

THE PHYTOPLANKTON POPULATION DYNAMICS
OF A SMALL RESERVOIR.

By

ANNETTE MARIE TRIMBEE, B.Sc., M.Sc.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University



November, 1983

PHYTOPLANKTON POPULATION DYNAMICS OF A SMALL RESERVOIR

DOCTOR OF PHILOSOPHY (1983)

(Biology)

McMaster University

Hamilton, Ontario

TITLE: The Phytoplankton Population Dynamics of a
Small Reservoir.

AUTHOR: Annette Marie Trimbee, B.Sc. (University of Winnipeg)

M.Sc. (University of Manitoba)

SUPERVISOR: ~~Professor G.P. Harris~~

NUMBER OF PAGES: xv, 208

ABSTRACT

Time series analysis was used to study the phytoplankton population dynamics of a small reservoir (Guelph Lake, southern Ontario). Three stations were sampled daily for one season (May 8 to August 20, 1981) and weekly at one station for 2 years (fall/1980 to fall/1982). Significant environmental variability was detected at time scales of days to weeks.

Time series analysis of the daily data from 3 stations (maximum separation - 1 km) demonstrated the existence of strong horizontal advection within the basin with a period of 2-3 days and 10-20 day cycles associated with changing weather systems. Rates and directions of horizontal advection varied among different variables. The algal biomass (chlorophyll a) at station 1 lagged that at station 3 by half a day. The time lag between station 1 and station 3 for Aphanizomenon flos-aquae was 7 days, whereas for Ceratium hirundinella station 1 led station 3 by 3 days indicating opposing motion by the species. Longer term (10-20 day) periodicities occurred in between and within station comparisons for soluble reactive phosphorus and total phosphorus. Periodicities in the average daily wind speed and water column stability showed that such lags or leads were due to vertical mixing.

Sedimentation traps were used to examine the settling of diatoms and the recruitment of summer blue-green species. The relationship between physical variables such as water column stability (N^2 , Richardson number) or wind stress and the vertical heterogeneity of

chlorophyll a, nutrients and phytoplankton species on a daily basis was examined. High Richardson numbers were better predictors of high vertical heterogeneity than low wind speed or N^2 alone. Higher correlations between physical variables and vertical heterogeneity were obtained in late summer. Relationships between environmental variables and phytoplankton population dynamics were examined on a daily and a weekly basis. Time lags occurred between changes in environmental variables and the abundance of particular phytoplankton as well as the rate of phytoplankton community change.

The results suggest that non-equilibrium conditions prevail in the phytoplankton community of Guelph Lake. Significant environmental variability was detected at time scales of the same magnitude as phytoplankton generation times, time lags occurred between changes in environmental variables and algal abundances and the majority of the increases in the rate of phytoplankton community change occurred in response to allogenic factors. Some of the problems encountered with the use of bivariate time series techniques in phytoplankton are then discussed.

ACKNOWLEDGEMENTS

I thank my thesis supervisor, Dr. G.P. Harris, for his contributions to the study of phytoplankton ecology and for his guidance and encouragement. I would also like to thank my committee members, Dr. C.D. Rollo and Dr. R. Vollenweider for their interest and support. Thanks are extended to Beryl Piccinin for her technical assistance and sincere friendship.

I would also like to thank Heidi Klein, Susan Hunter and Ruth Abrahams for their assistance in the field. I thank my husband Kevin for his assistance with field work, his interest in my work and his understanding throughout.

The Grand River Conservation Authority allowed access to the lake and supplied the hydrological data. Financial support from N.S.E.R.C. in the form of an operating grant to Dr. G.P. Harris and a scholarship to the author is gratefully acknowledged.

TABLE OF CONTENTS

I) Introduction	1
I-1 Paradox of the Plankton	1
I-2 Seasonal Succession	3
I-3 Models in Algal Ecology	6
I-4 Effects of Water Movements on Sampling	7
I-5 Demonstration of Non-Equilibrium Conditions	7
I-6 Use of Time Series Analysis	8
I-7 Objectives	10
II) Materials and Methods	12
II-1 Details of Site	12
II-2 Sampling Program	12
II-2-1 Daily Time Series	12
II-2-2 Weekly Time Series	15
II-3 Hydrology	15
II-4 Biomass Estimates	15
II-5 Chemical Analysis	18
II-6 Estimates of z_{eu}/z_m and Water Column Stability (N^2 and Richardson number)	19
II-7 Phytoplankton Diversity and Rate of Phytoplankton Community Change	21
II-8 Sedimentation Traps	21
II-9 Estimates of Vertical Heterogeneity	24
II-10 Time Series Analysis	24
III) Results	28
III-1 Temporal and Spatial Variability	28
III-1-1 Spectral Analysis of Temporal Variability	28
III-1-2 Time Series Analysis of Spatial Variability	42
III-1-2-1 Horizontal Advection	42
III-1-2-2 Redistribution by Vertical Mixing	72
III-1-3 Summary	75
III-2 Relationship between Environmental Variables and Phytoplankton Dynamics	79


III-2-1	Daily Time Series (May 8 to August 20, 1981)	79
III-2-1-1	General Description of Phytoplankton Dynamics	79
III-2-1-2	General Description of Environmental Variables	86
III-2-1-3	Sedimentation Trap Catches	93
III-2-1-4	Cross-correlations	113
III-2-1-5	Relationship between Physical Variables and Vertical Heterogeneity	131
III-2-2	Weekly Time Series	143
III-2-2-1	General Description of Phytoplankton Dynamics	143
III-2-2-2	General Description of Environmental Variables	149
IV)	Discussion	160
IV-1	Temporal and Spatial Variability	160
IV-1-1	Spectral Analysis of Temporal Variability	160
IV-1-2	Time Series Analysis of Spatial Variability	164
IV-1-2-1	Horizontal Advection	164
IV-1-2-2	Redistribution by Vertical Mixing	167
IV-2	Relationship between Environmental Variables and Phytoplankton Dynamics	167
IV-2-1	Daily Time Series	167
IV-2-2	Weekly Time Series	177
IV-3	General Discussion	182
IV-3-1	The Interpretation of Field Data	182
IV-3-2	Non-equilibrium versus Equilibrium	183
IV-3-3	Use of Bivariate Time Series Analysis	184
V)	Summary	188
V-1	Temporal and Spatial Variability	188
V-2	Relationship between Environmental Variables and Phytoplankton Dynamics	189
V-2-1	Daily Time Series	189
V-2-2	Weekly Time Series	190
V-3-1	Non-equilibrium versus Equilibrium	192
V-3-2	Use of Bivariate Time Series Analysis	192
VI)	References	194

List of Figures

Figure 1	Location of sites in Guelph Lake.	13
2	Power spectrum for temperature at 0m.	30
3	Power spectrum for temperature at 4m.	31
4	Power spectrum for chlorophyll a.	32
5	Power spectrum for water column stability.	34
6	Power spectrum for wind speed.	36
7	Power spectrum for z_{eu}/z_m .	37
8	Power spectrum for soluble reactive phosphorus.	38
9	Power spectrum for total phosphorus.	39
10	Power spectrum for silica.	40
11	Power spectrum for combined nitrate and nitrite.	41
12a	Cross-correlations for soluble reactive phosphorus, station 1 versus station 3.	44
12b	Phase spectrum for soluble reactive phosphorus, station 1 versus station 3.	45
12c	Cross-correlations for soluble reactive phosphorus, station 1 versus station 2.	46
12d	Phase spectrum for soluble reactive phosphorus, station 1 versus station 2.	47
12e	Cross-correlations for soluble reactive phosphorus, station 2 versus station 3.	48
12f	Phase spectrum for soluble reactive phosphorus, station 2 versus station 3.	49
13a	Cross-correlations for total phosphorus, station 1 versus station 3.	50
13b	Cross-correlations for total phosphorus, station 1 versus station 2.	51
13c	Cross-correlations for total phosphorus, station 2 versus station 3.	52
14	Cross-correlations for combined nitrate and nitrite, station 1 versus station 3.	54
15a	Cross-correlations for chlorophyll a, station 1 versus station 3.	55
15b	Phase spectrum for chlorophyll a, station 1	

versus station 3.	56
15c Cross-correlations for chlorophyll a, station 1 versus station 2.	57
15d Cross-correlations for chlorophyll a, station 2 versus station 3.	58
16a Cross-correlations for <u>Aphanizomenon</u> , station 1 versus station 3.	59
16b Phase spectrum for <u>Aphanizomenon</u> , station 1 versus station 3.	60
16c Cross-correlations for <u>Aphanizomenon</u> , station 1 versus station 2.	61
16d Phase spectrum for <u>Aphanizomenon</u> , station 1 versus station 2.	62
16e Cross-correlations for <u>Aphanizomenon</u> , station 2 versus station 3.	63
16f Phase spectrum for <u>Aphanizomenon</u> , station 2 versus station 3.	64
17a Cross-correlations for <u>Ceratium</u> , station 1 versus station 3.	66
17b Phase spectrum for <u>Ceratium</u> , station 1 versus station 3.	67
17c Cross-correlations for <u>Ceratium</u> , station 1 versus station 2.	68
17d Cross-correlations for <u>Ceratium</u> , station 2 versus station 3.	69
18 Cross-correlations for <u>Stephanodiscus</u> , station 1 versus station 3.	70
19 Cross-correlations for <u>Lyngbya</u> , station 2 versus station 3.	71
20 Auto-correlations for soluble reactive phosphorus at different depths.	73
21 Daily time series plots of chlorophyll a, phytoplankton diversity and rate of phytoplankton community change.	80
22 Daily time series plots of phytoplankton abundances	82
23 Daily time series plots of water column stability	

	($N^2(0-6)m$ and $N^2(0-10)m$).	84
24	Daily time series plots of environmental variables.	89
25	Accumulation rates of total phosphorus in the sedimentation traps (spring-fall, 1981).	94
26	Accumulation rates of <u>Stephanodiscus</u> in the sedimentation traps (April - mid-June, 1981).	97
27	Accumulation rates of <u>Asterionella</u> in the sedimentation traps (April-mid-June, 1981).	98
28	Accumulation rates of <u>Cyclotella</u> in the sedimentation traps (April-mid-June, 1981).	99
29	Accumulation rates of <u>Melosira</u> in the sedimentation traps (April-mid-June, 1981).	100
30	Accumulation rates of <u>Aphanizomenon</u> in the sedimentation traps (April-mid-June, 1981).	105
31	Accumulation rates of <u>Microcystis</u> in the sedimentation traps (July-August, 1981).	106
32	Accumulation rates of <u>Gomphosphaeria</u> in the sedimentation traps (July-August, 1981).	109
33	Accumulation rates of <u>Lyngbya</u> in the sedimentation traps (July-August, 1981).	110
34	Cross-correlations between N^2 and chlorophyll a.	114
35	Cross-correlations between N^2 and phytoplankton diversity.	119
36	Cross-correlations between N^2 and rate of phytoplankton community change.	121
37	Cross-correlations between N^2 and <u>Stephanodiscus</u> abundance.	124
38a	Cross-correlations between zeu/zm and <u>Cryptomonas erosa</u> abundance.	128
38b	Cross-correlations between zeu/zm and <u>Cryptomonas ovata</u> abundance.	129
38c	Cross-correlations between zeu/zm and <u>Rhodomonas</u> abundance.	130
39	Vertical profiles of <u>Aphanizomenon</u> abundance.	133
40	Vertical profiles of <u>Ceratium</u> abundance.	134
41	Vertical profiles of <u>Lyngbya</u> abundance.	135



42	Weekly time series plots of chlorophyll a and water column stability ($N^2(0-6)m$ and $N^2(0-10)m$).	144
43	A comparison of the phytoplankton diversity and rate of phytoplankton community change in the spring-summer of 1981 to that in 1982.	145
44	Phytoplankton diversity and rate of phytoplankton community change from May 9/ 1981 to September 29/ 1982.	146
45	Weekly time series plots of diatom abundances (spring-summer of 1981 and 1982).	147
46	Weekly time series plots of blue-green algal abundances (spring-summer of 1981 and 1982).	150
47	Weekly time series plots of temperature and pH at 0m and 10m and dissolved oxygen and ammonia at 10m (spring-summer of 1981 and 1982).	153
48	Operating rule in Guelph Lake (changes in lake level are shown).	155
49	Weekly time series plots of nutrients.	158
50	Power spectrum for temperature at 0m in Hamilton Harbour.	162

List of Tables

Table 1	Counting accuracy.	17
2	Significant cross-correlations between soluble reactive phosphorus time series obtained from different depths.	74
3	Significant cross-correlations between total phosphorus time series obtained from different depths.	76
4	Summary of between station and within station comparisons for soluble reactive phosphorus and total phosphorus and significant auto-correlations in wind speed.	78
5	Sinking rates from the upper 7m of Guelph Lake (Vd) and sinking rates into the upward facing sedimentation trap at 2m (Vt) for diatoms in the spring (1981) trapping periods.	101
6	Sinking rates (Vt) throughout the water column for diatoms in the spring (1981) trapping periods.	102
7	Cumulative sinking loss compared to maximum standing crop at station 1.	104
8	Specific migration activities of three summer blue-green algae at 2, 4 and 10m (station 1) during the late summer (1981) trapping periods.	111
9	Summary of the significant cross-correlations obtained when residuals of N^2 or dissolved oxygen were compared to residuals of the abundances of summer blue-greens.	132
10	Correlations between wind speed and water column stability.	137
11	Significant cross-correlations between N^2 and surface concentration or vertical heterogeneity.	138
12	Significant cross-correlations between wind speed and surface concentration or vertical heterogeneity.	140

- 13 Significant cross-correlations between Richardson number and surface concentration or vertical heterogeneity. 141
- 14 Correlations between surface concentration of total phosphorus or chlorophyll and abundance of Lyngbya. 142
- 15 Hydrological information, a comparison of the spring-summer of 1981 to 1982. 156
- 16 Ratio of combined nitrate and nitrite to soluble reactive phosphorus, a comparison of the spring-summer of 1981 to 1982. 159

Species List

Cyanophyceae

- Aphanizomenon flos-aquae Ralfs
Microcystis aeruginosa Kuetzing
Gomphosphaerium lacustris Chodat
Coelosphaerium Naegelianum Unger
Merismopedia tenuissima Lemmerman
Lyngbya Birgei G. M. Smith

Chlorophyceae

- Planktosphaeria gelatinosa G. M. Smith
Oocystis Borgei Snow

Peridineae

- Ceratium hirundinella (Mueller) Schrank

Chrysophyceae

- Dinobryon divergens Imhof
Ochromonas sp.

Cryptophyceae

- Cryptomonas erosa Ehrenberg
Cryptomonas ovata Ehrenberg
Rhodomonas minuta Skuja

Diatomeae

- Stephanodiscus astrea (Ehrenberg) Grunow
Asterionella formosa Hassall

Melosira granulata (Ehrenberg) Ralfs

Cyclotella Meneghiniana Kuetzing

I) INTRODUCTION

I-1 Paradox of the Plankton

Early views of the planktonic environment held that the environment was homogeneous and at equilibrium over large scales. Given this, however, the Competitive Exclusion Principle predicts one or only a few species of primary producers, yet the diversity of phytoplankton is much higher. The coexistence of numerous species in the same, apparently homogeneous, environment has been termed the "paradox of the plankton" (Hutchinson, 1961).

The Competitive Exclusion Principle assumes that the competing species are at equilibrium and that the two species are never exactly equivalent and therefore cannot have a competition coefficient of zero. Equilibrium has the following limiting assumptions: the population/environment is fully saturated with species so there is no temporary relaxation of selection favoring the optimal response, the optimum does not vary over time, the optimum is attainable and there is no limitation from the past history of the population (Harris, 1982). Equilibrium solutions to the paradox of the plankton based on resource utilization in chemostats (Titman, 1976, Tilman, 1977, 1980, Tilman et al., 1981), limit cycles (Hutchinson, 1965) and resource partitioning (Stewart and Levin, 1973, Peterson, 1975) have been suggested.

Non-equilibrium solutions have also been proposed. Hutchinson (1961) suggested that the main answer to the paradox of the plankton lies in the violation of the assumption that the competing species are at equilibrium. Hutchinson recognized that conditions change rapidly in aquatic habitats and perhaps one, and then another organism is the superior competitor, but that in such rapid succession that no species has the advantage long enough to eliminate the others. For competitive exclusion not to occur, the frequency of environmental fluctuations must be similar to the generation time of the organisms (Hutchinson, 1941, 1953, 1961, 1967). This principle has been re-stated in the theory of intermediate disturbance (Connell, 1978) which was proposed as a general non-equilibrium explanation of ecological diversity. This theory predicts that diversity is maximal when environmental perturbations disrupt competitive exclusion. The required scale of environmental perturbations depends on organism growth rates (Harris, 1980) and turnover times (Kemp and Mitsch, 1979). If environmental perturbations are long relative to growth rates diversity will be low, as competitive exclusion will lower diversity. If environmental perturbations are frequent relative to growth rates, an approach to equilibrium is possible and diversity will be reduced.

Richerson et al. (1970) proposed a contemporaneous disequilibrium model to explain the phytoplankton diversity. They proposed that water is patchy and particular species are favored in different patches. These patches are stable enough to permit a

considerable degree of overall patchiness to occur in phytoplankton, but are obliterated frequently enough to prevent the exclusive occupation of each niche by a single species. Richerson's hypothesis differs from Hutchinson's by stressing the spatial rather than the temporal heterogeneity of the plankton habitat.

I-2 Seasonal Succession

The cycle of species composition of the phytoplankton is termed their seasonal succession. This seasonal succession does not coincide exactly with the concept of terrestrial succession (e.g. Odum, 1971) in that a strongly directional component is not always well defined for the species composition observed (Lewis, 1978a). Water column stability plays a major role in the determination of phytoplankton diversity (Margalef, 1978). A typical progression in temperate lakes that stratify in the summer is from spring diatoms to summer species adapted to survive in stratified lakes. Reynolds et al. (1983) suggested that faster growing colonists and opportunistic species (r-selected) first dominate followed by slower-growing, loss-resistant species that compete more efficiently for the resources (K-selected). Diversity increases with the onset of stratified conditions due to increased spatial and temporal heterogeneity (Harris, 1980, Wall and Briand, 1980, Nalewajko et al., 1981).

This typical progression may be altered by changes in physical conditions. In the phytoplankton environment, succession consists of a

series of episodes of variable length (Margalef, 1967). An episode is initiated by an abrupt change in physico-chemical conditions, which is followed by a sudden change in phytoplankton composition. Successional change continues until an abrupt externally induced physico-chemical alteration initiates another episode. Lewis (1978a) found that tropical lakes such as Lake Lanao differed from comparable temperate lakes such as Lake Erken in the number of episodes. The lengths of episodes in Lake Lanao were shorter than Lake Erken. Variations in the supply of nutrients are much more irregular and numerous in Lake Lanao than in comparable temperate lakes where seasonal events are the dominant control mechanism. Reynolds (1980) suggests that phytoplankton community changes are brought about by a) true autogenic succession, under relatively constant physical conditions b) allogenic shifts, resulting from more permanent variations in physical structure and c) reversions, resulting from temporary perturbations, followed by a renewal of thermal stability. True autogenic succession is equivalent to the main sequence as described by Margalef (1978).

Indexes of succession rate have been formulated (Jassby and Goldman, 1974, Lewis, 1978b). The Jassby and Goldman (1974) index does not weight the species equally. Lewis(1978b) argued that since succession is a community phenomenon, that the changes in a given species should be expressed in relation to the abundance of all the species in the community and that all individuals therein are equally

weighted. Reynolds (1980) prefers to refer to this index as a rate of community change since it is sensitive to all major changes in community composition, whether they reflect true succession, or other, non-directional processes.

By examining the rates of phytoplankton community change and comparing these rates to changes in physical, chemical and biological variables it is possible to assess the relative contributions of these variables to the phytoplankton population dynamics observed. Equilibrium models of phytoplankton community structure assume that the observed seasonal succession is determined by strong competitive interactions (autogenic succession) whereas non-equilibrium models assume that external factors override competition and disrupt the approach to competitive exclusion (allogenic shifts). In the temperate lakes examined by Reynolds (1980), only half of the recorded changes in phytoplankton community structure coincided with changes in physical stability. Several transitions were directly consequential upon the rapid elimination of populations of smaller algae by grazing. Reynolds (1980) suggests that physical variables determine the direction of succession whereas chemical variables determine the rate and the starting point.

The abundance of a particular species depends on the balance between gain processes, such as growth and recruitment from the inflow and sediments and loss processes such as sedimentation, grazing, outwash and death and decomposition. It has been suggested that

differential loss rates discriminate between potentially competing species to an extent far greater than species differences in light and temperature optima, photosynthetic behaviour and nutrient uptake kinetics (Reynolds et al., 1982a). With advancing season, sedimentation is replaced by grazing and then by decomposition as the dominant sink for phytoplankton carbon (Gliwicz and Hillbricht, 1975, Reynolds et al., 1982a).

I-3 Models in Algal Ecology

Direct correlations between environmental variables and algal abundance are commonly sought. If non-equilibrium conditions prevail, however, time lags will occur between the environmental change and the phytoplankton response (Vollenweider, 1950, 1953, Allen, 1977, Harris, 1980, 1982). The factors leading to an algal bloom must be sought in samples taken during the growth phase rather than samples taken when the bloom is at its peak (Vollenweider, 1953). Harris (1980) demonstrated the existence of significant environmental variability at scales from seconds to years and showed that many equilibrium plankton models are invalidated by the existence of disequilibrium at scales much less than a few days. Levins (1979) argued that such temporal and spatial scales of variability are a resource to be exploited. Using principal component analysis (PCA) and a non-metric scaling technique (MDS), Harris and Piccinin (1980) found that there was rarely a precise correlation between the immediate environment and the species composition as there was a response lag of at least a week. In Hamilton Harbour phytoplankton

composition responded to changes in the ratio of the depth of the euphotic zone to the depth of the mixed layer (Z_{eu}/z_m) and major community changes occurred over a time scale of 2-6 weeks as well as seasonal time scales.

I-4 Effects of Water Movements on Sampling

The analysis of phytoplankton dynamics from samples taken from only one station is complicated by the fact that water motions and horizontal advection cause horizontal redistribution of the phytoplankton (Heaney, 1976, Heaney and Talling, 1980). Water bodies having density gradients theoretically exhibit countercurrent flow, that is, currents differing in magnitude and direction with depth (Kamykowski and Zentara, 1977). Since different phytoplankton species and nutrients may show different vertical distributions, different rates and direction of horizontal transport are to be expected under countercurrent flow conditions. Under conditions of mild to moderate wind stress, algal cells and nutrients that are positioned at the surface are likely to accumulate on the leeward side of the lake (George and Edwards, 1976, Heaney, 1976, Stauffer, 1982). Similarly, algal cells and nutrients that are positioned at a lower depth may be advected in the opposite direction and may accumulate on the windward shore.

I-5 Demonstration of Non-equilibrium conditions

To demonstrate that phytoplankton communities are

non-equilibrium systems it is first necessary to characterize the environmental variability over a wide range of time scales (Harris, 1982). The important time scales may range from minutes to days and weeks (Harris, 1978). For competitive exclusion to be disrupted, there must be significant environmental variability at scales of days to weeks since phytoplankton generation times are of this magnitude. If non-equilibrium conditions prevail, time lags will occur between changes in environmental variables and phytoplankton abundances, the majority of increases in phytoplankton succession rate will occur in response to allogenic factors and successional episodes will be initiated frequently.

I-6 Use of Time-Series Analysis

Time series analysis can be used to characterize the environmental and biological variability in a system. A time series is a sequence of numbers representing the progression of some variable in time (a stochastic process). The characteristic features of each time series may be determined by examining the autocorrelation function and power spectrum (Platt and Denman, 1975). The autocorrelation function provides information about how neighbouring points are correlated. The power spectrum provides information as to how the variance of a series of numbers about their mean is partitioned into contributions that are harmonics of the length of the data set. Power spectral analysis determines the dominant cycles in a system (Platt and Denman, 1975).

Theoretical studies (Kolmogorov 1941, Denman and Platt, 1976) suggest that the turbulent energy spectrum and the power spectrum for any passive scalar within the water flow field will show a $-5/3$ slope with increasing frequency or decreasing period, on a log-log plot within the inertial subrange. The inertial subrange is that range over which the velocity variance is transferred conservatively from lower to higher wave numbers until it reaches scales small enough for viscous dissipation to become important.

Bivariate time series analysis has been used to examine time lags between environmental fluctuations and phytoplankton responses (Sephton, 1980, Harris, 1982, Marra and Heinemann, 1982). The community structure may be considered to be a lagged damped function of the environmental spectrum (Harris, 1980). If more than one station has been sampled, the advection pattern for a given variable may be seen through station-to-station comparisons of the time series observed. The time series from one station may be considered the input and the time series from the second may be considered the output. Cross-correlations or cross-spectral analysis may be employed to compare an input time series to an output time series.

Time series analysis has been used to study the spatial and temporal variability and the phytoplankton ecology of Hamilton Harbour (Zarull, 1979, Sephton, 1980, Harris, 1982). Hamilton Harbour is a

eutrophic bay with high and continuous nutrient loadings which do not appear to limit algal growth and productivity (Harris et al., 1980a). Blue-green algae are not dominant in Hamilton Harbour in the late summer (Harris et al., 1980b, Sephton, 1980) as in other eutrophic lakes in temperate latitudes. Hamilton Harbour is connected to Lake Ontario by a narrow channel. Exchanges between the lake and harbour dominate the harbour's physical motions (Palmer and Poulton, 1976, Harris et al., 1980a). The lake oscillations are superimposed on the high frequency harbour motions resulting in chaotic mixing patterns. Sephton (1980) demonstrated that the phytoplankton community of Hamilton Harbour is a non-equilibrium system. There was significant environmental variability at scales of days and weeks and the daily or weekly environmental fluctuations represented the strongest temporal scale to which the algae responded.

I-7 Objectives

The object of this project was to test the generality that non-equilibrium conditions prevail in phytoplankton communities. To do this a lake that was less eutrophic than Hamilton Harbour, where blue-green algae were dominant in the late summer and where the physical motions were not complicated by exchange with a much larger body of water was chosen. Sampling was carried out daily at three stations for one spring-summer period and weekly at one station for approximately two years. Power spectral analysis was performed on time series of temperature, water column stability (N^2), wind speed, z_{eu}/z_m and

nutrients to determine the dominant physical and chemical cycles in the system. Power spectral analysis was also performed on the time series for chlorophyll a. Bivariate time series analysis was used to examine the spatial variability of chlorophyll a, nutrients and phytoplankton species. The characteristic horizontal and vertical mixing scales for Guelph Lake were then determined. The relationship between physical variables such as water column stability (N^2 , Richardson number) or wind stress and the vertical heterogeneity of chlorophyll a, nutrients and phytoplankton species on a daily basis was examined. Sedimentation traps were used to study both the loss of diatoms and the recruitment of summer blue-green algae from the sediments. Relationships between the environmental variability and the phytoplankton population dynamics were examined on both daily and weekly time scales.

2

9

II) MATERIALS AND METHODS

II-1 Details of site

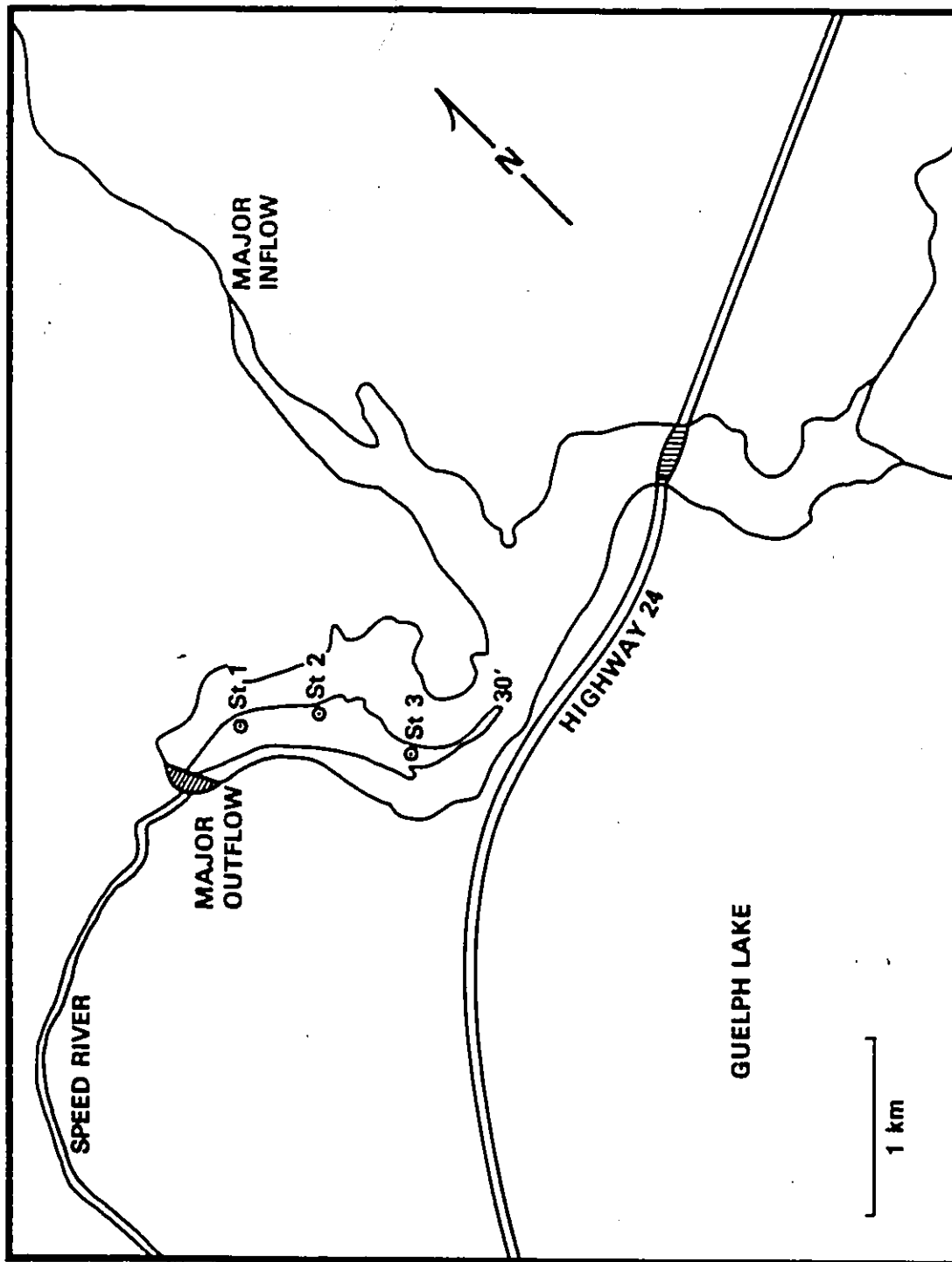
Guelph Lake is located in southern Ontario at a latitude of 43.33°N and a longitude of 80.15°W . The lake was created in 1976 by the damming of the upper Speed River and has an area of 360 hectares. In the first summer of impoundment the main part of the lake was deemed mesotrophic on the basis of oxygen saturation, secchi disc visibility, carbon content, chlorophyll content, primary productivity, phytoplankton abundance and diversity indices of rotiferan and crustacean zooplankton, benthos and fish (Mackie et al., 1976).

II-2 Sampling program

II-2-1 Daily time series

Sampling was carried out daily at 3 stations in the main basin for 105 days (May 8 to August 20, 1981). A raft was moored at station 1. Station 1 (outflow end) and station 2 had a maximum depth of 12m whereas station 3 (inflow end) had a maximum depth of 10m. The relative positions of the 3 stations are shown in Figure 1. Integrated samples (0-7m) were collected by way of a flexible plastic tube for the analysis

Figure 1 - Location of stations in Guelph Lake.



of chlorophyll-a, nutrient concentrations and phytoplankton population dynamics. Discrete vertical samples (surface, 1, 2, 3, 4, 5 and 10m) were also collected from station 1. Temperature and dissolved oxygen (DO) were recorded at each station using a YSI model 57 dissolved oxygen meter with a Clark type polarographic sensor and a built in thermistor. Light profiles of photosynthetically available radiation (P.a.r., 400 to 700 nm) were recorded at each station using a Li-Cor model LI-185 quantum meter. Daily wind speed data were obtained from the Elora research station located 5 km away. Wind speed data were obtained directly from station 1 for a subsample of the 105 days using a C.F. Casella and Co. Ltd. Sensitive Anemometer. The anemometer was clamped to a pole which extended vertically (2m) from one end of the raft. Counts per minute were converted to an average wind speed in m sec^{-1} using the conversion graphs provided by the manufacturer.

Temperature at station 1 was measured at 20 min intervals for a few days in July, 1981. Eleven YSI series 401 temperature probes were fastened together at 1m intervals to form a continuous cable. The cable was secured to and suspended through an opening in the raft floor. The temperature probes were fastened to an 18 channel stepping switch which selected the electrical signal sequentially from the temperature probes at 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10m. The complete cycle time of the switch was 112 seconds, or 6 seconds per thermistor probe. The stepping switch was connected to a Data Logger which was programmed to read information from the stepping switch every 20 minutes. The output from the data logger was calibrated and converted to °C.

II-2-2 Weekly time series

Station 1 was also sampled on a weekly basis for 111 weeks (August 20, 1980 to September 29, 1982). During the spring through fall an integrated sample (0-7)m and discrete vertical samples (surface, 1, 2, 3, 4, 5 and 10) were collected as in the daily time series. During the winter, the 7m tube could not be used because it was no longer flexible. Discrete vertical samples were taken at the surface, 1, 2, 3, 4, 5 and 1m from the bottom. The values from these samples were then averaged to approximate an integrated sample. Since lake levels were lower in the winter a discrete sample from 10m could not be obtained. When the ice was too thin to allow access to station 1, a surface sample was obtained as close to station 1 as possible.

II-3 Hydrology

Hydrological information was obtained from the Grand River Conservation Authority. Information concerning inflow rates, discharge rates, lake level and lake storage (volume) was available on a daily basis. A flushing time for the lake was calculated by dividing the lake storage by the discharge rate through the dam.

II-4 Biomass estimates

Subsamples of 20 ml from each water sample were preserved for

phytoplankton enumeration with a few drops of Lugol's iodide. After overnight sedimentation the relative abundances of the dominant phytoplankton species were determined by counting 20 fields at 2 magnifications using a Zeiss UPL inverted microscope (Utermöhl, 1958, Lund et al., 1958). The larger individual cells, colonies or filaments were counted at a magnification of 80x, whereas the smaller cells or colonies (Rhodomonas, Ochromonas, Cyclotella and Merismopedia) were counted at a magnification of 320X. The standard error of the mean (S.E.M.) may be determined by $\sqrt{\bar{x}/N}$, where \bar{x} is the mean number of individuals per field and N is the number of fields counted, assuming a Poisson distribution. Since the counting accuracy varies inversely with the square root of the number of fields counted, a quadrupled unit effort is required to doubly improve the accuracy (Lund et al., 1958). Due to the large number of samples which were to be counted, a decision was made to count 20 fields at each magnification. The abundances were calculated for each individual species by multiplying the total count in the 20 fields by the appropriate conversion factor (4.1 if counted at 80x and 16.4 if counted at 320x) to obtain the number of individuals ml⁻¹. Table 1 shows what the S.E.M. as a % of the mean is for individuals of different abundances, when 20 fields are counted at either low or high power. Note that the accuracy of the count doubles as the abundance quadruples. An abundance of 0 individuals ml⁻¹ for a particular species does not imply that it was not present at all, but merely that its abundance was below the detection limit of the counting technique used.

Table 1

Counting accuracy (Standard error of the mean (S.E.M.) as a % of the mean) obtained for different abundances (cells ml⁻¹) when 20 fields are counted at either low (80x) or high (320x) power.

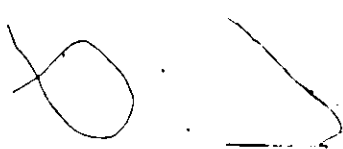
Low power			High power		
number of cells ml ⁻¹	\bar{x} /field	S.E.M. as a % of mean	number of cells ml ⁻¹	\bar{x} /field	S.E.M. as a % of mean
1230	15	5.8	4920	15	5.8
246	3	12.9	984	3	12.9
82	1	22.0	328	1	22.0
41	.5	31.6	164	.5	31.6

Chlorophyll-a concentrations were determined fluorometrically using a Turner Designs model 10 fluorometer after filtration (12 lbs in⁻²) of duplicate samples on Versapor filters (pore size = .45 μ m) and extraction in hot methanol (Talling, 1974). The range of values obtained between duplicate samples was usually between 2-5% of the mean. Calibration was done by comparison to chlorophyll-a concentrations determined spectrophotometrically.

II-5 Chemical analysis

A subsample of the unfiltered lake water from each sample was preserved by freezing for the analysis of total phosphorus (TP). Subsamples of 20 ml of the filtrate were preserved to analyse soluble reactive phosphorus (SRP) and soluble silica (Si) by the addition of 1 drop of concentrated HCl and then frozen. 20 ml subsamples to analyse combined nitrate and nitrite ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$) and ammonia (NH_3) were preserved by the addition of 1 drop of concentrated chloroform and then frozen.

TP and SRP were determined using the stannous chloride, ammonium molybdate method of Kramer et al. (1972) with an Autoanalyzer 11. The standard error for TP at 54.2 mg/l was 2.25%. Si was determined by the silicate-molybdate molybdenum blue reaction method (Technicon Corp., 1973). The standard error for Si at 1.36 mg/l was 5.4 %. $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ were determined using a cadmium column with the method outlined by the Technicon corporation (1971a) with an AAll. The standard error for



combined nitrate and nitrite at .31 mg/l was 1.48%. Ammonia was determined on the AAll using the sodium phenoxide, sodium hypochlorite and potassium tartrate reaction method (Technicon Corp, 1971b). The standard error for ammonia at .43 mg/l was 1.14%. Further details of the chemical methods may be found in Harris et al. (1980b).

pH measurements were made on samples brought back to the laboratory using a Radiometer Copenhagen pH meter 29.

II-6 Estimates of z_{eu}/z_m and water column stability (N^2 and Richardson numbers)

The depth of the euphotic zone (z_{eu}) was defined as the depth at which 1% of surface P.a.r. was observed. The mixing depth (z_m) was defined as the depth to the region of maximum temperature change over a 1m interval. $N^2(0-6)m$ and $N^2(0-10)m$ were calculated from:

$$1) -g/p * dp/dz,$$

where g is the acceleration due to gravity, p is the density of pure water at 4°C and dp/dz the density difference over the stated interval. A high value for N^2 means that buoyancy forces are high and as a result the resistance to mixing is high. More information as to the water column stability is obtained from a Richardson number than an N^2 value since a Richardson number gives an estimate of the ratio of buoyancy forces to turbulent kinetic energy inputs. A mixed layer Richardson number (Ri) is obtained from :

$$2) Ri = \frac{\alpha g \Delta T h}{w^{*2}}, \text{ (Fischer et al., 1979)}$$

where,

α = coefficient of thermal expansion of water

g = acceleration due to gravity

ΔT = temperature difference between the top and bottom of the depth interval

h = depth interval

w^* = friction velocity for the motion of surface water induced by wind.

$$3) w^* = (a C_d U^2 / w)^{1/2} \text{ (cm s}^{-1}\text{)}$$

where,

a = density of moist air

w = density of water

C_d = drag coefficient

U^2 = square of the wind speed

A rough form of a Richardson number for day i was calculated by dividing the change in temperature from the surface to 6m or 10m (11:00 AM on day i) by the wind speed² (wind speed from Elora = average of day i or wind speed from station 1 = average from 11:00 day i to 11:00 AM day $i + 1$). Wind speed² was used as the denominator since in the calculation of a

mixed layer Richardson number w^* is squared and w^* is a function of the wind speed. A high Richardson number indicates stable conditions.

II-7 Phytoplankton diversity and rate of community change

Phytoplankton diversity was calculated using the Shannon-Weaver diversity index (Shannon and Weaver, 1963) where,

$$4) H' = \sum_{i=1}^n \ln N_i/N * N_i/N.$$

Here, N_i is the abundance of the i th species and N is the number of individuals in the entire phytoplankton community. The rate of community change (succession rate) was calculated using Lewis's (1978a) SD (summed difference) rate where,

$$5) SD = \frac{\sum_{i=1}^n ((b_i(t_1)/B(t_1) - b_i(t_2)/B(t_2)))}{t_2 - t_1}.$$

Here $b_i(t)$ is the abundance of the i th species at time t and $B(t)$ is the size of the entire phytoplankton community.

II-8 Sedimentation traps

A series of sedimentation traps similar to those used by Reynolds (1975) was placed near station 1 to intercept floating and sinking phytoplankton cells. Black polyvinyl chloride cylinders (16.5cm x 8.0 cm in diameter) fitted with an inverted funnel at one end and a cap at the other end were anchored in pairs to a weighted rope such that one of each pair faced upwards and one faced downwards. The first pair was positioned at a depth of 2m, the second at 4m and the third pair at 10m.

The traps were recovered and emptied at approximately weekly intervals from April 22 to August 26, 1981. The traps were refilled with distilled water and repositioned. TP and phytoplankton abundances in the trap catches were determined as above.

Trap catches were used to determine the sinking rates (termed V_t) for some diatoms by the following formula (from Reynolds, 1976a):

$$6) V_t = \frac{C \times v}{P \times a} \text{ m/day}$$

$P \times a$

where C = daily increment of cells/ml collected in the trap

v = volume of the sedimentation trap (cm^3)

P = concentration of cells/ml in the station 1 (0-7)m

- sample taken on the day of trap removal

a = area of trap aperture (cm^2).

Sinking rates (termed V_d) for some diatoms were also determined through an analysis of population dynamics by the following formula (from Reynolds, 1976a):

$$7) V_d = a \times \left(1 - \sqrt[n]{P_2/P_1} \right) \text{ m/day}$$

where a = no. of m in integrated sample (7)

n = number of days in sampling interval

P_2 = concentration of cells/ml in the (0-7)m integrated sample after n days

P_1 = original concentration of cells/ml in the (0-7)m integrated sample.

Vt values could only be calculated when there was a measurable (0-7)m concentration of the species in question at the time of trap removal. Vd values could only be calculated when there was a decrease in the (0-7)m concentration of the algal species from the time the traps were set to the time the traps were removed.

The cumulative sinking loss could be compared to the maximum standing crop. The relative contribution of sinking to the loss of some diatom species could then be estimated. The total trap catches (cells/ml) in the upward trap at 10m were converted to a total areal flux (cells/cm²) by multiplying by the volume of the sedimentation chamber and dividing by the areal diameter of the chamber. The total areal flux was then compared to the maximum standing crop observed (maximum (0-7)m concentration of cells/ml x 1000 to get cells/cm² above the sedimentation trap).

Trap catches in upward versus downward traps with depth were used to examine the vertical activity ranges of some blue-green algae. Catches in downward facing traps would capture positively buoyant or motile individuals. Specific migration activities of floating versus sinking individuals (trap catch in colonies or filaments/ml / concentration of colonies or filaments at that depth/ml, from Konopka, 1982) were also calculated. The possibility of recruitment of summer blue-green algae from the sediments could then be examined.

II-9 Estimates of vertical heterogeneity

Estimates of vertical heterogeneity for chl_a, SRP and TP over the 105 day time interval were obtained by (standard deviation/ average) of the 6 depths and expressing as a % (as in Harris and Smith, 1977). Phytoplankton counts were done on daily vertical samples taken from July 21 to August 20, 1981 and vertical heterogeneity for selected algae was calculated in the same way.

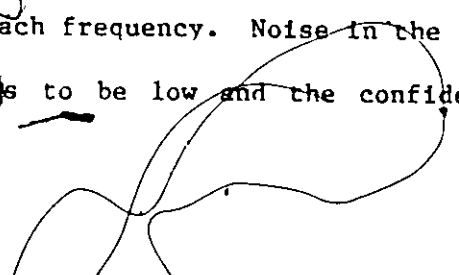
II-10 Time series analysis

Provided both the input and output series have been prefiltered to convert them into stationary time series (mean and standard deviation constant over time), the sample cross-correlation function may be used to test whether the 2 series are correlated and whether time lags or leads exist between them. Prefiltering is necessary since the cross-correlation is difficult to interpret when each of the 2 series are themselves correlated (Haugh and Box, 1977). The visual interpretation of cross-correlation estimates between 2 stationary time series is facilitated by the fact that the 95% confidence limits are approximately $\pm 2/\sqrt{n - k}$, where n = number of points and k = number of lags.

This prefiltering may be achieved through the application of ARIMA (p,d,q) models, that is, various combinations of autoregressive terms (p gives the number of autoregressive terms) differencing (d gives

the degree of differencing) and moving average terms (q gives the number of moving average terms)(Box and Jenkins, 1976). Loge transformations may also be used for biological variables. In autoregressive models, the current value of a process is expressed as a finite, linear aggregate of p previous values of the process and a current random shock. If the level or mean of a process varies with time, a first difference filter ($d = 1$) may be applied and the time series will become independent of the level and thereby stationary. If the level or mean as well as the slope of a process varies, a second difference filter ($d = 2$) may be applied to correct for this non-stationarity. In moving average models, the current value of a process is expressed as as a finite, linear aggregate of q previous shocks. In order to check if the residuals are stationary, the autocorrelation function of the residuals may be examined. The autocorrelation estimates of a stationary time series should be less than $+2/\sqrt{n}$ or $-2/\sqrt{n}$, where $n =$ number of points. The stationary residuals from each time series may then be cross-correlated.

If there is a tendency for periodic components to occur, cross-spectral analysis should also be employed. In cross-spectral analysis the correlation is estimated between pairs of variables as a function of frequency. A squared coherence spectrum and phase spectrum may be calculated (Jenkins and Watts, 1968). This corresponds to a knowledge of both the maximum cross-correlation and the corresponding lags or leads at each frequency. Noise in the system causes the squared coherence estimates to be low and the confidence limits on the phase



estimates to be correspondingly large. Prefiltering of the data sets is unnecessary as the squared coherence spectrum and the phase spectrum are equivalent when either the non-transformed data sets or equivalently prefiltered data sets are compared.

Significant cross-correlations at negative lags when a time series obtained from station 1 is compared to a time series obtained from station 3 suggest that changes at station 1 lag those at station 3 by k number of days. Significant cross-correlations at positive lags when a time series obtained from station 1 is compared to a time series obtained from station 3 suggest that changes at station 1 lead changes at station 3. Significant cross-correlations at a lag of 0 suggest that changes are occurring on the same day at both stations.

Lags or leads between stations could also be determined by calculating the slope of the phase spectrum and the time required for one cycle. A phase shift was referred to as a lag when station 1 followed station 3 (-ve slope on phase spectrum when station 1 was compared to station 3) and as a lead when station 1 lead station 3 (+ve slope on phase spectrum when station 1 was compared to station 3).

Programs used

A library program (Minitab) was used to determine autocorrelations, ~~cross-correlations~~ and to prefilter the data (calculations as outlined in Box and Jenkins, 1976). Spectral analysis

was done using the Biomedical library routines, BMD02T, BMDX92 and BMDX68 (Dixon, 1969). The number of lags that can be fitted to a data set is determined by $N/4$, where N is equal to the number of data points (Platt and Denman, 1975). Using BMD02T, the degrees of freedom are equal to $2.5 \times N/M$, where N is the number of data points and M is the number of lags. The degrees of freedom allows one to determine the 80 or 95% confidence intervals for the spectral estimates (Jenkins and Watts, 1968).

III) RESULTS

III-1 Temporal and Spatial Variability

III-1-1 SPECTRAL ANALYSIS OF TEMPORAL VARIABILITY

Individual spectra obtained from the different data sets (weekly, daily and at 20 minute intervals for temperature only) were combined in order to resolve the spectrum over a greater range of frequencies. The logarithm of the power spectral estimates was then plotted as a function of the logarithm of the frequency.

Temperature-

Three separate spectra were combined for temperatures at the surface and at 4m. The first spectrum was calculated using 111 weekly values with 20 lags and covered periods from 280 to 14 days. The second spectrum was calculated using 105 daily values with 20 lags and covered periods from 40 to 2 days. The third spectrum was calculated using 576 values taken at 20 minute intervals with 100 lags and covered periods from 2.8 to .028 days.

The power spectrum for temperature at 0m followed a slope of $-5/3$ with increasing frequency or decreasing period, when plotted on a log-log scale (Figure 2), as expected for a passive scalar within the flow field (Kolmogorov, 1941, Denman and Platt, 1976). The first point in the third spectrum fitted in with estimates from the second spectrum but was followed by a large increase in the power spectral estimate at a period of approximately 1 day.

The combined spectrum for the temperature at 4m was similar (Figure 3). A strong diurnal signal was also observed for the temperature at this depth. At higher frequencies the power spectral estimates were more variable at 4m than at 0m. This extra variability was likely due to internal waves.

Chlorophyll-a-

Two separate spectra (calculated from 111 weekly values and covering periods from 280 to 14 days and from 105 daily values and covering periods from 40 to 2 days) were combined. The power spectrum for chlorophyll-a also followed a slope of $-5/3$ from a period of approximately 93 down to 4 days, suggesting that at these time scales, chlorophyll-a behaved like a passive scalar within the flow field (Figure 4). Some flattening of the power spectrum for chlorophyll-a in Guelph Lake occurred at lower frequencies and at higher frequencies. Denman and Platt (1976) suggest that when the chlorophyll distribution is controlled by biological processes the variance of chlorophyll will

Figure 2 - Power spectrum for temperature at 0m (80% confidence limit at right). Note the large increase in the power spectral estimate at a period of 1 day.

- weekly data set
- daily data set
- 20 min. data set

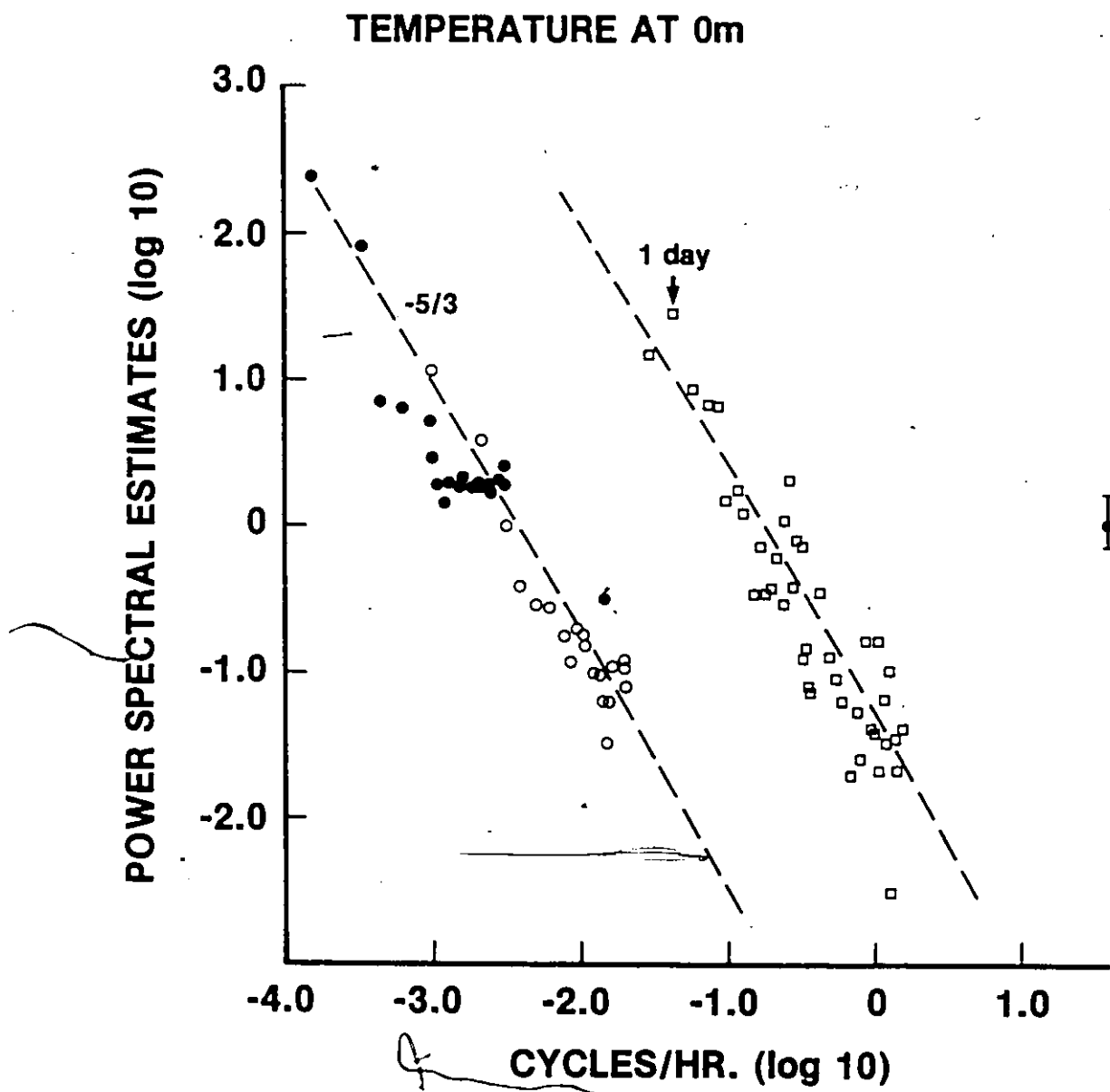


Figure 3 - Power spectrum for temperature at 4m (80% confidence limit at right). Note the large increase in the power spectral estimate at a period of 1 day.

