sampling; depth of open water in the pool; depth of peat basement of the pool; pool bottom character; floristic makeup of the pool fringe; pool bottom vegetation; vegetation types surrounding the pool area.

Permanent Bog Pool One (PB1)

Pool perimeter, 53 m; well defined and total length used for algal sampling; depth of open water, mostly 50-70 cm, maximum 80 cm; peat basement, 150 to 245 cm, mostly 180 cm; bottom texture variable, from fine organic floc to poorly decomposed plant residues; fringe overhanging, 20-40 cm deep, tight to loosely packed. Sphagnum subnitens/ nemoreum dominant, S. magellanicum Brid. and S. pulchrum (Lindb. ex. Braithw.) Warnst. in large patches. Drepanocladus fluitans (Hedw.) Warnst. and Sphagnum cuspidatum Ehrh. ex. Hoffm. in submerged areas, S. fuscum (Schimp.) Klinggr. in drier areas. Overgrown with Scirpus cespitosus L., interwoven with liverworts. Associated fringe species, Rhynchospora alba (L.) Vahl., Chamaedaphne calyculata (L.) Moench., Andromeda glaucophylla Link, Aster nemoralis Ait., Solidago uliginosa Nutt.,

Empetrum nigrum L., Sarracenia purpurea L., Ledum groenlandicum Retzius, Drosera rotundifolia L., Kalmia polifolia Wang., and Polytrichum juniperinum Hedw.; Pool bottom vegetation extensive, roots of Nuphar variegatum Engelm., and clumps of Eriocaulon septangulare With. and Sphagnum pulchrum, with a partial algal cover, when emergent. Nuphar and Eriocaulon covering ca. 20% and 30% of pool surface respectively; surrounding area to the north and west, wet flats, 15-20 small pools, Sphagnum tenellum Ehrh. ex. Hoffm., S. cuspidatum, and S. pulchrum abundant in pools and hollows, flats covered with Drosera. To the east, dry hummocks, Sphagnum fuscum and Scirpus cespitosus dominant, Rhacomitrium lanuginosum (Hedw.) Brid. and Juniperus communis L. present:

Permanent Bog Pool Two (PB2)

Pool perimeter 79 m; 47 m used for algal sampling, variably submerged flats forming parts of perimeter not used; depth of open water, 25-40 cm; pool peat basement, 150-225 cm thick; bottom texture homogeneous except for clumps of Eriocaulon roots. Three sediment layers discernable with depth. Top 2-2.5 cm, of algal and fine detrital material, next 1.5-2 cm, of fine dark grey-green floc, remainder of progressively coarser mix of decaying plant material; fringe tight-packed excepting patches of submerged Sphagnum, fringe overhanging slightly. Sphagnum subnitens/nemoreum dominant, S. magellanicum and S. pulchrum common, overgrown with Scirpus cespitosus and Rhynchospora

alba. Associated fringe species as for PB1; pool bottom vegetation of main body with only Eriocaulon septangulare roots, covering ca. 10% of surface when emergent. Complete bottom cover of a slime matrix, composed of algae and Gymnocolea inflata (Huds.) Dum, varying in color from yellow-green to dark purple. Bottom vegetation in areas of pool flats dominated by Drosera rotundifolia and Gymnocolea inflata, patches of Sphagnum cuspidatum, S. pulchrum and Utricularia cornuta Michx. present; surrounding vegetation as for the wet flats of PB1.

Permanent Bog Pool Three (PB3)

Pool perimeter, 61 m; fringe poorly defined, extensive margin areas of Drosera flats. Sub-perimeter of 34 m, defining margin of pool lacking Drosera flats used for algal sampling; depth of open water in main section 20-40 cm; peat basement, 110-220 cm in depth, mostly 190-200 cm; bottom cover a mix of fine organic floc and elevated patches of an algal matrix. Three sediment layers apparent with depth, top 2 cm, flocculent and light coloured, next 4 cm, lighter grey colour and finer, remainder, red-brown-grey plant residues becoming progressively coarser with depth; pool fringe of two types. Bordering Drosera flats, being loosely packed, composed of Sphagnum pulchrum, S. magellanicum and S. cuspidatum. Otherwise, variably packed from free growing Sphagnum shoots to being moderately tight, composed of Sphagnum subnitens/nemoreum, S. pulchrum and S. magellanicum. Associated fringe species as for PB2; no

rooted pool bottom vegetation in non Drosera flat area, ca. 40% covered in loose growth of Sphagnum pulchrum and patches of Gymnocolea inflata coated with algae; surrounding area flat, few to no hummocks, Sphagnum subnitens/nemoreum dominant, S. fuscum and Scirpus cespitosus abundant in drier areas. Associated species as for PB1.

Temporary Bog Pool One (TB1)

Pool perimeter 6.5 m; fringe well defined, all used for algal sampling; maximum depth of open water, 11 cm; pool peat basement, 50-75 cm in depth; bottom surface homogeneous, fine grey-green floc. Two sediment layers apparent, top 3.5 cm, fine grey-green floc, remaining depth, progressively coarser plant residues; fringe tight-packed, Sphagnum subnitens/nemoreum dominant with patches of S. tenellum, heavy growth of Scirpus cespitosus and Carex exilis Dewey. Associated fringe species, Aster nemoralis, Vaccinium oxycoccus L., Andromeda glaucophylla, Sarracenia purpurea, Drosera rotundifolia, Empetrum nigrum and Rhynchospora alba; pool bottom vegetation moderate, no restricted aquatic species; patches of Drosera rotundifolia, Eriophorum angustifolium Honckeny, Scirpus cespitosus and Utricularia cornuta; surrounding area of pool, to the north, large dry hummocks, Sphagnum fuscum dominant, important species, Kalmia spp., Ledum groenlandicum, Empetrum nigrum, Picea mariana, Larix laricina (Du Roc) K. Koch and Juniperus communis. Other directions, hummocks smaller and wetter, S. rubellum Wils and S. magellanium dominants.

Temporary Bog Pool Two (TB2)

Pool perimeter, 10 m; a 5 m subperimeter defining a section of pool not divided by peat islands used for algal sampling. Fringe well defined; maximum depth of open water, 7 cm; peat basement 34-44 cm in depth; bottom surface homogeneous and of a fine grey-green organic floc excepting for patches of sedge straw. Two sediment layers apparent, top 1.5 cm, fine grey-green organic floc, remainder, coarser and darker plant residues; fringe tight packed, forming high banks. Sphagnum subnitens/nemoreum dominant with S. tenellum and S. fuscum common, wet faces covered with Gymnocolea inflata, fringe overgrown with Scirpus cespitosus. Associated species, Carex exilis, Sarracenia purpurea, Aster nemoralis, Andromeda glaucophylla, Kalmia polifolia, Empetrum nigrum, Ledum groenlandicum, and Rhacomitrium lanuginosum; no pool bottom vegetation; surrounding area, dry and flat, Sphagnum fuscum and Scirpus cespitosus dominants.

Temporary Pen Pool One (TP1)

Pool perimeter 16.7 m; well defined and all used for algal sampling; maximum depth of open water, 12 cm; pool peat basement; 80-140 cm thick, mostly 110-120 cm; bottom surface homogeneous, of fine organic floc. Three sediment layers apparent, top 1.5 cm, a fine dark green organic floc, next 7 cm, similar, but a grey-green-brown colour, remainder, progressively coarser plant residues, fringe tight packed, Sphagnum subnitens/nemoreum dominant, S.

tenellum and S. magellanicum common, wet faces coated with Gymnocolea inflata. Associated fringe species, Scirpus cespitosus, Rhynchospora alba, Carex exilis, Drosera rotundifolia, Aster nemoralis, Myrica gale L., Chamaedaphne calyculata, Vaccinium oxycoccus, Similacina trifolia (L.) Desf.; bottom vegetation sparse, 4-5 clumps of Sarracenia purpurea and a patch of Myrica gale; surrounding area consisting of a wet flat with seven smaller pools, flat extending 3-7 m from pool perimeter. At the north edge of flat, stunted Picea mariana, Larix laricina and Juniperus communis, along the west edge, elevated dry peat hummocks, Sphagnum fuscum and Scirpus cespitosus dominants.

Temporary Fen Pool Two (TF2)

Pool perimeter, 4.8 m; well defined and all used for algal sampling; maximum depth of open water, 15 cm; no pool peat basement, 4-7 cm of sediment overlying bedrock; bottom surface homogeneous excepting for patches of vegetation and of a fine floc. Three sediment layers apparent, top 0.5-1.5 cm, a red brown to black fine iron + organic floc (Iron ochre: Malmer 1962a; Du Rietz, 1954) with embedded algal and detrital material, next 1 cm, a mix of surface layer and grey-green silty material, remaining 1.5-4 cm, of fine grained grey-green silt; fringe tight-packed, Sphagnum subnitens/nemoreum dominant, S. tenellum common, with a single submerged clump of Dicranum scoparium Hedw., associated fringe species, Scirpus cespitosus, Juncus canadensis J. Gay, Myrica gale, Chamaedaphne calyculata,

Aster nemoralis, Andromeda glaucophylla, Empetrum nigrum, Vaccinium oxycoccus and Carex exilis; pool bottom vegetation, 15-20 shoots of Eriophorum angustifolium, Myrica gale and Chamaedaphne calyculata also occurring; surrounding area, on the S and S-W edge large hummocks. Hummock tops of Sphagnum fuscum with mix of Sphagnum rubellum, Dicranum undulatum Brid., Pleurozium schreberi (Brid.) Mitt., bases and hollows of Sphagnum subnitens/nemoreum, and S. magellanicum, S. tenellum in wet areas. Associated hummock species, Eriophorum angustifolium, Scirpus cespitosus, Myrica gale, Vaccinium sp., Cornus canadensis L., Similacina trifolia, Ledum groenlandicum, Solidaga uliginosa, and Empetrum nigrum. Atypical hummocks of Sphagnum flavicomans (Card.) Warnst., S. imbricatum Hornsch ex. Russ, S. magellanicum and S. subnitens/nemoreum. Other directions, wet flats, extending 2-3 m from pool perimeter, vegetated similarly to fringe.

Temporary Fen Pool Three (TF3)

Pool perimeter, 4.3 m; well defined, all used for algal sampling; maximum depth of open water, 10 cm; pool peat basement lacking, 2-5 cm of sediment overlying bedrock; bottom surface variable, during summer ca. 60% covered in plant growth, remainder a fine floc. Two sediment layers apparent, top 0.5-1.5 cm a red-brown to black iron + organic material floc with embedded algal and detrital material, lower layer, fine grained grey-green silt; fringe thick, mostly loose packed, Sphagnum subnitens/nemoreum dominant,

S. tenellum common, overgrown with Juncus canadensis, Myrica gale, Chamaedaphne calyculata, Eriophorum angustifolium and Carex exilis. Associated fringe species, Drosera rotundifolia, Sarracenia purpurea, Eriophorum virginicum L., Polytrichum juniperinum; pool bottom vegetation dense, of non-aquatic restricted species; same as species overgrowing the fringe; surrounding pool, wet flat, extending 3-5 m from pool perimeter, vegetated as fringe. On the edges of flat, extensive band of hummocks similar to those given in TF2 but with Carex rostrata Stokes Carex paupercula Michx. and Sanguisorba canadensis L. present.

Temporary Fen Pool Four (TF4)

Pool perimeter, 10.8 m; well defined and all used for algal sampling; pool peat basement lacking, 2-4 cm of sediment overlying bedrock; bottom surface homogeneous, a few patches of sedge roots, otherwise a fine floc. Two sediment layers apparent, top 1-1.5 cm, red-brown to black iron + organic material floc with embedded algal and detrital material, lower layer, fine grained grey-green silt; fringes loose to tight packed, Sphagnum subnitens/ nemoreum dominant. Associated species, Kalmia polifolia, Carex paupercula, Sanguisorba canadensis, Juncus canadensis, Myrica gale, Eriophorum angustifolium, Scirpus cespitosus and Alnus sp.; pool bottom vegetation heavy but less so than in TF3, Juncus canadensis; Eriophorum angustifolium and Scirpus cespitosus present; surrounding area, of hummocks as

described in TF2. Five meters from pool perimeter to the north, a Carex rostrata dominated seepage track.

Permanent Fen Pool One (PF1)

Pool perimeter, 13 m; poorly defined due to flooding of margins, all of fringe used for algal sampling; maximum depth of open water, 30 cm, around pool edges, 18 cm; accumulation of organic material on pool bottom, 20-46 cm thick, but not consolidated to form a peat basement; bottom surface variable, large portions of sediment becoming buoyant with gas bubbles floating to surface, leaving depressions in sediment, 10-50% of surface affected, varying with time. Areas of intact bottom with fine red-brown-black iron + organic material floc embedded with aggregates of algal and detrital material. Areas of broken bottom, grey-black to green, non-fibrous clumps of organic material mixed with the iron + organic floc. Three sediment layers apparent, top 2 cm, of fine iron + organic floc, next 1 cm, a non-fibrous green-yellow coloured organic material, remainder, grey-black to green, non-fibrous organic material clumps; fringes variable, north end, loose bed of Sphagnum papillosum Lindb. with S. contortum, otherwise fringe ca. 20 cm wide of patches of S. contortum mixed with Eriophorum angustifolium, Scirpus cespitosus, Carex michauxiana Boeckl. and Juncus canadensis. Associated species, Myrica gale, Chamaedaphne calyculata, Similacina trifolia, Aster nemoralis, Sarracenia purpurea; pool bottom vegetation moderate; Carex michauxiana, Eriophorum angustifolium,

Juncus canadensis, Scirpus cespitosus and Myrica gale emergent, Utricularia intermedia Hayne and Sphagnum contortum free growing, concentrated around edges; surrounding area complex, pool lies in a depressed wet flat adjacent to main drainage channel of site (PF3), flat a mat of Sphagnum subnitens/nemoreum and Utricularia intermedia. South end of pool, overgrown drainage soak connecting with PF2, consisting of a bed of Utricularia intermedia overgrown with Juncus canadensis, Carex michauxiana, C. rostrata, Eriophorum angustifolium and Smilacina trifolia. North margin of main pool flat, high hummocks, mounds of Sphagnum magellanicum, S. subnitens/nemoreum and S. flavicomans, associated species Potentilla fruticosa L., Rosa nitida Willd., Sanguisorba canadensis, Similacina trifolia, Ledum groenlandicum, Pleurozium schreberi, Eriophorum angustifolium, Chamaedaphne calyculata and Vaccinium oxycoccus. West margin of main flat, elevated, drier and hummocky, vegetated as the hummocks of TF2.

Permanent Pen Pool Two (PF2)

Pool perimeter 12 m; well defined by a sedge border, all used for algal sampling; maximum depth of open water, 27 cm; consolidated peat basement lacking, with a false bottom of Nuphar variegatum rhizomes underlain with loose-packed organic material, 48-88 cm in depth; bottom surface as described for PF1. Three sediment layers apparent, top 1 cm, red-brown-black iron + organic material floc mixed with algal and detrital material, next 2 cm, a

mix of surface floc and non-fibrous clumps of organic material with a base of a pure thin layer (75 mm) of blue-green algae, remainder, non-fibrous clumps of organic material, grey-black to green in colour; fringe consisting of heavy growths of Carex michauxiana and C. exilis with Sphagnum contortum common. Associated fringe species, Similacina trifolia, Juncus canadensis, Andromeda glaucophylla, Myrica gale, Chamaedaphne calyculata, Aster nemoralis and Sarracenia purpurea; pool bottom vegetation heavy, Nuphar variegatum leaves covering 30-40% of pool surface, emergent growths of Carex michauxiana, Carex exilis, Eriophorum virginicum, Myrica gale, free floating growth of Sphagnum contortum and Utricularia intermedia; surrounding area comparable with PF1 with some exceptions. Wet flat surrounding pool has Sphagnum papillosum in addition to PF1 species, the wet soak section draining into PF2 has Viola pallens (Banks) Brainerd, Aster nemoralis, Sphagnum subnitens/nemoreum and S. tenellum in addition to PF1 species.

Permanent Fen Pool Three (PF3)

Pool perimeter 81 m; complete fringe of main pool body used for sampling, upper shallow flat not used; maximum depth of open water, 40 cm, most positions less, varies with development of pool vegetation; pool peat basement variable, 0.0-200 cm in depth, a false bottom of root and rhizome networks in some positions, loosely packed and waterlogged throughout; bottom surface variable, aggregates of plant

roots and decaying organic material, with a variable coat of iron + organic floc. Sediment layering obscure and variable, top layer of red-brown-black iron + organic floc, remainder, coarse non-fibrous organic material, black grey to green; fringe variable, four vegetation types. N edge, excepting outflow, and 50% of S edge, mats or clumps of Sphagnum papillosum. Near outflow, a mat of S. subnitens/ nemoreum. Lower south edge, pure Sphagnum mat, S. papillosum, S. contortum and S. fallax (Klinggr.) Klinggr. occurring. Mid south edge, a mat of S. subnitens/nemoreum and S. tenellum. Associated fringe species for all fringe types mostly as for hummock species of TF2; pool bottom vegetation dense and variable, a mix of Juncus sp., Menyanthes trifoliata L., Sparangium sp. and Utricularia intermedia, lesser amounts of Carex rostrata, Nitella sp. and Batrachospermum sp.; surrounding area, to the north, more elevated, with a mix of hummocks similar to those described for PF1. To the south, more elevated than pool area, with dry hummocks similar to those described for TF1. In area of pool outflow, a wet soak, dominated by Carex rostrata.

