PHYTOPLANKTON DYNAMICS IN LAKE MEMPHREMAGOG AND THEIR RELATIONSHIP TO TROPHIC STATE

by

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ABSTRACT

Netplankton species (>35µm) showed major seasonal shifts during the study period in Lake Memphremagog (Québec-Vermont), while nannoplankton species (<35µm, <10µm) were ubiquitous. Data from both Lake Memphremagog, which has a significant nutrient gradient, and from a literature survey of a number of lakes of different trophy showed that with increasing total biomass, there is a significant increase in nannoplankton biomass, but the relative proportion of nannoplankton (%) shows a significant decrease ($p<0.0001$). A similar highly significant relationship was found for nannoplankton (<35µm) and total chlorophyll, but not for production. Phytoplankton biomass in Lake Memphremagog (1976-1977) was dominated by Bacillariophyta, Cyanophyta and Cryptophyceae. Short-term fluctuations in the biomass and relative importance of each major taxonomic group were frequently not associated with changes in total phosphorus. This was also true at the species level, and within the range of nutrient levels observed in this lake (9-29µgl^{-1} total phosphorus), other factors appear to have a greater influence on the relative abundance of dominant algal groups and indicator species. Similarly, on a short-term basis, the dominant morphology of the netplankton fraction was not clearly related to total phosphorus. If the relative importance of individual species is measured using biomass rather than numerical abundance, within Lake Memphremagog, there was a significant decrease in the phytoplankton community diversity and evenness with increasing total biomass.

EXTRAIT

Les espèces de plancton de dimensions supérieures à 35µ m ont montré d'importants changements saisonniers durant 1976 et 1977 au Lac Memphrémagog (Québec-Vermont) tandis que les espèces appartenant à la fraction du nannoplancton (<35µm, < 10µm) ont été beaucoup plus omniprésentes. Des données recueillies sur ce lac, qui possède un gradient de matières nutritives d'importance, et suite à une revue de la littérature sur des lacs de différents niveaux trophiques, ont demontré qu'une augmentation significative de la biomasse du nannoplancton accompagne une augmentation de la biomasse totale quoique la proportion relative de nannoplancton (%) diminue de façon significative ($p<0.001$). De même, une relation très significative a été trouvée entre la fraction <35µm et la chlorophylle a totale du Lac Memphrémagog. Pourtant aucune relation significative ne se retrouve lorsqu'on utilise des évaluations de production primaire. Au cours des deux années 1976 et 1977, la biomasse du phytoplancton au Lac Memphrémagog était dominée par les Bacillariophytes, Cyanophytes et Cryptophycées. Les fluctuations à court terme de la biomasse et l'importance relative de chaque groupe taxonomique n'étaient généralement pas associées avec les changements du phosphore total. Cette observation s'applique aussi au niveaux de l'espèce, et à l'intérieur de la zone de niveaux de matière nutritive observés au lac Memphrémagog au cours de cette étude, des facteurs autre que le phosphore total semblent avoir une importance supérieure sur la distribution et l'abondance des principaux groupes taxonomiques et de l'espèce indicatrice d'un certain niveau trophique. De même, à court terme la morphologie dominante du plancton de dimension supérieure à 35µm n'était pas

clairement reliée à cette matière nutritive. Si l'importance des espèces individuelles est mesurée à partir de la biomasse au lieu de leur abondance numérique, les mesures de la structure de la communauté montre des rélations significatives avec le niveau trophique.

PREFACE

This thesis is presented in the form of two major sections, in accordance with thesis style regulations authorized by the Graduate Training Committee of the Department of Biology, McGill University. The first section investigates the relationship between phytoplankton size distributions and trophic level, and is written as a manuscript to be later submitted for publication. The second section, containing four chapters, further examines the relationship between phytoplankton community structure and lake trophy, and summarises the results and conclusions of Sections 1 and 2. Phytoplankton data from Lake Memphremagog and other lakes are presented in detail in a series of Appendices (A-D), together with an analysis of the error associated with different estimations of phytoplankton standing crop (Appendices E-G).

ACKNOWLEDGEMENTS

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FORWARD

Taxonomy has traditionally been used to investigate phytoplankton communities and, unlike measurements of standing crop or production, provides some insight into the nature of spatial and temporal shifts in algal assemblages. Although emphasis has often been placed on larger, more easily identified species (see Section 1), seasonal pulses of these forms represent only part of a more complex pattern of species succession involving both large and numerically more abundant forms (Hutchinson, 1967). However, a competent taxonomist can produce an overwhelming amount of detailed information about phytoplankton communities which can, and in fact often does, obscure the more general species patterns within and between lakes. Moreover, unless sampling, enumeration and data analysis are designed around a specific question, the application of sophisticated statistical analyses to such data sets is of limited value (e.g. Devaux, 1977). Nevertheless, Stoermer (1978) argues that detailed assessments of phytoplankton species assemblages provide the most appropriate measurements of water quality, since environmental conditions should be most immediately reflected in the predominant algal species. Similarly, other authors have attempted to relate algal groups, species or species quotients to trophic level (see Hutchinson, 1967).

A second, non taxonomic approach is to group species of a phytoplankton community into groups according to morphological characteristics. The most common criteria used has been cell size (Section 1). However, other aspects of cell morphology also appear to play a role in species succession, and can similarly be used as criteria

for division of species into groups; for example: motility, surface-to-volume ratio, and the morphology of colonies (Section 2).

Lastly, detailed information on phytoplankton species assemblages permit the computation of measurements of community structure such as species richness, diversity and equitibility (e.g. Margalef,1965; Tarapchak and Stoermer, 1976; Eloranta, 1976; Devaux, 1977) (Section 2).

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Section 1

Patterns of phytoplankton size fractions in relationship to trophic level and other factors.

Patterns of phytoplankton size fractions in relationship to trophic level and other factors*

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ABSTRACT

Netplankton species (>35 μm) showed major seasonal shifts during 1976 and 1977 in Lake Memphremagog (Québec-Vermont), while species belonging to the nannoplankton fractions (<35 μm, <10 μm) were much more ubiquitous. Data from both Lake Memphremagog, which has a significant nutrient gradient, and from a literature survey of lakes of differing trophy, showed that with increasing total biomass, there is a significant increase in nannoplankton biomass ($p < .0001$), but the relative proportion of nannoplankton (%) shows a significant decrease ($p < .0001$). A similar highly significant relationship was found between the <35 μm chlorophyll fraction and total chlorophyll within Lake Memphremagog, but no similar significant relationships were found between nannoplankton and total primary production. Although relative proportions (%) of nannoplankton biomass and chlorophyll showed some significant correlations with total phosphorus, light and temperature, the amount of unexplained variance in % nannoplankton was very large, suggesting that nutrients play a largely indirect role in size-selection. Fluctuations in the contribution of the nannoplankton are therefore more likely to be attributable to differential grazing losses.

EXTRAIT

Les espèces de plancton de dimensions supérieures à 35 µm montré d'importants changements saisonniers durant 1976 et 1977 au lac Memphrémagog (Qué-Vt) tandis que les espèces appartenant à la fraction due nannoplancton (< 35 µm, < 10 µm) ont été beaucoup plus omniprésentes. Des données recueillies et au lac Memphrémagog, qui possède un gradient de matières nutritives d'importance et suite à une revue de la littérature sur les lacs de différents niveaux trophiques, ont demontré qu'une augmentation significative de la biomasse du nannoplancton ($p < .0001$) accompagne une augmentation de la biomasse totale quoique la proportion relative du nannoplancton (%) diminue de façon significative ($p < .0001$). Une autre relation très significative a été trouvée entre la fraction < 35 µm et la chlorophylle a totale du lac Memphrémagog. Pourtant aucune relation significative ne se retrouve lorsqu'on utilise des évaluations de production primaire. Bien que quelques corrélations entre la proportion relative (%) de la chlorophylle a et de la biomasse du nannoplancton et le phosphore, la lumière et la température soient significatives, la quantité de variance inexplicable dans le % du nannoplancton est très grande, ce qui suggère un rôle très indirect joué par les matières nutritives dans la sélection de la taille. Les fluctuations dans la contribution du nannoplancton sont donc plus probablement attribuables, à des pertes différentielles causées par la nutrition des herbivores.

INTRODUCTION

One of the simplest criteria for grouping the component species of a phytoplankton community is cell size, an approach which is receiving more attention by fieldworkers (e.g. Lund, 1961; Pavoni, 1963; Gliwicz, 1967; Kristiansen, 1971; Gelin, 1971, 1975; Malone, 1971a,b; Semina, 1972; Kalff, 1972; Gelin and Ripl, 1978). In this study we looked for patterns in the spatial and temporal distributions of phytoplankton size fractions in relation to different physical and chemical characteristics both within Lake Memphremagog, and on a wider scale, using literature data. Our hypothesis was that the proportion of nannoplankton, as measured by biomass, chlorophyll a, and primary production should decrease with increasing trophy.

Phytoplankton have traditionally been divided into two main size-categories: net- and nannoplankton, based on their retention by plankton nets of a range of mesh sizes, rather than on any functional relationship to the community itself. From a taxonomic point of view, a great deal of emphasis has been placed on the netplankton fraction, since nannoplankton species are notoriously difficult to identify and enumerate well. However, more widespread use of better preservatives (e.g. Lugol's Iodine) and counting techniques (notably the Utermöhl technique) have greatly facilitated the enumeration of small forms, and it is becoming increasingly evident that they frequently make important contributions to both total community biomass and production (e.g. Kalff, 1972).

Cell size has been shown to be related to many of the factors associated with phytoplankton succession, and these relationships have been used by several authors to predict the outcome of size selection for a given set of environmental conditions (e.g. Parsons & Takahashi, 1973;

Shuter, 1979; Laws, 1975). However, these models have not been rigourously tested in the field, probably partly because of disagreement among authors on the appropriate size of natural phytoplankton communities, and on the relative importance of each factor in size-selection.

There are a number of problems associated with the division of natural phytoplankton community into size fractions. Size selection by screens is not precise (Sheldon and Sutcliffe, 1969); filamentous and elongate forms also pass through screens with a disporportionate frequency as the mesh size is increased (Watson, unpublished). With direct microscope counts, error can be significant, particularly for the nannoplankton fractions (Appendix E; Watson, 1979). Furthermore, the criterion for division into size classes varies among authors: the nannoplankton fraction is nominally delineated by a chosen maximum cell dimension (e.g. Granberg, 1970; Kristiansen, 1971; Gelin, 1975; Gelin & Ripl, 1978), but some authors, e.g. Pavoni (1963), include elongate and filamentous forms. If nannoplankton are defined as that fraction which is potentially ingestible by grazers (Gelin, 1975), the upper size limit will to some extent depend on the predominant species of both the nannoplankton (Schindler, 1971) and grazer populations (Burns, 1968). Zooplankton ingestion rates vary within the nanno fraction, and appear to be highest for extremely small sized particles (1-2μm) (Nadin-Hurley and Duncan, 1976; Gliwicz, 1977), with a maximum ingested particle diameter generally below 35-40μm (Burns, 1968), and most workers have used sizes below this limit to separate the nannoplankton fraction. We used mesh sizes of 10 μm and 35 μm to fractionate nannoplankton chlorophyll and primary production, and maximum cell dimensions of 10 and 35μm for estimating nannoplankton biomass in Lake Memphremagog.

Factors which appear to have a major influence on cell size distributions include nutrients, light, temperature, grazing and sinking. The role of nutrients in size selection remains unclear. While the literature so far suggests that there is a general decrease in the relative proportion of small cells with increasing trophy (e.g. Pavoni, 1963; Semina, 1972; Spodniewska, 1978, Gelin and Ripl, 1978), a direct relationship between nutrient concentration and cell size has not been demonstrated. There is evidence that nutrient uptake rates are size-dependent (e.g. Eppley et al., 1969), but intraspecific variation in kinetic constants indicate that uptake rates may be more closely linked to the local nutrient supply (Hecky and Kilham, 1974). In fact these latter authors suggest that any apparent relationship with cell size is generated by adaption to the increased nutrient diffusion associated with high sinking rates, and thus that nutrient uptake rates in motile or buoyant forms should be independent of cell size. Shuter (1979), however, argues that under most natural circumstances, cell movement relative to the medium should be insufficient to overcome nutrient diffusion limitation. In addition, ambient nutrient concentrations may not have an immediate influence on size distribution, since relative growth rate is more closely related to intracellular nutrient concentration than uptake (Fogg, 1975). On the other hand, nutrients may play a more indirect role by interacting with other size-selection factors. For example, under eutrophic conditions, a high algal biomass will greatly reduce light penetration (e.g. Carlson, 1977), and may cause a shift in grazing pressure towards smaller size fractions (Welch et al., 1975; Webster and Peters, 1978).

Light and temperature should be expected to influence the selection of optimal cell size, since both production and respiration rates per

unit biomass have been shown to decrease with increasing cell size (Banse, 1976; Laws, 1975). In addition, the interaction between these two factors may also be important. Small cells appear to be particularly sensitive to temperature-dependent respiration rates under low light levels (Shuter, 1979), such as are often found under eutrophic conditions, while recent evidence suggests that nannoplankton suffer significantly higher nocturnal respiration losses than netplankton (Paerl and MacKenzie, 1977).

Size-selection grazing has been demonstrated for a number of zooplankton species (Burns, 1968; Schindler, 1971; Gliwicz, 1977 and others), and has been considered to be largely responsible for the accumulation of the high standing crops of netplankton associated with eutrophic conditions (Welch et al., 1975; Porter, 1977; Kalff and Knoechel, 1978; Dillon et al., 1978). However, it is likely that the role of size-selection grazing is quite complex, since nutrient regeneration by zooplankton can make a significant contribution to the available nutrient pool (Peters, 1975; Welch et al., 1975).

Sinking losses have been considered by some as an important factor influencing cell size distributions (e.g. Parsons and Takahashi, 1973), since sinking rates increase with cell size (e.g. Hutchinson, 1967; Smayda, 1970). However, because many forms are motile or buoyancy regulating, sinking cannot be considered as strictly size-selective, although it may well play an important role in the succession between different taxa (e.g. Knoechel and Kalff, 1975).

In this paper, we examine the relationship between cell size and trophy on two levels:

1. Within one lake, using data collected from Lake Memphremagog during 1976-1977 (individual observations).

2. Between lakes, using literature data from a wide range of lakes (generally, seasonal average values).

As a measure of trophic level, we used total biomass, chlorophyll a (chla) and production, since these have all been shown to increase with nutrient loading (Kalff and Knoechel, 1978; Sakamoto, 1966; Vollenweider, 1968), and because data on the latter were largely unavailable for the lakes studied. Using data from Lake Memphremagog, we also explored the relationship betwen phytoplankton size distributions and phosphorus (total phosphorus (TP) and alkaline phosphatase activity), light and temperature.

LAKE MEMPHREMAGOG (Qué.-Vt.)

Lake Memphremagog is a narrow glacial lake lying on the Québec (Canada)-Vermont (U.S.A.) border at lat. 45°06'N, long. 72°17'W.

It is approximately 40km long, and is divided morphometrically into three basins, on the basis of mean depth (Fig. 1, Table 1). The lake receives an estimated 63% of its hydrological input and 84% of its phosphorus loading from three rivers entering at the southern end of the lake at Newport, Vt. resulting in a strong North-South nutrient gradient (Carlson et al., 1979; see also Table 8), also reflected in productivity and chla (Ross and Kalff, 1975).

Fig. 1: Location of four sampling stations in Lake Memphremagog (Qué.-Vt.).

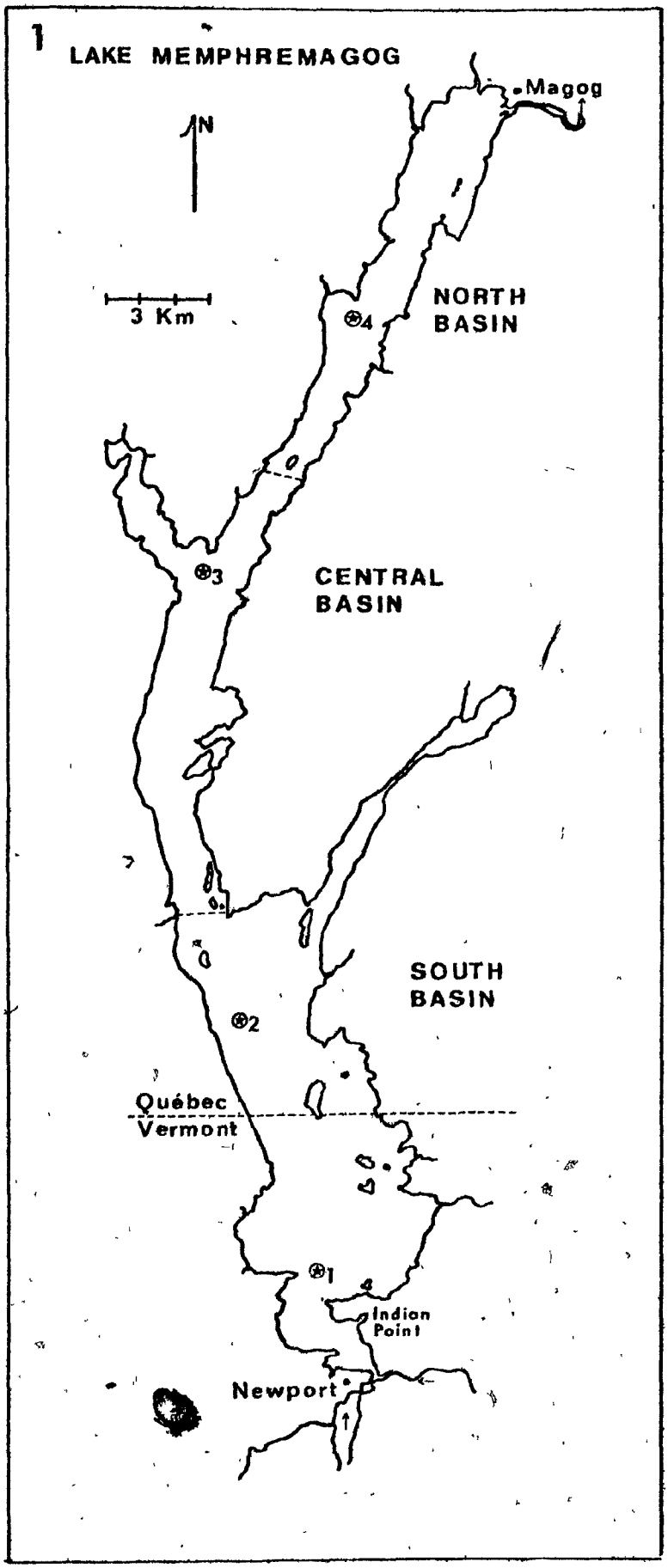

1
LAKE MEMPHREMAGOG
Magog
N
3 Km
NORTH BASIN
4
CENTRAL BASIN
3
SOUTH BASIN
2
Québec
Vermont
1
Indian Point
Newport

Table 1. General characteristics of Lake Memphremagog (Qué.-Vt.)

Basin	South	Central	North
Area (m^2)	4.4×10^7	2.2×10^7	1.9×10^7
Volume (m^3)	3.2×10^8	1.0×10^9	2.8×10^8
Mean depth (m)*	7.0	51.0	13.5
Depth of mixed layer (m)	7.0	10.5	9.5
Mean daily production* ($mg.C\ m^{-2}day^{-1}$)	1078	794	796
Maximum Chlorophyll-a* ($mg.Chla\ m^{-2}$)	28.5	11.2	9.3

* Ross and Kalff,1975

METHODS

Sampling was done at four stations in Lake Memphremagog, located along the phosphorus gradient such that station 1 (South Basin) was closest to the major nutrient input (Fig. 1). Weekly or biweekly samples were taken from May to October during 1976 and 1977. Average epilimnetic biomass was estimated from tube samples taken to the depth of the thermocline (measured on each occasion)[1] or to 15m when there was no stratification. In the shallow South Basin, samples were taken to 0.5m above the sediments. Subsamples were fixed with Lugol's Iodine, and later enumerated using the Utermöhl technique (Vollenweider,1969). Large species of low abundance were counted under low power across diagonal transects or over half the chamber area (minimum 26% total volume settled), while small or common species were counted under high power across one or two diagonal transects. Total, <35μm and <10μm biomass were calculated using mean cell volumes estimated for each species and assuming a density of 1.0. The distribution of organisms within the counting chamber was not always random, and transects were counted across any observed density gradients (e.g. Willén, 1976). Replicate counts showed a fairly low variance for total and nannoplankton biomass ($\pm$6%, $\pm$16%, $\pm$22% for total, <35μm and <10μm respectively). Chl*a*, primary production and TP were measured from samples taken at 0m, 1m, 2m, 3m, 5m, 7.5m and (where possible) 10m, using a Van Dorne water sampler. Chl*a* was determined fom 500ml subsamples filtered through Gelman GF-A/E filters, which were subsequently ground, extracted in 90% acetone, centrifuged, and the fluorescence read on a Turner model 110 fluorometer calibrated against a Spectronic 88 spectrophotometer at 665nm before and after addition of acid. Primary production was measured using the ^{14}C Method (Vollenweider,1969). Innoculated samples were incubated for

[1] marking the beginning of an increase in Δtemp to approximately $\geq 1^{\circ}C$ over 1m depth.

approximately 4 hours from mid-morning to early afternoon, and 50ml subsamples were filtered through Millipore 0.45 m filters and their activity measured using a Nuclear-Chicago gas-flow counter. Selective filtration through Nitex screens of mesh sizes 10μm, and 35μm were done for nannoplankton chl*a* and primary production using separate aliquots from the 2m samples. During 1976, 50ml subsamples were selectively filtered for both nannoplankton chl*a* and production while in 1977 the volume filtered for chl*a* was changed to 500ml and for production, to 25ml. Total phosphorus was measured using a persulfate digestion technique (Johnson, 1971), while alkaline phosphatase activity was determined fluorometrically using methyl-fluorescein phosphate as a substrate (Sproule and Kalff, 1979).

Insolation (I_o) was monitored with a YSI model 67 integrating pyranometer located at the McGill field-station near Georgeville, Qué. Underwater light extinction was measured using a Weston selenium photocell. The average light (or Effective light climate, E.L.C.) was calculated as in Riley (1957) from the equation:

$$E.L.C.(1y) = \frac{I_o'(1-e^{-EZ})}{EZ}$$

where: I_o' = photosynthetically available light immediately below the surface (=0.41(I_o); Ramberg, 1976)(1y.)

Z = depth of mixed layer (m).

E = extinction coefficient.

RESULTS

a) Spatial and seasonal patterns in phytoplankton biomass, chla and primary production in Lake Memphremagog.

Out of a total of 203 taxa (Table C-1, appendix C), only 22 accounted for 20% or more of the total biomass on at least one occasion (Table 2), although 86 taxa occurred in at least 50% of the samples examined for each station and year. Fluctuations in total biomass were mainly attributable to the netplankton fraction (>35µm) (Figs. 2A, B), and were generally more subdued at stations with lower concentrations of TP (3 and 4). The standing crop was also lower at these stations, particularly in 1976, when there was a significant N-S gradient in both total and nannoplankton biomass (Table 4).

Of all size fractions, the species composition of the netplankton was the most variable, both between stations, and particularly between years. During 1976, this fraction was dominated in spring by a high biomass of Diatoma tenue var. elongatum at all stations. This species was rapidly succeeded by a bloom of Oscillatoria Redekei, which maintained a fairly high standing crop throughout the summer, accompanied mainly by Ceratium hirundinella, Melosira italica subsp. subarctica and Oscillatoria cfa rubescens in the more eutrophic South Basin; by C. hirundinella and Fragilaria crotonensis in Central Basin; and by F. crotonensis, Rhizosolenia eriensis and Botryococcus Braunii in the North Basin. A late fall increase in M. italica subsp. subarctica observed in the South Basin occurred much later in the more oligotrophic Central Basin, and was more subdued (no late fall samples were taken at station 4 in North Basin).

Table 2. Taxa contributing ≥ 20% of total biomass in one or more samples. Values give % of total number of samples enumerated for a given station and year where the species accounted for ≥ 20% of the total biomass. Maximum % contribution to total biomass in parentheses.

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CYANOPHYTA - Chroococcales								
Coelosphaerium Naeglianum Ung.					5(21)		14(35)	8(29)
Misc. unicells <5 µm		6(24)						
- Hormogonales								
Anabaena flos-aquae (Lyng) Breb						5(23)	4(34)	
Oscillatoria Redekei Van Goor	29(65)	35(68)	28(72)	20(26)				
CHLOROPHYTA - Tetrasporales								
Gleococcus Shroeteri					5(25)		4(34)	8(34)
BACILLARIOPHYTA - Centrales								
Cyclotella bodanica Eulenst							4(22)	15(32)
Melosira italica subsp. *subarctica* O. Müll.	6(29)	12(20)			16(43)	5(24)	7(29)	
Rhizosolenia eriensis H.L.Smith								8(33)
Stephanodiscus astraea (Ehr.)Grun.	6(24)	6(21)			5(21)	9(22)		
Stephanodiscus hantzschii Grun.					5(31)	9(58)	25(51)	
- Pennales								
Asterionella formosa Hass.			6(24)					
Diatoma tenue var. *elongatum* Lyngb.	35(69)	25(70)	22(64)	20(42)		18(36)		

	1976				1977			
STATION	1	2	3	4	1	2	3	4
Fragilaria crotonensis Kitton				10(22)	71(27)	5(37)	14(37)	8(48)
Fragilaria cf. *vaucheriae* (Kutz)Peters							4(25)	
Synedra ulna var. *danica* (Kutz) Grun.								15(38)
CHRYSOPHYTA – Chromulinales								
Mallomonas elongata Reverdin					5(22)			
– Ochromonadales								
Uroglena cf. *volvox* Ehrnb.					5(23)			
– Prymesiales								
Chrysochromulina parva Lackey								8(20)
– Xanthophyceae								
Botryococcus braunii Kutz.								1(20)
PYRROPHYTA – Cryptophyceae								
Chryptomonas reflexa Skuja	6(23)	15(33)						
Rhodomonas minuta Skuja					5(26)		4(27)	
– Dinophyceae								
Ceratium hirundinella (O.F. Müll.) Schrank			12(35)					

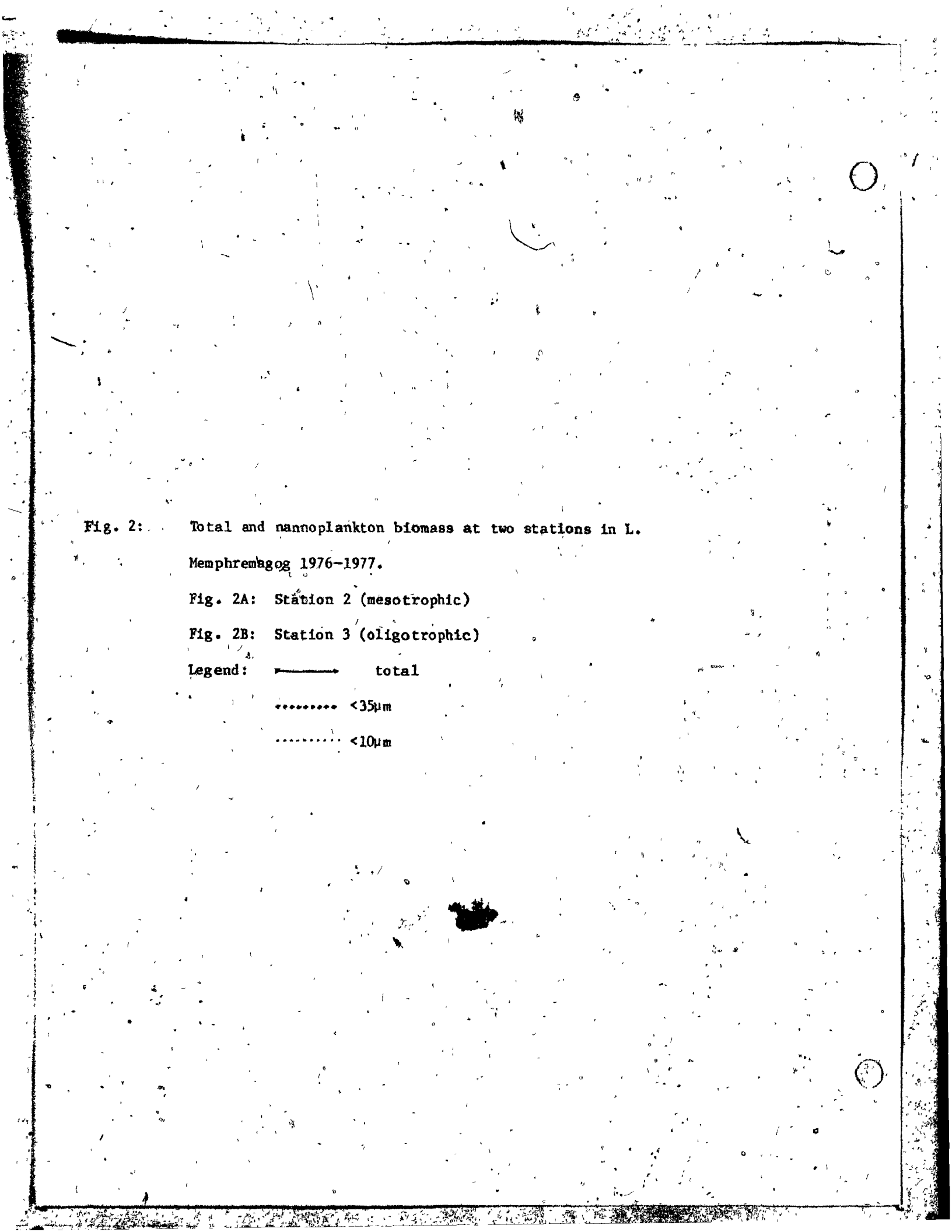


Fig. 2: Total and nannoplankton biomass at two stations in L. Memphremagog 1976–1977.

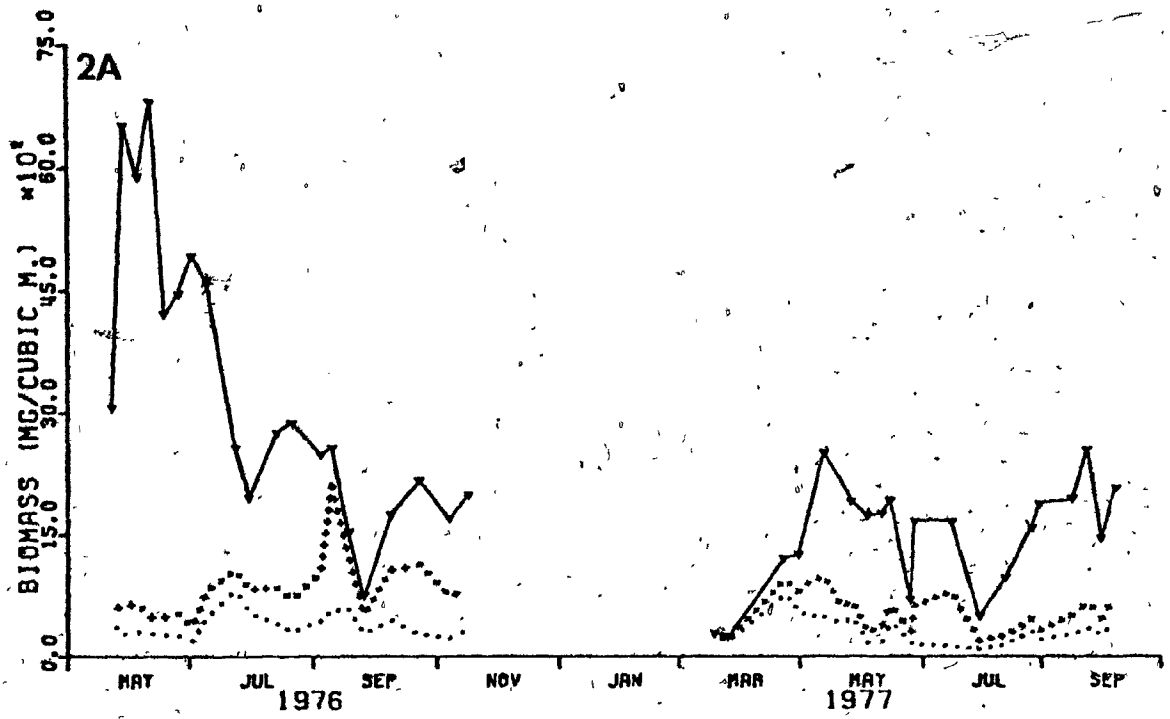
Fig. 2A: Station 2 (mesotrophic)

Fig. 2B: Station 3 (oligotrophic)

Legend: ——— total

••••••••• <35µm

····· <10µm


2A
BIOMASS (MG/CUBIC M.) ×10³
75.0
60.0
45.0
30.0
15.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

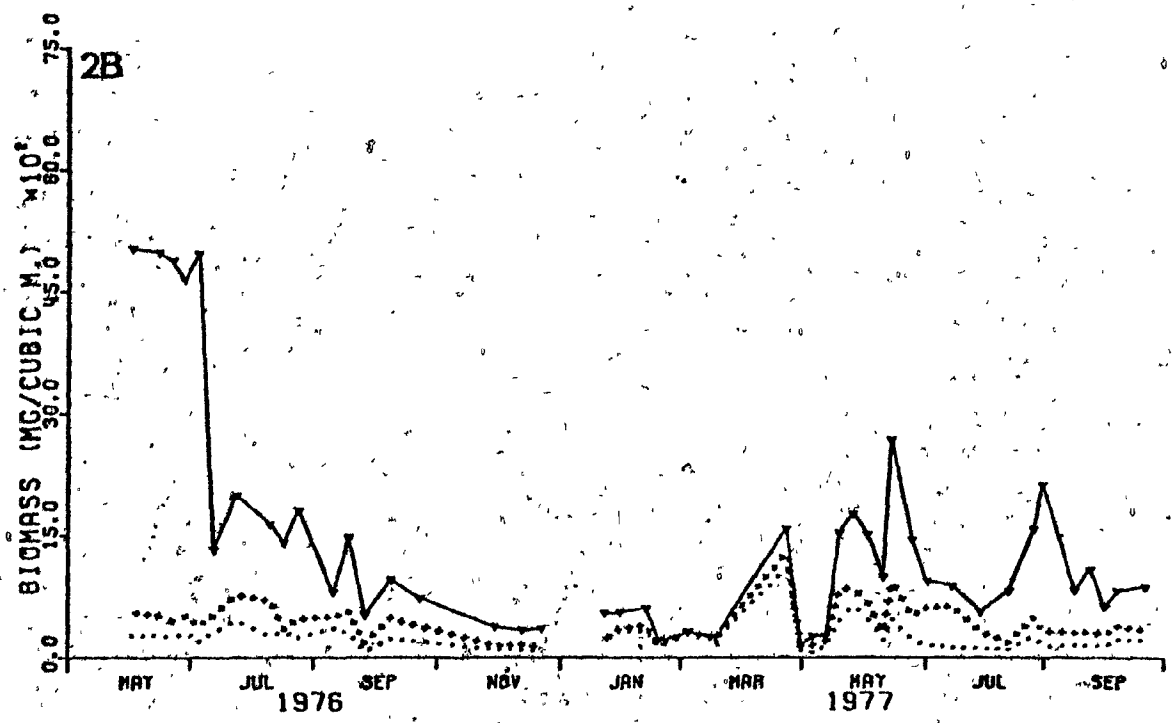

2B
BIOMASS (MG/CUBIC M.) ×10³
75.0
60.0
45.0
30.0
15.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Table 3. Taxa contributing ≥ 20% of nannoplankton biomass (<35µm and <10µm) in one or more samples. Values give % total number of samples enumerated for a given station and year where the species accounted for ≥ 20% nannoplankton biomass. Maximum % contribution to nannoplankton biomass in parentheses.