- weekly data set
- daily data set
- 20 min. data set

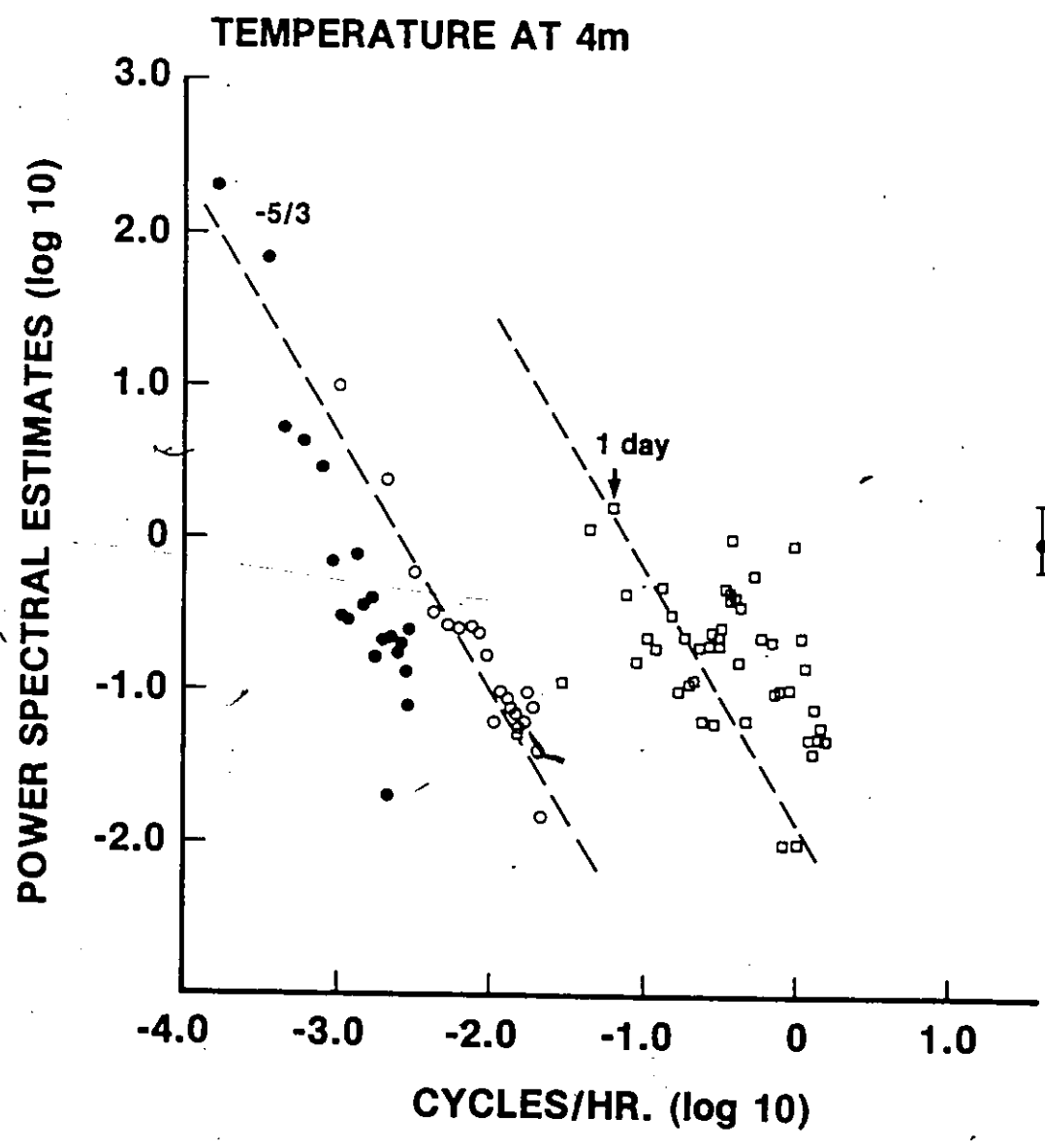


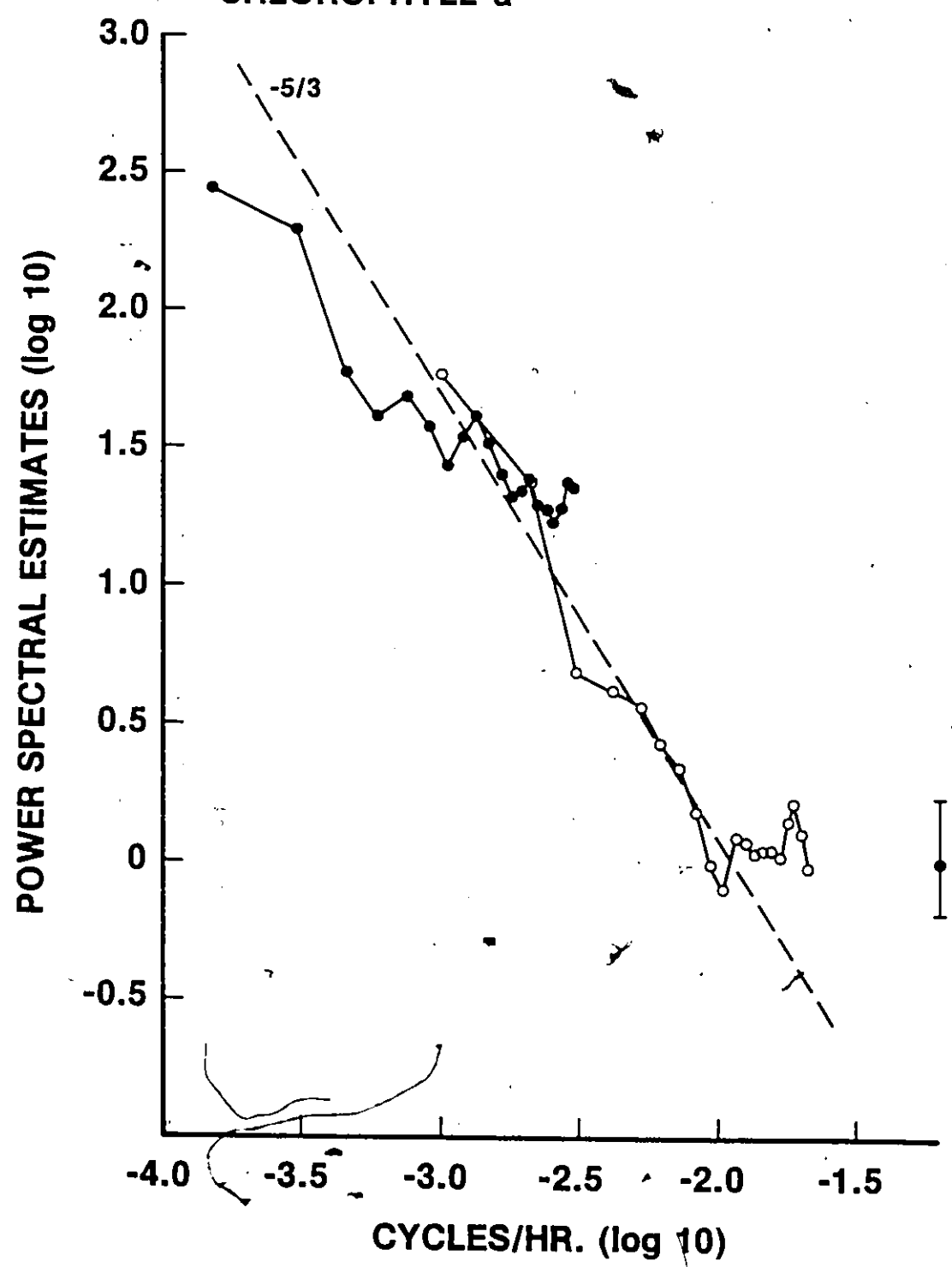
Figure 4 - Power spectrum for chlorophyll a, (0-7)m sample (80% confidence limit at right). Note the flattening of the power spectrum at higher and lower frequencies.

● weekly data set

○ daily data set

5

CHLOROPHYLL a



be a less decreasing function of wavelength than will be a passive scalar. This suggests that at those time scales where a flattening of the power spectrum occurred, biological processes were important.

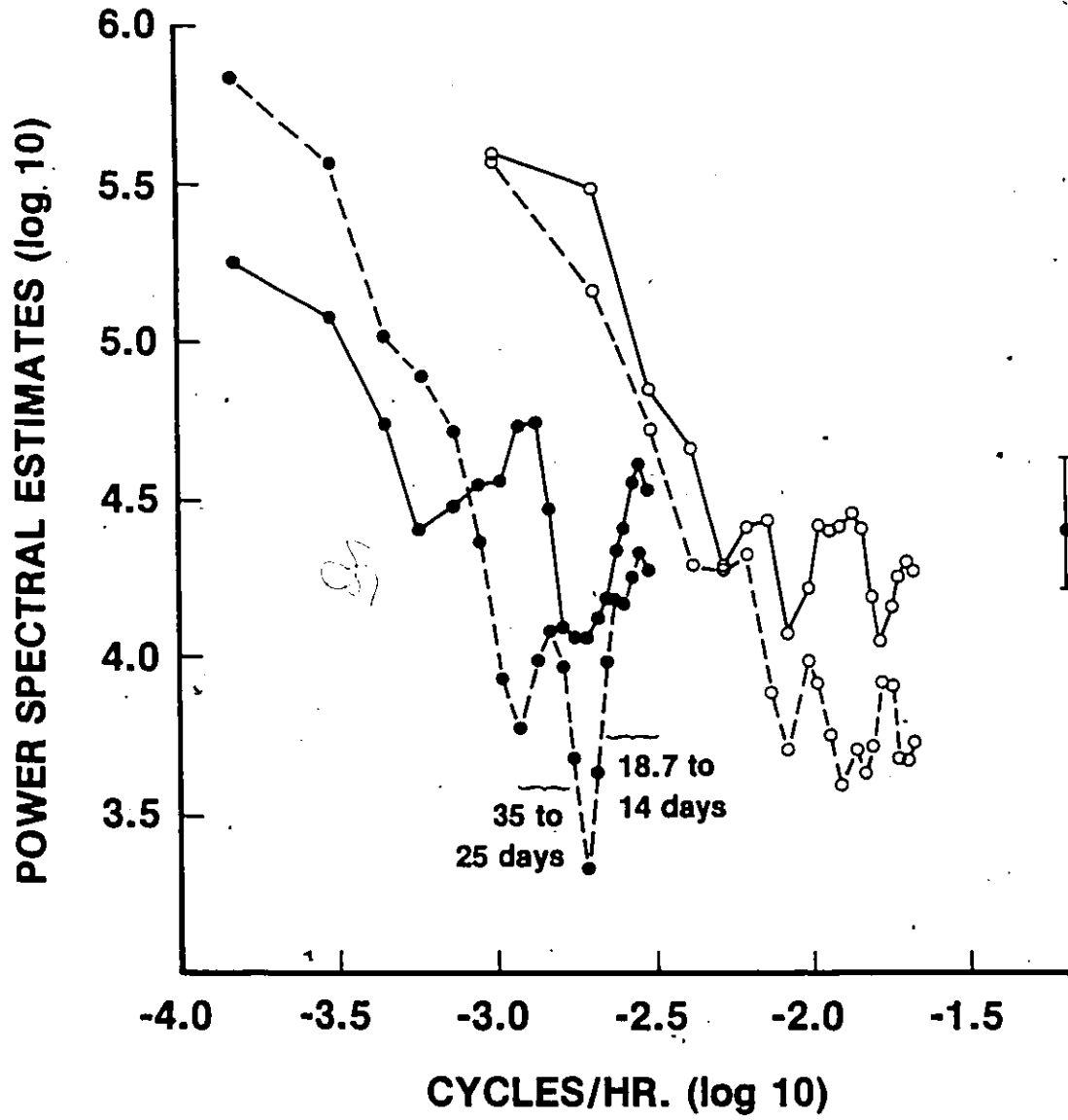
Water column stability (N^2)-

Two separate spectra spanning periods from 280 to 14 days and from 40 to 2 days were again combined for $N^2(0-6)m$ and $N^2(0-10)m$. The first 2 estimates for the second spectrum were much higher than estimates from the first spectrum. Increases in power spectral estimates occurred at periods of 4 weeks and 2 weeks (Figure 5). The slope of the spectrum observed for $N^2(0-10)m$ was much steeper than for $N^2(0-6)m$. This suggests that a lower proportion of the total variance for $N^2(0-10)m$ than for $N^2(0-6)m$ is found at higher frequencies.

Figure 5 - Power spectrum for water column stability, $N^2(0-6)_m$ and $N^2(0-10)_m$ (80% confidence limit at right).

- $N^2(0-6)_m$ weekly data set
- $N^2(0-10)_m$ weekly data set
- $N^2(0-6)_m$ daily data set
- $N^2(0-10)_m$ daily data set

WATER COLUMN STABILITY
($N^2(0-6)m$ and $N^2(0-10)m$)



Wind speed-

The power spectrum was calculated using 156 daily values with 39 lags. Increases in the power spectral estimates were observed at periods of 10-12, and 4-6 days (Figure 6).

zeu/zm-

The power spectrum was calculated using 105 daily values with 20 lags. Increases in the power spectral estimates were observed at periods of 5-7 and 2-3 days (Figure 7).

Nutrients-

Two separate spectra were again calculated for SRP, TP, Si and $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ (Figures 8,9,10,11). A sharp decrease in the power spectral estimates for TP and $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$, and to a lesser extent for SRP, was observed after a period of 140 days. This reflects the variability of these nutrients at seasonal time scales. The spectra observed for TP, $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ were quite flat after this period, suggesting that these substances were not merely behaving as passive scalars within the flow field and that biological processes were important at these time scales. Power spectral estimates for Si were roughly constant throughout the full range of frequencies examined. 4 week and 2 week periodicities were evident in the power spectra for SRP

Figure 6 - Power spectrum for wind speed (80% confidence limit
at right).

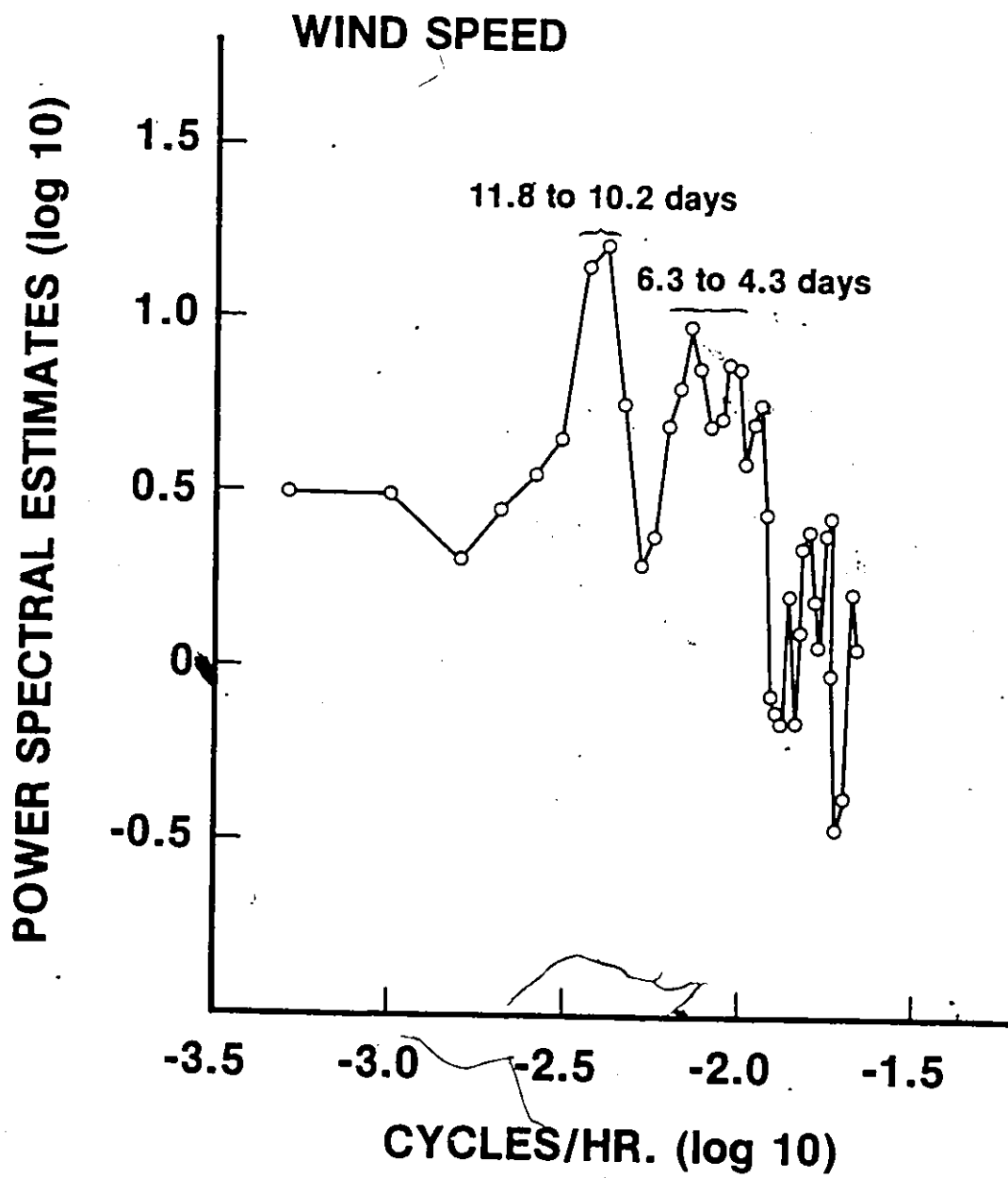


Figure 7 - Power spectrum for zeu/zm (80% confidence limit at right).

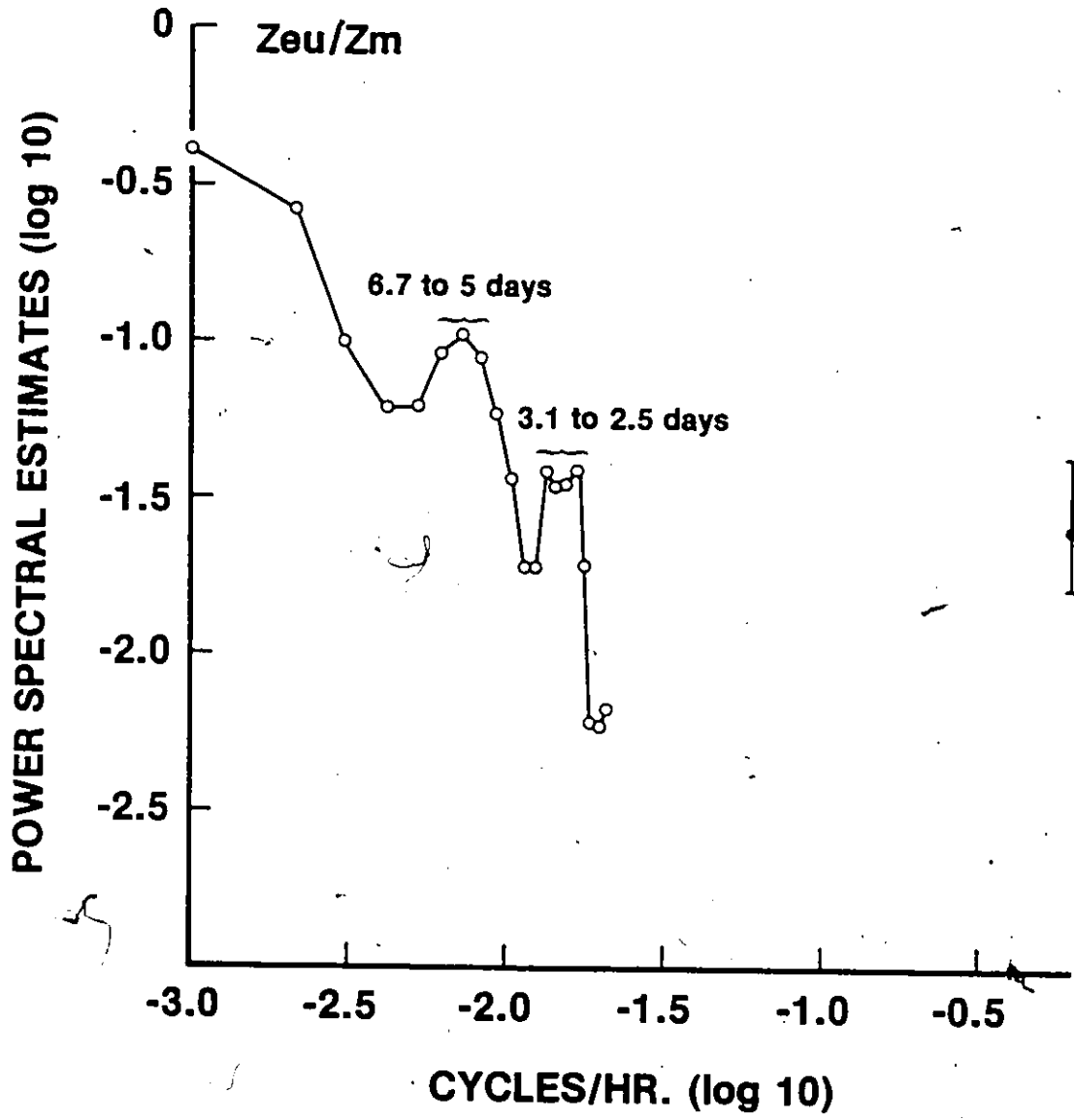


Figure 8 - Power spectrum for soluble reactive phosphorus (80% confidence limit at right). Note the increases in the power spectral estimates from the weekly data set at periods of approximately 2 and 4 weeks.

● weekly data set

○ daily data set

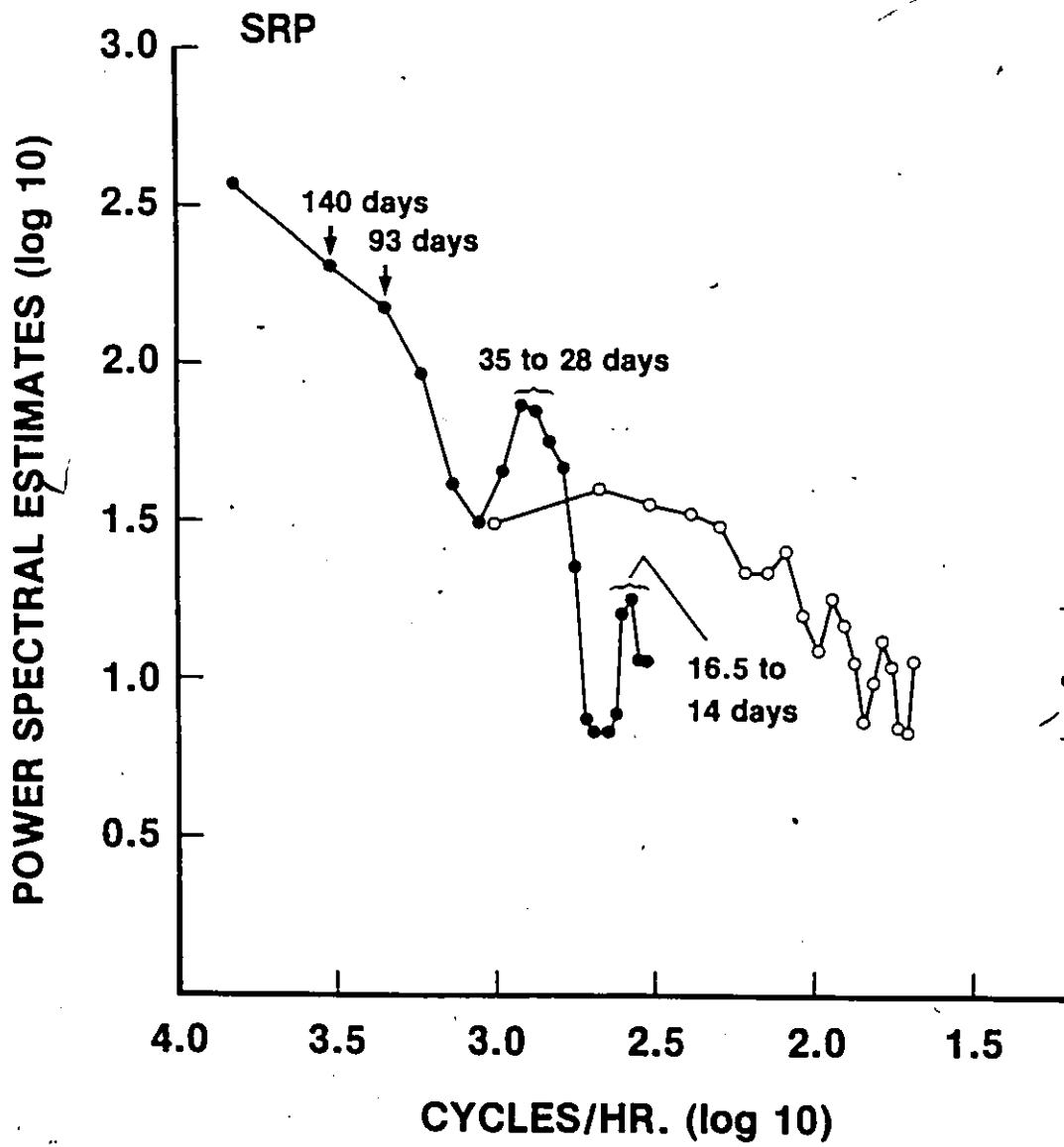


Figure 9 - Power spectrum for total phosphorus (80% confidence limit at right). Note the decrease in the power spectral estimates after a period of 140 days.

● weekly data set

○ daily data set

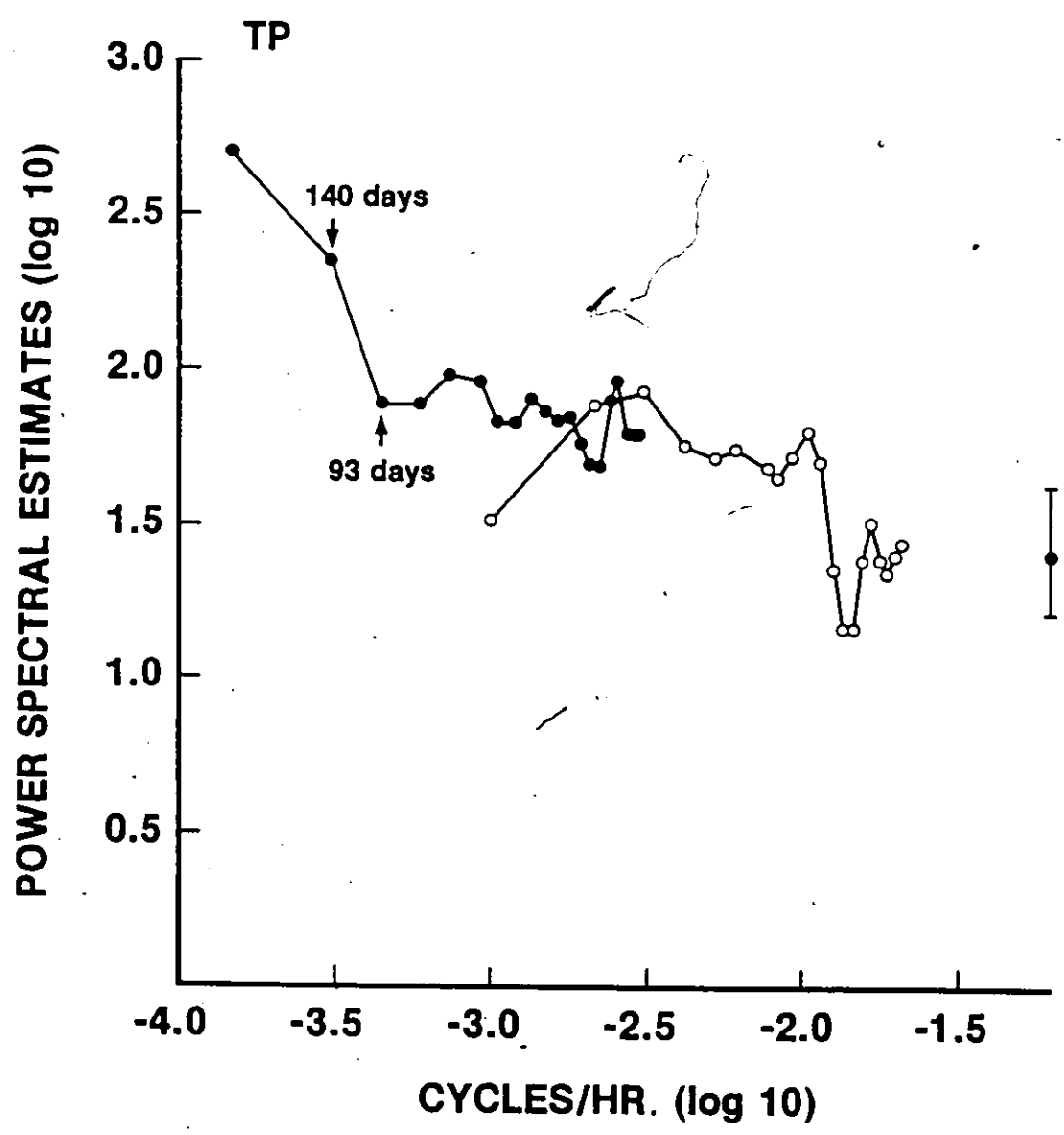


Figure 10 - Power spectrum for silica (80% confidence limit at right).

● weekly data set

○ daily data set

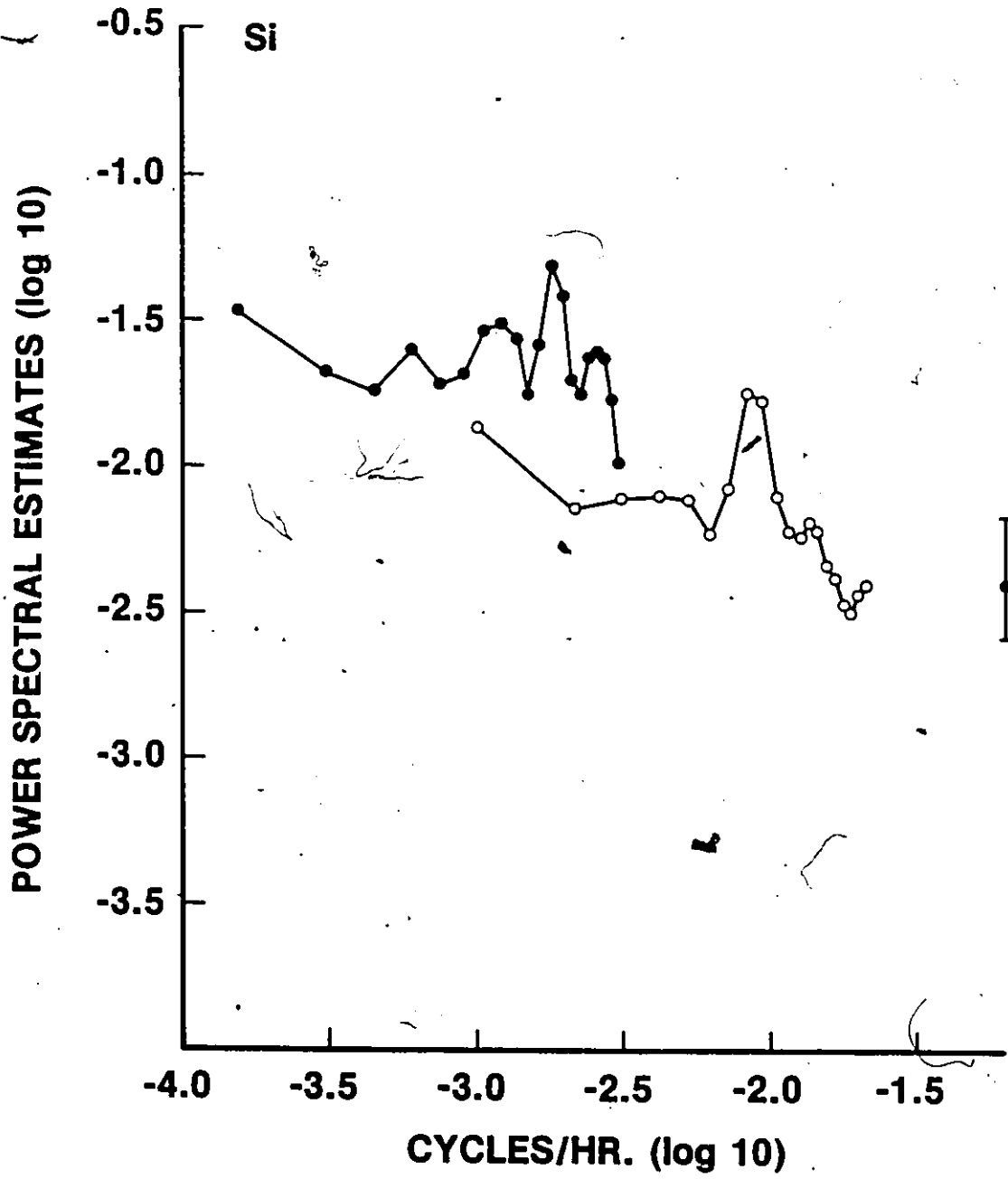
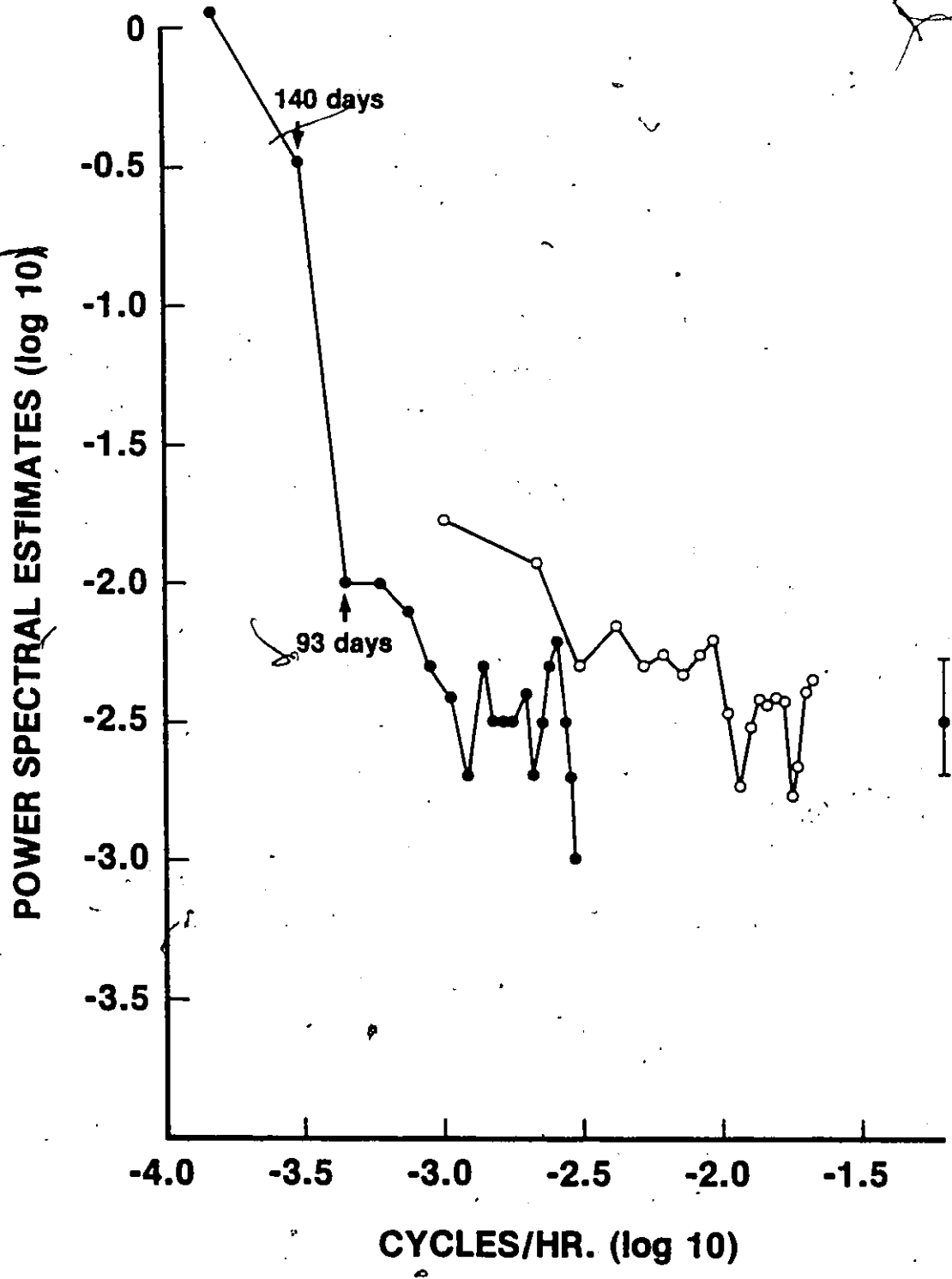


Figure 11 - Power spectrum for combined nitrate and nitrite (80% confidence limit at right). Note the drastic decrease in the power spectral estimates after a period of 140 days.

● weekly data set

○ daily data set

$\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$



calculated from the weekly data set, but not from the daily data set.

III-1-2 TIME SERIES ANALYSIS OF SPATIAL VARIABILITY

III-1-2-1 Horizontal Advection

The analysis of phytoplankton population dynamics from samples taken from only one station is complicated by the fact that water motions and horizontal advection cause horizontal redistribution of the phytoplankton (Heaney, 1976, Heaney and Talling, 1980). The advection pattern for any given variable may be seen through station-to-station comparisons of the time series observed. Different rates and directions of horizontal transport for different variables were observed in station-to-station comparisons for the daily time series.

Soluble reactive phosphorus (SRP)-

Results for cross-correlations of non-transformed data, 1st differenced data and residuals (after ARIMA modelling) indicated that the integrated SRP at station 1 lagged that at station 3 by 3 days (Figure 12a). Significant cross-correlations were also seen between the SRP at station 1 and that at station 3, 15 days later. Cross-spectral analysis of the non-transformed data (Figure 12b) also revealed a lag of 3 days between station 1 and station 3. This 3 day lag for SRP between

station 1 and station 3 (separation - 1 km) works out to an advection rate of .4 cm/s. The SRP at station 1 was found to be highly correlated with that at station 2 on the same day and 1 day earlier (Figure 12c). Significant cross-correlations were also observed at a lag of 10 days and a lead of 15 days. Examination of the phase spectrum suggested a less than one day lag between stations 1 and 2 (Figure 12d). The SRP at station 2 was found to be correlated with that at station 3, 3 days earlier, on the same day and 7 days later (Figure 12e). The phase spectrum revealed a 2-3 day lag as observed between station 1 and station 3 (Figure 12f).

Total phosphorus (TP)-

The TP at station 1 was significantly correlated with the TP at station 3 on the same day as well as 19 days earlier and 14 days later (Figure 13a). The TP at station 1 was significantly correlated with the TP at station 2 on the same day as well as 4 days earlier (Figure 13b). The TP at station 2 was significantly correlated with the TP at station 3, 15 days later (Figure 13c). Examination of the phase spectrums revealed no clear lags or leads since the coherences were low and as a result the confidence limits were wide.

Combined nitrate and nitrite ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$)-

No lags or leads between the stations were observed. For example, when the residuals from station 1 were compared to station 3

Figure 12a Cross-correlation estimates between SRP ARIMA (101) residuals from station 1 and SRP ARIMA (101) residuals from station 3 (at $k = 0$, r^2 for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$)

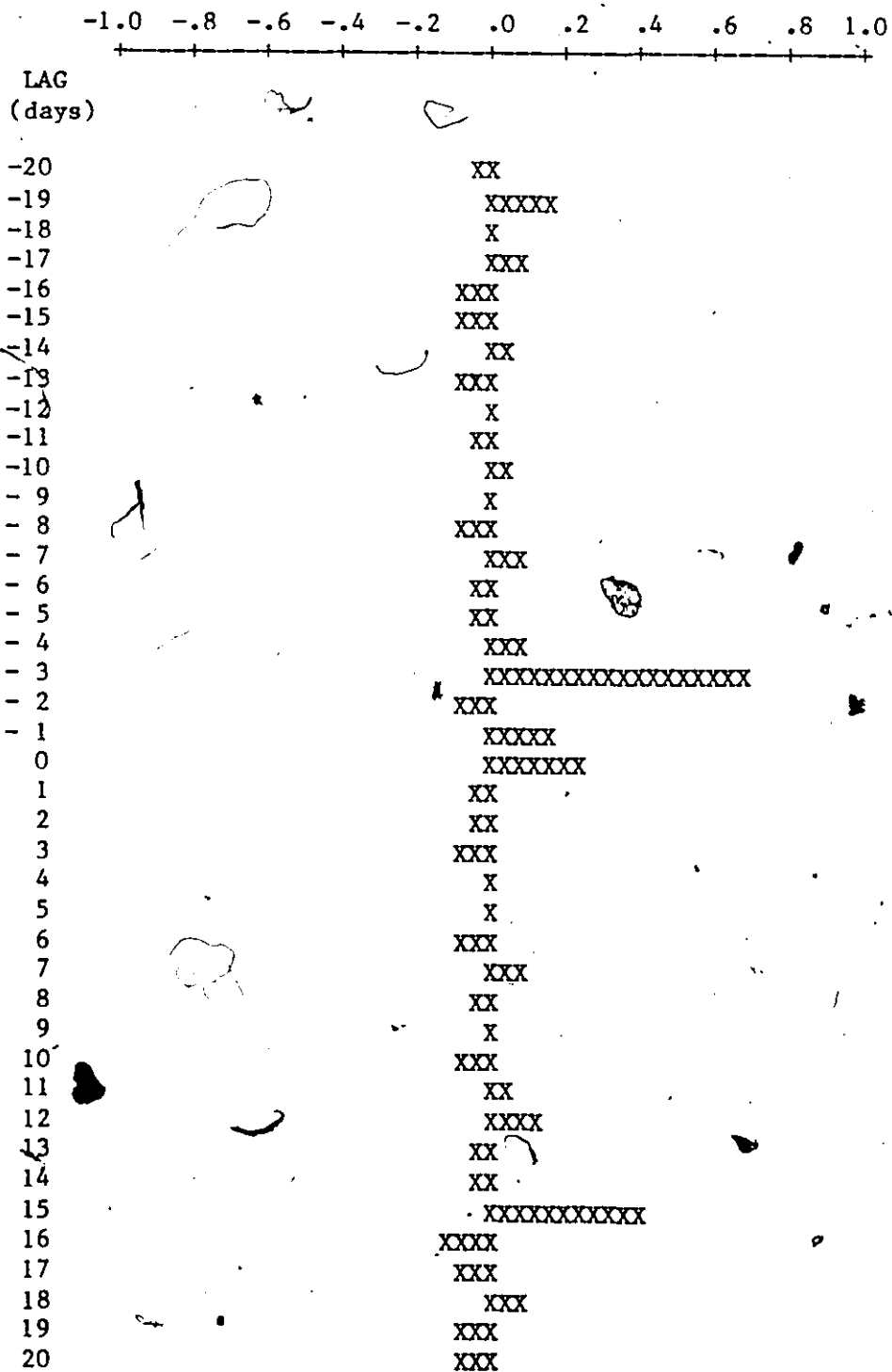


Figure 12b - Phase spectrum for soluble reactive phosphorus, station 1
versus station 3. (95% confidence limits). The -ve slope
suggests that station 1 lags station 3 by 3 days.

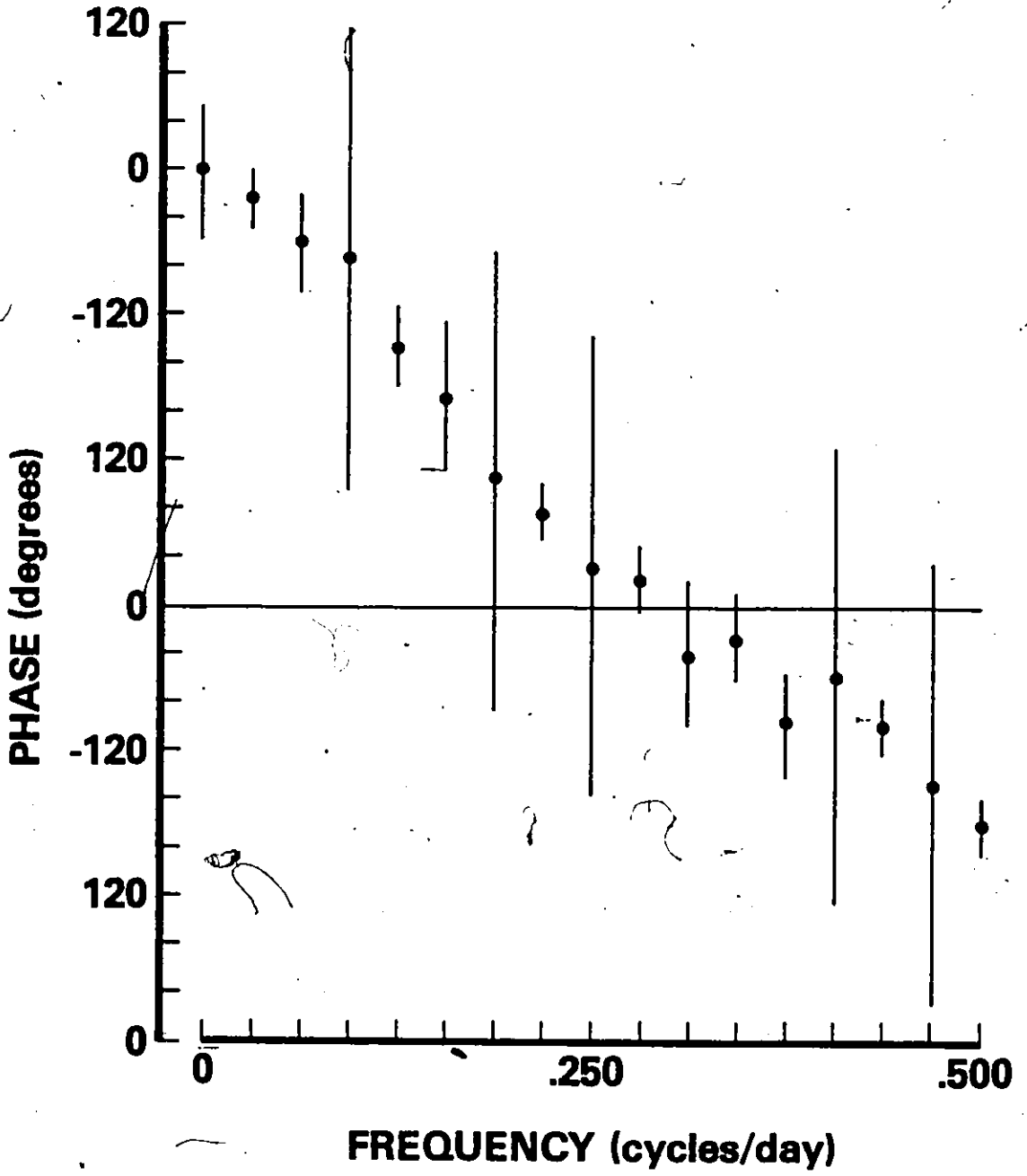


Figure 12c Cross-correlation estimates between SRP ARIMA (101) residuals from station 1 and SRP ARIMA (101) residuals from station 2 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

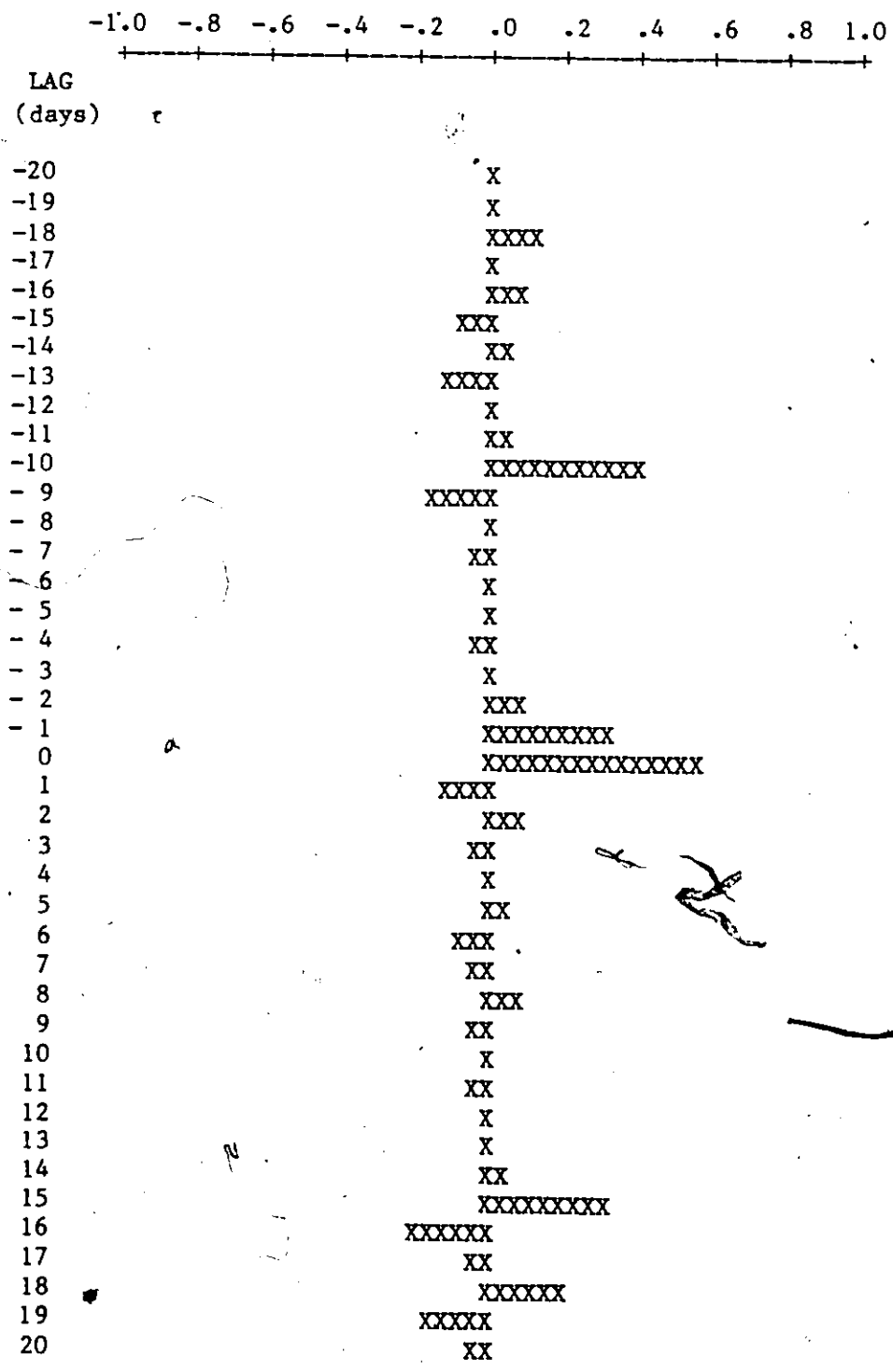


Figure 12d- Phase spectrum for soluble reactive phosphorus, station 1
verus station 2. (95% confidence limits). The -ve slope
suggests that station 1 lags station 2 by 1 day.

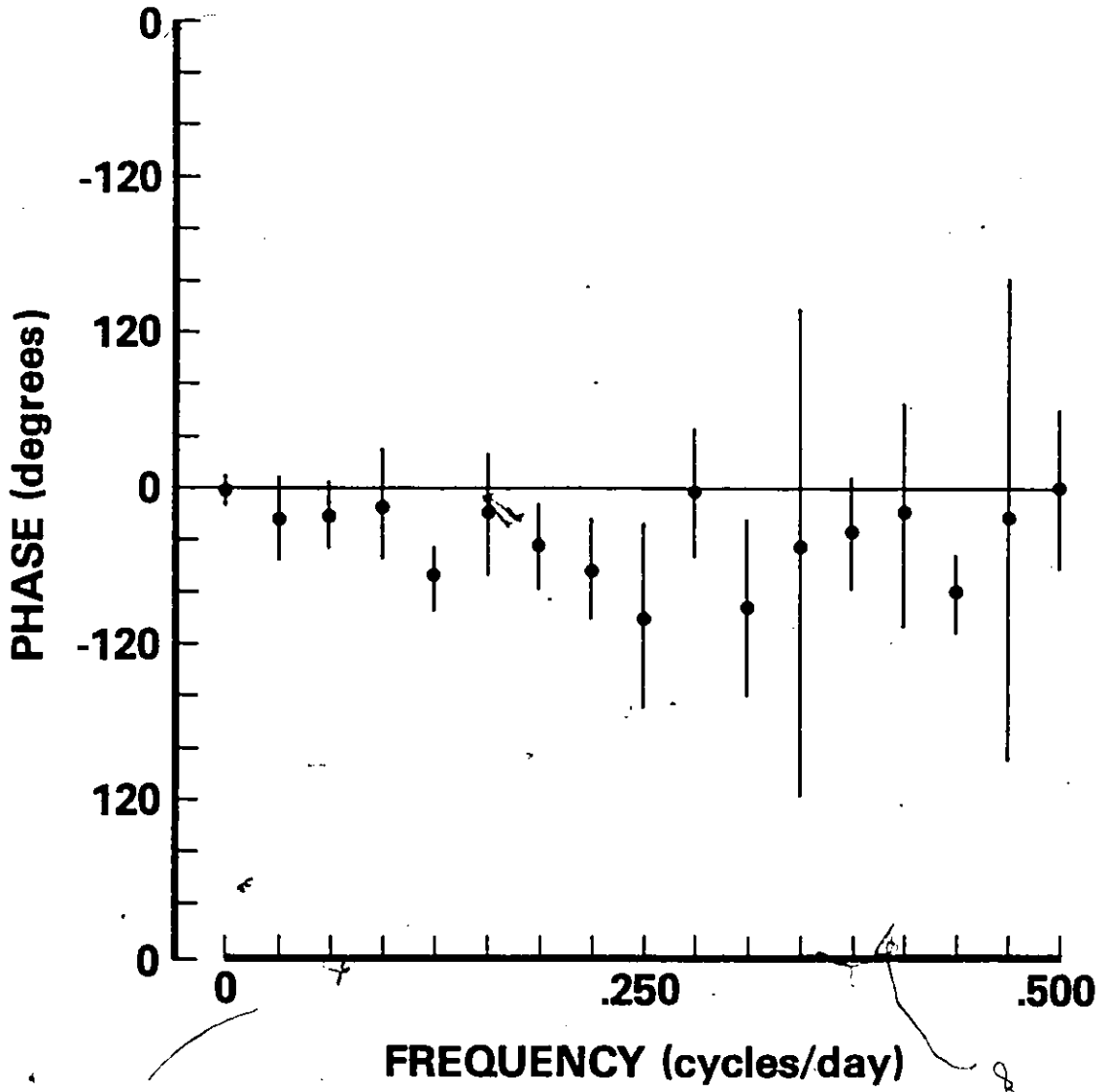


Figure 12e Cross-correlation estimates between SRP ARIMA (100) residuals from station 2 and SRP ARIMA (100) residuals from station 3 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

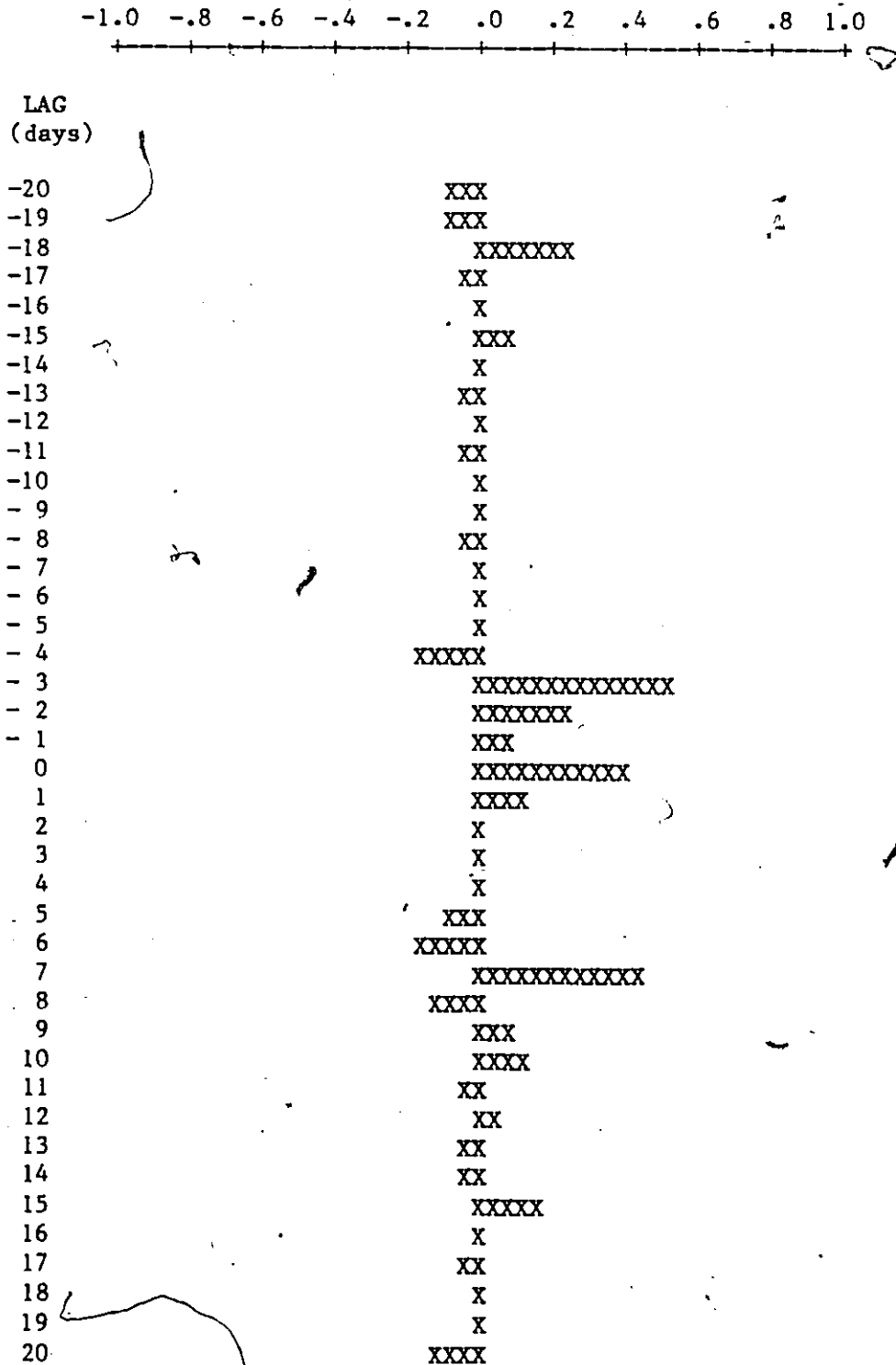


Figure 12f- Phase spectrum for soluble reactive phosphorus, station 2
versus station 3. (95% confidence limits). The -ve slope
suggests that station 2 lags station 3 by 2-3 days.