APPENDIX IV

A consideration of variables used in defining pool placement on spatial gradients of habitat variation

Of the three primary gradients of spatial variation considered important to water bodies of the North Harbour site, two are mostly apparent in the nature of the variation and in the ways they are assessed. The permanency gradient pertains to the degree of permanency of a water body and relates directly to its morphometry and positioning in the drainage system. The physical and biological consequences of such variation are strong and mostly obvious and will not be considered further.

The degree of surface water flow in peat pools is a source of strong physical and water quality variation given the degree of stagnancy possible in such pools. The evaluation of flow gradients are mostly apparent when the drainage system of the site is documented and interpreted. This may be complicated, however, by changes in water storage capacity of the peat site.

In peatlands, watershed water storage capacity depends greatly on the position of the water table in the peat profile, with little storage capacity at high water tables (Bay, 1969; Chapman, 1965). During high water tables rainfall input moves directly to outlets via drainage tracks (Bay, 1969). An example describing such a situation is given by Tallis (1973) from a Pennine blanket bog. He

observed large volumes of water to discharge from a drainage gully with heavy rain, but with flow subsiding quickly after cessation of rain. The flow rate changed by as much as 20-30 times within 24 h. During the study period, the water table of both North Harbour peat sites was at or very near the surface. Thus, evaluation of the flow gradient was based on conditions of greatest liklihood of flow.

Evaluation of the third gradient, the minerotrophic gradient is complex, and is not wholly apparent based on single physical or chemical variables of the habitat. The approach taken in evaluating the minerotrophic status of pools in this study uses a composite of physical variables of the surrounding peat and chemical variables of pool water composition.

The depth of peat forming a basement to a water body gives an idea of the potential for vertical percolation of mineral soil water. With a sediment base of < 10 cm between bedrock and water body, mineral soil water input is likely to be large. However, no empirical value can be developed for depth of peat basement and extent of percolation of mineral soil water, even for a specific location. The hydraulic conductivity of peat columns varies (Ingram, 1968); the degree of compaction, degree of mineralization and composition varies from location to location and even within a single peat column.

The position of the pool on the drainage slopes of the site also affects the extent to which a given depth of

peat will impede mineral soil water movement. The better-drained position will likely have less sub-surface water build-up compared with poorly drained areas. Greater sub-surface water will increase vertical percolation. Surface flow tracks to a pool can be located and traced to their origin, while sub-surface flows can be inferred from elevation contours of the site and evaluated by the condition of the surrounding peat.

The chemical compositions of waters of mineral soil and atmospheric origin differ strongly. Within the peatland pool, water composition is further modified through contact with the organic soil and by biological activity. Yet, pool water composition can be used as a measure of relative importance of mineral soil water versus atmospheric inputs.

Scatter plots of Ca + Mg against pH and Fe against the ratio of COD:tannins + lignins, plus the ratio of Ca: Mg were used to interpret relative degrees of minerotrophic influence of sample pools in this study.

pH values form an increasing series from ombrotrophic sites to sites of strong mineral soil water input (Sjörs, 1950; Gorham, 1950; Du Rietz, 1954). Exceptions are common (Du Rietz, 1954), with variables partially or completely independent of minerotrophic status affecting pH. Such variables include the extent of water movement (Sparling, 1966; Gorham, 1956) or the extent of acidification of precipitation (Vangenechten et al., 1981).

Tolenen & Hosiaisluoma (1978), studying Finnish peatland pools, observed pH to correlate positively with increasing degrees of minerotrophic influence, but were unable to use pH as a strict indicator of minerotrophic status because of overlapping ranges of values in pools with moderate to slight minerotrophic influence.

The levels of Ca and Mg similarly show a trend of increase from water of low mineral soil water input to waters of high input (Persson, 1962; Tolonen & Hosiaisluoma, 1978; Glaser et al., 1981). The supply of Ca and Mg to mineral soil water is greater than to atmospheric precipitation (YeFimov & YeFimova, 1973; Moore & Bellamy, 1974; Crisp, 1966). Du Rietz (1954) quotes Witting (1948) as giving a value of 1 mg/l Ca in pool water as an approximate boundary of mineral soil water influence. However, Tolenen & Hosiaisluoma (1978) were unable to distinguish pool minerotrophic status using Ca or Mg levels due to overlapping ranges of values for ombrotrophic and minerotrophic pools. The merit of using Ca and Mg measurements as indicators of minerotrophic status is supported by YeFimov & YeFimova (1973), who suggested that peat types can be discriminated by the amounts of Ca and Mg in pool and ground water after a scaling has been developed based on a large number of analyses.

Iron is the element which follows most closely the movement of mineral soil water in a peat column (Malmer, 1962a). Tolonen & Hosiaisluoma (1978) showed Fe levels to

correlate positively with an increasing degree of minerotrophic influence, but were unable to define the range of Fe values indicative of contact with mineral soil water. The strong seasonality observed in Fe levels in peat waters (Howell & South, 1981), due more to changing solubility than to supply, makes it necessary to consider the range of values over time when using Fe levels as an indicator of minerotrophic status.

The ratio of COD:tannins + lignins is a rough discriminator of pool minerotrophic status, being lowest in ombrotrophic waters and highest in minerotrophic waters. The COD level reflects the total organic component of the water and may be expected to vary in roughly predictable ways relative to tannins + lignins, which represent a more refractory component of the total organic material. The ombrotrophic pools were defined by heavy peat borders, typically with no through flow of water and with little flushing except for atmospheric input and snow melt. In contrast, minerotrophic pools were subject to greater water movement, either surface or subsurface, being less physically defined by peat basins. The tannins + lignins represent an organic fraction that is only slowly mineralized. Following release to the water mass through plant decomposition, they are changed by reaction with other organic material to form a component of humic and fulvic acids (Gjessing, 1975). Thus tannins + lignins can be expected to represent a greater proportion of the total COD

in poorly flushed (ombrotrophic) pools relative to better flushed (minerotrophic) pools, in general, due to a greater accumulation of tannins + lignins in poorly flushed pools.

A further parameter used to interpret relative degrees of mineral soil water to peat pools was the ratio of Ca:Mg. The ratio of exchangeable Ca to Mg in peat profiles was used by Chapman (1964) to distinguish the point at which the peat ceased contact with mineral soil water. The method was suggested by Mattson et al. (1944) on the basis of a similarity of the ratio of Ca to Mg in precipitation with that of sea water. The Ca:Mg ratio of precipitation varies with geographic location but favours Mg in oceanic locations (Gore, 1968; Allen et al., 1968).

The site used in this study is oceanic and from analysis of water from pools directly in contact with the mineral soil, Ca appears to strongly dominate over Mg in the mineral soil water. Thus the use of the Ca/Mg ratio in interpreting relative degrees of minerotrophic influence appears justified.

APPENDIX V

Bar graphs of the densities of dominant desmid species in sample pools over the nine sample dates.

Figure V-1: A bar graph of densities of dominant desmid species in pool TB1.

notes: undet. = the summed densities of all other desmid species in the sample.

▲ = a species of which 4-9 cells were seen in the counting procedure. The densities of such species are included with undet.

= column height is the mean of two replicates; extended line gives the value of the high density replicate. When counts of taxa were below the limit used for expression as a density in one of two replicates, the estimates were not average. The high replicate is given.

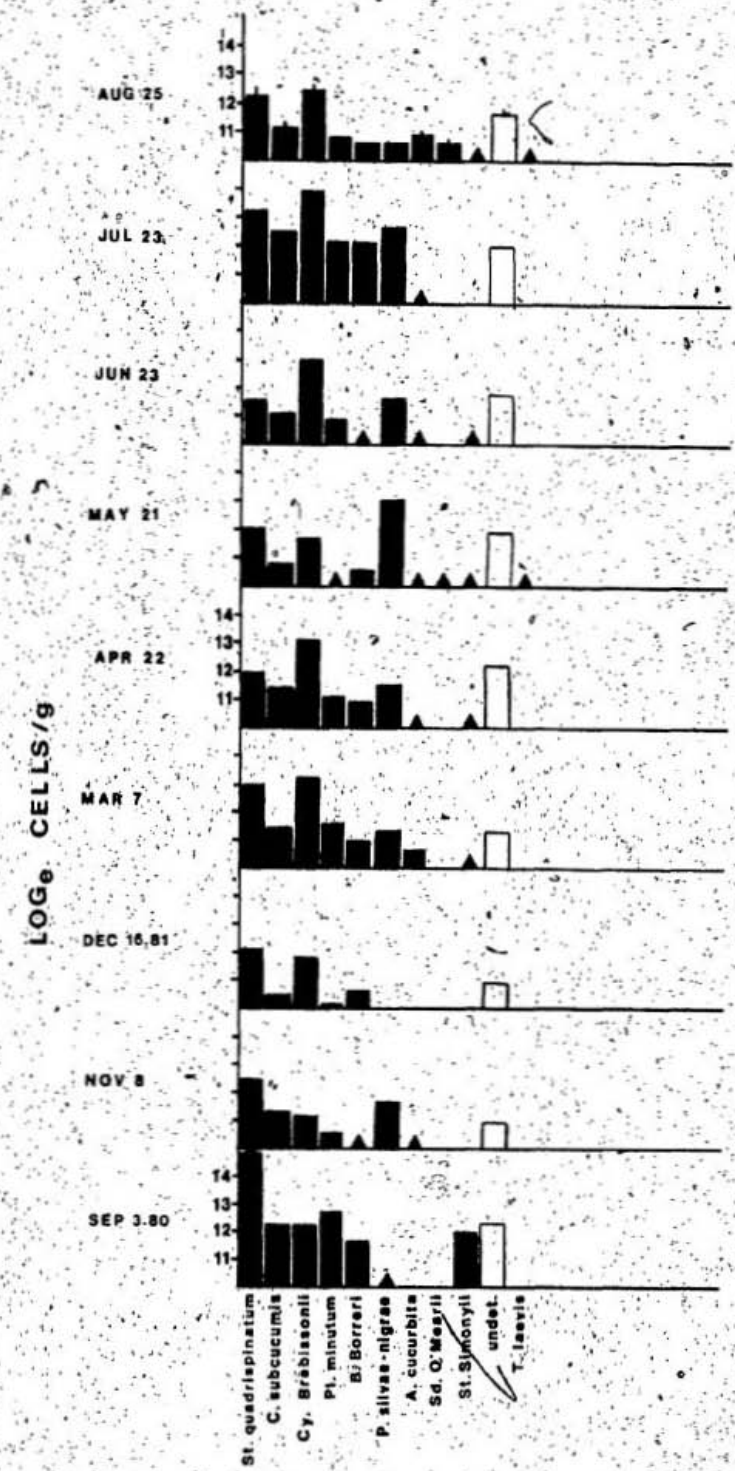

AUG 25
JUL 23
JUN 23
MAY 21
APR 22
MAR 7
DEC 16,81
NOV 8
SEP 3.80
LOGe CELLS/g
14
13
12
11
St. quadrispinatum
C. subcucumis
Cy. Brébissonii
Pl. minutum
Bi Borreri
P. silvae-nigrae
A. cucurbita
Sd. O'Neyrii
St. Simonyi
undet.
T. laevis

Figure V-2: A bar graph of densities of dominant desmid species in pool TB2.

notes: as per Figure V-1.

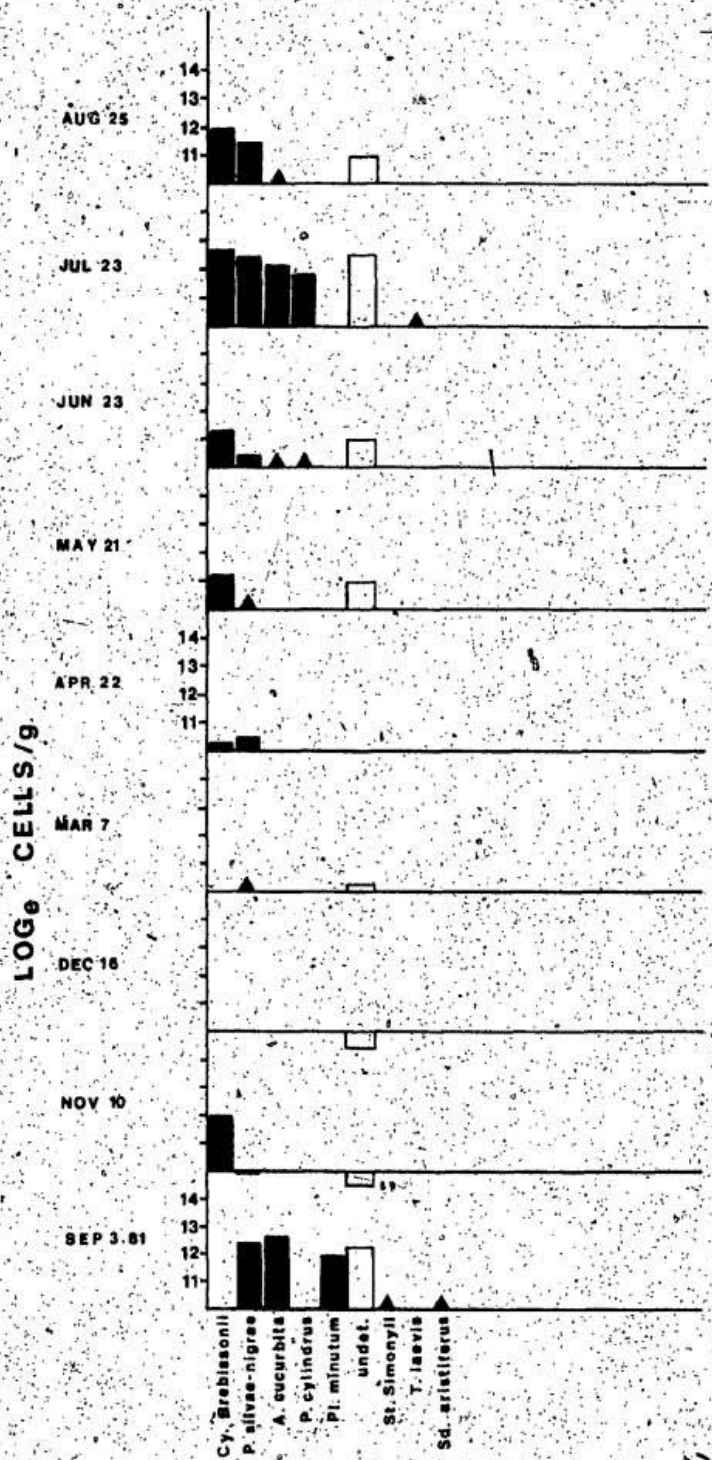

AUG 25
JUL 23
JUN 23
MAY 21
APR 22
MAR 7
DEC 16
NOV 10
SEP 3.81
14
13
12
11
LOGe CELLS/g.
Cy. brebissonii
P. silvae-nigrae
A. cucurbita
P. cylindrus
Pl. minutum
undet.
St. Simonyii
T. laevis
Sd. aristiferus

Figure V-3: A bar graph of densities of dominant desmid species in pool PB1.

notes: as per Figure V-1.