		1976				1977			
Biomass <35 µm	STATION	1	2	3	4	1	2	3	4
CYANOPHYTA									
Misc. unicells < 5 µm		6(23)		5(25)	10(22)			4(26)	
BACILLARIOPHYTA									
Cyclotella bodanica Eulenst				6(39)	10(30)	8(40)	27(31)	25(53)	46(74)
Stephanodiscus hantzschii Grun.						5(42)	9(66)	21(69)	
CHRYSOPHYTA									
Chrysochromulina parva Lackey				6(24)	20(28)	11(26)	18(51)	21(41)	23(47)
Misc. flagellates < 5 µm						11(27)			
Misc. non-flagellates < 5 µm				12(29)	10(25)	5(28)			
PYRROPHYTA									
Chryptomonas Marssonii Skuja		6(21)				5(25)	14(28)	4(20)	
Chryptomonas reflexa Skuja		41(42)	45(49)	28(27)	30(30)	5(22)	5(23)	4(45)	
Rhodomonas minuta Skuja		35(37)	40(41)	50(34)	50(27)	42(50)	59(52)	43(45)	31(31)

Biomass <10 µm	STATION	1976 1	1976 2	1976 3	1976 4	1977 1	1977 2	1977 3	1977 4
CYANOPHYTA									
Misc. unicells < 5 µm		6(30)	15(55)	22(39)	20(38)	16(26)	9(28)	4(42)	38(48)
CHLOROPHYTA									
Chlamydomonas sp.								4(30)	
Monoraphidium minutum (Nag.)		6(20)	6(27)						
BACILLARIOPHYTA									
Stephanodiscus hantzschii Grun.				6(21)		11(52)	14(83)	18(79)	
CHRYSOPHYTA									
Chromulina spp.			6(59)						
Chrysochromulina parva Lackey		12(23)	25(28)	28(27)	30(34)	32(43)	45(68)	64(53)	69(65)
Misc. flagellates < 5 µm						11(31)			
Misc. non-flagellates < 5 µm		6(23)	6(23)	12(54)	10(41)	5(32)			
PYRROPHYTA									
Rhodomonas minuta Skuja		82(65)	90(63)	89(69)	90(56)	79(74)	82(83)	75(69)	92(56)

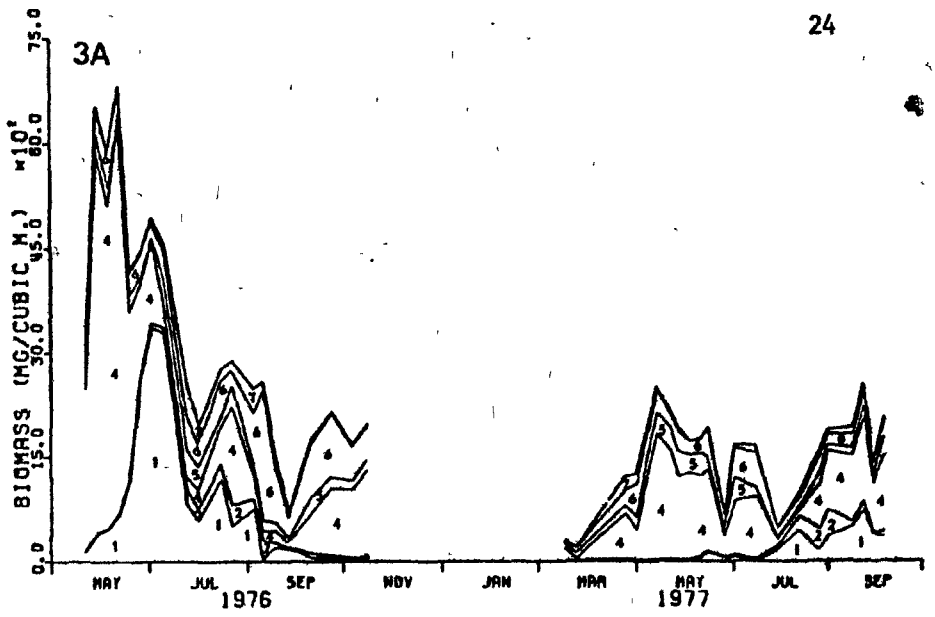
Table 4. Mean seasonal total and nannoplankton biomass (mg m^{-3}) and relative contribution (%) of nannoplankton fractions at the four stations in L. Memphremagog, May-Oct. 1976 and 1977 (tube samples).

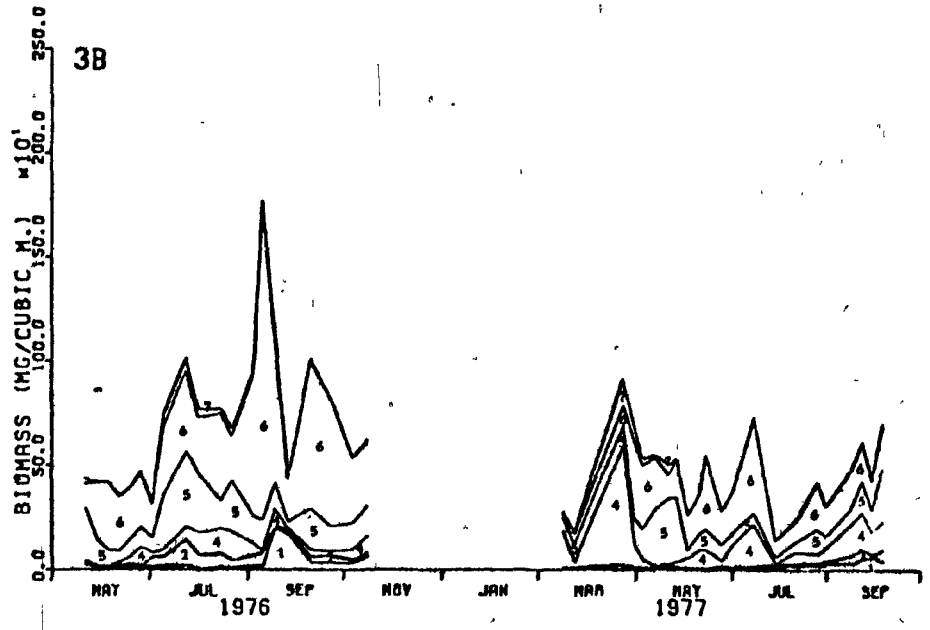
Station	Total biomass 1976	Total biomass 1977	Biomass <35 μ 1976 (%)	Biomass <35 μ 1977 (%)	Biomass <10 μ 1976 (%)	Biomass <10 μ 1977 (%)
1	2883.6	1610.9	820.5 (32)	493.3 (36)	344.5 (14)	249.8 (19)
2	3284.4	1664.6	829.1 (35)	574.9 (36)	378.6 (16)	317.5 (20)
3	2120.5	1112.5	425.4 (32)	470.8 (47)	232.4 (18)	259.0 (25)
4	1465.5	1105.6	426.6 (32)	506.0 (49)	238.1 (19)	235.1 (23)

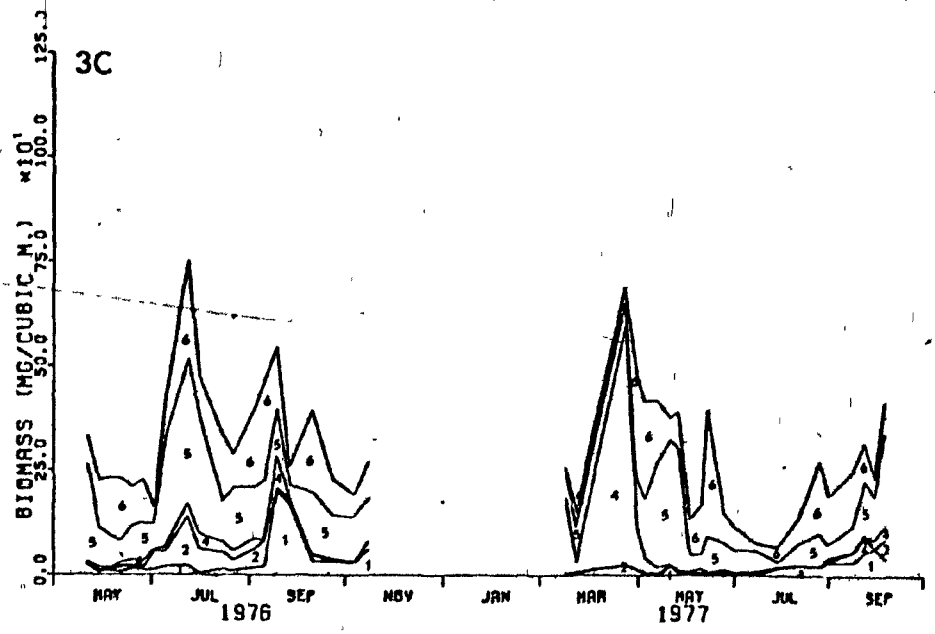
Significant differences ($p < 0.05$) between paired (individual) observations at different stations as determined using Wilcoxon matched-pairs signed ranks tests are indicated by arrows directed along the increasing gradient. It should be noted that these arrows do not indicate significant differences between the seasonal mean values shown in the table.

Figs. 3A-3C: Contribution of major taxonomic groups to total biomass (Fig. 3A), Biomass <35µm (Fig. 3B), Biomass <10µm (Fig. 3C) at station 2 (mesotrophic)

Legend: 1 - Cyanophyta; 2 - Chlorophyta; 3 - Euglenophyta; 4 - Bacillariophyta; 5 - Chrysophyta; 6 - Cryptopyceae (Pyrrophyta); 7 - Dinophyceae (Pyrrophyta).


3A
BIOMASS (MG/CUBIC M.) *10¹
0.0
15.0
30.0
45.0
60.0
75.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


3B
BIOMASS (MG/CUBIC M.) *10¹
0.0
50.0
100.0
150.0
200.0
250.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


3C
BIOMASS (MG/CUBIC M.) *10¹
0.0
25.0
50.0
75.0
100.0
125.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

The spring diatom pulse was much briefer the second year, and dominated less by D. tenue var elongatum, particularly towards the Northern end of the lake, where this species was increasingly replaced by the large diatom Synedra ulna var. danica. Oscillatoria Redekei did not appear after the spring diatom population, but was replaced by a brief pulse of Anabaena flos-aquae. The midsummer netplankton assemblage consisted of a larger number of co-dominant species than was seen in 1976, particularly in South Basin, where the major species were F. crotonensis, Stephanodiscus astraea, R. eriensis, Gleococcus Schroeteri and Coelosphaerium spp. Similar species were found at the less eutrophic stations 3 and 4, although S. astraea did not make a significant contribution to the total biomass at these stations. The fall pulse of M. italica subsp. subarctica was again smaller and observed later in Central Basin.

While the total phytoplankton community biomass was dominated by Cyanophyta and Bacillariophyta (Fig. 3A), the major groups contributing to the nannoplankton biomass were Chrysophyta and Pyrrophyta (Cryptophyceae), with the latter group being particularly important in the <35μm fraction (Figs. 3B,3C) (Appendix B). An average of 73% and 74% of the biomass of the <10μm and <35μm nannoplankton fractions (respectively) consisted of flagellate forms.

A total of 46 taxa were included in the <35μm fraction, and 38 in the <10μm fraction. Out of these, only 9 taxa contributed 20% or more of the <35 and <10μm nannoplankton biomass at least once (Tables 3 and 4). The dominant nannoplankton species remained quite constant, both between stations and years. The most important species in the <10μm fraction at all stations were Rhodomonas minuta and Chrysochromulina parva. An early

spring peak of Stephanodiscus hantzschii, particularly pronounced in the South Basin, contributed significantly to the <10μm biomass in 1977.

In addition to these nannoplankton species, important contributions to the <35μm biomass were made by Cryptomonas reflexa, C. Marsonii, C. erosa and Cyclotella bodanica.

Colourless species were not included in algal biomass estimates. However, the biomass of heterotrophic forms was comparatively low, generally ranging below 50 μgl^{-1} (compare to chlorophyllous biomass estimates, Table 4), and consisted mainly of nannoplankton forms, such as Katablepharis oxalis, Cryptaulax sp., Cyathomonas truncata and Desmatella spp.. Katablepharis ovalis was particularly ubiquitous, and on several occasions accounted for 10% or more of the total phytoplankton (chlorophyllous and non-chlorophyllous) biomass. Larger colourless species, such as Gymnodinium helveticum appeared infrequently and on these occasions, heterotrophs contributed up to 21% of the total phytoplankton biomass; however, this average contribution was very low (3% total chlorophyllous and non-chlorophyllous biomass).

Seasonal patterns in size fractions of biomass, chla and primary production showed little similarity. Correlation coefficients between these measurements were low, ranging from 0.16 to 0.6, although generally statistically significant (Table 5). While all fractions of chla exhibited highly significant decreases ($p = .01$) towards the Northern end of the Lake both in 1976 and 1977, production showed a similar significant gradient only for the total, and to a limited extent, for the <35μm fractions (Tables 6, 7).

Table 5. Pair-wise correlation coefficients between biomass, chl*a* and production for total and nannoplankton fractions.

Variables	Total	Fraction < 35μm	Fraction < 10μm
Biomass, chl*a*	0.32	0.58	0.45
Biomass, production	0.16(NS)	0.47	0.19(NS)
Chl*a*, production	0.40	0.52	0.60

All values significant at the $p < 0.05$ level, except where indicated (NS).

Table 6. Mean seasonal total and nannoplankton chla (mg m^{-3}) and relative contribution (%) of nannoplankton fractions at the 4 stations in L. Memphremagog, May-Oct. 1976 and 1977 (2m. samples).

Station	Total chla 1976	Total chla 1977	Chla < 35μ 1976 (%)	Chla < 35μ 1977 (%)	Chla < 10μ 1976 (%)	Chla < 10μ 1977 (%)
1	10.0	7.2	5.8 (56)	4.2 (59)	3.9 (41)	2.9 (40)
2		6.8		4.0 (60)		2.7 (43)
3	5.9	4.7	3.7 (65)	3.5 (75)	2.4 (43)	2.4 (49)
4		4.6		3.2 (72)		2.1 (45)

Significant differences ($p < 0.05$) between paired observations at different stations as determined using Wilcoxon matched-pairs signed-ranks tests are indicated by arrows directed along the increasing gradient. It should be be noted that these arrows do not indicate significant differences between the seasonal mean values shown in the table.

Table 7. Mean seasonal total and nannoplankton production (mg Cm^{-3} hr^{-1}) and relative contribution (%) of nannoplankton fractions at the 4 stations in L. Memphremagog, May-Oct. 1976 and 1977 (2m. samples).

Station	Total prodn. 1976	Total prodn. 1977	Prodn.<35μ 1976 (%)	Prodn.<35μ 1977 (%)	Prodn.<10μ 1976 (%)	Prodn.<10μ 1977 (%)
1	21.3	16.5	15.5 (67)	8.5 (50)	8.8 (42)	5.9 (34)
2		15.0		7.7 (50)		5.1 (33)
3	14.1	11.3	9.9 (77)	6.1 (57)	6.0 (45)	4.1 (38)
4		11.1		5.9 (57)		4.3 (43)

Significant differences ($p < 0.05$) between paired observations at different stations as determined using Wilcoxon matched-pairs signed-ranks tests are indicated by arrows directed along the increasing gradient. It should be noted that these arrows do not indicate significant differences between the seasonal mean values shown in the table.

Fig. 4A: Relationship between nannoplankton (<10μm) and total phytoplankton biomass within Lake Memphremagog 1976-1977, expressed by the equation $\log y = 0.37 \log x + 1.23$ ($r = 0.52$; $p < 0.0001$). Symbols represent individual stations and years:

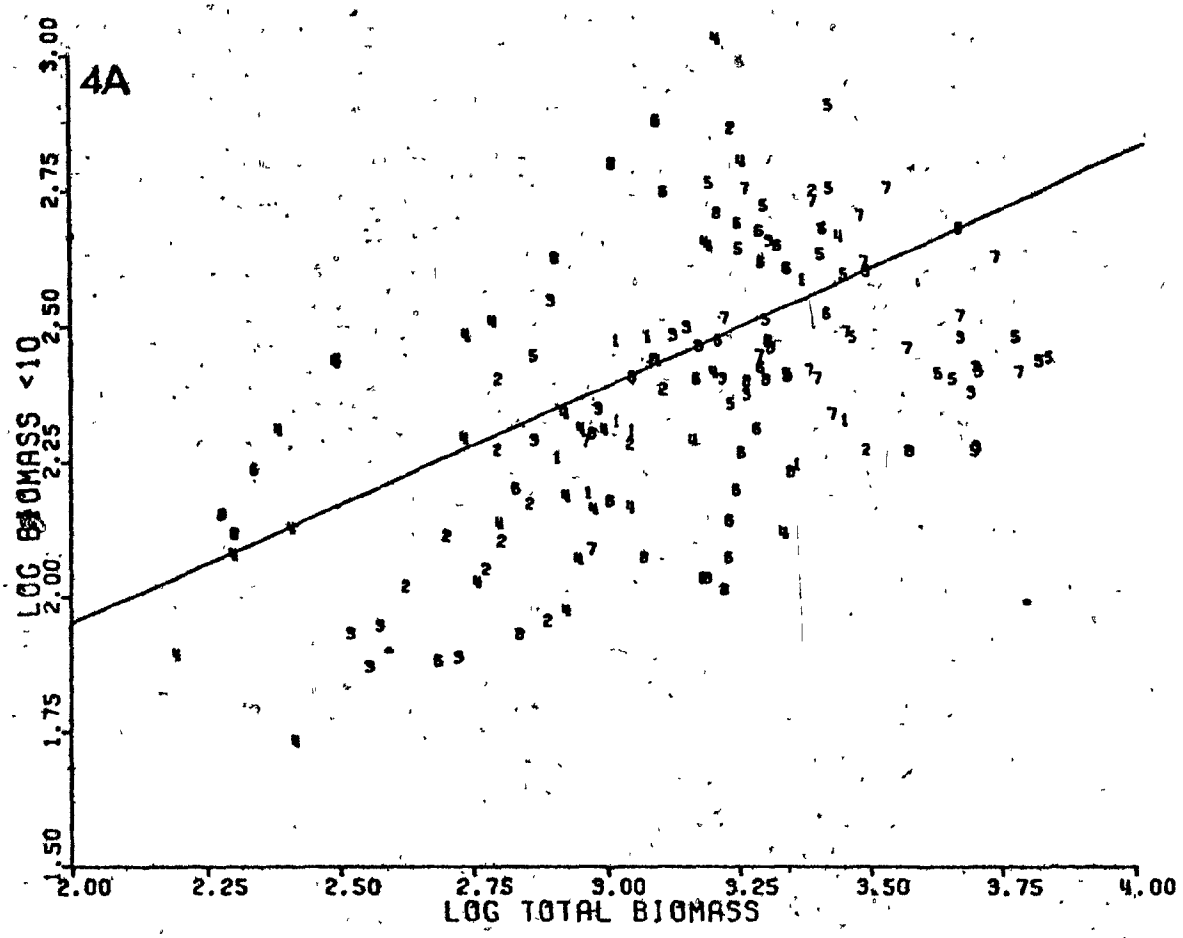
Station 1: 1 - 1976; 2 - 1977;

Station 2: 3 - 1976; 4 - 1977;

Station 3: 5 - 1976; 6 - 1977;

Station 4: 7 - 1976; 8 - 1977;

Fig. 4B: Relationship between % nannoplankton (<10μm) and total biomass within Lake Memphremagog 1976-1977, expressed by the equation $y = -33.0 \log x + 126.1$ ($r = 0.66$; $p < 0.0001$). Symbols as in 4A.


4A
LOG BIOMASS <10
3.00
2.75
2.50
2.25
2.00
1.75
1.50
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
LOG TOTAL BIOMASS

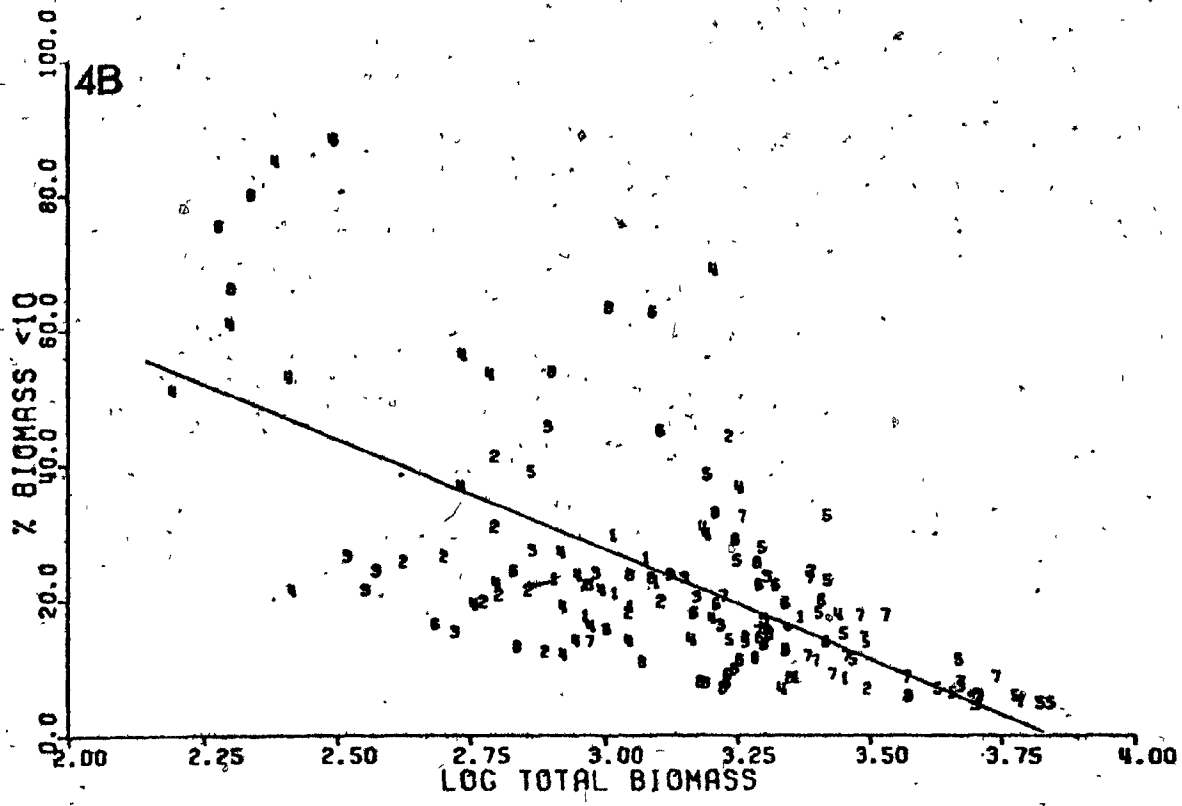
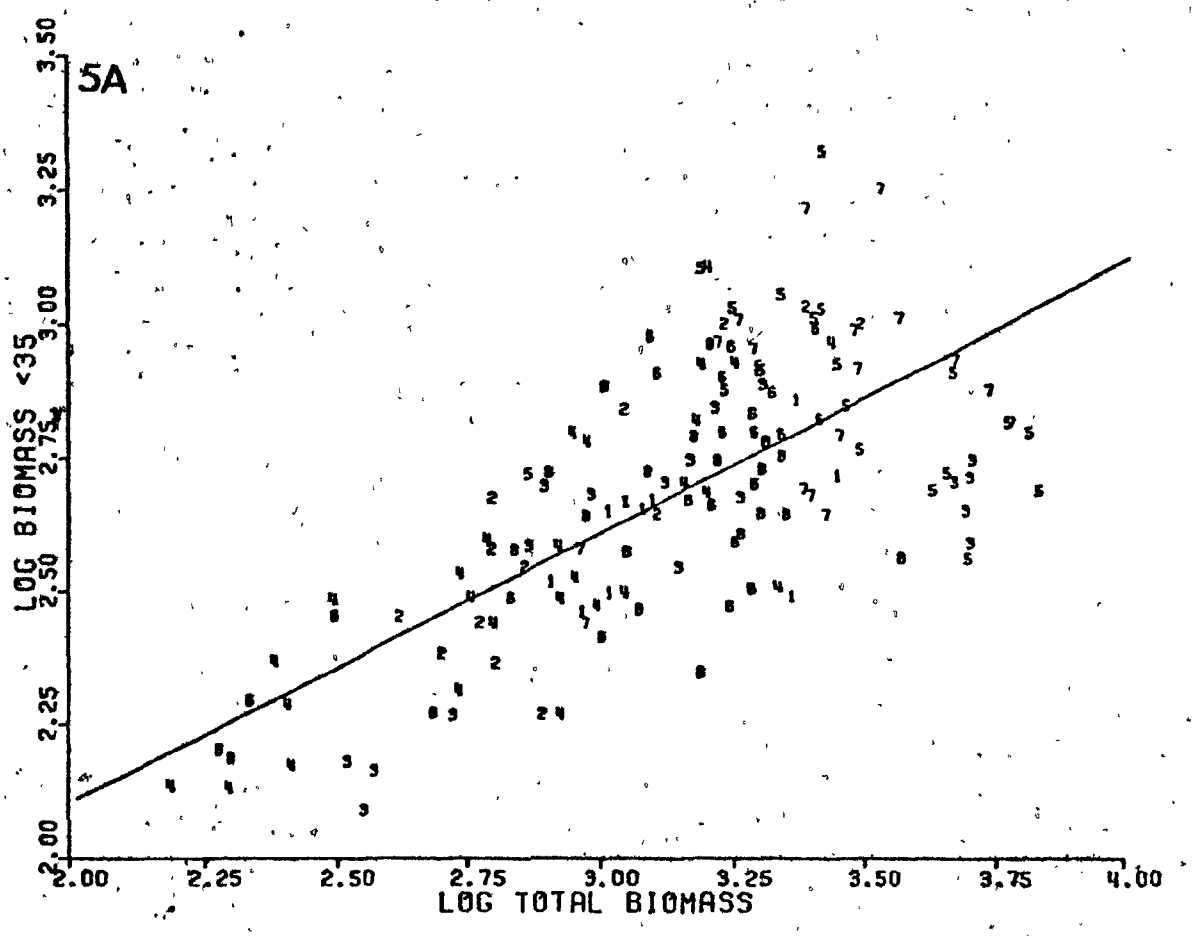

4B
% BIOMASS <10
100.0
80.0
60.0
40.0
20.0
0.0
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00
LOG TOTAL BIOMASS

Fig. 5A: Relationship between nannoplankton (<35µm) and total phytoplankton biomass within Lake Memphremagog 1976-1977; expressed by the equation log y = 0.48 logx + 1.17 ($r=0.68$; $p < .0001$).

Fig. 5B: Relationship between % nannoplankton (<35µm) and total biomass within Lake Memphremagog 1976-1977, expressed by the equation $y = -41.0 \log x + 169.1$ ($r = 0.69$, $p < 0.0001$).


5A
LOG BIOMASS <35
LOG TOTAL BIOMASS
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00

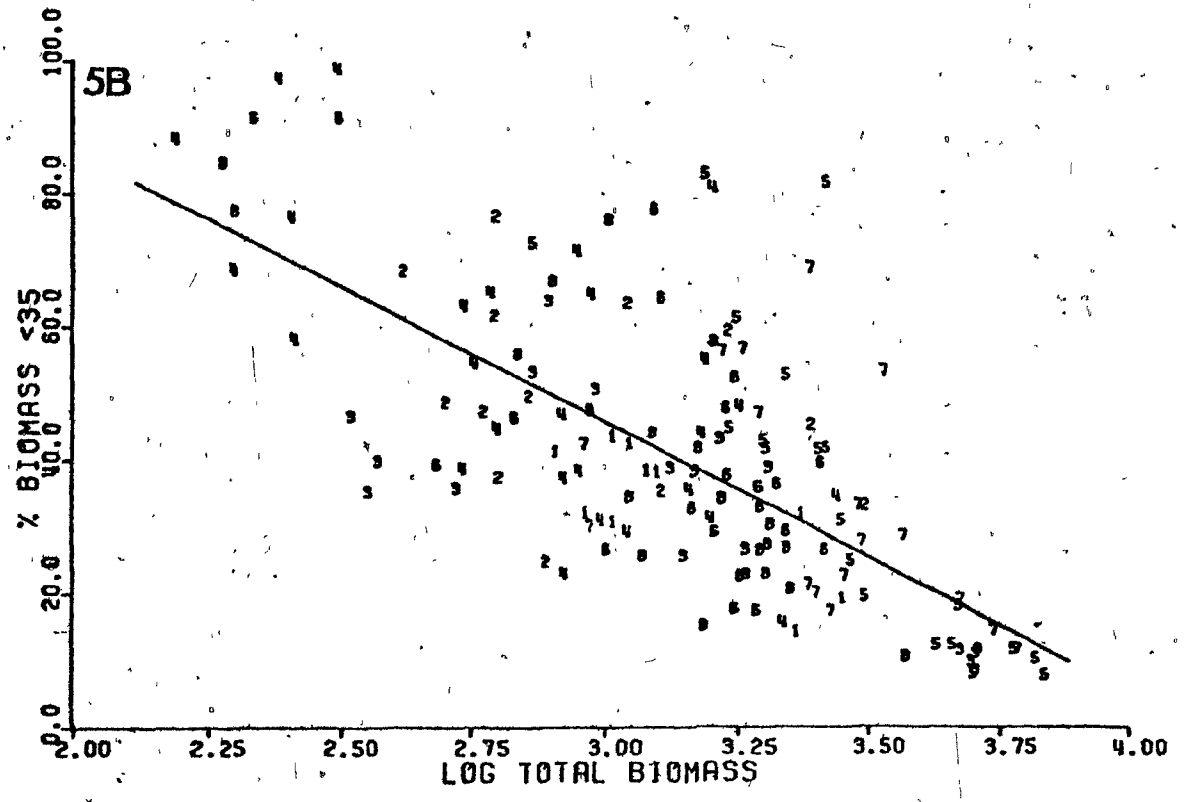

5B
% BIOMASS <35
LOG TOTAL BIOMASS
0.0
20.0
40.0
60.0
80.0
100.0
2.00
2.25
2.50
2.75
3.00
3.25
3.50
3.75
4.00

Fig. 6A: Relationship between nanoplankton and total biomass using literature data (generally seasonal average values) from a range of lakes of different trophy, expressed by the equation $\log y = 0.54 \log x + 1.02$ ($r = 0.78$, $p < .001$).

Symbols represent different authors:

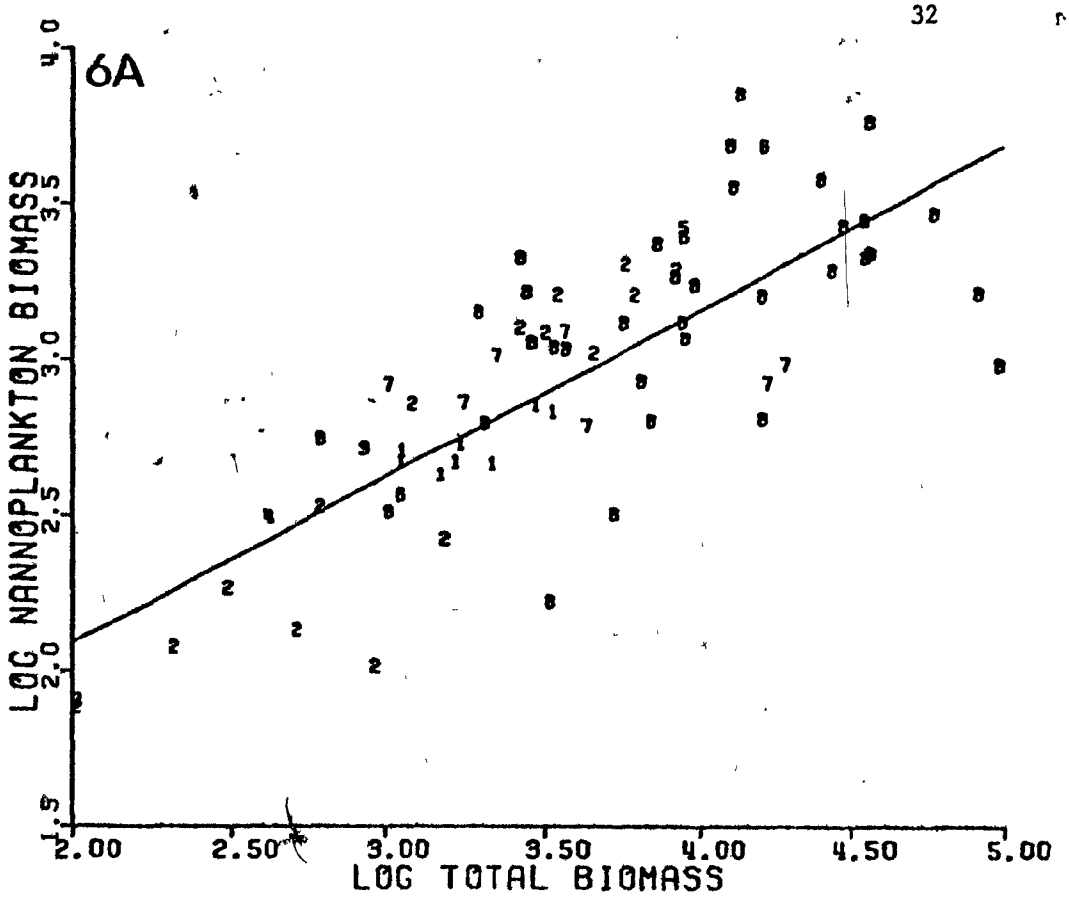
1 - Watson (1979); 2 - Munawar & Munawar (1975);

3 - Kalff (1972); 4 - Granberg (1970); 5 - Spodniewska

6 - Kristiansen (1971); 7 - Pavoni (1963)

8 - Spodniewska (1978).

Fig. 6B: Relationship between % nannoplankton and total biomass using literature data, expressed by the equation $y = -24.7 \log x + 120.0$ ($r=0.72$; $p < .0001$). Legend as in Fig. 6A.


6A
LOG NANNOPLANKTON BIOMASS
LOG TOTAL BIOMASS
4.0
3.5
3.0
2.5
2.0
1.5
2.00
2.50
3.00
3.50
4.00
4.50
5.00

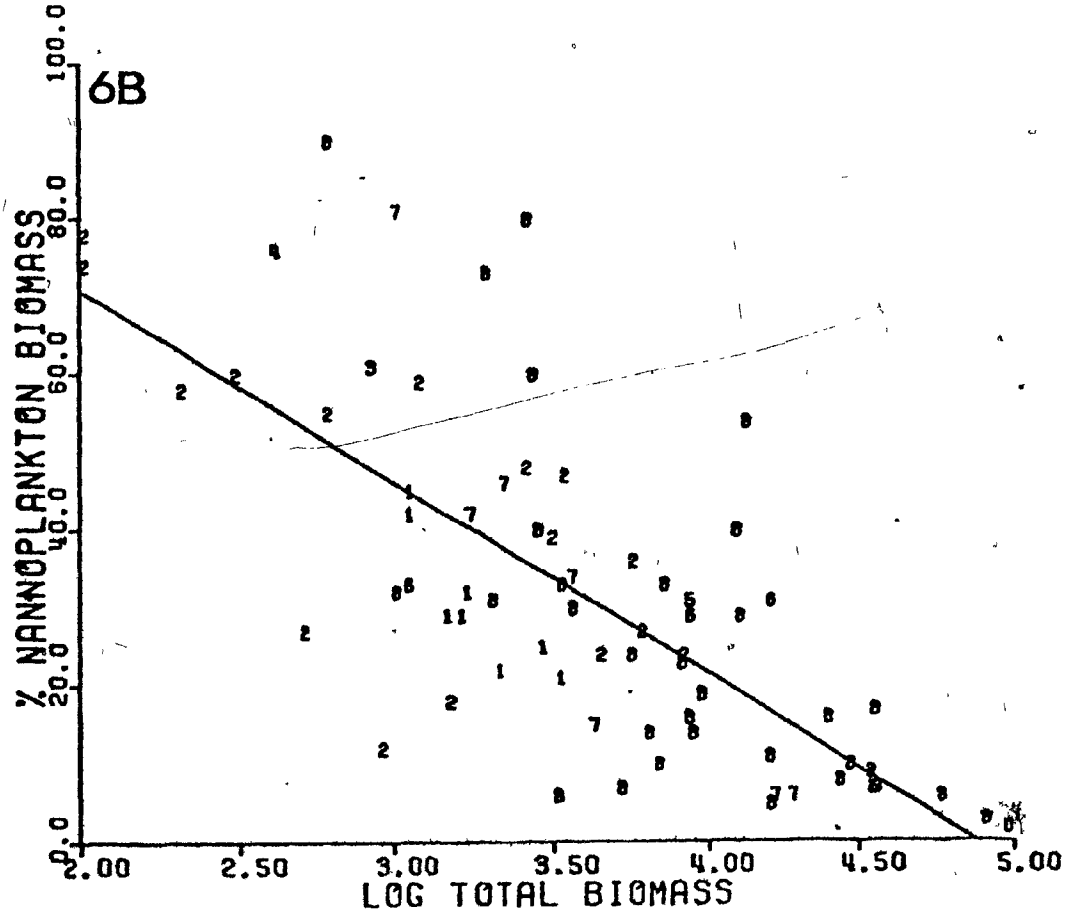
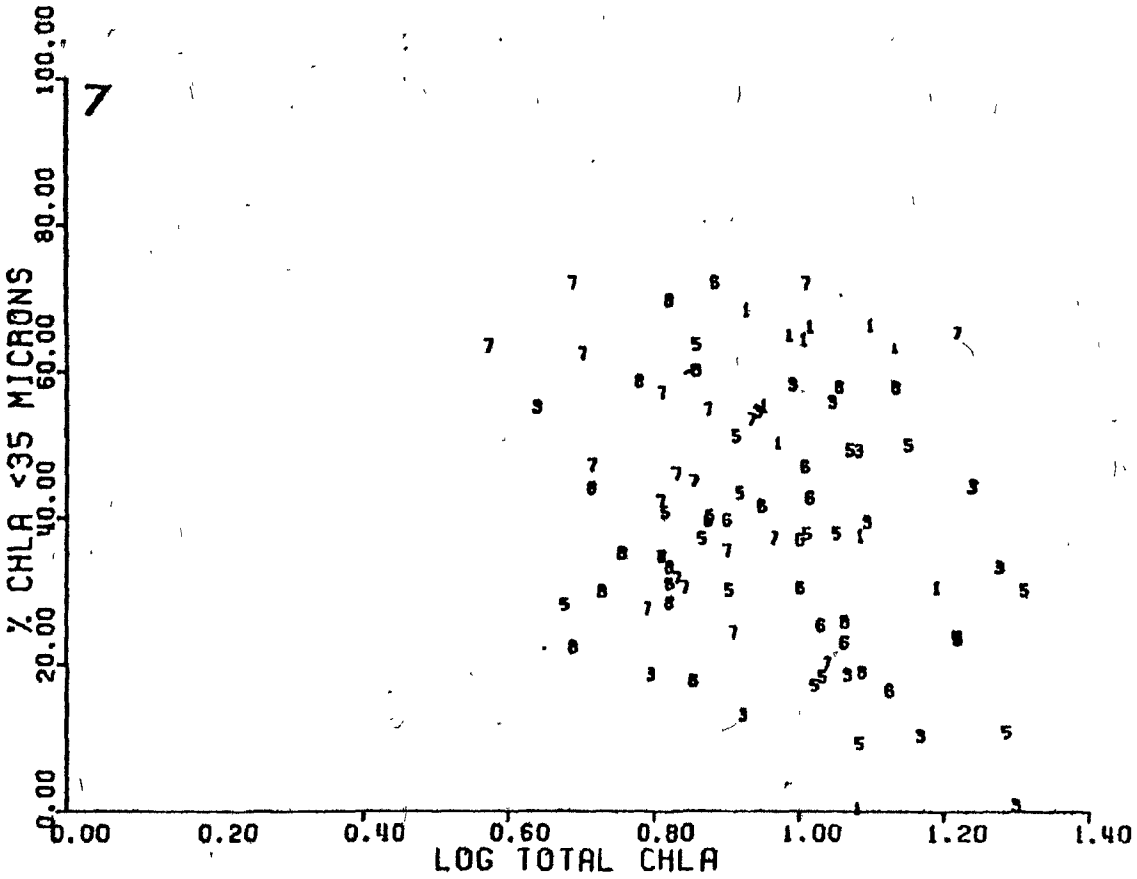

6B
% NANNOPLANKTON BIOMASS
LOG TOTAL BIOMASS
100.0
80.0
60.0
40.0
20.0
0.0
2.00
2.50
3.00
3.50
4.00
4.50
5.00

Fig. 7. Relationship between % chl*a* <35 µm and total chl*a* in Lake Memphremagog, 1976-1977. Symbols as in Fig. 4A.