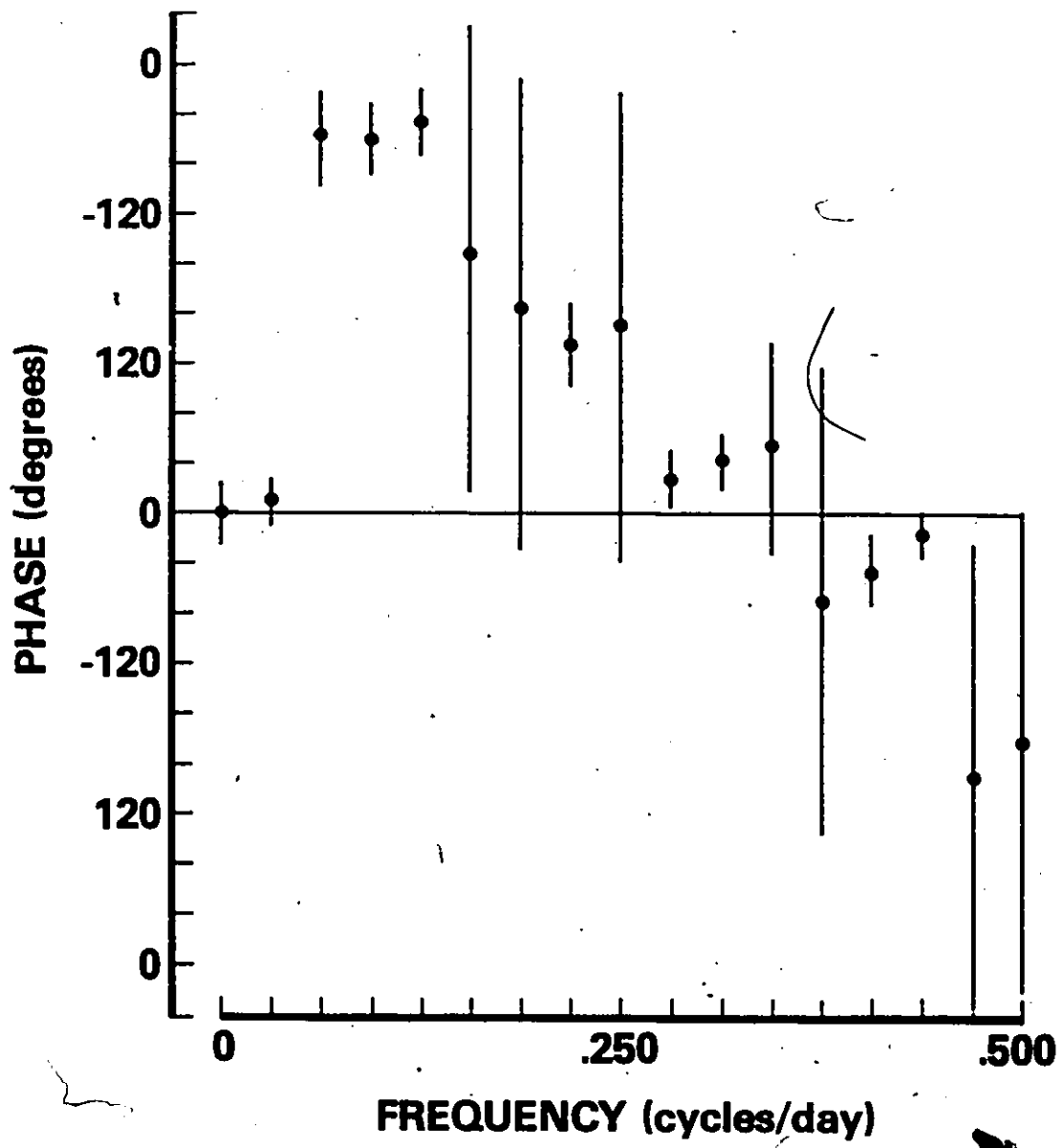


Figure 13a Cross-correlation estimates between TP ARIMA (101) residuals from station 1 and TP ARIMA (101) residuals from station 3 (at $k = 0$ for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

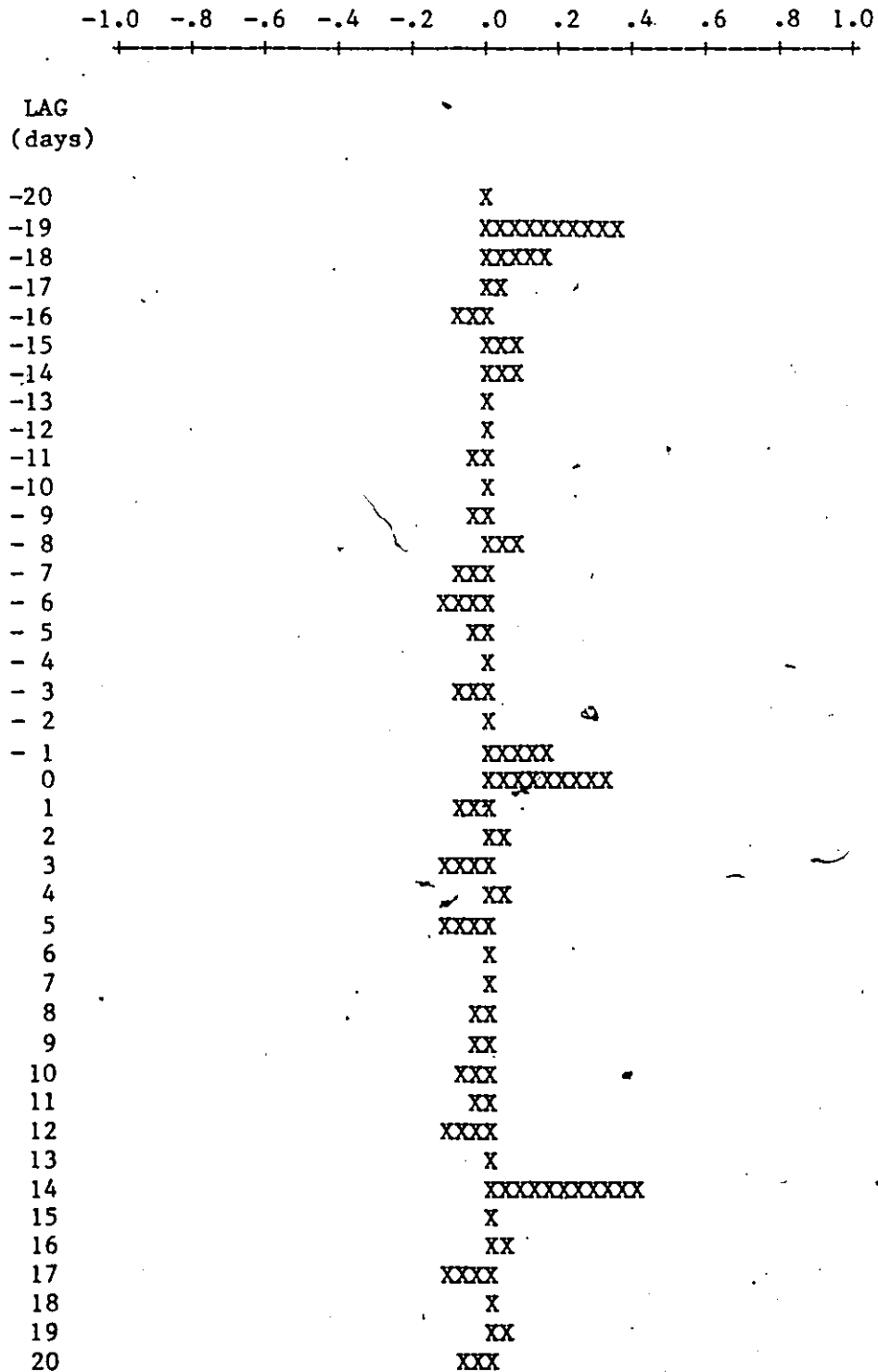


Figure 13b Cross-correlation estimates between TP ARIMA (101) residuals from station 1 and TP ARIMA (101) residuals from station 2 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

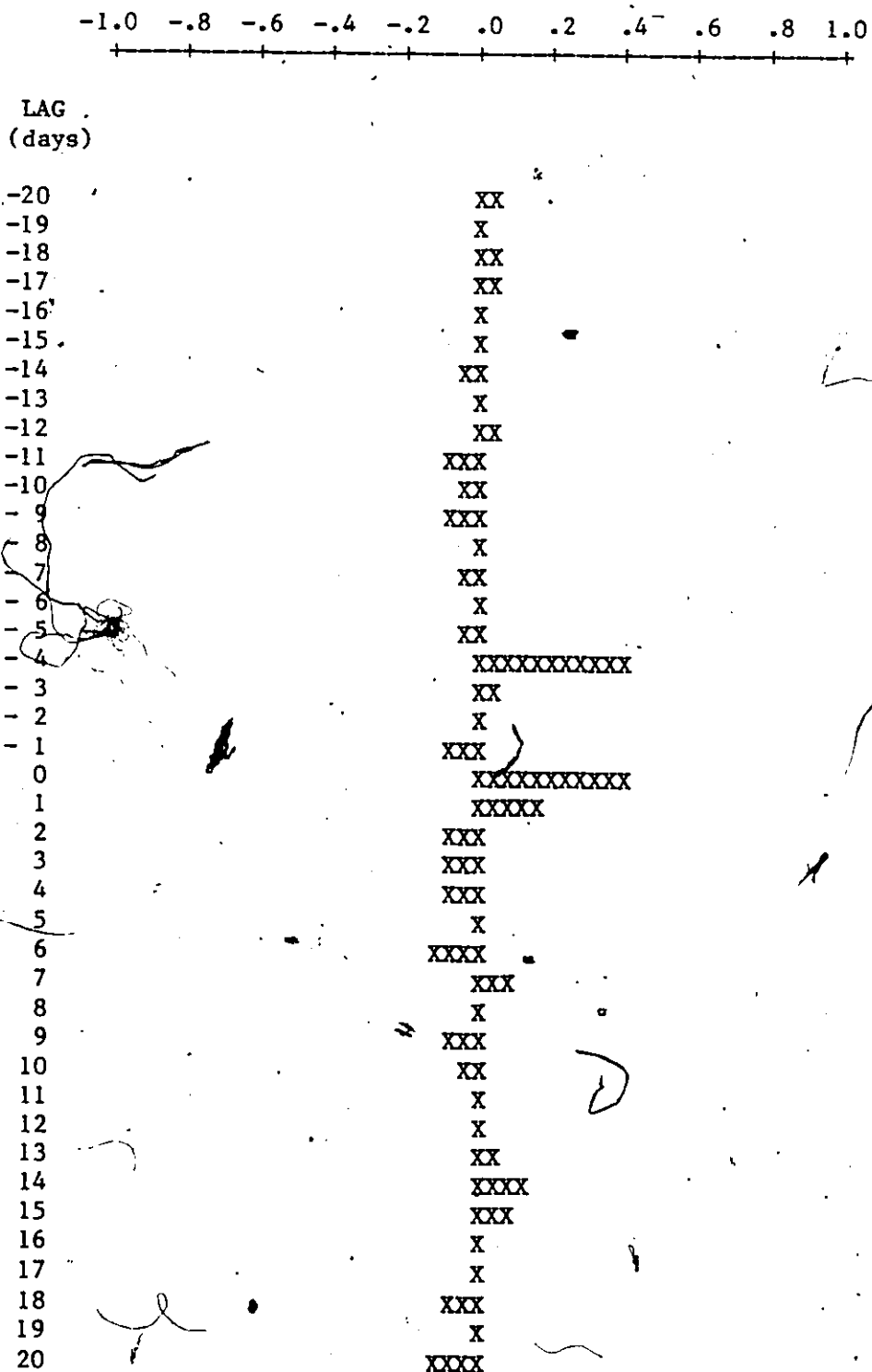
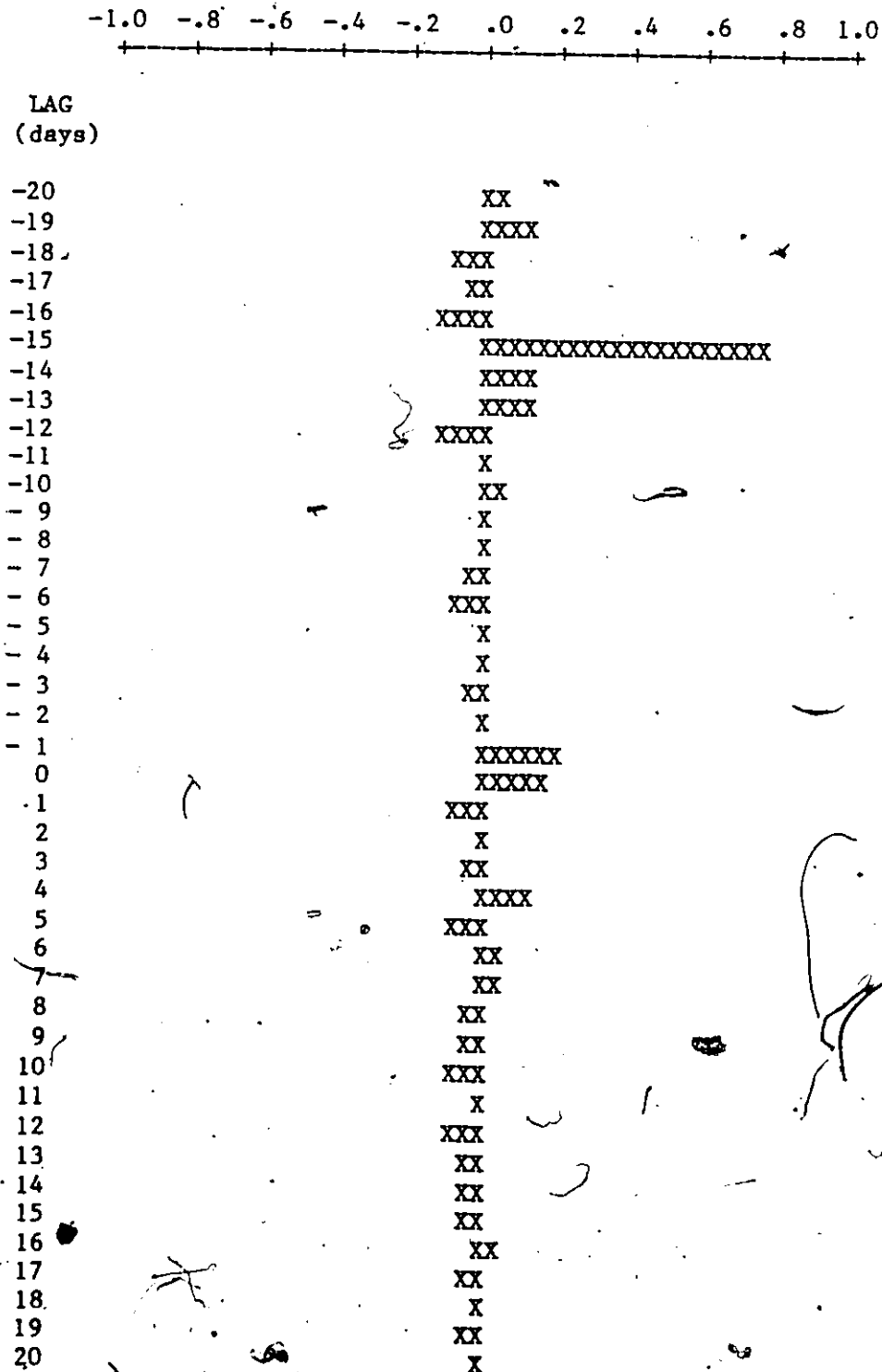


Figure 13c Cross-correlation estimates between TP ARIMA (101) residuals from station 2 and TP ARIMA (101) residuals from station 3 (at $k = 0$, for $p < .05$, $r^2 < .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).



the only significant value was that on the same day (Figure 14).

Chlorophyll-a-

Significant cross-correlations between the residuals from station 1 and station 3 were found on the same day as well as at a lag of one day (Figure 15a). Examination of the phase spectrum indicated a slight lag between the stations of 12 hours, suggesting an advection rate of 2.5 cm/s (Figure 15b). Similar results were obtained when station 1 was compared to station 2 (Figure 15c). No lag was observed between station 2 and station 3 (Figure 15d).

Aphanizomenon-

Cross-correlation estimates revealed that the relative abundances of Aphanizomenon at station 1 lagged those at station 3 by 7 days (Figure 16a) and those at station 2 by one day (Figure 16c). Examination of the phase spectra revealed a 6-7 day lag between station 1 and station 3, suggesting an advection rate of .2 cm/s (Figure 16b) and a 1-2 day lag between station 1 and station 2 (Figure 16d). A 6 day lag was observed between station 2 and station 3 when both the cross-correlation estimates (Figure 16e) and phase spectrum (Figure 16f) were examined.

Figure 14 Cross-correlation estimates between combined NO₃-N and NO₂-N ARIMA (111) residuals from station 1 and combined NO₃-N and NO₂-N ARIMA (111)₂ residuals from station 3 (at k = 20, for p < .05, r² > .195, at k = 20, for p < .05, r² > .217).

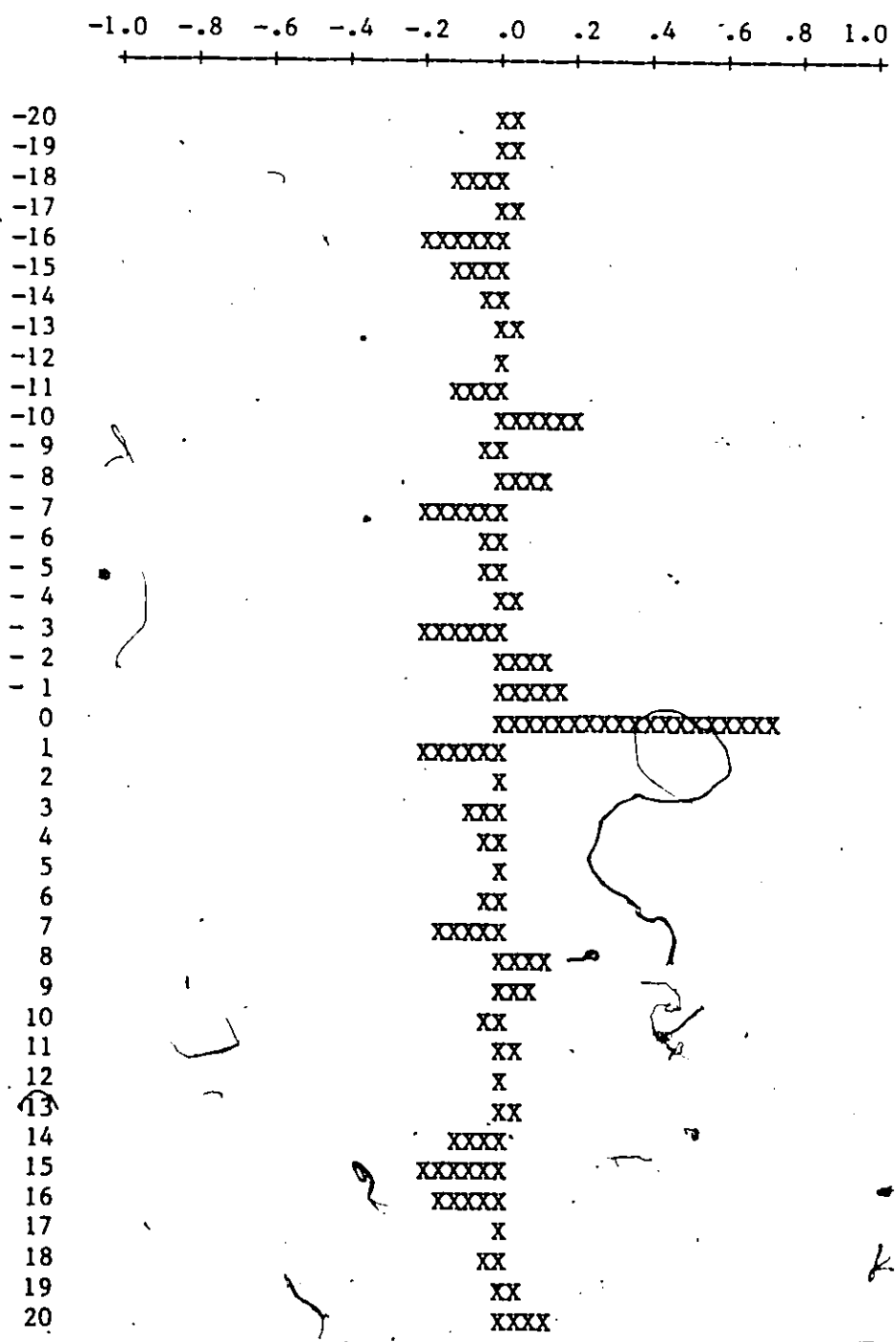


Figure 15a Cross-correlation estimates between log e transformed chlorophyll a ARIMA (101) residuals from station 1 and log e transformed chlorophyll a ARIMA (101) residuals from station 3 (at $k_2 = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

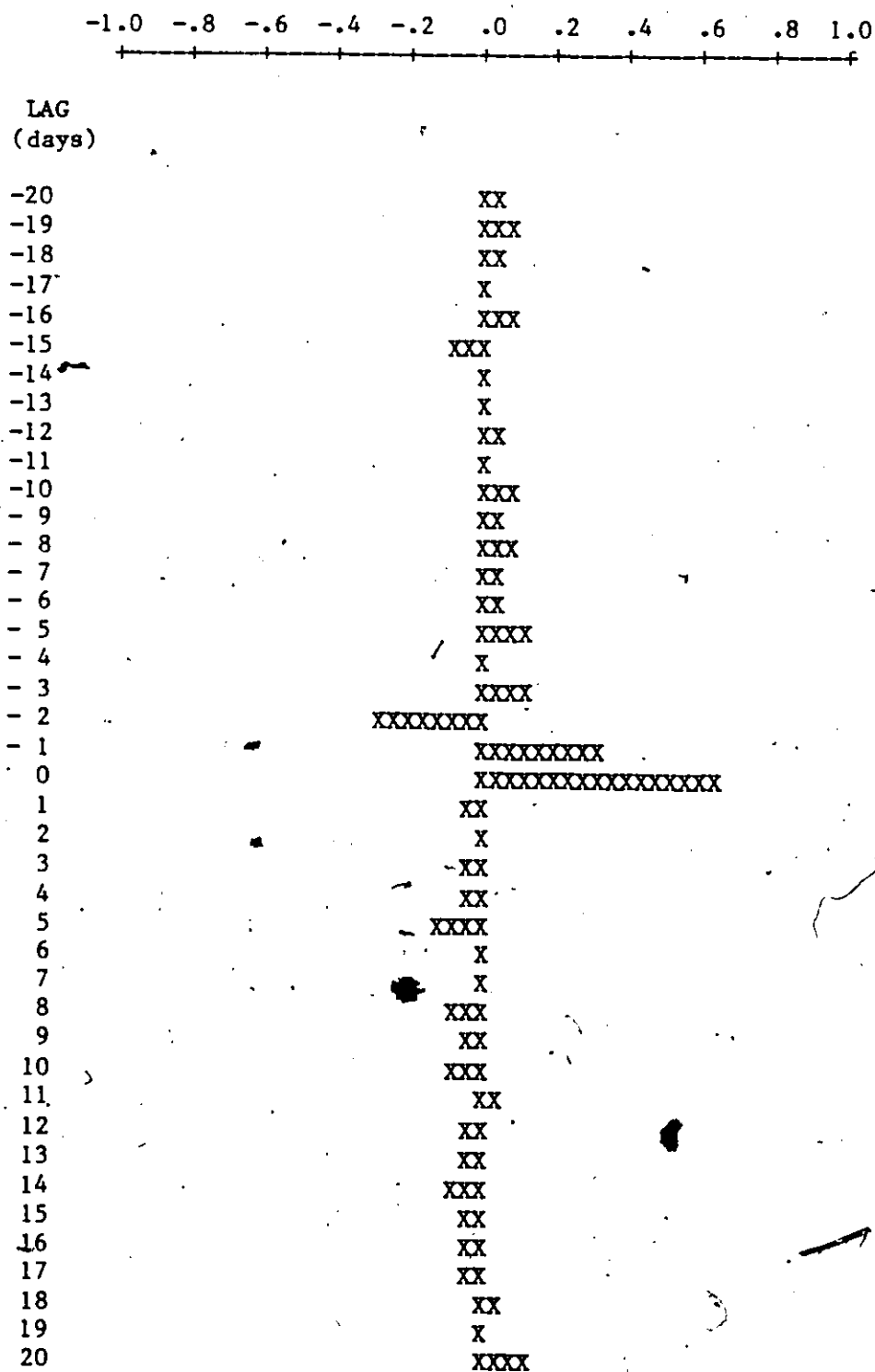


Figure 15b - Phase spectrum for chlorophyll a, station 1 versus station 3. (95% confidence limits). The -ve slope suggests that station 1 lags station 3 by .5 days.

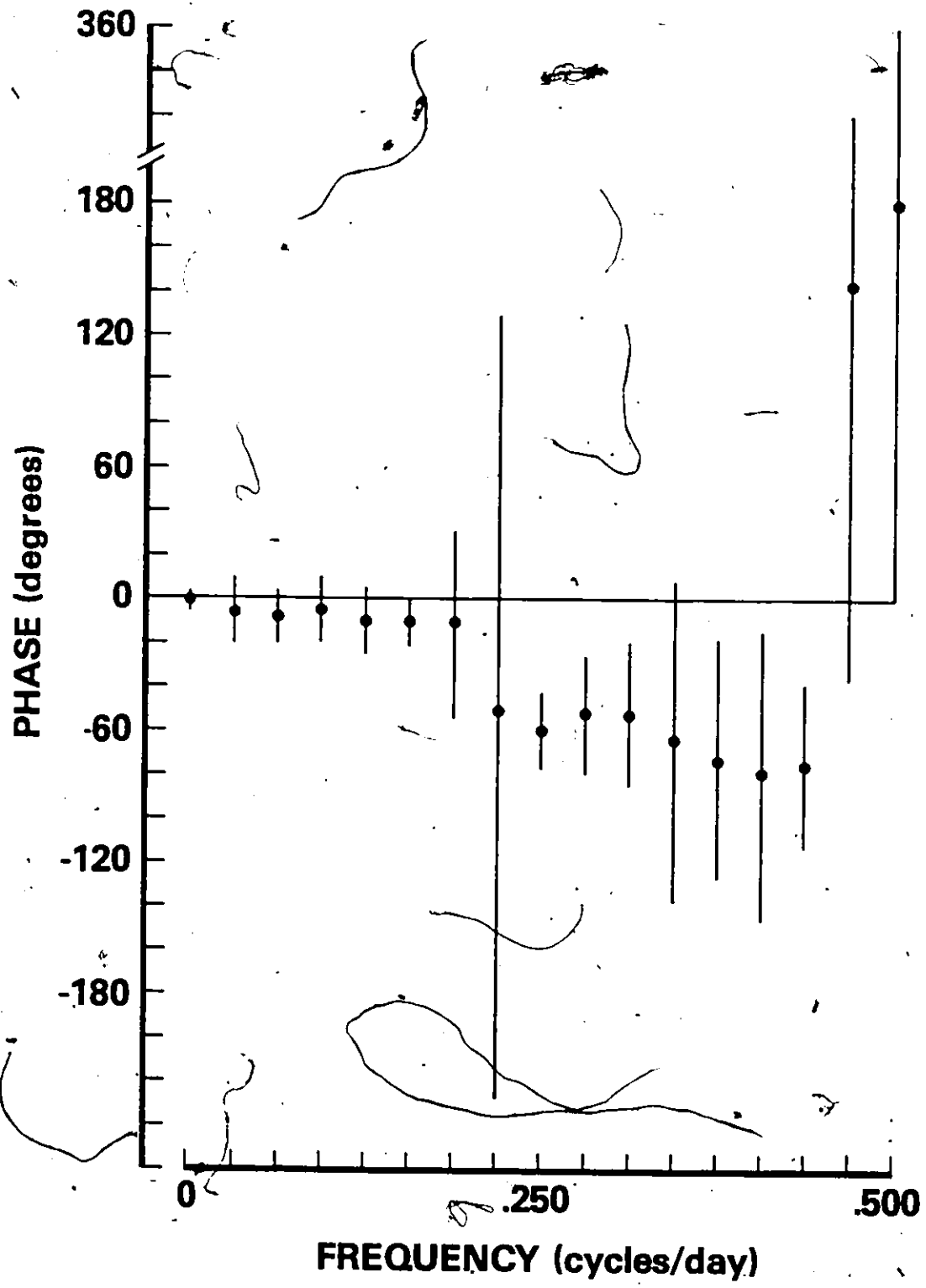


Figure 15c Cross-correlation estimates between log e transformed chlorophyll a ARIMA (101) residuals from station 1 and log e transformed chlorophyll a ARIMA (101) residuals from station 2 (at $k \neq 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

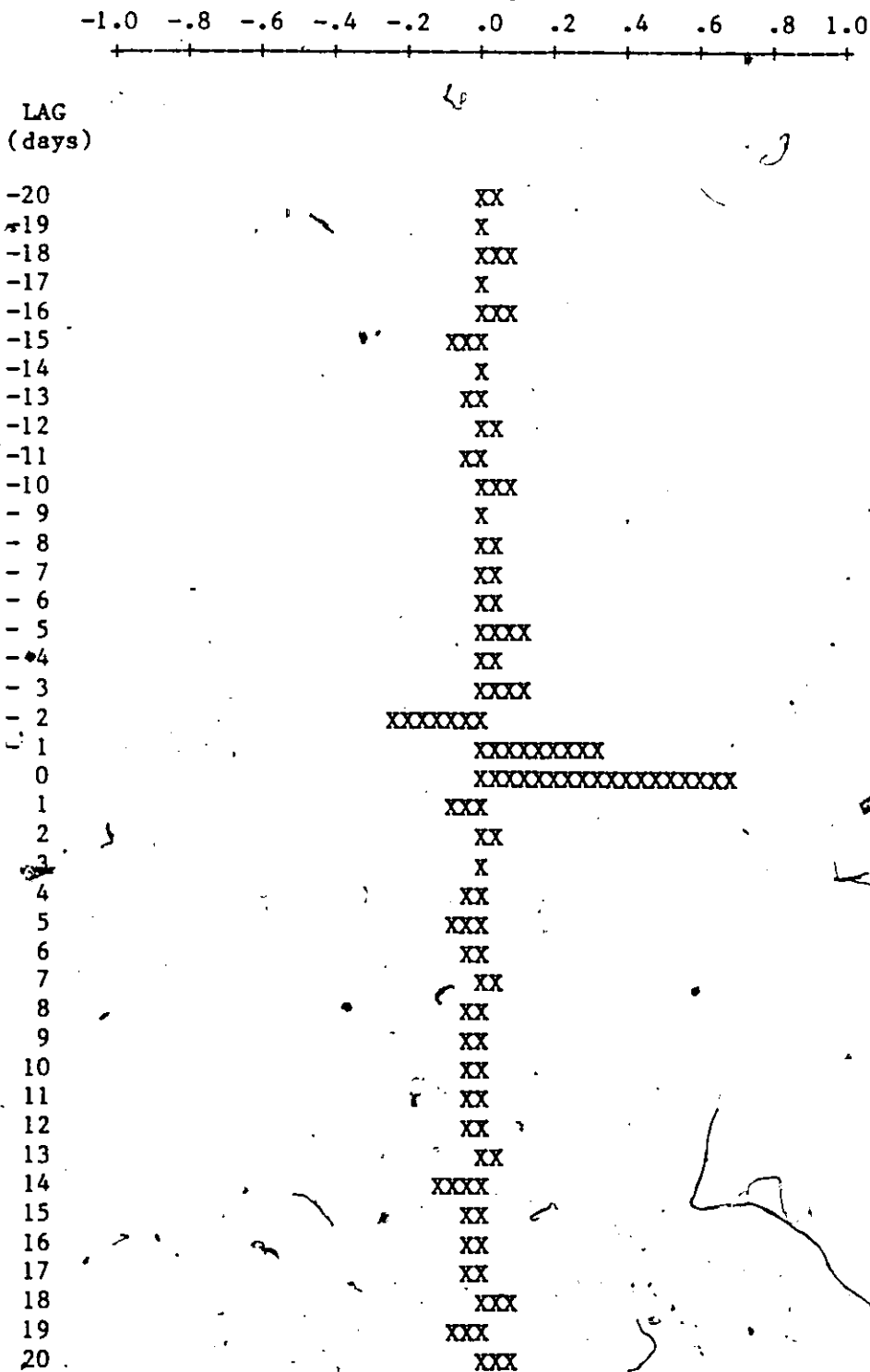


Figure 15d Cross-correlation estimates between log_e transformed chlorophyll a ARIMA (101) residuals from station 2 and log_e transformed chlorophyll a ARIMA (101) residuals from station 3 (at k = 0, for p < .05, r² > .195, at k = 20, for p < .05, r² > .217).

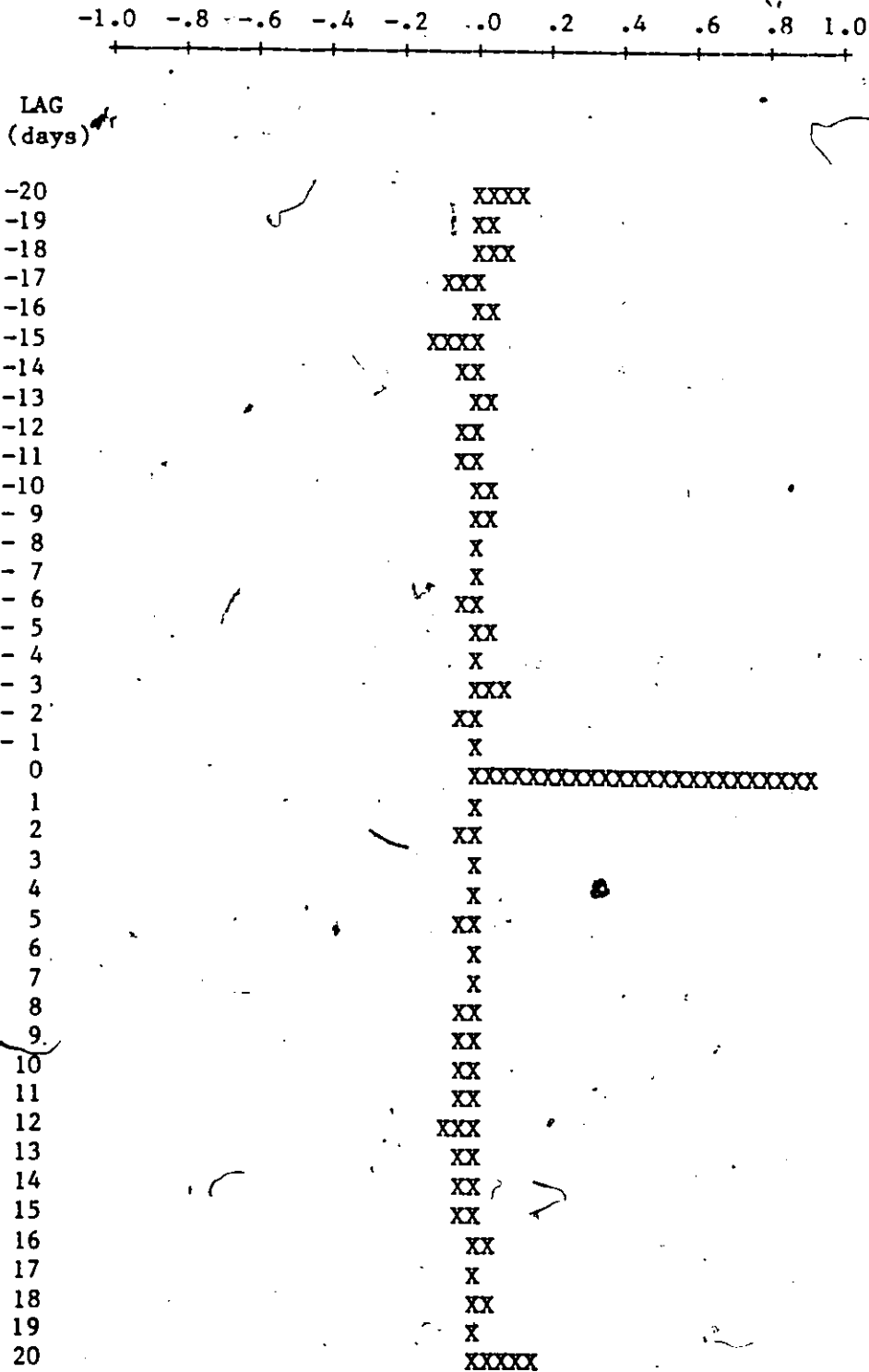


Figure 16a Cross-correlation estimates between Aphanizomenon
 ARIMA (101) residuals from station 1 and Aphanizomenon
 ARIMA (101)₂ residuals from station 3 (at $k = 0$, for
 $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 >$
 $.217$):

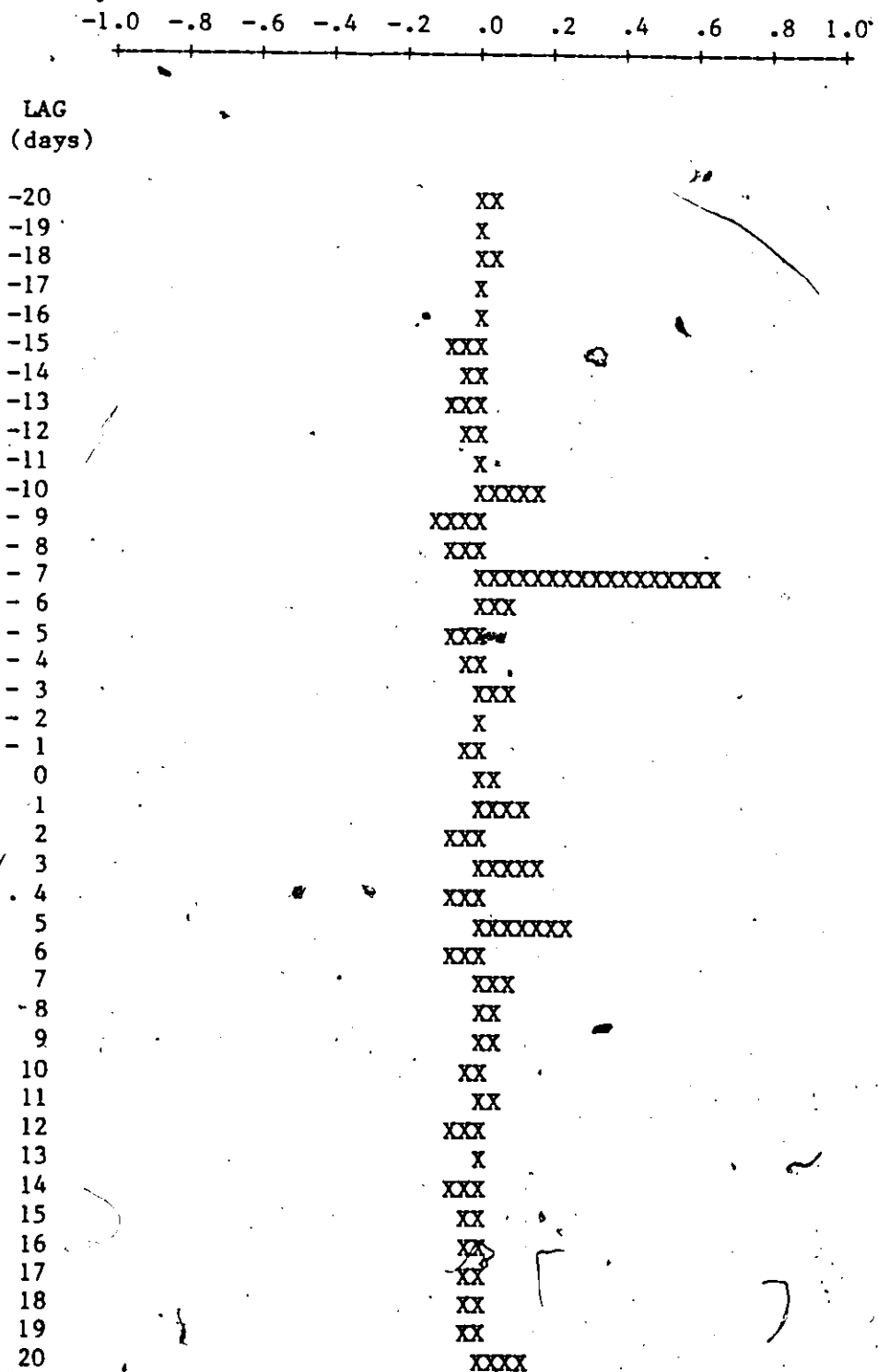


Figure 16b- Phase spectrum for Aphanizomenon, station 1 versus station 3. (95% confidence limits). The -ve slope suggests that station 1 lags station 3 by 7 days.

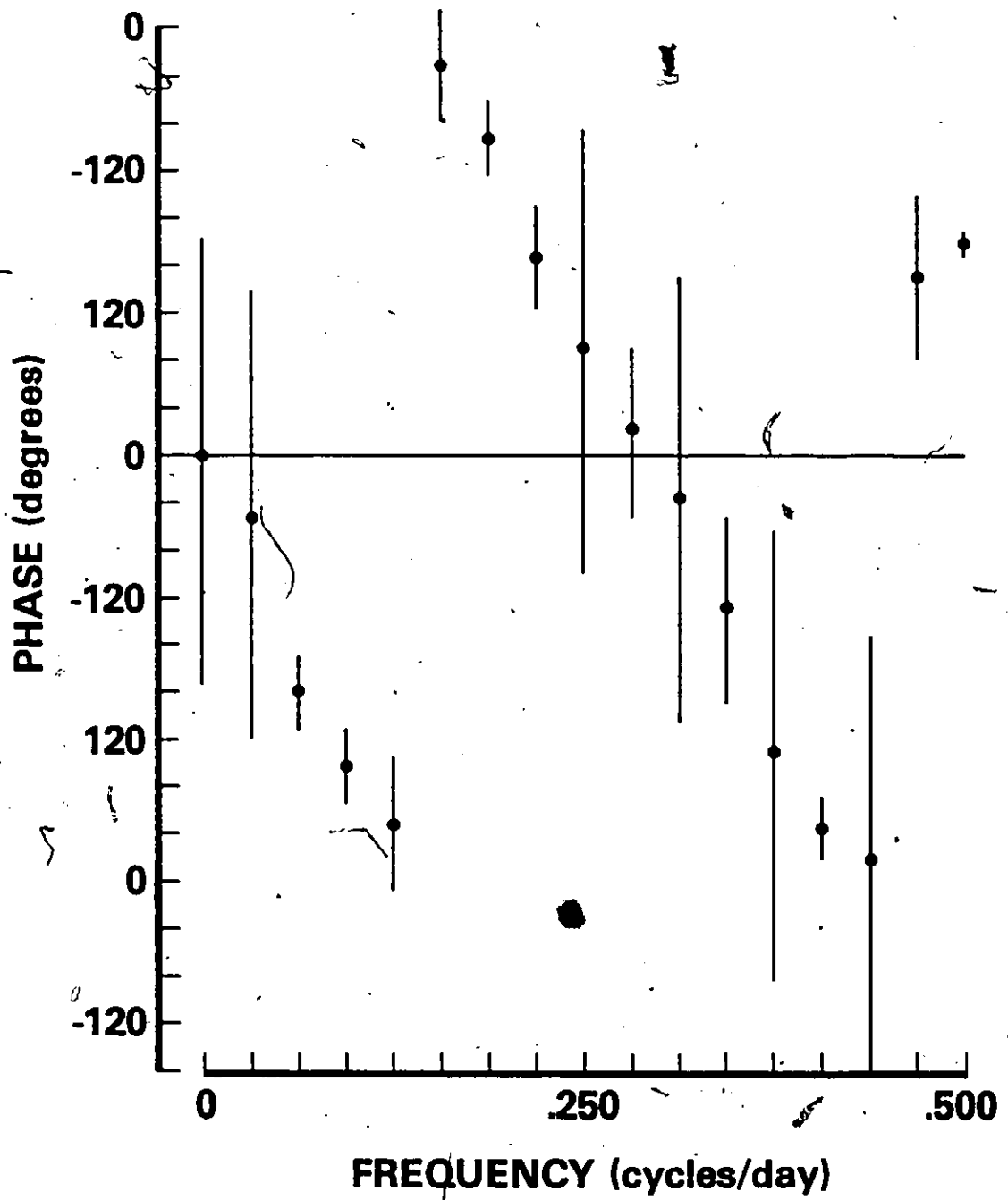


Figure 16c Cross-correlation estimates between Aphanizomenon ARIMA (101) residuals from station 1 and Aphanizomenon ARIMA (002) residuals from station 2 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

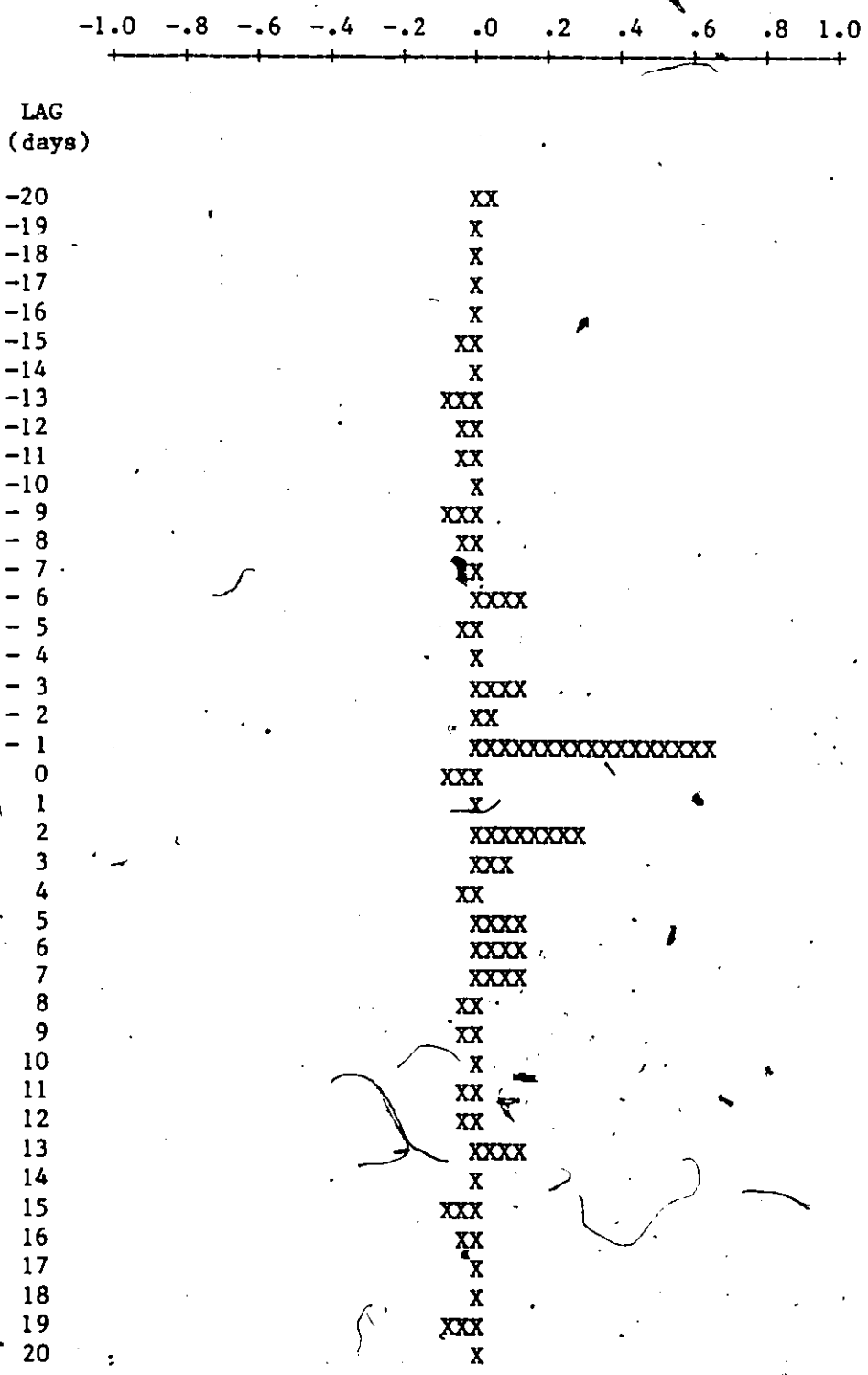


Figure 16d- Phase spectrum for Aphanizomenon, station 1 versus station 2. (95% confidence limits). The -ve slope suggests that station 1 lags station 2 by 1 day.

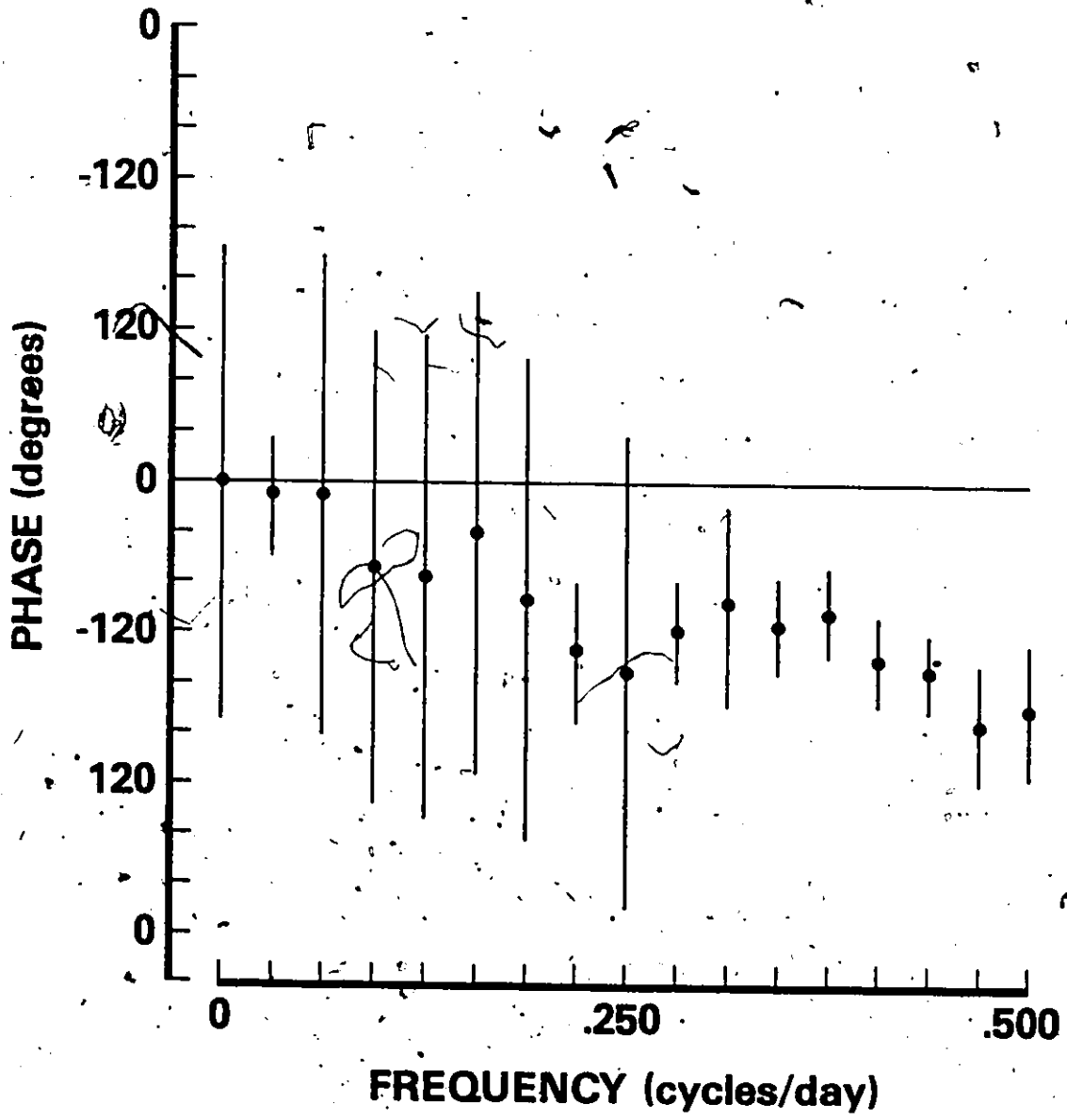


Figure 16e Cross-correlation estimates between Aphanizomenon ARIMA (002) residuals from station 2 and Aphanizomenon ARIMA (101) residuals from station 3 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

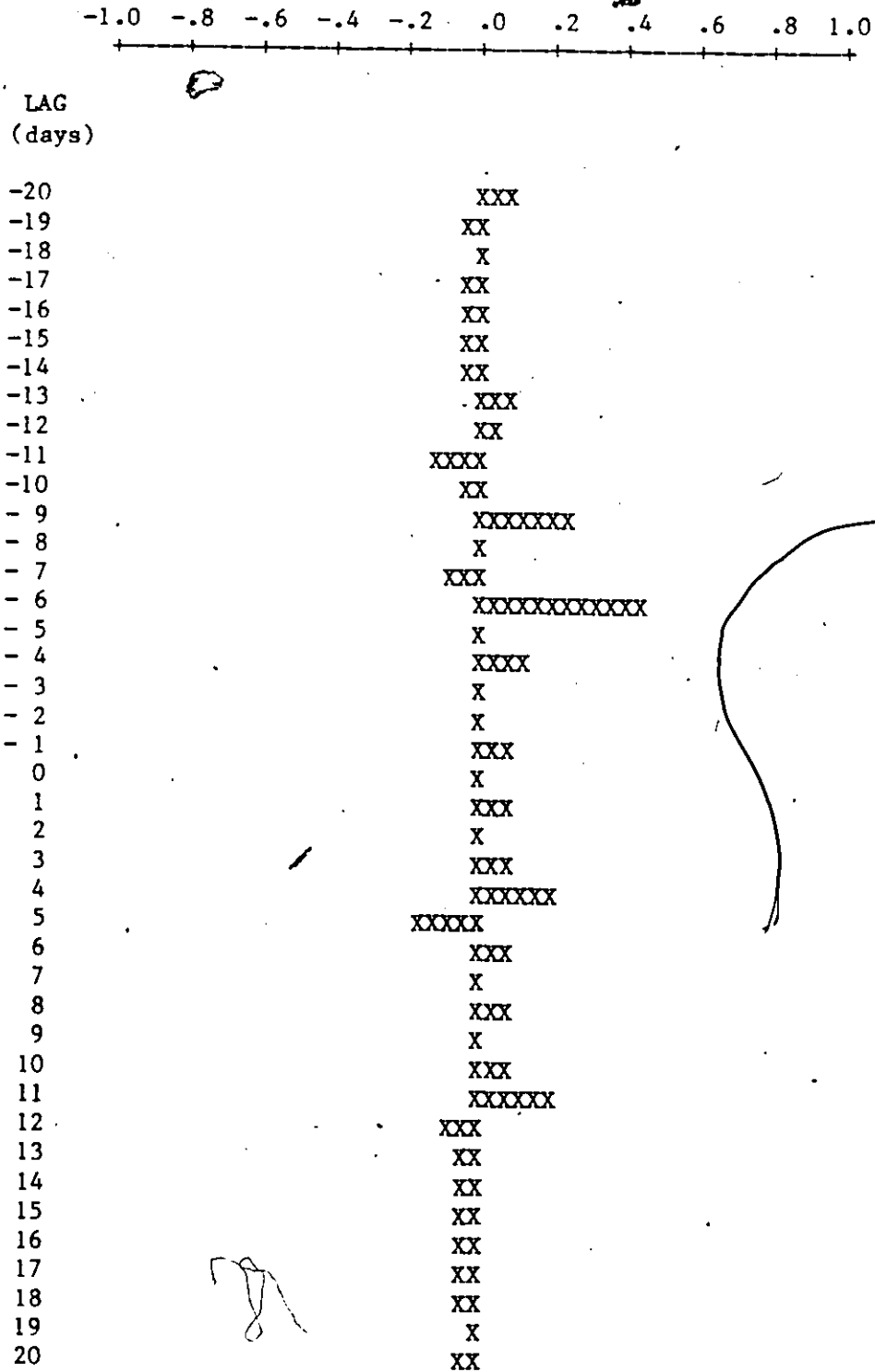
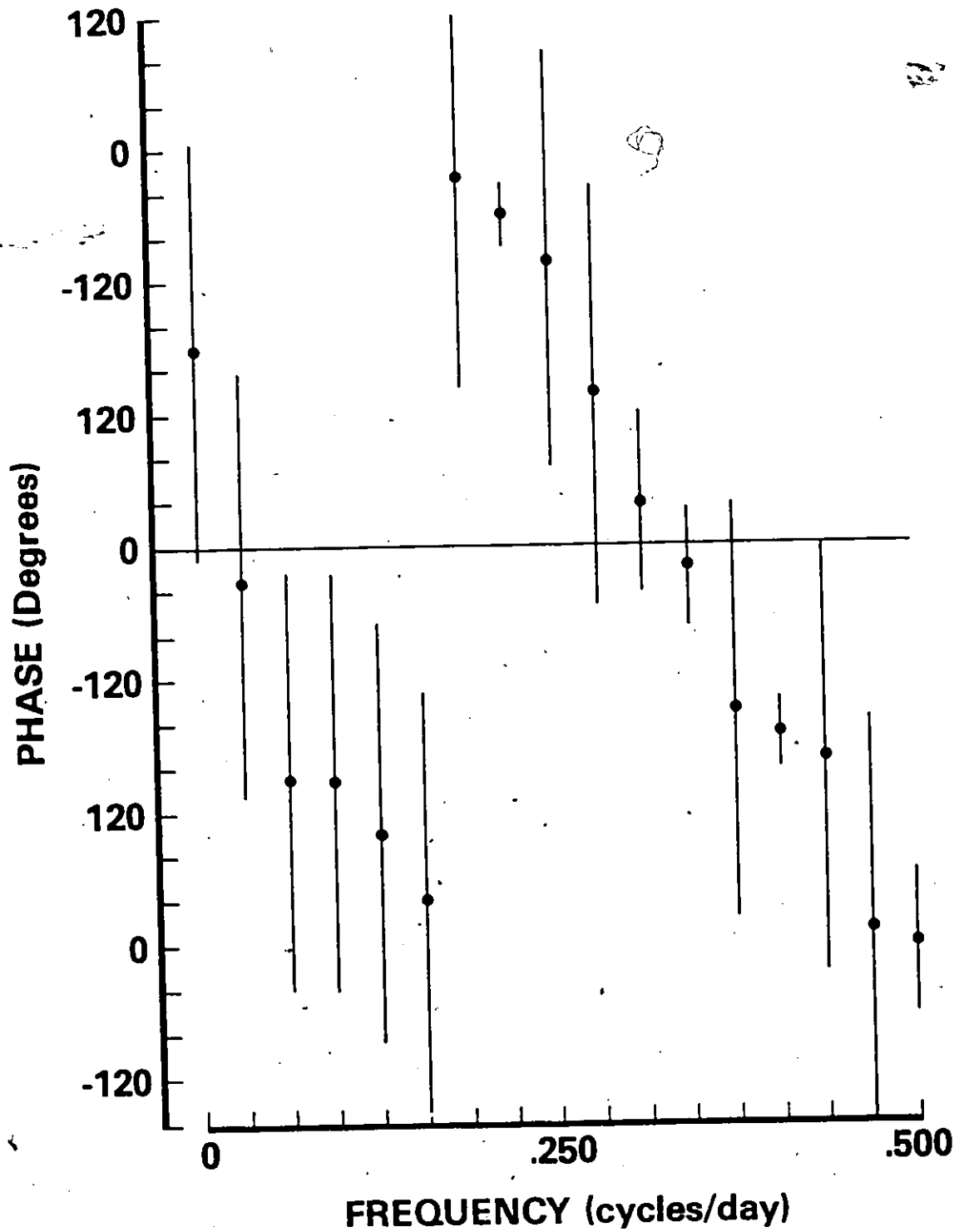


Figure 16f- Phase spectrum for Aphanizomenon, station 2 versus station 3. (95% confidence limits). The -ve slope suggests that station 2 lags station 3 by 6 days.