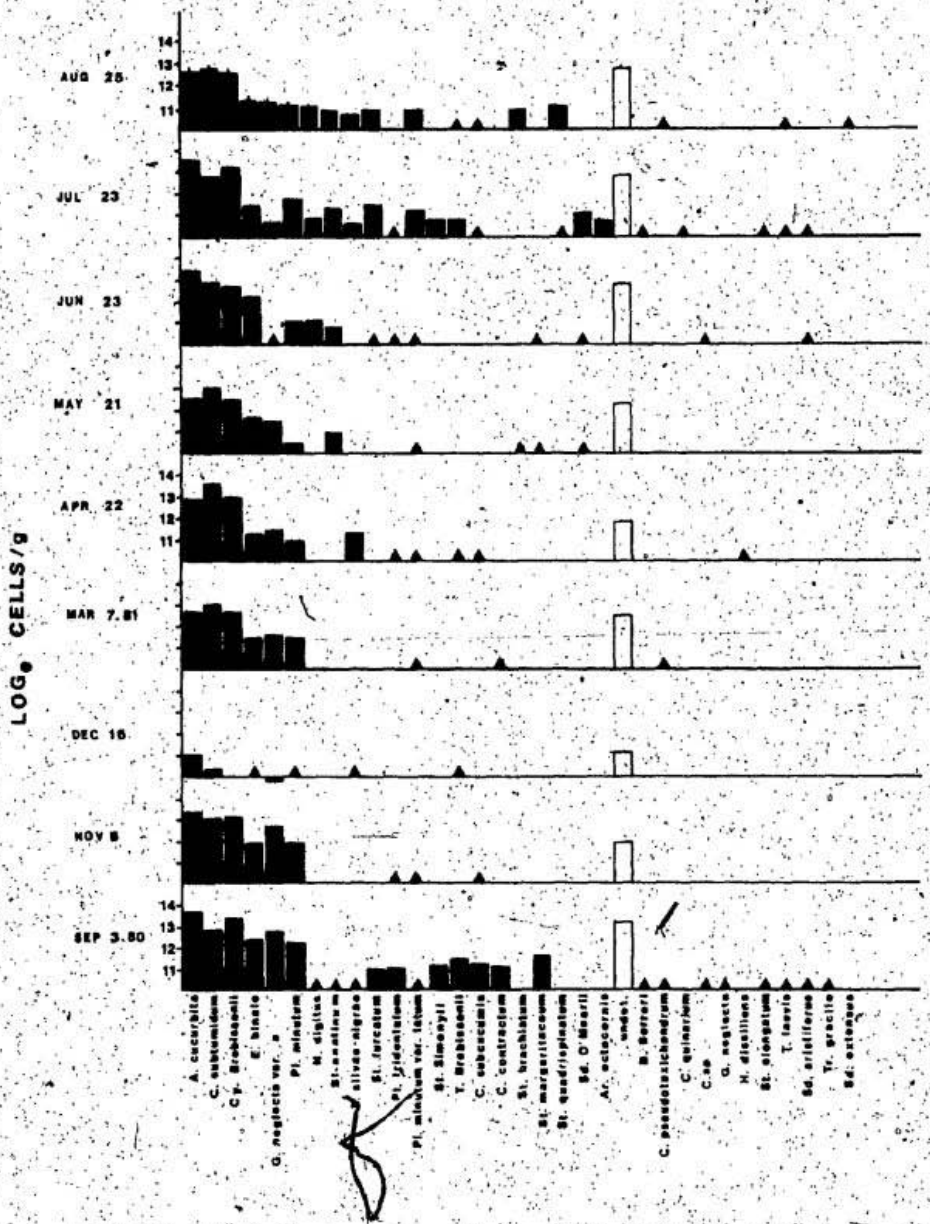

AUG 28
JUL 23
JUN 23
MAY 21
APR 22
MAR 7.81
DEC 16
NOV 5
SEP 3.80
14
13
12
11
LOG$_e$ CELLS/g
A. cucurbita
C. subtumidum
Cy. Brebissonii
E. bilaris
G. neglecta var. a
Pl. minutum
N. digitus
St. anabaenae
silvae-nigrae
St. furcatum
Pl. lybicum
Pl. minutum var. latum
St. Simonyi
T. Brebissonii
C. obscurissima
C. controversum
St. brachiatum
St. margaritaceum
St. quadripinatum
Bd. O'Meariil
Ar. octocornis
undul.
B. Berreri
C. pseudostrichondrum
C. quinarium
C. sp.
G. neglecta
H. distillans
St. elongatum
T. laevis
Bd. ariellformis
Tr. gracile
Bd. ostenfeldii

Figure V-4: A bar graph of densities of dominant desmid species in pool PB2.

notes: as per Figure V-1.

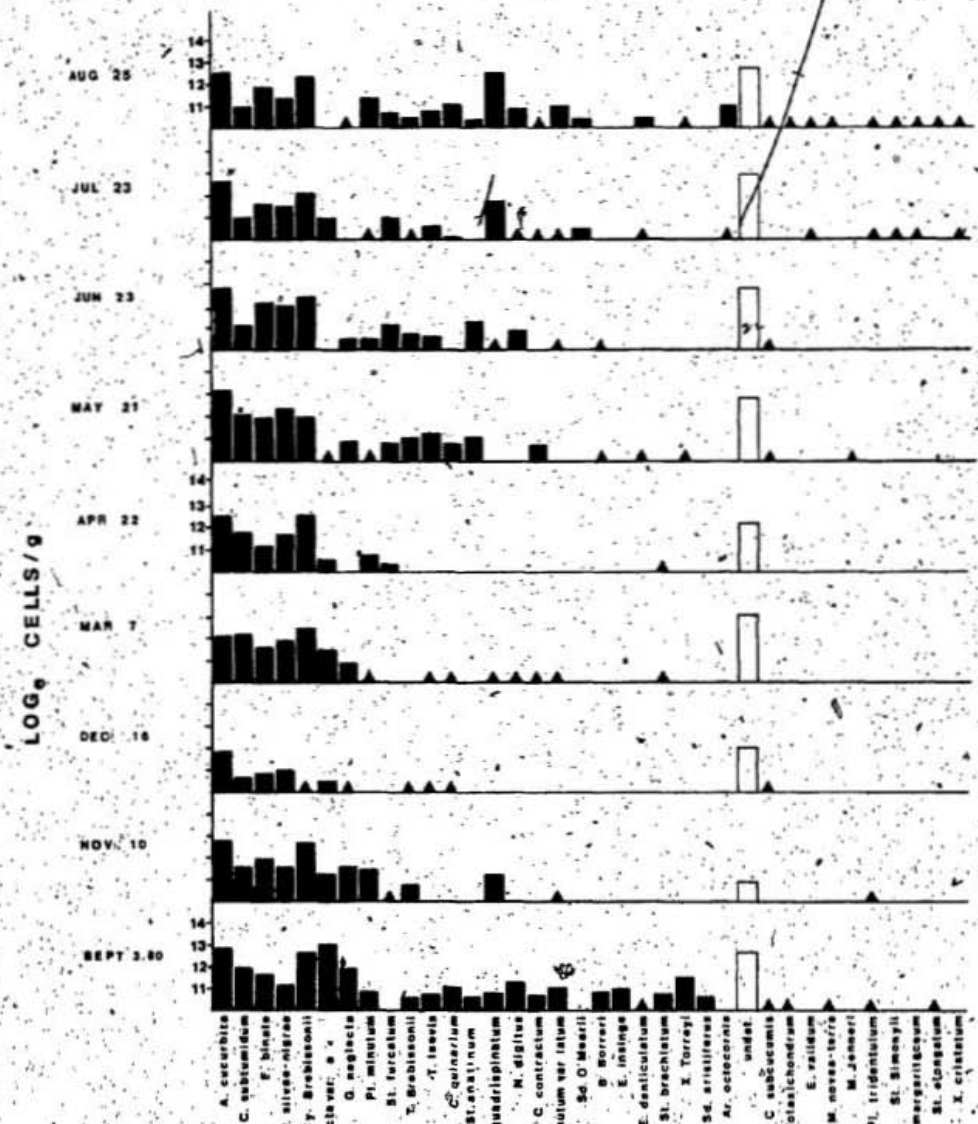

AUG 25
JUL 23
JUN 23
MAY 21
APR 22
MAR 7
DEC 16
NOV. 10
SEPT 3.80
LOG$_e$ CELLS/g
14
13
12
11
A. cucurbita
C. subtilissima
F. binale
P. silvae-nigrae
Cy. Brebissonii
G. neglecta var. a v
G. neglecta
Pl. minutum
St. furcatum
T. Brebissonii
T. laevis
C. quinarium
St. anatinum
St. quadrispinatum
N. digitus
C. contractum
Pl. minutum var latum
Sd. O'Meariі
B. Borreri
E. intinge
E. denticulatum
St. brachiatum
X. Torreyi
Sd. aristiferae
Ar. octocornis
undet.
C. subcucumis
C. pseudolaeichondrum
E. validum
M. nives-tatre
M. Jenneri
Pl. tridentulum
St. Simonyi
St. margaritaceum
St. elongatum
X. cristatum

Figure V-5: A bar graph of densities of dominant desmid species in pool PB3.

notes: as per Figure V-1.

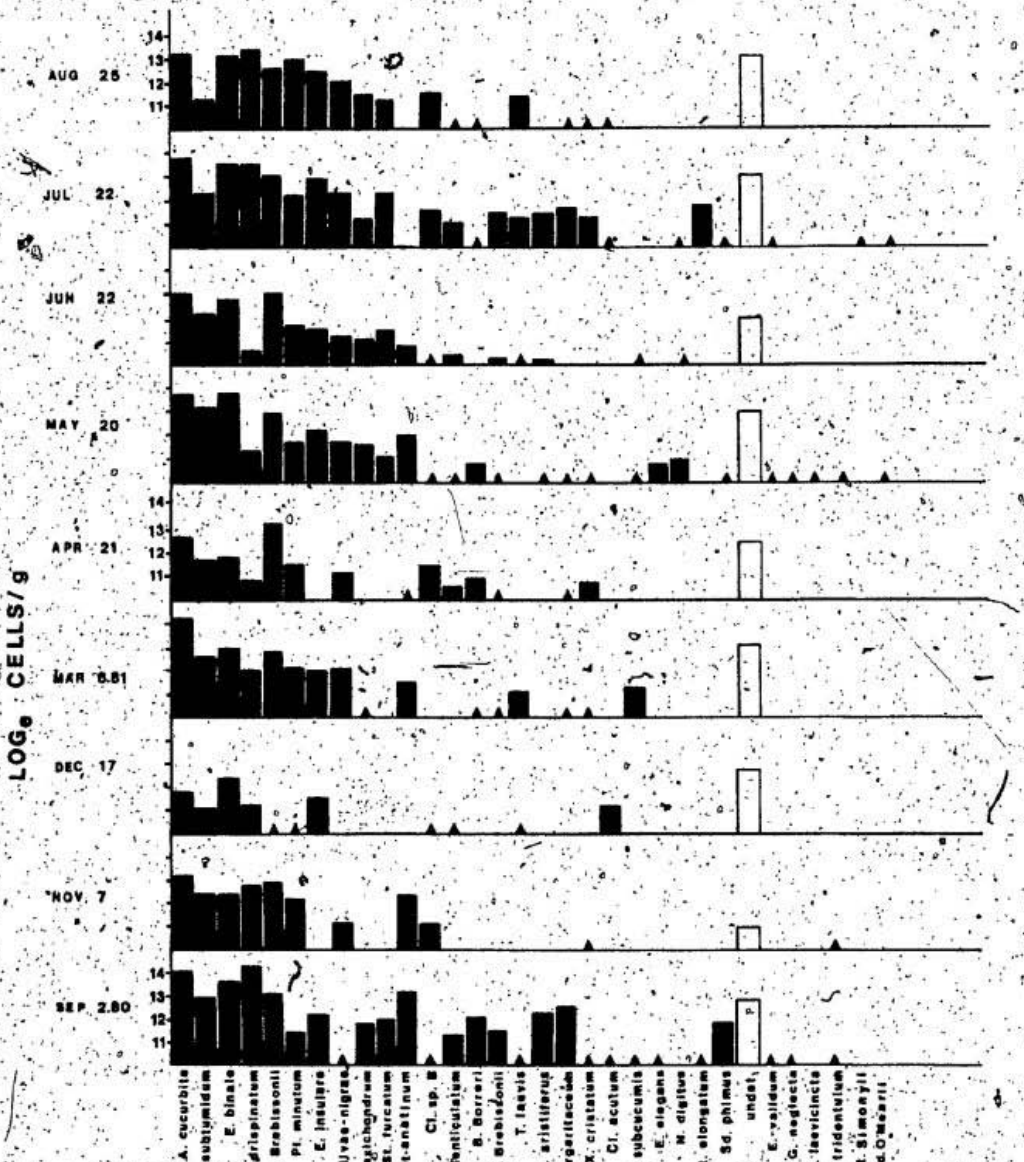

AUG 25
JUL 22
JUN 22
MAY 20
APR 21
MAR 6.81
DEC 17
NOV 7
SEP 2.80
LOGe CELLS/g
14
13
12
11
A. cucurbita
C. subtilissimum
E. binale
St. quadrisinatum
Cy. Brebissonii
Pl. minutum
E. intuitans
P. silvae-nigrae
C. pseudoglychoderum
St. furcatum
St. anatinum
Cl. sp. B
E. denticulatum
B. Borreri
T. Brebissonii
T. laevis
Sd. aristiferus
St. margaritaceum
X. cristatum
Cl. acutum
C. subcucumis
E. elegans
N. digitus
St. elongatum
Sd. phimus
undet.
E. validum
G. neglecta
H. laevicincta
Pl. tridentulum
St. Simonyi
Sd. O'Mearii

Figure V-6: A bar graph of densities of dominant desmid species in pool TP1.

notes: as per Figure V-1.

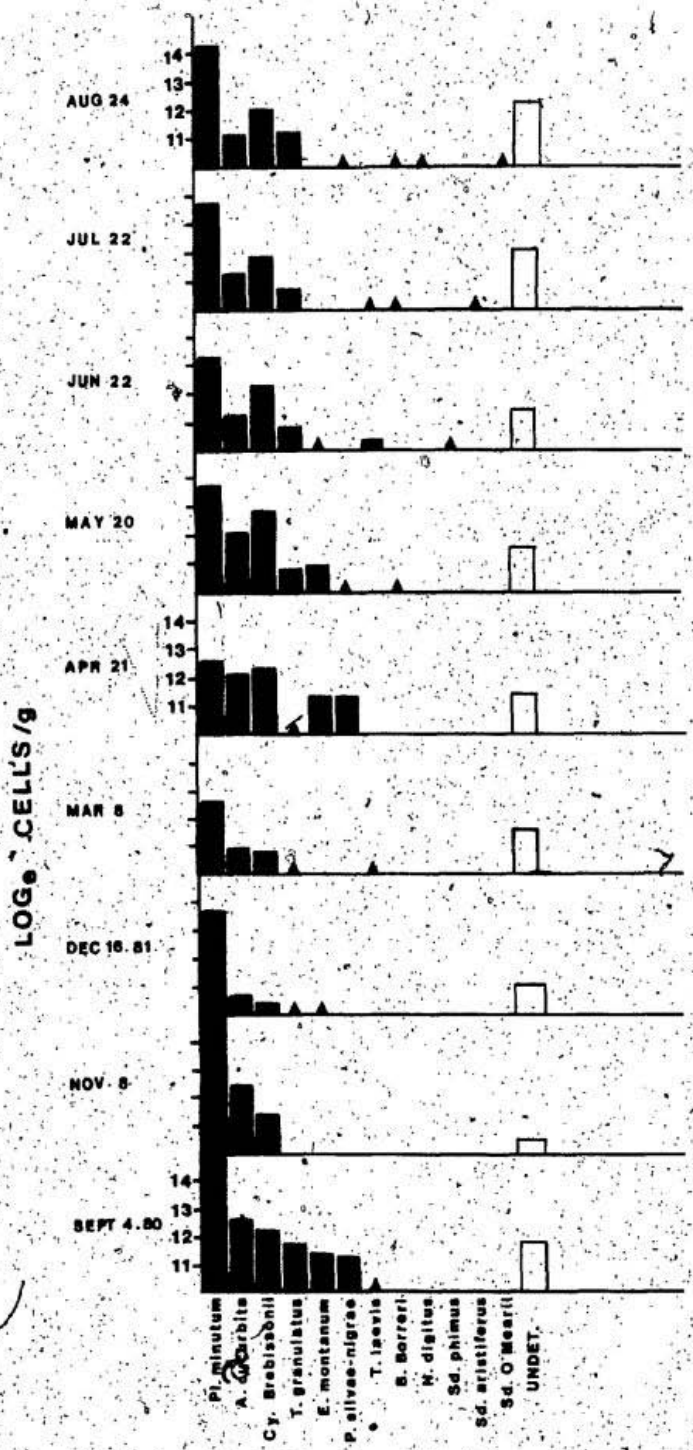

AUG 24
JUL 22
JUN 22
MAY 20
APR 21
MAR 8
DEC 16.81
NOV. 8
SEPT 4.80
14
13
12
11
LOGe CELLS/g
Pl. minutum
A. carbita
Cy. Brebissonii
T. granulatus
E. montanum
P. olivae-nigrae
T. laevis
S. Borreri
N. digitus
Sd. phimus
Sd. aristiferus
Sd. O'Mearii
UNDET.

Figure V-7: A bar graph of densities of dominant desmid species in pool TP2.

notes: as per Figure V-1.