% CHLA <35 MICRONS
100.00
80.00
60.00
40.00
20.00
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
LOG TOTAL CHLA

b) Relationship between size fractions and trophic level.

i). Lake Memphremagog.

There was a highly significant increase in both <10µm and <35µm nannoplankton biomass with increasing total biomass ($p=0.001$; Figs. 4A,5A), with correlation coefficients of 0.52 and 0.68 respectively. In addition, the slopes of both relationships were less than 1, indicating a significant decrease in the relative proportion of both nannoplankton fractions with increasing total biomass (Figs. 4B,5B). Analysis of covariance showed that differences between stations or years were not significant for any of these regressions.

In contrast, when using chla as a measure of standing crop, only the regression between %chla <35µm and total chla was significant (Fig. 7; $p=0.001$), and the correlation coefficient was extremely low ($r=0.4$). Differences in sample volumes filtered were not reflected in significant differences in slopes between years for any fraction (as determined by analysis of covariance).

Primary production showed even more unexplained variance: in fact no significant relationships were found between %nannoplankton (any size fraction) and total production. Again, analysis of covariance showed that differences between years was not significant for all size fractions.

ii). Between lakes.

On a 'between lake' level, a similar highly significant increase in nannoplankton biomass with increasing total biomass was observed (Fig. 6A), while again the relative proportion of nannoplankton biomass declined significantly (Fig. 6B). Analysis of covariance showed that differences between investigators or in nannoplankton size-range used did not make a

significant contribution towards the total variance in the nannoplankton fraction. Similarly, differences in surface area and mean depth, used as measures of morphometry and mixing depth, did not account for a significant amount of the total variance.

c) Environmental factors and their relationship with phytoplankton size fractions in Lake Memphremagog.

There was a significant N-S gradient in TP both years, although the average concentration declined appreciably 1977 (Table 8). Alkaline phosphatase data were only available for 1977 when there was an increase in mean activity towards the North in 1977, similar to the trend observed in 1975 (Sproule and Kalff, 1979). The mean effective light climate at each station showed little change between years, while average temperatures were generally lower in 1977 (Table 8).

The relationship between the relative contribution (%) of nannoplankton and TP, alkaline phosphatase activity, light and temperature were examined by analysis of covariance, which showed no single factor to have a dominant influence. Total phosphorus accounted for a statistically significant amount of the total variance in %biomass <10μm ($p=0.04$), and %chl*a* <35μm ($p=0.02$). Alkaline phosphatase activity showed no significant relationships with any nannoplankton fraction. Light was significantly related only to %chl*a* <35μm ($p=0.02$), while temperatures varied significantly with %biomass <10μm ($p=0.02$) and %production <35μm ($p=0.05$). The interaction between light and temperature did not account for a significant amount of the total variance in any nannoplankton fraction.

Table 8. Seasonal mean total phosphorus, alkaline phosphatase activity, temperature and light climate in L. Memphremagog, May-Oct. 1976 and 1977 (values averaged over the mixed layer).

	Total P ($mg\ m^{-3}$)		APA*	Temperature (^{o}C)		Light climate ($ly.day^{-1}$)	
Station	1976	1977	1977	1976	1977	1976	1977
1	28.6	15.0	0.66	18.0	15.8	61.6	59.3
2	22.4	14.4	0.73	17.3	15.8	40.9	46.1
3	13.2	10.8	0.81	17.4	15.4	37.1	40.5
4	-	9.2	0.95	18.3	16.2	51.1	53.4

* Alkaline phosphatase activity (µg methylfluorescein hr^{-1} µg chla; at 2m depth).

DISCUSSION

A major difference between the net and nannoplankton fractions is seen in the relative stability of their species assemblages. Several nannoplankton species, notably Rhodomonas minuta, Cryptomonas Marssonii, C. crosa, C. reflexa and Chrysochromulina parva, occurred in up to 100% of the samples examined at all stations, and frequently made significant contributions to both the nannoplankton and total biomass in Lake Memphremagog. This was also true of the samll heterotroph Katablepharis ovalis, which contributed significantly to total phytoplankton biomass (chlorophyllous and non-chlorophyllous) on a number of occasions. These nannoplankton species appear to be well adapted to the range of environmental conditions found within Lake Memphremagog. Furthermore, the same species are reportedly as ubiquitous over a much wider range of physical and trophic environments (e.g. Pavoni, 1963; Willén, 1969; Ahlgren, 1970; Granberg, 1970; Munawar and Munawar, 1975; Ramberg, 1976, Keskitalo, 1977; Reynolds, 1978).

In contrast, more conspicuous spatial and temporal shifts in L. Memphremagog were exhibited by species belonging to the netplankton fraction, which were characteristically periodic in their occurrences, although Cryptomonas rostratiformis, Asterionella formosa and Fragilaria crotonensis were present in most of the samples examined. However, while these particular species have also been reported from a range of lakes of different trophy, they are rarely found to be ubiquitous, except, to some extent, A. formosa (e.g. Lund, 1949; Reynolds, 1978). While the above implies that nannoplankton species are more plastic in their response to environmental changes, this fraction is not dominant as frequently as might be expected. In fact, from the regressions obtained, it is evident

that nannoplankton biomass increases significantly with increasing trophic level, (as measured by total biomass), but not as rapidly as the netplankton fraction (Figs. 4A,5A,6A). Therefore, the relative proportion (%) of nannoplankton biomass decreases significantly (Figs. 4B,5B,6B). However, there is considerable variance about these regression lines. Analysis of covariance indicates that within the literature data, this is not primarily attributable to diferences in technique between investigators or in morphometry between lakes (as measured by surface area and mean depth). Similarly, within Lake Memphremagog, morphometric differences between basins are not expressed in significant differences in slopes between stations. Furthermore, replicate biomass estimates (Watson, 1979, Appendix E-B) indicate that counting error is not sufficient to account for the range in variation observed about the regression lines (Figs. 4A,4B,5A,5B).

An increase in the relative abundance of large, more vacuolate forms associated with increasing total biomass may represent additional source of variance, since the relative proportion of non-cytoplasmic cell volume varies considerably not only between taxa, but according to the physiological condition of a given individual cell (Sicko-Goad et al., 1978). On the other hand, an increasing proportion of such netplankton species would in turn amplify any decrease in the relative proportion of nannoplankton biomass, and this in intself could account for some of the observed relationships between % nannoplankton and total biomass. If this is the case, we would expect the opposite to be true when chla and production are used as measurements, since specific values of both appear to be inversely related to cell size (Paasche, 1960 and Manney, 1972; Laws 1976, respectively). In fact, we observed a significant but less

pronounced decrease in % nannoplankton chl*a* with increasing total values (Fig. 7), but for the <35μm fraction only, and no similar significant relationship using % production. Again, there was considerable unexplained variance, even on a logarithmic scale. It thus seems likely that a very substantial difference in nutrient loading or trophic level is required to produce a recognisable change in the relative contribution of nannoplankton chl*a* and production, as was observed following the restoration of L. Trummen (Gelin and Ripl, 1978). In general, with less extreme seasonal changes in most lakes, the relative proportion of nannoplankton production remains fairly constant over the growing season (Kalff, 1972). A series of measurements taken on alternate days during the development and decline of the 1978 spring diatom assemblage in Lake Memphremagog supports this view by showing generally low short-term fluctuations in both % nannoplankton chl*a* (±10-15%) and production (±5-16%)), while total phosphorus varied between approximately 7.5-12.5 $\mu g l^{-1}$ (Watson, 1979, see Appendices F,G).

In retrospect, a lack of correlation between biomass (B), chl*a* (C) and production (P) might be expected, since these measures represent different attributes of the phytoplankton community which may vary both in the manner and particularly in the rate of their response to environmental changes. Thus, one observes considerable variability in the reported ratios of P/B (the "activity coefficient" e.g. Findenegg, 1965; Ahlegren, 1970; Kalff, 1972), P/C (the "assimilation number" e.g. Malone, 1971a,b; Fogg, 1975) and C/B (e.g. Paasche, 1960; Ahlgren, 1970, Manney, 1972; Willén, 1976; Tilzer et al., 1977; Nicholls and Dillon, 1978). The fact that none of the three measurements yields a very satisfactory representation of the relative contribution of different size-fractions

probably accounts for much of the scatter observed about the relationships between % nannoplankton and trophic level (Figs. 4A,5A,6A,7). On the other hand, this variance may signify that factors other than those related directly to trophic level play a significant role in determining the distribution of phytoplankton cell-size. Thus, the limited relationships we observe between total phosphorus and % nannoplankton in Lake Memphremagog which has been shown to be phosphorus deficient (Sproule and Kalff, 1979), indicate that the limiting nutrient has little influence on the relative proportion of nannoplankton in this lake. Further evidence that phosphorus is not a major size-selective factor in Lake Memphremagog is seen in the lack of correlation between any measurement of % nannoplankton and alkaline phosphatase activity, although the latter has been shown to be a good measure of phosphorus availability (Sproule and Kalff, 1979).

The assimilation number of phytoplankton population (AZ: $mgCm^{-3}hr^{-1}mg\ chla^{-1}$ at optimum depth) appears to be related to cell nutrient status, although some workers report a consistent increase and others a decrease in AZ with nutrient deficiency (Fogg, 1975). We therefore examined our data for any consistent differences in nanno- and netplankton (>10μm, >35μm) AZ which might indicate dissimilarities in their relative nutrient status. The results obtained showed consistent trends within each year, but marked differences between years (Table 9), which more recent data indicate were not simply an artifact of changes in sample volumes, and which were not reflected in significant differences in the slope of % nannoplankton vs. total standing crop for the two years. Thus, if these values AZ give an indication of the relative nutrient status of the net- and nannoplankton fractions (as defined by the different mesh sizes), they

Table 9. Comparison of the relative AZ (mg.C hr^{-1}/mg.Chl$\underline{a}$; at 2m depth) of the net- and nannoplankton fractions, using Wilcoxon matched-pairs signed-ranks tests.

Year / Station	Mesh 10µm	Mesh 35µm
1976		
1	-	Nanno > Net
3	-	Nanno > Net
1977		
1	Net > Nanno	Net > Nanno
2	Net > Nanno	Net > Nanno
3	Net > Nanno	Net > Nanno
4	-	Net > Nanno

Blanks indicate no significant differences between the two size fractions at the $p \leq 0.05$ level.

suggest that nutrients do not have an immediate and direct influence on phytoplankton size distribution in Lake Memphremagog. However, rather than having a direct influence, nutrients may well play an indirect role in size-selection. In L. Memphremagog. the differences between the relative AZ of the net- and nannoplankton fractions (Table 9) were not consistent with differences in total and available phosphorous (Table8; Peters, 1979). Furthermore, differences between the two size fractions (<10μm, >10μm) were not apparent in mesotrophic Lake Hinnasjön, (Gelin and Ripl, 1978), whereas the nannoplankton fraction (<10μm) exhibited a significantly higher AZ in highly eutrophic Lakes Vombsjön (Gelin, 1975) and Trummen (Gelin and Ripl, 1978). In addition, that nutrients (phosphorus) play an indirect role in size distribution is also evident from the highly significant relationships between % nannoplankton and total biomass and chl*a* (Figs. 4B,5B,6B,7). Nevertheless, the large amount of residual variance about these regression lines implicates interactions with factors other than light and temperature, since these parameters do not appear to play a major role in cell size-selection in Lake Memphremagog. Recent literature indicates that zooplankton grazing has a significant influence on nannoplankton standing crop: Haney (1973) measured average removal rates of particles <14μm of 80% day^{-1}. Although small cells have relatively rapid growth rates (Laws, 1975) and their renewal rates appear to be sufficient to offset these high grazing rates (Haney, 1973), short-term imbalances produced by grazing may well be responsible for much of the residual variance about the regression lines.

Thus, although phosphorus commonly limits total phytoplankton biomass (e.g. Vollenweider, 1968; Schindler, 1974), and we found a number of highly significant relationships between nannoplankton and trophic level (as measured by total biomass and chl*a*), our data suggest that the

relative proportion of nannoplankton is not primarily a function of the limiting nutrient (phosphorus), the nutrient status of the plankton as light and temperature. It therefore appears that in order to make better predictions of the contribution of the nannoplankton to phytoplankton standing crop, we require as yet unavailable information on the role played by selective zooplankton grazing.

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Section 2

The relationship between lake trophy and phytoplankton communities as examined using taxonomy, morphology and measurements of community structure.

ABSTRACT

During both 1976 and 1977, phytoplankton biomass in Lake Memphremagog at four stations located along a significant N-S nutrient gradient was dominated by Bacillariophyta, Cyanophyta, Cryptophyta, and to some extent, Chrysophyta. The mean seasonal contributions of these groups to total biomass were similar between stations each year but showed changes between 1976 and 1977, as did levels of total phosphorus. Seasonal patterns of the major taxonomic groups were generally more subdued at the more oligotrophic stations, and differed between the two years. Short-term fluctuations in the biomass and relative importance of each group were frequently not associated with changes in total phosphorus. This was also true at the species level and within the range of nutrient levels observed in Lake Memphremagog during the study, factors other than total phosphorus appeared to have a greater influence on the distribution and relative abundance of major taxonomic groups and indicator species. Similarly, on a short-term basis, the dominant morphology of the netplankton (<35 μm) fraction was not clearly related to this nutrient, although lower seasonal total phosphorus levels within Lake Memphremagog were accompanied by a decline in the relative importance of filamentous species, and an increase in the relative contribution of colonial forms. If the relative importance of individual species is measured using biomass rather than numerical abundance, within Lake Memphremagog, measurements of community structure showed significant relationships ($p<.01$) with trophic level, such that with increasing total biomass, there was a significant increase in the total number of species observed and a significant decrease in community diversity and evenness. It was also found that at

least 8 and up to 16 or 32 species should be enumerated to obtain a good estimate (>90%) of total phytoplankton biomass in this meso-oligotrophic lake.

EXTRAIT

Au cours des deux années 1976 et 1977, la biomasse du phytoplancton à quatre stations du lac Memphrémagog, situées le long d'un gradient de matières nutritives nord-sud signifacatif, était dominée par les Bacillariophytes, Cyanophytes, Cryptophycées et en partie par les Chrysophytes. La contribution saisonnière moyenne de ces groupes à la biomasse totale était semblable entre les stations à chaque année mais variait entre les années 1976 et 1977 tout comme les niveaux de phosphore total. Les modèles saisonniers des principaux groupes taxonomiques étaient généralement plus adoucis aux stations plus oligotrophiques et variaient pour les deux années. Les fluctuations à court terme de la biomasse et l'importance relative de chaque groupe n'étaient généralement pas associées avec les changements du phosphore total. Cette observation s'applique aussi au niveaux de l'espèce et à l'interieur de la zone de niveaux du matière nutritif observés au lac Memphrémagog au cours de cette étude. Des facteurs autre que le phosphore total semblent avoir une importance supérieure sur la distribution et l'abondance relative des principaux groupes taxonomiques et de l'espèce indicatrice d'un certain niveaux trophique. De même, à court terme la morphologie dominante du plancton de dimension supérieure à 35 µm n'était pas clairement relié à cette matière nutritive bien qu'une diminution de l'importance relative des espèces filamenteuses et un accroissement dans la contribution relative des formes coloniales accompagnassent des niveaux saisonniers inférieures de phosphore total. Si l'importance relative des espèces individuelles est mesurée à partir de la biomasse que de leur abondance numérique dans le

lac Memphremagog, les mesures de la structure de la communauté montre des rélations significatives ($p < .01$) avec le niveau trophique comme suite: une augmentation de la biomasse totale s'accompagne d'une accroissement significatif du nombre d'espèces observées et d'une diminution significative de la diversité et de la regularité de la communauté. Il a aussi été remarqué qu'au moins 8 sinon 16 ou 32 espèces devraient être enumérées afin d'obtenir une appréciation valable (>90%) de la biomasse du phytoplancton dans ce lac meso-oligotrophique.

Phytoplankton assemblages at four stations located along a North-South nutrient gradient in Lake Memphremagog (see Section 1) were investigated over a period of two years (1976-77). Sampling, enumeration and biomass calculations were performed as outlined in Section 1 and Appendix E. Here, the data obtained are examined in terms of:

i) seasonal patterns of the major species and taxonomic groups, and distributions of selected 'indicator species' (Chapter 1);

ii) distributions of different morphological groups (as defined by criteria other than size alone). (Chapter 2);

iii) measurements of community structure (Chapter 3).

Chapter 1

Seasonal patterns of major species and taxonomic groups and distributions of selected indicator species.

> "No deterministic modelling process will give intelligible predictions of these temporal or taxonomic details; ecosystems are simply too complex. Modelling efforts in ecosystems can best be restricted to simple ecosystem components." (Schindler, 1975).

Introduction

A number of authors have attempted to relate lake nutrient status to the quality of the underlying phytoplankton community using species quotients (e.g. Nygaard, 1949; Järnfelt, 1952), or 'indicator' species,

assemblages, or algal groups (e.g. Rawson, 1956; Hutchinson, 1967; Tarapchak and Stoermer, 1976; Stoermer, 1978; Nicholls, 1976). Quotients such as those developed by Nygaard (1949) generally do not give a complete representation of many phytoplankton communities, since they are based on species which are of low abundance in the majority of lakes (e.g. Rawson, 1956; Hutchinson, 1967; Kalff and Knoechel, 1978). On the other hand, while several authors (e.g. Rawson, 1956; Hutchinson, 1967; Tarapchak and Stoermer, 1976; Stoermer, 1978; Nicholls, 1976) consider that the distribution and relative abundance of dominant species, phytoplankton assemblages or taxonomic groups may be used as an indication of trophic level, the relative importance of each species in a given aquatic system will often greatly depend on the spatial and temporal frequency of sampling; the definition of relative abundance (i.e. as defined by numbers or biomass) and the taxomic competence of the investigator (Rawson, 1957; Tarapchak and Stoermer, 1976). Moreover, the relationship of particular algal assemblages with nutrient level (e.g. Hutchinson, 1967) may be obscured by the fact that neither the relative proportions of species in such assemblages, nor trophic level are quantitatively defined by most authors (e.g. Bradburg, 1975; Carlson, 1977). Furthermore, in some cases, phytoplankton communities may show little qualitative change in species composition with increasing eutrophication until some threshold nutrient level is reached (Tarapchak and Stoermer, 1976).

Thus, the concept of 'indicator' species, assemblages or groups remains confused. By examining the distributions of the major taxonomic

groups and algal species at the four stations in Lake Memphremagog in relationship to changes in total phosphorus and other factors, it is the purpose of this chapter to demonstrate that the use of such indices is an over-simplistic approach, both within and between lakes.

Methods

Methods of collection, preservation and enumeration of samples are outlined in Section 1, but it should be re-emphasised that since these were integrated tube samples, they represent the average contribution of the phytoplankton species over the depth of the mixed layers, or during turnover, the euphotic zone (15 m), not weighted for basin morphometry. A discussion of sampling and enumeration error is given in Appendix E. K_z, the vertical eddy diffusion coefficient was calculated using the relationship

$$K_z = 1 \times 10^{-9} (Z_T)^z (N^z)^{-0.5}$$ (Quay, 1977)

where Z_T = depth of mixed layer

N^2 (Brunt Vaisala frequency)

$$= \frac{-g}{\rho} \frac{\delta \rho}{\delta z}$$

ρ = water density

g = gravitational constant

z = depth interval (cm)

Results

A detailed description of spatial and temporal changes in major phytoplankton species at the four stations in Lake Memphremagog is given in Appendix A, and summarised in Section 1 and Figures A-1 through A-4.

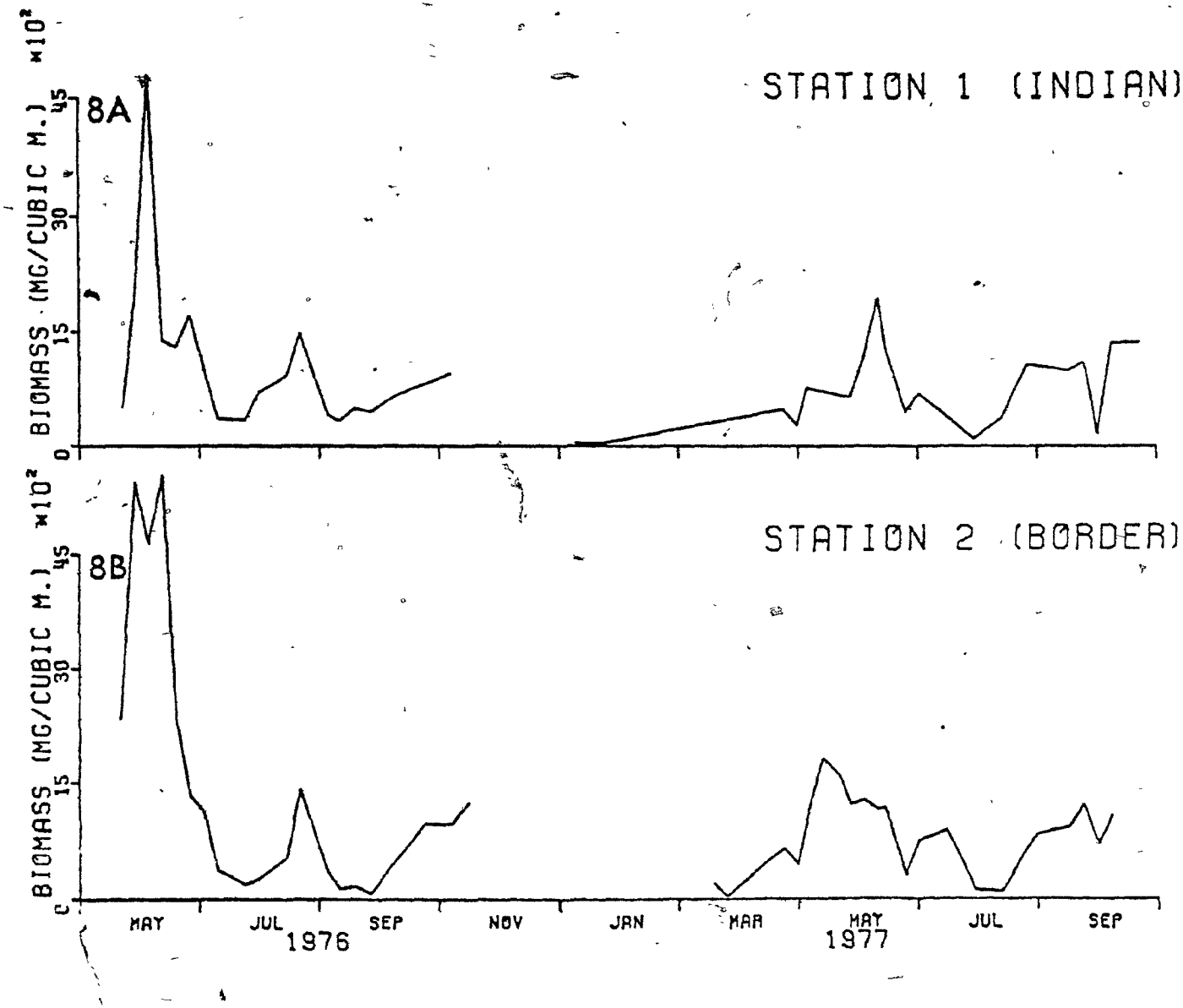
Discussion

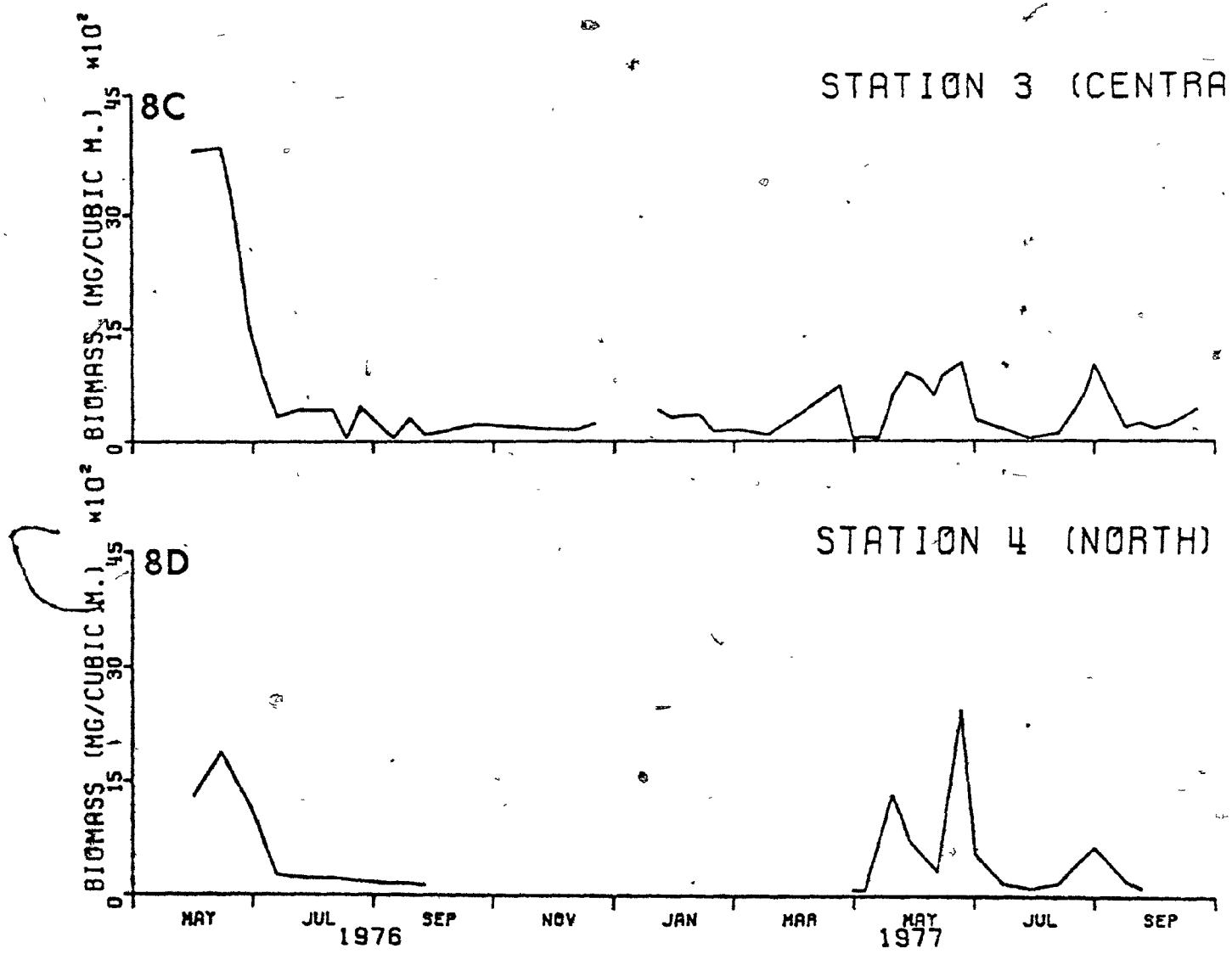
While decreasing levels of total phosphorus between stations and years appeared to correspond with a decline in the mean (absolute) biomass of the major taxonomic groups, the average % contribution of each group to total biomass was similar at all four stations each year, despite the N-S nutrient gradient, which was particularly significant in 1976 (Tables 8, 10). Both in 1976 and 1977, the dominant groups at all stations were Bacillariophyta (30-50% total biomass), Cryptophyceae (17-23%), Cyanophyta (10-26%), and to a lesser extent Chrysophyta (7-17%). Dinophyceae (4-9%), Chlorophyta (3-6%) and Euglenophyta (0-0.3%) generally contributed much less towards total biomass (Table 10; Figs. A-1 through A-4). Seasonal patterns of the major groups were quite similar throughout the lake but tended to be more subdued towards the more oligotrophic stations 3 and 4 (Figs. 8A-8D; 9A-9D; 10A-10D). However, in 1977, when levels of total phosphorus were generally lower (Table 8), the prominant spring maxima of Bacillariophyta and Cyanophyta observed the previous year were reduced or absent (Figs. 8A-8D; 9A-9D), as were the fall peaks in Cryptophyceae which occurred at the more eutrophic stations 1 and 2 in 1976 (Figs. 10A-10D). The relative importance of Chrysophyta showed little change between stations each year, although the average % contribution of this group did increase at stations 1 and 2 in 1977 (Table 10). However, in general, spatial and temporal differences in total phosphorus within Lake Memphremagog during 1976 and 1977 (Table 8) were not sufficient to produce a recognisable relationship between % Chrysophyta and total phosphorus, such as that observed by Nicholls (1977) for a number of Ontario lakes of different trophy.

Table 10. Mean biomass and average % contribution to total biomass of the major taxonomic groups in Lake Memphremagog, 1976-1977.

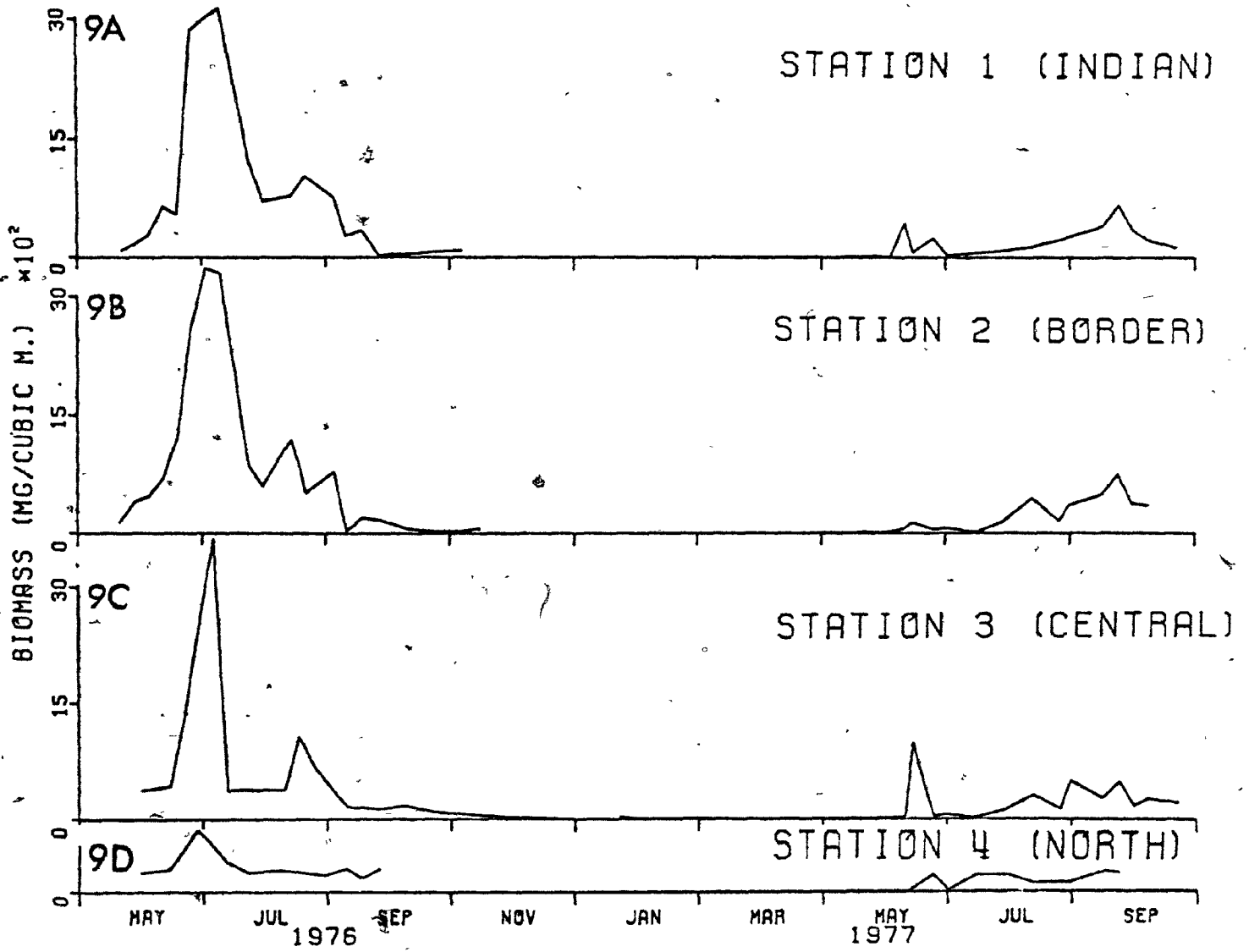
Station	Year	Cyanophyta	Chlorophyta	Euglenophyta	Bacillariophyta	Chrysophyta	Pyrrophyta	
							Cryptophyceae	Dinophyceae
1	1976	774 (22%)	93 (3%)	8 -	1107 (39%)	194 (8%)	565 (22%)	145 (5%)
1	1977	158 (10%)	62 (4%)	3 -	765 (46%)	190 (17%)	241 (18%)	49 (5%)
2	1976	811 (23%)	79 (3%)	4 -	1454 (39%)	194 (7%)	500 (21%)	141 (6%)
2	1977	158 (11%)	69 (5%)	1 -	823 (49%)	179 (13%)	245 (18%)	62 (5%)
3	1976	672 (26%)	74 (5%)	1 -	905 (35%)	145 (10%)	230 (16%)	114 (7%)
3	1977	140 (12%)	48 (5%)	1 -	406 (41%)	104 (11%)	192 (23%)	64 (8%)
4	1976	335 (25%)	98 (9%)	2 -	576 (31%)	146 (11%)	216 (16%)	93 (8%)
4	1977	112 (14%)	49 (7%)	1 -	521 (36%)	147 (13%)	201 (22%)	69 (8%)

Figs. 8A-8D. Seasonal biomass of BACILLARIOPHYTA at Stations 1 (Fig. 8A), 2 (Fig. 8B), 3 (Fig. 8C) and 4 (Fig. 8D) in Lake Memphremagog, 1976-1977.