(16f)



Ceratium-

Relative abundances of Ceratium at station 1 were found to lead those at station 3 by 2 days, suggesting an advection rate of .6 cm/s, when both the cross-correlation function (Figure 17a) and the phase spectrum (Figure 17b) were examined. Relative abundances of Ceratium at station 1 were found to lead those at station 2 by 1 day (Figure 17c). A 1 day lead was observed between station 2 and station 3 (Figure 17d).

Stephanodiscus-

A 3 day lag, suggesting an advection rate of .4 cm/s, was observed between station 1 and station 3 (Figure 18). No clear lags or leads were seen between stations 1 and 2 and 2 and 3.

Lyngbya birgei-

A 2 day lead, suggesting an advection rate of 1.1 cm/s, was observed between station 2 and station 3 (Figure 19). No clear lags or leads were seen between stations 1 and 2 and 1 and 3.

Figure 17a Cross-correlation estimates between Ceratium ARIMA (101) residuals from station 1 and Ceratium ARIMA (101) residuals from station 3 (at $k = 0$, for $p < .05$, $r^2 > .365$, at $k = 15$, for $p < .05$, $r^2 > .517$).

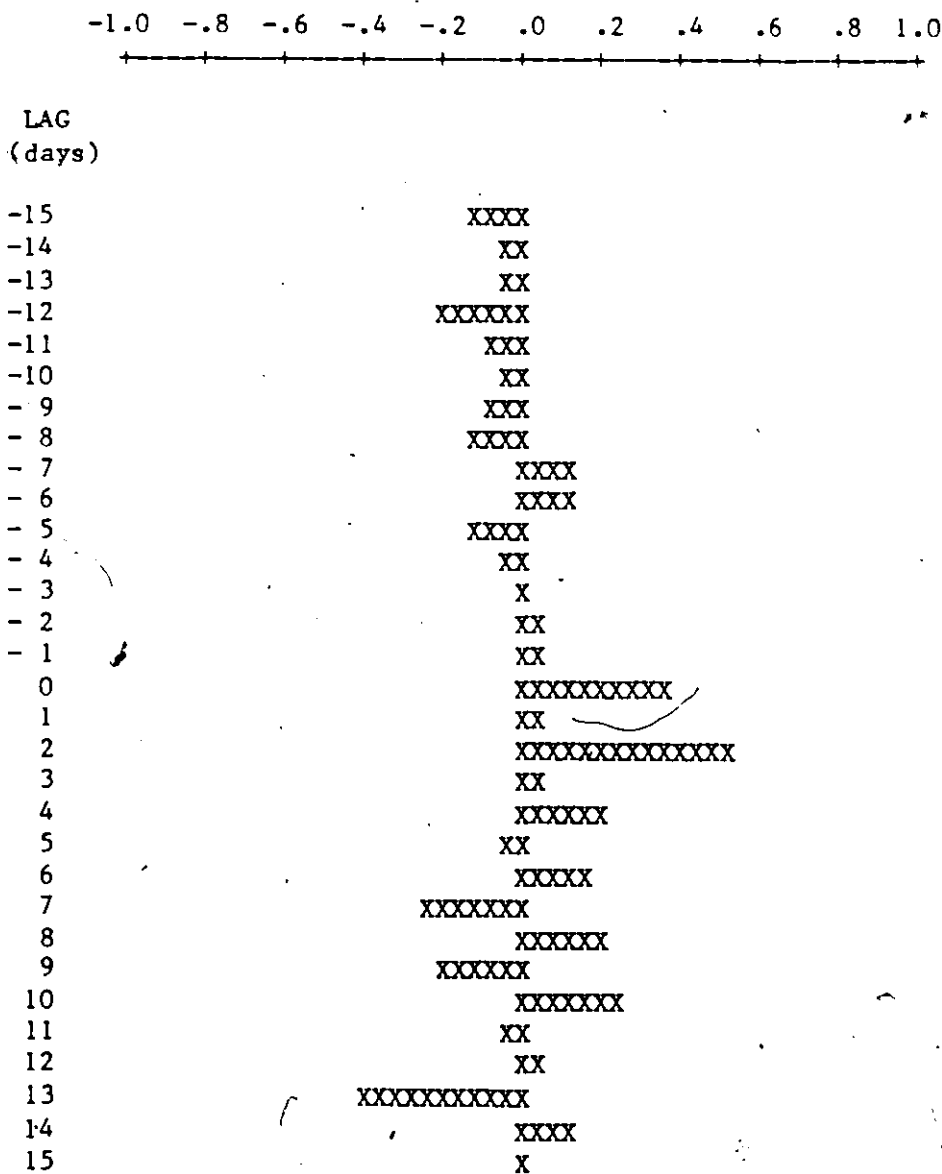


Figure 17b - Phase spectrum for Ceratium, station 1 versus station 3. (95% confidence limits). The +ve slope suggests that station 1 leads station 3 by 2 days.

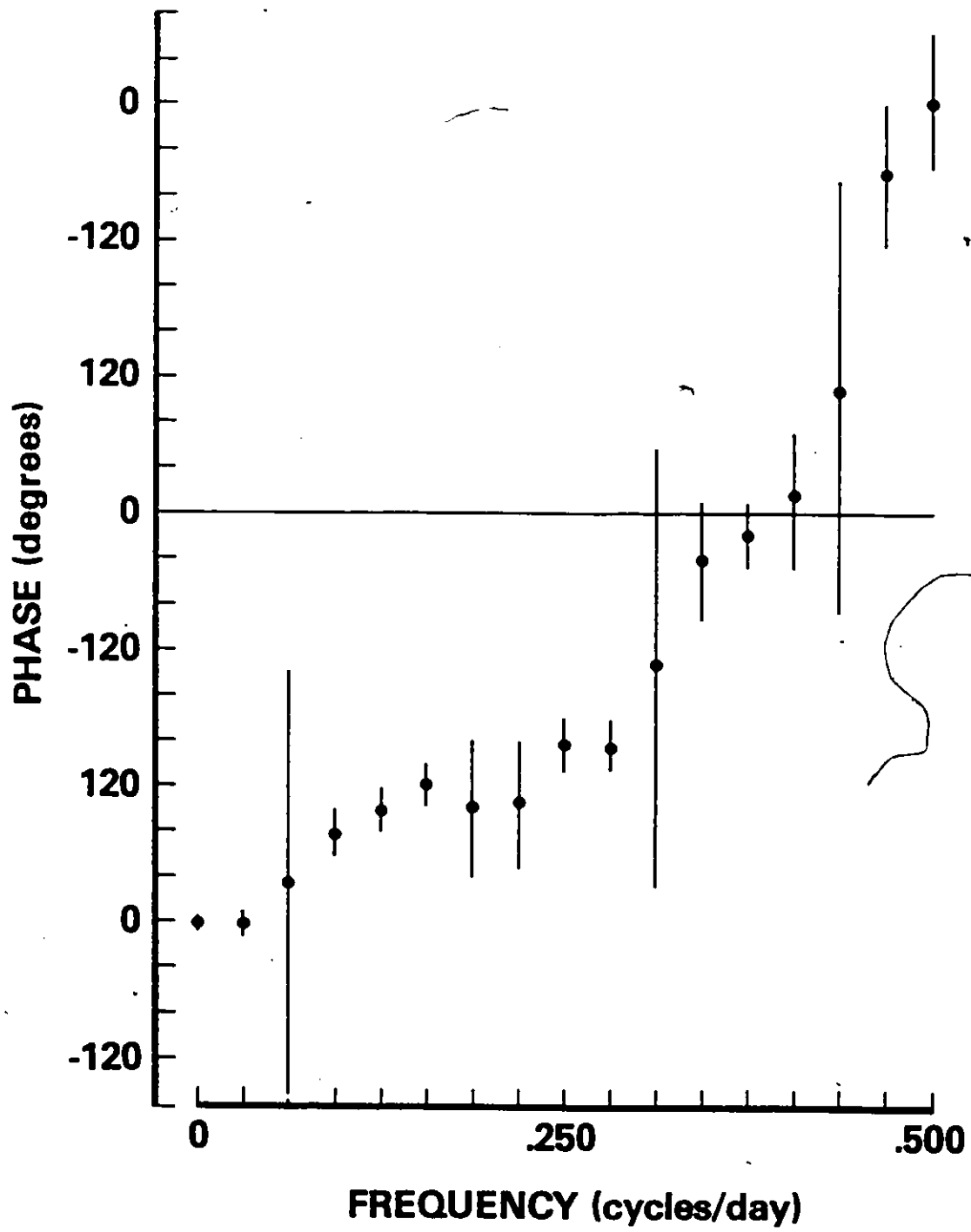


Figure 17c Cross-correlation estimates between Ceratium ARIMA
 (101) residuals from station 1 and Ceratium ARIMA
 (101) residuals from station 2 (at $k = 0$, for p
 $< .05$, $r^2 > .365$, at $k = 15$, for $p < .05$, $r^2 > .517$).

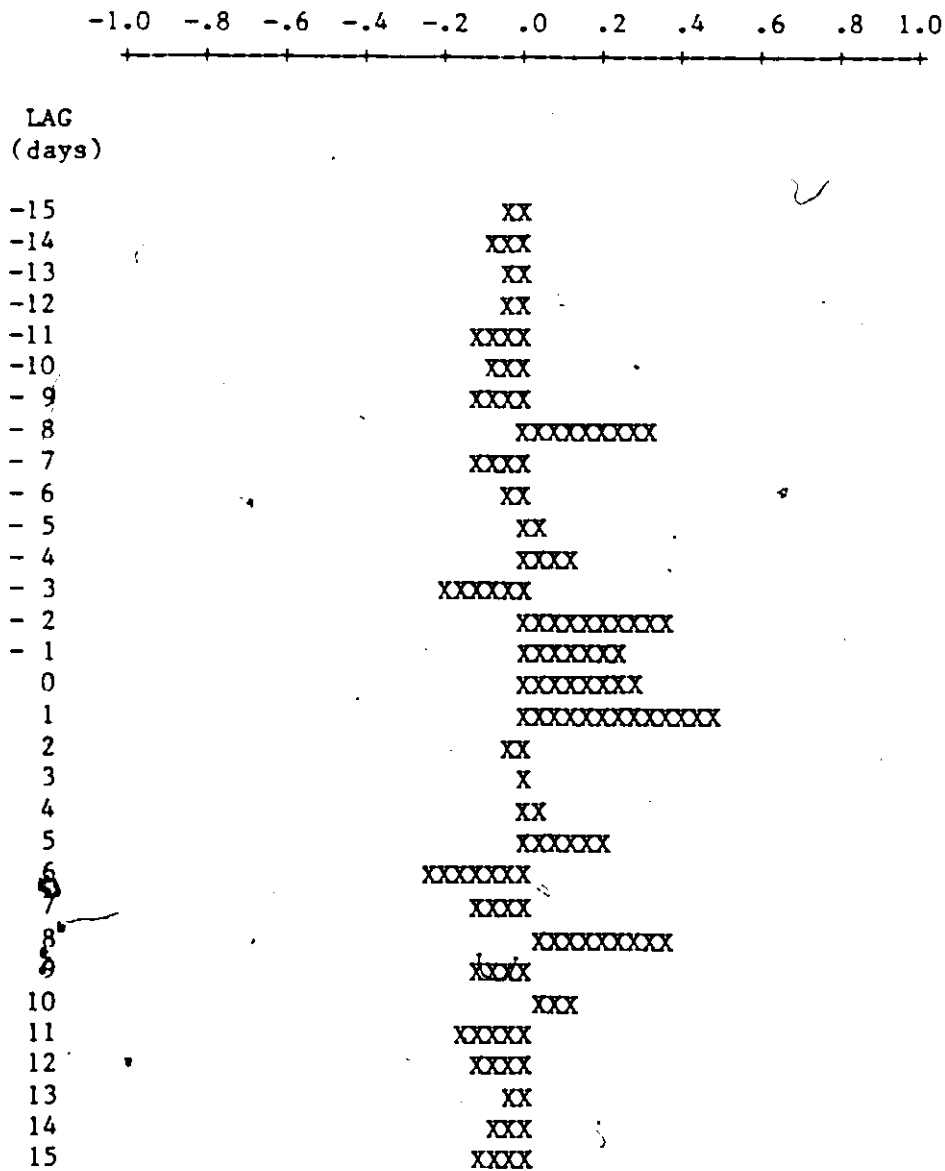


Figure 17d Cross-correlation estimates between Ceratium ARIMA
 (101) residuals from station 2 and Ceratium ARIMA
 (101) residuals from station 3 (at $k = 0$, for p
 $< .05$, $r^2 > .365$, at $k = 15$, for $p < .05$, $r^2 > .517$).

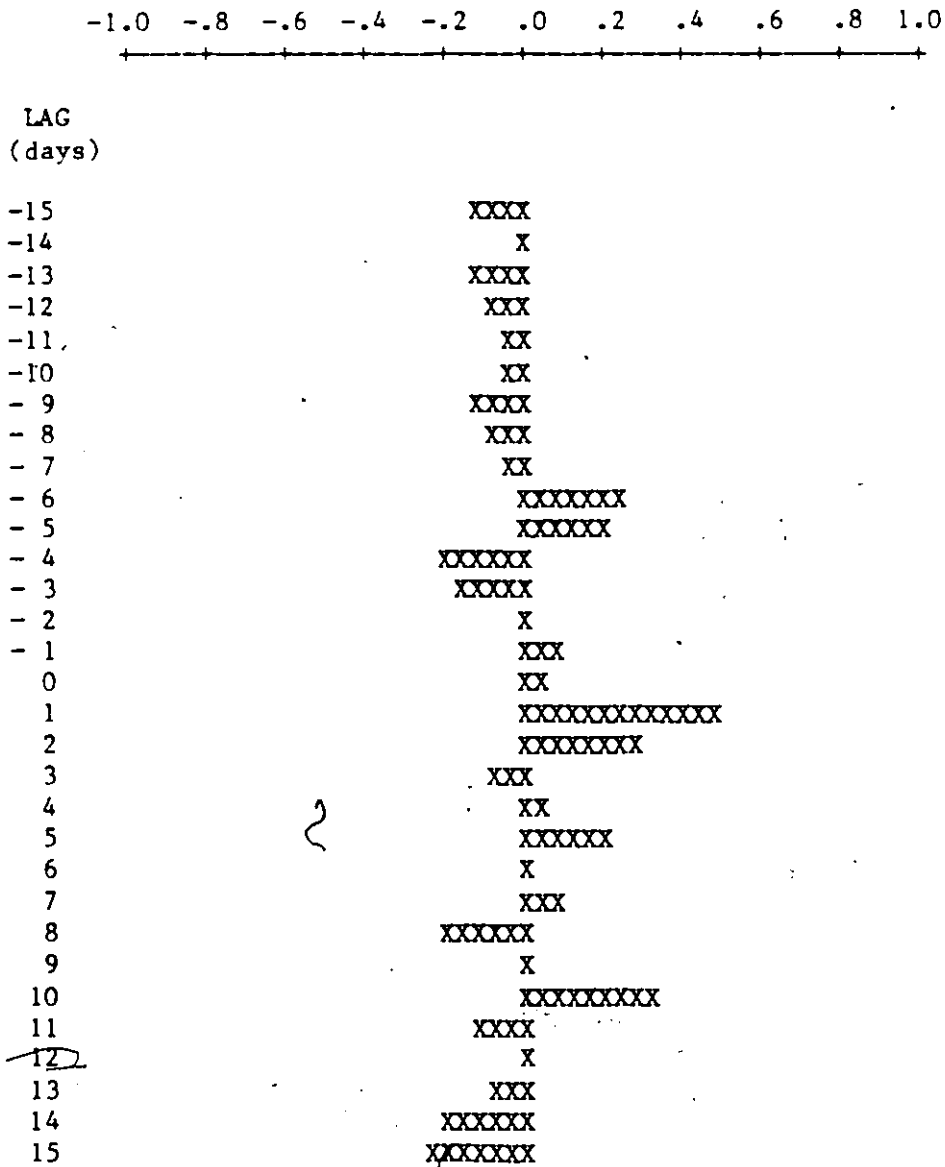


Figure 18 Cross-correlation estimates between Stephanodiscus ARIMA (101) residuals from station 1 and Stephanodiscus ARIMA (101) residuals from station 3 (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 15$, for $p < .05$, $r^2 > .217$).

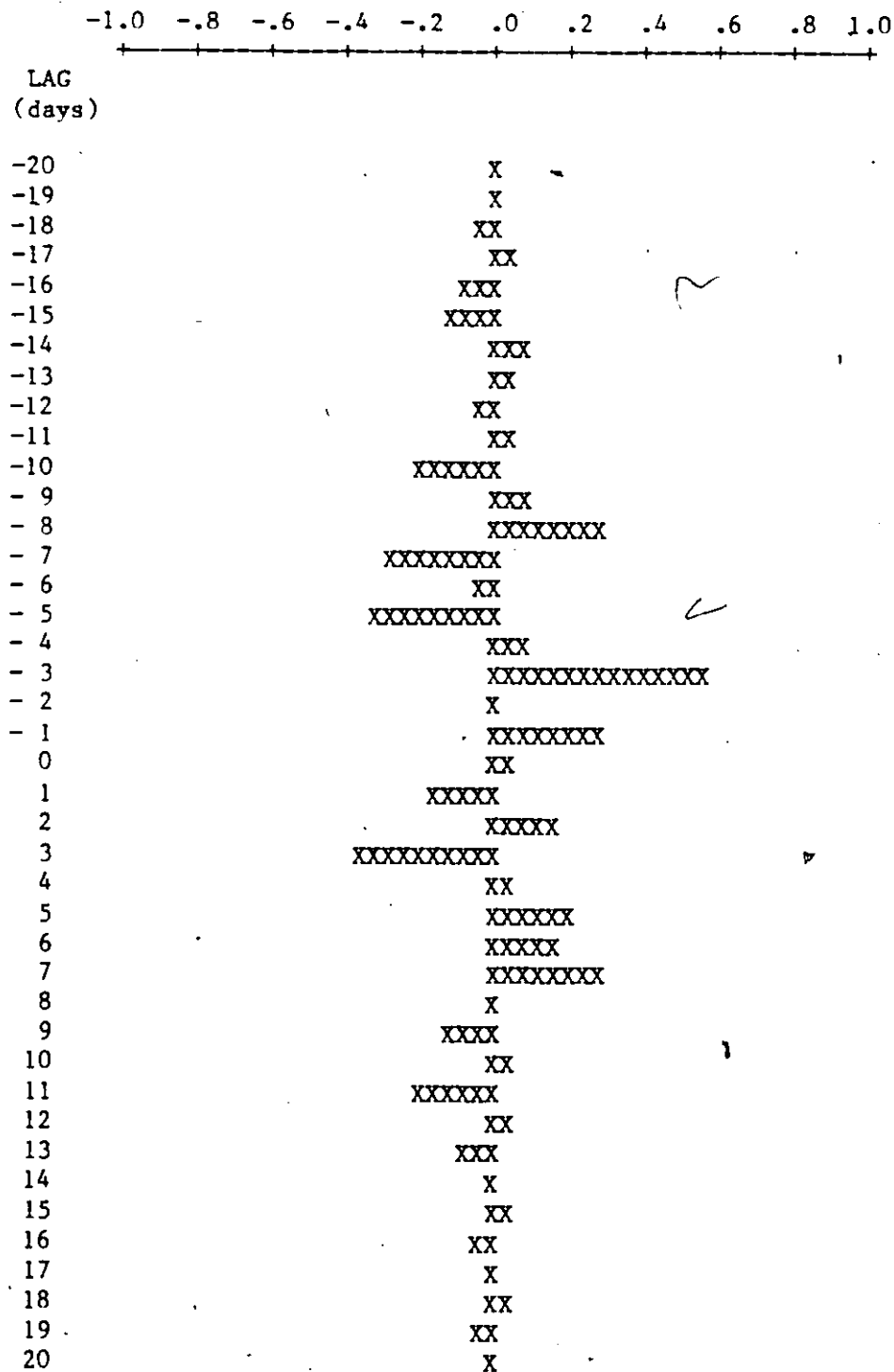
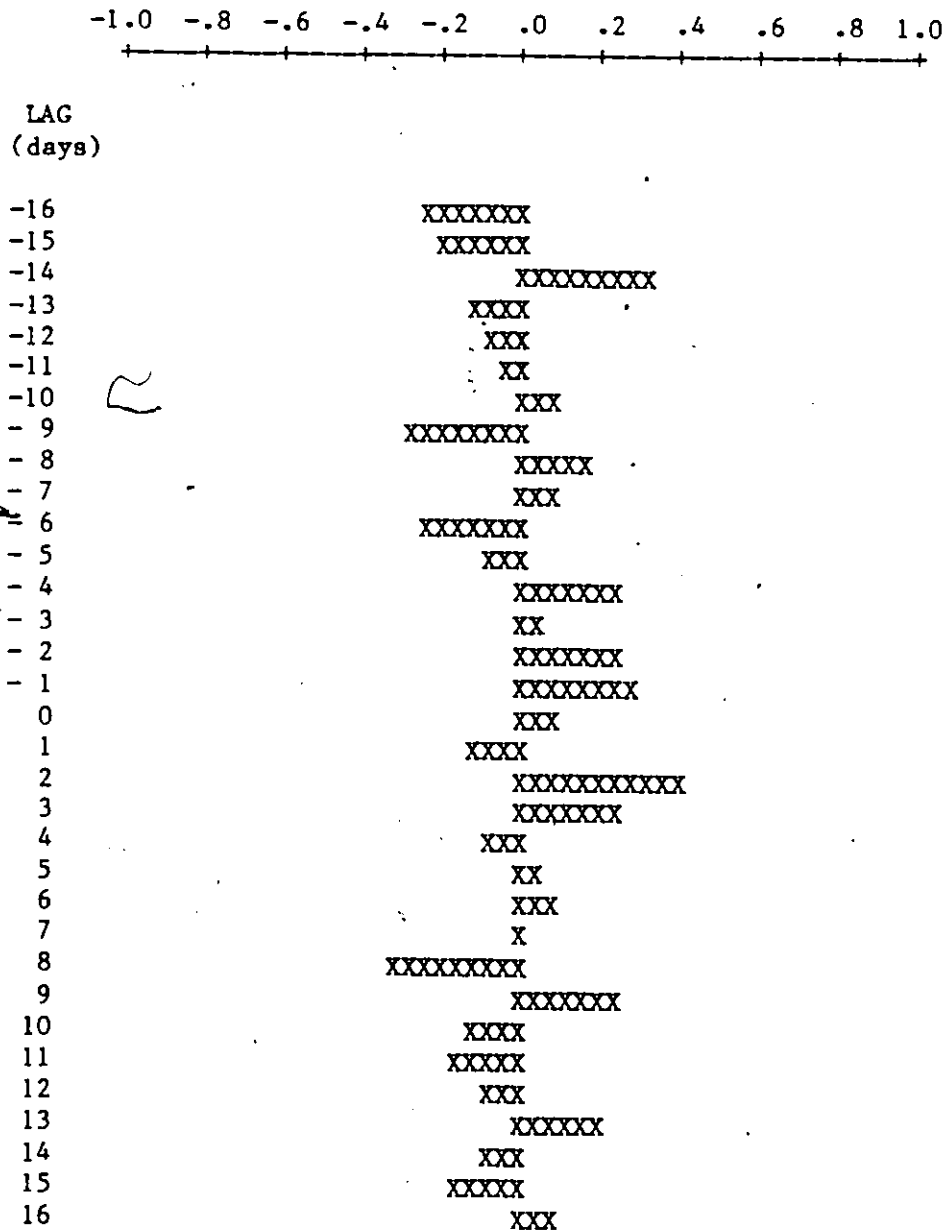


Figure 19 Cross-correlation estimates between Lyngbya
 ARIMA (101) residuals from station 2 and Lyngbya
 ARIMA (101) residuals from station 3 (at $k = 0$,
 for $p < .05$, $r^2 > .269$, at $k = 16$, for $p < .05$,
 $r^2 > .321$).



III-1-2-2 Redistribution by vertical mixing

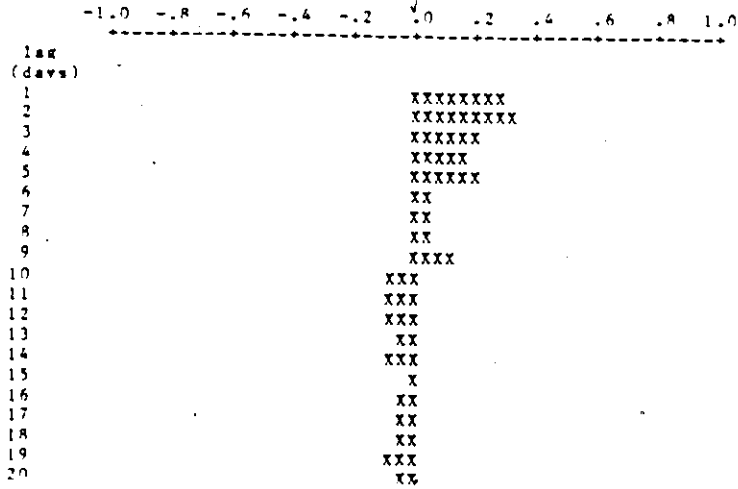
Within station 1 depth comparisons for SRP and TP-

The results obtained from the cross-correlations between different depths at station 1 and the auto-correlations of SRP at each depth suggested that on average over the 105 days examined, the upper 2m was not mixed with the rest of the water column with regards to SRP concentrations. This suggests that biological processes have an important affect on the SRP concentrations in the upper layers. The auto-correlation estimates of the time series of SRP at 0, 1 and 2m were significant up to lags of a few days (Figure 20). In contrast, the auto-correlation estimates of the time series of SRP from greater depths were non-significant except at lags of 20 days (Figure 20). A summary of the significant cross-correlations obtained when the SRP time series from different depths were compared is shown in Table 2. Cross-correlations were high on the same day when the SRP at 0m was compared to the SRP at 1m and the SRP at 1m was compared to the SRP at 2m. Cross-correlations were high on the same day when the SRP at 3, 4 or 5m was compared to the SRP at 10m. Cross-correlations were also high at longer negative and/or positive lags. For example, the SRP from 5m at station 1 and the SRP from 10m at station 1 were significantly cross-correlated on the same day ($r^2 = .894$, for $p < .05$, $r^2 > .195$), 20 days earlier ($r^2 = .435$, for $p < .05$, $r^2 > .217$), 10 days earlier ($r^2 = .208$, for $p < .05$, $r^2 > .205$) and 20 days later ($r^2 = .252$, for $p < .05$, $r^2 > .217$).

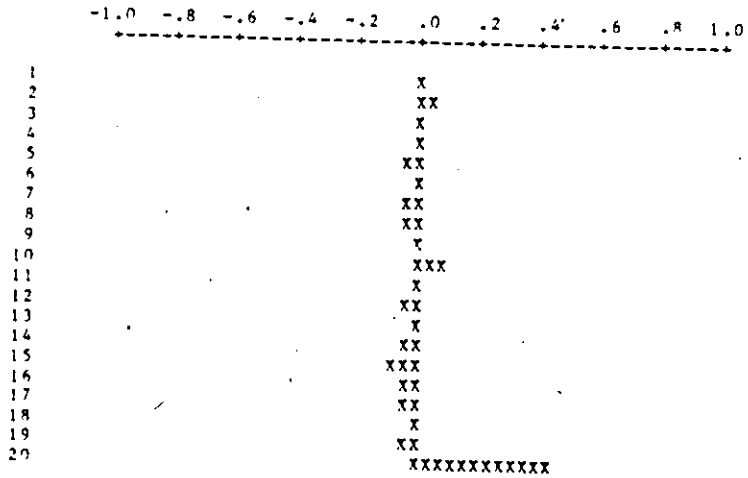
Figure 20

Auto-correlations of SRP at various depths
 (daily time series, May 8 to August 20, 1991)
 (at $k = 0$, for $p < .05$, $r^2 > .195$,
 at $k = 20$, for $p < .05$, $r^2 > .217$).

A) surface



B) 5m



C) 10m

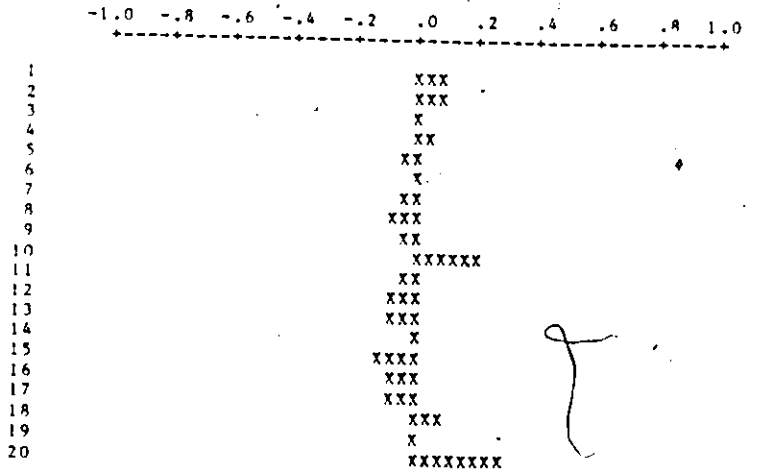


Table 2

Significant cross-correlations between soluble reactive phosphorus (SRP) time series obtained from different depths at station 1 (daily time series, May 8 to August 20, 1981)
 (at $k = 0$, for $p < .05$, $r^2 > .195$,
 at $k = 20$, for $p < .05$, $r^2 > .217$).

Depths compared	Lag (cross-correlation estimate)				
0m to 1m	0 (.441)				
0m to 2m	n.s.				
0m to 5m	-1 (.356)	-3 (.258)	10 (.225)	17 (.315)	19 (.395)
1m to 2m	0 (.574)				
1m to 3m	n.s.				
2m to 3m	0 (.358)				
2m to 5m	0 (.225)				
2m to 10m	0 (.273)	-12 (.234)	1 (.276)		
3m to 10m	0 (.759)	10 (.308)	20 (.245)		
4m to 10m	0 (.604)	-18 (.212)			
5m to 10m	0 (.894)	-20 (.435)	-10 (.208)	20 (.252)	

When TP values from 0, 5 and 10m were cross-correlated all combinations had a maximum cross-correlation on the same day (Table 3). Significant cross-correlations were also seen at longer lags and leads. For example, the TP from 5m at station 1 and the TP from 10m at station 1 were significantly correlated on the same day ($r^2 = .485$, for $p < .05$, $r^2 > .195$) and 18 days earlier ($r^2 = .220$, for $p < .05$, $r^2 > .214$).

III-1-3 SUMMARY .

The object of using power spectral analysis on time series of temperature, N^2 , wind speed, zeu/zm and nutrients was to determine the dominant physical and chemical cycles in the system. Four-week and two-week periodicities were evident in the power spectra obtained from the weekly data sets for $N^2(0-6)m$ and $N^2(0-10)m$. The power spectrum for wind speed decreased with increasing frequency with increases seen at periods of 10 and 4-6 days. The power spectrum for zeu/zm decreased with increased frequency with increases seen at periods of 5-7 and 2-3 days. Longer term periodicities in wind speed and zeu/zm may have been resolved if a power spectrum was calculated from a weekly data set. The power spectral estimates for $NO^3-N + NO^2-N$ and TP were roughly constant except for increases seen at seasonal time scales. The power spectral estimates for Si were roughly constant throughout all time scales examined. In contrast, 4-week and 2-week periodicities were evident in

Significant cross-correlations between total phosphorus (TP) time series obtained from different depths at station 1 (daily time series- May 8 to August 20, 1981) (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

Depths compared	Lag (cross-correlation estimate)		
0m to 5m	0 (.568)	-17 (.227)	-20 (.232)
5m to 10m	0 (.485)	-18 (.220)	

the power spectrum for SRP calculated from the weekly data set.

The data clearly shows the existence of short-term (2-3 day) lags and leads between stations as nutrients, biomass and individual species moved within the basin. Significant cross-correlations at longer lags and/or leads were also observed in the station-to-station comparisons and within station 1 depth comparisons for both SRP and TP. Longer term lags and leads would arise if all stations showed similar fluctuations at these time scales: fluctuations driven by basin wide events such as the entrainment of hypolimnetic water and major readjustments in the depth of the thermocline. The periodicities observed in N^2 and in the wind speed data showed strong evidence for 10-20 day fluctuations which are known to be associated with the passage of atmospheric weather systems through temperate latitudes (Boyce, 1974). The periodicities in the stability of the surface waters are driven by periodic fluctuations in wind speed. A summary of the significant cross-correlations obtained in station-to-station and within station 1 (0,5 and 10m) depth comparisons for SRP and TP is shown in Table 4. Chi-square analysis revealed that the frequencies of significant cross-correlations at lags or leads greater than 4 were not as expected by chance at a significance level of $p < .05$. The data suggests that high cross-correlations at lags or leads greater than 10 days are likely due to vertical mixing rather than being statistical outliers of no significance.

Table 4 - Summary of between station and within station comparisons for soluble reactive phosphorus (SRP) and total phosphorus (TP) and significant autocorrelations in wind speed. Significant cross-correlations ($p < .05$) between stations and within station 1 at different depths for SRP and TP have been tabulated. A + sign indicates a significant cross-correlation at a positive lag and a - sign indicates a significant cross-correlation at a -ve lag. If a time series from station 1 is compared to a time series from station 3, a significant cross-correlation at a -ve lag suggests that changes at station 1 lag those at station 3 by k number of days, where $k = \text{lag}$. Similarly, a significant cross-correlation occurring at a +ve lag, suggests that changes at station 1 lead those at station 3. The lags having significant autocorrelation estimates for wind speed are indicated by a *.

Table 4- Summary of between station and within station comparisons for soluble reactive phosphorus (SRP) and total phosphorus (TP) and significant autocorrelations in wind speed.

LAG (days)	Station to Station				Within station							
	SRP		/ TP		SRP		/ TP					
	station number		station number		depth (m)							
	1,3	1,2	2,3	1,3	1,2	2,3	0,5	5,10	0,10	0,5	5,10	0,10
0	-		-		-			-		-		-
1		-							-	+		-
2			-							+		
3			-							+		
4	-				-				-			
5												
6												
7			+									
8												
9												
*10		-					+	-				-
*11												
*12												
13												
14				+		-			+			
*15	+	+										
16												
17												
18			-								-	-
*19				-			+		+			
20								+, -		-		

Chi-square test:

Pooled classes	Observed frequency	Expected frequency
5-9	1	6
10-15	9	7.2
16-20	10	6

The expected frequency of significant cross-correlations ($p < .05$) at any one lag is $2/40 * 12$ (number of runs) $* 2$, since the -ve and + lags have been combined in 1 row. $\chi^2 = 7.29$. For 2 degrees of freedom, at $p = .05$, $\chi^2 = 5.99$ and at $p = .01$, $\chi^2 = 9.21$. The results of this test suggest that the frequency of significant cross-correlations at lags greater than 4 are not as expected by chance.

III-2 Relationship between environmental variables and phytoplankton dynamics

III-2-1 DAILY TIME SERIES

III-2-1-1 General description of phytoplankton dynamics (May 8 to August 20, 1981)

Integrated chlorophyll-a concentrations were higher at the beginning (May 8-27) and the end of the time series (late July- August) (Figure 21). The average chlorophyll-a concentration was 8,4 $\mu\text{g/l}$. The phytoplankton diversity increased in May, decreased in mid-June, increased again in early July and then decreased towards the end of the time series (Figure 21). The rates of community change were low in early May and from mid-July through to the end of the daily time series (Figure 21). Increases in the rate of community change occurred in late May, mid-June and early July. The (0-7)m abundances of several phytoplankton species over the 105 days are shown in Figure 22. The phytoplankton dynamics observed during this time interval can be described in terms of 4 periods:

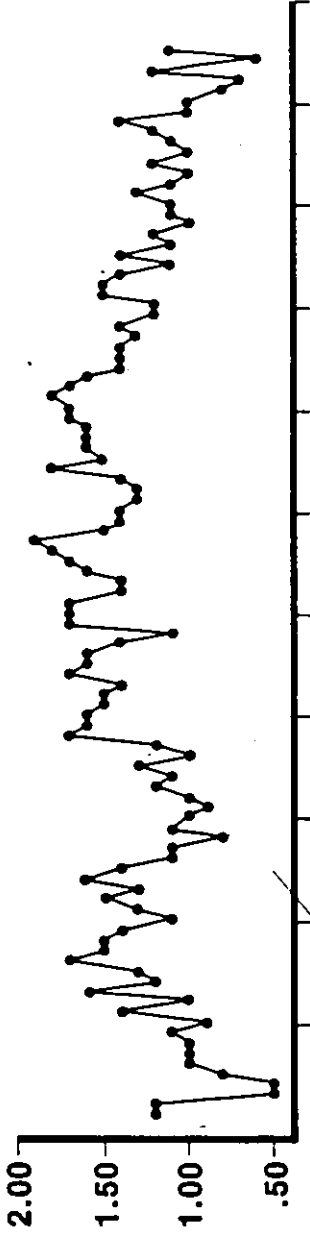
May 8 to May 27-

At the onset of daily sampling, diatoms such as Stephanodiscus and Asterionella were present and on the decline. By May 27, abundances of these diatoms were low to non-measurable. The blue-green alga

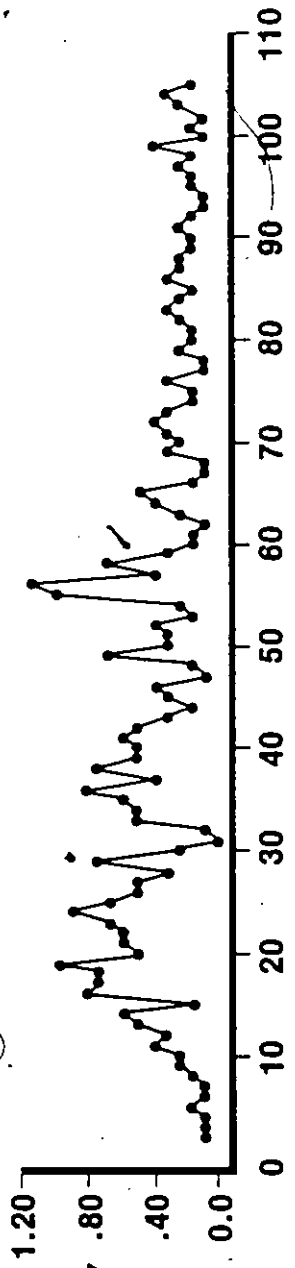
Figure 21 - Time series plots (May 8 - August 20, 1981) of chlorophyll
a , phytoplankton diversity (Shannon-Weaver index, 1963)
and rate of phytoplankton community change (Lewis, 1978)
(station 1, integrated sample).



CHLOROPHYLL a
(0-7)m (µg/l)



SHANNON-WEAVER
DIVERSITY (H')



RATE OF COMMUNITY
CHANGE (SD)

May 17 May 27 June 6 June 16 June 26 July 6 July 16 July 26 Aug 5 Aug 15

1981

Aphanizomenon was also present and declined in abundance by the end of May. Other algae present and declining included Dinobryon and Ochromonas.

May 27 to July 6-

Cryptomonas erosa and Cryptomonas ovata increased to a peak in early June and then decreased throughout the rest of this period. Rhodomonas increased until early June and remained present throughout this period. Planktosphaeria and Ochromonas began to increase in mid-June. Ceratium and Oocystis first appeared towards the end of June. An increase in the abundance of Dinobryon was observed in the later part of June.

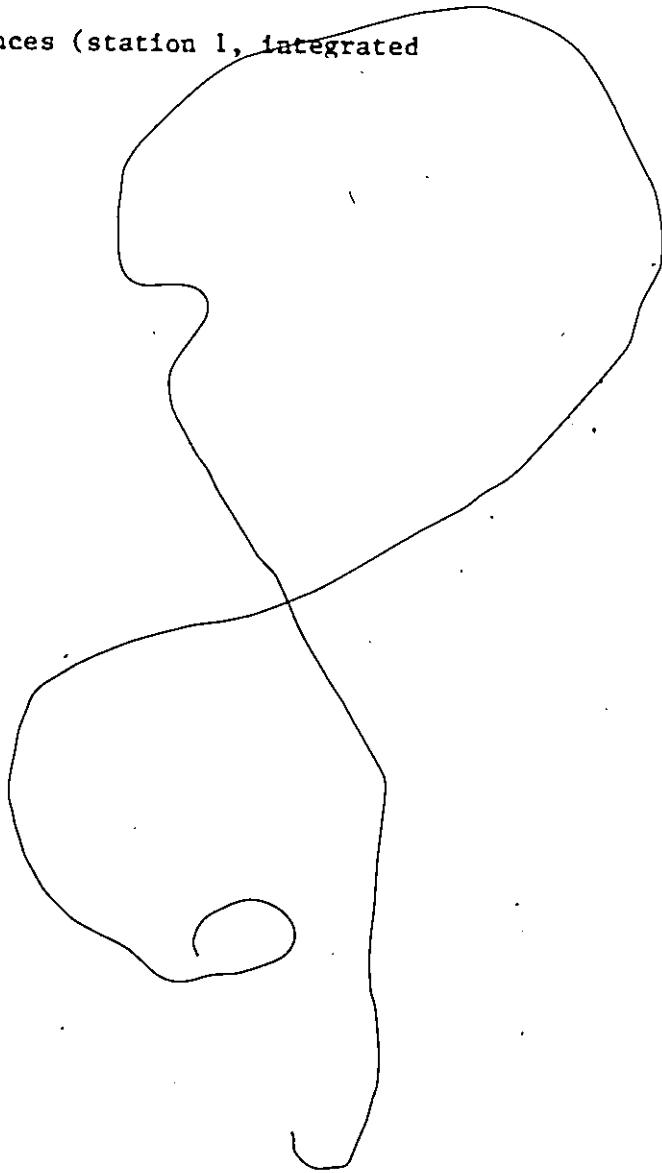
July 6 to July 26-

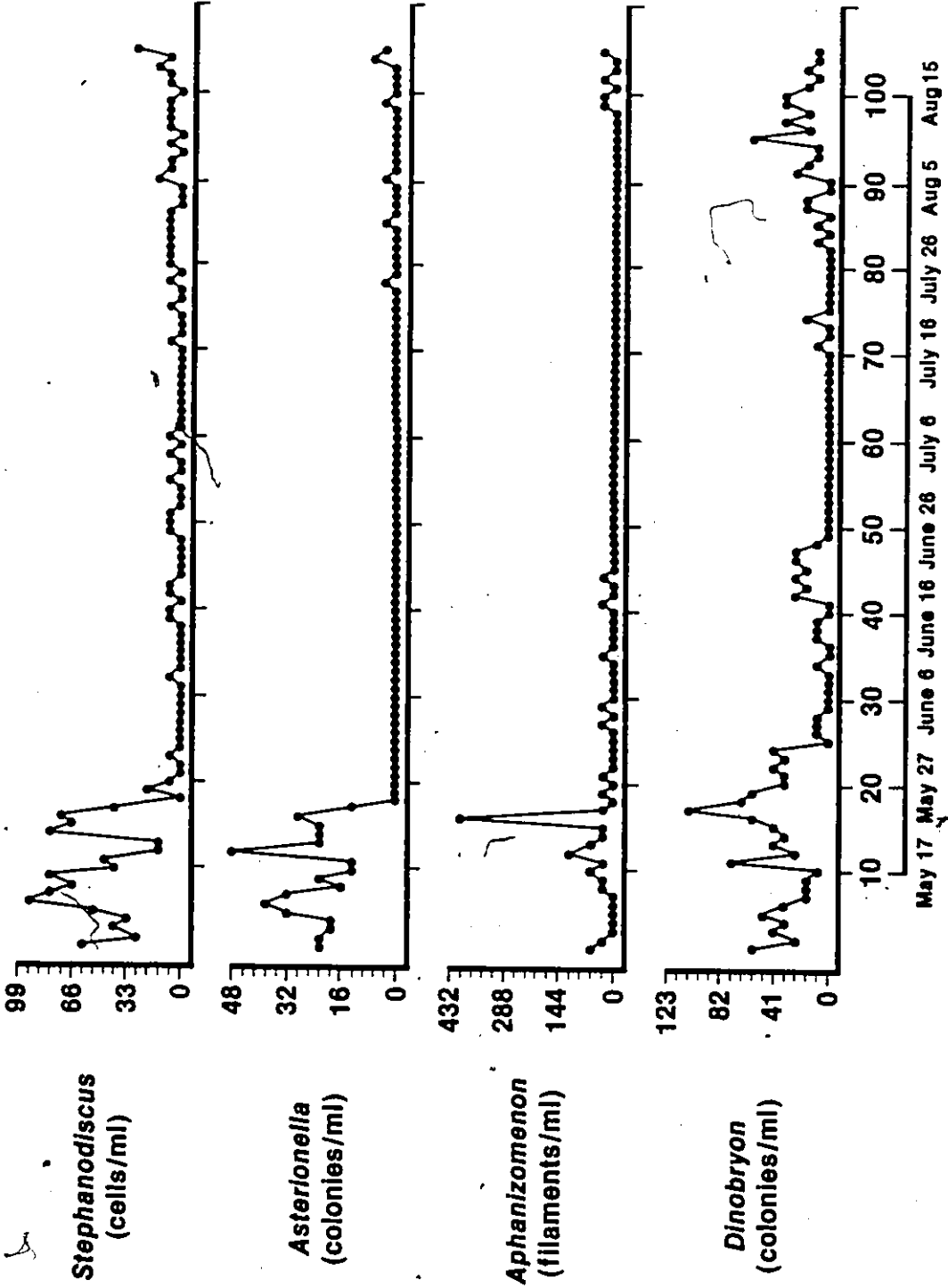
Several blue-green algae (Microcystis, Gomphosphaeria, Coelosphaerium, Lyngbya and Merismopedia) appeared and continued to increase throughout this period. Ceratium continued to increase. Green algae such as Oocystis and Planktosphaeria peaked mid-way through this period and declined to low-levels by July 26.

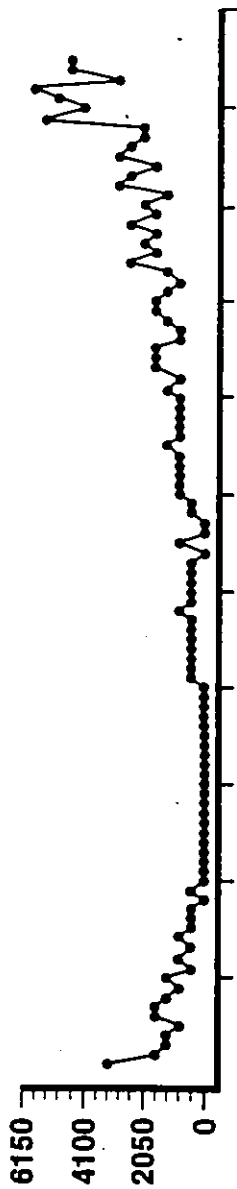
July 26 to August 20-

Melosira, Dinobryon and Aphanizomenon began to increase again. Ceratium decreased after July 26. Merismopedia decreased from July 26

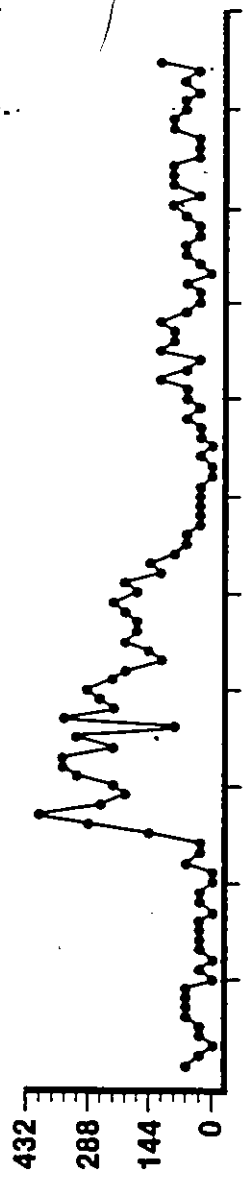
Figure 22 - Time series plots (May 8 - August 20, 1981) of phytoplankton abundances (station 1, integrated sample).