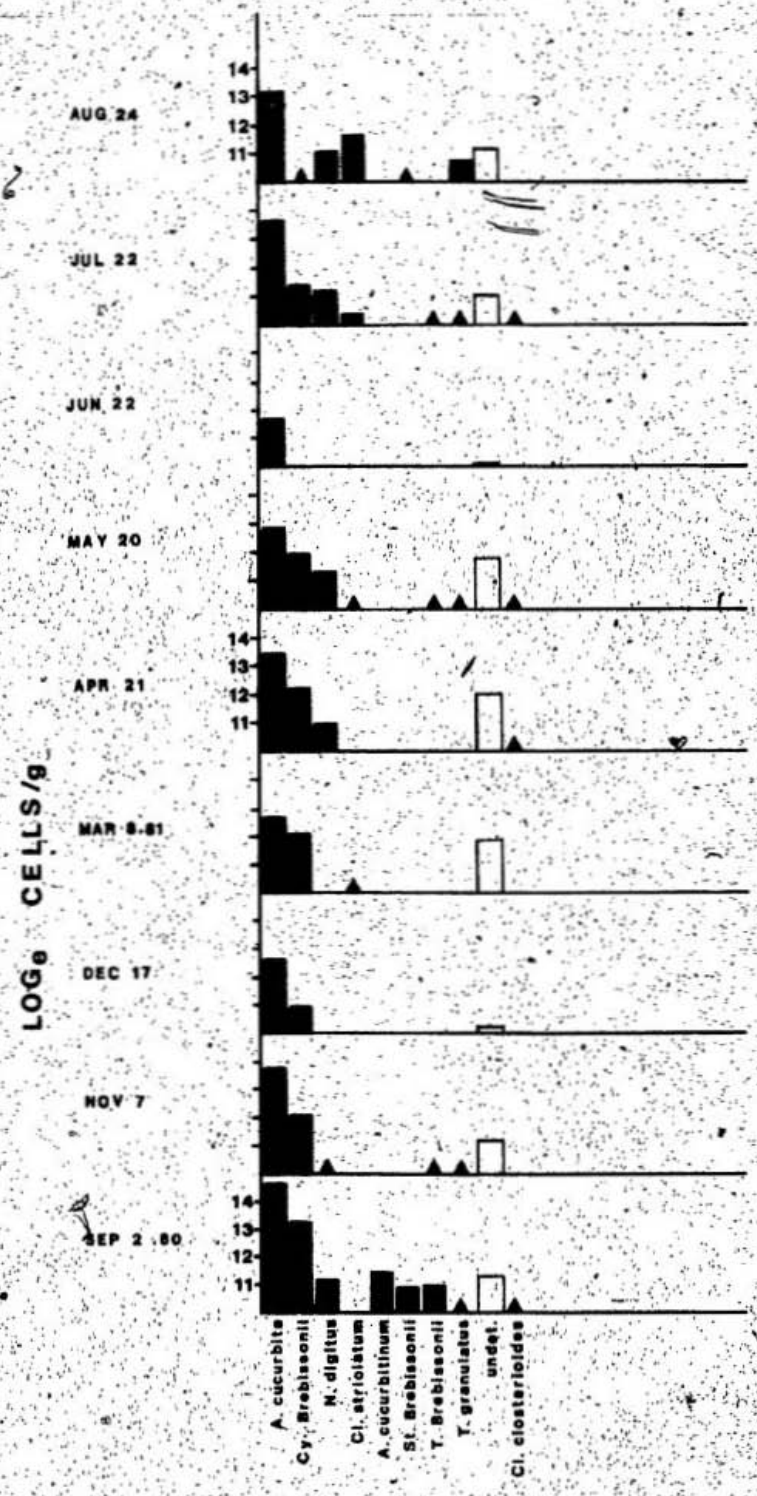

AUG 24
JUL 22
JUN 22
MAY 20
APR 21
MAR 8-81
DEC 17
NOV 7
SEP 2 80
LOG10 CELLS/g
14
13
12
11
A. cucurbita
Cy. Brebissonii
N. digitus
Cl. striolatum
A. cucurbitinum
St. Brebissonii
T. Brebissonii
T. granulatus
undet.
Cl. closterioides

Figure V-8: A bar graph of densities of dominant desmid species in pool TF3.

notes: as per Figure V-1.

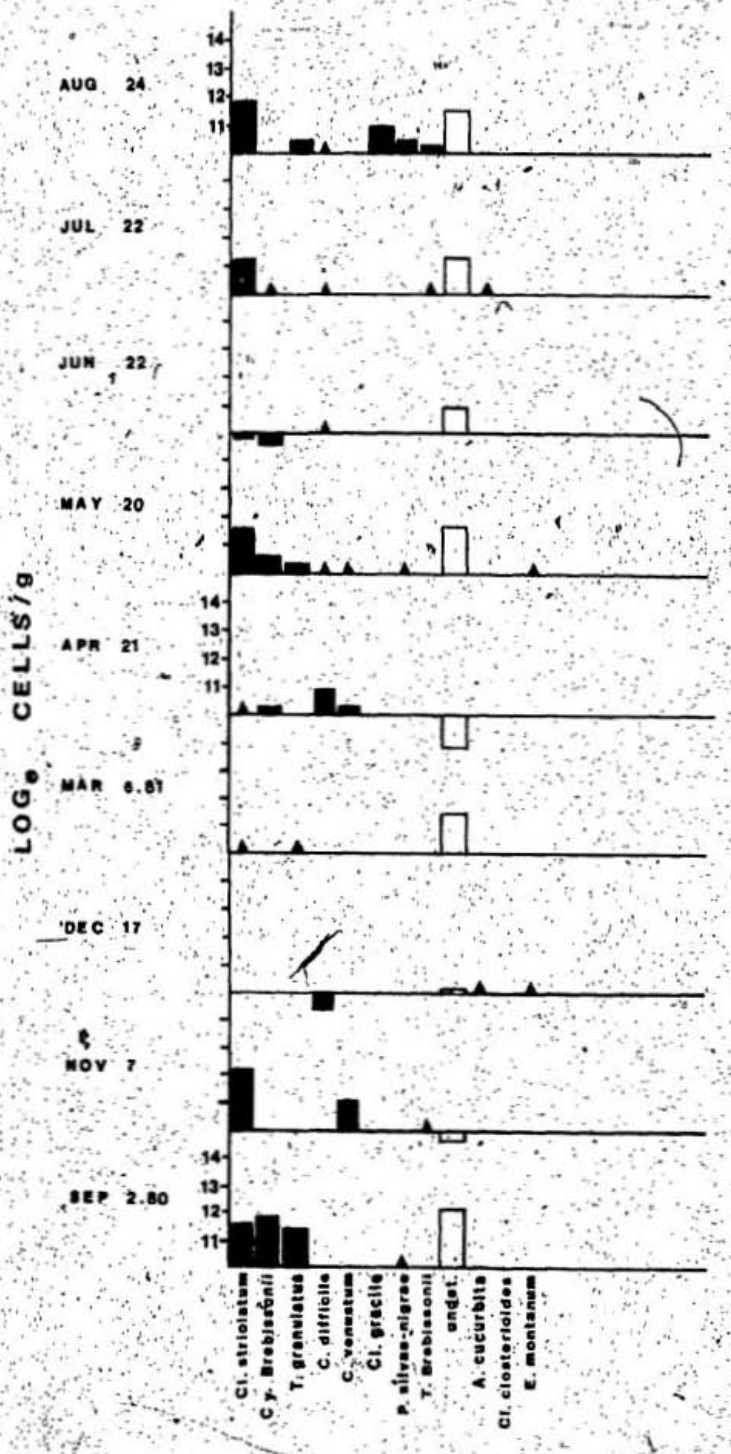

AUG 24
JUL 22
JUN 22
MAY 20
APR 21
MAR 6.81
DEC 17
NOV 7
SEP 2.80
LOGe CELLS/g
14
13
12
11
Cl. striolatum
Cy. Brebissonii
T. granulatus
C. difficile
C. venustum
Cl. gracile
P. silvae-nigrae
T. Brebissonii
angst.
A. cucurbita
Cl. closterioides
E. montanum

Figure V-9: A bar graph of densities of dominant desmid species in pool TP4.

notes: as per Figure V-1.

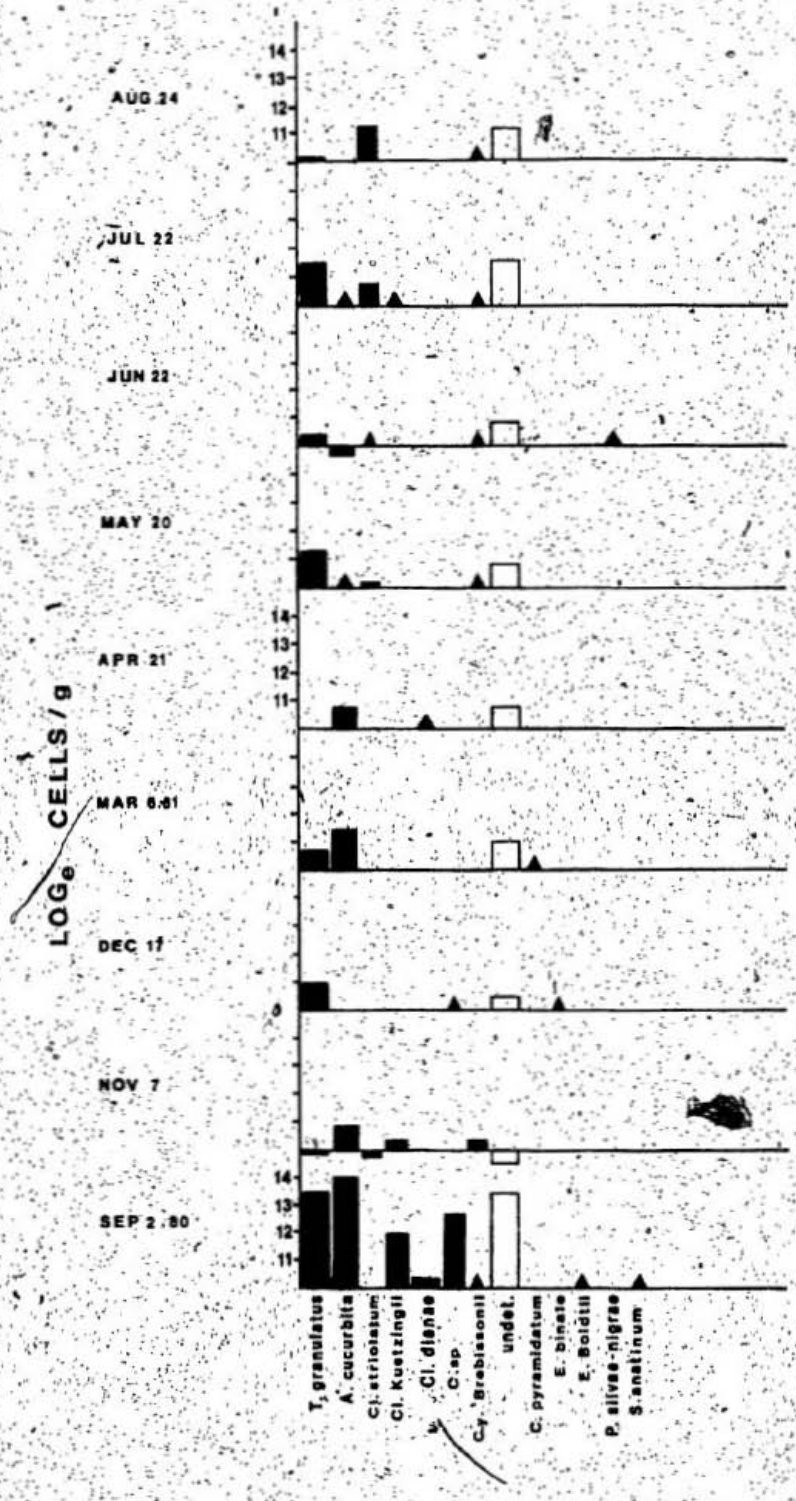

AUG 24
JUL 22
JUN 22
MAY 20
APR 21
MAR 6.81
DEC 17
NOV 7
SEP 2.80
LOGe CELLS / g
14
13
12
11
T. granulatus
A. cucurbita
Cl. striolatum
Cl. Kuetzingii
Cl. dianae
C. sp
Cy. Brebissonii
undet.
C. pyramidatum
E. binate
E. Bolditi
P. olivae-nigrae
S. anatinum

Figure V-10: A bar graph of densities of dominant desmid species in pool PP1.

notes: as per Figure V-1.

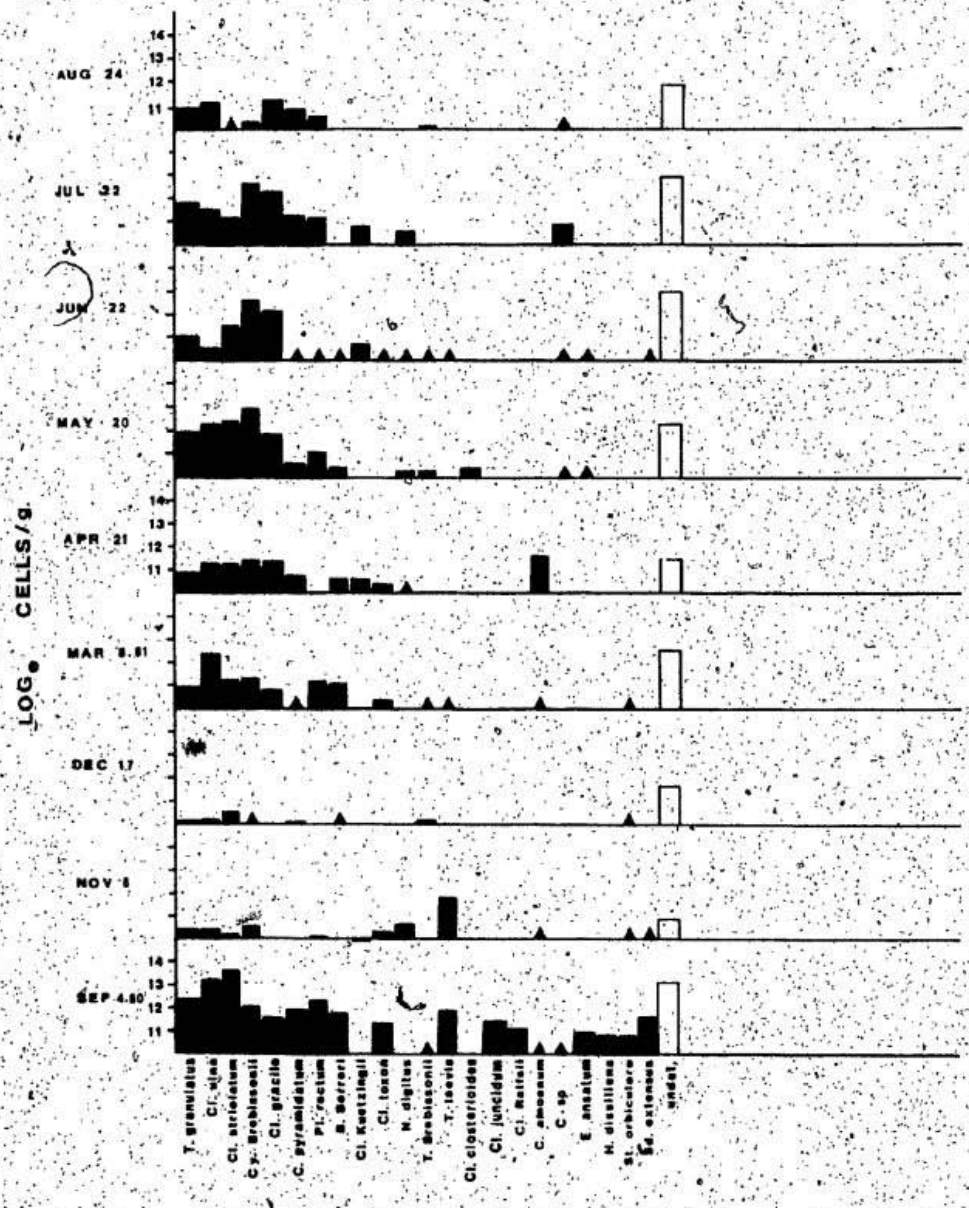

AUG 24
JUL 23
JUN 22
MAY 20
APR 21
MAR 5.81
DEC 17
NOV 5
SEP 4.80
LOG CELLS/g
T. granulatus
Cl. elos
Cl. acicularum
Cy. Brebissonii
Cl. gracile
C. pyramidatum
Pl. rectum
B. Borreri
Cl. Kuetzingii
Cl. laxum
N. digitus
T. Brebissonii
T. laevis
Cl. closterioides
Cl. juncidum
Cl. Ralfsii
C. amoenum
C. sp
E. anomalum
H. distillens
St. orbiculare
Ed. ostenses
undet.

Figure V-11: A bar graph of densities of dominant desmid species in pool PF2.

notes: as per Figure V-1.