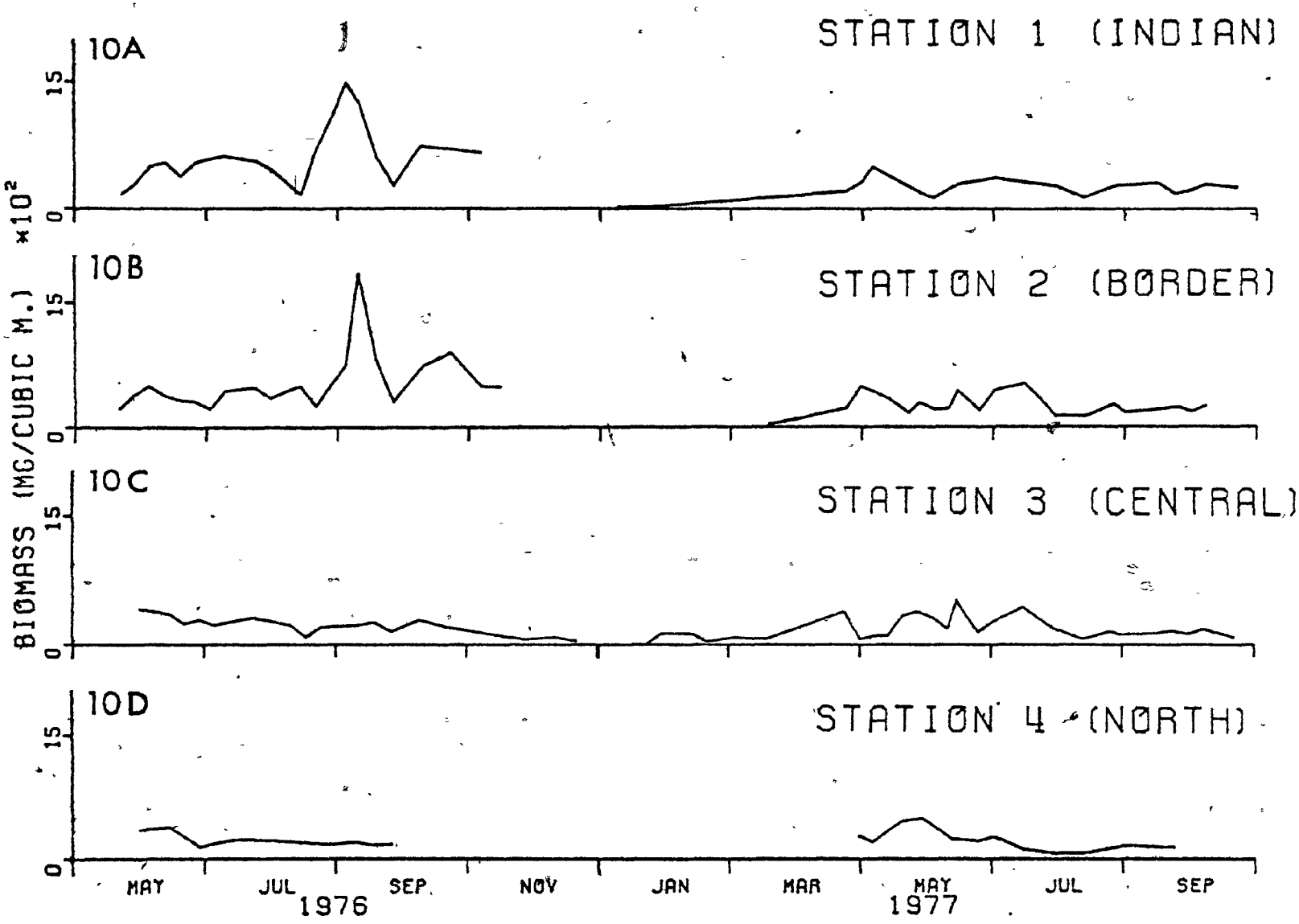

8A
STATION 1 (INDIAN)
BIOMASS (MG/CUBIC M.) ×10²
45
30
15
0
8B
STATION 2 (BORDER)
BIOMASS (MG/CUBIC M.) ×10²
45
30
15
0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


8C
STATION 3 (CENTRAL)
BIOMASS (MG/CUBIC M.) ×10²
45
30
15
0
8D
STATION 4 (NORTH)
BIOMASS (MG/CUBIC M.) ×10²
45
30
15
0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Figs. 9A-9D. Seasonal biomass of CYANOPHYTA at Stations 1 (Fig. 9A), 2 (Fig. 9B), 3 (Fig. 9C) and 4 (Fig. 9D) in Lake Memphremagog, 1976-1977.


9A
STATION 1 (INDIAN)
9B
STATION 2 (BORDER)
9C
STATION 3 (CENTRAL)
9D
STATION 4 (NORTH)
BIOMASS (MG/CUBIC M.) *10²
30
15
0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Figs. 10A-10D. Seasonal biomass of CRYPTOPHYCEAE at Stations 1 (Fig. 10A), 2 (Fig. 10B), 3 (Fig. 10C) and 4 (Fig. 10D) in Lake Memphremagog, 1976-1977.


10A
STATION 1 (INDIAN)
10B
STATION 2 (BORDER)
10C
STATION 3 (CENTRAL)
10D
STATION 4 (NORTH)
BIOMASS (MG/CUBIC M.) ×10²
15
0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Thus, while changes in the average % contributions of the major taxonomic groups were observed at each station between 1976 and 1977 (Table 10), the proportions of each groups were very similar at all four stations each year. However, relative differences in mean total phosphorus concentrations between stations each year were generally equivalent to or greater than changes at individual stations between years (Table 8). It is apparent, therefore, that the seasonal average proportions of the major taxonomic groups do not necessarily reflect changes in nutrient status, at least within the range of total phosphorus concentrations observed within Lake Memphremagog during 1976 and 1977 (9-29 $\mu g l^{-1}$; Table 8).

On the species level, responses to changes in mean seasonal phosphorus concentrations were also not always clear-cut. In 1976, Diatoma tenue var. elongatum accounted for a major portion of the diatom maximum at all stations, but decreased in both absolute biomass and relative importance towards the more oligotrophic North Basin (Table C-2; Figs. A-1-A-4). The following spring, this species showed a marked reduction in both absolute and relative biomass throughout the lake, again particularly in North Basin (Tables C-1, C-2). D. tenue var. elongatum is not commonly reported as a dominant form, although it has recently become abundant in Lake Michigan, particularly in the more eutrophic inshore areas, which are also characterised by elevated chloride levels (Tarapchak and Stoermer, 1976). However, the absolute and relative abundance of this species in Lake Memphremagog appears to be primarily influenced by changes in phosphorus levels rather than the ability of this species to tolerate increased salinity, since chloride levels are generally low throughout this lake (5-6 $\mu g l^{-1}$; Carlson, unpublished).

The absolute and relative abundance of many other important diatom species do not show similar relationships to total phosphorus both in Lake Memphremagog and in other lakes. For example, changes in the spatial and temporal distribution and relative importance of Asterionella formosa show little correspondance with levels of total phosphorus in Lake Memphremagog. Although A. formosa did not attain a particularly high biomass at any station in 1976 or 1977 (Table C-2; Figs. A-1-A-4), it was ubiquitous, and even showed an appreciable development (300 $\mu g l^{-1}$) under ice-cover in the Central Basin, demonstrating the ability of this species to cope with a wide range of environmental changes. Its abundance in both oligotrophic and eutrophic lakes further attests to this flexibility and has created some confusion concerning its status as a trophic 'indicator' (Hutchinson, 1967). However, this species is one of several (diatom) species which with increasing eutrophication, show a general shift away from perennial occurrences towards strong seasonal maxima (Stoermer, 1978), supporting the hypothesis that species showing a high relative abundance under oligotrophic conditions do so because they have a greater ability to cope with low nutrient concentrations, and not because of a preference for such nutrient regimes (e.g. Kalff and Knoechel, 1978). This may explain some of the apparent contradiction concerning trophic preferences of so-called 'indicator' species. Thus patterns in the abundance of Fragilaria crotonensis, described as an 'indicator' or eutrophy (Nicholls, 1976), mesotrophy (Rawson, 1956; Tarapchak and Stoermer, 1976) and oligotrophy (Hutchinson, 1967) showed little apparent relationship to levels of total phosphorus within Lake Memphremagog, and

Table 11. Maximum abundance of selected diatom species in Lake Memphremagog, 1976 and 1977.

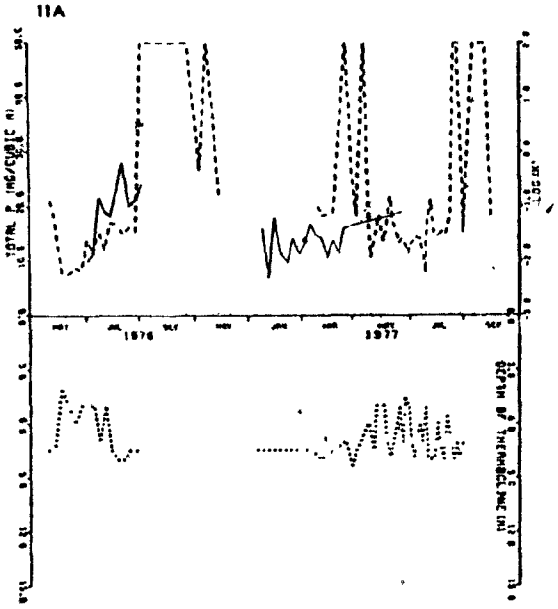
	Year	Indian	Border	Central	North
Cyclotella bodanica	1976	72	115	259	130
	1977	187	202	246	721
Rhizolenia eriensis	1976	285	127	116	127
	1977	230	224	126	411
Asterionella formosa	1976	196	214	110	123
	1977	125	260	300	46
Synedra ulna var. *danica*	1976	219	176	157	82
	1977	127	164	270	923
Fragilaria crotonensis	1976	275	270	224	492
	1977	984	625	742	1485
Melosira italica	1976	670	439	77	28
	1977	857	490	888	186
Melosira granulata	1976	150	237	13	3
	1977	348	217	218	9
Stephanodiscus astraea	1976	459	419	61	31
	1977	477	429	72	20
Diatoma tenue var. *elongatum*	1976	4100	4770	3200	1660
	1977	223	900	297	85

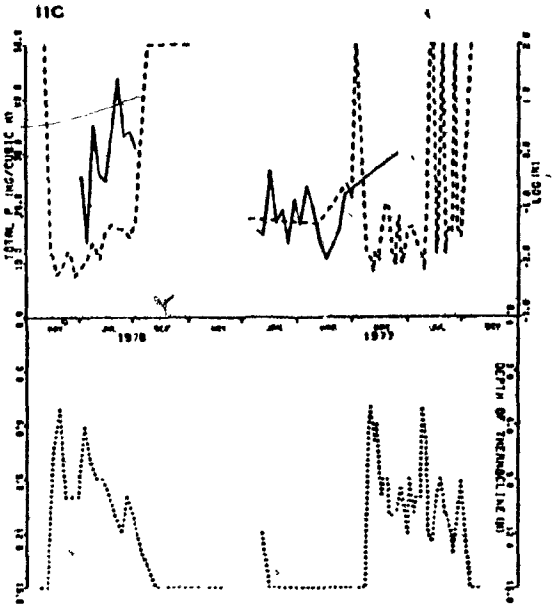
Figs. 11A-11D. Mean epilimnetic total phosphorus concentrations, depth of thermocline and vertical eddy diffusion coefficient at Stations 1 (Fig. 11A), 2 (Fig. 11B), 3 (Fig. 11C) and 4 (Fig. 11D) during 1976 and 1977 in Lake Memphremagog.

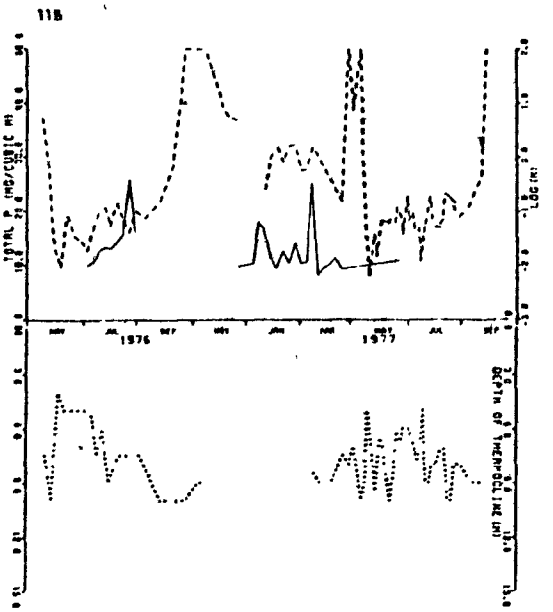
Legend: ———— total phosphorus

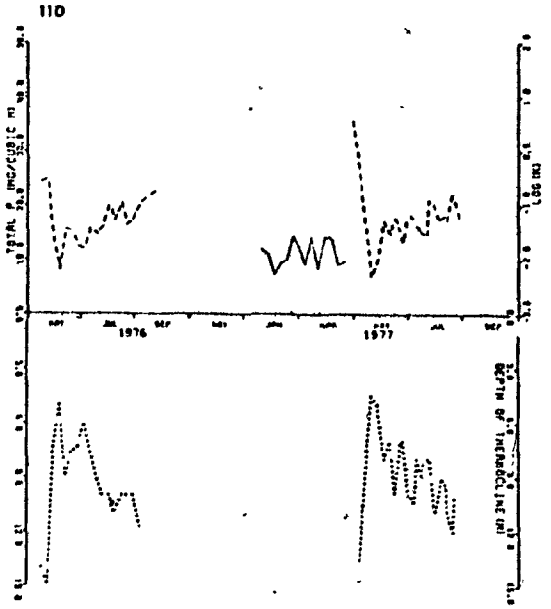
---------- depth of thermocline (Z_T)

... . vertical eddy diffusion coefficient (K)


11A
1976
1977


11C
1976
1977


11B
1976
1977


11D
1976
1977

this species was also very ubiquitous (Table C-1). In fact F. crotonensis even exhibited a general increase in relative abundance where seasonal levels of total phosphorus were reduced (Table C-2), together with other major diatom species considered by some authors to be eutrophic or meso-eutrophic indicators, notably Rhizosolenia eriensis, Synedra ulna var. danica, Melosira italica and M. granulata (Rawson, 1956; Tarapchak and Stoermer, 1974). Several of these species also attained a higher seasonal (absolute) maximum biomass at the most oligotrophic station 4 mainly in 1977(Table 11), even though sampling frequency was lowest at this station and hence in many cases, the true maximum biomass may not have been detected. Since it is unlikely that nutrient levels at the more eutrophic stations in this lake during 1976 and 1977 were inhibitory (max. 29 $\mu g l^{-1}$) total phosphorus in fall 1976, at Station 1; Fig. 11A), it would appear that other factors have a greater influence on the distribution and abundance of these diatoms. In fact, the increase in absolute and relative abundance of many of these species during the second, more nutrient-deficient year could reflect reduced sinking losses since there was a general increase in turbulence (K_2) and mixing depth (Z_T) during the stratified period in 1977 (Figs. 11A-11D). However, it should be noted that increased turbulence is usually associated with changes in other factors (e.g. local nutrient supply, light, temperature, seiche activity), which may also influence the distribution of these and other phytoplankton species.

Several of the more common species of filamentous blue-green algae reported to be typical of eutrophic conditions (e.g. Rawson, 1956; Hutchinson, 1967; Findlay and Kling, 1975) appear to be better indicators of general

trophic conditions in Lake Memphremagog, particularly Oscillatoria Redekei, O. rubescens, Aphanizomenon flos-aquae and A. gracile. All of these species showed decreased mean seasonal and absolute abundances with lower total phosphorus levels (Figs. A-1-A-4; Table 2). However, on a finer scale, the decline of the large populations of Oscillatoria Redekei in July 1976 at Stations 1-3 was not immediately associated with changes in average epilimnetic total phosphorus but appeared to correspond with a decrease in the relative stability of the water column (Figs. 11A-11D), in general keeping with the theory that buoyancy-regulating blue-greens require well-stratified conditions for optimal growth (e.g. Fogg et al., 1973). Similarly, small surface blooms of Anabaena flos-aquae in June 1977 at Stations 1-3 appeared to correspond more with increased turbulence than any consistent changes in levels of total phosphorus at these stations (Figs. 8-A-C; B-6a, b, c, Appendix B). Surface blooms of A. flos-aquae were also observed subsequent to this study in Central Basin in 1978 and 1979, when there was a further decrease in phosphorus levels throughout the lake (Kalff, unpublished), and even as early as 1881[1] (Cushing, 1925), when nutrient levels in Lake Memphremagog were also probably lower[2]. Thus it

---

[1]The species was described as "a gelatinous ball (of) numerous unbranched beaded filaments", and actually diagnosed by Sir William Osler as Nostoc minutissimum, although this is probably incorrect since Nostoc is not generally found in open water habitats, while Anabaena flos-aquae appears to be typical of this lake.

[2]In 1975, the Newport Sewage Plant contributed an estimated minimum of 30% of the total phosphorus loading to the lake as a whole (Carlson et al., 1979).

appears that the distribution of A. flos-aquae within Lake Memphremagog bears little relationship to the general trophic status of the lake, although dense populations of this species are usually associated with eutrophic conditions (e.g. Hutchinson, 1967). However, it should again be pointed out that the collection method (i.e. tube, surface or discreet depth samples) may greatly influence the apparent relative contribution of each species to total phytoplankton biomass, particularly that of buoyancy-regulating forms. Thus, for example in 1977, over the entire epilimnion, A. flos-aquae showed only brief dominance at some stations (Figs. A-1-A-4) although the surface bloom was visible at most stations for approximately 3 weeks.

To reiterate, spatial and temporal changes in levels of total phosphorus in Lake Memphremagog were not consistently reflected by the patterns in the relative abundance of the major phytoplankton species and taxonomic groups; moreover, fairly appreciable shifts in the taxonomic composition of the phytoplankton communities were not always attributable to changes in total phosphorus. It appears that the range of phosphorus concentrations during the period of this study was not sufficient to produce recognisable changes in the dominant algal species, and that within this range, other factors had a more immediate influence on species distributions.

Thus, the occurrence of so-called 'indicator' species generally shows little relationship to lake trophic status, mainly because the concept of an indicator species remains poorly defined, although it is generally considered (e.g. Rawson, 1956; Hutchinson, 1967; Tarapchak and Stoermer, 1976) that such species should be high in relative abundance. However,

from the ubiquitous distributions of some diatom and Cryptophycean (see Section 1) species it is apparent that a high relative abundance under oligotrophic conditions is not necessarily indicative of a trophic preference: such species may show a more seasonal, but equally high relative contribution to total biomass with increasing eutrophication. In addition, the overall contribution of major species to total biomass may be largely biased by sampling frequency and technique, particularly where there are strong seasonal or spatial differences in species composition. Therefore, in order to assess trophic level on the basis of species assemblages, a more meaningful definition of trophic preference is required, which would take such factors into account and require standard sampling and enumeration techniques. Even so, the interpretation of changes in the phytoplankton species composition may still be confounded by the seemingly intrinsic variability of natural systems, which may defy predictions on a species level. For example, Schindler (1975) found that the addition of similar quantities of fertilizer to two Shield lakes of comparable morphometry and original chemistry and phytoplankton flora resulted in the production of major blooms in both lakes, but with the dominant species and timing of the blooms differing between lakes and even in the same lake between years. It is evident from this and the previous Section (1) that major shifts in species composition and dominant cell morphology may be related to changes in factors other than, or in addition to, nutrients and thus the use of 'indicator' species as a gauge of trophic level will have limited success: trophy is more suitably measured by simpler parameters, such as total biomass, chl*a* or total

phosphorus (e.g. Vollenweider, 1969; Schinder, 1975; Carlson, 1977) since these are more sensitive to general changes in the aquatic community.

Chapter 2

The relationship between the distribution of phytoplankton morphological groups and trophic level within Lake Memphremagog, 1976-1977.

Introduction

One of the simplest morphological characteristics of a phytoplankton community is cell size, which has been shown to be significantly related to trophic level (Section 1). However, from the considerable scatter about the regression lines (Figs. 4B-6B), it is apparent that factors other than nutrients also influence phytoplankton size distribution. Similarly, in the previous chapter it was found that within the range of total phosphorus levels encountered in Lake Memphremagog during 1976-1977, shifts in algal species composition were not necessarily associated with changes in nutrient concentrations.

Since aspects of cell morphology in addition to size should influence the interaction of species with their immediate environment, they should also play a role in phytoplankton succession. For example, sinking rates may be modified by buoyancy-regulating devices such as flagella and gas vacuoles (e.g. Fogg, 1975), cell shape and the presence of extensions or protuberances (e.g. Hutchinson, 1967; Smayda, 1970), and colony size and morphology (e.g. Fogg et al., 1973; Titman and Kilham, 1976). Sinking rates may in turn affect nutrient uptake (e.g. Smayda, 1970; Hecky and Kilham, 1974) and photosynthetic rates (e.g. Fogg et al., 1973). Cell or colony shape also appear to influence zooplankton

ingestion and assimilation rates (e.g. Porter, 1977; Gliwicz, 1977; Webster and Peters, 1978).

This chapter briefly examines the data obtained from phytoplankton samples at the four stations in Lake Memphremagog during 1976 and 1977 for any relationship between trophic level (total algal biomass) and the distribution of a number of groups defined by different morphological criteria.

Methods

Sampling and enumeration techniques are as outlined and discussed in Chapter 1 of this section. Phytoplankton species were assigned to one of the following morphological groups (see Table C-1):

- P: non-flagellate, <10 µm (diatoms, greens, blue-greens)
- Q: flagellate, <10 µm (Chrysophyta, Cryptophyceae, greens)
- A: non-flagellate, <35 µm (blue-greens, greens, diatoms)
- B: flagellate, <35 µm (Chrysophyta, Cryptophyceae, green algae)
- C: colonial, low surface-to-volume ratio (s/v) (generally spherical and ellipsoidal greens, blue-greens and Chrysophyta; often in a gelatinous matrix)
- D: colonial, high s/v (generally star or chain-forming diatom and Chrysophyta species; some coenobia)
- E: flagellate, >35 µm (greens, dinoflagellates, cryptoflagellates, some Chrysophyta)
- F: filamentous (blue-greens, greens, diatoms)
- G: non-flagellate, >35 µm, low s/v (some diatoms, desmids and greens)

H: non-flagellate, >35 μm, high s/v (diamtoms, greens)

Results and discussion.

The seasonal contributions of the morphological groups to total biomass at each station are shown in Figs. 12A-12D. The nannoplankton fractions (groups P, Q, A and B) are dealt with in detail in Section 1. Within the netplankton fraction (<35 μm), flagellates (group E) and non-flagellates with low s/v (group G) contributed little towards total phytoplankton biomass and exhibited no distinguishable trends between stations and years (Figs. 12A-12D). Non-flagellates with a high s/v (group H) made greater relative contributions to total biomass, and while their mean seasonal % contribution declined at all stations in 1977, when total phosphorus levels in the lake were generally lower (Table 8), the relative importance of this group showed no patterns between stations either year despite significant N-S nutrient gradients. Thus, distributions of unicellular netplankton groups within Lake Memphremagog during 1976-1977 do not appear to have been primarily influenced by changes in levels of total phosphorus.

The two groups of colonial forms (with low and high s/v; groups C and D respectively) showed generally similar trends in mean seasonal % contribution to total phytoplankton biomass, increasing towards the more oligotrophic North Basin both years (Table 12), and at all stations during the second, more phosphorus-deficient year (Table 8, Section 1). While increases in the relative importance of these two groups did not always coincide, they both showed a greater relative and absolute abundance in mid- to late summer (Figs. 12A-12D), particularly in 1977, when total phosphorus

Table 12. Relative contribution to total phytoplankton biomass (%) of major morphological groups within the netplankton (<35 µm) at the 4 stations in Lake Memphremagog, 1976–1977.

Station	Year	C colonial low s/v	D colonial high s/v	E <35µm flagellate	H <35µm non-flagellate high s/v	F filament
1	1976	2.5	5.4	9.1	17.4	31.9
	1977	9.9	10.6	7.1	9.0	17.7
2	1976	1.2	6.7	6.6	19.7	27.0
	1977	9.7	11.9	5.4	13.6	13.3
3	1976	4.1	11.2	10.2	15.3	24.3
	1977	11.0	16.4	6.1	6.0	7.0
4	1976	12.2	10.3	5.0	15.4	19.3
	1977	14.5	12.3	3.9	11.9	5.4

levels were generally relatively low (Figs. 11A-11D). Thus, while it has been suggested that a high s/v should facilitate nutrient uptake (e.g. Findenegg, 1965), during this period of study within Lake Memphremagog, there was no clear resolution between patterns of unicellular and colonial netplankton groups broadly divided according to their s/v in relationship to changes in total phosphorus, and it is likely that other factors (e.g. turbulence, grazing pressure) also play an important role in selecting for optimal s/v.

Filamentous species (group F) accounted for a fairly large proportion of total biomass in 1976 at all stations (Table 12; Figs. 12A 12D), but showed a general decrease in their relative importance towards the North Basin both years, and at all the stations between 1976 and 1977. Seasonal patterns in the relative abundance of this group were generally similar between stations each year, but differed between years. In 1976, the % contribution of filamentous forms to total biomass was high throughout most of the growing season, while in 1977, the relative importance of this group did not show any conspicuous increase until late summer (Figs. 12A-12D). However, since short term changes in the abundance of the dominant filamentous species in 1976 (Oscillatoria Redekei) did not appear to be directly related to fluctuations in total phosphorus (Chapter 1, Section 2), it is likely that differences between years in the seasonal patterns of this group were more immediately influenced by other factors.

Thus, while the relative abundance of several morphological groups within the netplankton of Lake Memphremagog showed little relationship with

Fig. 12A-12D. % contribution to total phytoplankton biomass of morphological groups at Station 1 (Fig. 12A), Station 2 (Fig. 12B), Station 3 (Fig. 12C) and Station 4 (Fig. 12D) in Lake Memphremagog, 1976-1977. Legend (see text):

10 - <10 µm

35 - <35 µm

C - colonial, low s/v

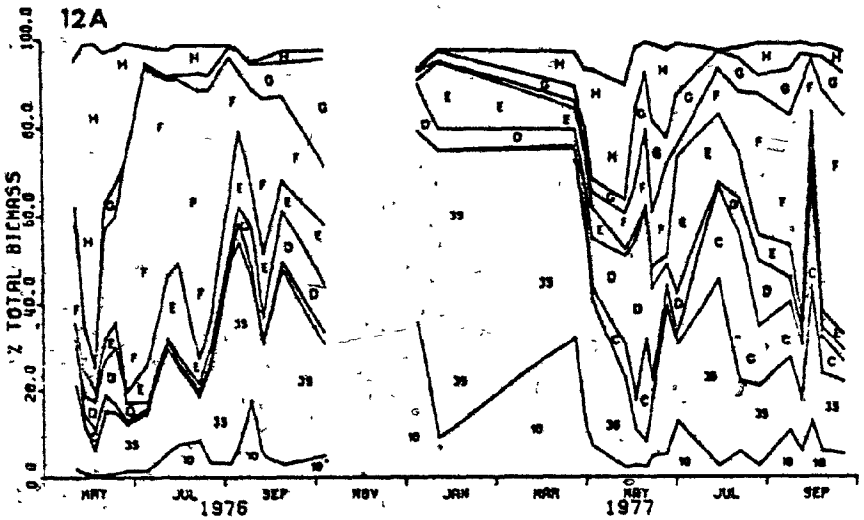
D - colonial, high s/v

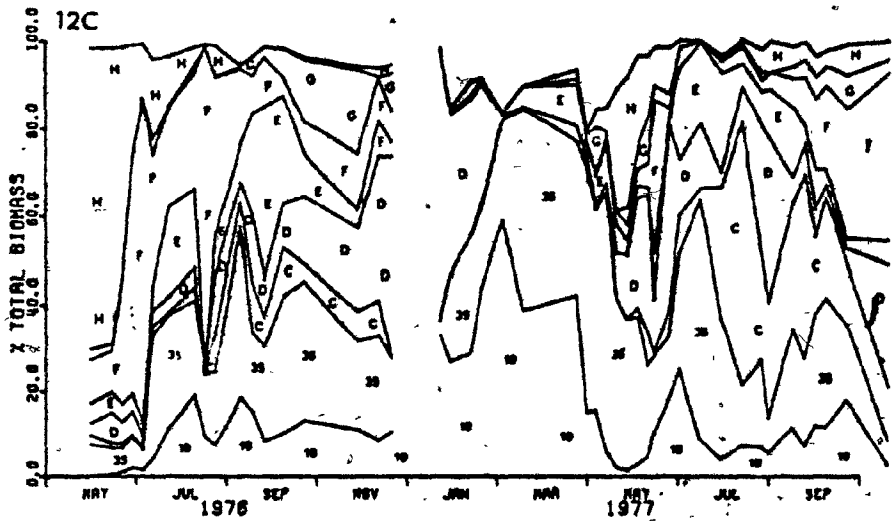
E - flagellate, >35 µm

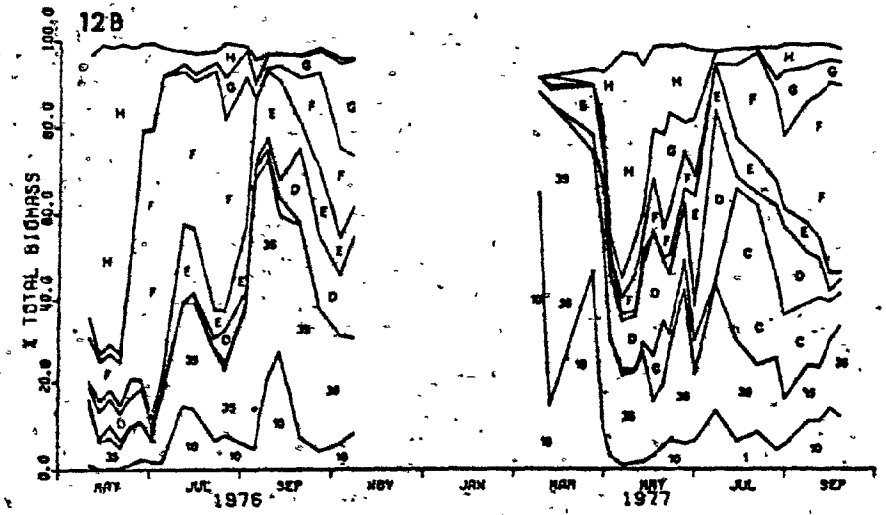
F - filamentous

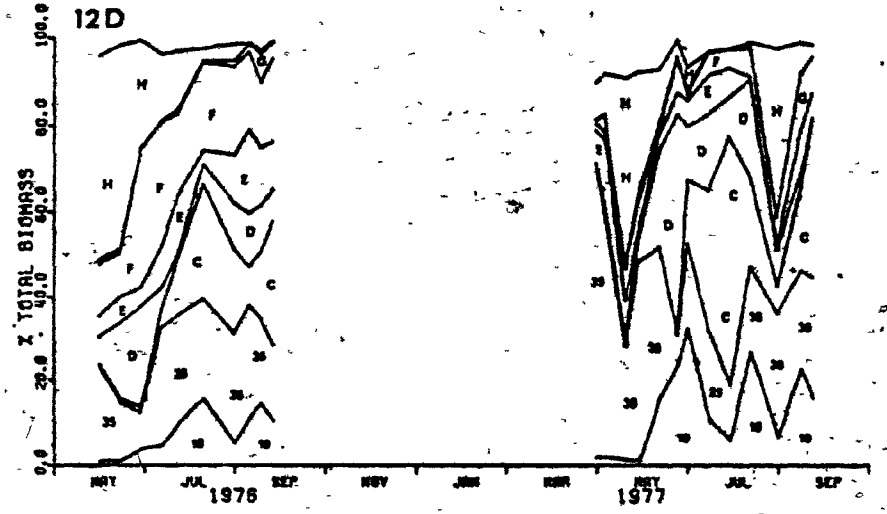
G - non-flagellate, >35 µm, low s/v

H - non-flagellate, >35 µm, high s/v


12A
% TOTAL BIOMASS
100.0
60.0
40.0
20.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


12C
% TOTAL BIOMASS
100.0
60.0
40.0
20.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


12B
% TOTAL BIOMASS
100.0
60.0
40.0
20.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


12D
% TOTAL BIOMASS
100.0
60.0
40.0
20.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

mean seasonal concentrations of total phosphorus during 1976 and 1977, decreasing levels of this nutrient did appear to be associated with an increase in the mean relative importance of colonial species, and a decrease in that of filamentous forms. However, seasonal patterns of phytoplankton grouped according to broad morphological criteria do not appear to be primarily attributable to short-term changes in total phosphorus concentrations.

Chapter 3

Measurements of community structure

Introduction

Any single given index of species richness, diversity or equitability will not provide a comprehensive measurement of community structure (e.g. Kalff and Knoechel, 1978), since some indices are more strongly influenced by the total number of species observed by the investigator, while others are more sensitive to species-evenness, or the distribution of the dominant species in the sample (Hill, 1973; Eloranta, 1976). However, even where several indices have been used, little relationship between phytoplankton community structure and trophic level has been found (e.g. Taraphak and Stoermer, 1976; Willén, 1976; Eloranta, 1976). This may be because, as has been pointed out (Hill, 1973; Eloranta, 1976, 1978; Kalff and Knoechel, 1978), these indices are usually calculated using numerical abundance as a measure of the relative importance of each species; although even numerical abundance is not clearly definable for filamentous and colonial forms (Eloranta, 1978). Furthermore, cell numbers generally over emphasise the relative proportion of smaller size fractions (Paasche, 1960), since nannoplankton frequently account for a major proportion of the total cell numbers even under eutrophic conditions (e.g. Pavoni, 1963; Kristiansen, 1971). However, the relative abundance of the nannoplankton fraction generally decreases with increasing trophic level (Section 1; Figs. 4 B, 5 B, 6 B) and measurements of community structure may show some significant response to nutrient changes if these measurements are based on relative biomass rather than numerical abundance (Eloranta, 1976, 1978); in fact, Eloranta (1978) found a significant negative relationship between species evenness and total biomass

if the index was calculated using biomass as a measure of relative importance, while the relationship was not significant if cell number was used. Furthermore, Margalef (1965) argues that species evenness should decrease with increasing trophy, and while several authors report that relatively few species generally account for a major portion of phytoplankton biomass (e.g. Kalff et al., 1975; Jumppanen, 1976; Willén, 1976), this number does appear to be higher in nutrient-poor waters (Willén, 1976).

Using species data obtained from the four stations in Lake Memphremagog, the relationships between community structure and trophic level (as measured by total biomass) were examined to test the hypothesis that species evenness and diversity should decrease with increasing eutrophy if biomass is used as a measure of the relative importance of individual species. Diversity was expressed by diversity numbers (after Hill, 1973), which are based on the more commonly used Shannon-Weaver and Simpson's index.

Methods

Three diversity numbers were calculated, N_o, N_1 and N_2, where:

N_o = total number of species present

N_1 = exp (H), where H is the Shannon-Weaver index given by the equation: $H = \Sigma p_i \ln p_i$

$N_2 = \frac{1}{c}$ where c is Simpson's index, given by the equation: $c = \Sigma(p_i)^2$

The relative importance of each species, p_i, was measured by its relative biomass rather than its numerical abundance. Evenness was calculated

according to the equations:

$$E_1 = \frac{N_1}{N_o} \qquad E_2 = \frac{N_2}{N_1}$$, which according to Hill (1973)

generally gives a better measure of this aspect of community structure than the more commonly used J (where $J = \ln (N_1)/\ln (N_o)$; Pielou, 1969).

The relationships between these indices and total biomass (B) were examined using the models

$$\text{Log } (B) = a + bN_o + cN_1 \qquad -1)$$

$$\text{Log } (B) = a + bN_o + dN_2 \qquad -2)$$

$$\text{Log } (B) = a + bN_o + cE_1 \qquad -3)$$

$$\text{Log } (B) = a + bN_o + CE_2 \qquad -4)$$

These regressions were calculated using all data from each station and year, for separate years, and for individual stations within each year.

In addition, seasonal patterns in the relative proportions of total biomass accounted for by the 1, 2, 4, 8, 16 and 32 most dominant species was examined for each of the four stations.

Results

Regressions 1), 2) and 3) showed significant slopes for all data ($p < .01$), for individual years ($p < .01$) and for individual stations within years. The fourth model did not provide a good fit to the data. For all regressions, the coefficient of N_o was positive, indicating that with increasing total biomass, there was a significant increase in the numbers of species N_o ($r = 0.57$, $p < .001$ for all samples). Conversely, the coefficients of N_1, N_2 and E_1 were all negative ($r = 0.83$, $r = 0.76$,

$r = 0.89$; $p < .001$; respectively), implying a significant decrease in diversity numbers N_1 and N_2 and evenness E_1 with increasing total biomass.