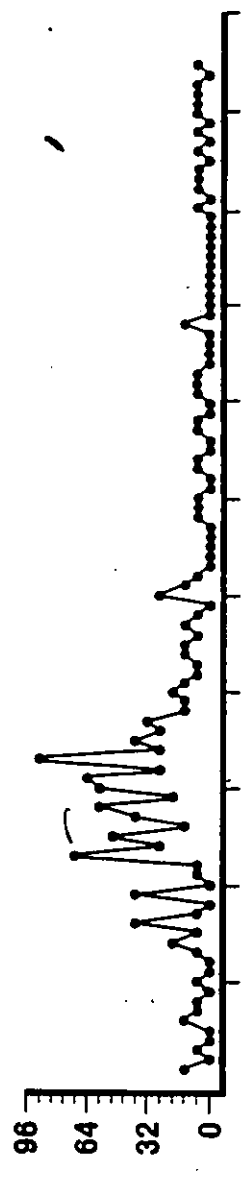




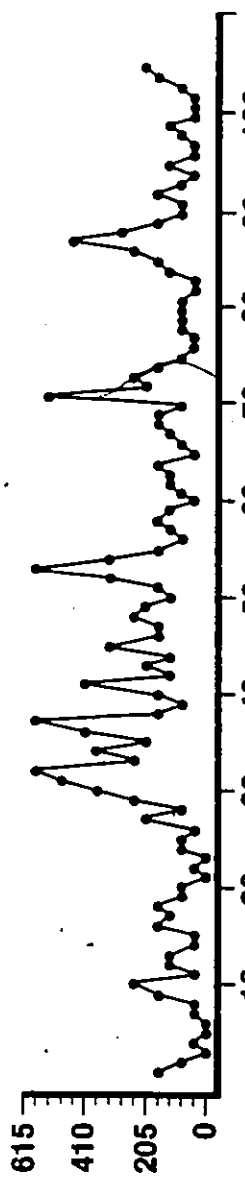
Ochromonas
(cells/ml)



Cryptomonas erosa
(cells/ml)



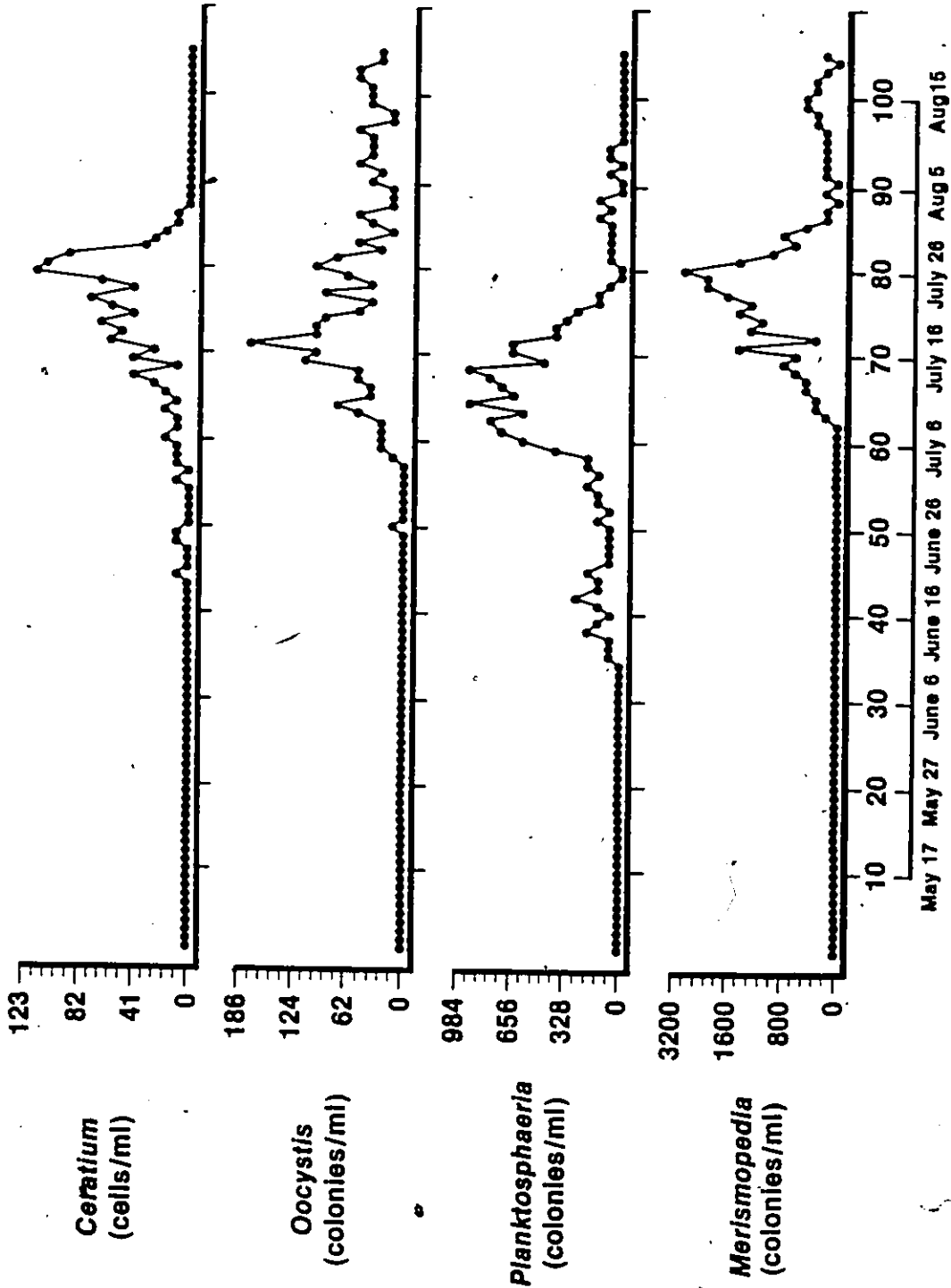
Cryptomonas ovata
(cells/ml)



Rhodomonas
(cells/ml)

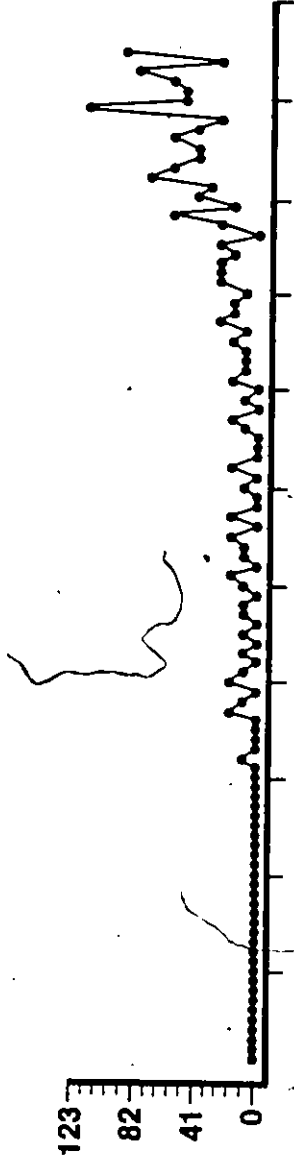
May 17 June 6 June 16 June 26 July 6 July 16 July 26 Aug 5 Aug 15

1981

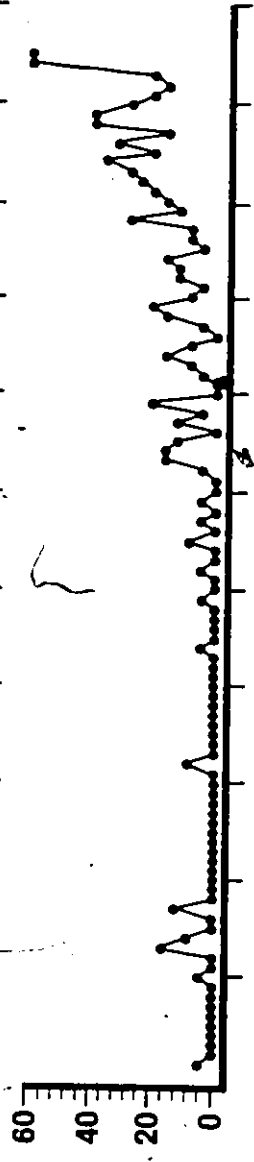


1981

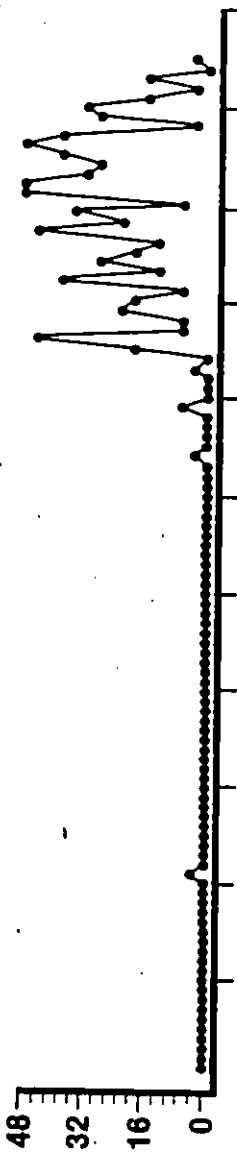
Gomphosphaeria
(colonies/ml)



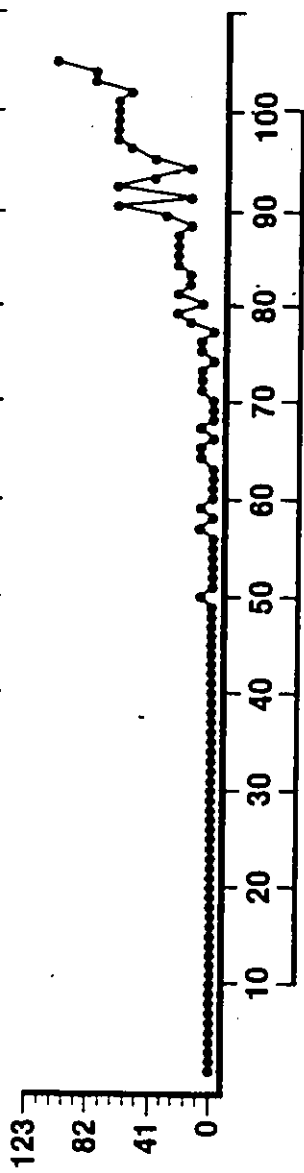
Coelosphaerium
(colonies/ml)



Lyngbya
(filaments/ml)



Microcystis
(colonies/ml)



May 17 May 27 June 6 June 16 June 26 July 6 July 16 July 26 Aug 5 Aug 15

1981

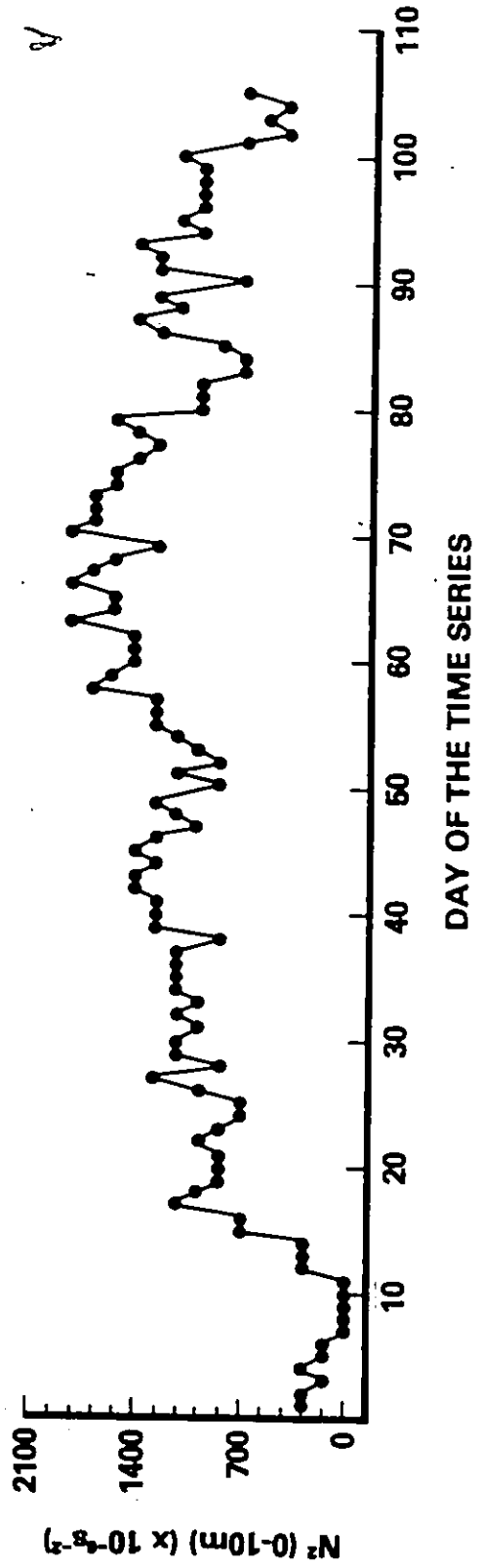
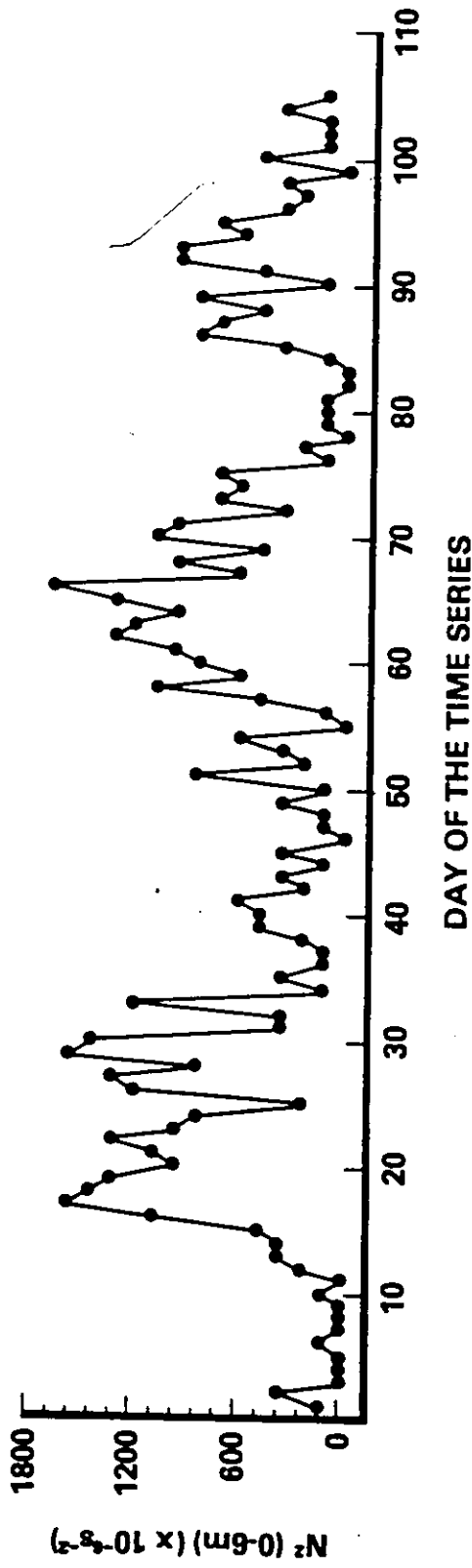
to August 5, increased again until August 15 and then decreased. Lyngbya began to decline in the second half of this period whereas Microcystis, Coelosphaerium and Gomphosphaeria continued to increase.

III-2-1-2 General description of environmental variables (May 8 to August 20, 1981)

Time series plots of environmental variables over the 105 days are shown in Figures 23 and 24. $N^2(0-6)m$ began to increase in mid-May but fluctuated between high and low values with a cycle of approximately 20-30 days throughout the daily time series. $N^2(0-10)m$ began to increase in mid-May, reached a maximum in late July, and then decreased. Wind speeds were higher in May ($\bar{x} = 8.7$ mph) and June ($\bar{x} = 8.8$ mph) than in July ($\bar{x} = 6.9$ mph) and August ($\bar{x} = 6.0$ mph). Richardson numbers were consistently low for the first 50 days and became more variable in the last 55 days. zeu/zm ratios were low ($< .7$) except for 4-5 weeks starting in mid-June. The proportion of illuminated and dark water that a phytoplankton cell is circulated in is a function of the zeu/zm ratio. As the zeu/zm ratio decreases, the proportion of dark water that a phytoplankton cell is circulated in, increases.

Surface water temperature began to increase in mid May, reached a maximum ($^{\circ}25$ C) and levelled off in early July. Surface pH was relatively constant (8.4 - 8.7) until July 26 and then decreased. The water at 10m became anoxic at the beginning of July and remained anoxic throughout the rest of the daily sampling period. NH_3 concentrations

Figure 23 - Time series plots (May 8 - August 20, 1981) of water column stability ($N^2(0-6)_m$ and $N^2(0-10)_m$ at station 1). Note the periodic fluctuations in $N^2(0-6)_m$.

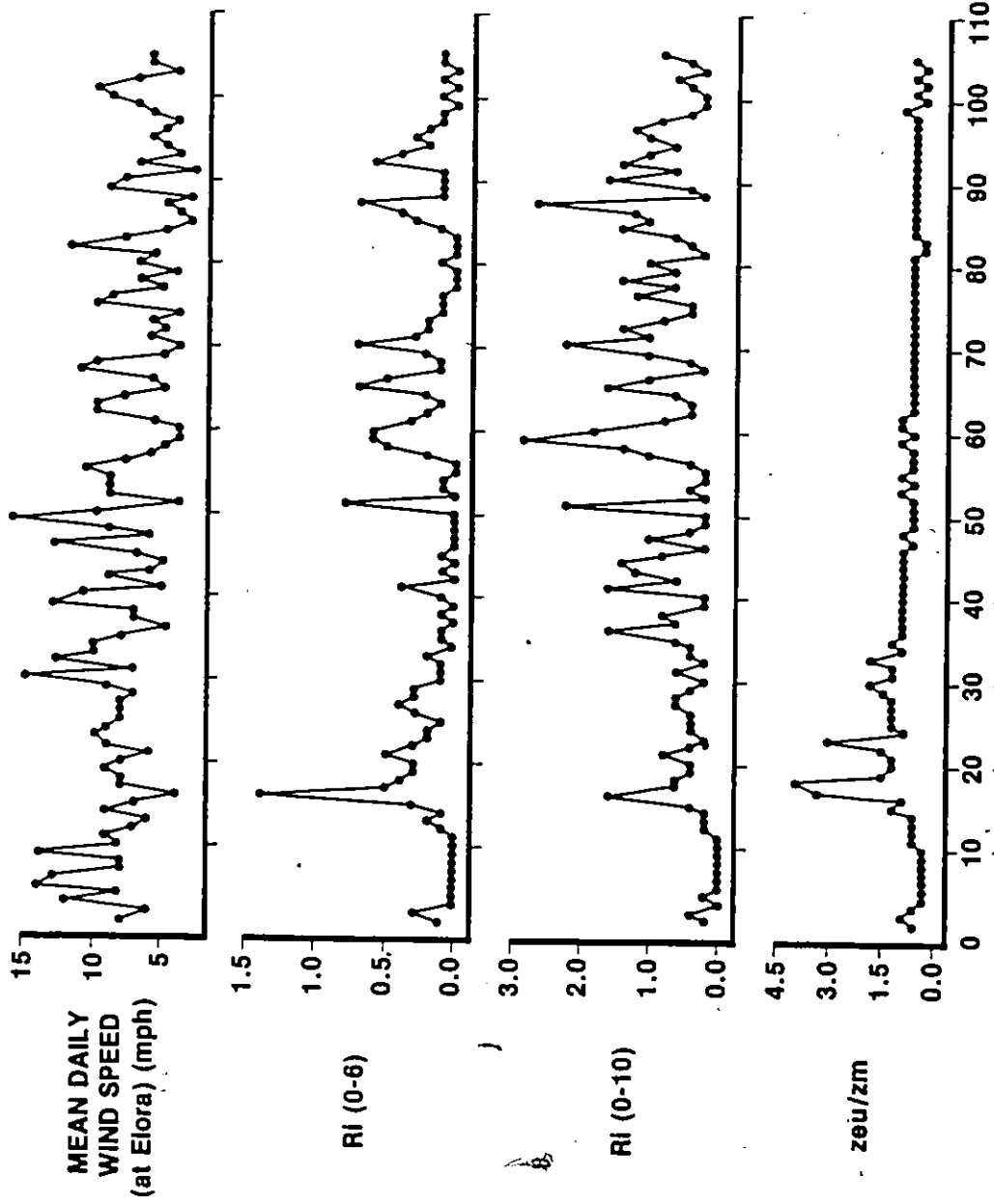


increased with the development of anoxic conditions at 10m.

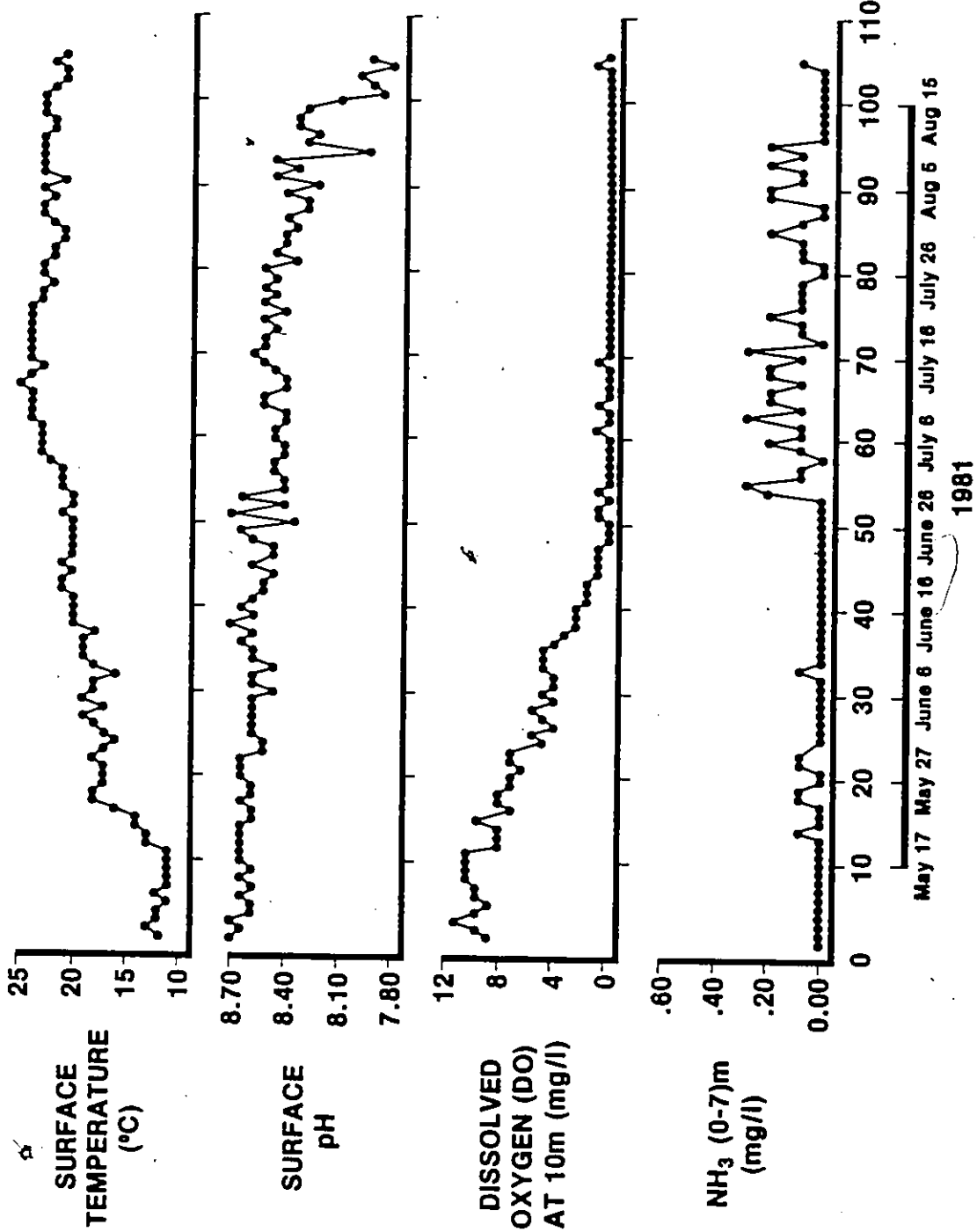
SRP and TP concentrations were highly variable throughout the sampling period. The average concentration of SRP in the integrated sample was 7.52 $\mu\text{g}/\text{l}$ (sd = 7.85). The average concentration of TP in the integrated sample was 24.8 $\mu\text{g}/\text{l}$ (sd = 11.4). Results from station-to-station and within station 1 depth comparisons for SRP and TP suggested that periods of vertical mixing and therefore increases in SRP and TP in the integrated sample occurred every 10-20 days. Power spectral estimates for SRP and TP dropped sharply after a period of 140 days. Four week and 2 week periodicities were evident in the power spectrum for SRP, but not for TP, obtained from the weekly data sets. Si levels were highest in mid to late August. The power spectrum for Si was roughly constant over the range of periods or frequencies examined. $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ concentrations declined at a steady rate (.01 mg/l/day) from an initial value of 1.35 mg/l down to .19 mg/l throughout the 105 days. The power spectral estimates for $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ decreased sharply after a period of 140 days and were then roughly constant with decreasing period.

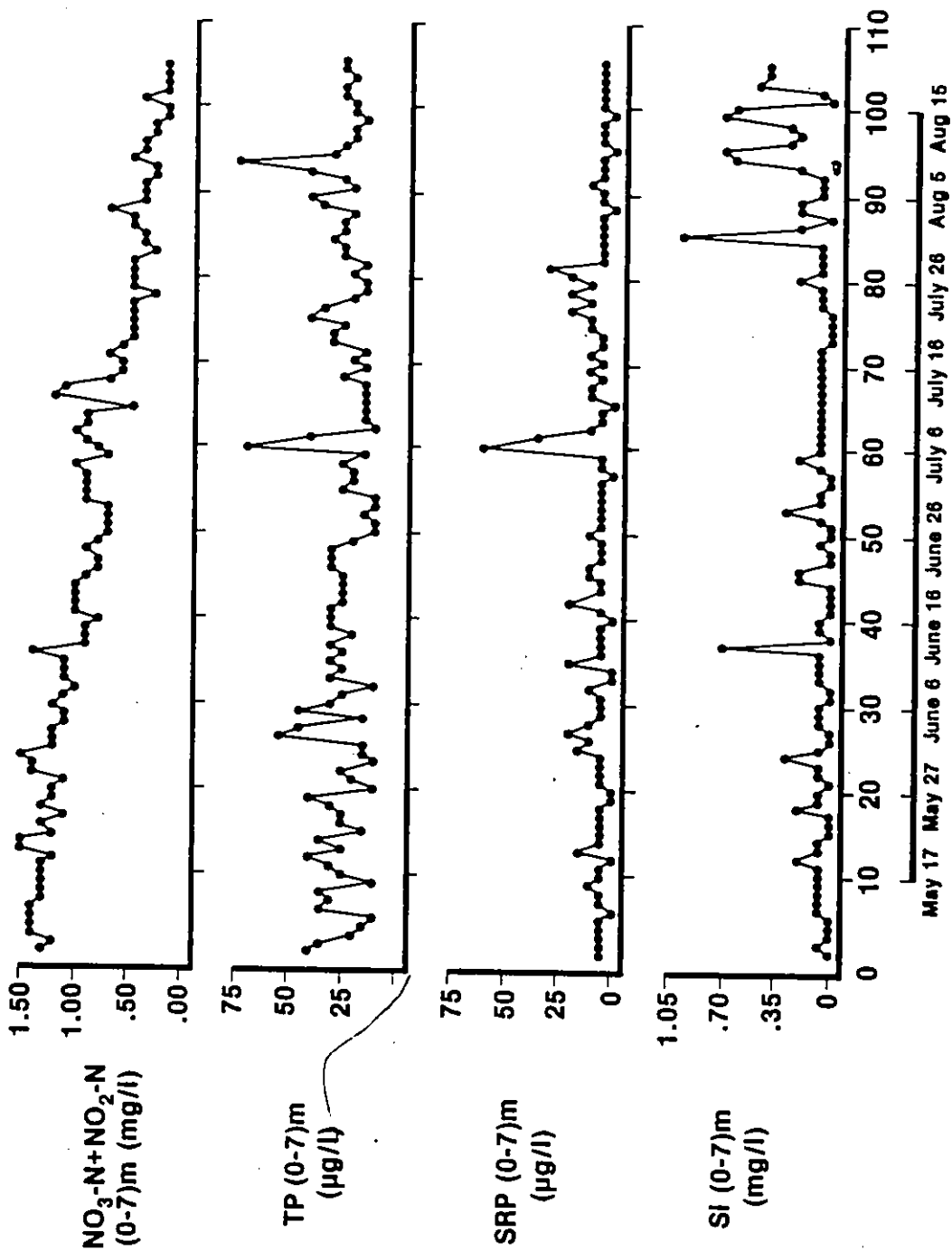
The lake level declined from May 8 through to July 5. A sharp increase back to the level observed on May 8 followed. Increased levels of SRP and TP occurred at this time. The lake level then continued to decline. Inflow rates were highest in mid-May, early July and late August. The flushing time of the lake ranged from 90 to 300 days with an average time of 165 days, suggesting that over the 105 days it may be

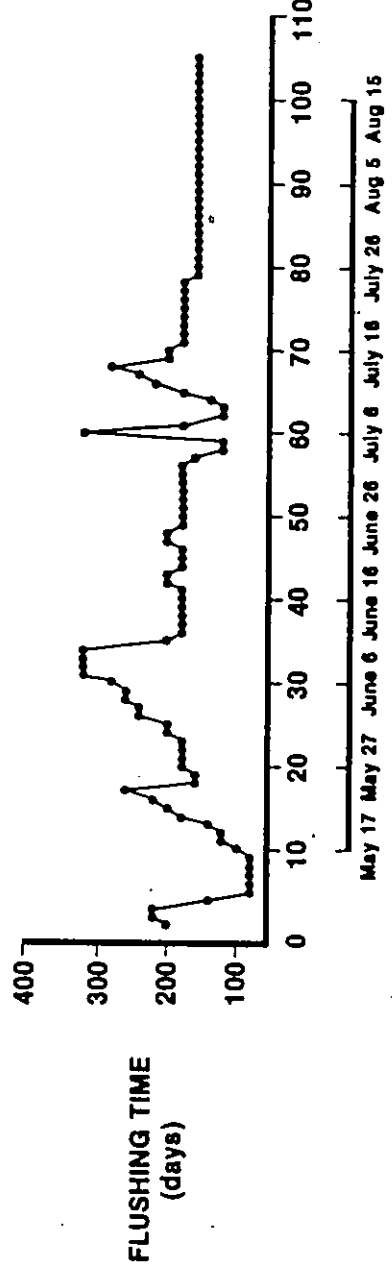
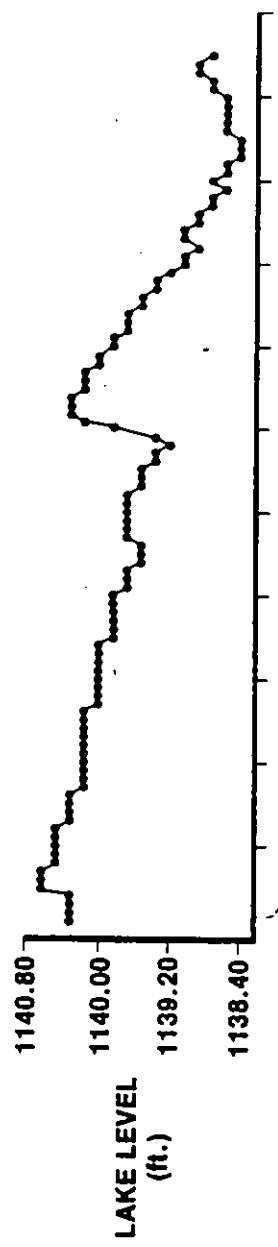
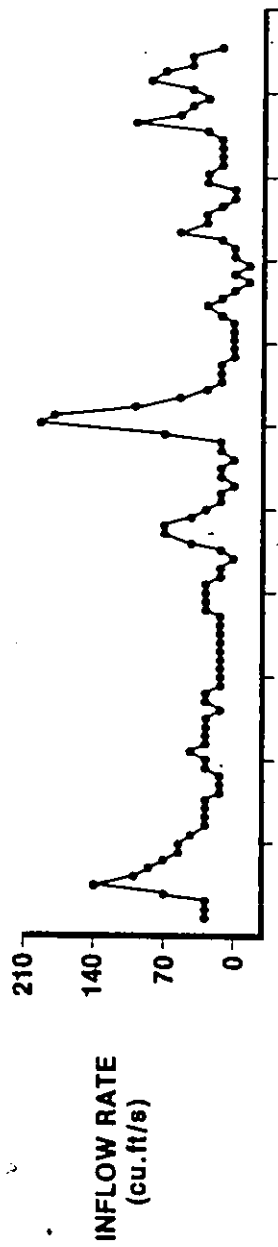
Figure 24 - Time series plots (May 8 - August 20, 1981) of
environmental variables.



May 17 May 27 June 6 June 16 June 26 July 6 July 16 July 26 Aug 5 Aug 15
1981







May 17 May 27 June 6 June 16 June 26 July 6 July 16 July 26 Aug 5 Aug 15

1981

ca

considered a closed basin.

III-2-1-3 Sedimentation trap catches

Accumulation rates of total phosphorus-

The rates of accumulation of TP in the upward facing trap at 2m were generally higher than those in the downward facing trap at this depth (Figure 25). Rates were highest in April to early May and in early August with a slight peak in mid-June. The same pattern was observed for the sedimentation traps placed at 4m. The rates of accumulation of TP in the upward facing trap at 10m did not show a clear seasonal pattern but rather varied up and down throughout the sampling period with a peak in mid-June. Increased rates of TP accumulation were observed in the downward facing traps at 10m in late July and August suggesting that resuspension of material from the bottom sediments was occurring at this time.

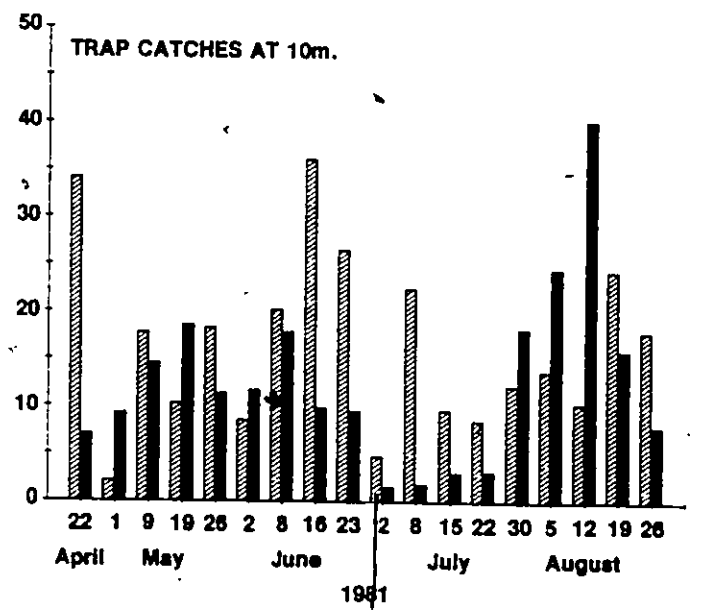
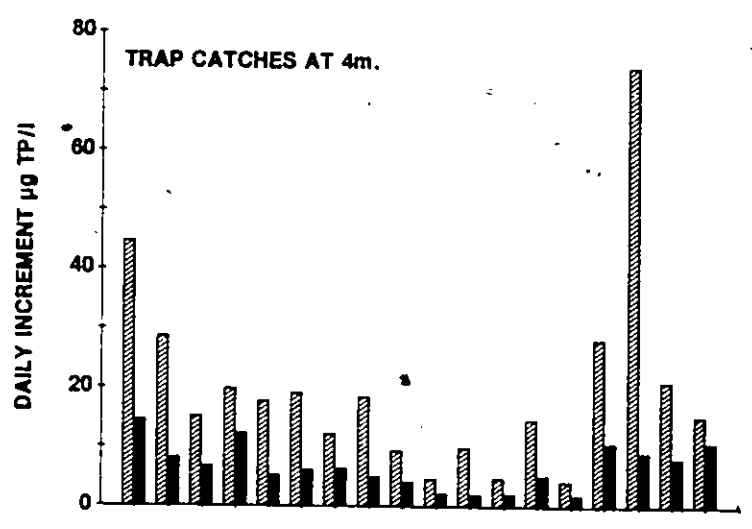
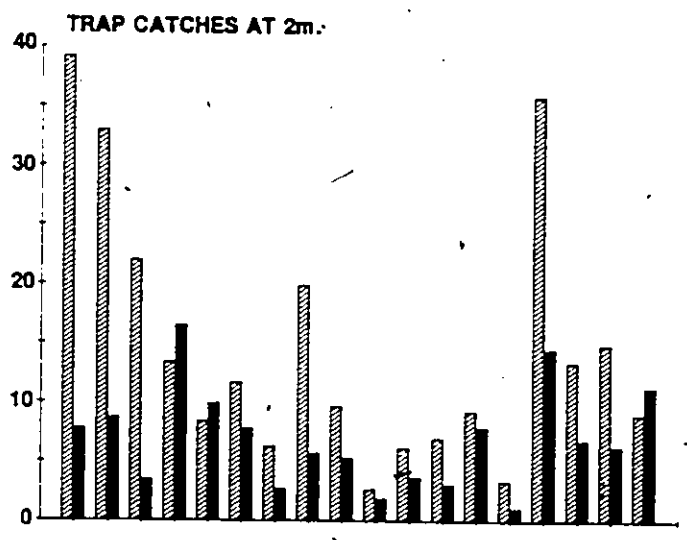
Phytoplankton counts-

Diatoms were most abundant in upward facing traps recovered from April 22 to mid-June. The trap catches of diatoms during this period are shown in Figures 26, 27, 28, 29. Catches increased in late August. Catches in downward traps were low except for some occasions in the traps at 4m. Green algae were most abundant in traps recovered in mid-July. Blue-green algae such as Microcystis, Gomphosphaeria and

Figure 25 - Accumulation rates of total phosphorus (TP) in the upward and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap
solid bar = downward facing trap





1961

Lyngbya were recovered in low amounts through June and early July and to a much greater extent in late July and August. Figures 31, 32, 33 show the trap catches of these blue-green algae in July and August. Aphanizomenon was recovered in traps from April 22 to mid-June (Figure 30) and late August as with diatoms.

Information obtained from the trap catches was used to calculate the sinking rates for some diatom species and the relative contribution of sedimentation to the loss of these species. Information from the trap catches of blue-green algae in the upward versus downward facing traps, was used to examine the vertical activity ranges of these algae. The depth range in which a particular species shows up in the traps may be interpreted as a vertical activity range (Reynolds, 1976b). Positively buoyant individuals would accumulate in the downward facing traps. The specific migration activities of floating versus sinking individuals of Microcystis, Gomphosphaeria and Lyngbya were calculated. The possibility of the recruitment of these algae from the bottom sediments was then examined.

Loss of Diatoms-

Sinking rates-

By the end of May, the abundances of diatoms were low to non-measurable (Figure 22). The sinking rates for four species of diatoms were calculated as outlined in the methods. V_t values (based on

trap catches) could only be calculated when there was a measurable (0-7)m concentration of the species in question at the time of trap removal. Vd values (not based on trap catches) could only be calculated when there was a decrease in the (0-7)m concentration of the algal species from the time the traps were set to the time the traps were removed. Results of Vt values (using the upward trap catch at 2m) and Vd values for some of the diatom species observed are given in Table 5.

Different species had different sinking rates. Rates for individual species varied from one trapping interval to the next. An increase in the sinking rates (both Vt and Vd) of Asterionella, Stephanodiscus and Melosira was observed from April 22 to May 1. A further increase in sinking rates was observed for Asterionella and Stephanodiscus from May 1 to May 9. Sinking rates for Cyclotella increased from April 16 to May 9.

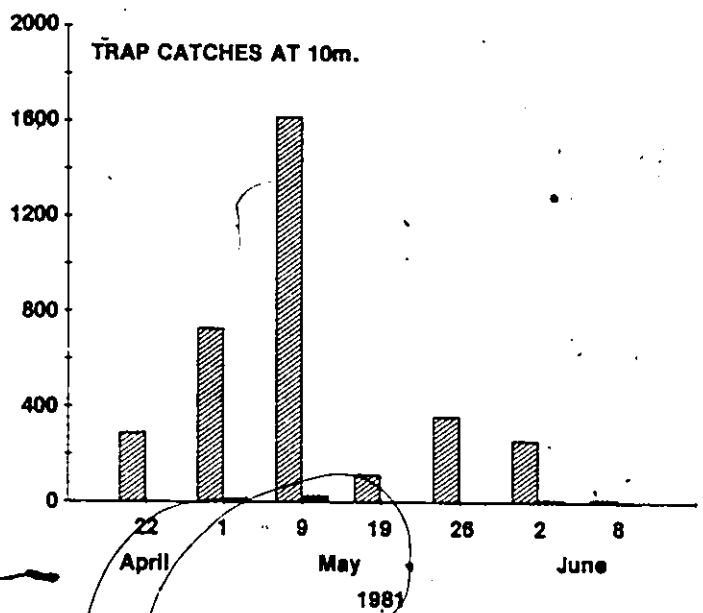
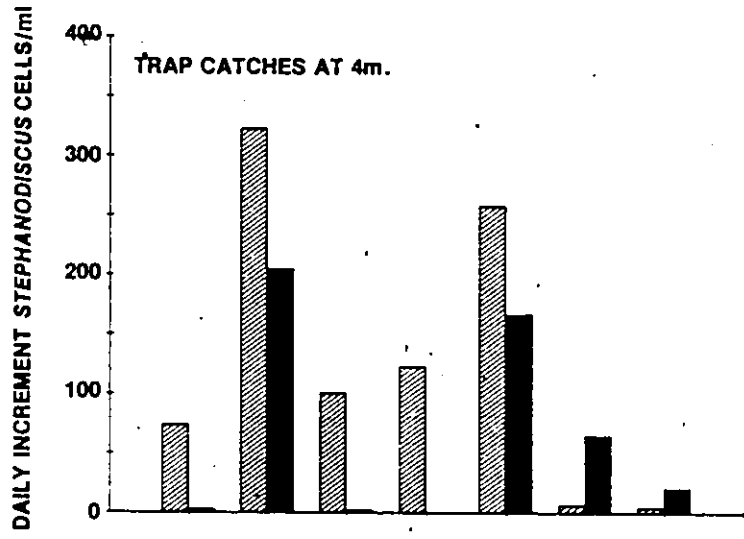
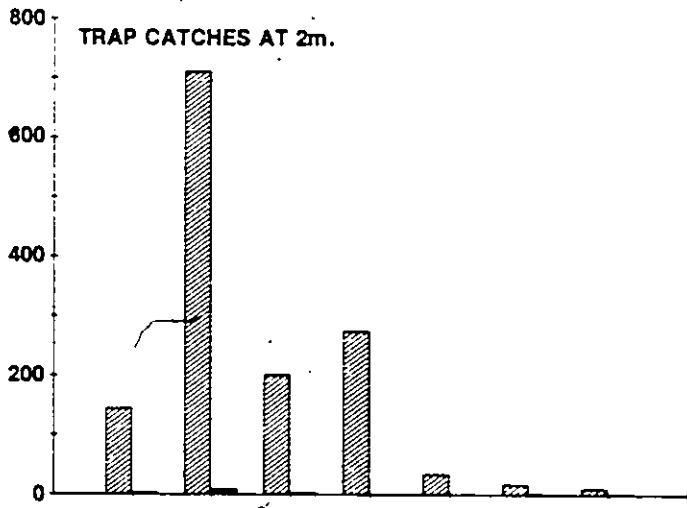
Different Vt values for a given species on a given date were obtained when the upward facing trap catches at the three different depths were used (Table 6) suggesting that sinking rates varied with depth. Very high sinking rates at the 10m depth were observed for Stephanodiscus, Asterionella and Melosira on May 9.

High trap catches of diatoms in the upward facing trap at 2m were generally followed by high trap catches in the upward facing trap at 10m, 1 trapping interval later (Figures 26, 27, 28, 29).

Figure 26 - Accumulation rates of Stephanodiscus cells in the upward and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap



22 April
1 May
9 May
19 May
26 May
2 June
8 June
1981

Figure 27 - Accumulation rates of Asterionella colonies in the upward and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap

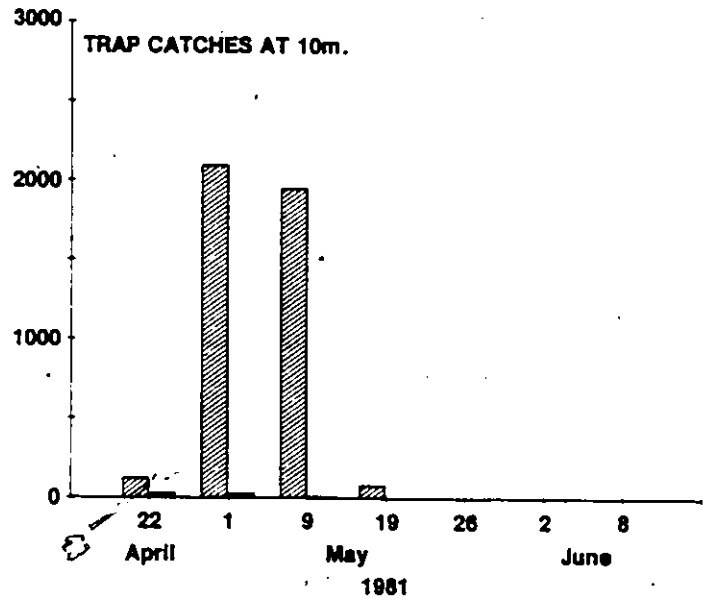
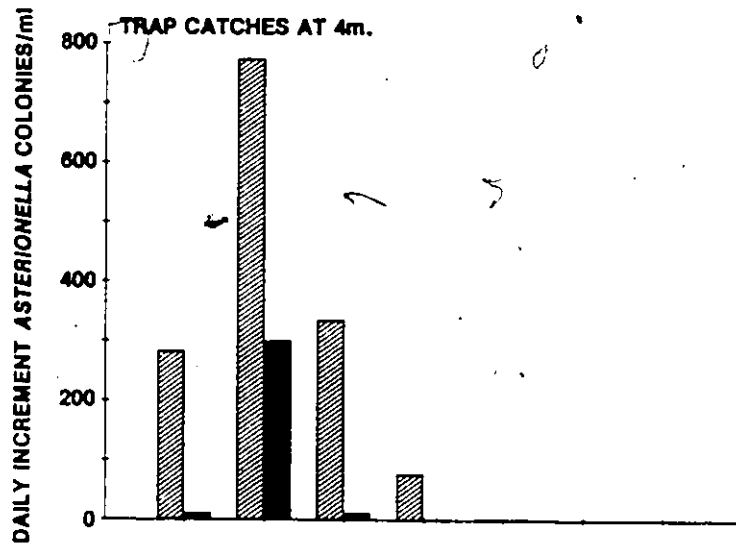
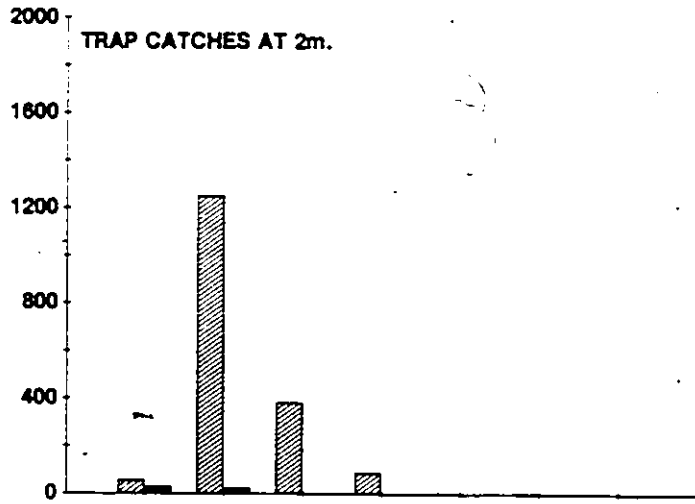


Figure 28 - Accumulation rates of Cyclotella cells in the upward
and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap

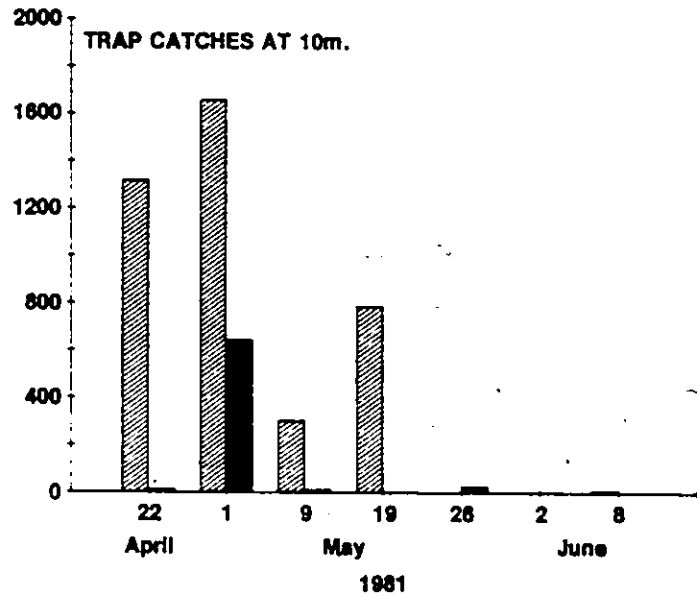
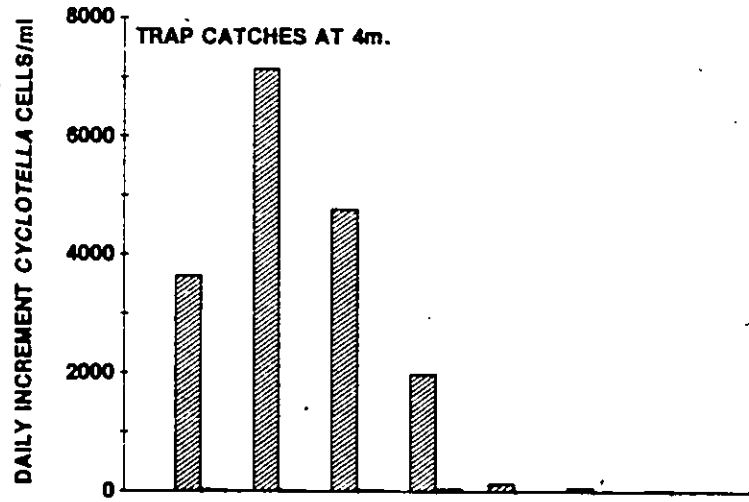
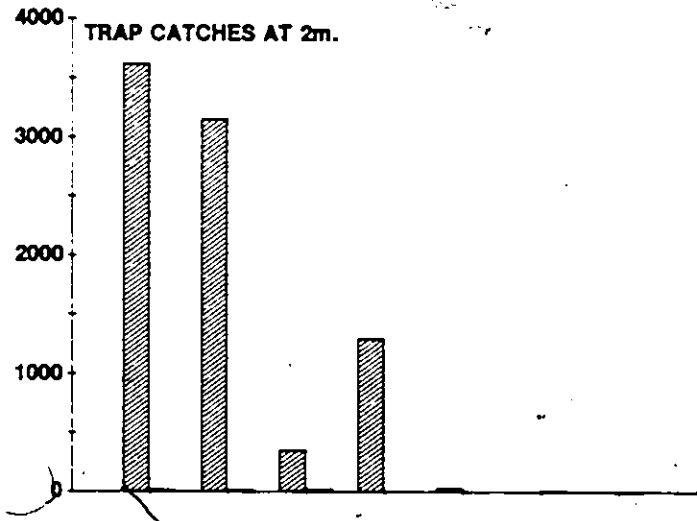


Figure 29 - Accumulation rates of Melosira filaments in the upward
and downward facing sedimentation traps at 2, 4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap

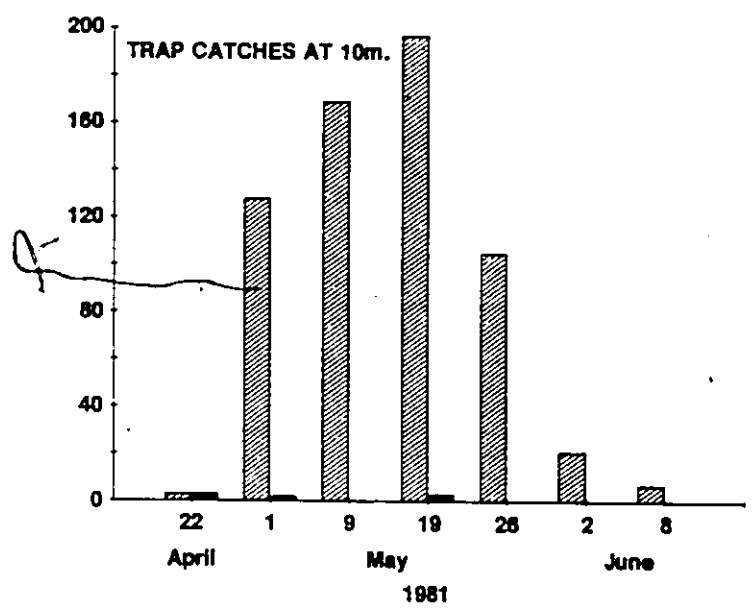
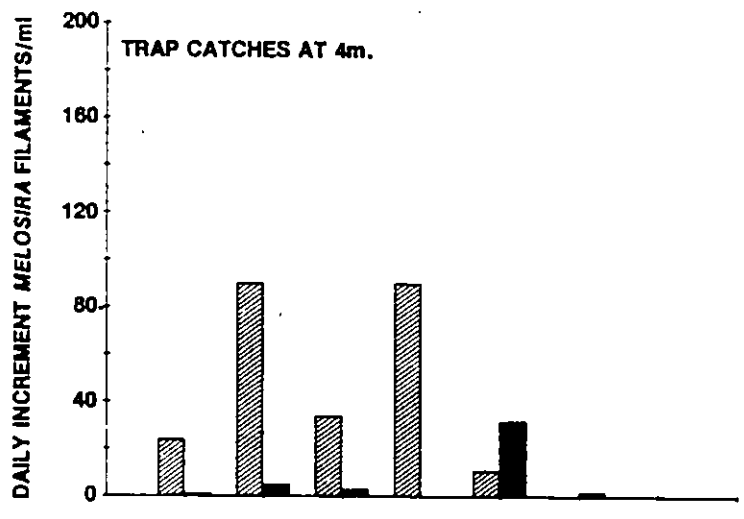
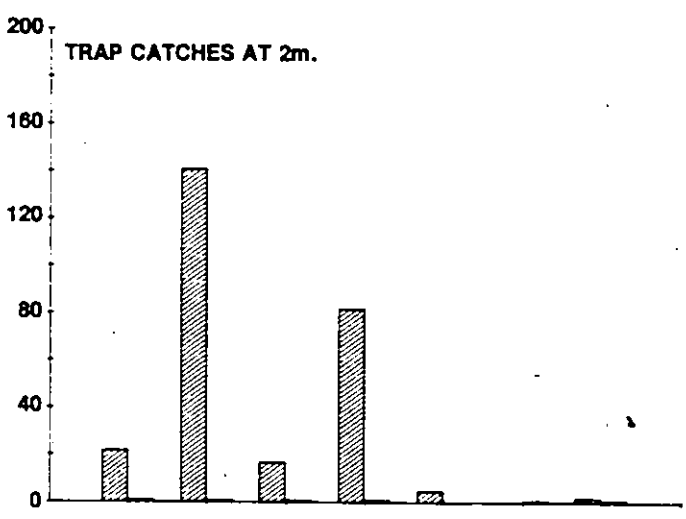


Table 5

Sinking rates from the upper 7m of Guelph Lake (Vd) and sinking rates into the upward facing trap at 2m (Vt), for the spring (1981) trapping periods (rates in m/day).

Period	<u>Stephanodiscus</u>		<u>Asterionella</u>		<u>Cyclotella</u>		<u>Melosira</u>	
	Vd	Vt	Vd	Vt	Vd	Vt	Vd	Vt
16-22 April		.12		.01	1.69	3.10		.15
22-1 May	.28	.85	.23	.35	1.90		1.08	4.20
1-9 May	1.60	1.93	2.28	3.66			.17	
9-19 May		1.34						4.90
19-26 May	2.99							

Sinking rates (Vt values) throughout the water column in the spring (1981) trapping period (rates in m/day).

Depth of trap (m)	<u>Stephanodiscus</u>			<u>Asterionella</u>			<u>Cyclotella</u>			<u>Melosira</u>		
	2	4	10	2	4	10	2	4	10	2	4	10
Period												
16-22 April	.1	.1	.2	.0	.1	.0	3.1	4.7	3.1	.2	.2	.0
22-1 May	.9	.4	.9	.3	.2	.6				4.2	2.7	3.8
1-9 May	1.9	1.0	15	3.7	3.2	18				.2	.4	1.7
9-19 May	1.3	.6	.6	.9	.7	.8				4.9	5.4	12

Cumulative sinking loss compared to maximum standing crop-

Results here (Table 7) show agreement between the proposed sedimentary fluxes of diatoms and the corresponding maximal standing crop. The proposed areal fluxes for Stephanodiscus and Melosira were 2 - 3 times greater than the corresponding maximal standing crop, but since the maximal standing crops may have been underestimated by weekly sampling, this is not unreasonable. The flux and crop estimates agreed more closely for Asterionella and Cyclotella. The maximum standing crop for the two green algae examined far exceeded the detected sedimentary flux. The maximum standing crop of Lyngbya was also much greater than the detected sedimentary flux.