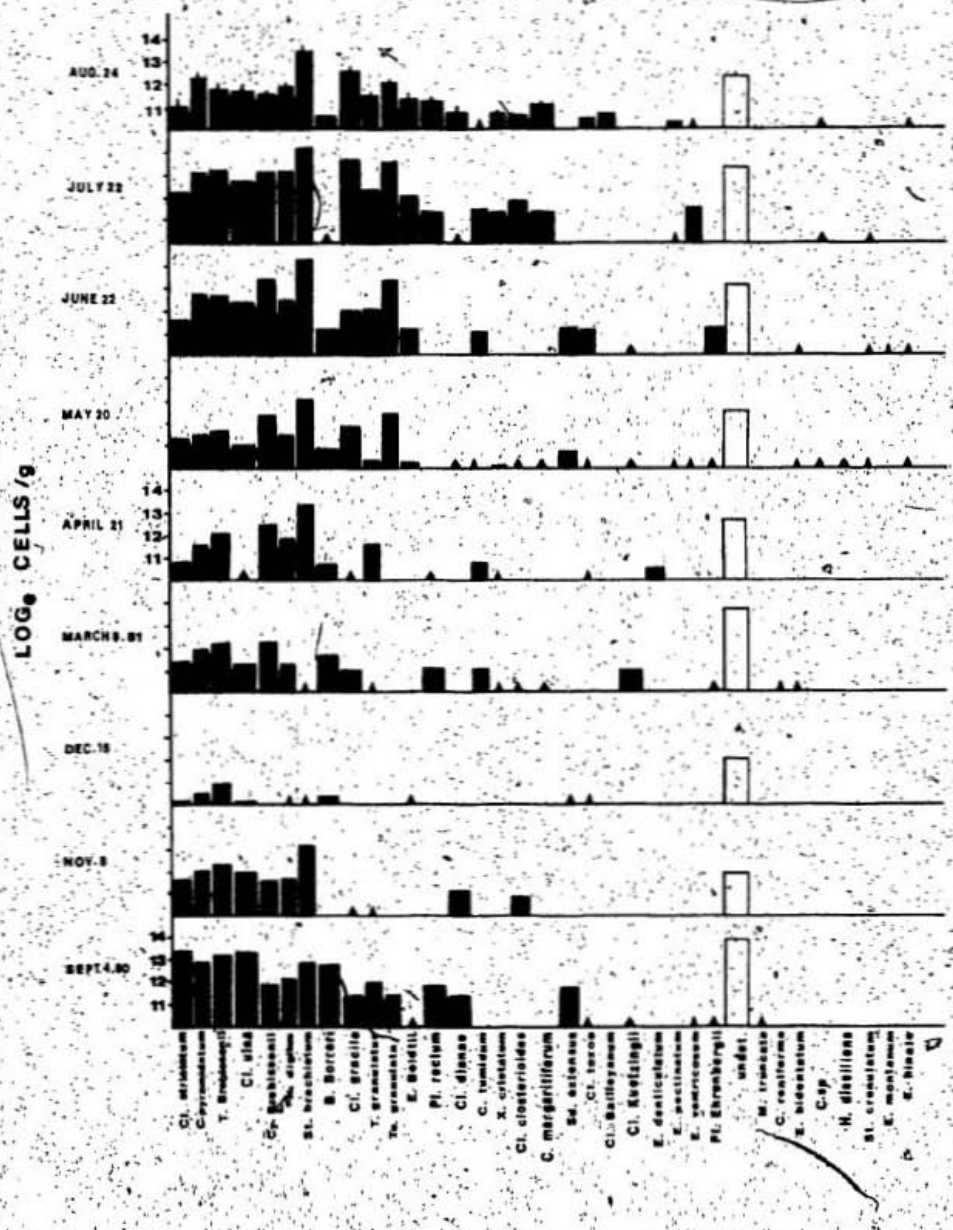
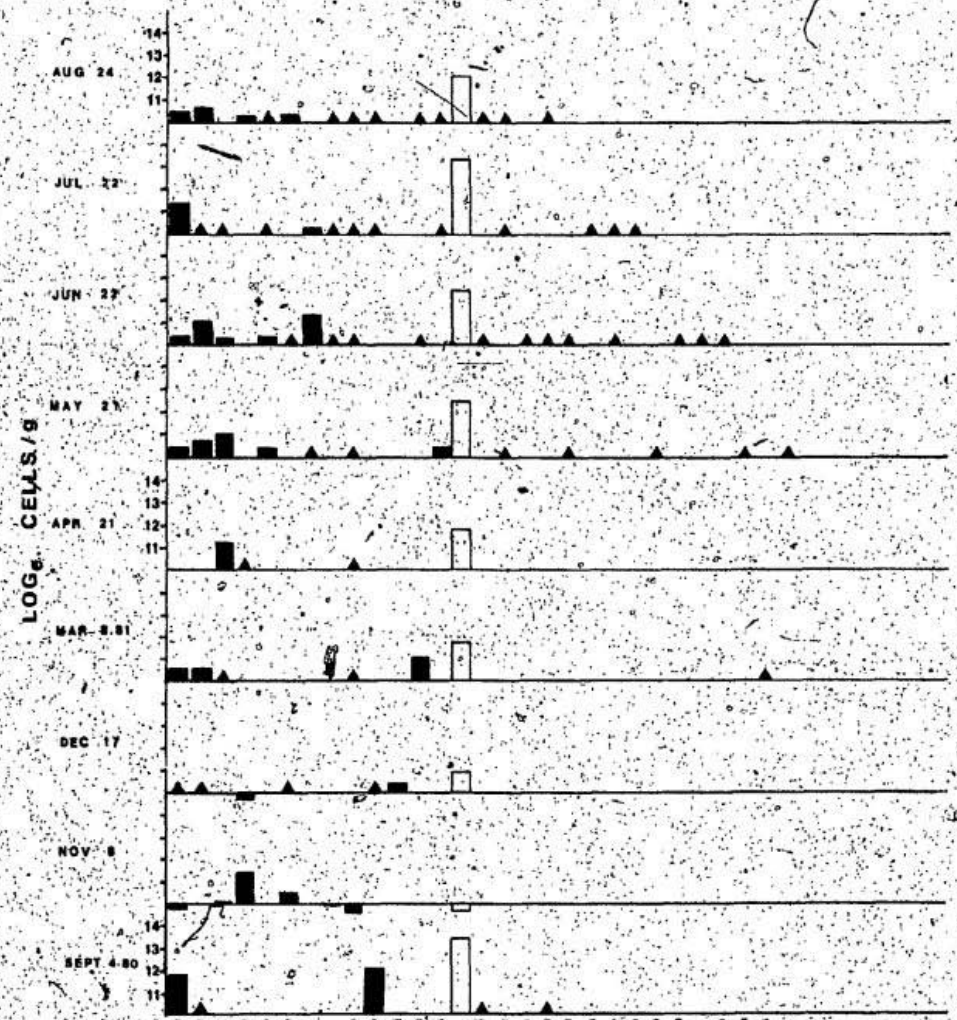

AUG. 24
JULY 22
JUNE 22
MAY 20
APRIL 21
MARCH 8, 81
DEC. 15
NOV. 8
SEPT. 4, 80
14
13
12
11
LOG$_e$ CELLS/g
Cl. striatum
C. pyrenoidosum
T. Bindereanum
Cl. ulna
Cr. ehrenbergii
Ta. diplon
St. brachiatum
B. Borreri
Cl. gracile
T. granulata
Ta. granulata
E. Boleitii
Pl. rectum
Cl. dianae
C. tumidum
X. crintatum
Cl. closterioides
C. margaritiferum
Sd. ostenseus
Cl. turris
Cl. Ballyanum
Cl. Kuetzingii
E. denticulatum
E. pectinatum
E. gemicosum
Pl. Ehrenbergii
undet.
M. truncata
C. reniforme
N. bidentatum
C. sp.
H. distillens
St. crenulatum
E. montanum
E. Binale

Figure V-12: A bar graph of densities of dominant desmid species in pool PF3.

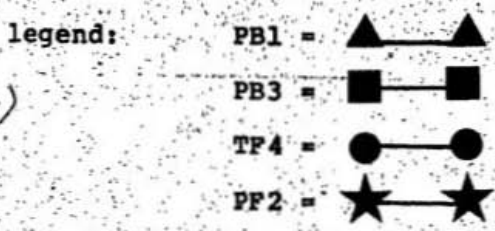
notes: as per Figure V-1.


AUG 24
JUL 22
JUN 22
MAY 21
APR 21
MAR 8.81
DEC 17
NOV 8
SEPT 4-80
LOG10 CELLS/g
14
13
12
11
C. pyramidatum
Cl. striolatem
Cy. Brebissonii
A. cocurbita
Cl. diamas
P. silvae-nigrae
Te. granulata
C. sp.
N. digitus
Pl. miniatum
St. Brebissonii
T. Brebissonii
T. granulatus
vindet.
Cl. gracile
Cl. intermedium
Cl. Kützingii
Cl. archarianum
C. lunulum
C. amoenum
E. bilunata
E. monianum
Pl. colonatum
St. brachiatum
St. anatinum
St. margaritaceum
S. japonicum
T. laevis

APPENDIX VI

Temporal variations in water quality were examined using a graphical analysis. All regularly measured water quality parameters are given. The results from some pools have been averaged. In all such cases the pools had mostly comparable absolute levels and temporal variations in water quality.

Figure VI-1: Temporal variations in sulphate, sodium, and chloride in four pools, with a comparison of levels in all pools.



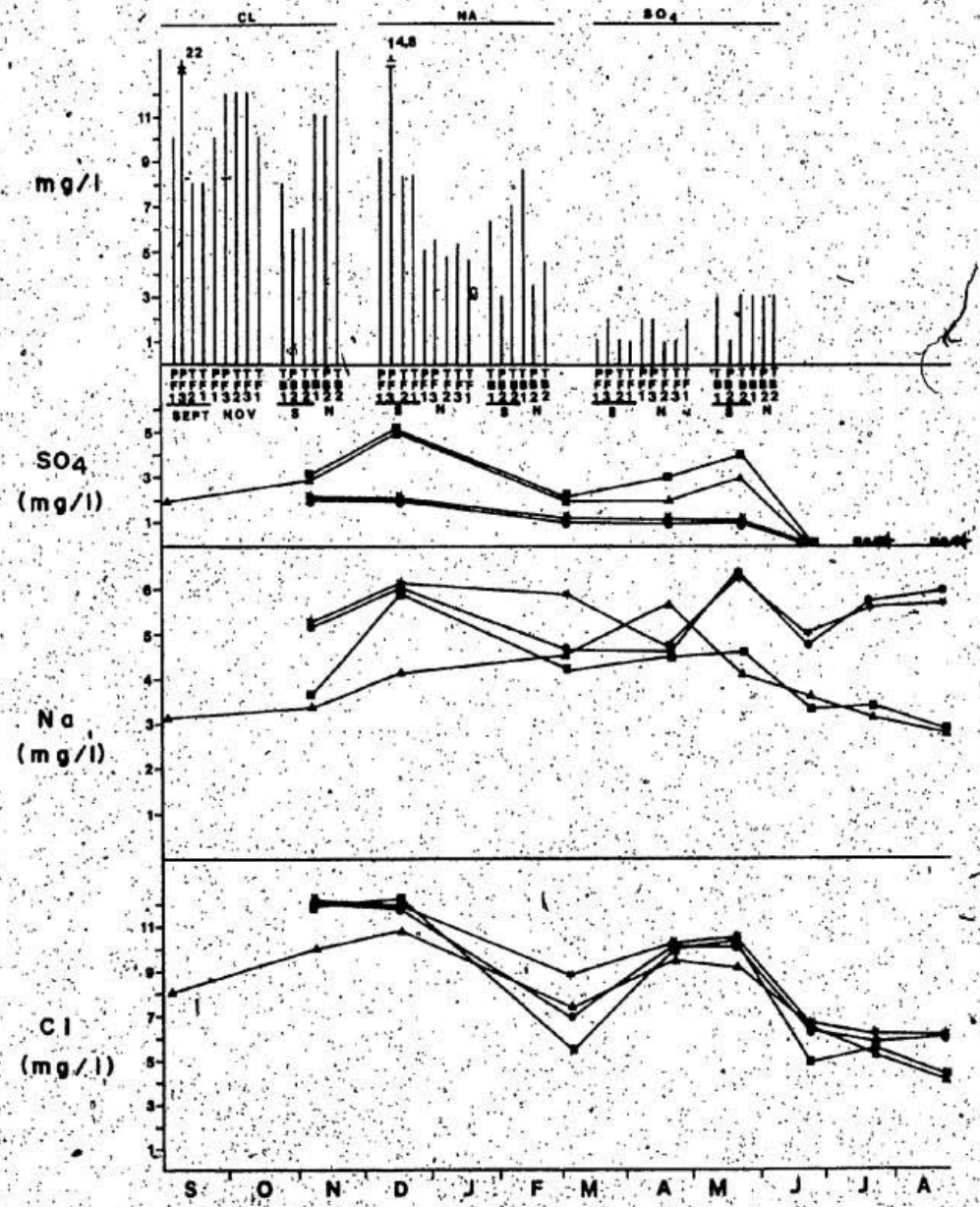
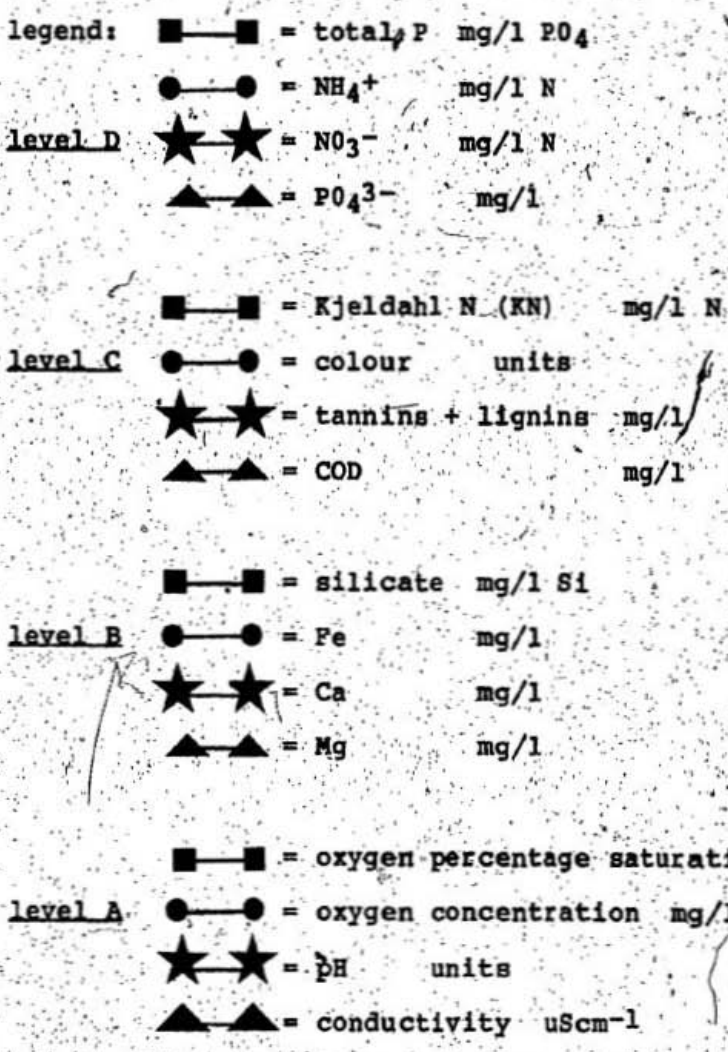

CL
NA
SO4
22
14,8
mg/l
SEPT NOV
SO4 (mg/l)
Na (mg/l)
Cl (mg/l)
S O N D J F M A M J J A

Figure VI-2: Temporal variatoin in water quality in pools PB1 and PB2.



notes: 1) values are averages.

2) a break in the plot indicates a missing sample.