In general, the single most dominant species accounted for 30% or less of the total biomass (Figs. 11A-11D) although in spring and early summer, 1976 relatively high proportions (60-70%) of the total biomass were attributable to one species at Station 1, 2 and 3 (Diatoma tenue var. elongatum, followed by Oscillatoria Redekei -- see Appendices A and C). Furthermore, to obtain 90% of the total estimated biomass up to 16 or even 32 species had to be normally enumerated (Figs. 11A-11D).

Discussion

A significant increase in the total numbers of species N_o with increasing total biomass was similarly observed by Eloranta (1978), who noted that this relationship may be reversed if the number of individuals counted is kept constant, since the numbers of species encountered per unit volume of water generally decreases with increasing total biomass. However, since N_o is generally dependent on sample size (Hill, 1973; Eloranta, 1978), it is perhaps not surprising to find that this diversity number alone shows a weaker correlation with total biomass ($r = 0.57$) than when combined in a model with N_1 and N_2 ($r = 0.83$, $r = 0.76$), since the indices H and c on which these latter two are based are less influenced by sample size, except for very small samples (Eloranta, 1978). However, despite an increase in the total number of species (N_o) with increasing total biomass, N_1 and N_2 show a significant decrease, implying the observed decrease in species evenness E_1, or an increase in the relative importance

of the most abundant species. This is graphically illustrated in Figs. 13A-13D, where many of the peaks in total biomass coincide with an increase in the relative distribution of one or a few species. Willén (1976a) suggests that it is necessary to enumerate only about 6 of the most abundant species in water samples from eutrophic lakes (of mean total biomass between 2300-7000 μgl^{-1}; Willén, 1976b) and 7-8 in samples from oligotrophic lakes (mean total biomass of 200 μgl^{-1}; Willén, 1976b) to obtain an estimate of approximately 90% of the total phytoplankton biomass. However, in Lake Memphremagog, even at extremely high levels of total biomass (6000-7000 μgl^{-1}), approximately 90% of the total biomass was attributable to at least 8 species, and under conditions of lower total biomass, to between 16-32 species. It is therefore apparent that although species diversity and evenness (calculated using biomass as a measure of the relative importance of each species) show a significant decrease with increasing total biomass, caused by an increase in the relative dominance of one or more of the most abundant species, even under conditions of very high total biomass, at least 8 species should be enumerated to obtain a good approximation of total biomass in Lake Memphremagog. Where phytoplankton standing crop is lower, this number should be increased to between 16 and 32 species.

Figs. 13A-13D. % total biomass attributable to 1, 2, 4, 8, 16 and 32 species (below) at the four stations and associated total biomass.

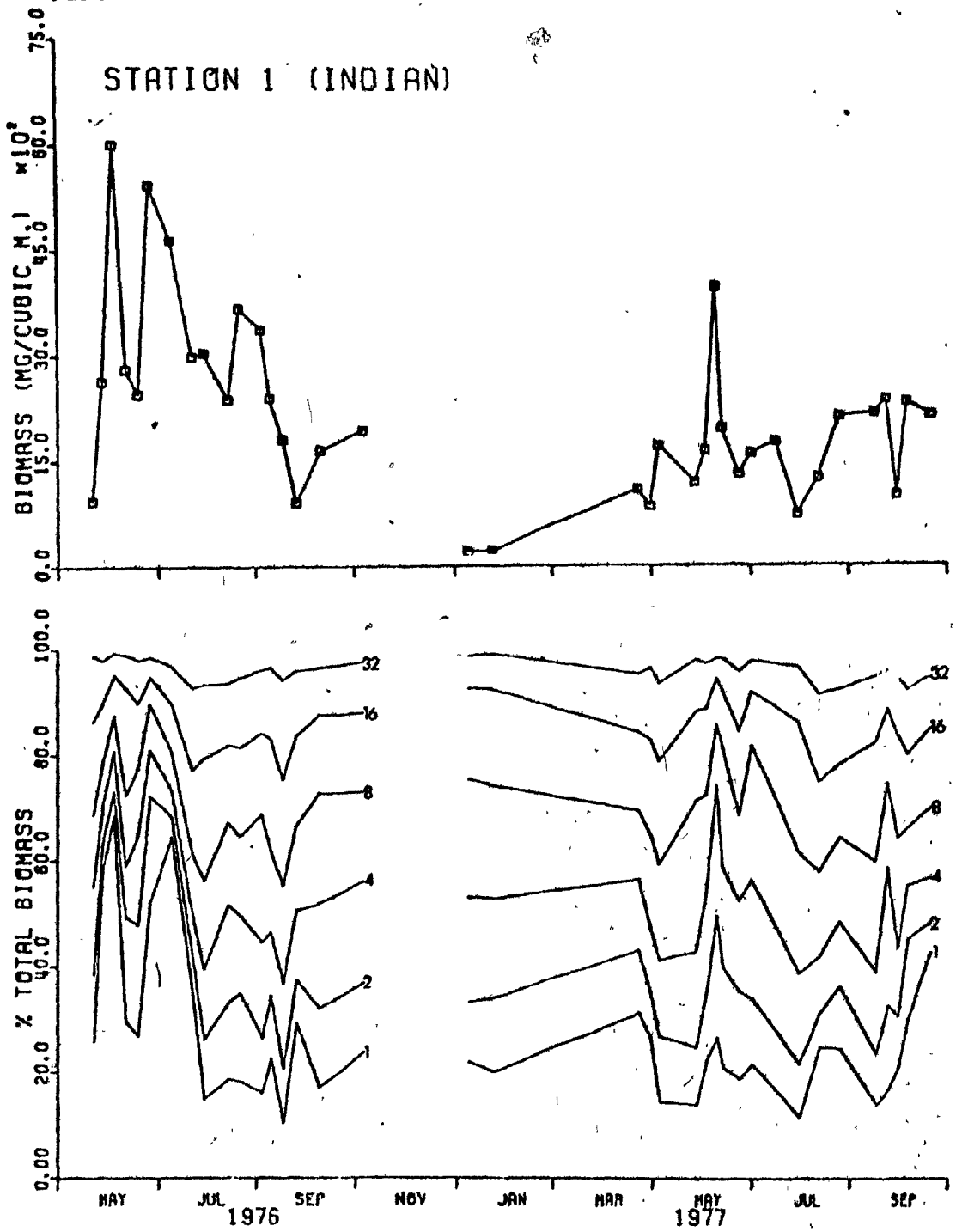
12A - Station 1 (mesotrophic)

12B - Station 2 (mesotrophic)

12C - Station 3 (oligotrophic)

12D - Station 4 (oligotrophic)

13A


STATION 1 (INDIAN)
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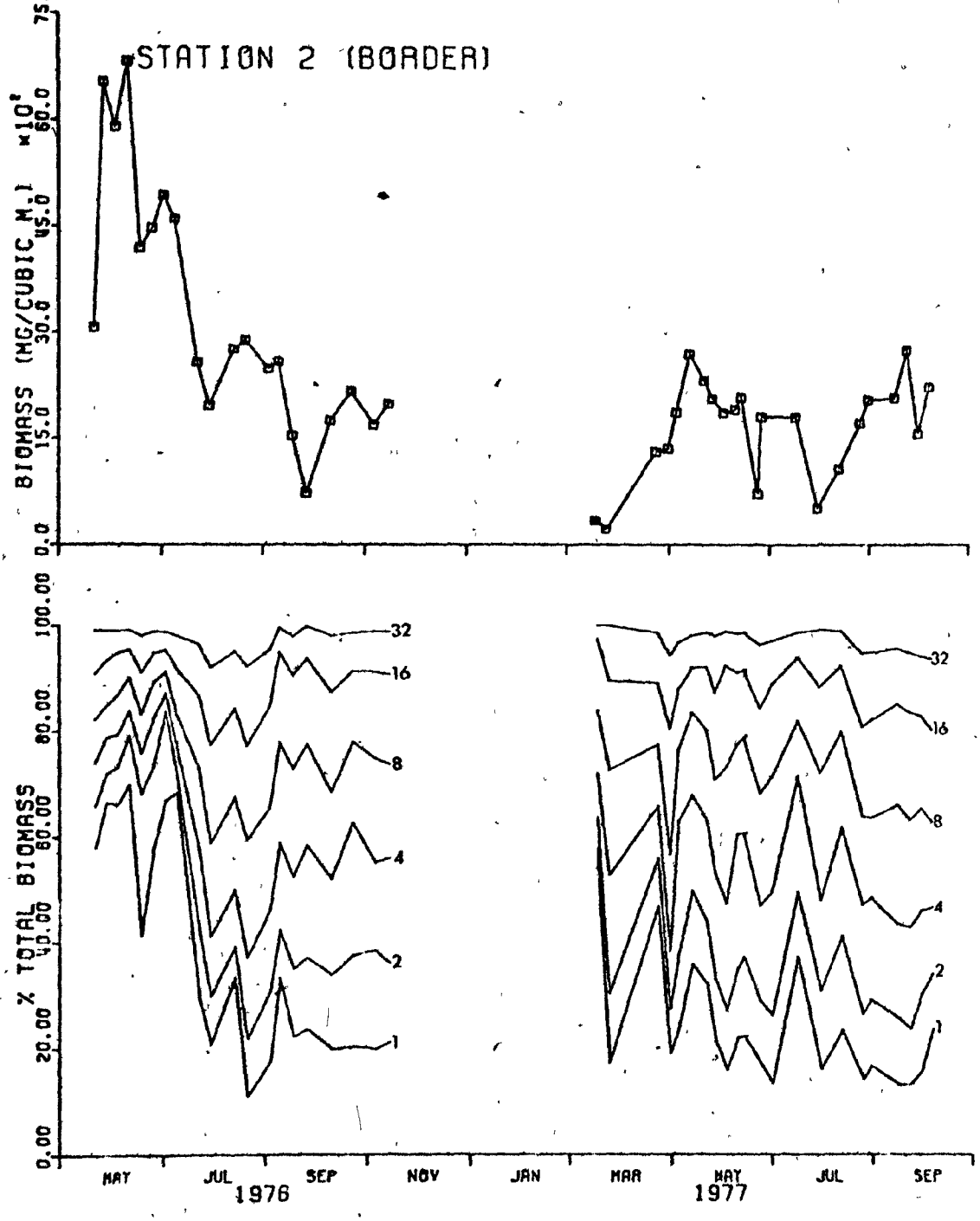
75.0
60.0
45.0
30.0
15.0
0.0
% TOTAL BIOMASS
100.0
80.0
60.0
40.0
20.0
0.00
32
16
8
4
2
1
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

13B


STATION 2 (BORDER)
BIOMASS (MG/CUBIC M.) x10
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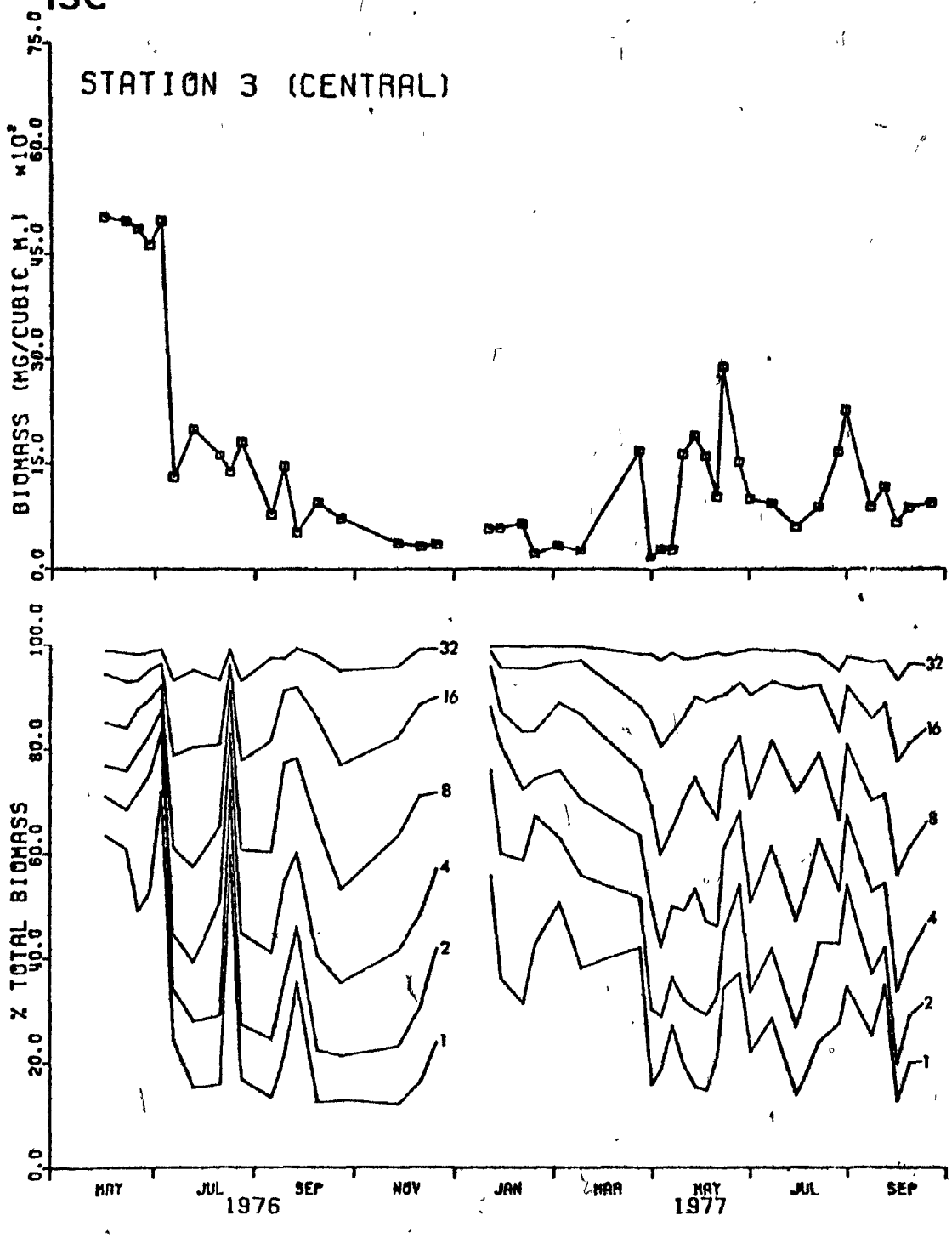
60.0
45.0
30.0
15.0
0.0
% TOTAL BIOMASS
100.00
80.00
60.00
40.00
20.00
0.00
32
16
8
4
2
1
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

13C


STATION 3 (CENTRAL)
BIOMASS (MG/CUBIC M.) ×10³
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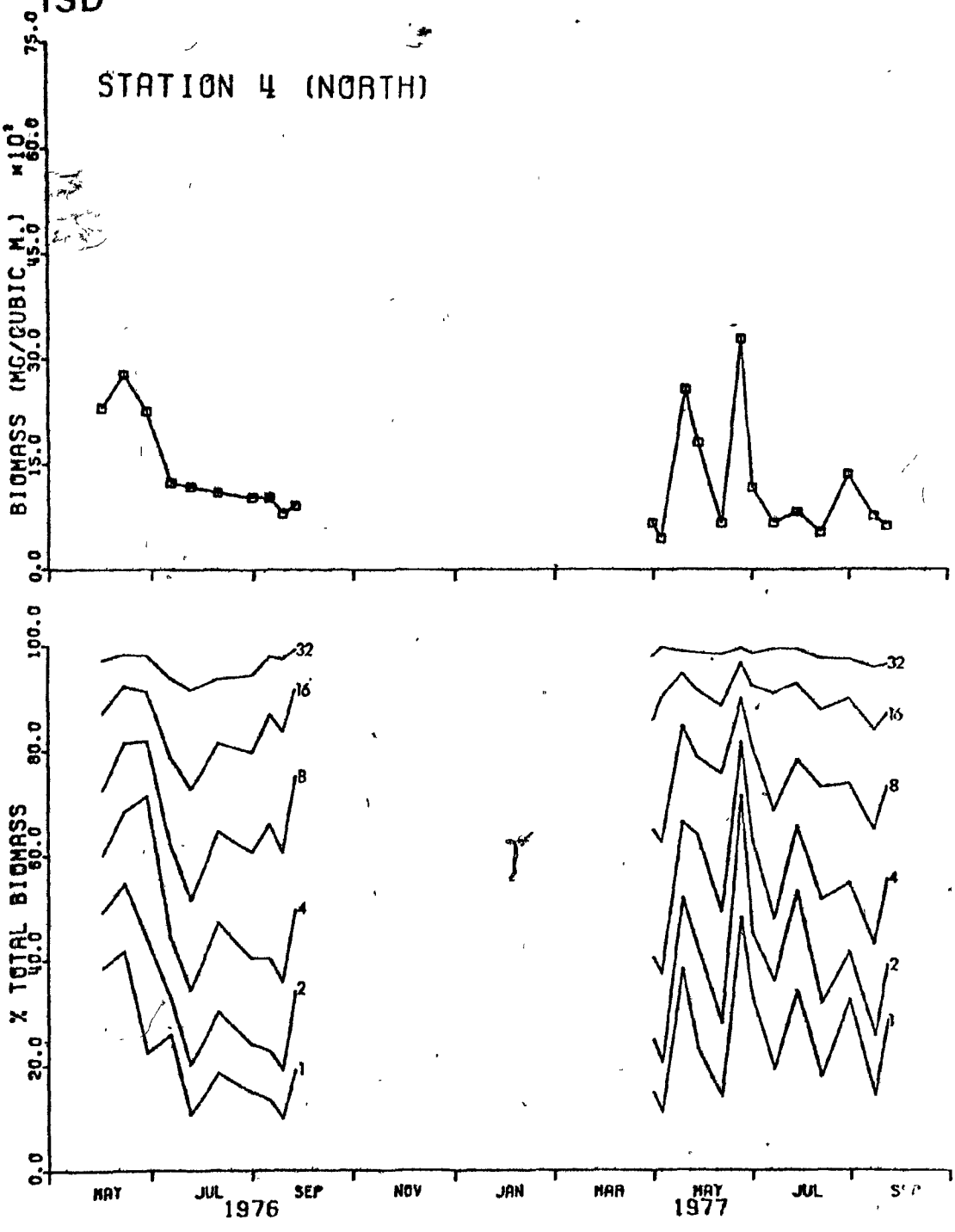
60.0
45.0
30.0
15.0
0.0
% TOTAL BIOMASS
100.0
80.0
60.0
40.0
20.0
0.0
32
16
8
4
2
1
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

13D


STATION 4 (NORTH)
BIOMASS (MG/CUBIC M.) ×10³
75.0
60.0
45.0
30.0
15.0
0.0
% TOTAL BIOMASS
100.0
80.0
60.0
40.0
20.0
0.0
32
16
8
4
2
1
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
1976
1977

Chapter 4

General summary of the results and conclusions of Sections 1 and 2.

Within Lake Memphremagog (1976-1977), netplankton species (> 35 μm) showed a greater tendancy towards seasonal occurrences, while nannoplankton species (< 35 μm) were generally more ubiquitous. With increasing total biomass, there is a significant increase in nannoplankton biomass ($p < .0001$), but a significant decrease in the relative proportion of this fraction ($p < .0001$) both within Lake Memphremagog and among a number of lakes covering a wide range of trophic levels. A similar significant relationship was found for % nannoplankton (<35 μm) and total chla within Lake Memphremagog, but not for production. Although some correlations between % nannoplankton biomass and total phosphorus, light and temperature were statistically significant, the large amount of residual variance indicated that nutrients have a more indirect influence on phytoplankton size distributions, and it is suggested that differential grazing losses may play an important role in phytoplankton size selection.

Spatial and temporal changes in total phosphorus levels within Lake Memphremagog were not always reflected by the major taxonomic groups and dominant species, particularly on a short-term basis. Conversely, conspicuous shifts in dominant phytoplankton assemblages were frequently not associated with changes in total phosphorus, which was similarly true of the distribution and relative abundance of a number of 'indicator' species. It appears that within the range of total phosphorus concentrations observed during 1976-1977 in Lake Memphremagog (9-29 $\mu g l^{-1}$), factors other than this nutrient have a more immediate influence on the

taxonomic composition of the phytoplankton community. Similarly, there was no clear-cut relationship between total phosphorus levels and the dominant morphology of the netplankton fraction (>35 μm), although decreased levels of this nutrient were reflected in a general decrease in the relative importance of filamentous species, and an increase in the relative abundance of colonial forms.

Thus, while total phosphorus measurements may be used to predict long-term changes in total phytoplankton biomass, they frequently bear little relationship to short-term fluctuations in species composition.

Measurements of community structure showed significant relationships with trophic level (total biomass) within Lake Memphremagog if biomass (rather than numerical abundance) was used as a measure of the relative importance of each species. With increasing total biomass, there was a significant increase in the number of species observed, but a significant decrease in community diversity and evenness. Furthermore, to obtain a good estimate of total phytoplankton biomass (> 90%) at least 8 and, where biomass is low, up to 16 or 32 species should be enumerated.

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APPENDIX A.

Phytoplankton succession at the four stations in Lake Memphremagog.

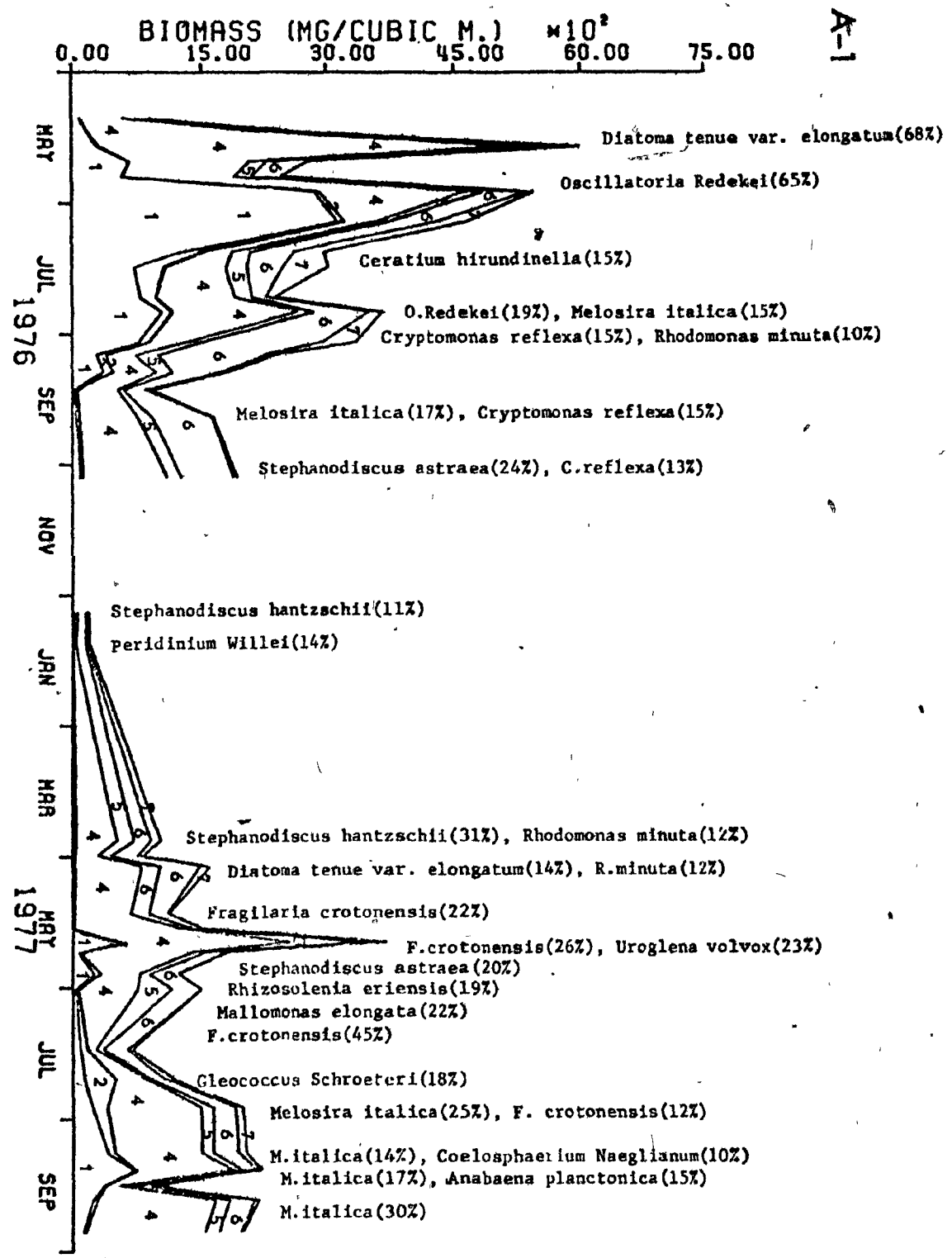
A complete listing of all species and their relative frequency of occurrence is given in Appendix C (Table C-1), together with those species contributing to 10% or more of the total (Table C-2) and nannoplankton biomass (Tables C-3, C-4).

Station 1: Indian Point

In 1976, ice-out occurred between the first and second week in April in South Basin, but sampling did not begin until late May. Early samples at this most eutrophic (Table 8, Section 1) and shallow station ($z = 9.5$ m) were marked by a sharp increase in Diatoma tenue var. elongatum, which peaked early in June (4/6/76) at approximately 4000 $\mu g l^{-1}$ (70% total biomass) (Fig. A-1). Its subsequent decline followed the onset of a period of stratification (Fig. 11A, Section 2), and was initially accompanied by an increase in the abundance of other diatoms (Fragilaria crotonensis, Stephanodiscus astraea and Rhizosolenia eriensis), small flagellates (Rhodomonas minuta), and a filamentous blue-green (Oscillatoria Redekei). The latter subsequently increased rapidly and became dominant in early July (maximum 3000 $\mu g l^{-1}$; 65% total biomass), following which it showed a fairly consistent decline coincident with an increase in turbulence (Fig. 11A, Section 2), although it still accounted for 17% of the total biomass by mid August (Fig. A-1). The decrease in the abundance of O. Redekei was initially followed by an increase in Cryptophyceae (Cryptomonas reflexa, C. Marssonii and Rhodomonas minuta) and large

Fig. A-1. Contribution of major taxonomic groups and dominant species to total phytoplankton biomass at Station 1 (mesotrophic) in Lake Memphremagog, 1976-1977.

Legend: 1 - Cyanophyta; 2 - Chlorophyta; 3 - Euglenophyta; 4 - Bacillariophyta; 5 - Chrysophyta; 6 - Cryptophyceae (Pyrrophyta); 7 - Dinophyceae (Pyrrophyta).


BIOMASS (MG/CUBIC M.) ×10²
0.00
15.00
30.00
45.00
60.00
75.00
A1
MAY
JUL
1976
SEP
NOV
JAN
MAR
MAY
1977
JUL
SEP
Diatoma tenue var. elongatum(68%)
Oscillatoria Redekei(65%)
Ceratium hirundinella(15%)
O.Redekei(19%), Melosira italica(15%)
Cryptomonas reflexa(15%), Rhodomonas minuta(10%)
Melosira italica(17%), Cryptomonas reflexa(15%)
Stephanodiscus astraea(24%), C.reflexa(13%)
Stephanodiscus hantzschii(11%)
Peridinium Willei(14%)
Stephanodiscus hantzschii(31%), Rhodomonas minuta(12%)
Diatoma tenue var. elongatum(14%), R.minuta(12%)
Fragilaria crotonensis(22%)
F.crotonensis(26%), Uroglena volvox(23%)
Stephanodiscus astraea(20%)
Rhizosolenia eriensis(19%)
Mallomonas elongata(22%)
F.crotonensis(45%)
Gleococcus Schroeteri(18%)
Melosira italica(25%), F. crotonensis(12%)
M.italica(14%), Coelosphaerium Naeglianum(10%)
M.italica(17%), Anabaena planctonica(15%)
M.italica(30%)

dinoflagellates (Peridinium Willei and especially Ceratium hirundinella), and in August, by an assemblage of filamentous species, notably O. Redekei, Mougeotia sp., Aphanizomenon gracile, Melosira granulata, M. italica subsp. subarctica (hitherto referred to a M. italica), and Oscillatoria rubescens. Melosira italica showed a continued increase to a maximum in mid-August (18% total biomass), when it was codominant with O. Redekei. In September, these species were succeeded by a second increase in Cryptophyceae (Cryptomonas reflexa and Rhodomonas minuta), dinoflagellates (Ceratium hirundinella) and blue-greens (Oscillatoria rubescens). The Cryptophyceae dominated until late September, when there was a complete break-down of stratification (Fig. 11A, Section 2) and a second brief pulse of M. italica. This was also accompanied by an increase in Fragilaria crotonensis and Stephanodiscus astraea, with the last becoming the dominant species early in November 24% total biomass) (Fig. A-1).

No further samples were collected at this station before ice-cover, first observed in South Basin on December 4th. Subsequently, two 5 m tube samples were collected through the ice in January, 1977 and examined. Total biomass was very low on both occasions (200 μgl^{-1}), and dominated by small flagellates (Chromulina, Ochromonas spp.) and Stephanodiscus hantzschii. At the end of January, Peridinium Willei and Asterionella formosa had become present in low numbers.

The first open water sample in 1977 (24/4/77) was taken approximately 1-2 weeks after ice-out in South Basin. The water column was well-mixed (Fig. 11A, Section 2) and total biomass was already 1000 μgl^{-1}, dominated by S. hantzschii (30% total biomass) and Rhodomonas minuta. The former

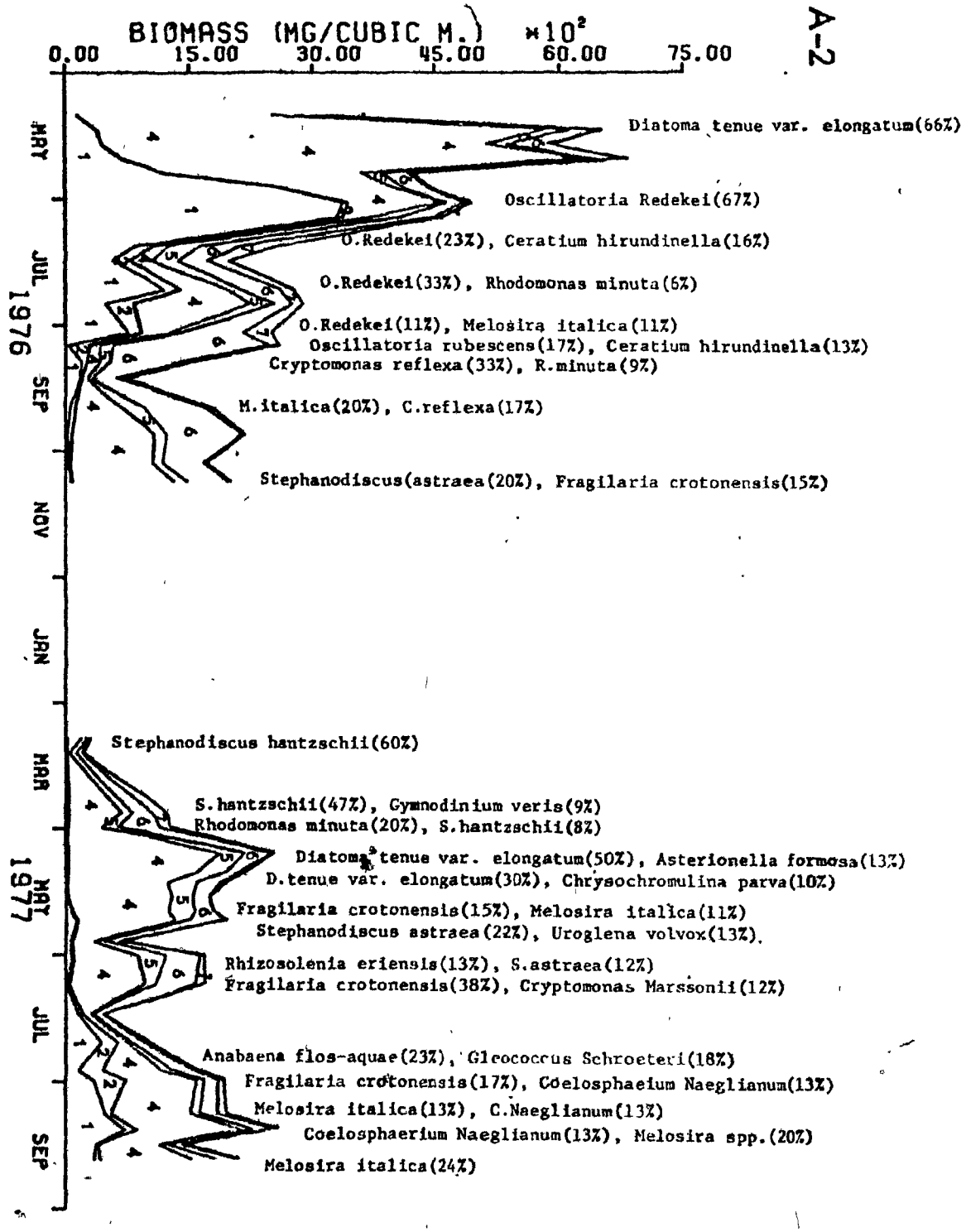
species showed a rapid decline and by the second week in May, Diatoma tenue var. elongatum was dominant (14% total biomass). However, this species did not reach the biomass observed the previous spring, and following the onset of stratification (approximately 12/5), declined to a low abundance by the end of May. Other concurrent species which also made significant contributions to the total biomass during May were D. tenue var. tenue, Asterionella formosa and Synedra ulna var. danica. In June, the dominant diatom species shifted to Fragilaria crotonensis and Stephanodiscus astraea, which peaked the second week, accompanied by a brief pulse of Uroglena volvox and Anabaena flos-aquae. This coincided with a small increase in mixing depth (Fig. 11A, Section 2) and resulted in an increase in total biomass to 3000 $\mu g l^{-1}$. The decline in abundance of these species was followed by a rapid succession: Rhizosolenia eriensis and Oscillatoria limnetica (25/6), Mallomonas elongata and Cyclotella bodanica (2/7), Fragilaria crotonensis (16/7), Cryptomonas Marssonii (30/7) and Gleococcus Schroeteri (13/8) (Fig. A-1). From mid-July onward, there were frequent break downs of stratification (Fig. 11A, Section 2). As in 1976, Melosira italica appeared in late August, but remained dominant and continued to increase in biomass until the end of October, accompanied by a shifting species assemblage of Fragilaria crotonensis (26/8), Coelosphaerium Naeglianum, Melosira granulata and Anabaena planctonica. As in the previous year, there was also an increase in Stephanodiscus astraea towards the end of October.

Station 2: Border

Station 2 is characterized by somewhat lower levels of total

phosphorus (Table 8, Section 1) and is slightly deeper (z = 9.5 m) than the more southerly Station 1, but species patterns at the two stations were very similar and, in fact, biomass was generally higher at Border (Figs. A-1, A-2; Table 4, Section 1). The spring peak in 1976 of Diatoma tenue var. elongatum was larger (4700 μgl^{-1}) and extended to mid-June when this species was again succeeded by Oscillatoria Redekei; stratification was established the first week of June (Fig. 11B, Section 2). Oscillatoria Redekei attained dominance by late June at this station, reaching 3300 μgl^{-1}, a similar maximum biomass to that observed further south. Its subsequent decline in abundance coincided with a slight decrease in the relative stability of the water column (Fig. 11B, Section 2), although this species again remained dominant until late August. This decline was again associated with an increase in dinoflagellates (Ceratium hirundinella) and Cryptophyceae (Rhodomonas minuta); and in addition, with Chrysochromulina parva (Fig. A-2). As at Station 1, these species were succeeded by an assemblage of filaments: O. Redekei, Aphanizomenon gracile, Mougeotia sp., Melosira italica and M. granulata. Total biomass was generally lower than at Indian Point during this period, and M. italica did not show a sharp increase in August; moreover, Oscillatoria rubescens dominated briefly at the beginning of September prior to the second development of Cryptophyceae (Cryptomonas reflexa, Rhodomonas minuta) and dinoflagellates (Ceratium hirundinella). Fall turnover at this station again occurred at the end of September (Fig. 11B, Section 2); however, in contrast to Station 1, C. reflexa was not replaced by Melosira italica until mid-October. The

Fig. A-2. Contribution of major taxonomic groups and dominant species to total phytoplankton biomass at Station 2 (mesotrophic) in Lake Memphremagog, 1976-1977. Legend as in Fig. A-1.