Vertical Activity Ranges of Blue-Green Algae

Aphanizomenon-

Filaments were recovered almost exclusively in the downward facing traps suggesting that the majority of the filaments, if not all, were positively buoyant (Figure 30, April 22 to mid-June). Catches in the downward facing trap at 2m were not significantly correlated ($r^2 = .276$, $p > .10$) to the (0-7)m concentration of filaments at the time of trap removal, whereas the trap catches in the downward facing trap at 4m ($r^2 = .991$, $p < .005$) and the downward facing trap at 10m ($r^2 = .967$, $p < .01$) were significantly correlated to the (0-7)m concentration of filaments. Catches in the downward facing trap at 2m were correlated (r^2

Table 7

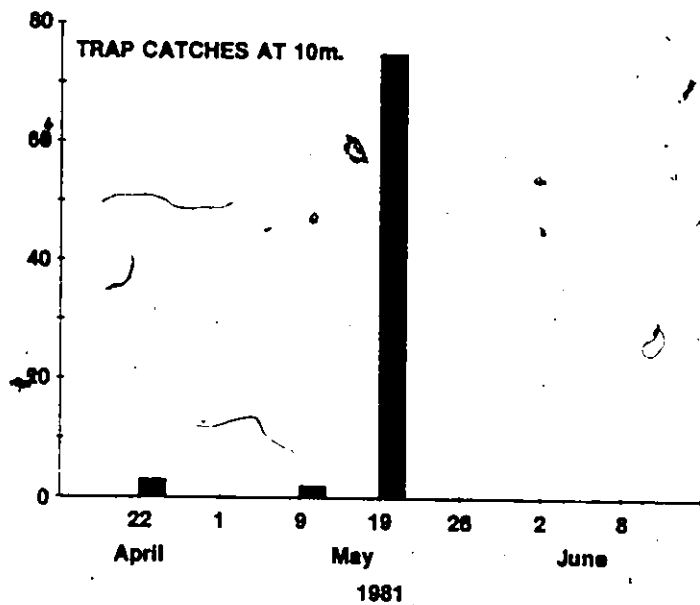
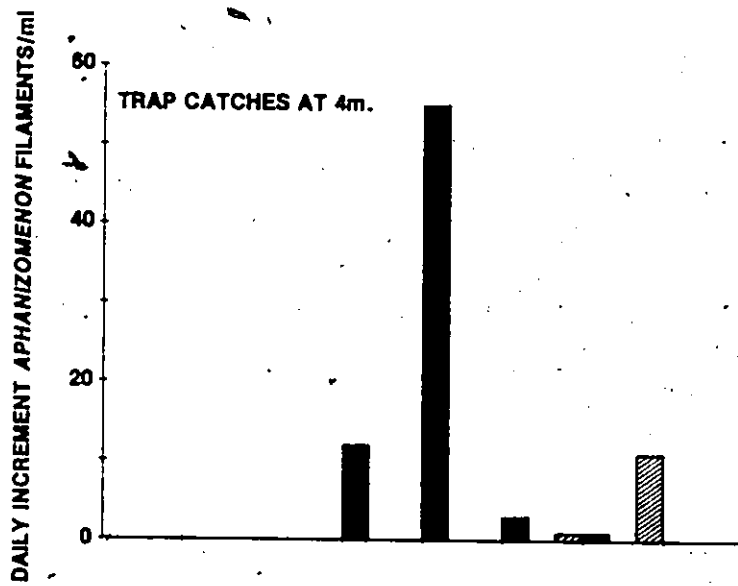
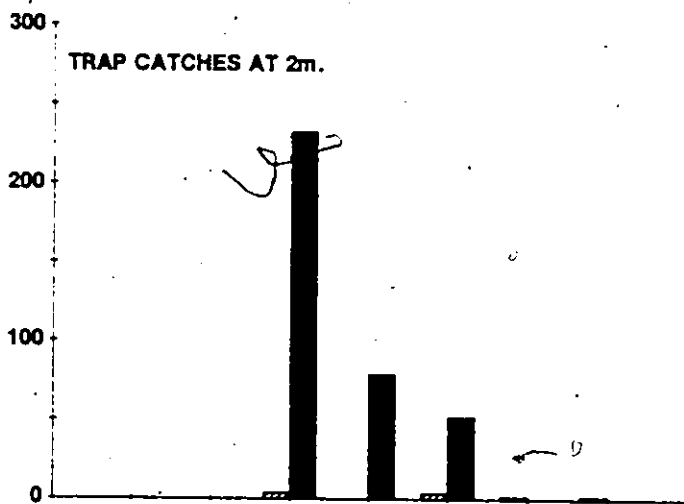
Cumulative sinking loss (cells/cm² in upward sedimentation trap
(at 10m) compared to maximum standing crop
(cells/cm²) at station 1.

Species	Cumulative sinking loss (C)	Maximum standing crop (P)	C/P as a %
<u>Stephanodiscus</u>	6.0×10^5	2.9×10^5	207
<u>Asterionella</u>	8.6×10^5	11.6×10^5	74
<u>Melosira</u>	9.5×10^4	3.4×10^4	282
<u>Cyclotella</u>	3.6×10^6	4.3×10^6	84
<u>Planktosphaeria</u>	4.6×10^3	943×10^3	.5
<u>Oocystis</u>	9.7×10^3	168×10^3	6
<u>Lyngbya</u>	1.1×10^3	336×10^3	.3

Figure 30 - Accumulation rates of Aphanizomenon filaments in the
upward and downward facing sedimentation traps at 2,4 and
10m.

hatched bar = upward facing trap

solid bar = downward facing trap



= .914, $p < .10$) to the total catch in the downward facing traps at 4m and 10m at the next trapping interval. These results suggested that Aphanizomenon filaments appeared near the level of the first trap prior to the levels of the second and third traps and prior to the increase in the (0-7)m concentration of filaments.

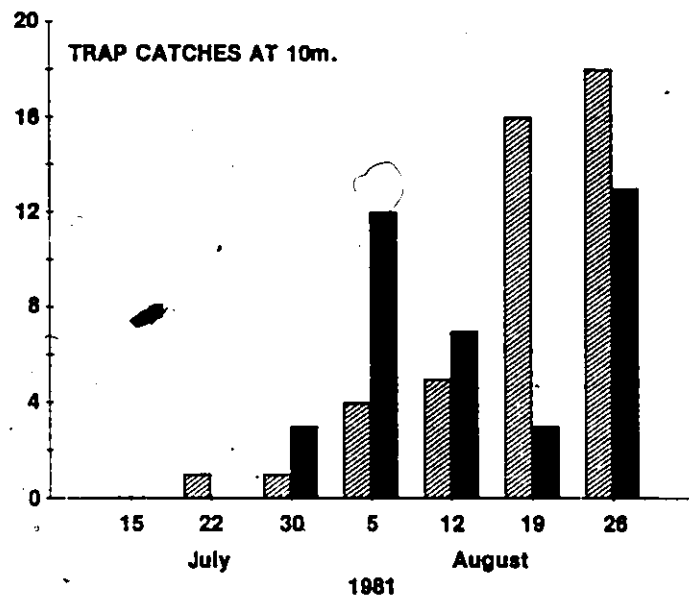
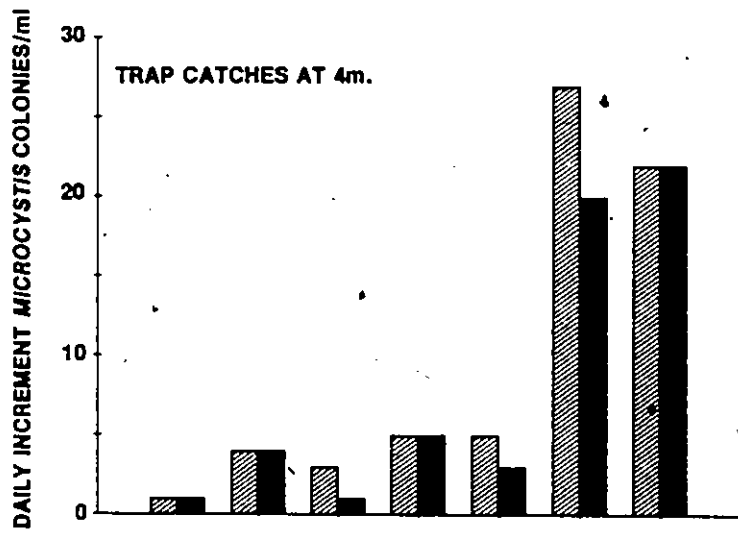
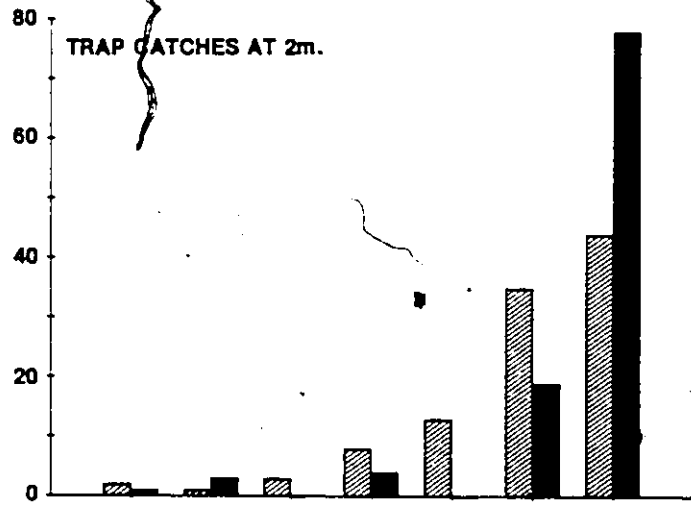
Microcystis-

Colonies were recovered in greatest amounts in late July and August (Figure 31). Since daily phytoplankton counts were done for this time period, the catches in the downward traps were compared to the mean (0-7)m concentration of colonies during the trapping interval. The catches in the downward facing trap at 2m ($r^2 = .883$, $p < .05$) and the downward facing trap at 4m ($r^2 = .917$, $p < .02$) were significantly correlated to the mean concentration of colonies during the trapping interval whereas the trap catches in the downward facing trap at 10m ($r^2 = .588$, $p > .10$) were not. There did not appear to be a clear shift from high trap catches in the downward facing trap at 10m to high trap catches in the downward facing trap at 2m or vice versa. Specific migration rates were calculated (Table 8). High specific migration rates for floating and sinking colonies at 10m were seen on August 5. Floating rates exceeded sinking rates at this depth suggesting that over this sampling interval Microcystis colonies were recruited from the sediments.

Figure 31 - Accumulation rates of Microcystis colonies in the upward and downward facing sedimentation traps at 2, 4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap



Gomphosphaeria-

Colonies were recovered in greatest amounts in late July and August (Figure 32). The total downward trap catches were significantly correlated ($r^2 = .954$, $p < .02$) to the mean (0-7)m concentration of colonies during the trapping interval. The trap catches in the downward facing trap at 10m alone, were correlated to the downward facing trap catches at 2m ($r^2 = .956$, $p < .02$), those at 4m ($r^2 = .928$, $p < .05$) and to the mean colony concentration of colonies ($r^2 = .852$, $p < .10$) during the next trapping interval. These results suggest an upward shift of colonies. High specific migration activities were seen from August 12 through to August 19, especially for floating colonies, again suggesting an upward shift of colonies from the sediments.

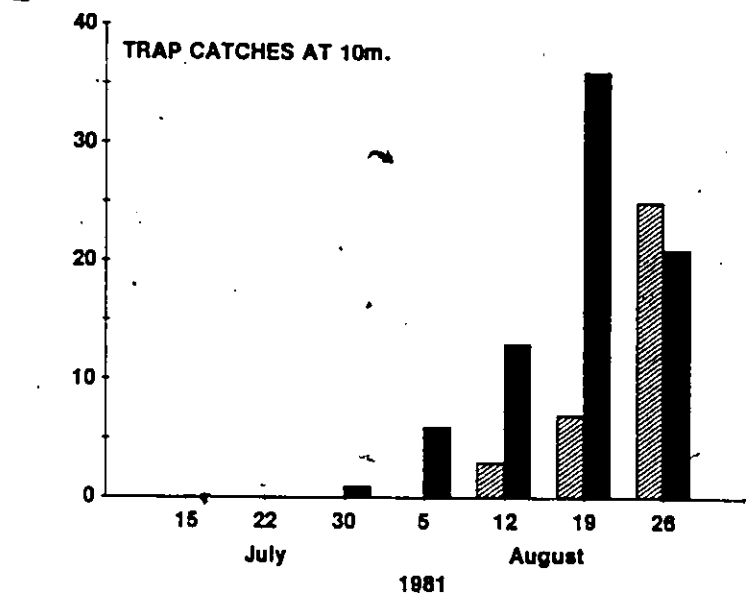
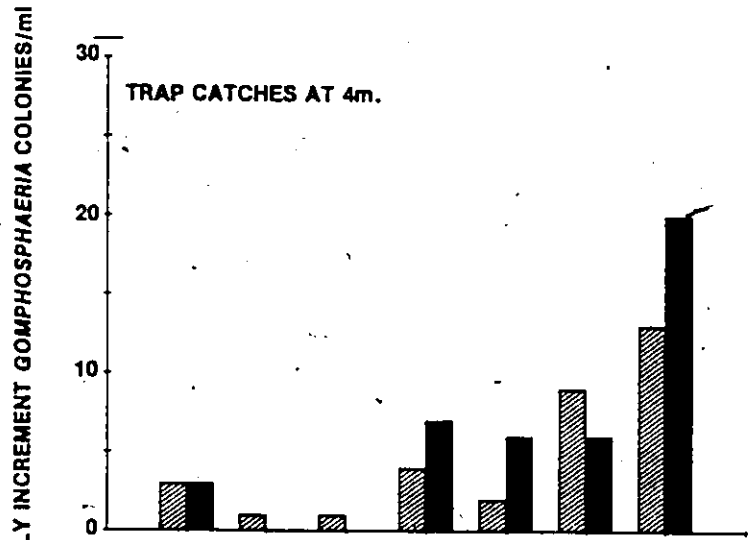
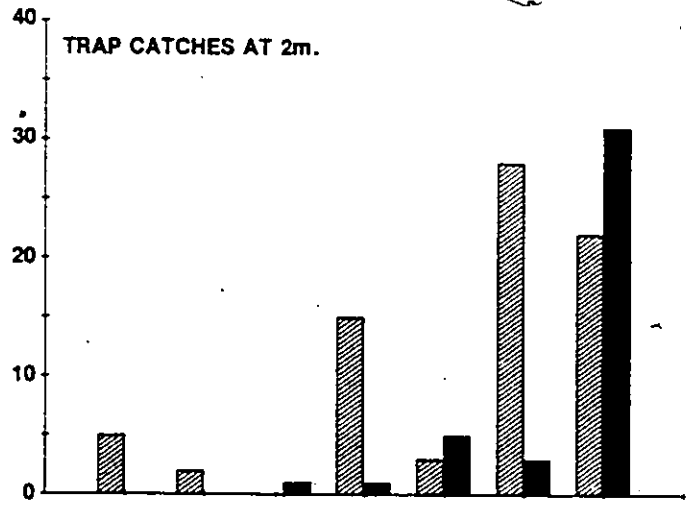
Lyngbya-

Filaments were recovered in greatest amount in late July and August (Figure 33). Trap catches in the downward trap at 2m ($r^2 = .093$) were not significantly correlated to the (0-7)m concentration of filaments during the trapping interval whereas the catches in the downward trap at 4m ($r^2 = .938$, $p < .05$) and the downward trap at 10m ($r^2 = .975$, $p < .01$) were significantly correlated to the mean (0-7)m concentration of filaments. High specific migration rates occurred at 10m from July 30 through to August 19, with floating rates exceeding sinking rates on July 30 and August 12, suggesting recruitment of filaments from the bottom sediments. Sinking rates exceeded floating

Figure 32 - Accumulation rates of Gomphosphaeria colonies in the upward and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap



U

2

Figure 33 - Accumulation rates of Lyngbya filaments in the upward and downward facing sedimentation traps at 2,4 and 10m.

hatched bar = upward facing trap

solid bar = downward facing trap

✓

1

✓

+

Q

✓

✓

✓

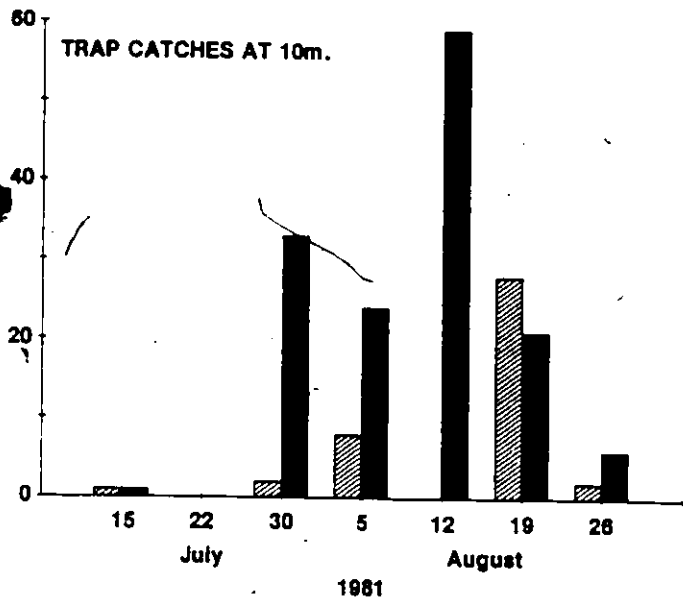
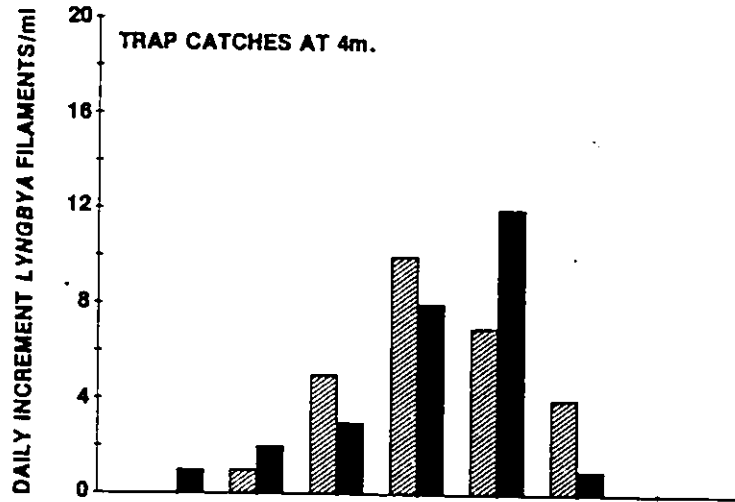
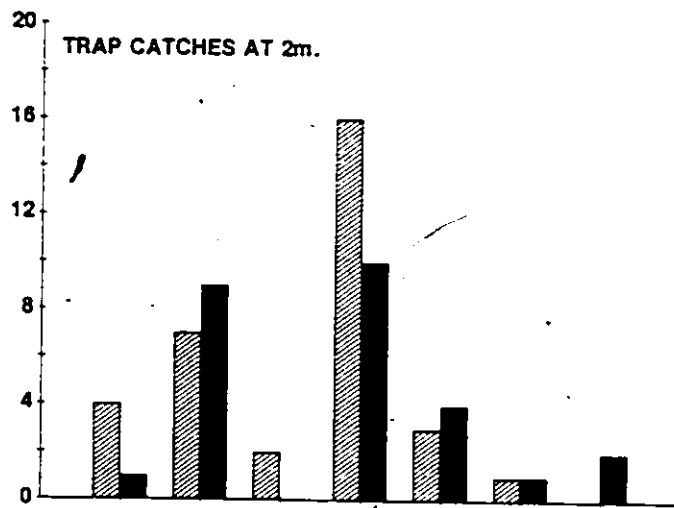


Table 8

Specific migration activities of three summer blue-green algae at 2, 4 and 10m (station 1) during the late summer (1981) trapping periods.

Depth (m)	Date of trap removal				
	July 22	July 30	August 5	August 12	August 19
<u>1) Microcystis</u>					
Sinking					
2	.1	.3	.7	.2	.6
4	1.0	.4	.2	.1	.2
10	.3	.1	4.0	.4	.4
Floating					
2	.1	.01	.3	.02	.3
4	.3	.1	.2	.1	.2
10	.03	.2	12.0	.6	.1
<u>2) Gomphosphaeria</u>					
Sinking					
2		.2	1.3	.2	.5
4		1.0	1.0	.04	.3
10		.1	.1	.4	1.8
Floating					
2		.02	.1	.3	.1
4		.02	1.8	.1	.2
10		.02	.5	1.6	9.0
<u>3) Lyngbya</u>					
Sinking					
2	7.0	.03	1.3	.04	1.0
4	.1	.3	.3	.1	4.0
10	0	.1	2.0	0	28.0
Floating					
2	9.0	.01	.8	.1	1.0
4	.3	.1	.2	.2	1.0
10	0	1.6	6.0	59.0	21.0

rates at 10m on August 19 suggesting a net loss of filaments to the sediments at this time.

Summary

Information from the sedimentation trap catches was used to determine sinking rates of diatoms and to estimate the relative contribution of sedimentation to the loss of these species. Sinking rates varied with time and depth. The results showed good agreement between the proposed sedimentary fluxes of diatoms and the corresponding maximal standing crop.

Information from the trap catches was also used to examine the possibility of recruitment of summer blue-green species from the sediments. The high specific migration rates of floating colonies of Microcystis and Gomphosphaeria and of Lyngbya filaments at 10m suggested that in Guelph Lake a fair number of colonies and filaments were recruited from the sediments. The high rates of accumulation of TP in the downward facing trap at 10m provided further evidence that resuspension of material from the sediments occurred at this time.

III-2-1-4 Cross-correlations

Influence of water column stability (as N^2) on chlorophyll, diversity and rate of community change.

Time series of $N^2(0-6)m$ or $N^2(0-10)$ were cross-correlated to time series of integrated chlorophyll-a, phytoplankton diversity and the rate of phytoplankton community change. It is not possible to statistically interpret the cross-correlation function obtained when 2 non-stationary data sets are compared. Therefore, the time series were modelled (as outlined in section 11-10-2) to obtain stationary residuals. Significant cross-correlations at positive lags suggest that changes in water column stability lead changes in the second variable. Significant cross-correlations at negative lags suggest that changes in water column stability lag changes in the second variable.

Cross-correlations between non-stationary $N^2(0-6)m$ or $N^2(0-10)m$ and non-stationary integrated chlorophyll were negative at lower negative or positive lags (Figure 34a,34b). Significant negative cross-correlations between stationary residuals of $N^2(0-6)m$ and stationary residuals of integrated chlorophyll were found at lags of 1 and 3 days (Figure 34c). Cross-correlations between stationary residuals of $N^2(0-10)m$ and stationary residuals of integrated chlorophyll were not significant (Figure 34d).

Cross-correlations between non-stationary $N^2(0-10)m$ and

Figure 34a Cross-correlation estimates between non-transformed
 $N^-(0-6)m$ and non-transformed integrated, chlorophyll a.

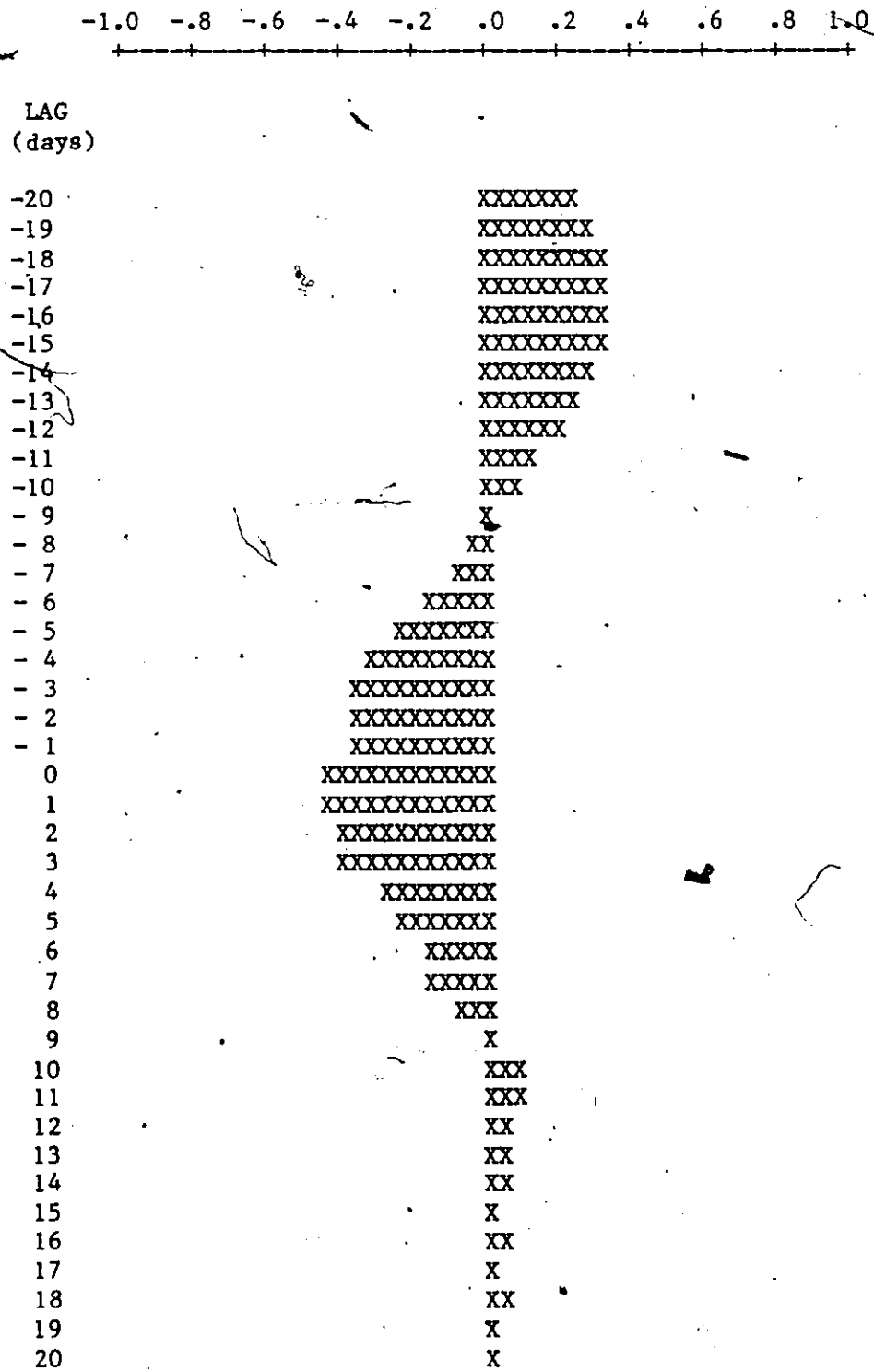


Figure 34b Cross-correlation estimates between non-transformed $N^2(0-10)m$ and non-transformed integrated chlorophyll
a.

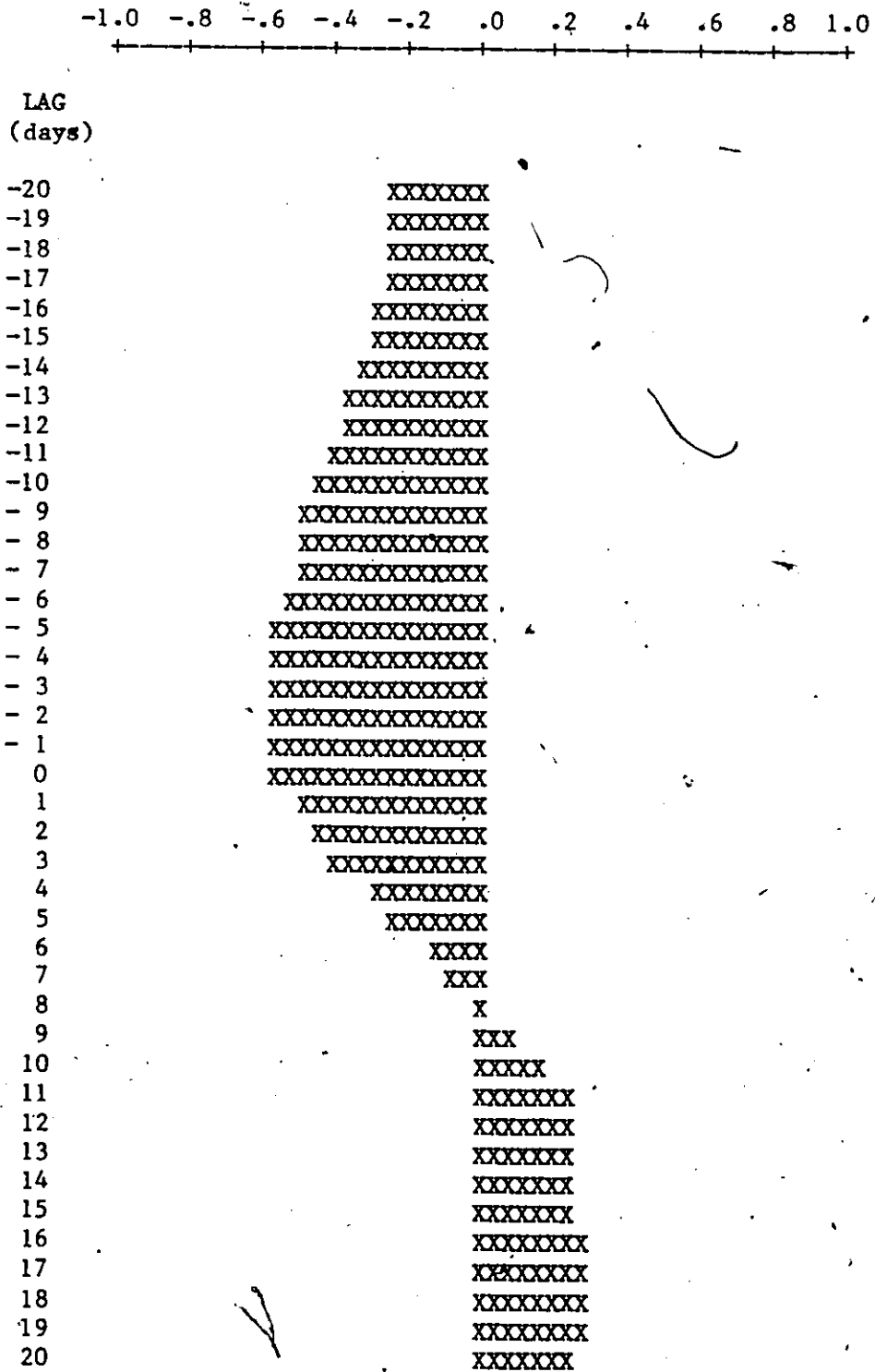
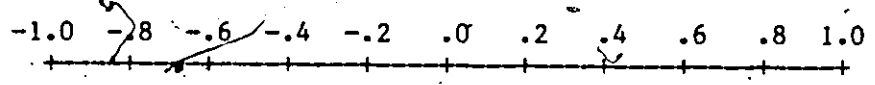


Figure 34c Cross-correlation estimates between N²(0-6)m ARIMA (101) residuals and integrated chlorophyll a loge ARIMA (101) residuals (at k = 0, for p < .05, r² > .195, at k = 20, for p < .05, r² > .217).



LAG
(days)

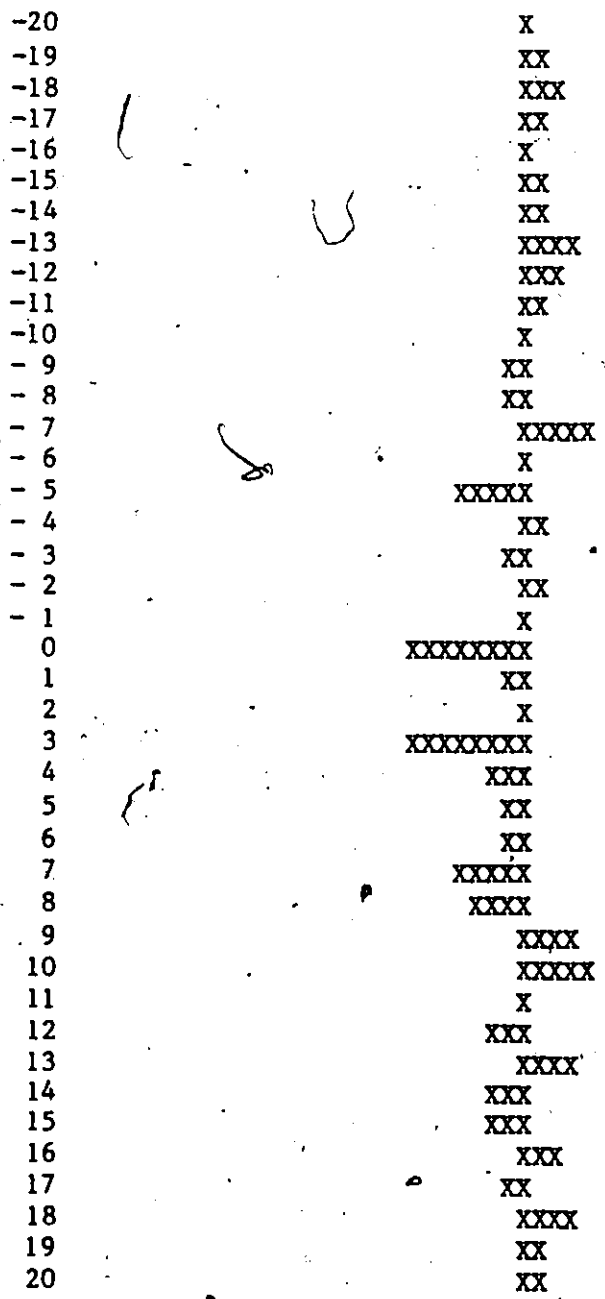
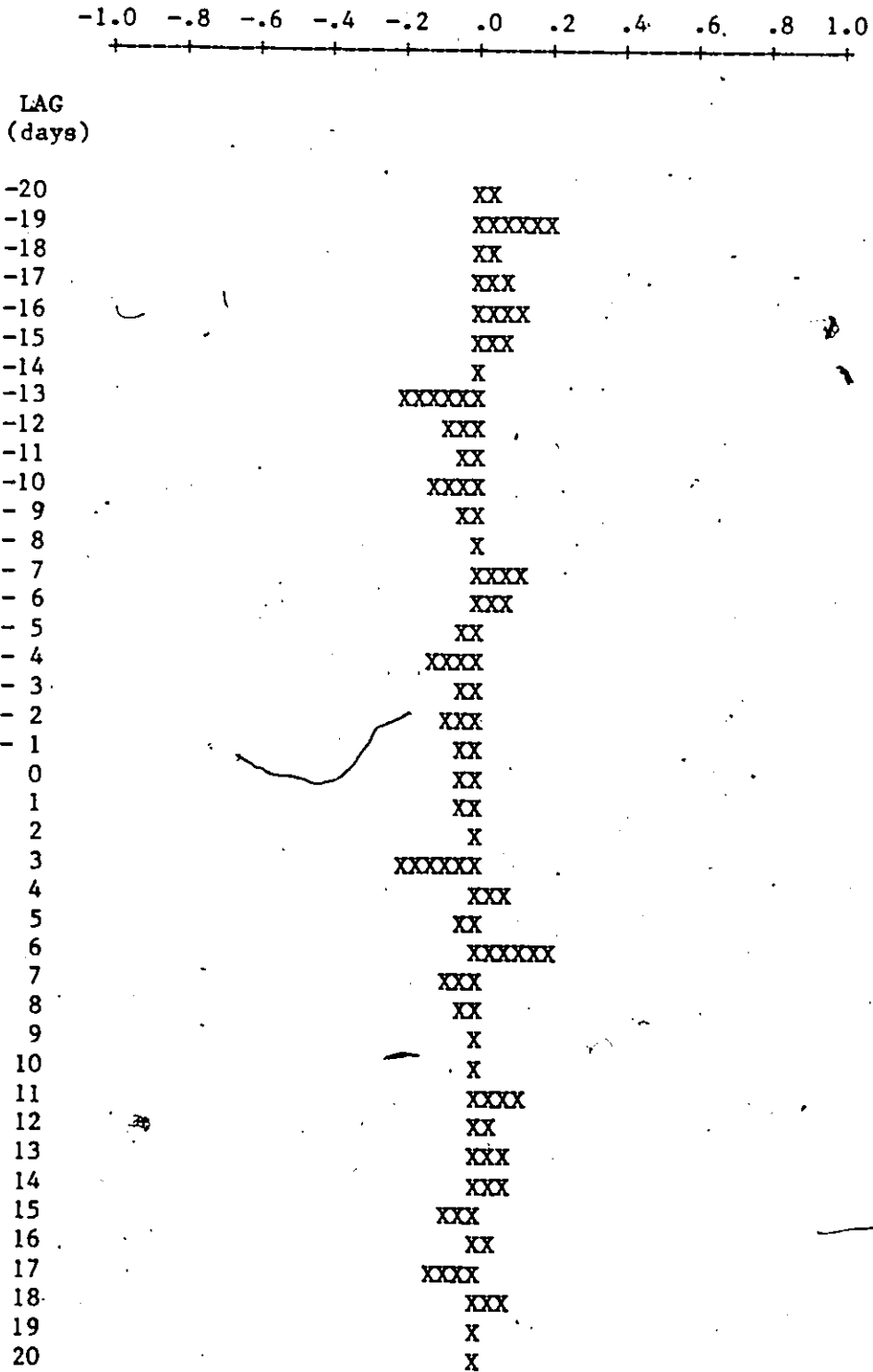


Figure 34d Cross-correlation estimates between $N^2(0-10)m$ ARIMA (111) residuals and integrated chlorophyll a ARIMA (111) residuals (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).



non-stationary diversity were positive with a maximum value at a lag of -2 (Figure 35a). Similarly, the cross-correlations between stationary residuals of $N^2(0-10)_m$ and stationary residuals of diversity showed a maximum value at a lag of -2 ($r^2 = .246$, for $p < .05$, $r^2 > .198$) (Figure 35b). This suggests that changes in $N^2(0-10)$ actually lagged, rather than led, increases in diversity by 2 days.

Cross-correlations between non-stationary $N^2(0-6)_m$ and non-stationary rate of phytoplankton community change were positive at lower negative and positive lags with a maximum at a lag of -5. However, the cross-correlations between stationary residuals of $N^2(0-6)_m$ and stationary residuals of the rate of community change were not significant (Figure 36a). Cross-correlations between non-stationary $N^2(0-10)_m$ and non-stationary rate of community change were positive at negative lags and negative at longer positive lags with a maximum at a lag of 14 days. Significant cross-correlations between stationary residuals of $N^2(0-10)$ and stationary residuals of the rate of community change were observed at lags of 5 ($r^2 = -.280$, for $p < .05$, $r^2 > .200$) and 8 days ($r^2 = -.256$, for $p < .05$, $r^2 > .202$) (Figure 36b). This suggests that increases in $N^2(0-10)_m$ led decreases in the rate of community change by 5-8 days.

Loss of diatoms-

The decline of the diatom populations coincided with an increase in N^2 . Cross-correlations between non-stationary $N^2(0-6)_m$ and

Figure 35a Cross-correlation estimates between non-transformed $N^2(0-10)m$ and non-transformed phytoplankton diversity (105 days).

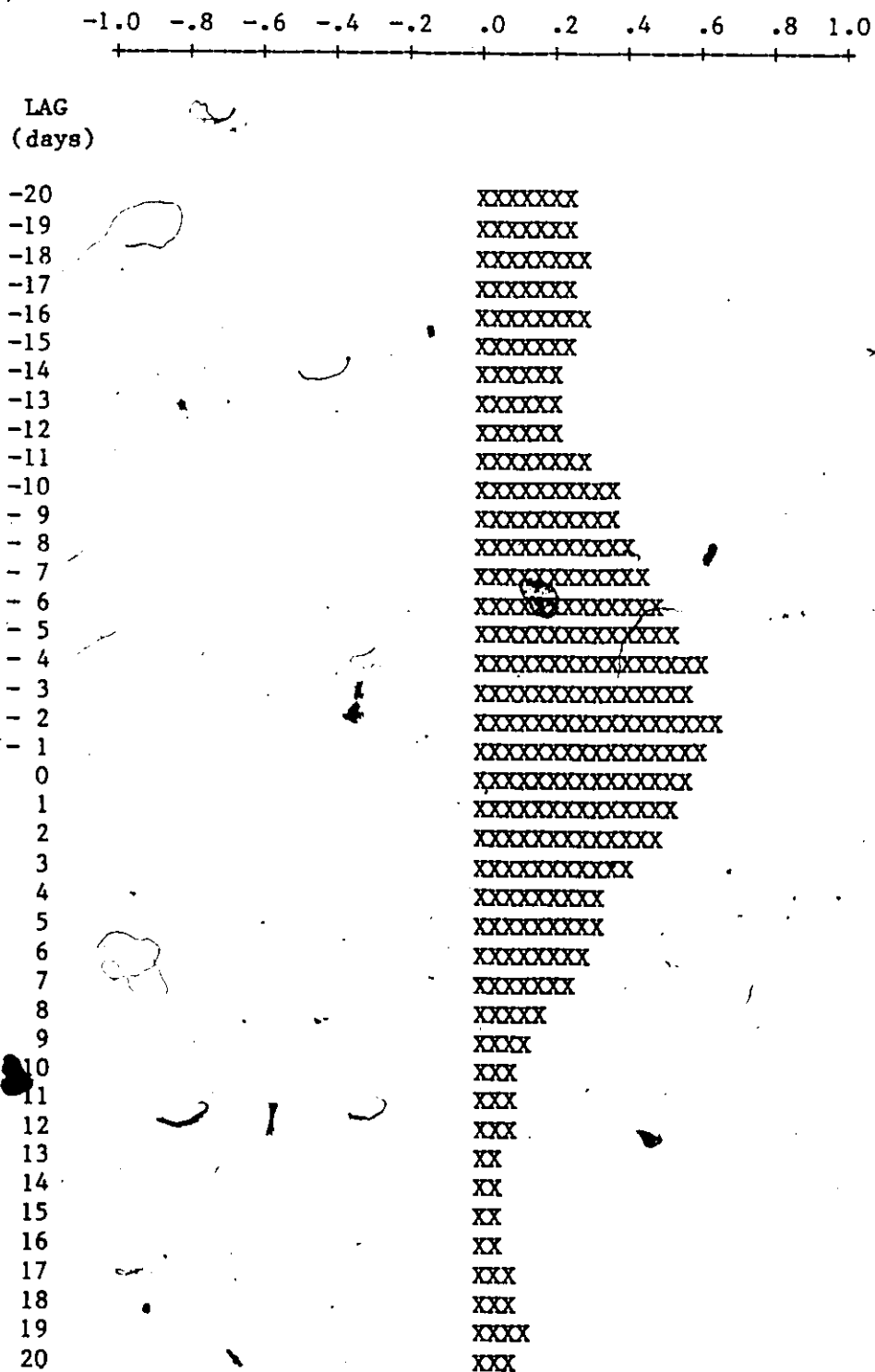


Figure 35b Cross-correlation estimates between $N^2(0-10)_m$ ARIMA (111) residuals and phytoplankton diversity ARIMA (110) residuals (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

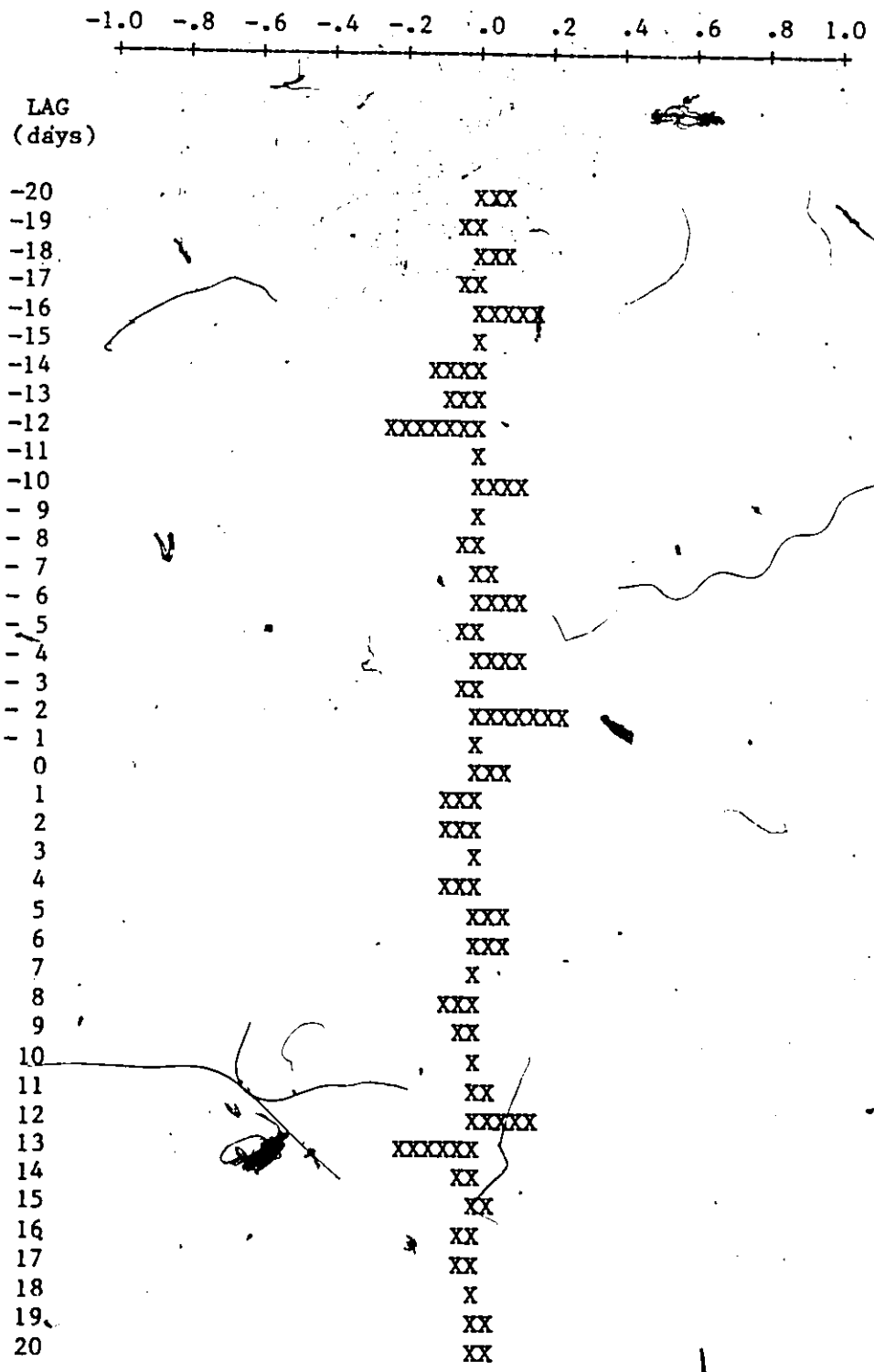


Figure 36a Cross-correlation estimates between $N^2(0-6)_m$ ARIMA (101) residuals and the rate of phytoplankton community change ARIMA (101) residuals (at $k = 0, 2$ for $p < .05$, $r^2 > .195$, at $k = .20$, for $p < .05$, $r^2 > .217$).

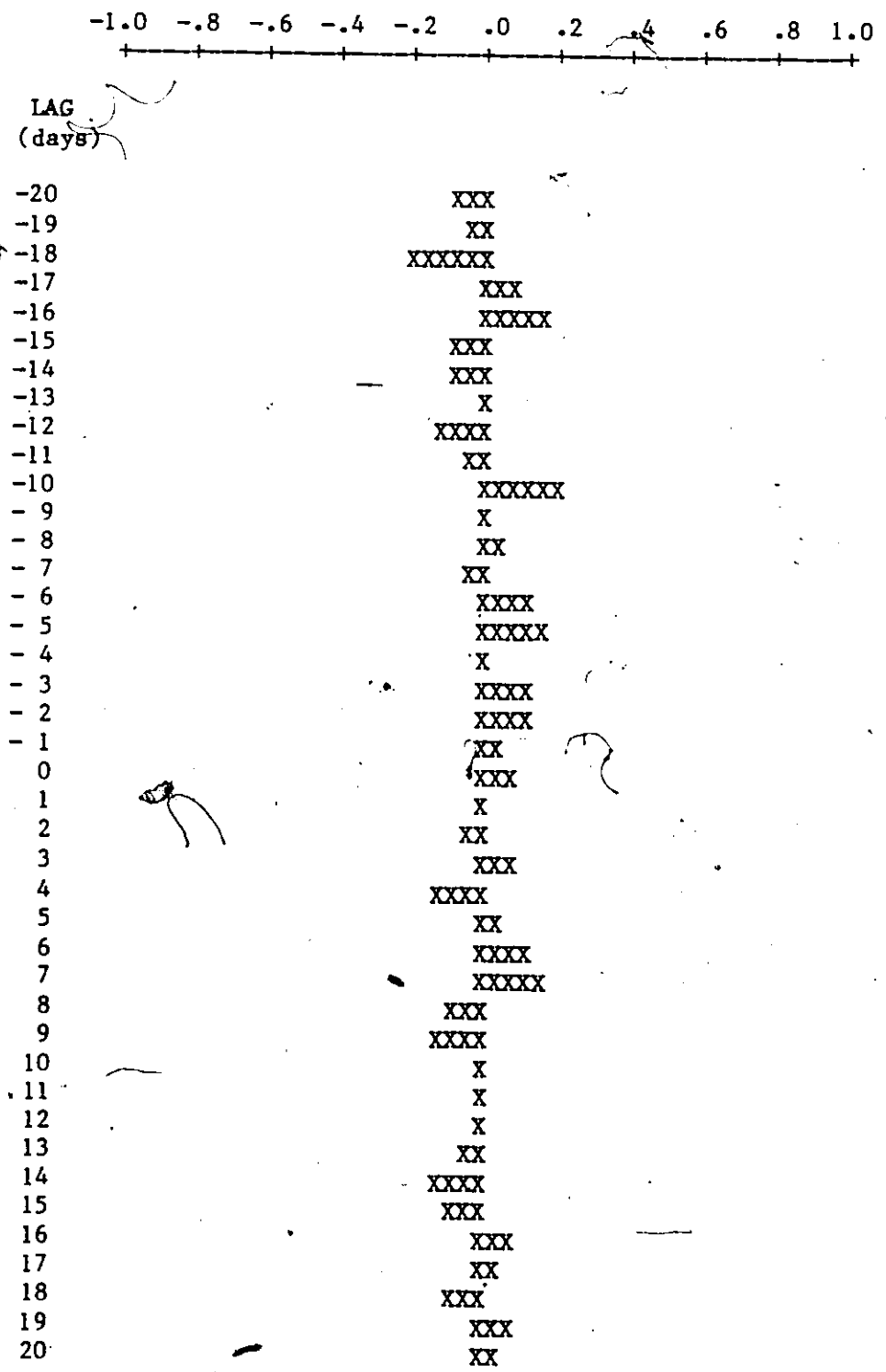
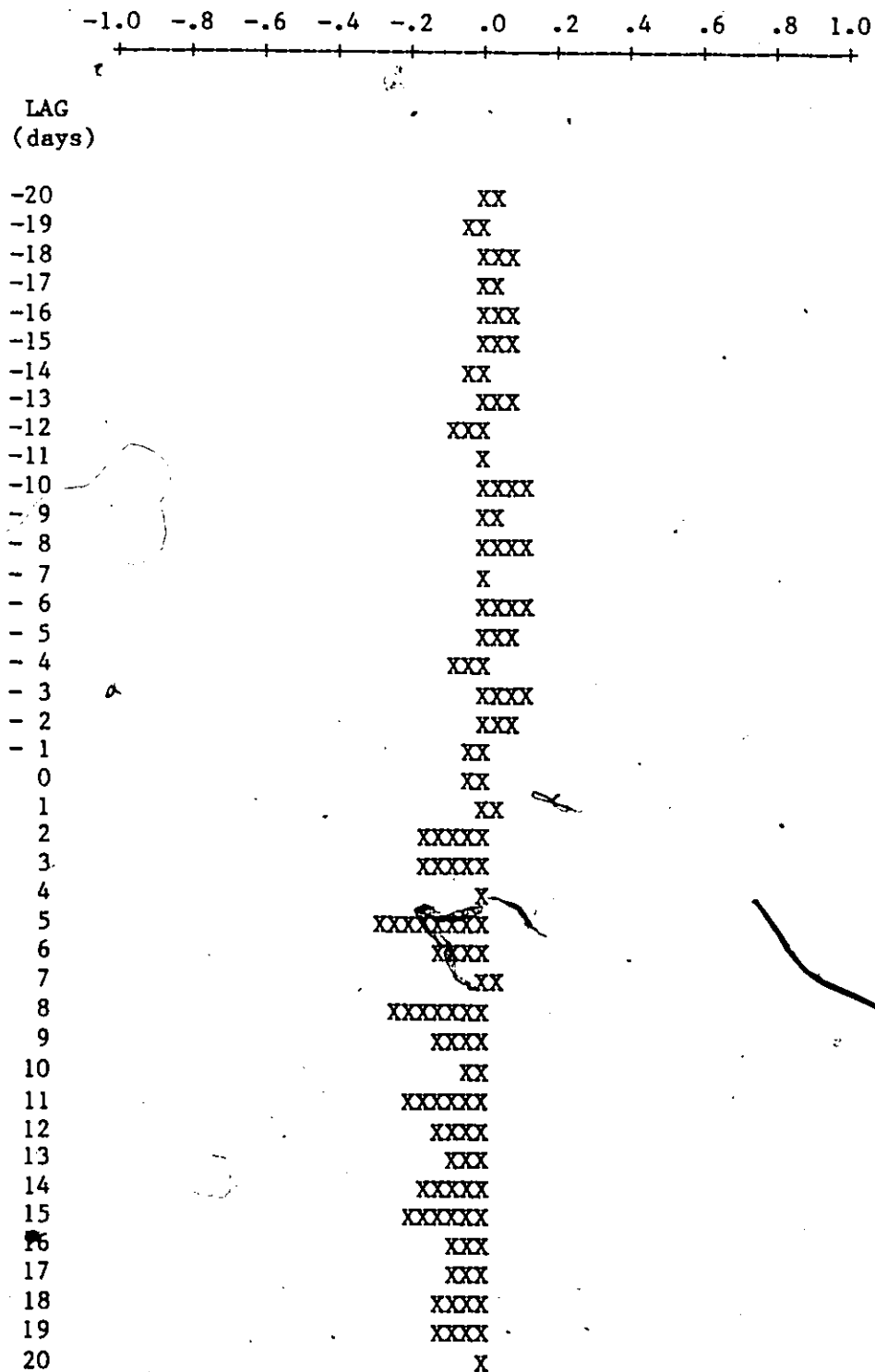


Figure 36b Cross-correlation estimates between $N^2(0-10)m$ ARIMA (002) residuals and rate of phytoplankton community change ARIMA (101) residuals (at $k \neq 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).



non-stationary Stephanodiscus values from May 8 to June 6 were negative with a maximum on day 2 (Figure 37a). Only a subset of the total time series was used since diatom abundances were low to non-measurable by early June. However, when the residuals from each data set were compared no significant cross-correlations were observed (Figure 37b). Similar results were obtained when $N^2(0-10)m$ was compared to Stephanodiscus (Figure 37c and 37d).

Emergence of Cryptomonads-

The decline of the diatoms was followed by an increase in z_{eu} and a decrease in z_m which resulted in an increase in z_{eu}/z_m (Figure 24). Cryptomonads were abundant 1-2 weeks later (Figure 22). Significant cross-correlations were observed between stationary residuals of z_{eu}/z_m and stationary residuals of Cryptomonas erosa (maximum on day 9, $r^2 = .409$, for $p < .05$, $r^2 > .204$) (Figure 38a), Cryptomonas ovata (maximum on day 10, $r^2 = .494$, for $p < .05$, $r^2 > .205$) (Figure 38b) and Rhodomonas (maximum on day 14, $r^2 = .418$, for $p < .05$, $r^2 > .210$) (Figure 38c).

Emergence of summer blue-greens-

Blue-green algae such as Microcystis, Lyngbya, and Gomphosphaeria first appeared in early July (Figure 22) when $N^2(0-10)m$ was at its maximum (Figure 23) and the water at 10m had become anoxic (Figure 24). A summary of the significant cross-correlations obtained when the residuals of $N^2(0-6)m$, $N^2(0-10)m$ or DO at 10m were compared to the residuals of Microcystis, Lyngbya and Gomphosphaeria is shown in

Figure 37a Cross-correlation estimates between non-transformed $N^-(0-6)m$ and non-transformed Stephanodiscus (days 1-30).