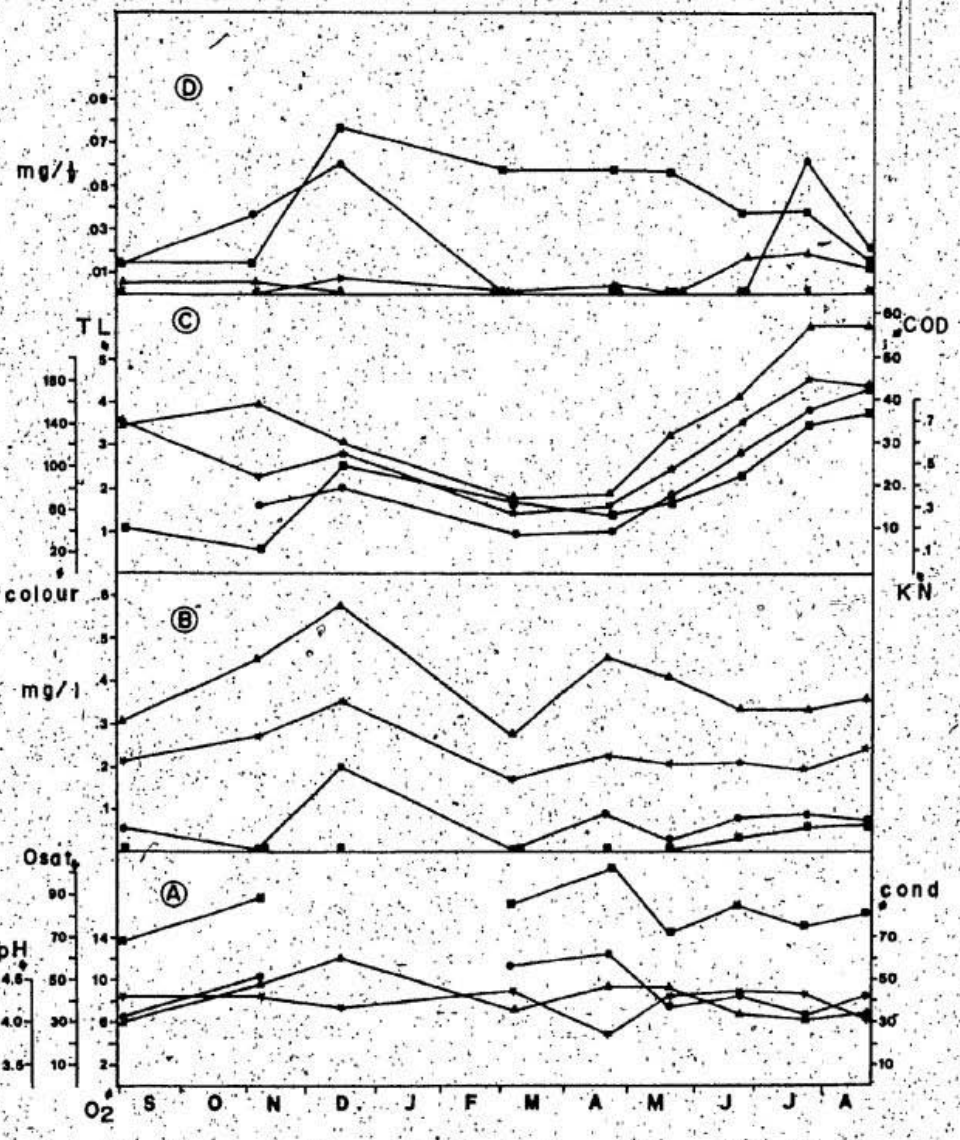

D
mg/l
.09
.07
.05
.03
.01
C
TL
180
140
100
80
60
colour
COD
60
50
40
30
20
10
KN
.7
.5
.3
.1
B
mg/l
.6
.5
.4
.3
.2
.1
A
Osat
90
70
50
30
10
pH
4.5
4.0
3.5
cond
14
10
6
2
O2
S
O
N
D
J
F
M
A
M
J
J
A

Figure VI-3: Temporal variation in water quality in pool PB3.

legend:

level D
- ■ = total P mg/l PO_4
- ● = NH_4^+ mg/l N
- ★ = NO_3^- mg/l N
- ▲ = PO_4^{3-} mg/l

level C
- ■ = Kjeldahl N (KN) mg/l N
- ● = colour units
- ★ = tannins + lignins mg/l
- ▲ = COD mg/l

level B
- ■ = silicate mg/l Si
- ● = Fe mg/l
- ★ = Ca mg/l
- ▲ = Mg mg/l

level A
- ■ = oxygen percentage saturation
- ● = oxygen concentration mg/l O_2
- ★ = pH units
- ▲ = conductivity uScm-1

note: a break in the plot indicates a missing sample.

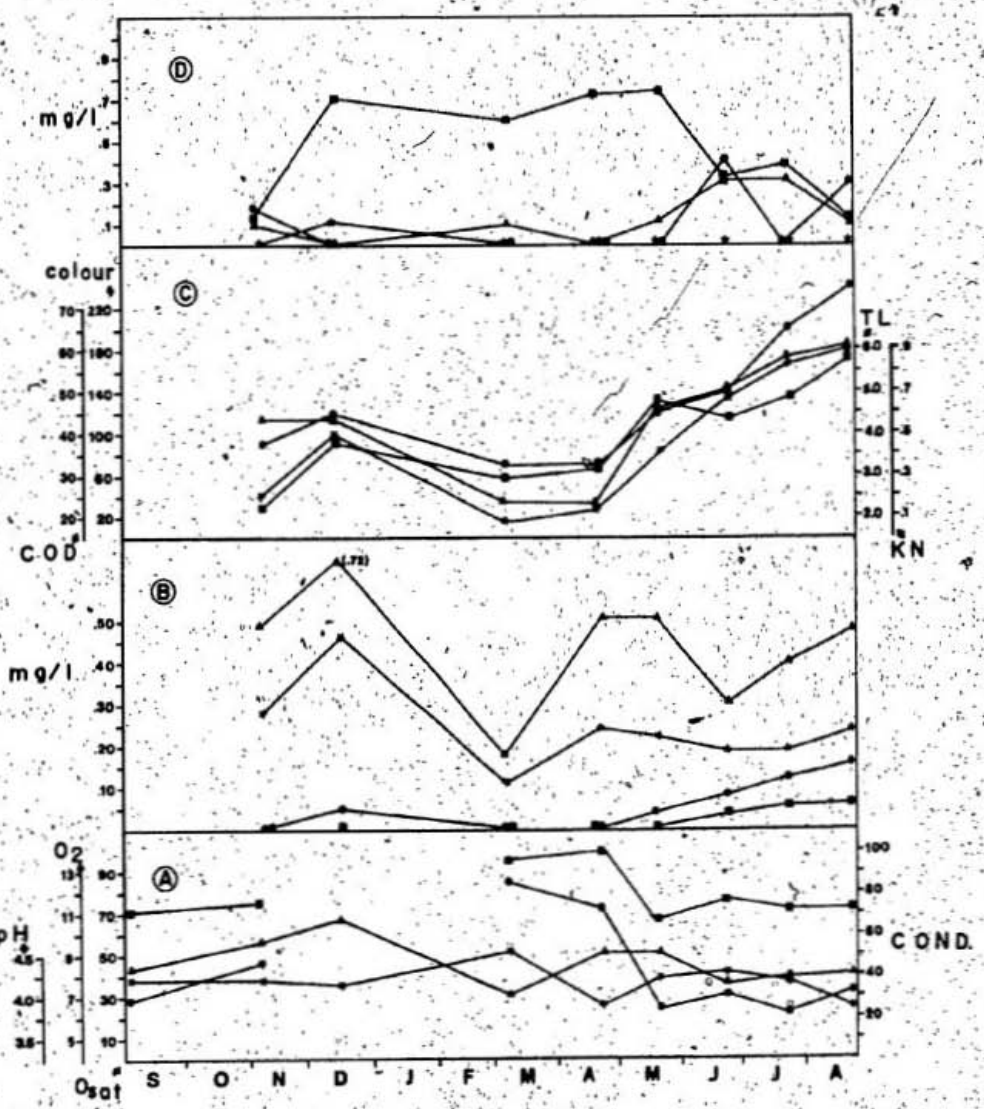
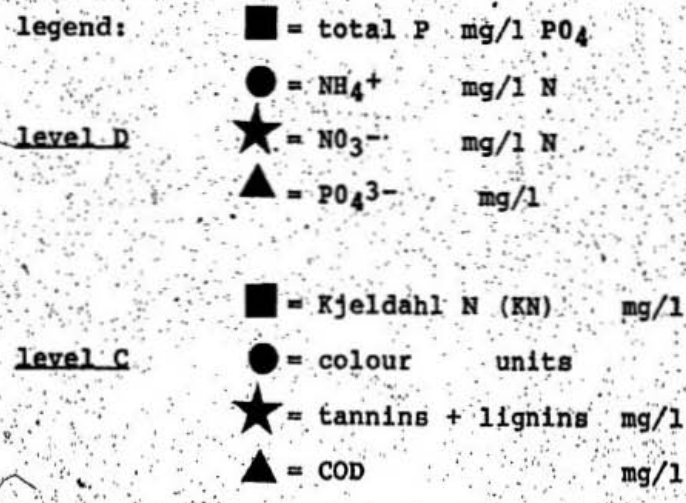

D
mg/l
colour
C
TL
COD
KN
B
mg/l
O2
A
pH
COND.
Osat
S O N D J F M A M J J A

Figure VI-4: Temporal variations in water quality in pool TB1.



note: break in plot indicates a missing sample.

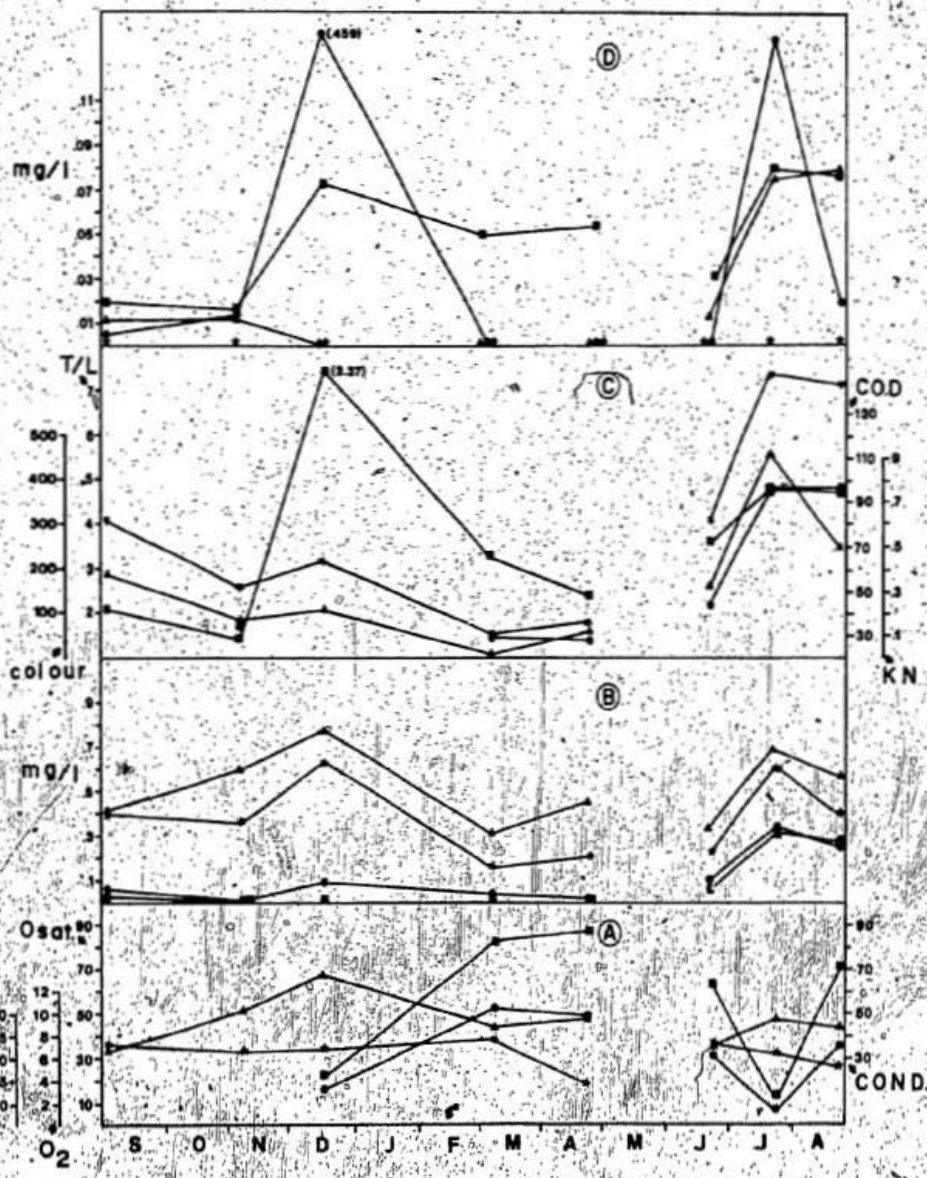
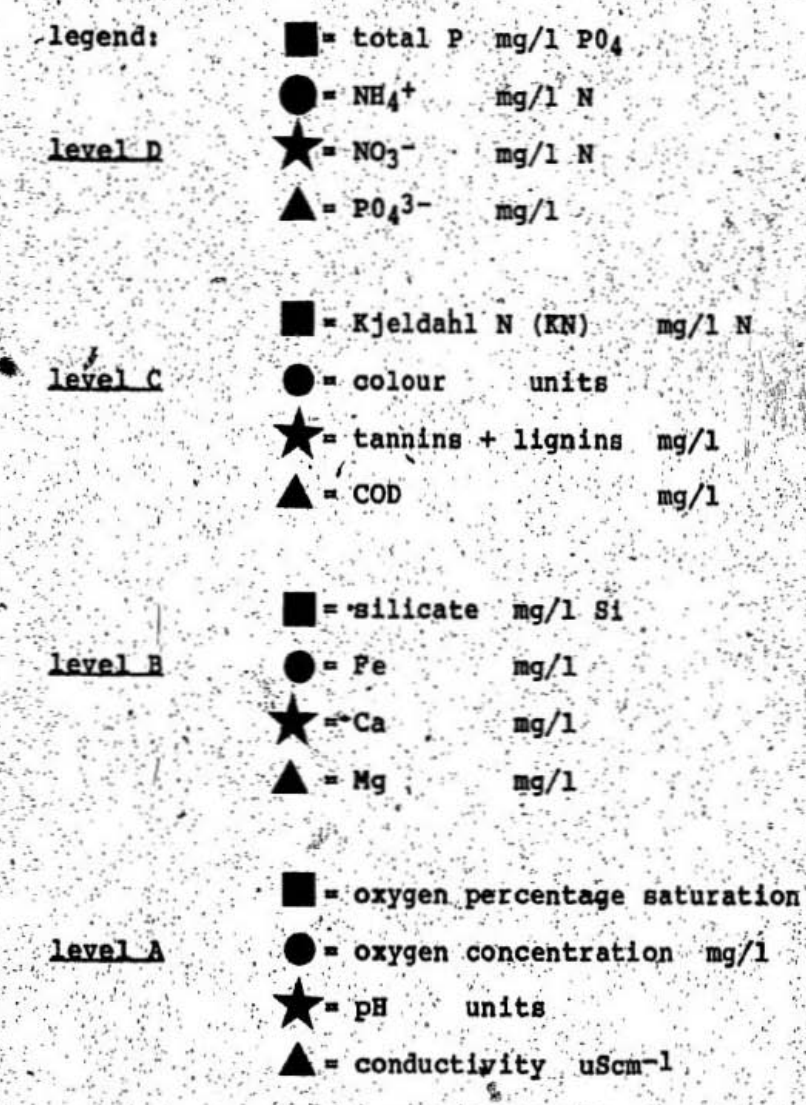

D
mg/l
T/L
C
COD
KN
colour
B
mg/l
Osat
A
pH
O2
COND.
S O N D J F M A M J J A

Figure VI-5: Temporal variation in water quality in pool TB2.



note: a break in the plot indicates a missing sample.