BIOMASS (MG/CUBIC M.) ×10²
0.00
15.00
30.00
45.00
60.00
75.00
A-2
MAY
JUL
1976
SEP
NOV
JAN
MAR
MAY
1977
JUL
SEP
Diatoma tenue var. elongatum(66%)
Oscillatoria Redekei(67%)
O.Redekei(23%), Ceratium hirundinella(16%)
O.Redekei(33%), Rhodomonas minuta(6%)
O.Redekei(11%), Melosira italica(11%)
Oscillatoria rubescens(17%), Ceratium hirundinella(13%)
Cryptomonas reflexa(33%), R.minuta(9%)
M.italica(20%), C.reflexa(17%)
Stephanodiscus(astraea(20%), Fragilaria crotonensis(15%)
Stephanodiscus hantzschii(60%)
S.hantzschii(47%), Gymnodinium veris(9%)
Rhodomonas minuta(20%), S.hantzschii(8%)
Diatoma tenue var. elongatum(50%), Asterionella formosa(13%)
D.tenue var. elongatum(30%), Chrysochromulina parva(10%)
Fragilaria crotonensis(15%), Melosira italica(11%)
Stephanodiscus astraea(22%), Uroglena volvox(13%)
Rhizosolenia eriensis(13%), S.astraea(12%)
Fragilaria crotonensis(38%), Cryptomonas Marssonii(12%)
Anabaena flos-aquae(23%), Gleococcus Schroeteri(18%)
Fragilaria crotonensis(17%), Coelosphaeium Naeglianum(13%)
Melosira italica(13%), C.Naeglianum(13%)
Coelosphaerium Naeglianum(13%), Melosira spp.(20%)
Melosira italica(24%)

latter species remained dominant until the second week in November, when it was succeeded by Stephanodiscus astraea and Fragilaria crotonensis, as at Station 1.

Two under-ice samples from late March 1977 showed a slightly higher biomass (200 μgl^{-1}) to that found in January at Station 1, but a similar species assemblage, predominated by Stephanodiscus hantzschii, Rhodomonas minuta, and small Chrysophycean flagellates.

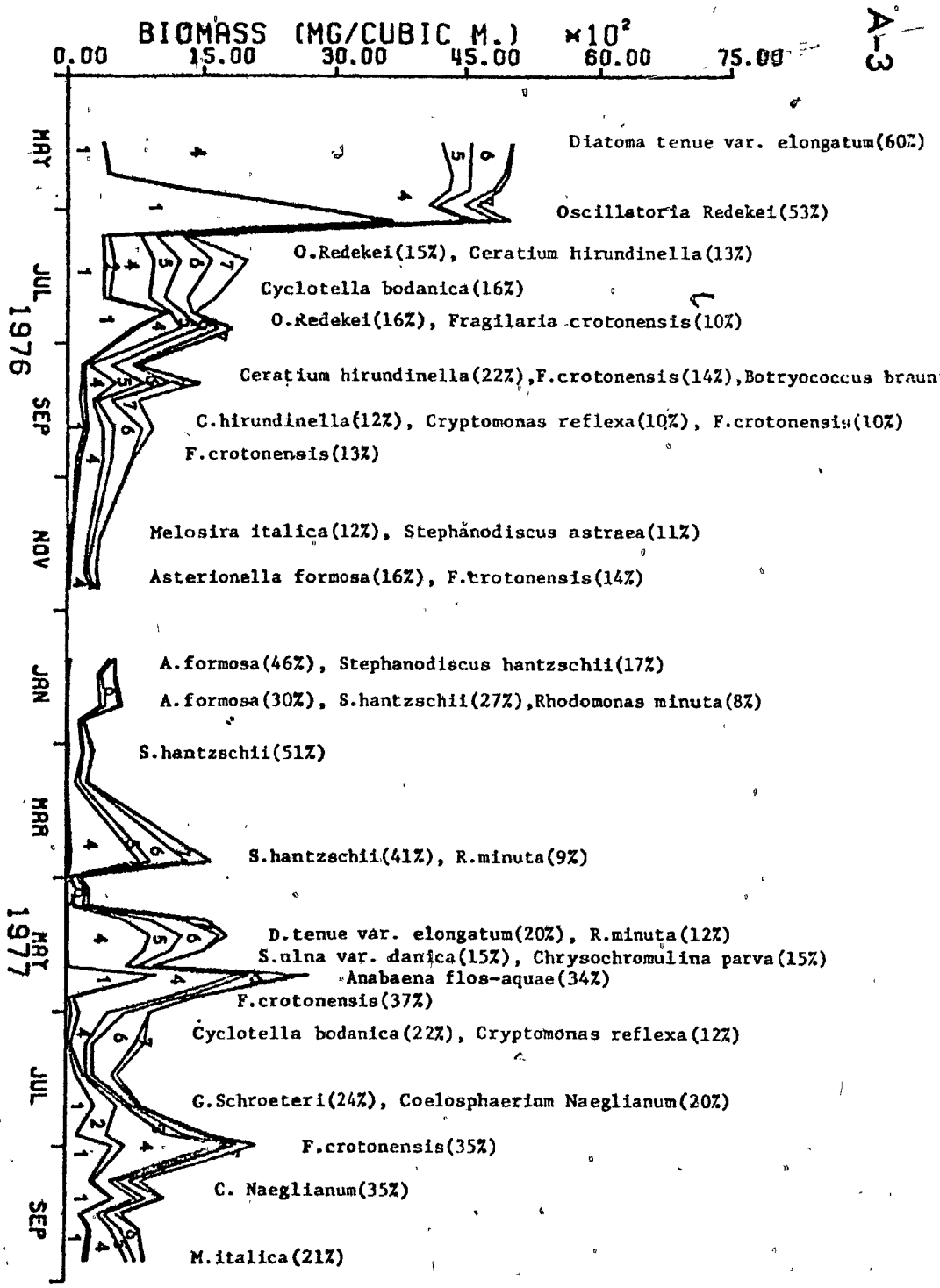
The first open-water sample (24/4/77) at Border was similar to that at Station 1 (1200 μgl^{-1}) and predominated by S. hantzschii (47% total biomass), together with Gymnodinium veris and Peridinium aciculiferum (Fig. A-2). Stephanodiscus hantzschii was again rapidly succeeded by Diatoma tenue var. elongatum, D. tenue var. tenue and Asterionella formosa. Chrysochromulina parva also made a significant contribution to the total biomass during this period. Diatoma tenue var. elongatum did not reach the high levels of biomass in 1977 observed the previous spring although it again showed a higher and more extenuated peak at this station than further south at Station 1. Stratification was established during mid-May (Fig. 11B, Section 2). At the end of May, there was a shift to Fragilaria crotonensis, Stephanodiscus astraea and Rhizosolenia eriensis. In fact, these species remained dominant until the end of July: the pulse Uroglena volvox and Anabaena flos-aquae observed at Station 1 was not as pronounced at Border, and similarly, Oscillatoria limnetica, Mallomonas elongata and Cyclotella bodanica remained at relatively low biomass (Figs. A-1, A-2). There was a brief increase in Anabaena flos-aquae the second week in August. Following fall-turnover in the third week of this month, the dominant

species were Gleococcus Schroeteri (26/8) and Fragilaria crotonensis (31/8). Melosira italica became dominant from mid-September onward, approximately two weeks after its appearance at Station 1, and was accompanied by a species assemblage similar to that observed further south, although Coelosphaerium Naeglianum showed a more pronounced increase in absolute biomass and dominated briefly in late September (24/9/77).

Station 3: Central

Total phosphorus concentrations at this station, which has the greatest depth (z = 100 m), are much lower than those in the more eutrophic South Basin (Table 8, Section 1). In general, levels of phytoplankton biomass in 1976 and 1977 were also reduced (Figs. A-1, A-2, A-3; Table 4, Section 1), although the spring maximum of Diatoma tenue var. elongatum (3000 $\mu g l^{-1}$) was only slightly lower than that observed in the South Basin. Ice-out occurred the third week in April in this basin and although stratification was established at the beginning of June (Fig. 11C, Section 2), D. tenue var. elongatum did not show any appreciable decline until the third week of this month (Fig. [redacted] The subsequent peak of Oscillatoria Redekei (3500 $\mu g l^{-1}$) in early July was similar in magnitude to those observed at the more eutrophic, southern stations, but showed an earlier decline, again coinciding with an increase in mixing depth (Fig. 11C, Section 2). However, this species similarly remained dominant throughout most of the summer. Its initial decline was followed by an increase in Cryptophyceae (Cryptomonas reflexa, Rhodomonas minuta) similar to that seen at Stations 1 and 2, with a rapid succession to a

Fig. A-3. Contribution of major taxonomic groups and dominant species to total phytoplankton biomass at Station 3 (oligotrophic) in Lake Memphremagog, 1976-1977. Legend as in Fig. A-1.


BIOMASS (MG/CUBIC M.) ×10²
0.00
15.00
30.00
45.00
60.00
75.00
A-3
MAY
JUL
1976
SEP
NOV
JAN
MAR
MAY
1977
JUL
SEP
Diatoma tenue var. elongatum(60%)
Oscillatoria Redekei(53%)
O.Redekei(15%), Ceratium hirundinella(13%)
Cyclotella bodanica(16%)
O.Redekei(16%), Fragilaria crotonensis(10%)
Ceratium hirundinella(22%),F.crotonensis(14%),Botryococcus braunii(10%)
C.hirundinella(12%), Cryptomonas reflexa(10%), F.crotonensis(10%)
F.crotonensis(13%)
Melosira italica(12%), Stephanodiscus astraea(11%)
Asterionella formosa(16%), F.crotonensis(14%)
A.formosa(46%), Stephanodiscus hantzschii(17%)
A.formosa(30%), S.hantzschii(27%),Rhodomonas minuta(8%)
S.hantzschii(51%)
S.hantzschii(41%), R.minuta(9%)
D.tenue var. elongatum(20%), R.minuta(12%)
S.ulna var. danica(15%), Chrysochromulina parva(15%)
Anabaena flos-aquae(34%)
F.crotonensis(37%)
Cyclotella bodanica(22%), Cryptomonas reflexa(12%)
G.Schroeteri(24%), Coelosphaerium Naeglianum(20%)
F.crotonensis(35%)
C. Naeglianum(35%)
M.italica(21%)

mixed assemblage of Ceratium hirundinella, Rhizosolenia eriensis, Rhodomonas minuta, Chrysochromulina parva, Synedra ulna var. danica and Cyclotella bodanica. The shift to a predominance of filamentous forms observed in the South Basin was not as marked at this station and did not occur until mid-August, following a brief dominance by Cyclotella bodanica (Fig. A-3). Furthermore, only two filamentous species, Oscillatoria Redekei and Aphanizomenon gracile, appeared in any abundance; Mougeotia sp., Melosira spp., and Oscillatoria rubescens were not observed. Ceratium hirundinella and Fragilaria crotonensis also made important contributions to the total biomass during late August and eventually became dominant in mid-September, accompanied by a brief pulse of Botryococcus Braunii. The fall increase in Cryptophyceae observed in the South Basin was very subdued at this station and Melosira italica also remained at very low biomass. Ceratium hirundinella dominated until mid-October and the onset of fall turnover (Fig. 11C, Section 2), following which phytoplankton biomass remained low (700 $\mu g l^{-1}$) and consisted mainly of Fragilaria crotonensis, Stephanodiscus astraea and Melosira italica (Fig. A-3).

During December, there was a slow increase in Asterionella formosa, which became dominant prior to the establishment of ice cover at the end of the month (between 28-31 December), although total biomass remained low (300 $\mu g l^{-1}$). In the first under-ice sample (22/1), total biomass had increased to 540 $\mu g l^{-1}$) and consisted mainly of A. formosa (46%) and Stephanodiscus hantzschii (Fig. A-3). Subsequent samples showed a gradual decline in A. formosa and by mid-February, S. hantzschii remained as the dominant species, together with Rhodomonas minuta, and to a lesser extent,

Chrysochromulina parva.

The first open-water sample (24/4/77), collected approximately 4 days after ice-out, already showed a significant increase in total biomass (1600 μgl^{-1}), which was predominated by S. hantzschii (41%), Rhodomonas minuta and Gymnodinium veris. This was followed by an extremely abrupt decline in these species, with total biomass remaining very low (200 μgl^{-1}) until the onset of stratification, the third week in May (Fig. 11C, Section 2) when Diatoma tenue var. elongatum increased briefly. This species was immediately followed by a rapid succession of diatoms; notably Synedra ulna var. danica (not observed in any abundance in the South Basin during this period), Asterionella formosa, Fragilaria crotonensis and Cyclotella bodanica (Fig. A-3). Uroglena volvox and Stephanodiscus astraea did not show as significant an increase at this station; however, the development of Anabaena flos-aquae in mid June was greater in magnitude than that observed in the more eutrophic South Basin. A decline in the predominant diatom species towards the beginning of July was accompanied by an increase in Cryptophyceae (Cryptomonas reflexa, Rhodomonas minuta and C. rostratiformis). The plankton was dominated in August by a more extensive development of colonial greens (Gleococcus Schroeteri) and blue-greens (Coelospharium Naeglianum, C. Kützingianum) than seen in the South Basin. These species were again briefly replaced by Fragilaria crotonensis in late August, but then continued to dominate until late October, when there was a more extensive development of Melosira italica than seen in the previous year at this station (Fig. A-3). Fall overturn commenced during the middle of September (Fig. 11C, Section 2).

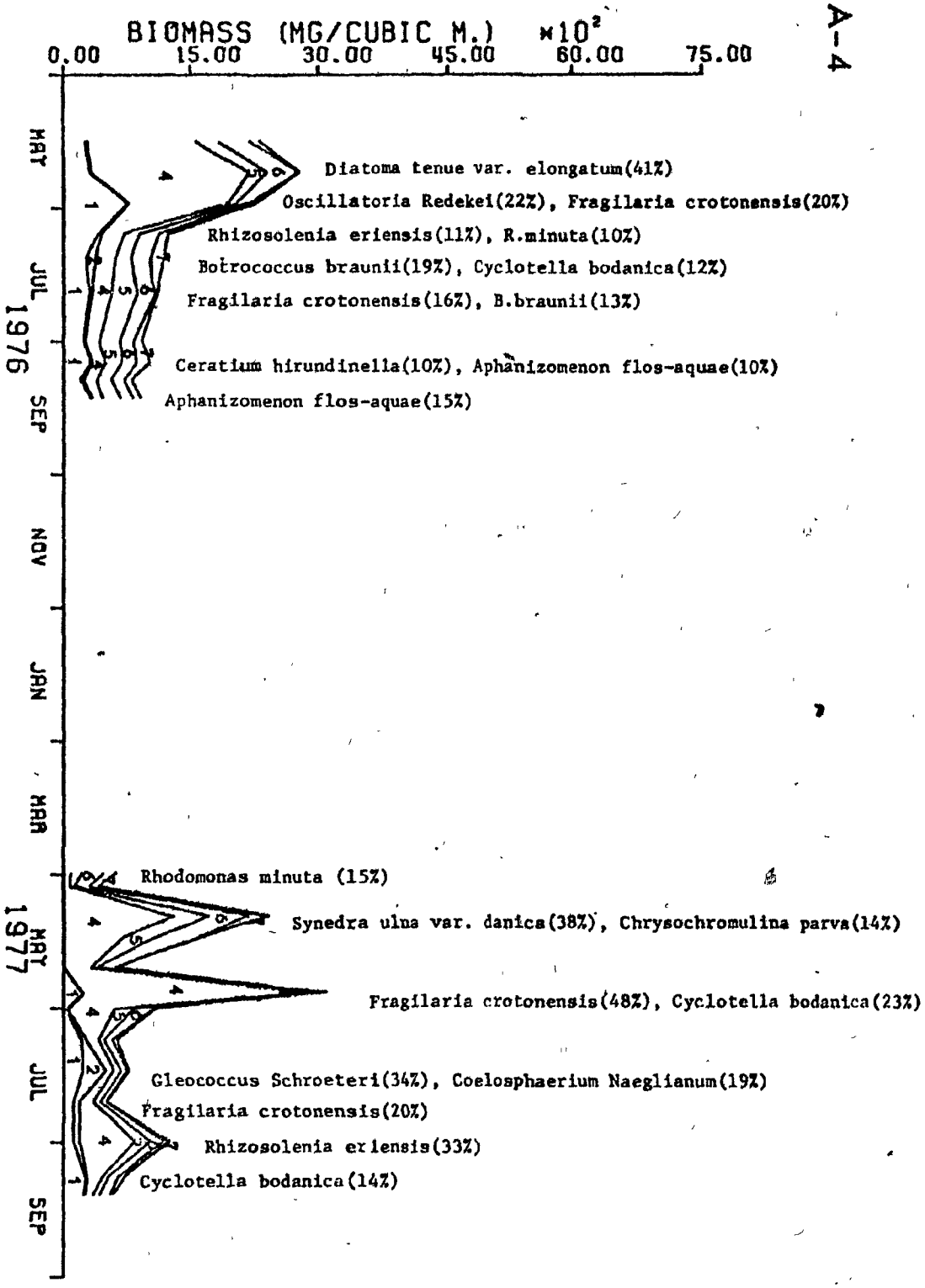
Station 4: North

This station is comparable in depth to Station 2 in South Basin ($z = 14.5$ m), but exhibits the lowest levels of total phosphorus and phytoplankton biomass, although in 1977, differences between Stations 3 (Central Basin) and 4 were significantly reduced (Tables 8, 4; Section 1).

Diatoma tenue var.elongatum showed a much less pronounced spring maximum (1170 $\mu g l^{-1}$) at this station in 1976 than observed in the South and Central Basins (Figs. A-1, A-2, A-3, A-4), and declined approximately 2 weeks after the onset of stratification, which occurred at the beginning of June (Fig. 11D, Section 2). In addition, the ensuing development of Oscillatoria Redekei was comparatively small (max. 500 $\mu g l^{-1}$) and short-lived. This species had decreased significantly by the end of July, when there was an increase in turbulence and mixing depth (Fig. 11D, Section 2), although as at other stations remained fairly abundant (approx. 10% total biomass) until late August (Fig. A-4). Following the initial decline of O. Redekei, there was no appreciable increase in Cryptophyceae, although as in Central Basin, there was a slight development of diatoms (Rhizosolenia eriensis, Cyclotella bodanica) and dinoflagellates (Ceratium hirundinella). The mid-summer predominance of filamentous forms which occurred at the other stations was absent in the North Basin; instead there was a rapid succession of species, notably Botrococcus Braunii (9/8) and Fragilaria crotonensis (30/8). No fall pulse of Cryptophyceae was observed and the plankton was dominated by Ceratium hirundinella at the commencement of overturn (Fig. 11D, Section 2) during the first half of September, succeeded

Fig. A-4. Contribution of major taxonomic groups and dominant species to total phytoplankton biomass at Station 4 (oligotrophic) in Lake Memphremagog, 1976–1977. Legend as in Fig. A-1.

A-4


BIOMASS (MG/CUBIC M.) ×10²
0.00
15.00
30.00
45.00
60.00
75.00
MAY
JUL
1976
SEP
NOV
JAN
MAR
MAY
1977
JUL
SEP
Diatoma tenue var. elongatum(41%)
Oscillatoria Redekei(22%), Fragilaria crotonensis(20%)
Rhizosolenia eriensis(11%), R.minuta(10%)
Botrococcus braunii(19%), Cyclotella bodanica(12%)
Fragilaria crotonensis(16%), B.braunii(13%)
Ceratium hirundinella(10%), Aphanizomenon flos-aquae(10%)
Aphanizomenon flos-aquae(15%)
Rhodomonas minuta (15%)
Synedra ulna var. danica(38%), Chrysochromulina parva(14%)
Fragilaria crotonensis(48%), Cyclotella bodanica(23%)
Gleococcus Schroeteri(34%), Coelosphaerium Naeglianum(19%)
Fragilaria crotonensis(20%)
Rhizosolenia eriensis(33%)
Cyclotella bodanica(14%)

by Aphanizomenon flos-aquae. No late fall samples were collected at this station.

In spring 1977, the first ice-out sample at Station 4 was taken a week later than at other stations, and it showed no evidence of Stephanodiscus hantzschii, which at that time was abundant but already declining in South and Central Basins. Instead, the plankton was dominated by small flagellates (Rhodomonas minuta, Chrysochromulina parva). This was followed at the onset of stratification in mid-May (Fig. 11D, Section 2) by Synedra ulna var. danica which attained a higher maximum biomass at Station 4 (900 $\mu g l^{-1}$) than a similar population of this diatom in Central Basin (Figs. A-3, A-4). However, this species was not accompanied by a development of Diatoma tenue var. elongatum as observed at Station 3. Synedra ulna var. danica continued to dominate until early June when it was succeeded by Fragilaria crotonensis and Cyclotella bodanica, which accounted for 50% and 20% respectively of a sharp increase in total biomass (3100 $\mu g l^{-1}$) towards the end of June (Fig. A-4). The accompanying development of Anabaena flos-aquae was relatively minor (200 $\mu g l^{-1}$). There was an increase in Uroglena volvox at the beginning of July, as observed in the South Basin, although this species did not show a similar development at Station 3 (Central Basin). In mid-July, colonial species (Coelosphaerium Kützingianum, Gleococcus Schroeteri) increased, as in Central Basin but in contrast to events at Station 3, these species were replaced in early August by a series of diatoms (Fragilaria crotonensis, Rhizosolenia eriensis and Cyclotella bodanica), although there was a similar development of Coelosphaerium Naeglianum towards the end of September (Fig. A-4),

corresponding with the onset of fall overturn.

APPENDIX B.

Total and nannoplankton biomass and contribution of major taxonomic groups to total and nannoplankton biomass within Lake Memphremagog, 1976-1977.

This appendix contains all graphs of total and nannoplankton biomass and the contribution of major taxonomic groups to total and nannoplankton biomass at the stations in Lake Memphremagog (1976-1977) not included in the main body of the thesis.

Fig. B-1. Total and nannoplankton biomass at two stations in Lake Memphremagog 1976-1977.

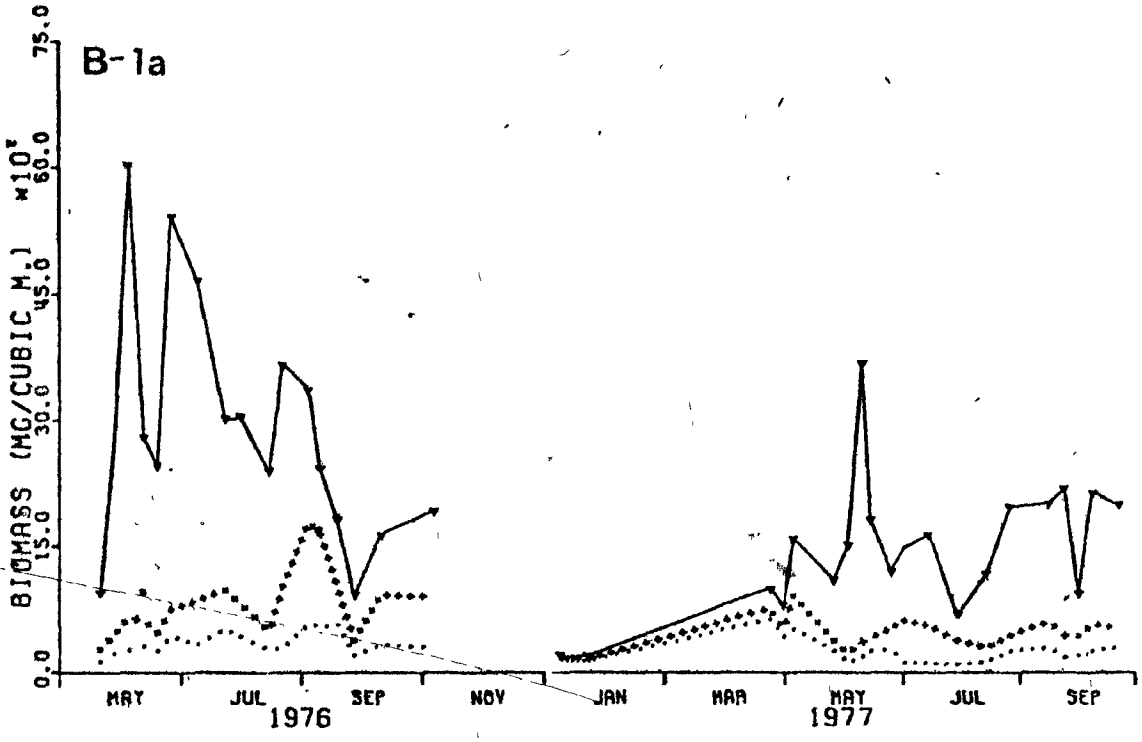
Fig. B-1a - Station 1 (mesotrophic);

Fig. B-1b - Station 4 (oligotrophic).

Legend: ←——— total

·····<35 µm

·····<10 µm


B-1a
BIOMASS (MG/CUBIC M.) *10²
75.0
60.0
45.0
30.0
15.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

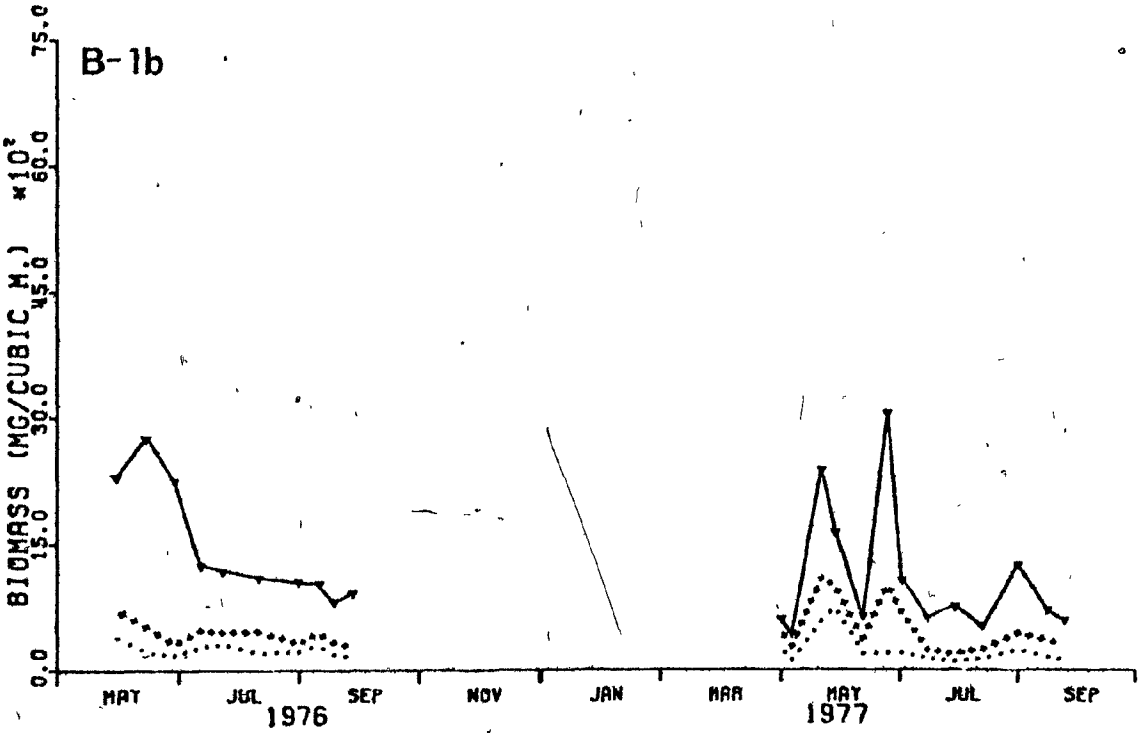
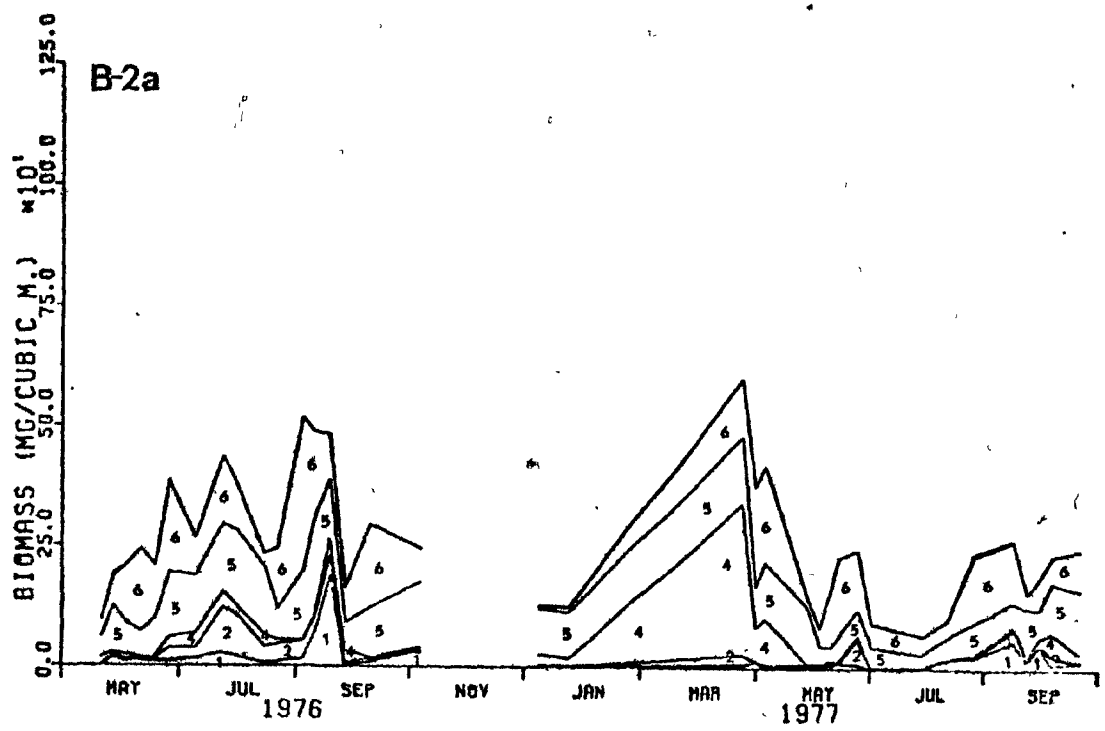

B-1b
BIOMASS (MG/CUBIC M.) *10²
75.0
60.0
45.0
30.0
15.0
0.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Fig. B-2. Contribution of major taxonomic groups to Biomass <35 µm (Fig. B-2a) and Biomass <10 µm (Fig. B-2b) at Station 1 (mesotrophic) in Lake Memphremagog 1976-1977.

Legend: 1 - Cyanophyta; 2 - Chlorophyta; 3 - Euglenophyta; 4 - Bacillariophyta; 5 - Chrysophyta; 6 - Cryptophyta (Pyrrophyta); 7 - Dinophyceae (Pyrrophyta).


B-2a
BIOMASS (MG/CUBIC M.) ×10'
0.0
25.0
50.0
75.0
100.0
125.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

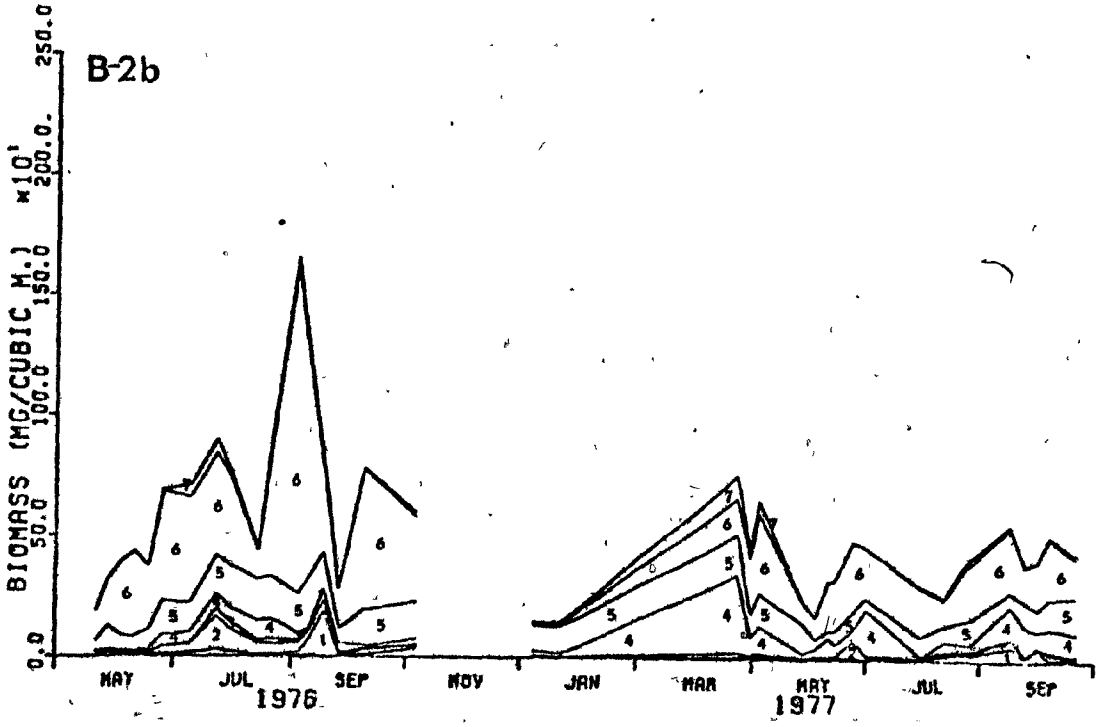
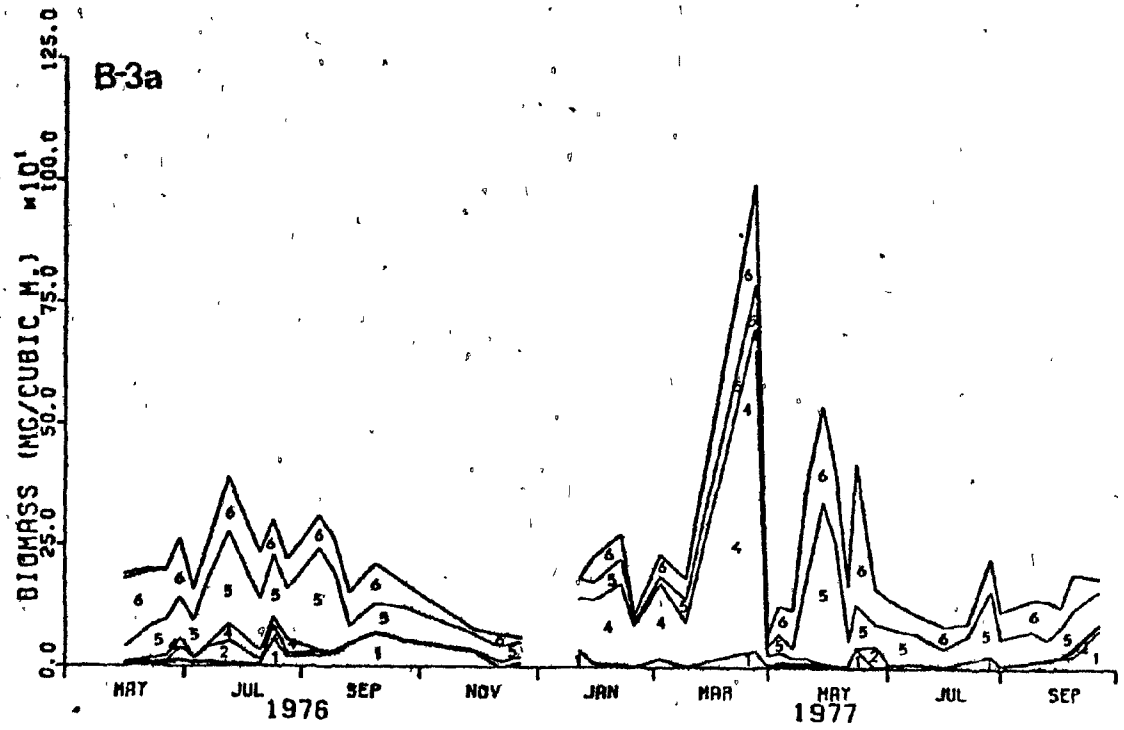

B-2b
BIOMASS (MG/CUBIC M.) ×10'
0.0
50.0
100.0
150.0
200.0
250.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Fig. B-3. Contribution of major taxonomic groups to Biomass <35 µm (Fig. B-3a) and Biomass <10 µm (Fig. B-3b) at Station 3 (oligotrophic) in Lake Memphremagog 1976-1977. Legend as in Fig. B-2.