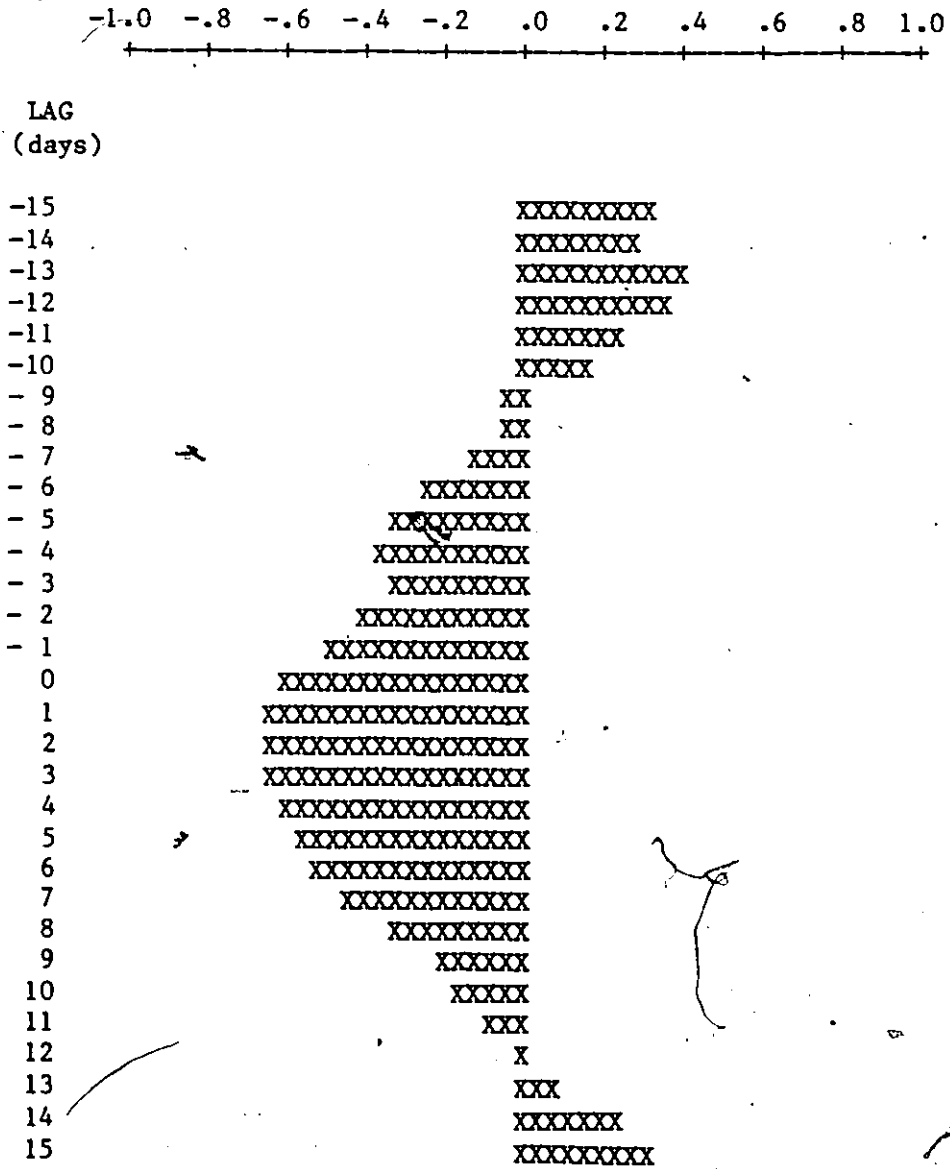


Figure 37b Cross-correlation estimates between $N^2(0-6)_m$ ARIMA (101) residuals and Stephanodiscus ARIMA (101) residuals (at $k = 0$, for $p < .05$, $r^2 > .365$, at $k = 15$, for $p < .05$, $r^2 > .517$).

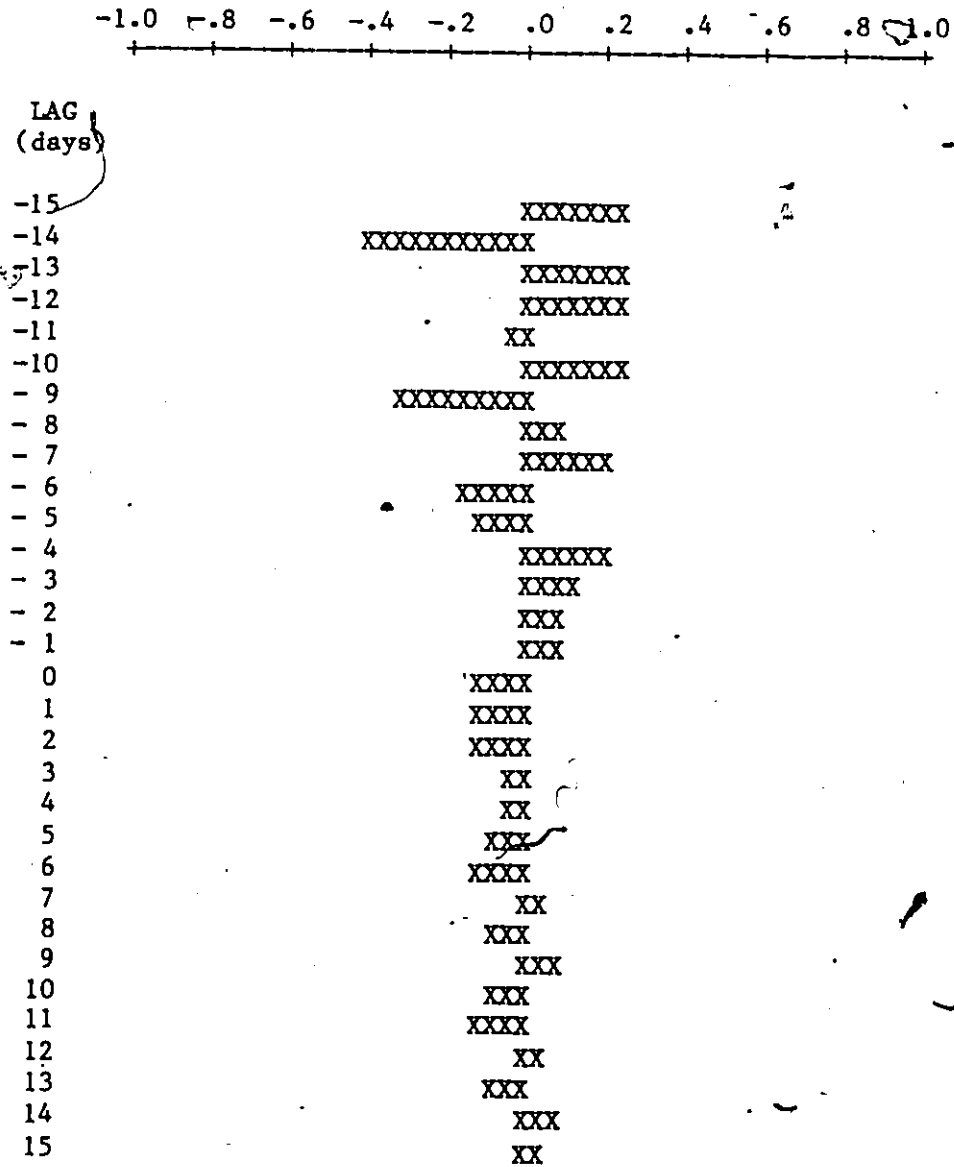


Figure 37c Cross-correlation estimates between non-transformed $N^2(0-10)m$ and non-transformed Stephanodiscus (days 1-30).

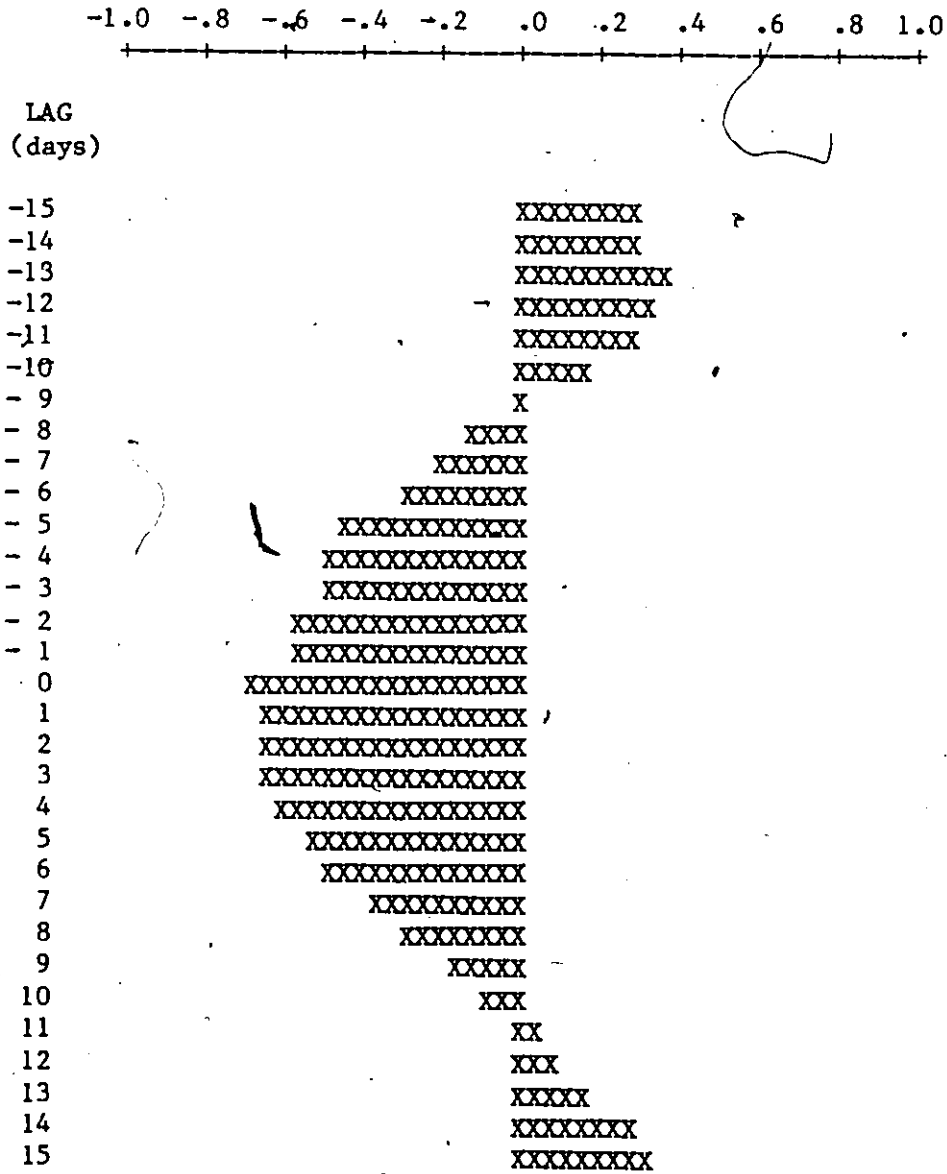


Figure 37d Cross-correlation estimates between $N^2(0-10)$ ARIMA (111) residuals and Stephanodiscus ARIMA (111) residuals (at $k = 0$, for $p < .05$, $r^2 > .365$, at $k = 15$, for $p < .05$, $r^2 > .517$).

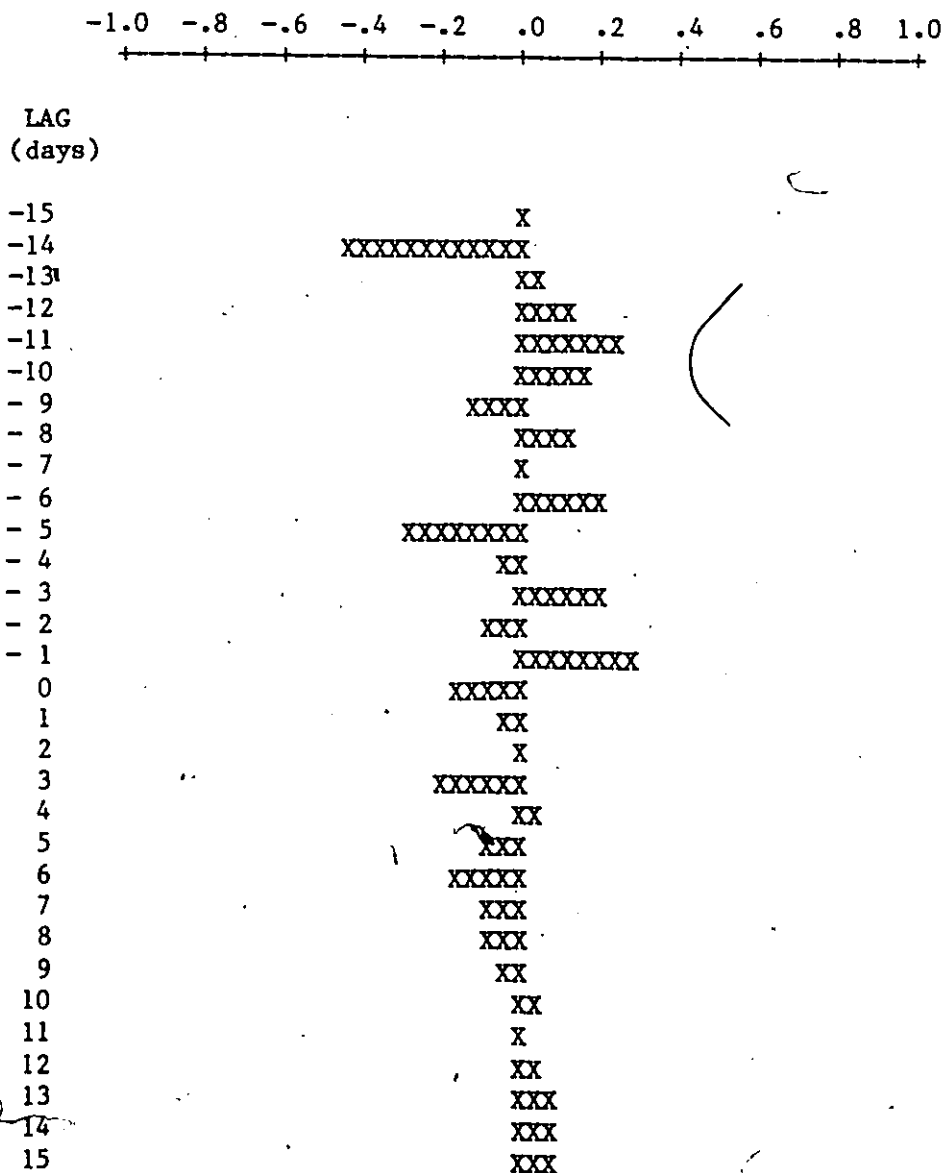


Figure 38a Cross-correlation estimates between zeu/zm ARIMA (100) residuals and *Cryptomonas eroga* ARIMA (100) residuals (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 15$, for $p < .05$, $r^2 > .217$).

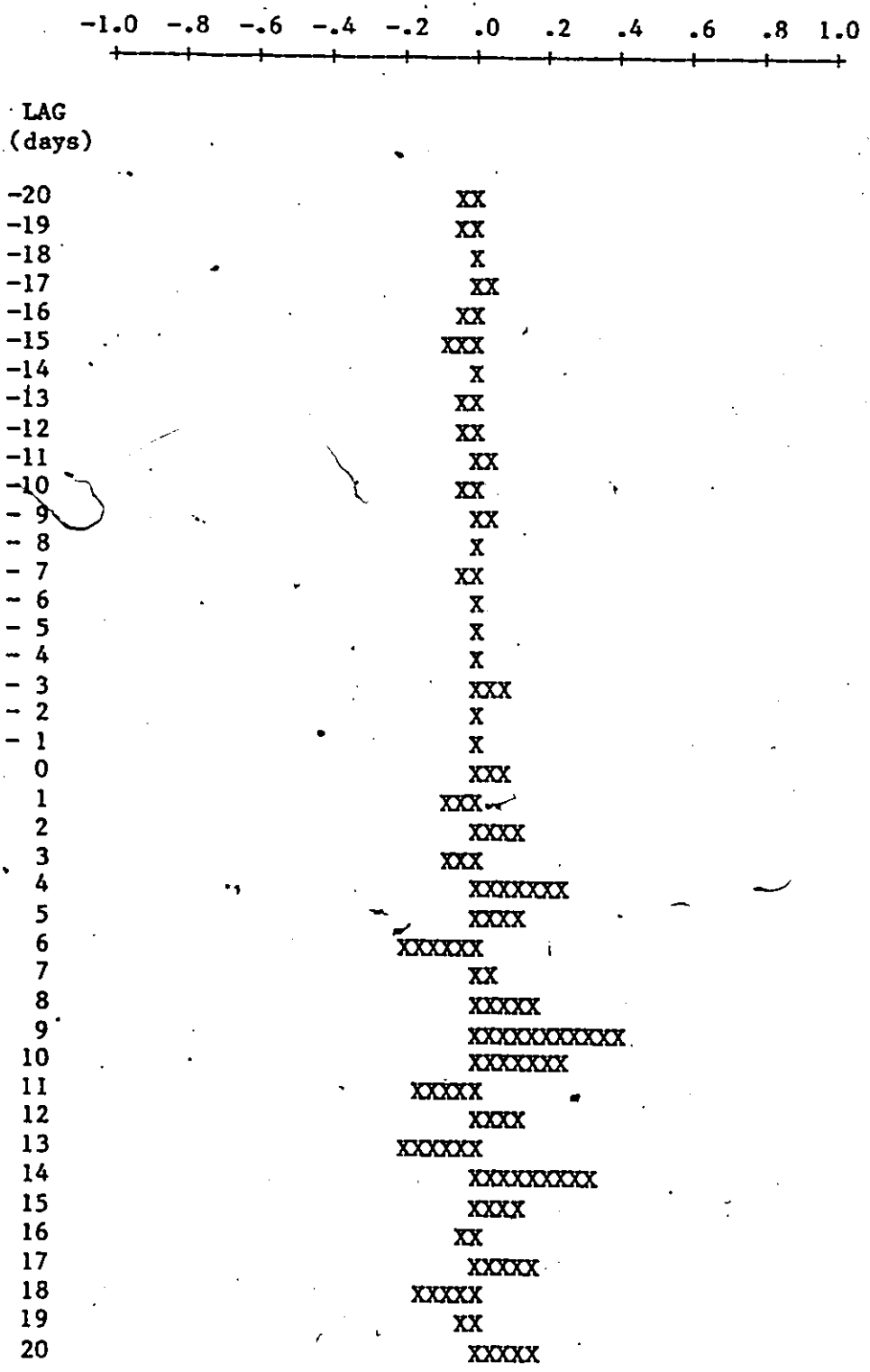
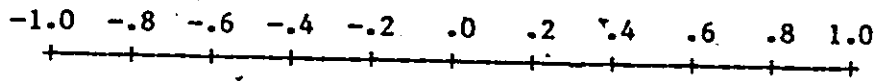


Figure 38b Cross-correlation estimates between *zeu/zm* ARIMA (100) residuals and *Cryptomonas ovata* ARIMA (100) residuals (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).



LAG (days)

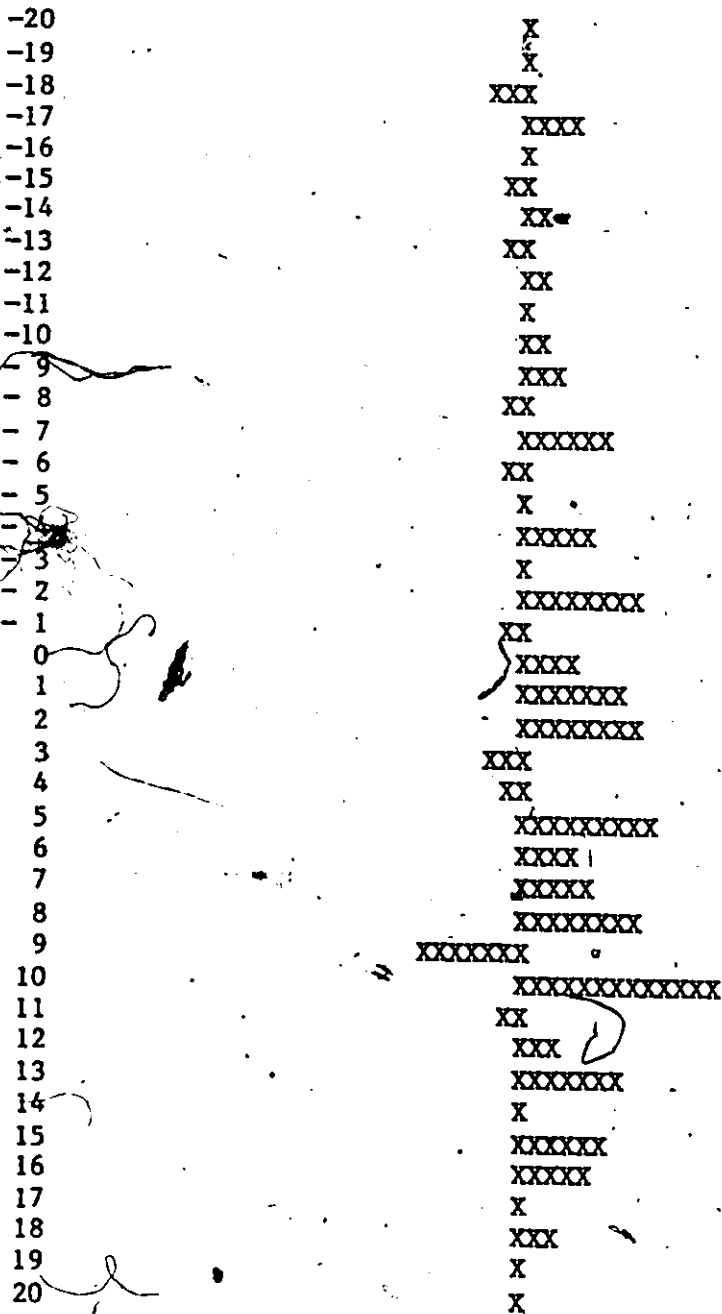


Figure 38c Cross-correlation estimates between *zeu/zm* ARIMA (100) residuals and *Rhodomonas* ARIMA (100) residuals (at $k = 0$, for $p < .05$, $r^2 > .195$, at $k = 20$, for $p < .05$, $r^2 > .217$).

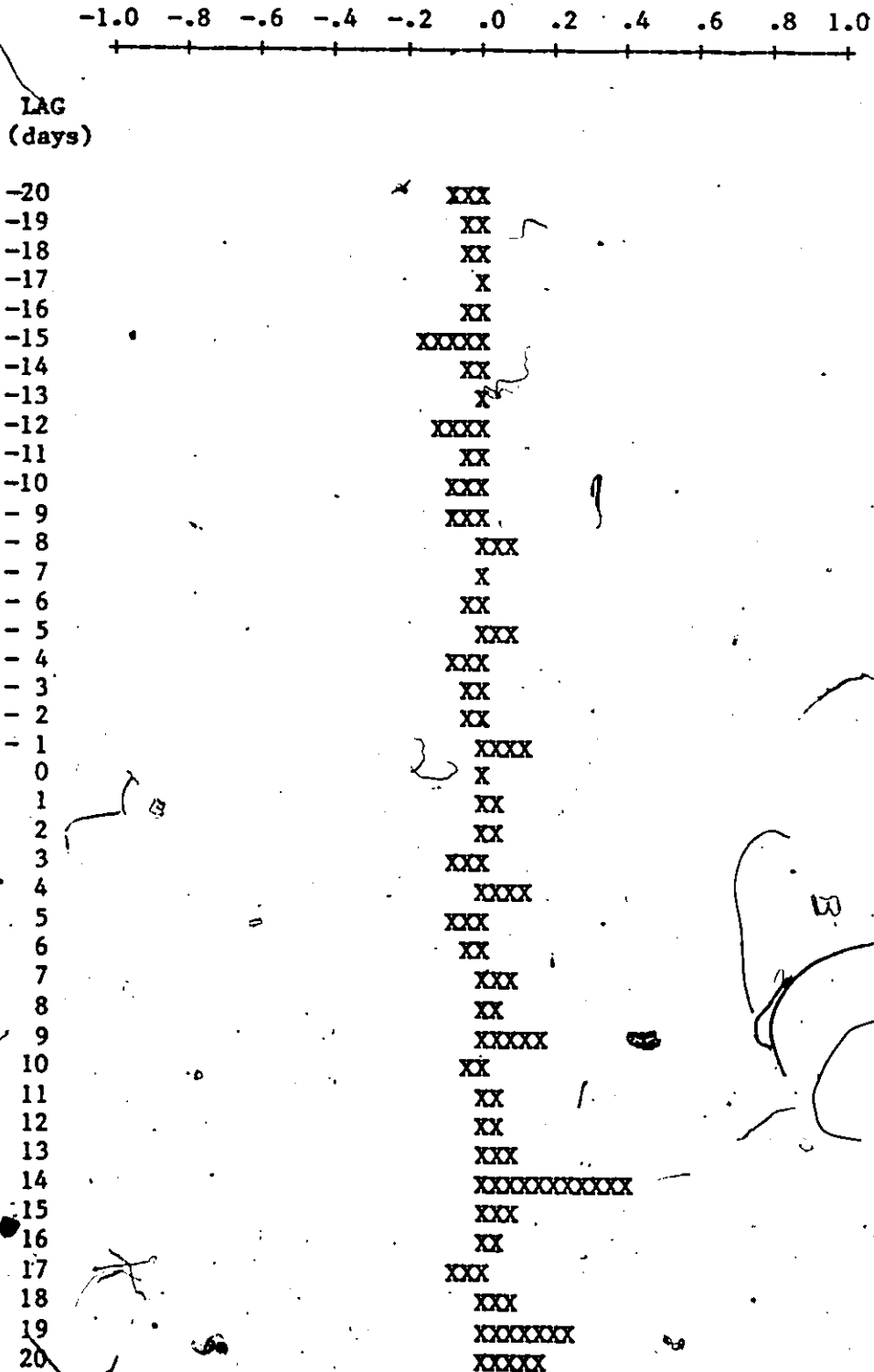


Table 9. Significant negative cross-correlations were obtained between $N^2(0-10)m$ and the abundance of Microcystis 2 days later and between $N^2(0-10)m$ and the abundance of Lyngbya 1 day earlier. Significant negative cross-correlations were also observed between DO at 10m and the abundance of Microcystis 11 days later and between DO at 10m and the abundance of Gomphosphaeria 4 days later.

III-2-1-5 Relationships between physical variables and vertical heterogeneity

N^2 values are expected to influence the degree of vertical heterogeneity in phytoplankton species and in nutrients, as are wind speed and Richardson number. Some algal species may regulate their position in the water column through buoyancy regulation (blue-green algae) or active migration (for example, Ceratium). Algal species that cannot actively regulate their position, as well as inanimate seston may accumulate just in or below the layers where their sinking speed slows down, for example, in colder waters (Margalef, 1978). Examples of vertical profiles of the blue-green algae Aphanizomenon and Lyngbya, as well as the dinoflagellate Ceratium (Figures 39,40,41), showed that surface accumulations as well as peaks at a lower depth were possible. A high degree of vertical heterogeneity would be expected when N^2 is high, wind speed is low, or Richardson number is high. Water column stability also influences the formation of surface blooms. Stable conditions favor the development of surface blooms.

Summary of the significant cross-correlations obtained when the residuals from $N^2(0-6)_m$, $N^2(0-10)_m$ or DO at 10m were compared to the residuals of the abundances of summer blue-greens (days 50-105 of the daily time series were considered, at $k = 0$, for $p < .05$, $r^2 > .267$, at $k = 15$, for $p < .05$, $r^2 > .321$). The abbreviation n.s. stands for no significant cross-correlations. The first number gives the value of the lag where the significant cross-correlation was observed. The number in brackets gives the value of the cross-correlation.

	$N^2(0-6)_m$ ARIMA(101)	$N^2(0-10)_m$ ARIMA(101)	DO at 10m ARIMA(101)
<u>Microcystis</u> loge, ARIMA(001)	n.s.	2(-.324)	11(-.363)
<u>Lyngbya</u> loge, ARIMA(001)	n.s.	-1(-.352)	n.s.
<u>Gomphosphaeria</u> loge, ARIMA(001)	n.s.	n.s.	4(-.288)

Figure 39 - Vertical profiles of Aphanizomenon abundance (station 1).

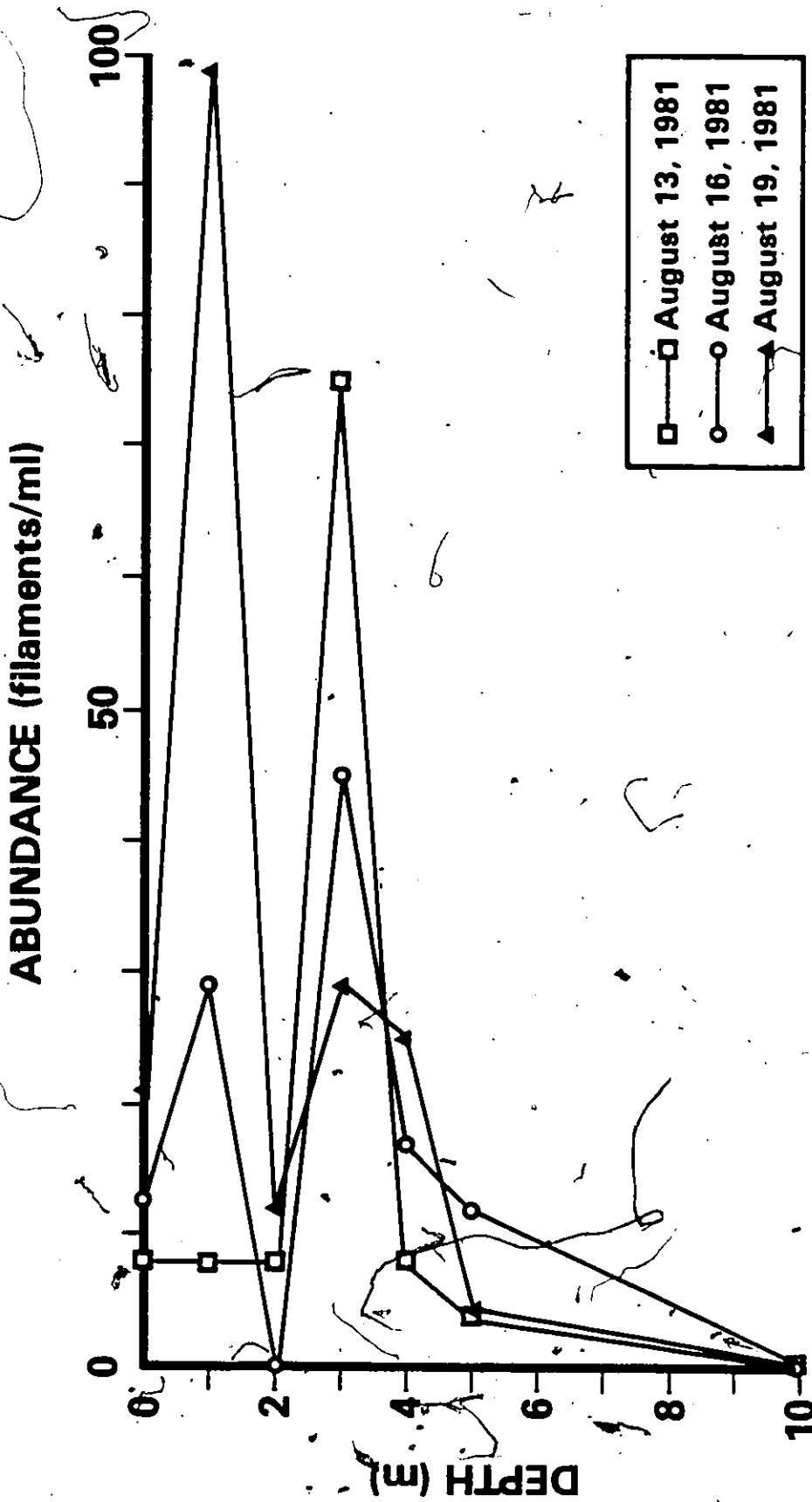


Figure 40 - Vertical profiles of Ceratium abundance (station 1).



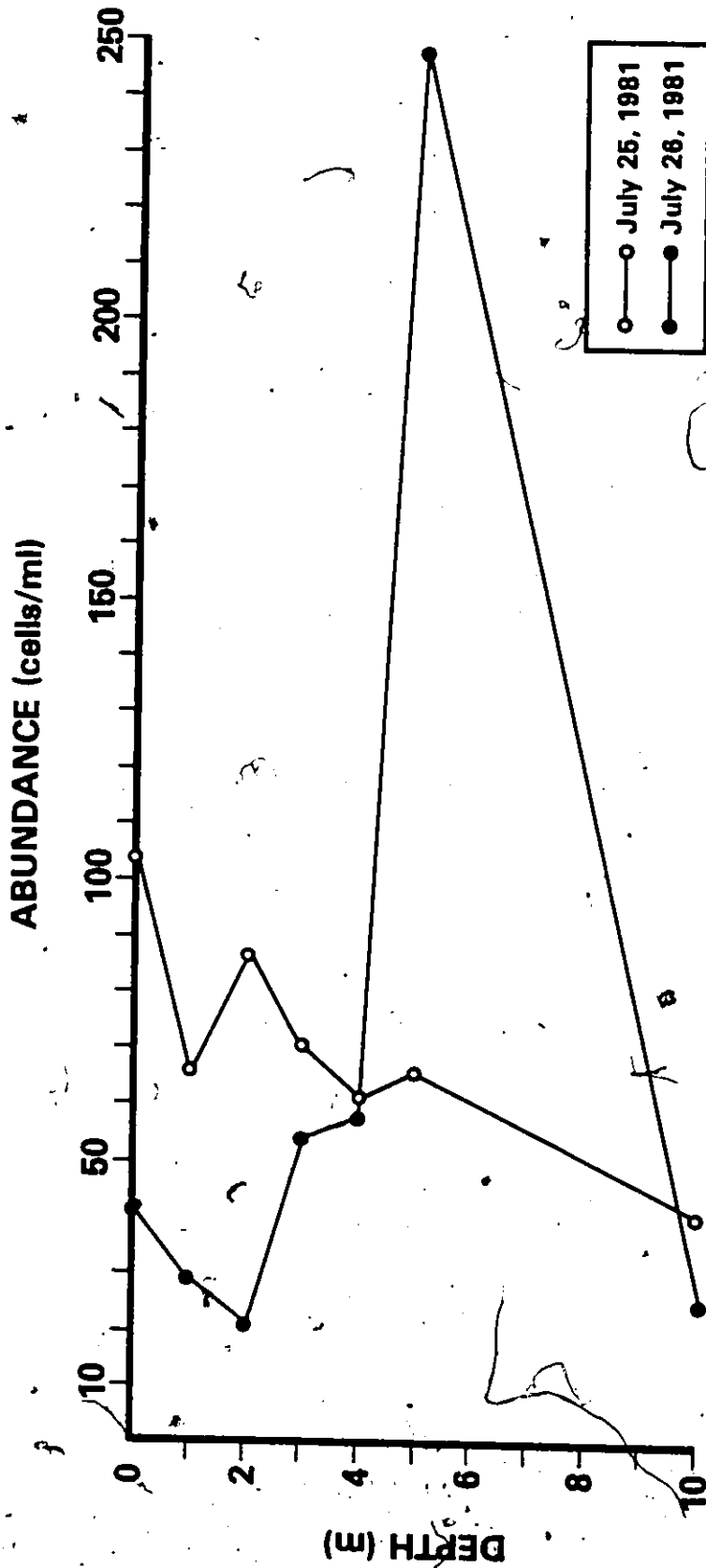
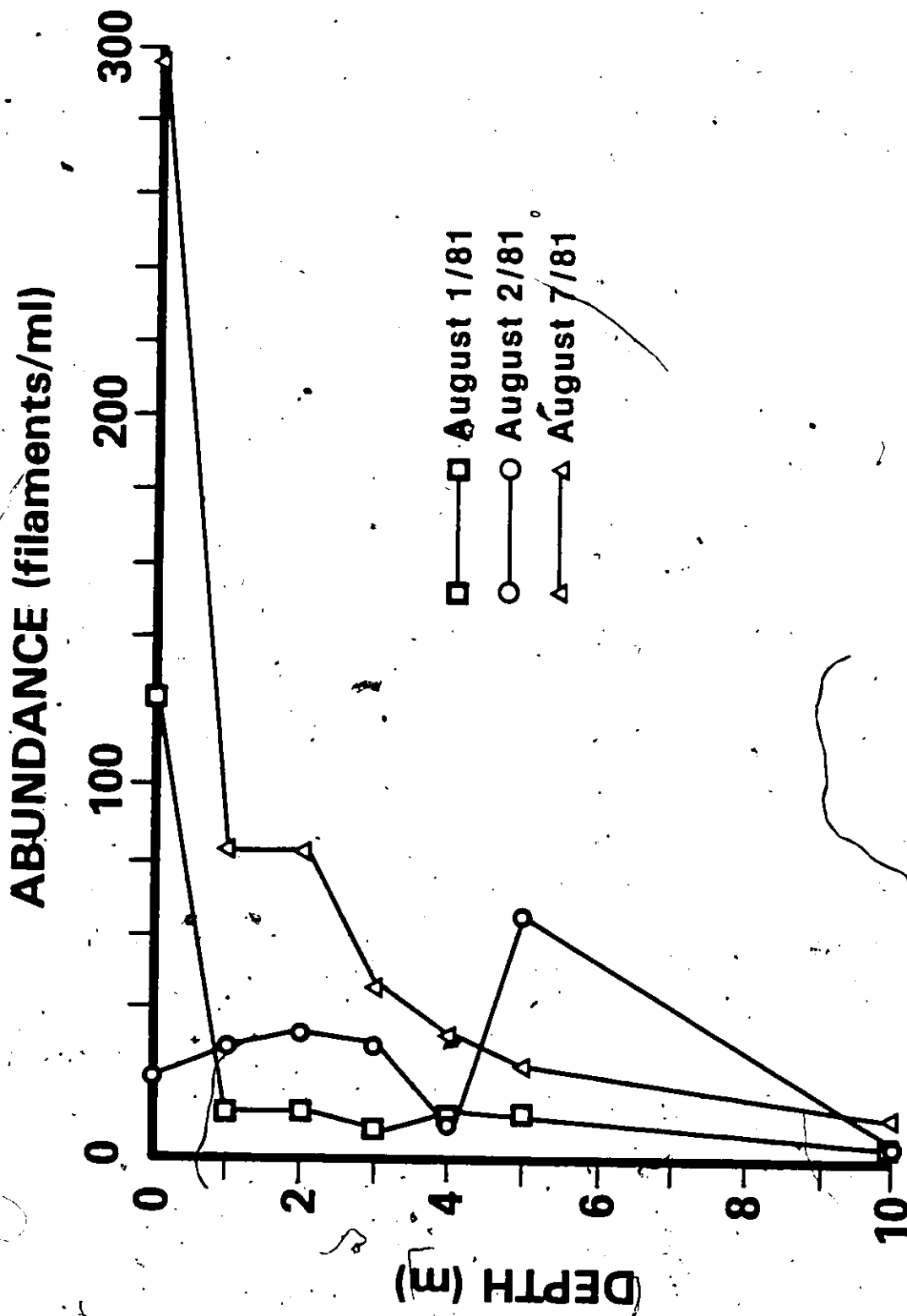


Figure 41 - Vertical profiles of Lyngbya abundance (station 1).



$N^2(0-6)m$ was significantly negatively correlated to the average wind speed over the prior 24 hours, whereas $N^2(0-10)m$ was significantly negatively correlated to the average wind speed over the prior 72 hours (Table 10). This suggests that $N^2(0-10)$ is more resistant to alteration from energy inputs than $N^2(0-6)m$. Windy conditions must persist for a longer time period for $N^2(0-10)m$, than for $N^2(0-6)m$ to decrease. Consequently, $N^2(0-6)m$ was more variable than $N^2(0-10)m$ over the daily time series.

Cross-correlations were done between physical variables (N^2 , wind speed and Richardson number) and the degree of vertical heterogeneity or surface accumulation of chlorophyll, TP, SRP and several phytoplankton species.

Significant cross-correlations between N^2 and surface concentration or between N^2 and vertical heterogeneity over the full 105 days were not observed. Significant cross-correlations were observed if a subsample from early to mid-August was considered. During this time N^2 was positively correlated to increases in surface concentrations of chlorophyll or TP, as well as the vertical heterogeneity of chlorophyll a or TP on the same day and 1 day earlier. These results suggested that chlorophyll and TP could respond more rapidly than N^2 to the change in the physical environment that caused N^2 to increase. N^2 was positively cross-correlated to the Lyngbya surface abundance on the same day (Table 11).

Table 10

Correlations between wind speed and water column stability.
(August 1 - August 19) (for $p < .05$, $r_2 > .456$)

- 1) Wind speed (average over past 24 hours) to $N^2(0-6)m$,
 $r^2 = -.648$.
- 2) Wind speed (average over past 3 days) to $N^2(0-10)m$,
 $r^2 = -.666$.

Table 11

Significant cross-correlations between N^2 and surface concentrations or vertical heterogeneity (sd/\bar{x}) (July 30 - August 19)₂ (at $k = 0$, for $p < .05$, $r^2 > .437$, at $k = 1$, for $p < .05$, $r^2 > .447$).

	$N^2(0-6)_m$	$N^2(0-10)_m$
0m chl	-1 (.572) 0 (.480)	n.s.
chl sd/\bar{x}	-1 (.577) 0 (.506)	-1 (.457)
0m <u>Lyngbya</u>	0 (.649)	0 (.490)
<u>Lyngbya</u> sd/\bar{x}	n.s.	n.s.
0m SRP	n.s.	n.s.
SRP sd/\bar{x}	n.s.	n.s.
0m TP	-1 (.566) 0 (.479)	n.s.
TP sd/\bar{x}	-1 (.533)	-1 (.524)

The first number is the lag (k)₂ in days and the number in brackets is the corresponding r^2 value. A significant cross-correlation at a lag of -1 means that changes in the vertical heterogeneity or surface concentration of that particular variable actually lead changes in N^2 by 1 day.

* the letters n.s. stand for no significant cross-correlations

Over the full 105 days significant cross-correlations between wind speed (from Elora field station) and chlorophyll vertical heterogeneity were not observed. 2 subsamples of wind speed data were obtained from station 1. Set A was taken from June 23 to July 8 and Set B was taken from July 30 to August 19. A significant negative cross-correlation was observed between the average wind speed of the previous 24 hours and surface chlorophyll for Set B but not for Set A. Calm conditions may be a resource that is not necessarily exploited. Buoyancy regulating species must be present for surface accumulations to occur under calm conditions. The average wind speed (Set B) from the previous 24 hrs was also significantly negatively cross-correlated to surface abundance of Lyngbya and vertical heterogeneity of Lyngbya, chlorophyll, SRP and TP (Table 12).

~~When~~ Richardson numbers were compared to vertical heterogeneity significant cross-correlations were seen even in the larger subsamples. Richardson numbers in early to mid August were highly positively cross-correlated to surface concentrations and vertical heterogeneity of TP, SRP, chlorophyll and Lyngbya the next day (Table 13). Surface chlorophyll, TP and Lyngbya were highly significantly correlated at this time (Table 14). Significant cross-correlations were not observed between Richardson numbers and surface concentrations or vertical heterogeneity of Microcystis, Gomphosphaeria, Rhodomonas, Ochromonas, Oocystis and Planktosphaeria.

Table 12

140

Significant cross-correlations between wind speed (obtained from raft) and surface concentration or vertical heterogeneity (sd/\bar{x}) (July 30 - August 19) (at $k = 1$, for $p < .05$, $r > .447$).

	wind speed
0m chl	1 (-.492)
chl sd/\bar{x}	1 (-.512)
0m <u>Lyngbya</u>	1 (-.589)
<u>Lyngbya</u> sd/\bar{x}	1 (-.579)
0m SRP	n.s.
SRP sd/\bar{x}	n.s.
0m TP	n.s.
TP sd/\bar{x}	1 (-.459)

The first number refers to the $lag_2(k)$ in days and the number in brackets gives the corresponding r value. A significant cross-correlation at a lag of 1, means that changes in the vertical heterogeneity or surface concentration lag changes in the wind speed by 1 day.

Table 13

Significant cross-correlations between Richardson numbers and surface concentration or vertical heterogeneity.

- a) Days 50 to 105 of the daily time series. Richardson numbers were calculated using wind data from the Elora field station. (at $k = 1$, for $p < .05$, $r^2 > .272$, at $k = 4$, for $p < .05$, $r^2 > .280$).

	Ri (0-6)m	Ri (0-10)m
chl sd/x	1 (.284)	n.s.
SRP sd/x	0 (.369)	n.s.
TP sd/x	n.s.	n.s.

- b) Days 84 to 104 of the daily time series (July 30 to August 19). Richardson numbers were calculated using wind data from station 1₂ (at $k = 1$, for $p < .05$, $r^2 > .447$, at $k = 4$, for $p < .05$, $r^2 > .485$).

	Ri (0-6)m	Ri (0-10)m
Om chl	1 (.585)	1 (.828)
chl sd/x	1 (.513)	1 (.697)
Om <u>Lyngbva</u>	1 (.732)	1 (.876)
<u>Lyngbva</u> sd/x	n.s.	1 (.524)
Om SRP	1 (.525)	1 (.682)
SRP sd/x	4 (.576)	4 (.568)
Om TP	1 (.571)	1 (.786)
TP sd/x	1 (.681)	1 (.725)

The first number gives the lag in days and the number in brackets gives the corresponding r^2 value.

Table 13

Significant cross-correlations between Richardson numbers and surface concentration or vertical heterogeneity.

- a) Days 50 to 105 of the daily time series. Richardson numbers were calculated using wind data from the Elora field station. (at $k = 1$, for $p < .05$, $r^2 > .272$, at $k = 4$, for $p < .05$, $r^2 > .280$).

	R1 (0-6) _m	R1 (0-10) _m
chl sd/x	1 (.284)	n.s.
SRP sd/x	0 (.369)	n.s.
TP sd/x	n.s.	n.s.

- b) Days 84 to 104 of the daily time series (July 30 to August 19). Richardson numbers were calculated using wind data from station 1₂ (at $k = 1$, for $p < .05$, $r^2 > .447$, at $k = 4$, for $p < .05$, $r^2 > .485$).

	R1 (0-6) _m	R1 (0-10) _m
0m chl	1 (.585)	1 (.828)
chl sd/x	1 (.513)	1 (.697)
0m <u>Lyngbya</u>	1 (.732)	1 (.876)
<u>Lyngbya</u> sd/x	n.s.	1 (.524)
0m SRP	1 (.525)	1 (.682)
SRP sd/x	4 (.576)	4 (.568)
0m TP	1 (.571)	1 (.786)
TP sd/x	1 (.681)	1 (.725)

The first number gives the lag in days and the number in brackets gives the corresponding r^2 value.

Correlations between surface concentrations (July 30 - August 19)
(for $p < .05$, $r^2 > .433$).

	r^2 (Pearson)	r^2 (Spearman)
0m chl 0m <u>Lyngbya</u>	(.892)	(.684)
0m chl 0m TP	(.916)	(.605)
0m <u>Lyngbya</u> 0m TP	(.861)	(.491)

III-2-2 WEEKLY TIME SERIES

III-2-2-1 General description of phytoplankton dynamics

Chlorophyll-a maxima were observed in mid-October and in late March-early May (Figure 42). The fall blooms reached higher chlorophyll levels than the spring blooms. The weekly rates of phytoplankton community change for the spring through fall of 1981 and 1982 are shown in Figure 43. In 1981, increases in the rate of community change occurred in late May, mid-June, early July and late July. Rates were low in August and September. In contrast, in 1982, increases in the rate of community change were observed in mid-July, early August, late August and late September. In 1982, rates of community change were low in May and June. The phytoplankton diversity was lower in mid-May to early August in 1982 than in 1981 (Figure 43). Figure 44 is a plot of the phytoplankton diversity index and the rate of community change from May 8/1981 through to September 29/1982. During the winter months the phytoplankton diversity and rate of phytoplankton community change were lower than in the spring, summer and fall.

The spring diatom bloom occurred later in 1982 than in 1981. Diatoms were present throughout the summer in higher amounts in 1982 than in 1981 (Figure 45). Diatom abundances increased again in August, 1982 as in 1981.

The most obvious difference in the phytoplankton communities

Figure 42 - Weekly time series plots of chlorophyll a and
water column stability ($N^2(0-6)m$ and $N^2(0-10)m$).

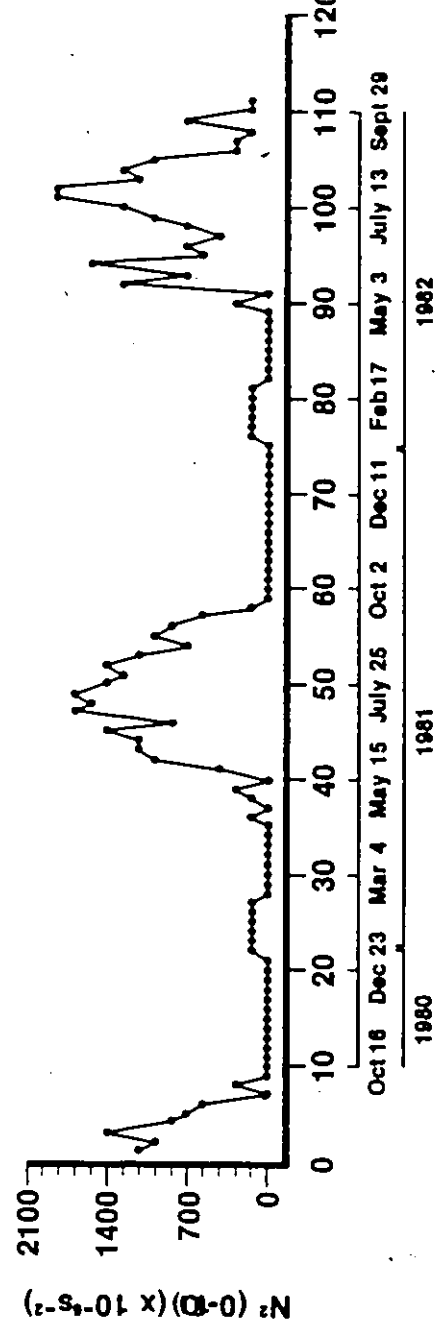
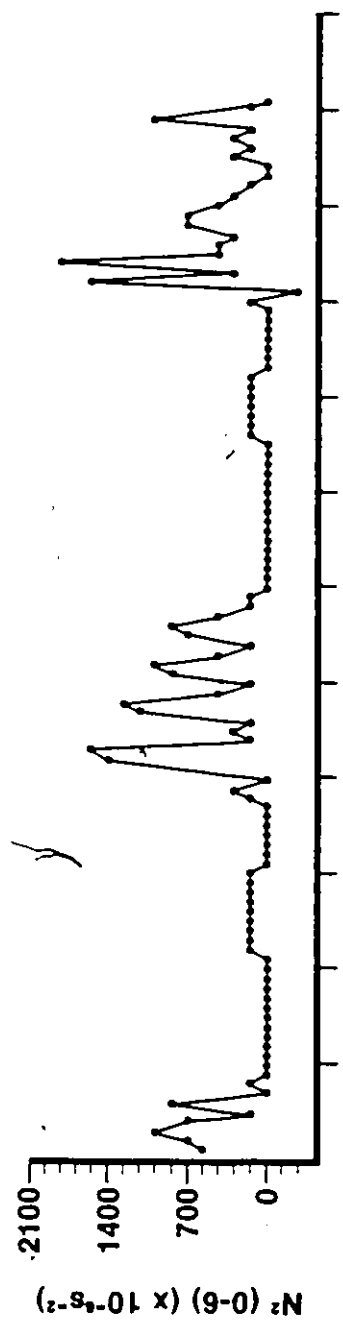
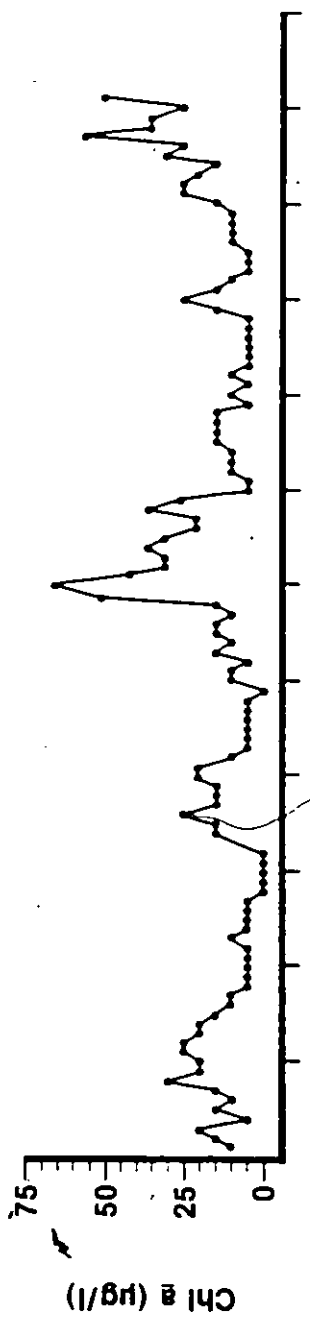
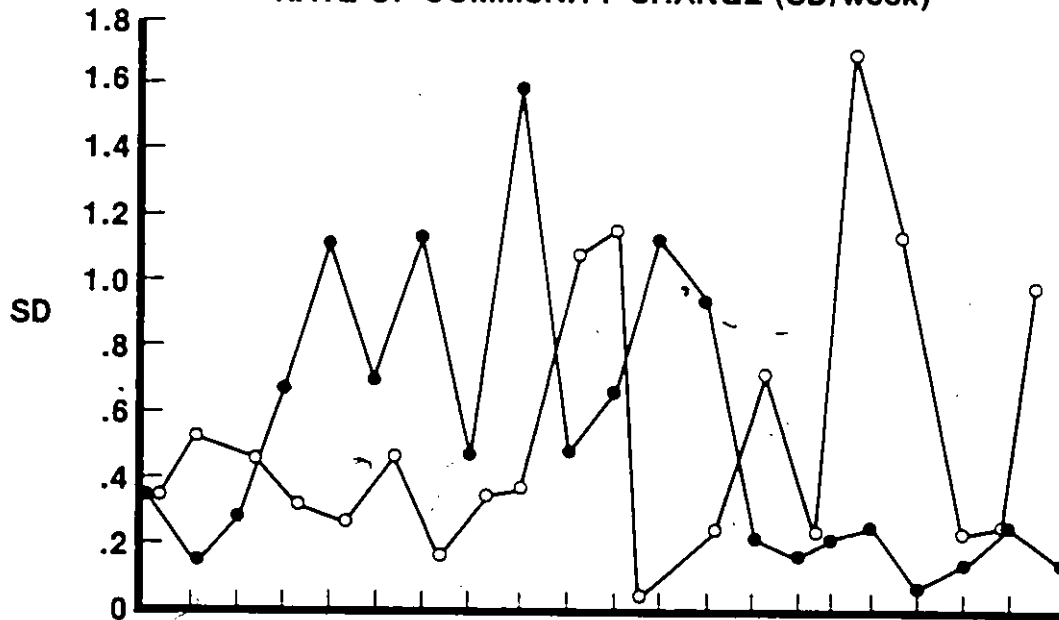


Figure 43- A comparison of the phytoplankton diversity (Shannon-Weaver, 1963) and rate of phytoplankton community change (Lewis, 1978b) in the spring-summer of 1981 to that in 1982.

RATE OF COMMUNITY CHANGE (SD/week)



SHANNON - WEAVER DIVERSITY (H')

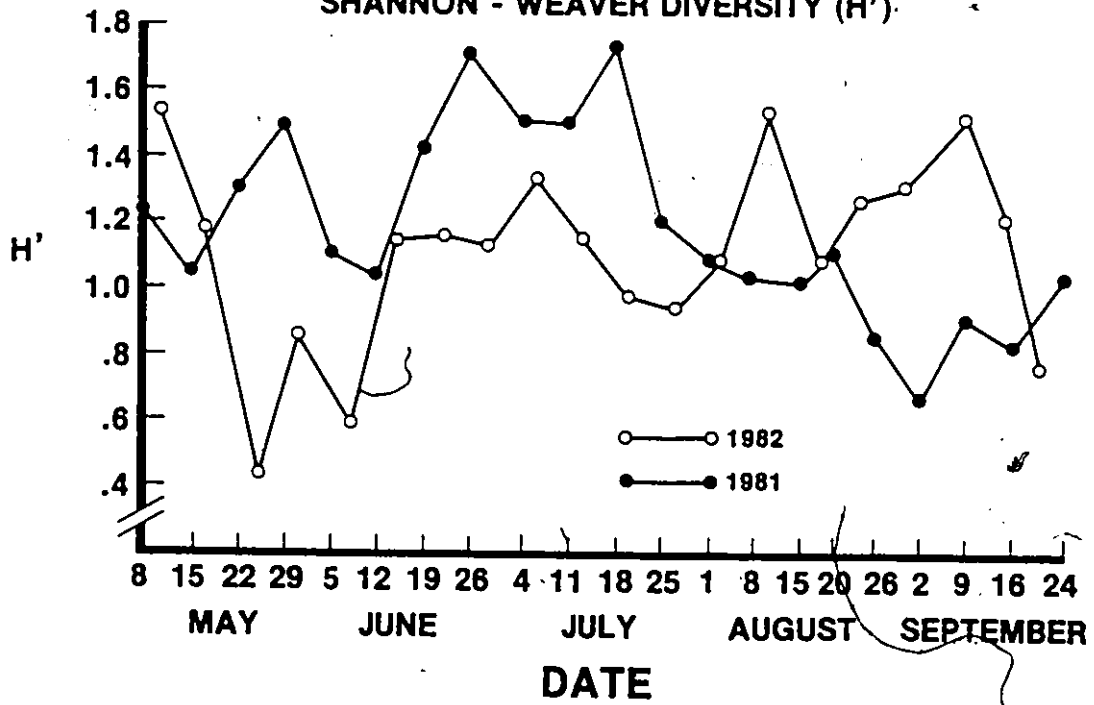


Figure 44- Phytoplankton diversity (Shannon-Weaver, 1963) and rate
of phytoplankton community change (Lewis, 1978) from
May 9/ 1981 through to September 29/ 1982.