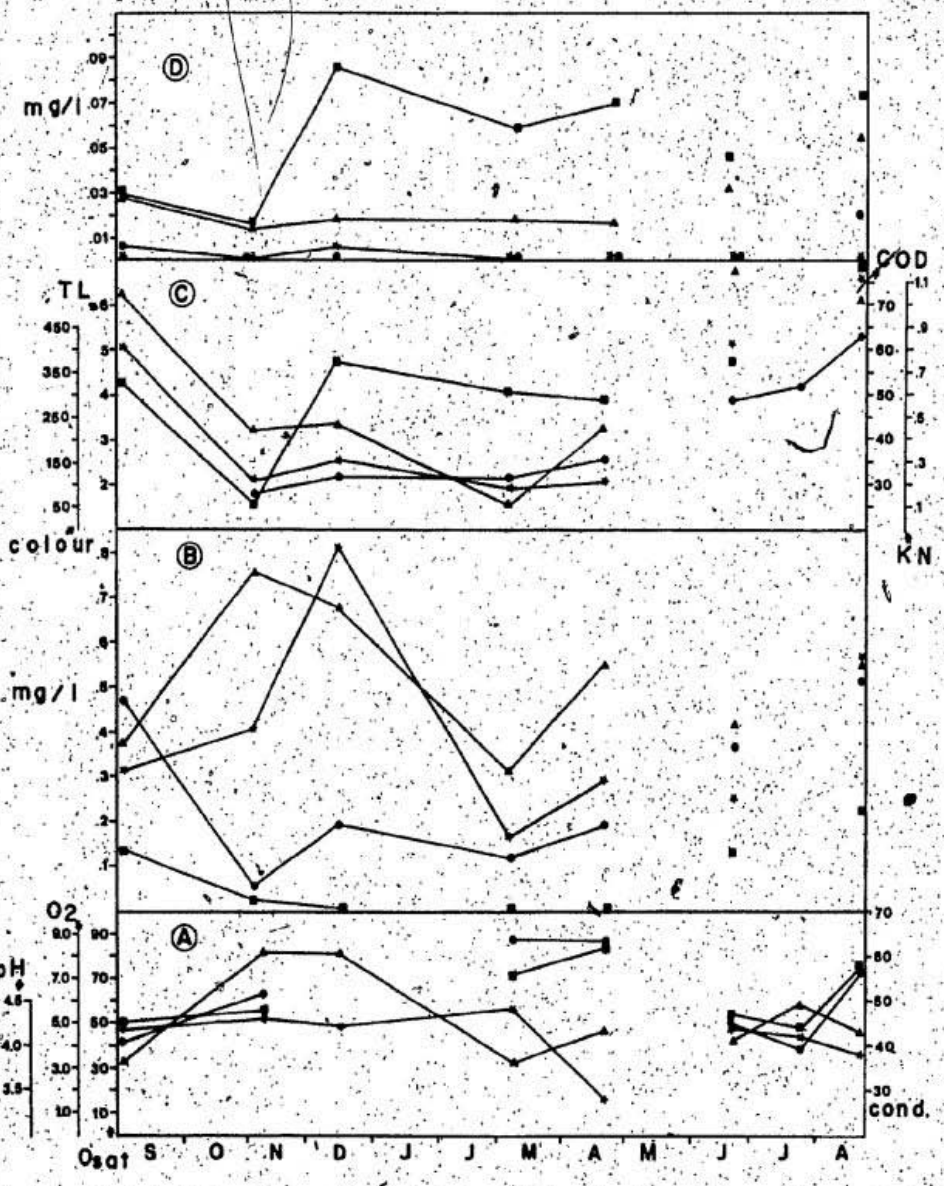
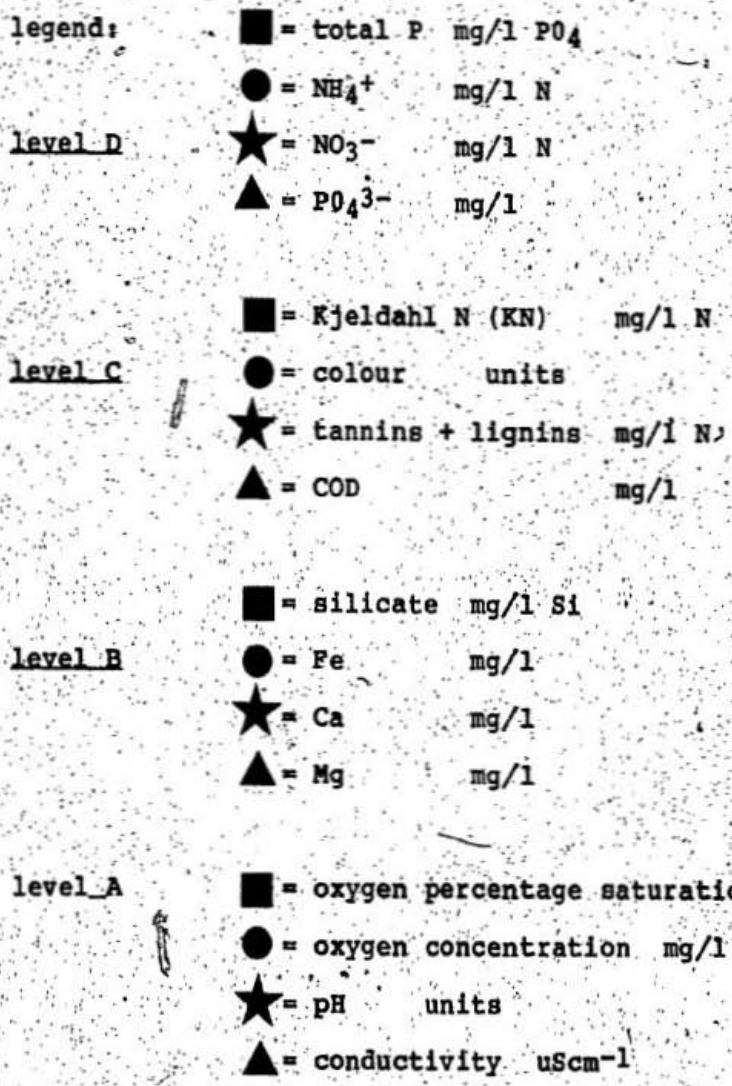

D
mg/l
.09
.07
.05
.03
.01
COD
TL
C
450
350
250
150
50
colour
1.1
.9
.7
.5
.3
.1
KN
B
mg/l
O2
A
pH
4.5
4.0
3.5
90
70
50
30
10
cond.
Osat
S O N D J J M A M J J A

Figure VI-6: Temporal variation in water quality in pool TF1.



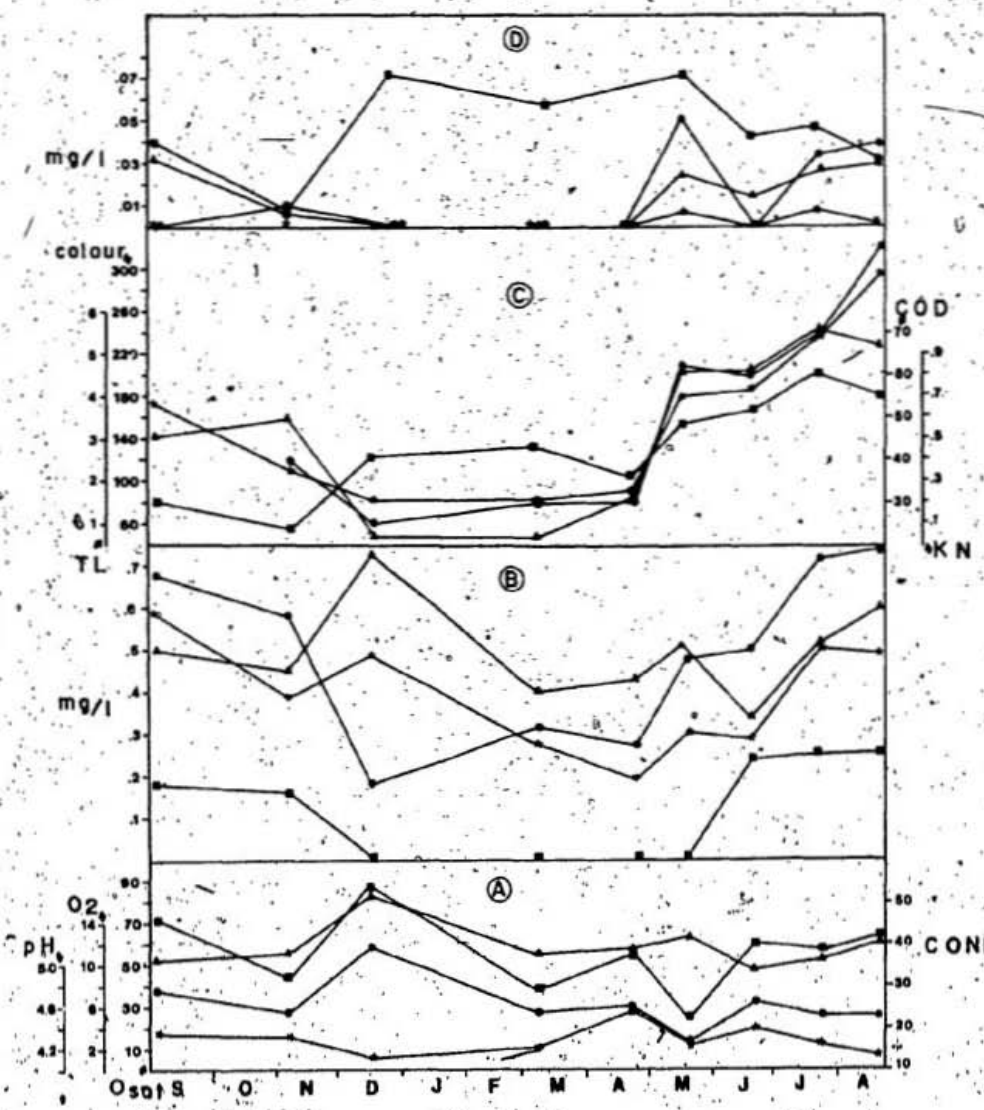

D
mg/l
.07
.05
.03
.01
colour
C
COD
KN
TL
B
mg/l
A
O2
pH
COND.
O S J S O N D J F M A M J J A

Figure VI-7: Temporal variations in water quality in pool TF2.

legend:

level D
- ■ = total P mg/l PO_4
- ● = NH_4^+ mg/l N
- ★ = NO_3^- mg/l N
- ▲ = PO_4^{3-} mg/l

level C
- ■ = Kjeldahl N (KN) mg/l N
- ● = colour units
- ★ = tannins + lignins mg/l
- ▲ = COD mg/l

level B
- ■ = silicate mg/l Si
- ● = Fe mg/l
- ★ = Ca mg/l
- ▲ = Mg mg/l

level A
- ■ = oxygen percentage saturation
- ● = oxygen concentration mg/l O_2
- ★ = pH units
- ▲ = conductivity $uScm^{-1}$

note: a break in the plot indicates a missing sample

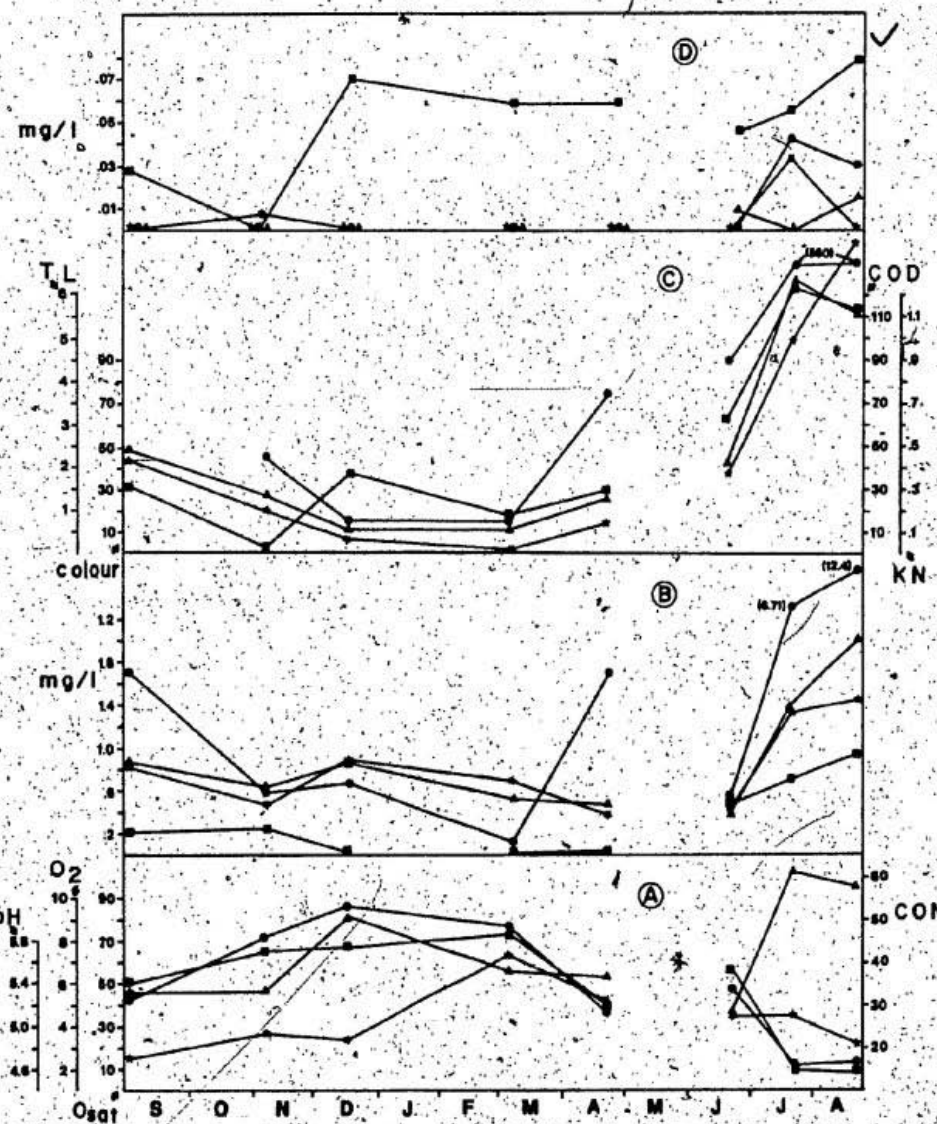
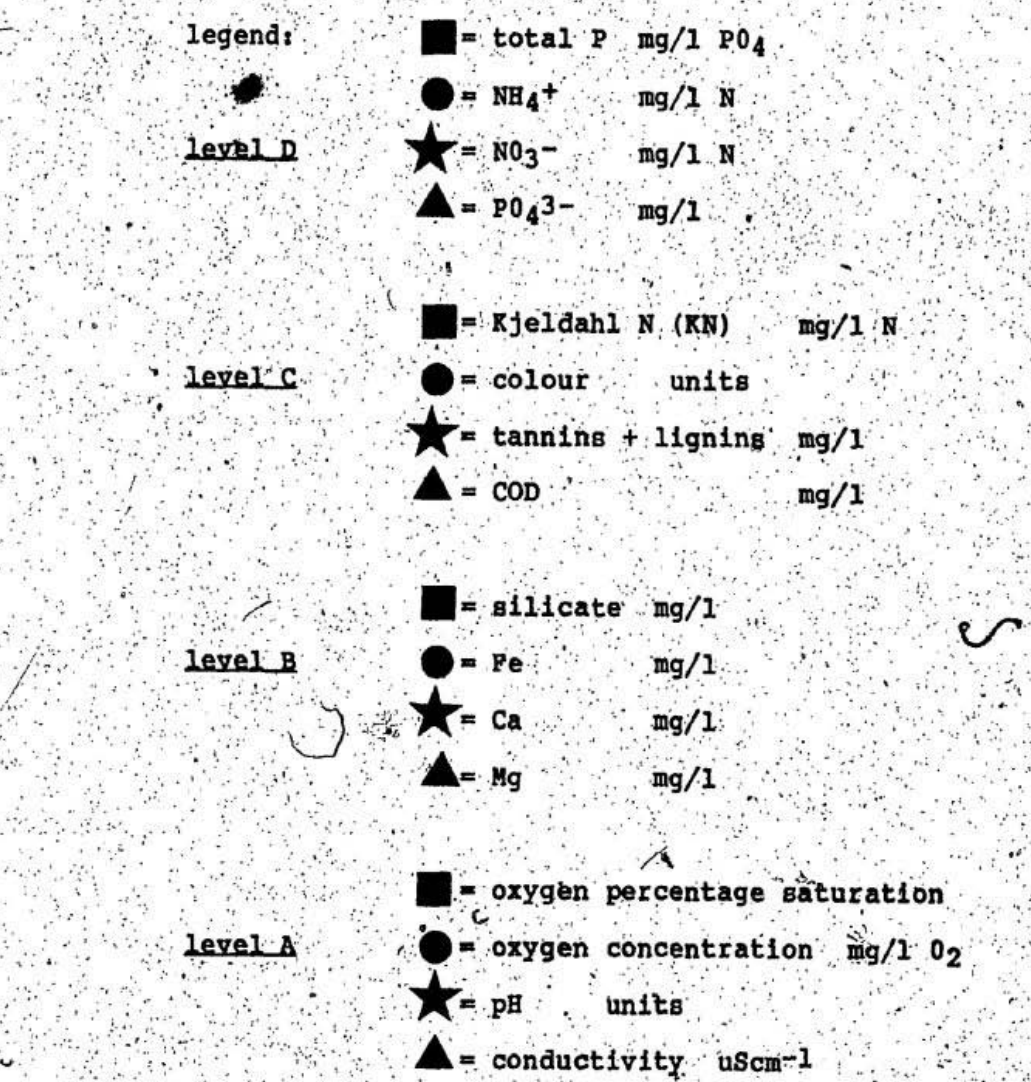

D
mg/l
.07
.05
.03
.01
C
T.L
colour
COD
KN
B
mg/l
A
O2
pH
Osat
COND.
S O N D J F M A M J J A

Figure VI-8: Temporal variation in water quality in pools TF3 and TF4.



note: values are averages.