B-3a
BIOMASS (MG/CUBIC M.)
*10¹
0.0
25.0
50.0
75.0
100.0
125.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

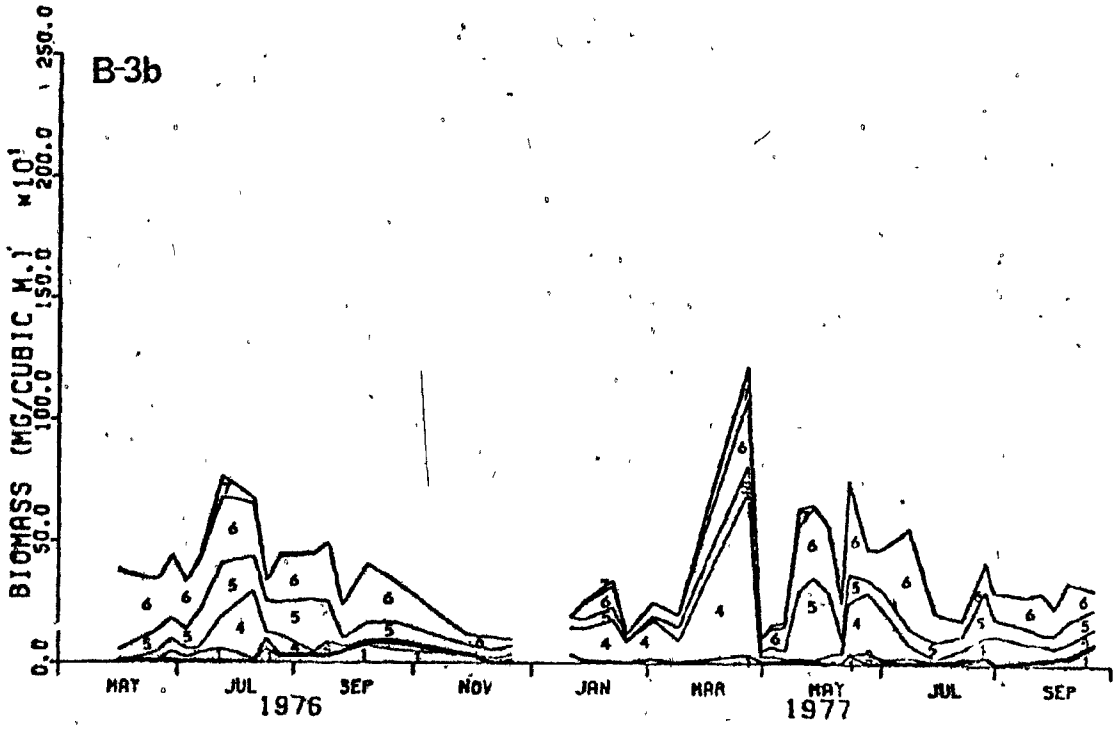
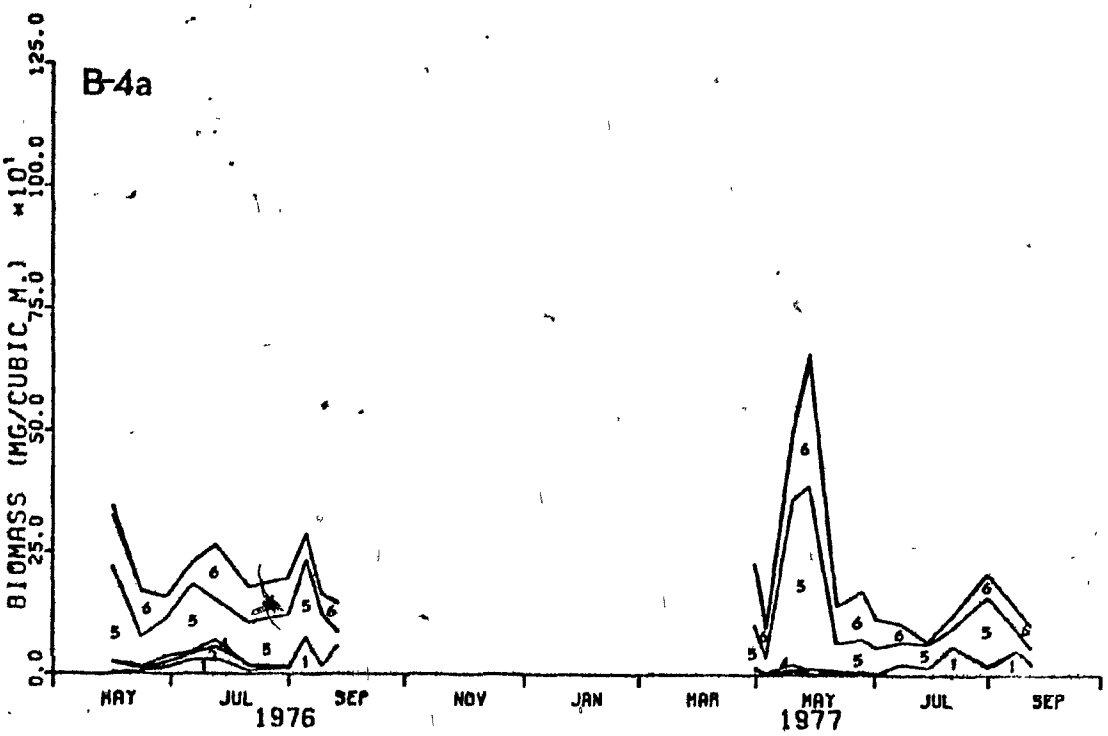
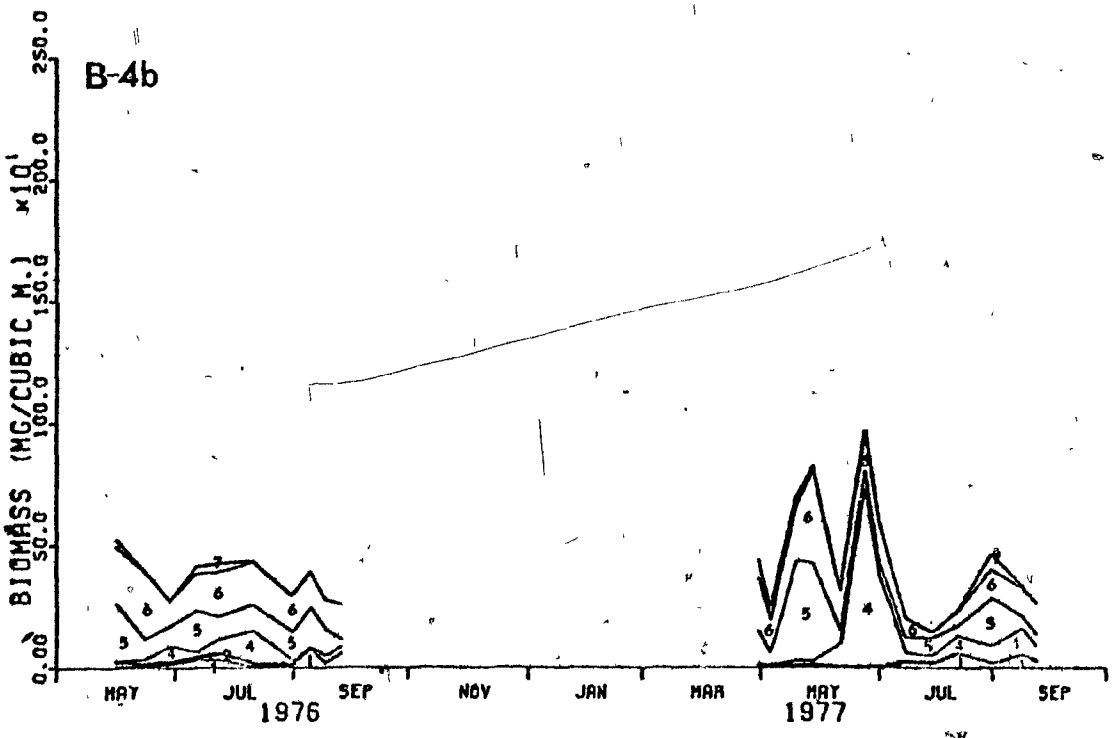

B-3b
BIOMASS (MG/CUBIC M.)
*10¹
0.0
50.0
100.0
150.0
200.0
250.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

Fig. B-4. Contribution of major taxonomic groups to Biomass <35 µm (Fig. B-4a) and Biomass <10 µm (Fig. B-4b) at Station 4 (oligotrophic) in Lake Memphremagog 1976-1977. Legend as in Fig. B-2.


B-4a
BIOMASS (MG/CUBIC M.) ×10¹
0.0
25.0
50.0
75.0
100.0
125.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977


B-4b
BIOMASS (MG/CUBIC M.) ×10¹
0.00
50.0
100.0
150.0
200.0
250.0
MAY
JUL
SEP
NOV
JAN
MAR
MAY
JUL
SEP
1976
1977

APPENDIX C.

Table C-1. Listing of all phytoplankton species found at the four stations (Fig. 1) within Lake Memphremagog to date. Morphological grouping and average volume given for more common species 1976-1977, together with % samples for each station and year in which species were found. Species identified by author in samples from 1973 indicated (73); those identified by H. Kling in 1973 samples indicated (73,K).

Note: volumes of colonial species determined according to footnotes (see NOTES at end of table, p.135).

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CYANOPHYTA						
Chroococcales - Chroococcaceae						
Aphanocapsa cf. *delicatissima* W. & G.S. West	C	○15% col.				
Aphanothece cf. *clathrata* W. and G.S. West	C	○15% col.				
Chroococcus limneticus Lemm.	C	95				77(54%)
Coelosphaerium Kuetzingianum Naeg.	C	■10/cell; 5 cells/ 156μ^2 S.A.		76(50%)		76(80%) 77(62%)
Coelosphaerium Naeglianum Ung.	C	■outer 5μ depth of colony	76(94%) 77(53%)	76(60%) 77(55%)	76(94%) 77(57%)	76(100%) 77(54%)

	Group	Av. vol. (μ^3)	% samples present (if ≥50%) for each year			
			1	2	3	4
CYANOPHYTA						
Chroococcales - continued						
Gleocapsa vesiculosa	A,P	15/cell				
Gomphosphaeria aponina Kg.	C	100/cell				76(100%)
Gomphosphaeria lacustris Chod.	C	3/cell				
Microcystis flos-aquae (Wittr.) Kirchn.	C	0.15% col.				
Misc. unicells <5 µm (mainly *T. inconstans*)	A,P	50	76(95%)	76(100%)	76(94%)	76(100%)
Hormogonales - Nostacaceae						
Anabaena flos-aquae (Lyng) Bréb.	F	33/µ	77(74%)	77(59%)	77(54%)	77(70%)
Anabaena planctonica Brunnth	F	40/µ	76(59%) 77(68%)		76(67%)	
Anabaena spiroides Kleb.	F	34/µ			76(50%)	
Aphanizomenon flos-aquae (L.) Ralfs	F	20/µ				
Aphanizomenon gracile Lemm.	F	13/µ				
- Rivulariaceae						
Gleotrichia echinulata (J.E. Smith) P. Richter						

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CYANOPHYTA						
Hormogonales - Oscillatoriaceae						
Lyngbya Birgei G.M. Smith	F	175/μ				
Oscillatoria limnetica Lemm.	F	5/μ	76(71%) 77(53%)		76(50%)	77(62%)
Oscillatoria Redekei Van Goor.	F	13/μ	76(76%)	76(70%)	76(67%)	76(80%)
Oscillatoria cf. *rubescens* D.C.	F	20/μ	76(100%)	76(85%)	76(83%)	76(80%)
- Pelanemataceae						
Pelonema subtillissimum Skuja						
CHLOROPHYTA						
Protablepharidales - Protablepharidaceae						
Gyromitus cordiformis Skuja	O	530	76(82%) 77(84%)	76(70%) 77(91%)	76(78%) 77(64%)	76(90%) 77(92%)
Polymastigales - Paramastigaceae						
Paramastix conifera Skuja						

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Volvocales - Chlamydomonadaceae						
Carteria sp.	B	3400				
Chlamydomonas cf. *gleophilia* Skuja	B,Q	50				
Chlamydomonas cf. *oviformis* E.G. Pringsh	B,Q	40	76(47%)			
Chlamydomonas sp. 1	B,Q	525	76(100%) 77(84%)	76(100%) 77(91%)	77(95%)	77(54%)
Chlamydomonas sp. 2	B	150	76(47%)			
Chlorogonium maximum Skuja	E	2600				
- Volvocaceae						
Pandorina morum (Müller) Bory	C	200/cell				
Eudorina cf. *unicocca*	C	220/cell				
Tetrasporales - Tetrasporaceae						
Gleococcus Schroeteri (Chod.) Lemm.	C	▽270/daught.col or 220/mature cell.	76(60%) 77(74%)	76(50%) 77(77%)	76(67%)	76(80%) 77(77%)
Gleocystis bacillus Teiling	C	300/cell				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Tetrasporales - Tetrasporaceae						
Gleocystis planctonica (W. & G.S. West) Lemm.	C	▽220/cell				
Tetraspora sp.						
- Hydrodictyaceae						
Pediastrum Boryanum (Turp.) Menegh	D	$\pi r^2 x 5\mu$				
Pediastrum duplex Meyen	D	$(\pi r^2 x 5)^{1}/_{2}$				
Pediastrum tetras (E) Ralfs (73,K)	D					
- Oocystaceae						
Franceia droescheri (Lemm.) G.M. Smith	A	1150				
Langerheimia gevenensis Chodat	A	30	76(47%)			
Micractinium sp.	D	65				
Oocystis lacustris Chodat	C	1050	76(65%)	76(65%)	76(50%)	76(50%)
Oocystis gigas var. *incrassata* W. & G.S. West	G	33x17.5				
Nephrocytium lunatum W. West	C	▽550/cell				
Tetraëdron limneticum Borge	A	2200				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Tetrasporales - Oocystaceae						
Tetraëdron minimum (A.Br.) Hansg.	A,P	250	76(47%)			76(60%)
Tetraëdron trigonum (Naegeli) Hansg.	G	2250				
Tetraëdron trigonum var. *gracile* Reinsch.	A	3500				
Tetraëdron victoriae var. *major*	G	6400				
- Coelastraceae						
Ankistrodesmus acicularis var. *heteropolis* Skuja	A	350	77(84%)	76(55%) 77(59%)	76(61%) 77(75%)	76(50%) 77(62%)
Ankistrodesmus bibranalus (Reinsch.) Kors	C	50				
Ankistrodesmus falcatus (Corda) Ralfs	D	50				
Ankistrodesmus fasciculatus Lundb. Kom-Legn.	D	50				
Ankistrodesmus fusiformis Corda *sensu* Kors.						
Coelastrum cambricum Archer	C	▽34/cell				
Coelastrum microsporum Naeg.	C	▽34/cell				
Coelastrum octaëdron Skuja	C	▽220/cell				
Coelastrum probiscideum Bohlin	C	▽34/cell				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Tetrasporales - Coelastraceae						
Crucigenia irregularis Wille	D	▽100/cell				
Crucigenia quadrata Morren	D,A	▽5/cell				
Crucigenia truncata G.M. Smith	D	▽25/cell				
Crucigenia cf. *tetrapedia* (Kirchn.) W. & G.S. West						
Dictyosphaerium elegans Bachmann	C	▽50/cell				
Dictyosphaerium pulchellum Wood	C	▽50/cell				
Elakatothrix gelatinosa Wille		▽200/cell				
Elakatothrix viridis (Snow) Printz	C	▽200/cell	76(88%) 77(79%)	76(95%) 77(82%)	76(89%) 77(68%)	76(90%) 77(69%)
Monoraphidium contortum (Thurs in Breb) Kom-Legn.	H	15				
Monoraphidium inrregulare (G.M. Smith) Kom-Legn.	H	15				
Monoraphidium minutum (Näg.) Kom-Legn.	A,P	50	76(82%)	76(70%)	76(67%)	76(50%)
Monoraphidium pusillum (Printz) Kom-Legn.	H	50	76(65%)			
Monoraphidium setiforme (Nyg.) Kom-Legn.	H	20	76(52%)			

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Tetrasporales - Coelastraceae						
Quadrigula cf. *Pfitzeri* Schroed.	C	80				
Scenedesmus acuminatus (Lagerm.) Chod.	A	▽40/cell				
Scenedesmus denticulatus Lagerm.	A	▽160/cell				
Scenedesmus denticulatus var. *linearis* Hansg.	A	▽160/cell	76(65%)	76(55%) 77(55%)		
Scenedesmus cf. *ecornis* (Ralfs) Chod.	A	▽125/cell	76(53%)			
Scenedesmus intermedius var. *acaudatus* Hortob.	A,P	▽35/cell	76(53%)	76(70%)		76(50%)
Scenedesmus intermedius var. *bicaudatus* Hortob.	A	▽35/cell				
Scenedesmus quadricauda Chod.	A	▽80/cell	76(88%) 77(53%)	76(50%)		
Scenedesmus spinosus Chod.	A	▽80/cell				
Treubaria triappendiculata Bernard	A,P	▽20	76(53%)			
Ulotrichales - Ulotrichaceae						
Hormidium sp.	F					
Ulothrix sp.	F	45μ				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHLOROPHYTA						
Zygnematales - Zygnemataceae						
Mougeotia sp.	F	12/μ	76(65%)	76(55%)	76(56%)	76(70%)
Desmidiales - Desmidiaceae						
Arthrodesmus sp.	H	7850				
Closterium aciculare var. *aciculare* West.	H	3800				
Closterium acerosum var. *acerosum* (Schrank) Erenb.	G	200000				
Closterium acutum var. *variable* (Lemm.) Krieger	H	525				
Cosmarium cf. *depressum* (Naeg.) Lund						
Cosmarium sp.	G	7100				
Staurastrum cuspidatum (Bréb) (73)						
Staurastrum dejectum Bréb	G	11000				
Staurastrum cf. *erasum* (Bréb)						
Staurastrum longipes (Nordst.) Teil	G	6350			76(50%)	
Staurodesmus sp.	G	27500				
Spondylosum planum (Wolle W. & G.S. West	F	1700			76(50%)	
Xanthidium antilopaeum (Bréb) Kutz (73,K)						

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
EUGLENOPHYTA						
Euglenales - Euglenaceae						
Euglena spp.	E	1000				
Trachelomonas cf. *cylindrica* E. Sec. Playf.						
Trachelomonas cf. *macropunctata* (Skv.) Defl.						
Trachelomonas cf. *volvocina* Ehrenb.	B	1800	76(53%)			76(50%) 77(54%)
Trachelomonas spp.	B	4000	76(53%)	76(55%)		
BACILLARIOPHYTA						
Centrales - Coscinodiscaceae						
Cyclotella bodanica Eulenst.	A	6600	76(82%) 77(89%)	76(90%) 77(86%)	76(89%) 77(79%)	76(90%) 77(100%)
Cyclotella sp.	A,P	500				
Melosira granulata (Ehr.) Ralfs	F	50/µm	76(53%) 77(63%)	76(65%) 77(59%)		
Melosira granulata var. *angustissima* Müll.	F	20/µm	76(53%)	76(55%)		
Melosira italica subsp. *subarctica* O. Müll.	F	55/µ	76(100%) 77(100%)	76(90%) 77(77%)	76(72%) 77(61%)	76(70%) 77(77%)

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
BACILLARIOPHYTA						
Centrales - Coscinodiscaceae						
Melosira varians C.A. Ag.	F					
Stephanodiscus astraea (Ehr.) Grun.	G	26000	76(88%) 77(79%)	76(95%) 77(82%)	76(72%) 77(50%)	
Stephanodiscus Hantzschii Grun.	A,P	150	76(94%) 77(79%)	76(90%) 77(77%)	76(78%) 77(75%)	76(50%)
- Soleniaceae						
Attheya Zachariasi J. Brun.	G	3500	76(59%)			
Rhizosolenia eriensis H.L. Smith	H	3010	76(88%) 77(74%)	76(85%) 77(73%)	76(83%) 77(54%)	76(80%) 77(62%)
Rhizosolenia longiseta Zach.						
Pennales - Fragilariceae						
Asterionella formosa Hassall	D	650	76(100%) 77(100%)	76(100%) 77(100%)	76(94%) 77(100%)	76(100%) 77(100%)
Diatoma tenue var. *elongatum* Lyngb.	H	2250	76(76%) 77(53%)	76(65%) 77(50%)	76(67%)	76(60%)
Diatoma tenue var. *tenue* Patrick	H	800				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
BACILLARIOPHYTA						
Pennales - Fragilariceae						
Diatoma vulgare Bory	H	225				
Fragilaria crotonensis Kitton	D		76(94%) 77(95%)	76(95%) 77(91%)	76(100%) 77(86%)	76(100%) 77(92%)
Fragilaria cf. *vaucheriae* (Kütz) Peters	D		76(59%)	76(70%)	76(61%)	
Meridion circulare Agardh.	G	800				
Synedra acus Kütz		500				
Synedra acus var. *angustissima*	H	540	76(94%) 77(95%)	76(80%) 77(91%)	76(78%) 77(68%)	76(80%) 77(85%)
Synedra acus var. *radians*						
Synedra berolinensis Lemm.	D	200				
Synedra rumpens Kütz (73)						
Synedra ulna (Nitsch) Ehr.	G	40000				
Synedra ulna var. *danica* (Kütz) Grun.	H	8300	76(76%) 77(89%)	76(70%) 77(82%)	76(67%) 77(71%)	76(60%) 77(69%)
Tabellaria fenestrata (Lyngb.) Kütz	D	3000		76(50%)	76(67%)	76(70%)
Tabellaria flocculosa (Roth) Kütz	D	2000				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
BACILLARIOPHYTA						
Pennales - Achnanthaceae						
Achnanthes minutissima Kütz	A,P	30*				
Rhoicosphenia curvata (Kütz) Grun.	G	1500				
Rhapalodia gibba (Ehr.) O. Müll.		500				
- Naviculaceae						
Cymbella affinis Kütz	G	850*				
Cymbella cf. *aspera* (Ehr.) Cleve		4000		*		
Cymbella spp.	G	calc.				
Navicula cryptocephala var. *venetia*						
Navicula oblonga Kütz						
Navicula cf. *radiosa* Kütz (73)	G	18000				
Navicula cf. *Reinhardtii* Grun.		6700				
Navicula spp.	G	1000				

*A. Cattaneo, pers. comm.

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
BACILLARIOPHYTA						
Pennales - Nitschiaceae						
Nitschia cf. *cicularis* W. Smith	H	500	77(63%)	77(50%)		
Nitschia cf. *dissipata* (KUtz) Grun.	G	4000				
Nitschia spp.	G	500				
- Surirellaceae						
Cymatopleura solea						
Surirella sp.						
CHRYSOPHYTA						
Chromulinales - Euchromulinaceae						
Chromulina cf. *sphaeridia* Schiller						
Chromulina cf. *ovalis* Klebs			76(100%) (94%) (59%)	76 (90%) (95%) (90%) (60%)	76(100%) (100%) (100%) (50%)	76(100%) (100%) (70%)
			77(100%) (100%) (73%)	77(100%) (95%) (59%)	77(100%) (93%)	77(100%) (100%)
Chromulina vestita Schiller	B,Q	200				
Chromulina spp.	B,Q	50-200				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHRYSOPHYTA						
Chromulinales - Euchromulinaceae						
Chrysococcus radians Conrad	B,Q	300				
Chrysococcus spp.	B,Q	100				
Kephyrion cf. *rubri-claustri* var. *amphora* Conrad						
Kephyrion cf. *sitta* Pascher		50				
Kephyrion sp.	B,Q	65				
- Mallomonadaceae						
Mallomonas cf. *acaroides* Perty	B	2000				
Mallomonas akrokomos Ruttner	B	210	76(53%) 77(79%)	77(68%)	77(68%)	
Mallomonas caudata Iwanoff	B	2350	76(71%) 77(89%)	76(75%) 77(82%)	76(67%) 77(64%)	76(70%) 77(85%)
Mallomonas elongata Reverdin	E	5890	76(65%) 77(79%)	76(75%) 77(73%)	76(67%) 77(57%)	76(70%)
Mallomonas cf. *insignis* Pernad	E	2000	76(65%)	76(65%)	76(72%)	76(60%)
Mallomonas pseudocoronata Prescott	E	2750	76(53%)			76(70%)

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHRYSOPHYTA						
Isochrysidales - Isochrysodaceae						
Erkenia subaequiciliata Skuja	B,Q	100				
- Synuraceae						
Synura uvella Ehrnberg & Korschikon	C	530	76(76%) 77(58%)			76(50%)
Ochromonadales - Ochromonadaceae						
Ochromonas cf. *miniscula* Conrad						
Ochromonas spp.	B,Q		76(76%) 77(100%)	76(85%) 77(91%)	76(89%) 77(79%)	76(90%) 77(69%)
Uroglena cf. *volvox* Ehrnb.	C	100	77(58%)	77(55%)		
- Lepochromonadaceae						
Chrysoikos angulatus	B	50				
Chrysoikos skujai (Nauwerk) Willen	B	50				
Dinobryon bavaricum Imhof.	D	200	76(64%)	76(60%)	76(50%)	76(70%)
Dinobryon cylindricum var. *alpinum* (Imhof.) Bachmann	D	100				
Dinobryon divergens Imhof.	D	100	76(76%)			

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHRYSOPHYTA						
Ochromonadales - Lepochromonadaceae						
Dinobryon sociale Ehrnb.	D	100				
Dinobryon sociale var. *americanum* (Brunnth) Bachm.	D	100	76(59%)			
Rhizochrysidales - Rhizochrysidaceae						
Chrysamoeba mikrokonta Skuja	B,Q	180				
Chrysamoeba radians Klebs	B,Q	500				76(60%)
Prymesiales - Prymesialaceae						
Chrysochromulina parva Lackey	B,Q	80	76(100%) 77(100%)	76(100%) 77(91%)	76(89%) 77(100%)	76(100%) 77(100%)
Chrysocapsales - Bitrichiaceae						
Bitrichia chodatii (Reverdin) Chodat	H	200			76(50%)	76(60%)
Chrysosphaeriales - Stichogleaceae						
Stichoglea delicatula (West) Skuja	C	525				
Craspedomonadales - Bicoecaceae						
Bicoeca crystallina Skuja	O	25				
Bicoeca mitra Pott	O	130				

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
CHRYSOPHYTA						
Craspedomonadales - Bicoecaceae						
Bicoeca tubiformis Skuja	O	130				
Bicoeca spp.	O	100				
- Craspedomonadaceae						
Aulomonas Lackey	O	35	77(53%)	77(50%)		
Conocladium umbellatum (Tatem) Stein	O	100				
Desmarella sp.						
Salpingoeca elegans (Bachm.) Lemm.						
Stelexomonas dichotoma Lackey	O	100				
Misc. flagellates <5 µm	B,Q		76(100%) 77(100%)	76(100%) 77(95%)	76(100%) 77(96%)	76(100%) 77(100%)
Misc. non-flagellates <5 um	A,P		76(76%) 77(84%)	76(95%) 77(82%)	76(100%) 77(82%)	76(100%) 77(69%)
- Xanthophyceae						
Botrococcus Braunii Kütz	C					76(60%)

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
PYRROPHYTA CRYPTOPHYCEAE						
Cryptomonadales - Cryptomonadaceae						
Chilomonas cf. *oblonga* Pascher						
Chroomonas cf. *Norstedtii* Hansgirg	B,Q	250				
Cryptomonas erosa Ehrenbg.	B	1050	76(100%) 77(100%)	76(95%) 77(100%)	76(89%) 77(100%)	76(100%) 77(100%)
Cryptomonas Marssonii Skuja	B	800	76(100%) 77(100%)	76(95%) 77(95%)	76(100%) 77(96%)	76(100%) 77(100%)
Cryptomonas obovata Skuja	B	1100	76(94%) 77(89%)	76(85%) 77(86%)	76(94%) 77(82%)	76(90%) 77(77%)
Cryptomonas ovata Ehrenberg	B	2250	76(53%)	76(60%)		
Cryptomonas reflexa Skuja	B	2250	76(100%) 77(89%)	76(95%) 77(91%)	76(100%) 77(100%)	76(100%) 77(100%)
Cryptomonas rostratiformis Skuja	E	3560	76(100%) 77(100%)	76(95%) 77(91%)	76(94%) 77(93%)	76(100%) 77(85%)
Rhodomonas minuta Skuja	B,Q	150	76(100%) 77(100%)	76(100%) 77(100%)	76(100%) 77(100%)	76(100%) 77(100%)
Katablepharidaceae						
Katablepharis ovalis Skuja	O	150	76(100%) 77(100%)	76(100%) 77(100%)	76(100%) 77(100%)	76(100%) 77(100%)

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
PYRROPHYTA CRYPTOPHYCEAE						
Cryptomonadales - Senniaceae						
Cryptaulax sp.	O	250				
Cyathomonas truncata (Fres.) From.	O	250				
PYRROPHYTA DINOPHYCEAE						
Gymnodiniales - Gymnodinaceae						
Amphidinium cf. *luteum* Skuja	B,Q	500				
Gymnodinium helveticum Penard	O	8500	76(53%)		76(50%) 77(68%)	76(50%)
Gymnodinium Lantzschii Itermöhl	O	600		76(55%) 77(64%)	76(50%) 77(74%)	77(85%)
Gymnodinium mirabilis Penard (73,K)						
Gymnodinium palustre Schilling (73,K)						
Gymnodinium uberrimum (Allman) Kofoid & Swezy	E	14000	77(68%)	77(64%)	77(68%)	77(62%)
Gymnodinium cf. *veris* Lindem	B	3225	76(82%) 77(63%)	76(75%) 77(68%)	76(61%) 77(68%)	76(90%)

	Group	Av. vol. (μ^3)	% samples present (if >50%) for each year			
			1	2	3	4
PYRROPHYTA DINOPHYCEAE						
Peridinales - Peridinaceae						
Ceratium hirundella (O.F. Müller) Schrank	E	50000	76(59%)	76(65%)	76(78%)	76(80%)
Peridinium aciculiferum (Lemm.) Lemm.	E	4330	77(53%)	77(50%)	76(50%)	
Peridinium goslaviense Woloszynska (73,K)						
Peridinium Willei Huitf-Kaas	E	25000	76(53%)	76(55%) 77(55%)	76(50%)	76(70%) 77(54%)
Peridinium wisconsiense (Eddy) (73,K)						
- Glenodinaceae						
Glenodium oculatum	B	1750	76(100%) 77(84%)	76(100%) 77(91%)	76(83%) 77(89%)	76(70%) 77(92%)

NOTES ON VOLUME DETERMINATIONS

◆ volume determined from colony dimensions measured for each specimen enumerated; approximated to a sphere or ellipsoid on each occasion.

○ where gelatinous matrix extensive and ind. cells difficult to enumerate, 15% of the above determined volume taken as actual volume (after Reynolds,C.S. 1973. Growth and buoyancy of Microcystis aeruginosa Kutz.emend.Elenkin in a shallow eutrophic lake.Proc R. Soc. Lond.B.184:29-50).

■ where cells largely peripheral and difficult to count, total volume ind. cell volumes,
i) ind. volumes of cells, where #cells a predetermined function of colony surface area(5 cells per 156 ^{2} S.A.)
ii) volume of outer 5 m depth of colony, calculated for each specimen enumerated.

▽ total volume ind. cell volumes, where #cells/colony determined on each occasion; or where daughter colonies are formed, total volume volumes of daughter cols. volumes of mature cells volumes of juvenile cells. in gelatinous matrix.

Table C-2. Taxa contributing to 10% or more of the total biomass on at least one occasion for a given station and year. Values give % samples where contribution >10%; numbers in parentheses represent maximum % contribution to total biomass.

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CYANOPHYTA-Chroococcales								
Coelosphaerium kützingianum Naeg.						23(10)	7(19)	15(19)
C. naeglianum Ung.					16(21)	18(15)	29(35)	15(29)
Misc. unicells <5 μ	6(10)	10(24)						8(12)
-Hormogonales								
Anabaena flos-aquae (Lyng) Breb					5(12)	5(23)	4(34)	
A. planctonica Grunnth.					5(15)			
Aphanizomenon flos-aquae (L) Ralfs			6(11)	20(15)				
A. gracile Lemm.	6(12)		17(12)					
Oscillatoria limnetica Lemm.					5(17)			
O. Redekei Van Goor	47(65)	40(68)	44(72)	50(26)				
O. cf. rubescens D.C.	12(10)	5(18)						

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CHLOROPHYTA-Tetrasporales								
Gleococcus Schroeteri					11(25)	9(18)	11(24)	8(34)
BACILLARIOPHYTA - Centrales								
Cyclotella bodanica Eulenst			6(16)	10(12)	5(12)	5(13)	7(22)	46(32)
Melosira granulata (Ehr) Ralfs					11(16)	13(14)		
M. italica subsp. *subarctica* O.Mull	7(29)	20(20)	11(10)		32(43)	36(24)	7(29)	
Rhizosolenia eriensis H.L.Smith				10(11)	16(19)	18(17)		8(33)
Stephanodiscus astraea (Ehr) Grun	6(24)	10(21)	6(11)		21(21)	13(33		
S. hantzschii Grun	6(11)				5(31)	13(58)	29(51)	
-Pennales								
Asterionella formosa Hass			11(24)	11(10)	23(13)	18(56)		
Diatoma tenue var. *elongatum* Lyngb	35(69)	35(70)	33(64)	30(42)	11(14)	18(36)	7(19)	
D. tenue var. *tenue* Patrick						9(14)		
Fragilaria crotonensis Kitton	6(11)	20(15)	39(18)	20(22)	21(27)	36(37)	18(37)	39(48)
F. cf. vaucheriae (Kutz) Peters							4(25)	
Synedra ulna var. *danica* (Kutz) Grun					5(11)		4(15)	15(38)

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CHRYSOPHYTA-Chromulinales								
Chromulina spp.					5(11)	5(13)		
Mallomonas elongata Reverdin					5(22)	5(11)		
-Ochromonadales								
Uroglena cf. *volvox* Ehrnb					5(23)	9(13)		8(13)
-Prymesiales								
Chrysochromulina parva Lackey						9(12)	7(15)	23(20)
Misc. flagellates <5 µm					5(20)	5(11)		
Misc. non flagellates <5 µm					5(22)		4(13)	
Xanthophycaea								
Botryococcus braunii Kutz							7(10)	23(19)
PYRROPHYTA-Cryptophyceae								
Cryptomonas Marssonii Skuja					5(11)	5(12)		
C. reflexa Skuja	24(23)	25(33)	11(29)	10(10)				
C. rostratiformis Skuja	12(13)	5(13)			5(10)	5(13)	7(13)	8(10)
Rhodomonas minuta Skuja	12(11)	5(11)		10(10)	2(126)	27(19)	39(27)	31(15)

	1976				1977			
STATION	1	2	3	4	1	2	3	4
PYRROPHYTA-Dinophyceae								
Ceratium hirundinella (O.F. Muller) Schrank	12(15)	15(14)	28(35)	20(13)			7(12)	

Table C-3. Taxa contributing ≥ 10% of nannoplankton biomass <35µm in one or more samples. Values give % of total number of samples enumerated for a given station and year where the species accounted for ≥ 10% of the biomass <35µm. Maximum contribution to biomass <35µm given in parentheses.

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CYANOPHYTA								
Misc. unicells <5 µm	6(23)	5(18)	28(26)	20(22)	11(12)	18(13)	4(26)	31(15)
CHLOROPHYTA								
Monoraphidium minutum (Nag) Kom-Legn	12(10)	10(13)						
BACILLARIOPHYTA								
Cyclotella bodanica Eulenst	6(13)	15(15)	33(39)	50(30)	53(40)	55(31)	46(53)	69(74)
Stephanodiscus hantzschii Grun			11(13)		26(42)	18(66)	29(69	
CHRYSOPHYTA								
Chromulina spp.					10(15)	5(15)	11(13)	
Chrysochromulina parva Lackey	24(11)	25(16)	28(24)	60(28)	21(26)	41(51)	43(41)	69(47)
Mallomonas caudata Iwanoff							4(14)	7(17)
Ochromonas spp.	6(14)				5(11)	5(11)		

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CHRYSOPHYTA-continued								
Misc. flagellates <5 µm					11(27)			
Misc. non flagellates <5 µm	12(19)	10(17)	11(29)	8(25)	11(28)			
PYRROPHYTA								
Cryptomonas erosa Ehrnbg	35(14)	20(17)			11(12)	5(14)		
C. Marssonii Skuja	59(21)	45(16)	17(12)	10(10)	32(25)	18(28)	11(20)	8(13)
C. reflexa Skuja	88(42)	80(49)	83(27)	70(30)	42(22)	18(23)	32(45)	46(18)
Rhodomonas minuta Skuja	88(37)	90(41)	94(34)	100(27)	74(50)	82(52)	86(45)	77(31)

Table C-4. Taxa contributing ≥ 10% of nannoplankton biomass <10μm in one or more samples. Values give % of total number of samples enumerated for a given station and year where the species accounted for ≥ 10% of the biomass <10μm. Maximum % contribution to biomass <10μm given in parentheses.

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CYANOPHYTA								
Misc. unicells <5 μm	18(30)	26(66)	35(39)	40(38)	16(26)	32(28)	21(42)	39(48)
CHLOROPHYTA								
Chlamydomonas sp.					5(16)		4(30)	
Monoraphidium minutum (Nag)	24(20)	20(27)	17(12)			9(12)		
BACILLARIORHYTA								
Achnanthes minutissima Kutz	6(10)	6(13)	6(12)					
Stephanodiscus hantzschii Grun	6(13)		11(21)		32(52)	18(83)	32(79)	
CHRYSOPHYTA								
Chromulina spp.		6(60)			11(17)	5(18)		8(11)
Chrysochromulina parva Lackey	53(23)	82(28)	61(27)	80(34)	58(43)	79(68)	54(53)	92(65)
Ochromonas spp.			6(13)		5(13)	4(13)	4(12)	

	1976				1977			
STATION	1	2	3	4	1	2	3	4
CHRYSOPHYTA - continued								
Misc. flagellates <5 µm	59(17)	41(15)	44(15)	30(14)	26(31)	16(16)	11(27)	15(12)
Misc. non flagellates <5 µm	24(23)	20(23)	39(54)	30(41)	11(32)		7(18)	
PYRROPHYTA								
Chroomonas cf. *Norstedii* Hansgirg		5(12)						15(17)
Rhodomonas minuta Skuja	88(65)	100(63)	94(69)	100(56)	90(74)	91(73)	93(69)	92(56)

Table C-5. Mean % contribution of major taxonomic groups to total phytoplankton biomass <35 µm at the four stations in Lake Memphremagog, 1976-1977.

Station, Year	Cyanophyta	Chlorophyta	Euglenophyta	Bacillariophyta	Chrysophyta	Pyrrophyta	
						Cryptophyceae	Dinophyceae
1 1976	3.6	4.6	1.1	5.9	20.4	61.8	2.6
1977	3.6	2.9	0.7	18.0	27.7	43.7	3.3
2 1976	5.6	4.5	0.3	7.3	23.3	56.2	2.8
1977	4.1	2.8	0.1	20.7	26.7	41.9	3.7
3 1976	7.3	3.6	0.2	11.3	26.9	48.4	2.4
1977	4.4	2.4	0.2	28.2	23.1	38.4	3.3
4 1976	7.3	2.5	0.4	10.5	31.5	44.9	2.9
1977	6.1	1.6	0.2	23.4	27.6	35.7	5.3

Table C-6. Mean % contribution of major taxonomic groups to total phytoplankton biomass <10 µm at the four stations in Lake Memphremagog, 1976-1977.

Station,	Year	Cyanophyta	Chlorophyta	Euglenophyta	Bacillariophyta	Chrysophyta	Pyrrophyta	
							Cryptophyceae	Dinophyceae
1	1976	7.1	7.6	0.0	6.0	37.9	41.0	0.2
	1977	7.2	3.3	0.0	9.1	41.1	39.0	0.4
2	1976	11.1	6.8	0.0	4.4	40.2	37.1	0.3
	1977	7.7	3.2	0.0	10.8	38.3	40.0	0.1
3	1976	11.9	3.7	0.0	5.7	42.5	35.8	0.4
	1977	7.3	2.8	0.0	18.2	34.8	36.8	0.2
4	1976	12.1	3.9	0.0	1.9	47.8	33.8	0.6
	1977	13.0	1.2	0.0	0.8	45.1	39.6	0.2

APPENDIX D.

Table D-1: Literature survey of total and nannoplankton biomass from a range of lakes of different trophy.

No.	Lake	Author(s)	Total Biomass mgl^{-1}	% Nanno. Biomass	Definition of Nannoplankton Fraction	Mean Depth $\bar{z}$(m)	Surface Area SA(ha)	$SA/\bar{z}$
	Memphremagog	Watson (1979)						
1	Station 1 ('76)		2884	24	<35 µm	7	2020	288.6
2	2 ('76)		3284	20		7	2390	314.3
3	3 ('76)		2121	21		50	2166	43.3
4	4 ('76)		1466	28		13.5	1880	139.3
5	1 ('77)*		1611	28		7	2020	288.6
6	2 ('77)		1665	31		7	2390	314.3
7	3 ('77)		1112	44		50	2166	43.3
8	4 ('77)		1106	41		13.5	1880	139.3
9	Sup. ins.	Munawar &	100	73	"Phytoflagellates"	145	8330000	57450
10	Sup. off.	Munawar (1975)	100	77		145	8330000	57450
11	Whitefish		200	57		145	8330000	57450
12	Duluth		300	59		76	8330000	57450
13	Huron off.		500	26		76	5951000	78300
14	Ontario off.		1000	54		91	1876000	20620
15	Huron (B.Pen.)off.		900	11		76	5951000	78300

No.	Lake	Author(s)	Total Biomass mgl^{-1}	% Nanno. Biomass	Definition of Nannoplankton Fraction	Mean Depth $\bar{z}$(m)	Surface Area SA(ha)	SA/$\bar{z}$
16	Ontario in.		1200	58		91	1876000	20620
17	Huron (B.Pen.)in.		1500	17		76	5951000	78300
18	Erie off. cen.		2600	47		21	2582000	122952
19	Erie ins. E.		3100	38		21	2582000	122952
20	Erie off. S.		3400	46		21	2582000	122952
21	Erie ins. cen.		4400	23		21	2582000	122952
22	Erie ins. W.		5600	35		21	2582000	122952
23	Erie ins.(B.Isc.)		6000	26		21	2582000	122952
24	Huron (Sagin)		8200	23		76	5951000	78300
25	Hertel	Kalff (1972)	830	60	<64 µm	~3	29	~10
26	Pääjarvi	Granberg (1970)	400	75	<60 µm	14.4	1340	93.1
27	Mikolajskie	Spodniewska et al.(1973)	8600	30		11.0	460	41.4
28	Esrom	Kristiansen (1971)	1100 (est.)	32	<45 µm	22 (max.)		
29	Bavelse		8600 (est.)	28		8 (max.)	110	13.8
30	Tystrup		15700 (est.)	30		21	640	30.5
31	Brienzersee	Pavoni (1963)	1000	80		176	2918	16.6

No.	Lake	Author(s)	Total Biomass mgl^{-1}	% Nanno. Biomass	Definition of Nannoplankton Fraction	Mean Depth $\bar{z}$(m)	Surface Area SA(ha)	$SA/\bar{z}$
32	Thunersee		1700	41		135	4808	35.6
33	Walensee		3600	33		103	2327	22.6
34	Sempachersee		4200	14		46	1437	31.2
35	Zurichsee		2200	45		54	6700	124.1
36	Hallwilersee		16200	5		21	1029	49
37	Pfaffikersee		18600	5		18	325	18.1
38	Rynskie	Spodniewska (1978)	34200	6	<30 µm	136	620	45.6
39	Szymon		28900	9		1.1	154	140.0
40	Szymoneckie		26700	7		<1.0	181.1	181
41	Kotek		24400	15		<1.0	42.1	42.1
42	Jagodne		15600	4		8.7	936	107.6
43	Boczne		15500	10		8.7	189.8	21.8
44	Guzianka Wielka		12100	39		6.5	72.0	11.1
45	Mikolaskie		9300	18		11.1	460	41.4
46	Beldany		8700	13		10.0	780	78.0
47	Tajty		8500	15		7.6	251-2	33.1

No.	Lake	Author(s)	Total Biomass mgl^{-1}	% Nanno. Biomass	Definition of Nannoplankton Fraction	Mean Depth $\bar{z}$(m)	Surface Area SA(ha)	SA/$\bar{z}$
48	Sniardwy		8100	22		5.9	10598	1796.3
49	Niegocin		7100	32		10.0	2498.8	249.9
50	Taltowisko		6300	13		14.0	323.4	23.1
51	Talty		5500	23		7.6	1160	152.6
52	Nidzkie		5100	6		6.2	1724	278.1
53	Guzianka Mala		2600	79		2.6	42	16.2
54	Haneza		2000	30		38.7	311.4	8.1
55	Gieladzkie		92700	1		7.9	416	52.7
56	Biale		78600	2		9.4	374	39.8
57	Zdruznd		56600	5		4.7	246.8	52.5
58	Walpunskie		35200	6		3.0	49.5	16.5
59	Kujnd		34900	16		2.0	30.0	15.0
60	Dluzec		33700	8		7.4	127.0	17.2
61	Gardynskie		13000	53		2.2	107	48.6
62	Zyzdroj Welki		12400	28		5.0	200.1	40
63	Lampasz		6800	9		9.2	76	8.3

No.	Lake	Author(s)	Total Biomass mgl^{-1}	% Nanno. Biomass	Definition of Nannoplankton Fraction	Mean Depth $\bar{z}$(m)	Surface Area SA(ha)	$SA/\bar{z}$
64	Łąpackie		3600	29		9.4	278	29.6
65	Gant		3300	32		10.3	37.8	3.7
66	Uplik		3200	5		3.4	61.9	18.2
67	Zyzdroj Maly		2800	39		3.8	42.3	11.2
68	Zyndackie		2700	59		4.0	35.0	8.8
69	Babiety Wielkie		1900	72		22.9	271.1	11.8
70	Mokre		1000	31		13.1	797.8	60.9
71	Pilakno		600	89		14.6	278.7	19.1

APPENDIX E.

Variance associated with estimates of total biomass.

Total biomass was estimated from weekly or bi-weekly tube samples taken to the depth of the epilimnion during stratification, or to a maximum depth of 0.5m above the sediments in South Basin, and 15m in Central and North Basins.

Since tube samples represent the average concentration or biomass of the water column sampled, and are not weighted for basin morphometry, they cannot be used to calculate areal biomass, particularly in South Basin, which has a relatively large littoral area. In addition, the degree of spatial heterogeneity in phytoplankton biomass around each station was not investigated, hence the samples analysed can only be considered as representative of the biomass of the station itself, and not necessarily of the associated basin.

Individual estimates of total biomass include error associated with sampling, subsampling and enumeration, as well as that arising from the computation of mean volumes for each unicellular or colonial species (Lund et al., 1958). However, according to these authors, confidence limits calculated from mean counts of individually sedimenting units (e.g. cells, colonies and filaments) give a reasonable estimate of the total error, providing that the distribution of these units within the counting chamber is Poisson.

Methods.

Total variance, including sampling, subsampling and counting error, was estimated from two sets of three replicate tube samples, taken under

conditions of low and high phytoplankton biomass (11/5/78 and 28/5/78 respectively) in Central Basin. Measurements of total biomass were obtained in the usual manner for each sample (see section on net and nannoplankton distribution). In addition, three subsamples were settled for each of the three samples of high biomass, and the distribution of organisms within the counting chamber examined using counts of four selected species across 20 diagonal transects. These species were chosen as representative of a numerically abundant unicellular form (Cryptomonas reflexa), a rare unicellular form (Gymnodinium helveticum), a filamentous species (Melosira italica) and a colonial species (Dinobryon cylindricum var. alpinum). A two-tailed Binomial test was used to test whether the distribution of these four species within the chamber was significantly different from a Poisson. Furthermore, differences between tube samples and replicate subsamples were tested for using nested ANOVAs, on both transformed and untransformed data ($x = \sqrt{x}$; $x = \sqrt{x+1}$ for low counts). A non-parametric Kruskal-Wallis test (Siegel, 1957) was also used to test for differences between subsamples, assuming a mutual independence between transects.

Results and discussion.

There was close agreement between total biomass estimates for replicate tube samples, both for high and low phytoplankton density (± 1% and ± 6% (2SE) respectively), although the nannoplankton factions (<10 µm and <35 µm) showed higher relative variance (±10% and ±26% respectively for the low biomass samples; ±26% and ±18% respectively for the high

biomass samples; Table E-1). The variance associated with individual species was also higher, particularly for large, rare forms (e.g. Peridinium aciculiferum, Synedra ulna, Melosira italica). There was very little difference in the number of taxa observed in the replicate tube samples.

Using the Binomial test on counts of the four species from the high biomass tube samples, the distributions of these organisms within the counting chamber were found to differ significantly from a Poisson in 45% of the subsamples for the filamentous and colonial species, 37% for the common unicellular form and 9% for the rare, unicellular form (Table E-2). Analysis of variance on these counts from replicate subsamples showed no significant differences in the abundance of each of the four species between replicate tube samples for both transformed and untransformed data. However, in each case, differences between subsamples from tube samples were highly significant ($p < 0.01$). Significant differences between subsamples were also found one in three times for all four species using the Kruskal-Wallis test (Table E-2). Thus, it appears that most of the variance associated with estimates of total biomass in this study is attributable to subsampling, sedimentation and counting error. Because of non-random settling of organisms within the counting chamber, the variance cannot be calculated directly from the mean, as in Lund et al., 1958). However, counts from the two sets of triplicate tube samples, and other replicate counts made on routine samples, indicate that the replicability of biomass estimates is good, although the variance for individual species may be quite high. Furthermore, paired comparisons between stations show highly significant differences in both total and nannoplankton biomass in 1976 and

Table E-1. Estimates of biomass and numbers from triplicate tube samples taken under conditions of low (11/5/78) and high (28/5/78) biomass in Central Basin, Lake Memphremagog.

LOW BIOMASS TUBE SAMPLES (11/5/78)	Tube 1.	Tube 2	Tube 3	$\bar{x}$	2SE (%)
Total biomass ($\mu g l^{-1}$)	193.4	192.4	194.4	193.6	1.5 (.8%)
Total # l^{-1}	1053630	1063060	1054030	1056906	6158 (.6%)
Total # filaments l^{-1}	1571	1178	393	1047	693 (66.0%)
Biomass 10 m ($\mu g l^{-1}$)	61.8	65.1	73.3	66.7	6.8 (10.0%)
Biomass 35 m ($\mu g l^{-1}$)	121.0	122.1	139.4	127.5	12 (9.0%)
Chrysochromulina parva ($\mu g l^{-1}$)	23.4	16.6	19.6	19.9	3.9 (19.0%)
Cryptomonas reflexa ($\mu g l^{-1}$)	15.0	11.5	16.8	14.4	3.1 (22.0%)
Coelosphaerium naeglianum ($\mu g l^{-1}$)	14.7	21.0	14.7	16.8	4.2 (25.0%)
Melosira italica subsp. *subarctica* ($\mu g l^{-1}$)	14.0	6.5	-	6.8	8.1(119.0%)
Gymnodinium veris ($\mu g l^{-1}$)	13.9	16.5	21.5	17.3	4.5 (26.0%)
Peridinium aciculiferum ($\mu g l^{-1}$)	13.6	11.9	1.7	9.1	7.4 (82.0%)
Rhodomonas minuta ($\mu g l^{-1}$)	11.3	14.1	18.4	14.6	4.1 (38.0%)
Total # taxa observed in sample	39	42	41		

HIGH BIOMASS TUBE SAMPLES (28/5/78)	Tube 1	Tube 2	Tube 3	$\bar{x}$	2SE (%)
Total biomass (μgl^{-1})	2026.6	2123.6	2264.4	2137.5	136.8 (6%)
Total # l^{-1}	6260820	7834890	9552230	7882647	1900895 (24%)
Total # filaments l^{-1}	27882	35344	29060	30762	30762 (15%)
Biomass <10 µm (μgl^{-1})	488.3	564.4	746.4	599.7	153.6 (26%)
Biomass <35 µm (μgl^{-1})	762.9	895.4	1047.9	902.6	164.6 (18%)
Melosira italica subsp. *subarctica* (μgl^{-1})	510.8	467.2	367.2	448.4	84.9 (19%)
Chrysochromulina parva (μgl^{-1})	229.9	279.0	349.9	286.3	69.6 (24%)
Diatoma tenue var. *elongatum* (μgl^{-1})	121.9	63.6	016.0	97.2	34.8 (36%)
Rhodomonas minuta (μgl^{-1})	111.7	113.1	171.1	132.0	39.3 (30%)
Asterionella formosa (μgl^{-1})	110.3	87.3	123.7	107.1	21.3 (20%)
Synedra ulna (μgl^{-1})	109.9	-	157.1	89.0	93.1(105%)
Cryptomonas reflexa (μgl^{-1})	60.9	90.1	87.5	79.5	18.5 (23%)
Total # taxa observed in sample	72	74	74		

Table E-2. Kruskal-Wallis and Binomial Tests on replicate counts of 4 species (High biomass tube-samples) across 20 diagonal transects.

Species	KRUSKAL-WALLIS TEST (differences between subsamples) Tube 1	Tube 2	Tube 3	BINOMIAL TEST (Poisson dist.) p<.05	p<.005
Cryptomonas reflexa	A	A	R	63%	82%
Gymnodinium helveticum	R	A	A	91%	100%
Melosira italica subsp. *subarctica*	R	A	A	55%	64%
Dinobryon cylindricum var. *alpinum*	A	R	R	55%	100%

Kruskall-Wallis test: A = H_o accepted, i.e. no significant differences between subsamples ($p<.05$).

R = H_o rejected

Binomial test: % samples in which distribution not significantly different from Poisson at level of significance indicated.

1977 (Table 4), indicating that the variance associated with individual estimates is not sufficient to obscure significant differences in total biomass.

Error associated with estimates of mean cell volume.

No formal estimate of this error could be made. Mean cell dimensions were obtained from a minimum of 50 specimens of the most common species, fewer for rarer forms, from samples taken at all stations. Cell volumes were calculated from the most suitable combination of geometric shapes (e.g. Kling and Holmgren, 1972). The cell volume of Ceratium hirundinella was obtained from Kling and Holmgren, 1972. No corrections was made for the non-cytoplasmic volume of individual cells (e.g. Smayda, 1965; Devaux, 1977). Although this volume can be appreciable, it varies considerably between species of a single taxonomic group and, furthermore, with the physiological condition of a given individual cell (Sicko-Goad et al., 1977). Filament biomass was estimated from volume per µm length, calculated from mean filament diameter, or for species with appreciable constriction at cell junctions (e.g. Anabaena planctonica), from the average volume of individual cells and the mean number of cells per unit length. The length of each filament enumerated was measured to the nearest 25 µm and the total biomass computed. Fragilaria species were classified as filaments (and thus included in counts of total filament concentrations), but biomass for these species was calculated from individually measured filaments (approximated to the nearest 20 µm for both length and height), assuming a mean valve width, and using a correction factor for spaces between individual frustules (Fragilaria crotonensis).

Where possible, the biomass of colonial forms was obtained by counting the number of cells in each colony enumerated, and using mean volumes of mature, or (when present in any abundance) daughter cells (e.g. G. schroeteri). Where cell counts were extremely difficult, colony dimensions were measured to the nearest 25 µm, and colonies approximated to a spherical or ellipsoidal shape. Unless there was very close association between cells (e.g. newly formed daughter colonies; some coenobia), corrections were made for non-cellular volume (Microcystis, Aphanocapsa, Aphanthece, Coelasphaerium and Gomphosphaeria spp.)

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APPENDIX F.

Variance associated with chlorophyll a measurements.

The variance associated with chla measurements can be considered under two general categories — sampling error, and that attributable to the technique.

Sampling error was examined using total and nannoplankton (<10 μm, <20 μm, <35 μm, <64 μm) chla measurements from two sets of triplicate tube samples taken under conditions of low and high phytoplankton biomass (see section of variability in biomass estimates).

The variance associated with technique (also encompassing subsampling error) was investigated from triplicate subsamples from tube samples taken during 1977 and 1978 (total chla only). In addition, the calibration between absorbance (at 665 nm) on the Spectronic 88 spectrophotometer and fluorescence on the Turner model 110 fluorometer was checked using samples taken from a range of phytoplankton densities and species assemblages in 1976-77 (a total of 101 samples).

The short-term variability in % nannoplankton chla was also examined using 2 m samples taken during the development and decline of the spring diatom population in 1978 (see section of variance associated with production measurements).

Results and discussion.

The variance among triplicate tube samples was appreciable, particularly for low chla concentrations (Table F-1), where it ranged up to ± 46% (for the fraction <64 μm), and averaged around ± 20%. The resolution between the nannoplankton fractions was poor; in fact, in one series the

Table F-1. Mean chla (mg m^{-3}) for the different size-fractions in two series of replicate tubes taken under conditions of low and high biomass at Station 3 (Central Basin) in 1978.

Fraction	11/5/78 (low biomass)			28/5/78 (high biomass)		
	$\bar{x}$	±2SE	(%)	$\bar{x}$	±2SE	(%)
TOTAL	0.95	0.17	(18%)	5.45	0.13	(2%)
64µm	0.78	0.36	(46%)	3.93	0.99	(25%)
35µm	0.57	0.12	(21%)	2.78	0.58	(21%)
20µm	0.51	0.06	(12%)	3.6	0.31	(9%)
10µm	0.50	0.03	(6%)	-	-	-

Table F-2. Replicate chla measurements on triplicate subsamples from tube samples taken in 1977 and 1978 at 4 stations in L. Memphremagog. Values in mg.chla m^{-3}.

Station	Tube (m)	Date	Replicate 1	2	3	$\bar{x}$	±2SE	(%)
3	(8.5)	4/6/77	3.5	3.6	3.9	3.7	0.2	(7%)
1	(7.5)	11/6/77	12.8	11.4	12.4	12.2	0.8	(7%)
2	(8.5)	11/6/77	6.9	6.3	6.7	6.6	0.4	(5%)
2	(8.5)	18/6/77	9.0	7.4	6.4	7.6	1.5	(20%)
3	(10)	18/6/77	5.1	4.5	5.1	4.9	0.4	(8%)
1	(7.5)	25/6/77	5.1	5.8	5.1	5.3	0.5	(9%)
2	(8.5)	2/7/77	6.4	4.3	5.4	5.4	1.2	(23%)
2	(8.5)	6/8/77	4.5	3.7	3.6	3.9	0.6	(15%)
1	(7.5)	16/9/77	8.9	7.4	9.8	8.7	1.4	(16%)
2	(8.5)	16/9/77	6.2	6.9	7.5	6.9	0.8	(11%)
3	(8.5)	16/9/77	3.6	3.7	3.6	3.6	0.1	(2%)
2	(8.5)	1/10/77	4.9	4.6	4.6	4.7	0.2	(4%)
4	(13)	1/10/77	3.4	3.0	2.8	3.1	0.4	(12%)
3	(15)	11/5/78	1.1	0.8	0.9	1.0	0.2	(18%)
3	(15)	18/5/78	1.0	0.8	0.9	0.9	0.2	(16%)
3	(15)	22/5/78	1.1	1.1	1.0	1.1	.04	(4%)
3	(15)	23/5/78	2.1	1.9	2.3	2.1	0.2	(11%)
3	(15)	24/5/78	3.1	4.3	3.2	3.5	0.7	(21%)
1	(7.5)	24/5/78	5.1	5.2	3.4	4.6	1.1	(25%)
2	(8.5)	24/5/78	4.5	5.2	4.9	4.9	0.4	(8%)
3	(15)	25/5/78	3.8	3.6	3.6	3.7	0.1	(4%)
3	(10)	25/5/78	4.0	3.7	3.8	3.8	0.2	(5%)
1	(7.5)	31/5/78	3.8	3.4	4.3	3.8	0.5	(13%)
3	(12)	15/6/78	2.5	2.5	2.5	2.5	-	(0%)
							$\bar{x}$	(11%)

Table F-3. Relative contributions to total chl*a* (%) of nannoplankton fractions <64μm, <35μm, <20μm and <10μm at 2m depth in Lake Memphremagog (Station 3), spring 1978.

	Mesh size (μm)			
Date	64	35	20	10
15/5/78	62	80	66	47
18/5/78	109	138	88	-
22/5/78	-	82	67	-
25/5/78	93	80	73	-
27/5/78	75	66	57	53
29/5/78	78	66	68	59
30/5/78	103	76	89	70
1/6/78	98	77	76	64
3/6/78	80	91	91	68
5/6/78	-	-	-	-
10/6/78	85	84	-	
12/6/78	74	62	43	-
$\bar{x}$	86	82	72	61
2SE	9	12	10	6
(%)	(11)	(15)	(13)	(10)

fraction passing through a 20 µm mesh exhibited a higher chl*a* content than that passing through a 35 µm mesh size. This was also observed in a number of samples taken during the progression of the spring diatom population in 1978 (Table F-3). Similar overlap was shown by corresponding fractions of nannoplankton production on fewer occasions, but differences between the fractions were frequently very small (Table F-3). This suggests that the error associated with the chl*a* technique obscures small differences between nannoplankton size-fractions that are better resolved by the ^{14}C technique.

Measurements of total chl*a* from triplicate subsamples of single tube samples also indicate that there is considerable variability associated with this technique, with an average range in variation of ± 11% (2SE) and a maximum of ± 25% (Table F-2). This may account for the fact that no significant change in the calibration between the spectrophotometer and the fluorometer was found throughout 1976-77, despite shifts in species assemblages and hence in associated pigments.

However, despite the greater error associated with chl*a* measurements, the relative contributions (%) of the nannoplankton fractions to total chl*a* and total production at 2m showed very similar temporal patterns (Figs. F-1a, b, c, d) and significant correlations were found between % total chl*a* and % total production for the fractions <10 µm, <20 µm, <35 µm ($r = 0.83, 0.65, 0.71$ respectively; $p < .05$). In addition, the nannoplankton fractions accounted for similar proportions of total chl*a* ($\bar{x}$ = 61%, 72%, 82% and 86% respectively; Table F-3) and total production ($\bar{x}$ = 49%, 70%, 72% and 79% respectively; Table G-3) over the month long period of these measurements. This indicates that while the chl*a* technique is not sensitive to small

Figure F-1. Relative contribution (%) of nannoplankton fraction to total chl*a* (————) and production (·····) at 2M at Station 3 (Central) in Lake Memphremagog, May-June, 1978.

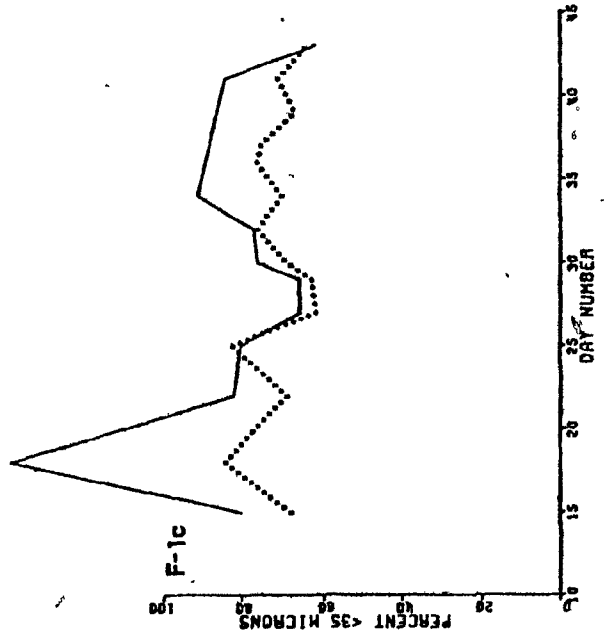
Day number from May 1st, 1978. Mesh sizes as follows:

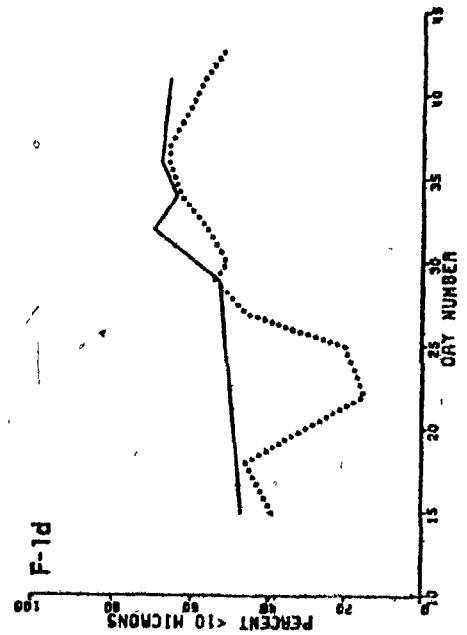
Fig. F-1a : 64 µm

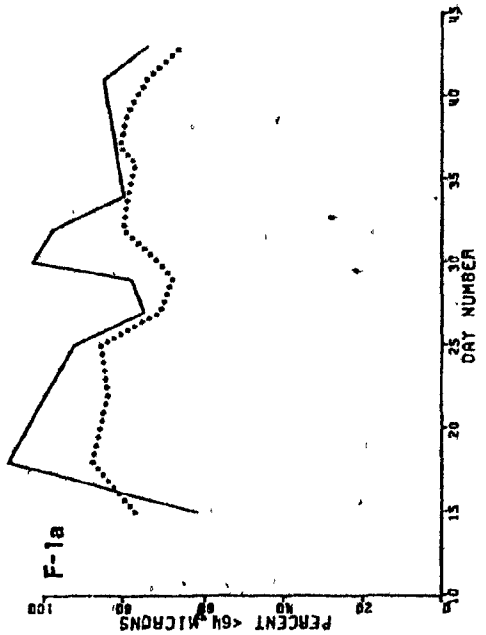
Fig. F-1b : 35 µm

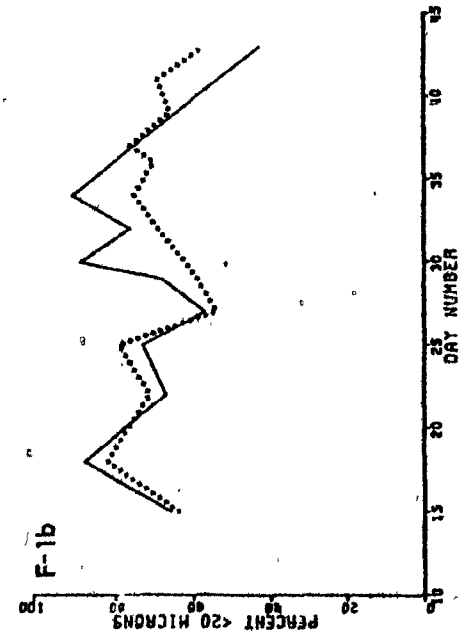
Fig. F-1c : 20 µm

Fig. F-1d : 10 µm


F-1c
PERCENT <35 MICRONS
DAY NUMBER


F-1d
PERCENT <10 MICRONS
DAY NUMBER


F-1a
PERCENT <64 MICRONS
DAY NUMBER


F-1b
PERCENT <20 MICRONS
DAY NUMBER

differences between size fractions, larger temporal fluctuations are reflected by these measurements. Furthermore, although the relative contributions of nannoplankton to total chl*a* and total production may show little correlation over the entire season (see Section 1), significant correlations between these measurements are found over a short time period, such as that covered by the duration of these experiments.

APPENDIX G.

Variance associated with primary production estimates, using the ^{14}C technique.

In general, there appear to be three major sources of variance in production estimates: error associated with sampling and technique (including counting error), and the natural variance associated with fluctuations in insolation, biomass and photosynthetic capacity (e.g. Vollenweider, 1969). Two series of experiments were run to obtain some estimate of variance associated with sampling and technique, particularly for the nannoplankton fractions. The effects of diurnal variation in insolation, biomass and photosynthetic capacity were not examined; however, samples were routinely incubated at the same time of day (mid-morning to early afternoon), for 3-4 hours. In addition, for the purpose of this study, production rates were not extrapolated to a daily basis, but are reported as hourly rates.

Methods.

The method used for production estimates in these experiments is as outlined in Section 1. In the first experiment, two series of triplicate production runs were done on consecutive days at station 3 in May, 1978. In the first series, three subsamples were taken from one Van Dorne water bottle at each depth, while in the second series, subsamples were taken from three separate water bottles at each depth. Triplicates were innoculated with ^{14}C and suspended at each depth simultaneously, such that there were 3 light bottles at every sampling depth, and 3 dark bottles at alternate depth. Following incubation, triplicate samples were filtered simultaneously and

and subsamples from the 2m light bottles were selectively filtered through screens of mesh sizes 10 µm, 20 µm, 35 µm and 64 µm.

In the second experiment, the temporal variability of nannoplankton production at 2m depth was investigated more closely. Primary production was measured approximately every second day from mid May to mid June, 1978, at station 3 (Central Basin). This period coincided with the development and decline of a spring diatom assemblage of Synedra acus var. angustissima, Asterionella formosa and Diatoma tenue var. elongatum, which was monitored by chla measurements and visual inspections of samples under the microscope.

Results and discussion.

The results of the first experiment have not been converted to production rates, but are reported as sample activity (c.p.m. per 50 ml of sample, corrected for background and differences in the volume of ^{14}C innoculated), all other factors being constant between replicates except pH and alkalinity in the second series, which showed a maximum variation of ± 0.08% and ± 3%, respectively (Table G-1).

Variations between replicate bottles from the same water samples was fairly low, ranging up to ± 16% (2SE), and averaging about ± 10%; variability between dark bottles was slightly lower (Table G-1). Replicate selective filtrations showed very close agreement, both for measured activity (max of ± 7%), and %total (max of ± 7%) at 2m. Tangled lines resulted in the loss of several bottles in the second series but the remaining samples also showed relatively low variability (max of ± 10%). Selective filtrations showed greater discrepancies in this run, especially for the fractions <20 µm and <35 µm for both activity (± 12%) and %total activity (± 14%)

Table G-1. Mean activity and range of variance at each depth for two series of triplicate production runs on 5/6/78 (triplicates from the same sample), and 6/6/78 (triplicates from separate samples) at station 3, L. Memphremagog.

Depth (m)	Triplicates from same sample: light bottles cpm	±2SE (%)	dark bottles cpm	±2SE (%)	Triplicates from separate samples: light bottles cpm	±2SE (%)	dark bottles cpm	±2SE (%)	alkalinity $mg.m^{-3}$	±2SE(%)	pH	± 2SE(%)
0	1956	83 (4%)			1886	163 (9%)			43.3	1.0(3%)	8.03	.03(.4%)
1	1491	228 (15%)	42	2 (6%)			57	3 (5%)	43.7	0.6(1%)	8.02	.03(.4%)
2	818	43 (5%)			2424	90 (4%)			43.1	0.5(1%)	8.05	.06(.7%)
3	516	47 (9%)	39	2 (5%)	2468	219 (10%)			43.2	1.1(2%)	8.01	.04(.4%)
5	175	28 (16%)							43.4	0.1(.2%)	8.0	.06(.7%)
7.5	62	7 (11%)	34	3 (9%)			53	4 (8%)	43.9	1.0(2%)	7.9	-

Table G-2. Mean activity and % total activity for nannoplankton fractions <10 µm, <20 µm, <35 µm, and <64 µm at 2m depth from two series of triplicate production runs, 5/6/78 and 6/6/78 at station 3, L. Memphremagog.

mesh (µm)	Triplicates from same sample: cpm	±2SE	(%)	%total	±2SE	(%)	Triplicates from separate samples: cpm	±2SE	(%)	%total	±2SE	(%)
10	562	19	(3%)	66	3	(5%)	1663	59	(4%)	66	6	(11%)
20	599	38	(6%)	70	2	(4%)	1911	230	(12%)	74	10	(14%)
35	647	44	(7%)	76	2	(3%)	1876	222	(12%)	74	10	(14%)
64	668	7	(11%)	76	6	(7%)	2035	12	(1%)	80	4	(4%)

Table G-3. Relative contributions to total production (%) of nannoplankton fractions <64µm, <35µm, <20µm and ≤10µm at 2m depth in Lake Memphremagog (Station 3), spring 1978.

	Mesh size (µm)			
Date	64	35	20	10
11/5/78	97	80	88	49
15/5/78	77	68	64	39
18/5/78	88	84	82	46
22/5/78	84	69	71	15
25/5/78	86	82	79	20
27/5/78	71	62	54	46
29/5/78	68	63	59	54
30/5/78	71	69	62	51
1/6/78	80	76	69	56
3/6/78	79	70	75	63
5/6/77	77	76	70	66
6/6/78	81	75	76	66
8/6/78	79	67	66	61
10/6/78	74	71	69	57
12/6/78	66	64	57	51
$\bar{x}$	79	72	70	49
2SE	4	4	5	8
(%)	(5)	(5)	(7)	(16)

(Table G-2). The resolution in activity between these mesh sizes was low in both production runs; however, the fact that a large difference in variability between replicates was not observed between the two experiments indicates that sampling error is small compared to that associated with technique.

In the first experiment, the difference in the relative contribution (%) of each size fraction to total production between the two days was small (variation in actual activity reflecting a marked difference in incident radiation received during each incubation). Similar lack of temporal variability in the relative contributions of the different size fractions was more effectively demonstrated in the 15 consecutive production measurements of the second experiment (Table G-3; Figs. F-1a, b, c, d), in which the highest variance was shown by the faction <10 μm (± 16%). However, similar temporal patterns were exhibited by the relative contributions of the nannoplankton fractions to both total chla and production (Figs. F-1a, b, c, d; see also Appendix F); and it appears that these fluctuations were not simply due to random error, but real and detectable despite the general variability associated with both techniques.

REFERENCES

Vollenweider, R.A. 1969. (Ed.) A Manual on Methods for Measuring Primary Production in Aquatic Environments. I.B.P. Handbook No. 12. Blackwell Scientific Publication. Oxford. 213 pp.