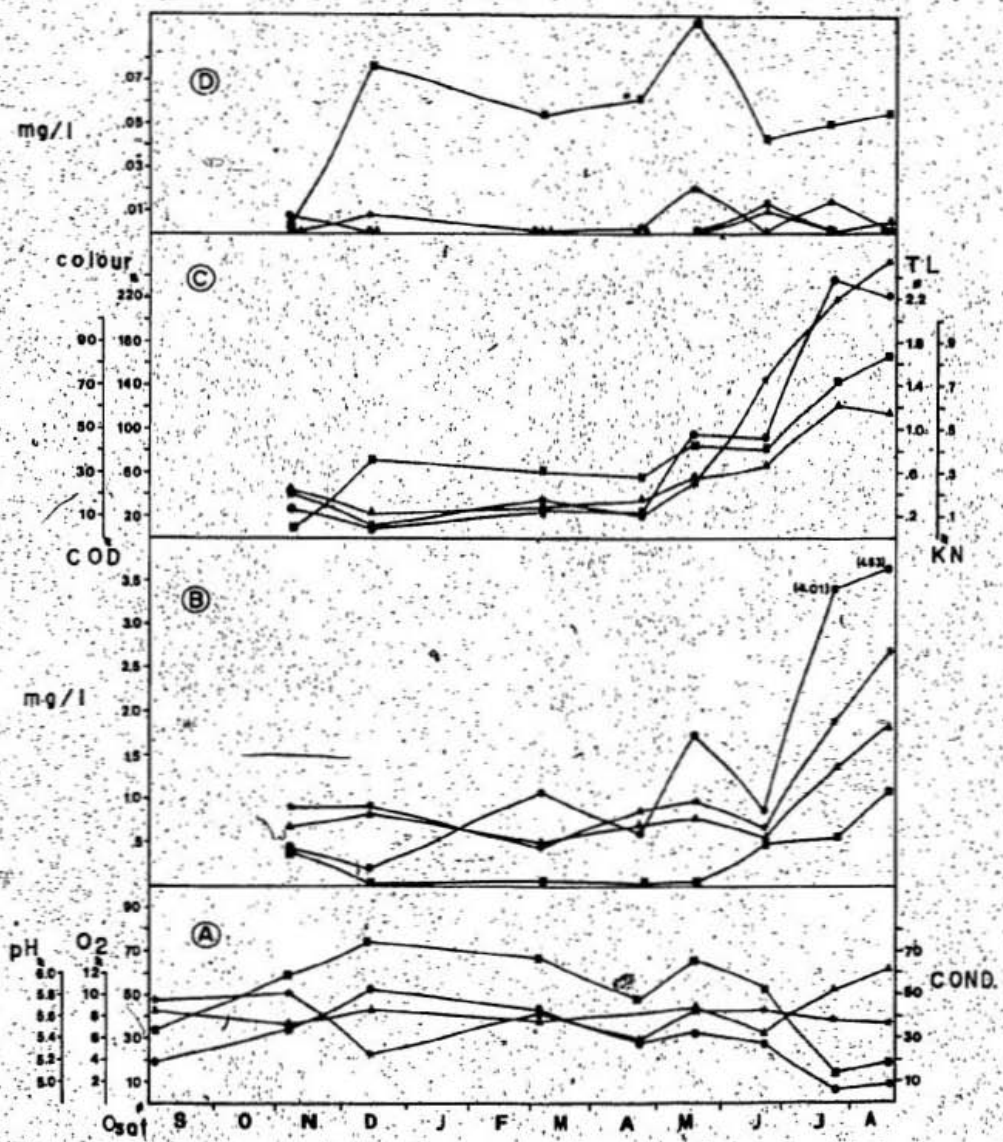
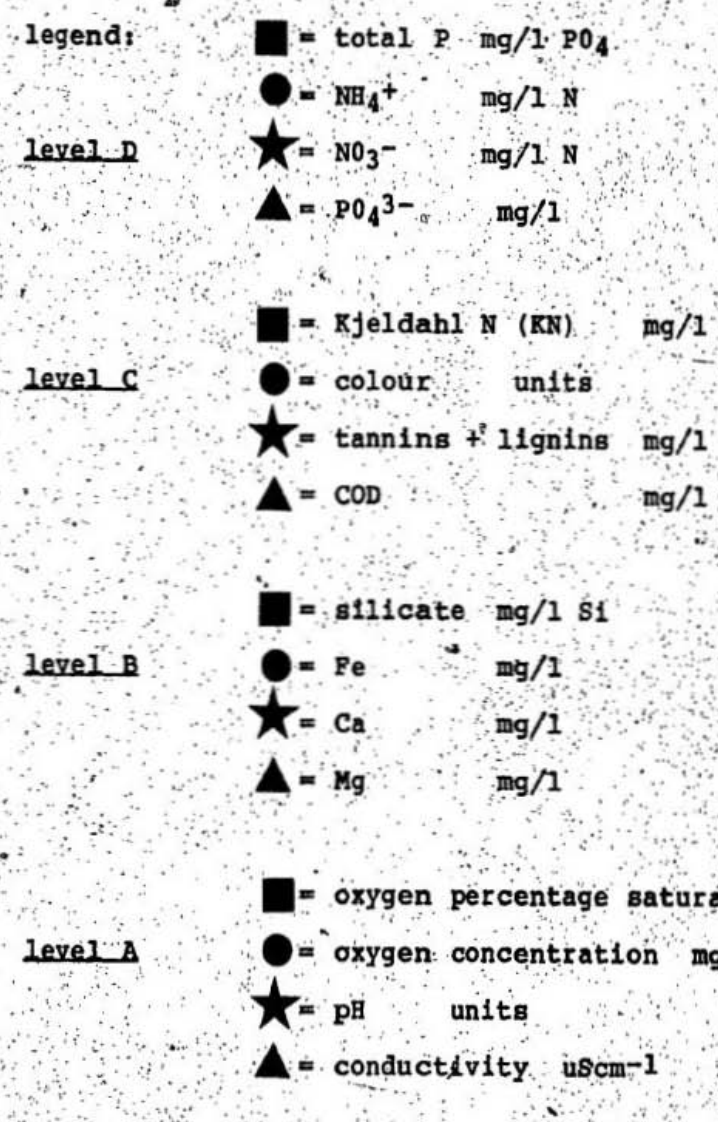

D
mg/l
.07
.05
.03
.01
colour
Pt
220
180
140
100
60
20
90
70
50
30
10
C
TL
2.2
1.8
1.4
1.0
.6
.2
.9
.7
.5
.3
.1
COD
KN
B
(4.01)
(4.83)
3.5
3.0
2.5
2.0
1.5
1.0
.5
mg/l
A
pH
6.0
5.8
5.6
5.4
5.2
5.0
O2
12
10
8
6
4
2
90
70
50
30
10
COND.
70
50
30
10
Osat
S
O
N
D
J
F
M
A
M
J
J
A

Figure VI-9: Temporal variation in water quality in pools PF1 and PF2.



note: values are averages.

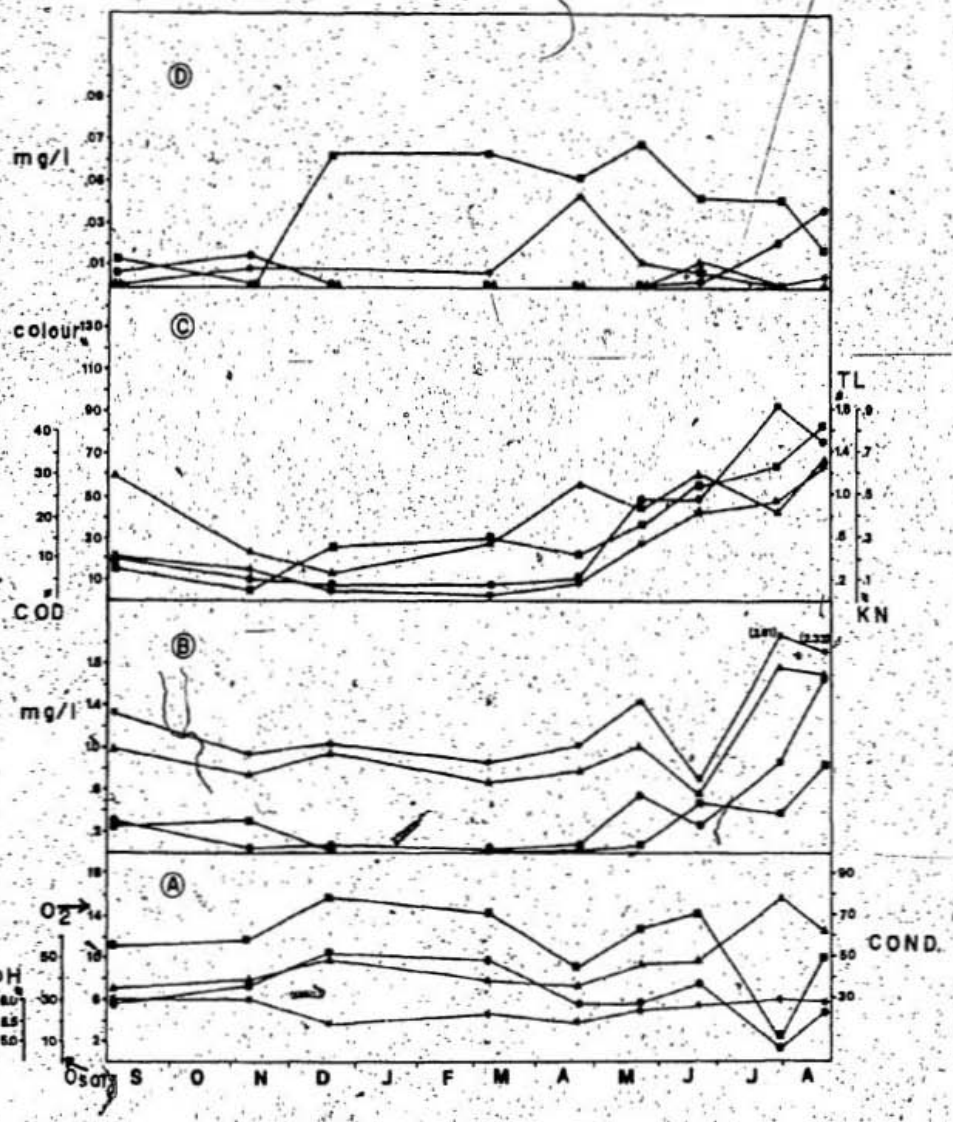
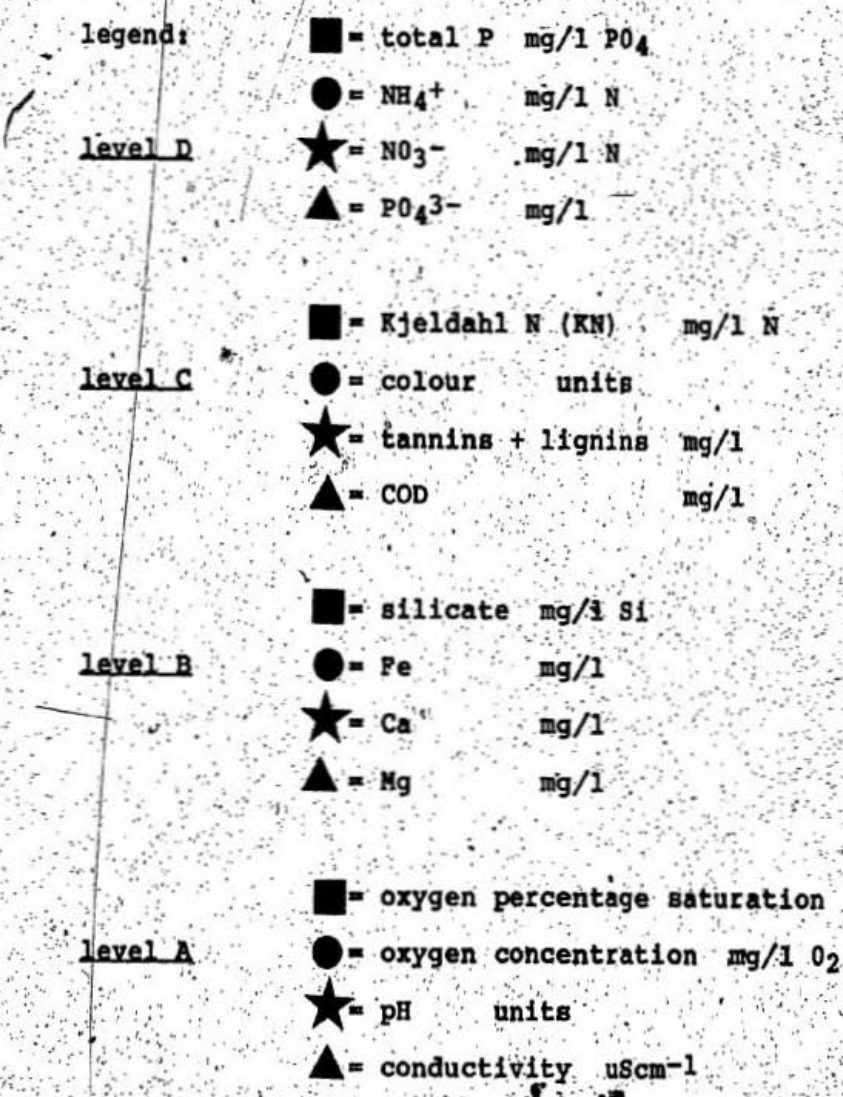
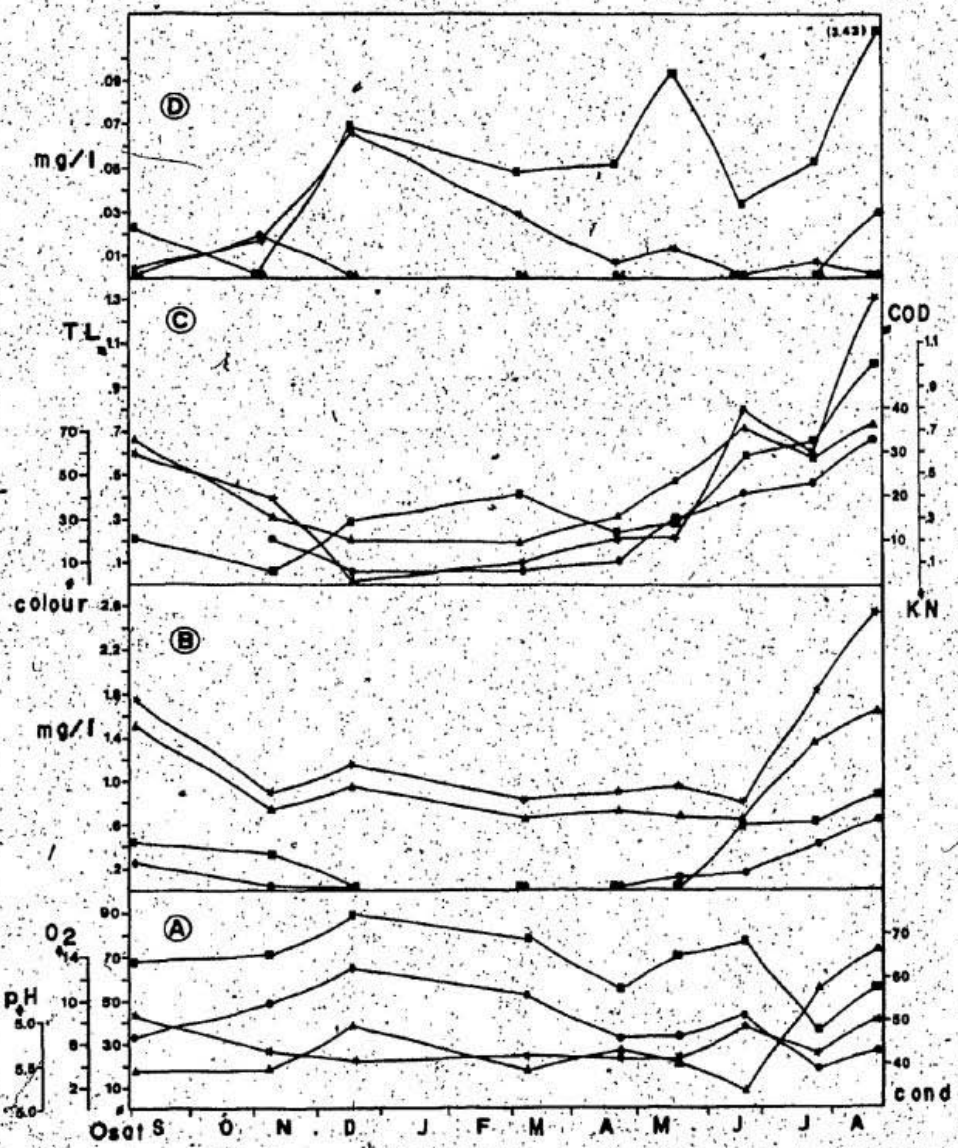

D
mg/l
.09
.07
.05
.03
.01
C
colour
130
110
90
70
50
30
10
COD
40
30
20
10
TL
1.8
1.4
1.0
.6
.2
.9
.7
.5
.3
.1
KN
B
mg/l
18
14
10
6
2
A
O2
pH
8.0
8.5
9.0
50
30
10
COND.
90
70
50
30
Oson
S
O
N
D
J
F
M
A
M
J
J
A

Figure VI-10: Temporal variation in water quality in pool PF3.




(3.43)
D
mg/l
C
TL
COD
KN
colour
B
mg/l
A
O2
pH
cond
Oset S O N D J F M A M J J A