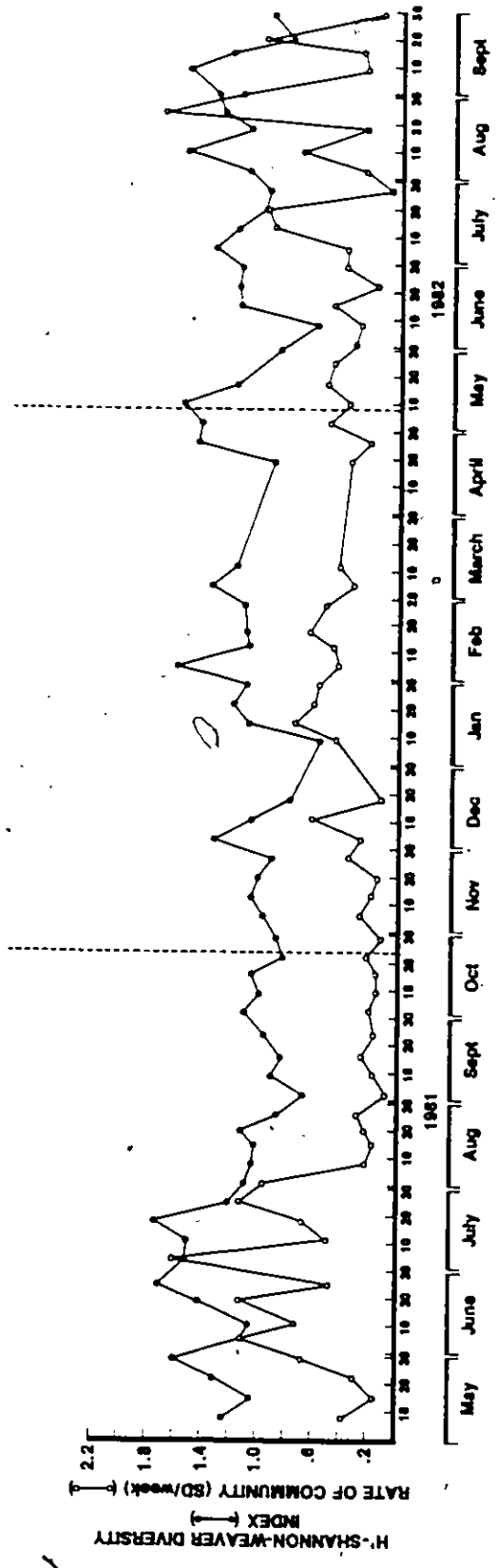
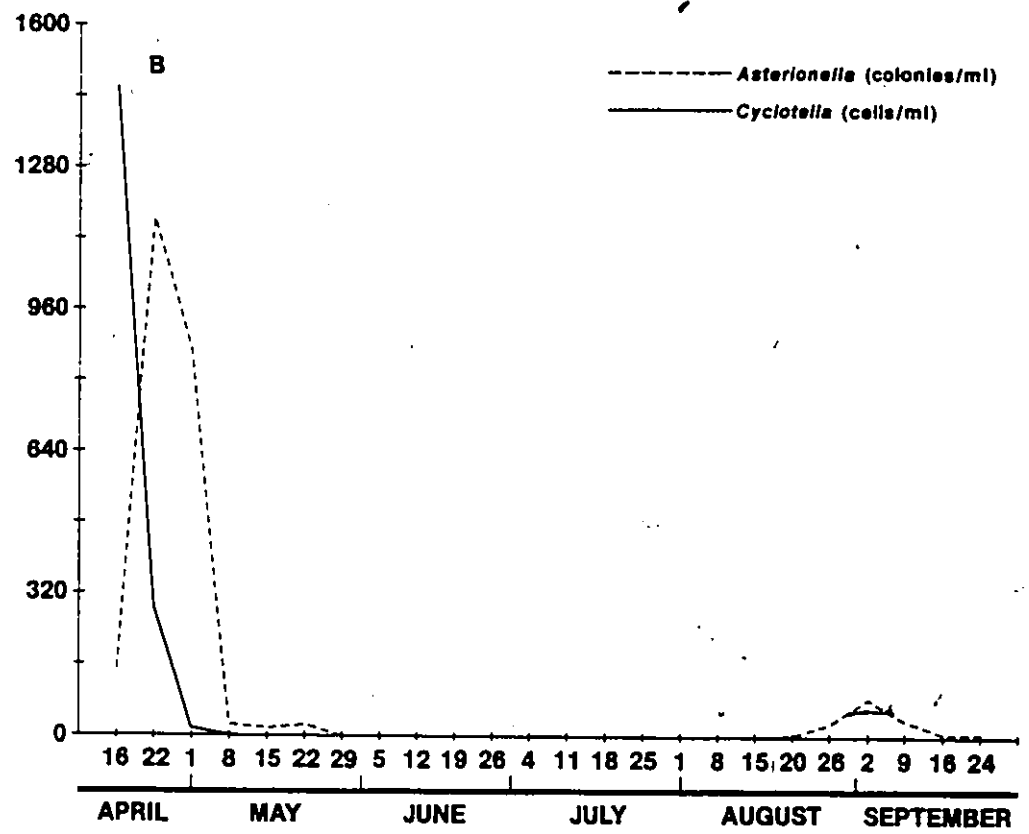
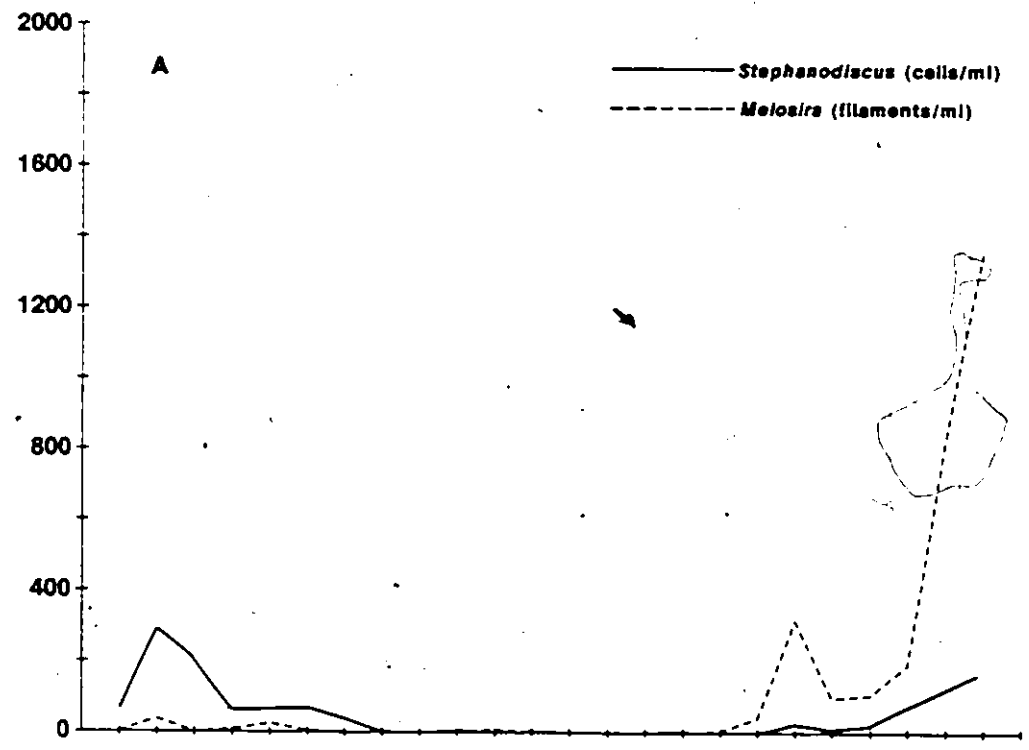
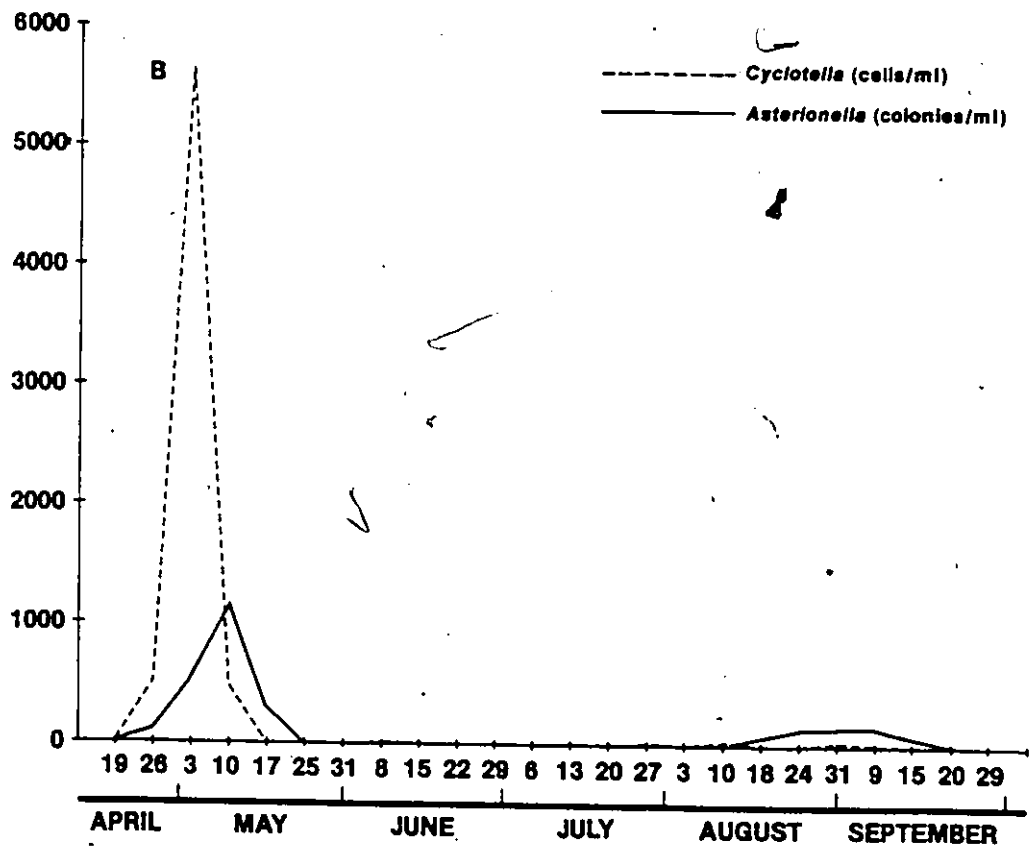
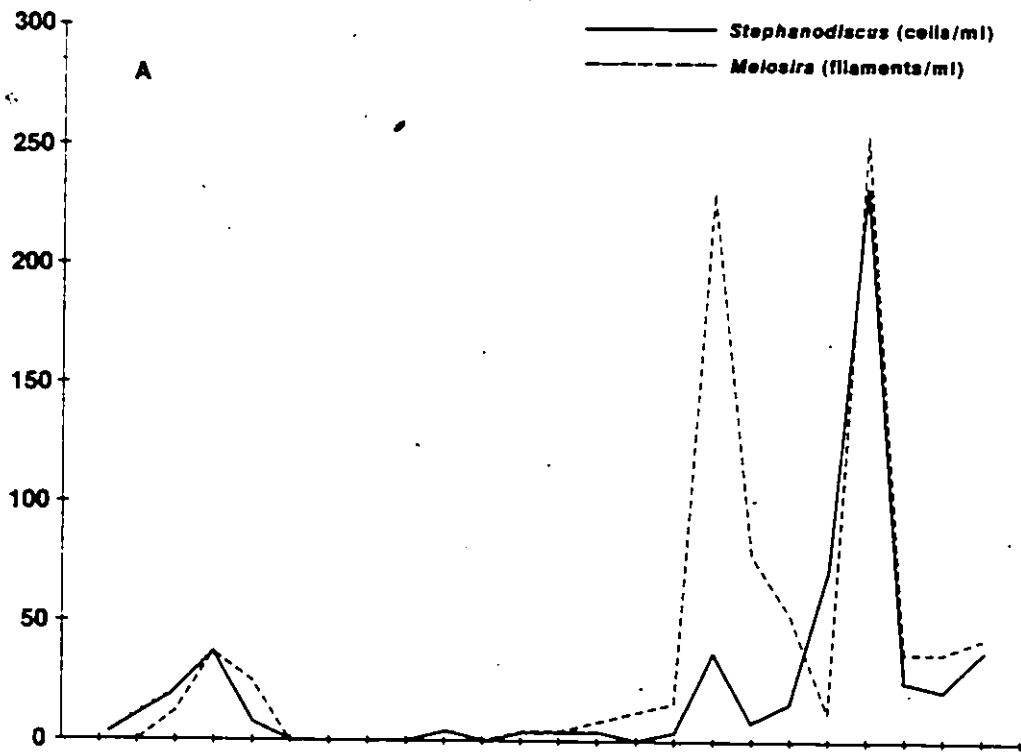


Figure 45 - Weekly time series plots of diatom abundances (spring-
summer of 1981 and 1982).





observed in the two summers was the much greater abundance of Aphanizomenon in 1982. In 1982, Aphanizomenon appeared in May and continued to increase until mid-August, decreased for 2 weeks and then increased again in late August (Figure 46). In 1981, Aphanizomenon appeared in May but decreased to low amounts by early June and did not increase again until late August (Figure 46).

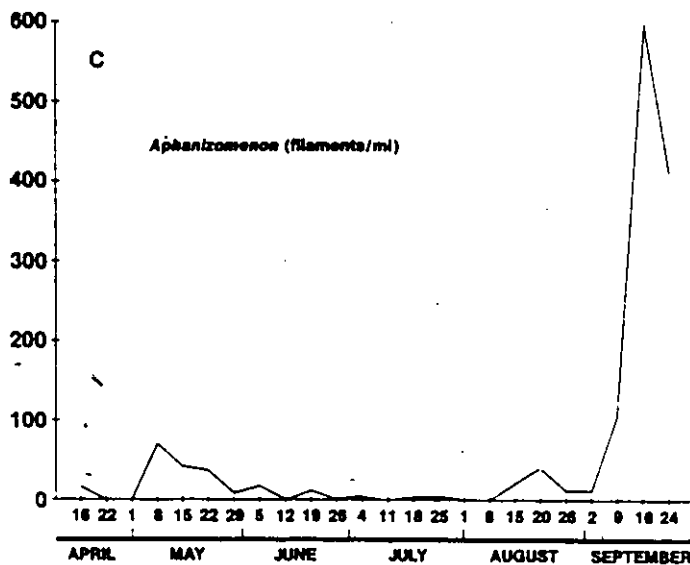
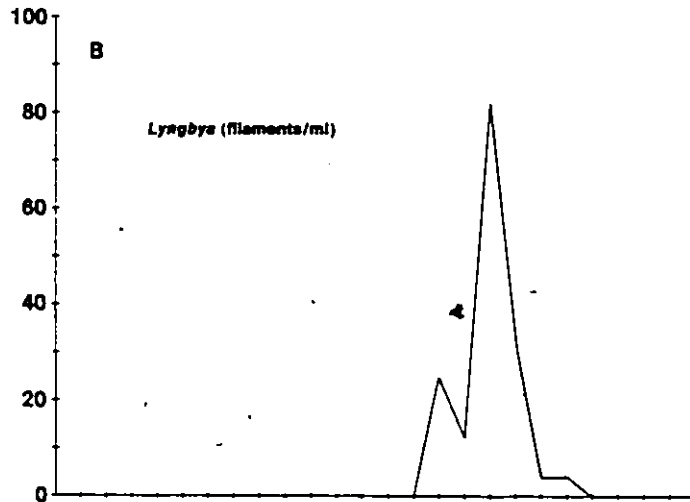
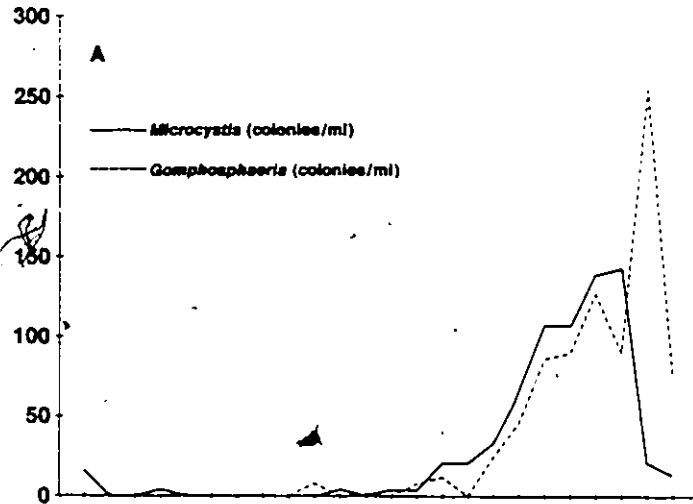
Blue-green algae such as Microcystis and Gomphosphaeria appeared earlier on in the year in 1982 (Figure 46) than in 1981, but did not immediately increase as in 1981. Lyngbya was less abundant in 1982 than in 1981 (Figure 46).

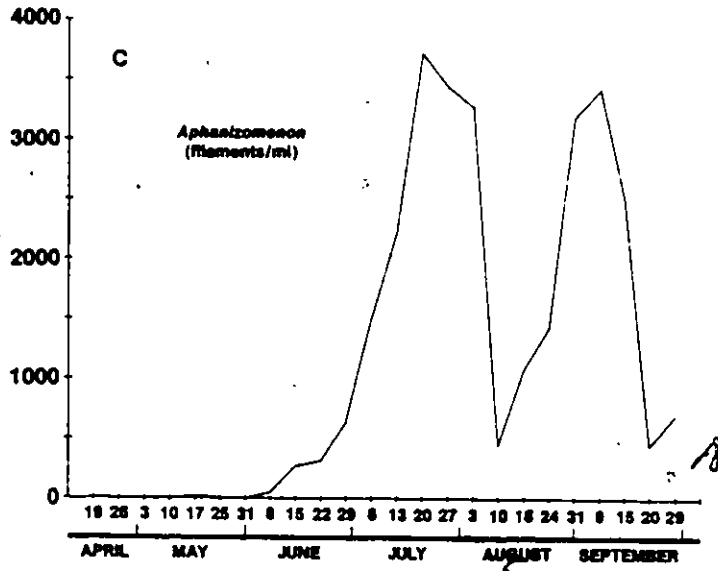
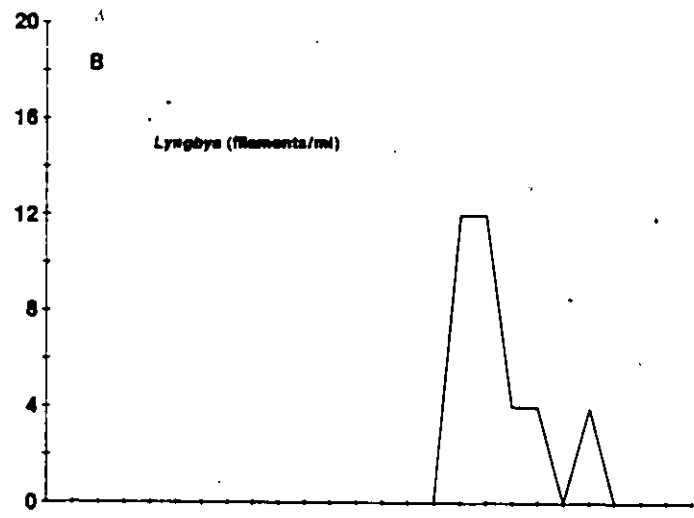
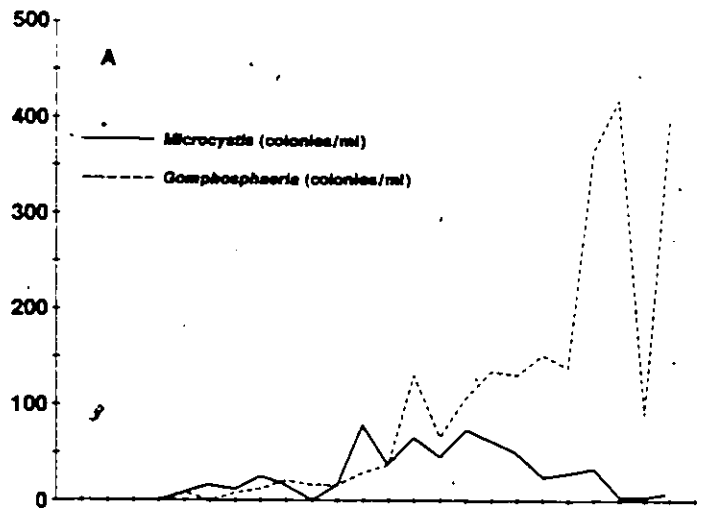
III-2-2-2 General description of environmental variables.

$N^2(0-6)m$ was low throughout the winter of 1980-1981, increased in mid-May and alternated between high and low values with a cycle of approximately 4 weeks throughout the summer. Values were low throughout the next winter and increased again in May, 1982. A regular cycle of high and low values was not observed, as in 1981, but rather $N^2(0-6)m$ was low throughout July and August of 1982 (Figure 42).

$N_2(0-10)m$ was low throughout the winter of 1980-1981, increased in mid-May to a maximum value in late July and decreased again to a minimum value in October, 1982. $N_2(0-10)m$ increased again in May, 1982, but did not follow the same clear seasonal pattern as observed in 1981. Decreases were seen at the beginning of July and in mid-August (Figure

Figure 46- Weekly time series plots of blue-green algal abundances
(spring-summer of 1981 and 1982).





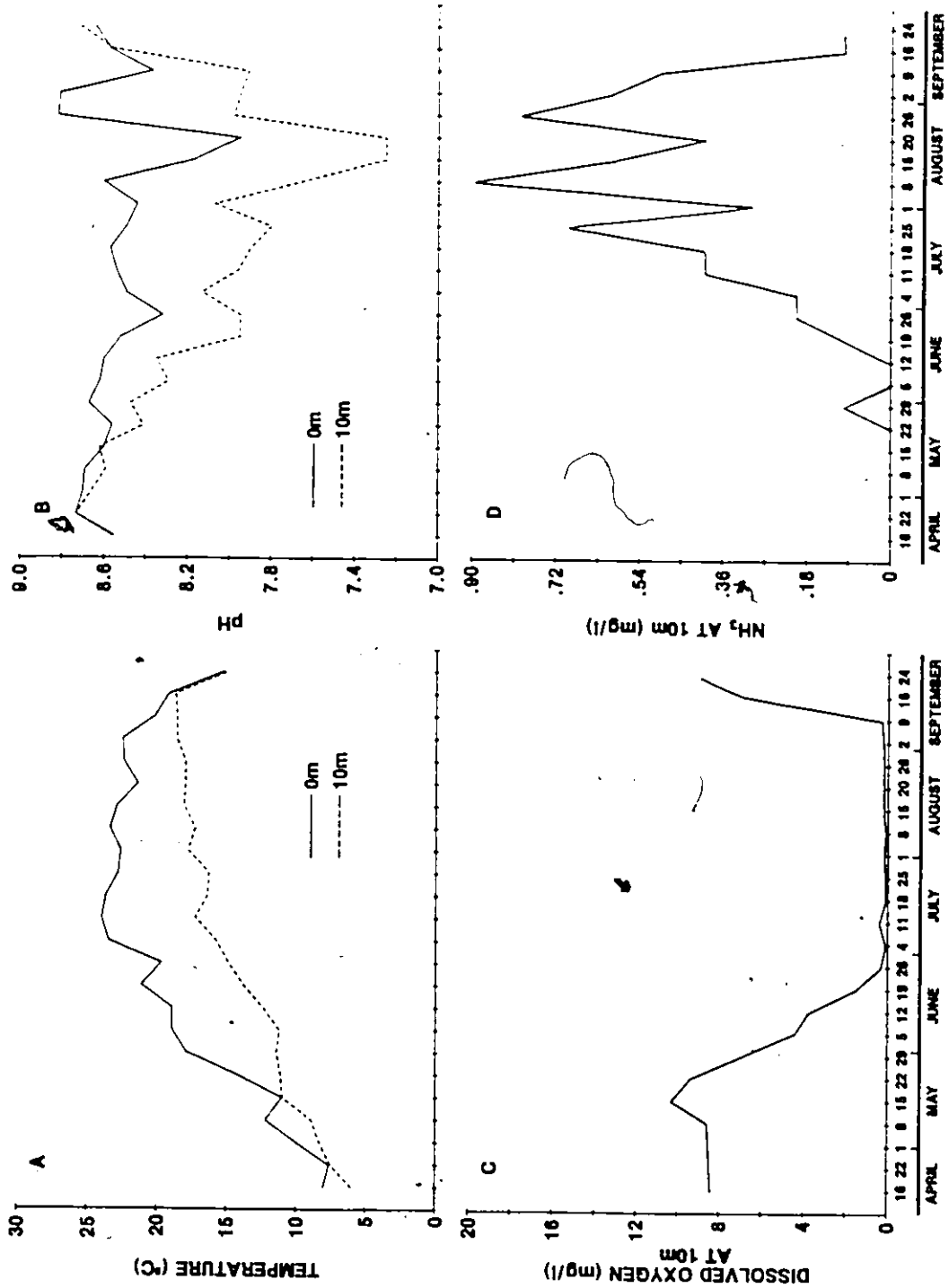
42).

Time series ~~plots~~ of temperature at 0m and 10m, pH at 0m and 10m, dissolved oxygen (DO) at 10m and NH_3 at 10m on a weekly basis for the spring through summer of 1981 and 1982 are shown in Figure 47. The conditions at 10m were very different for the two summers. In 1981, the water at 10m became anoxic at the beginning of July and remained anoxic until mid-September. NH_3 concentrations at 10m were high ($> .2$ mg/l) from July 4 to October 22 in 1981. In contrast, in 1982, the water at 10m became anoxic for only a week or two in late July and NH_3 concentrations were high only from August 3 to August 24.

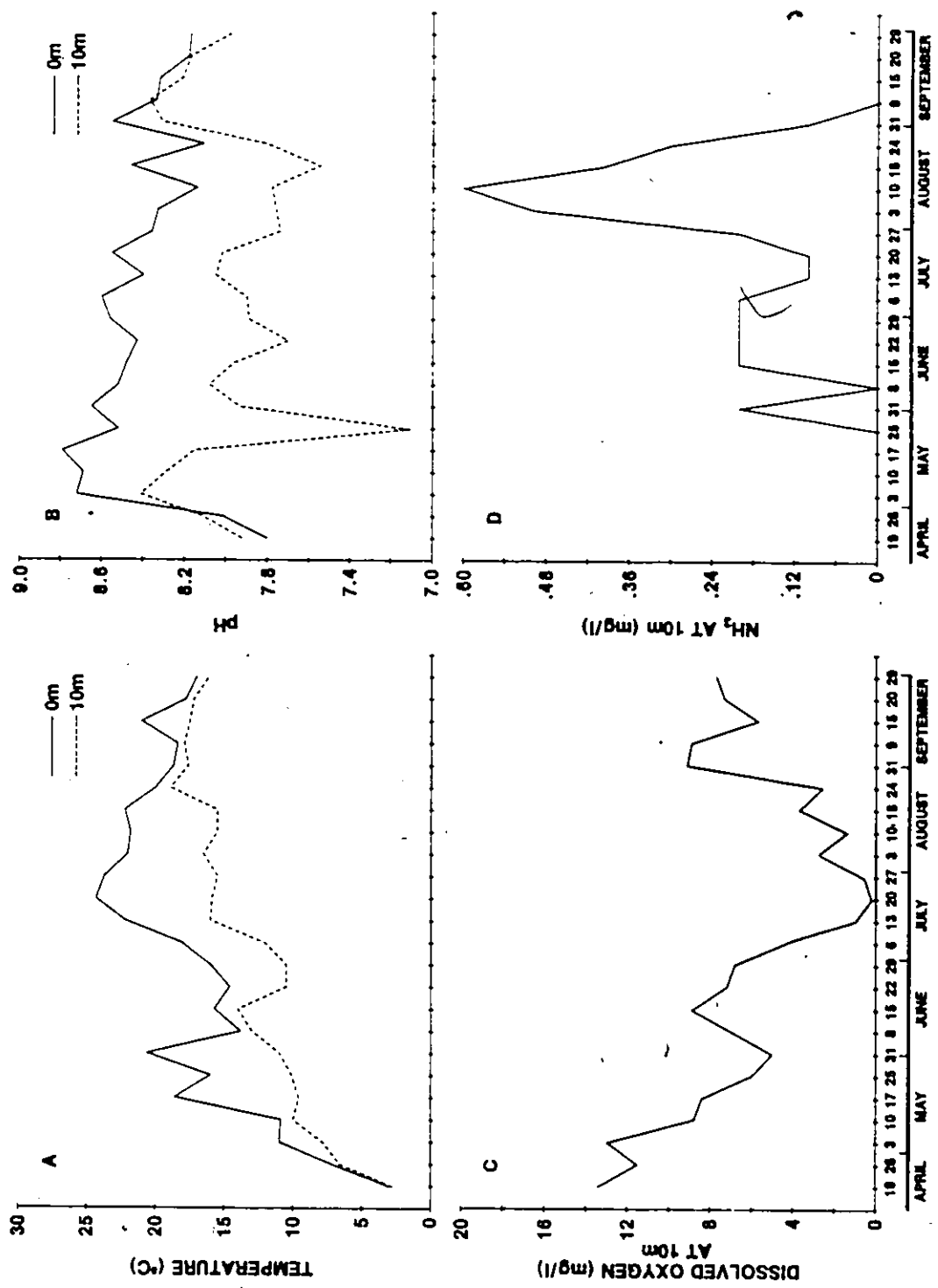
The flow rates through the dam in Guelph Lake are altered in the winter months to decrease the lake level in preparation for the high inflow rates which occur in the spring. In 1980, the lake level was lowered at a slow steady rate from September through December and at a more rapid rate in January and February of 1981 (Figure 48). Lake level was rapidly restored in late February, 1981. The pattern of draw-down was similar in the fall of 1981, however, the lake level was not restored until late March, 1982. The average lake level from May 8 to August 20 was slightly lower in 1982 than in 1981. However, the average flushing time from May 8 to August 20 in 1982 was not significantly different from that in 1981 (Table 15).

In 1981, the highest $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$ levels were observed on April 9. Levels then declined at a rate of .07 mg/l/week to reach a minimum

Figure 47- Weekly time series plots of temperature and pH at 0 and 10m and dissolved oxygen (DO) and ammonia (NH_3) at 10m (spring-summer of 1981 and 1982).



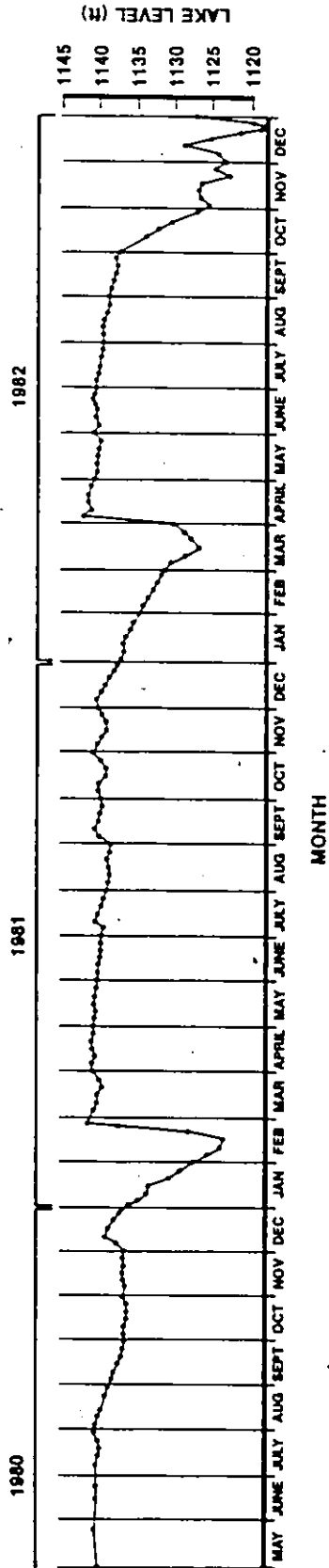
1981



1982

Figure 48- Operating rule in Guelph Lake. Changes in the lake level
are shown.

OPERATING RULE - GUELPH DAM



Hydrological Information

A comparison of spring-summer in 1981 to 1982
(May 8 - August 20, daily records for both years)

	1981	1982
Lake level (ft.)		
mean	1140.0	1139.6
sd	.4	.6

Flushing time (days)

mean	165	180
sd	76	49

in late July and August. In 1982, the levels and rates of decline appeared very similar (Figure 49). SRP levels fluctuated throughout the spring and summer of 1982 and 1981 in a similar manner (Figure 49). N/P ratios as $(\text{NO}_3\text{-N} + \text{NO}_2\text{-N}/\text{SRP})$ were more variable and higher in the spring and summer of 1981 than in 1982, especially during the first 10 weeks of this period (Table 16).

Figure 49- Weekly time series plots of nutrients (soluble reactive phosphorus(SRP), total phosphorus(TP), combined nitrate and nitrite ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N}$) and silica(Si) over the 111 weeks sampled.

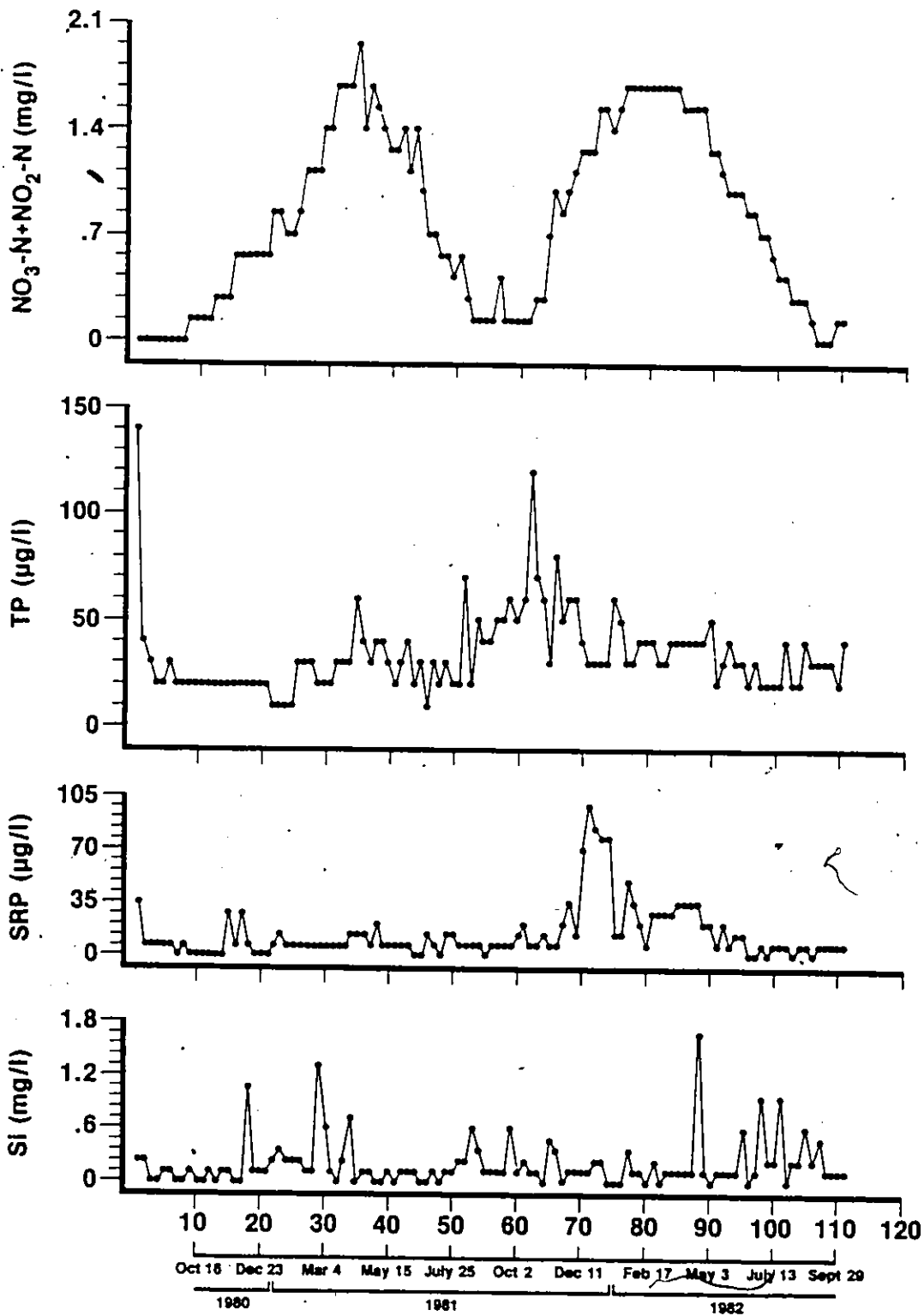


Table 16

Ratio of combined nitrate and nitrite to soluble reactive phosphorus ($\text{NO}_3\text{-N} + \text{NO}_2\text{-N} / \text{SRP}$ in the (0-7)m integrated sample)

Weekly values
(spring-summer of 1981 and spring-summer 1982).

Date	Ratio	Date	Ratio
1981		1982	
April 9	174	April 8	42
16	130	19	41
22	177	26	78
May 1	82	May 3	71
8	185	10	124
15	250	17	57
22	202	25	144
29	381	31	66
June 5	198	June 8	84
12	519	15	275
19	286	22	269
26	64	29	179
July 4	114	July 6	212
11	600	13	140
18	54	20	98
25	41	27	90
Aug. 1	76	Aug. 3	88
8	42	10	45
15	44	18	42
20	29	24	44
26	61	31	7

The spring-early summer (first 9 weeks) means for the $\log_{10} \text{NO}_3\text{-N} + \text{NO}_2\text{-N} / \log_{10} \text{SRP}$ were significantly different, however, the means over the whole spring-late summer were not significantly different.

(IV) DISCUSSION

IV-1- Temporal and Spatial Variability

IV-1.1- Spectral Analysis of Temporal Variability

In this study, spectra obtained from different data sets (111 weekly values, 105 daily values and for temperature only, 576 values taken every 20 min.) were combined. The more correct, although impractical way of looking at a spectrum covering the same time scales as the combined spectrum, would have been to sample at the higher frequency interval over the full 111 weeks.

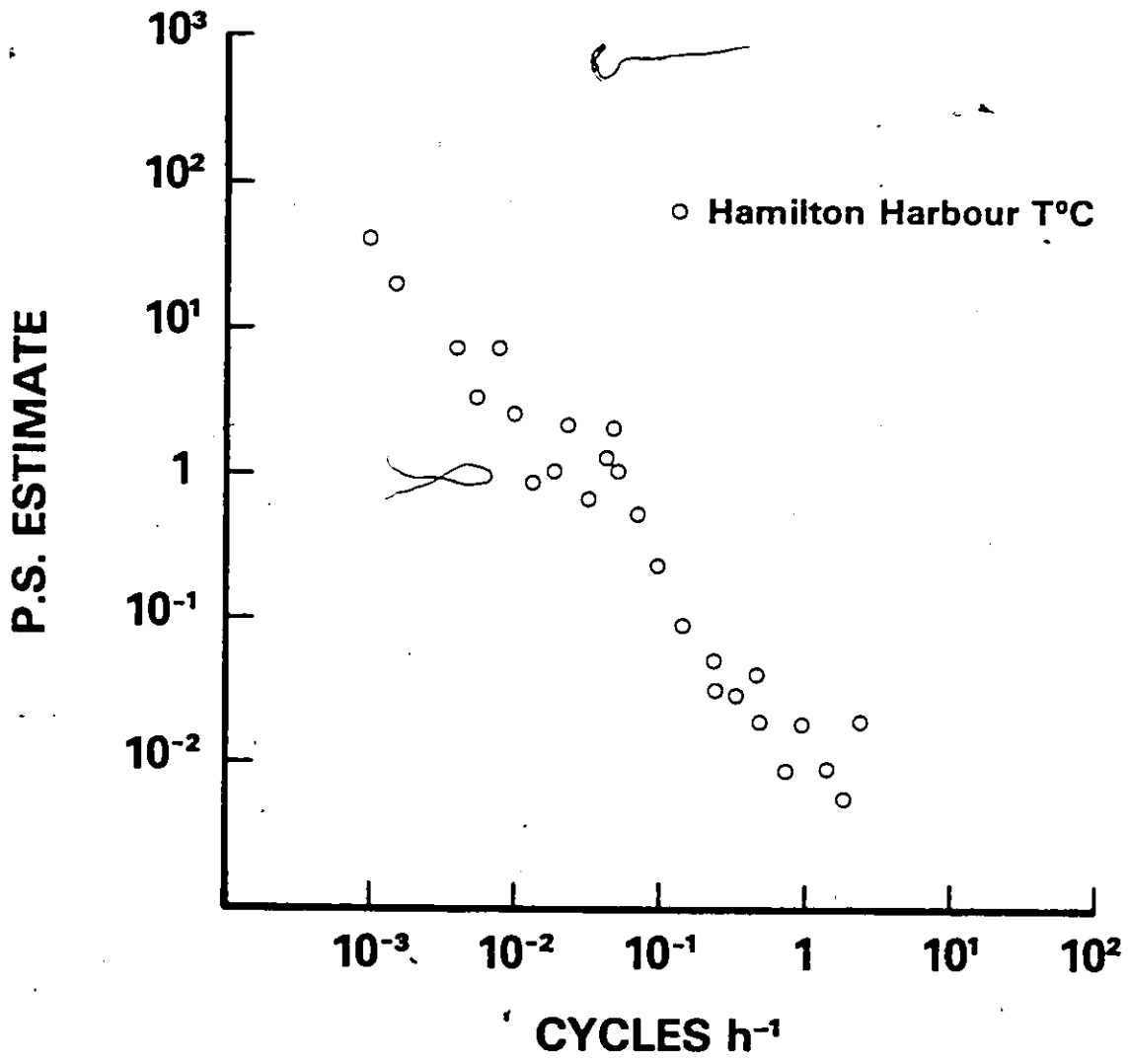
The power spectra for temperature at 0m and temperature at 4m followed a slope of $-5/3$ with increasing frequency, on a log-log plot, as expected for a passive scalar within the flow field, from a period of 280 days down to 2 days. A large increase was then observed at a period of 1 day. This strong diurnal periodicity is not representative of the daily variability on average over the year. It does serve to demonstrate that in July, 1981, daily temperature differences were only an order of magnitude less than yearly differences. Blue-green algae which have the ability to regulate buoyancy would be favored under such thermal conditions. Under conditions of high thermal stratification

algal cells which could not regulate buoyancy might sink out of the euphotic zone. The possession of gas-vacuoles by blue-green algae would tend to increase the probability of their re-entry into the euphotic zone during periods of intense stratification (Ganf, 1974). The power spectral estimates for the temperature at 0m and at 4m continued to decrease at a slope of $-5/3$, from a period of 1 day down to .028 days. At these periods, the power spectral estimates at 4m were noisier than at 0m. This extra noise was likely due to internal waves.

In contrast, the power spectrum for temperature at 0m in Hamilton Harbour does not show this strong diurnal periodicity (Figure 50). In the late summer, blue-green algae become dominant in Guelph Lake but not in Hamilton Harbour.

In a turbulent environment horizontal and vertical diffusion ensure that time and space are interrelated. Dye diffusion studies have suggested that a patch size of 1 km is approximately equal to a period of 1 day (Bowden, 1970, Okubo, 1971, Boyce, 1974). Other workers (Platt and Denmann, 1975, Richerson et al., 1975, Powell et al., 1975, Denmann and Platt, 1976, Demers et al., 1979) have studied power spectra for chlorophyll-a calculated from time series obtained by continuously sampling one station and found that in different environments there was a range of length scales for which chlorophyll behaved as a passive scalar whose local abundance was controlled by physical transport. For example, in the Gulf of St. Lawrence, Platt and Denman (1975) found that at length scales < 5 km, chlorophyll-a behaved like a passive scalar

Figure 50 Power spectral estimates for the temperature at 0m
in Hamilton Harbour.



within the flow field and that at length scales > 5 km biological processes became important. In Lake Tahoe, Powell et al. (1975) found that at length scales < 100 m, chlorophyll-a behaved like a passive scalar and that at length scales > 100 m, biological processes became important. Some flattening of the power spectrum for chlorophyll-a in Guelph Lake occurred at higher frequencies and lower frequencies suggesting that at these length scales biological processes were important.

The object of using power spectral analysis on time series of N^2 , wind speed, z_{eu}/z_m and nutrients was to determine the dominant physical and chemical cycles in the system. Environmental variability was detected at scales of days to weeks.

IV-1-2- Time Series Analysis of Spatial Variability

IV-1-2-1- Horizontal Advection

The data clearly shows the existence of short-term (2-3 day) leads and lags between stations as nutrients, biomass and individual species moved within the basin. Two factors which are likely to be of importance are 1) the origin and 2) the vertical distribution of each variable. Whether the nutrient enters the lake mainly as a point source or as a diffuse source will influence station-to-station comparisons. Similarly, some phytoplankton species may grow more favorably or be recruited more heavily from one end of the lake. Blue-green algae may be recruited from the bottom muds or the inflow in the form of vegetative filaments, colonies or akinetes (Sirenko et al., 1969, Reynolds and Rogers, 1976, Jones, 1979, Livingstone and Jaworski, 1980, Fallon and Brock, 1981) or from the resuspension of algal material deposited on the lake edges (Topachevskij et al., 1969). Dinoflagellates such as Ceratium may be recruited from the germination of cysts or overwintering cells (Heaney and Talling, 1980).

The vertical distribution of the nutrient or phytoplankton species will also affect its rate and direction of horizontal advection. Some algal species may regulate their position in the water column through buoyancy regulation (blue-green algae) or active migration (for example, Ceratium). Algal species that cannot actively regulate their position, as well as inanimate seston may accumulate just in or below

the layers where their sinking speed slows down, for example, in colder waters (Margalef, 1978). The rate of sedimentation depends on particle size, shape and density (Smayda, 1970). Under conditions of mild to moderate wind stress, algal cells and nutrients in the surface waters are likely to accumulate on the leeward side of the lake (George and Edwards, 1976, Heaney, 1976, Stauffer, 1982). Similarly, algal cells and nutrients that are positioned at a lower depth may be advected in the opposite direction and may accumulate on the windward shore. A knowledge of the diel migration patterns of Ceratium hirundinella has been used to predict the horizontal patchiness of this organism in Esthwaite (Heaney, 1976, Harris, Heaney and Talling, 1979, Heaney and Talling, 1980). When Ceratium was concentrated in the surface waters, transport was downwind. When concentrated at a lower depth, transport was in the opposite direction. George and Edwards (1976) also found that they could predict the horizontal distribution of blue-green algae and crustacean plankton from a knowledge of their vertical distributions.

Since Guelph Lake is a reservoir, the direction of net horizontal transport would likely be from station 3 (inflow end) to station 1 (outflow end). Lags between station 1 and station 3 would be expected for variables originating mainly from the inflow end of the lake. The 3-day lags between station 1 and station 3 (separation - 1 km) for SRP and Stephanodiscus suggest an advection rate of .4 cm/s. Longer lags could occur for such variables if the net horizontal advection from station 3 to station 1 were delayed. This was observed

for Aphanizomenon where the advection rate was .2 cm/s. Aphanizomenon appeared to be preferentially recruited from the shallower (station 3) end of the lake. A possible mechanism for this delay is vertical stratification at such a depth that transport occurred for periods of time in the opposite direction. Examples of vertical profiles of Aphanizomenon abundance at station 1 show that this algae is capable of strong layering (Figure 39). Periods of high water column stability where countercurrent flow across the thermocline is theoretically possible, did occur at times throughout the 105 days (Figure 23).

Leads of the order of a few days would be expected if the variable originated mainly from the outflow end and its vertical distribution was such that the majority of its advection was in the opposite direction to Aphanizomenon. Leads of this time scale were observed for Ceratium (advection rate = .6 cm/s) and Lyngbya (advection rate = 1.1 cm/s). Examples of vertical profiles of abundances for both of these species at station 1 (Figures 40, 41) showed that surface accumulations as well as peaks at lower depth were possible. Shorter lags could occur if the variable were not originating preferentially from one end of the lake but rather as a diffuse source (for example, $\text{NO}_3^- \text{-N} + \text{NO}_2^- \text{-N}$). Similarly, the 12 hour lag observed for chlorophyll-a (advection rate = 2.5 cm/s) may be explained by assuming that phytoplankton growth is occurring throughout the basin but, more importantly, the chlorophyll pattern is made up of a number of species which may be advected in different directions simultaneously.

IV-1-2-2- Redistribution by vertical mixing

Significant cross-correlations at longer lags and leads (10-20 days) would arise if all stations showed similar fluctuations at such time scales: fluctuations driven by basin-wide events such as the entrainment of hypolimnetic water and major readjustments in the depth of the thermocline. The periodicities observed in water column stability and in the wind speed data showed strong evidence for 10 - 20 day fluctuations which are known to be associated with the passage of atmospheric weather systems through temperate latitudes (Boyce, 1974). These results suggested that the significant cross-correlations obtained in the between station and within station comparisons for SRP and TP were due to periods of vertical mixing rather than being statistical outliers of no significance.

IV-2- Relationship between environmental variables and phytoplankton dynamics

IV-2-1- DAILY TIME SERIES (Spring-summer, 1981)

The phytoplankton dynamics observed in Guelph Lake in the spring and summer of 1981 (Figure 21) showed a typical progression where spring diatoms gave way to summer species better adapted to survive in stratified lakes. Reynolds et al. (1983) suggest that faster growing colonists and opportunistic species (r-selected) are among the first to dominate and that there follows a change towards slower growing

loss-resistant species that compete more efficiently for the available resources (K-selected).

Influence of water column stability on chlorophyll, diversity and rate of community change-

The observation that cross-correlations between non-stationary N^2 and non-stationary chlorophyll were negative at lower positive and negative lags (Figure 34) is as expected. High chlorophyll values are expected when N^2 values are low and chemical status is high (Round, 1971). The observation that cross-correlations between non-stationary N^2 and non-stationary diversity were positive (Figure 35) is in agreement with the generally accepted idea that diversity increases under stratified conditions (Harris, 1980, Wall and Briand, 1980, Nalewajko et. al., 1981) due to the increased spatial and temporal heterogeneity. Cross-correlations between stationary residuals of N^2 and stationary residuals of diversity, however, suggested that diversity increased prior to the increase in N^2 . Calm conditions may have resulted in algal cells moving upward and thereby increasing the phytoplankton diversity in the integrated sample, prior to increases in N^2 . Increases in the rate of community change on a daily basis were observed in late May (loss of diatoms), mid-June (emergence of Cryptomonads) and early July (emergence of summer blue-greens). The rate of community change was low throughout the rest of the daily time series (Figure 21). The observation that cross-correlations between non-stationary $N^2(0-10)m$ and non-stationary rate of community change are negative at longer positive

lags (Figure 36) is in agreement with Reynolds' (1980) observation that rates of community change were lowest during the late phases of thermal stratification. However, an increase in the rate of community change occurred coincident with the initial onset of thermal stratification, here, suggesting a positive correlation between water column stabilization and rate of community change.

Loss of diatoms-

The sedimentation traps were placed in Guelph Lake near the peak of the Asterionella, Stephanodiscus and Melosira populations (Figure 45). Initial sinking rates were low (Table 5). Sinking rates of Asterionella and Stephanodiscus increased after May 1 and were high until the end of May. The sinking rates for Melosira increased by May 1, decreased again by May 9 and increased again by May 19. Cyclotella had already started to decline in abundance before the traps were set (Figure 45). The sinking rates observed for Cyclotella were high throughout.

Possible reasons for the increase in sinking rate include the population stage of growth and physical conditions. Exponentially growing diatom cells have slower sinking rates than stationary phase cells (Titman and Kilham, 1976, Jaworski et al., 1981, Reynolds and Wiseman, 1981). Laboratory studies have shown that the sinking rate of Asterionella formosa can be increased by limiting CO₂ uptake either by CO₂ depletion or by the addition of DCMU (Jaworski et al., 1981).

Sinking rates have been shown to increase with the onset of summer stratification (Walsby and Reynolds, 1979).

The population of Cyclotella (Figure 45) began to decline when surface pH values began to increase (Figure 47) and before the onset of summer stratification (Figure 42). The most drastic declines of Stephanodiscus and Asterionella occurred between May 1 and May 9 (Figure 45) coincident with the onset of summer stratification (Figure 42), increases in surface water temperature and high pH values (Figure 47). Increases in the V_t values calculated from the upward trap catches at 10m, were seen from May 1 to May 9 (Table 6). This suggested that prior to this a metalimnetic barrier may have prevented cells from sinking to this 10m depth. Reynolds (1973) has presented evidence that metalimnetic layers can delay temporarily the settling of planktonic diatoms.

Increases in N^2 were followed by decreases in diatom abundance. Cross-correlations between N^2 and Stephanodiscus abundance (daily values May 8 - June 6) were negative with a peak on the same day. However, when the stationary residuals from each data set were cross-correlated, no significant values were observed (Figure 37).

The results here show good agreement between the proposed sedimentary fluxes of diatoms and the corresponding maximal standing crop (Table 7) as in Reynolds et al. (1982a and 1982b), Livingstone and Reynolds (1981) and Reynolds and Wiseman (1982). It may be concluded

that for Stephanodiscus, Asterionella, Melosira and Cyclotella, most of the accountable cells were eventually removed intact to the sediments and that the sediment traps provided a reasonable estimate of their sedimentary flux into Guelph Lake.

Emergence of Cryptomonads-

Increases in zeu and decreases in zm resulting in an increased zeu/zm ratio (Figure 24) were observed after the diatoms had declined. Significant, positive cross-correlations were observed when zeu/zm residuals were compared to Cryptomonas erosa (9 days), Cryptomonas ovata (10 days) and Rhodomonas (14 days) residuals (Figure 38). Haffner, Harris and Jarai (1979) also observed an increase in the abundance of Cryptomonads in Hamilton Harbour after a phase of rapid warming which resulted in an increase in the zeu/zm ratio. Small flagellates have growth rates of 4-10 divisions per week (Lund and Reynolds, 1982). Harris et al. (1982) suggested that small flagellates such as Rhodomonas are photosynthetically inefficient cells that are capable of growing rapidly if there is sufficient solar energy.

Emergence of blue-green algae-

Information from the trap catches may be useful in determining the origin of the summer bloom forming populations of blue-green algae. Preston et al. (1980) and Reynolds et al. (1981) working with experimental enclosures have suggested that summer populations of

Microcystis aeruginosa originate from vegetative colonial stock that overwinters on the bottom sediment each year. Information from both upward and downward facing sedimentation traps near the bottom surface and sediment areal concentrations of Microcystis colonies led Reynolds et al. (1981) to conclude that there was no mass transfer of overwintering colonies to the water column but rather that intensive growth from individual cells in the old colonies lead to the formation of new infective colonies. The early recoveries of colonies in downward facing traps were consistent with an input of similar order from the sediments and exceeded contemporary catches in upward facing traps, at least while the plankton population was small. However, there was no decrease in the benthic population. They suggested that it was impossible to distinguish between chance trappings of colonies dislodged from and sinking back to the sediments as opposed to directed migratory movements. Livingstone and Reynolds (1981) working on the relatively deep Rosetherne Mere also suggested that it was unlikely that many of the overwintering Microcystis colonies returned to the plankton the next year.

In Guelph Lake, Lyngbya, Microcystis and Gomphosphaeria started to increase in abundance in mid-July (Figure 22, 46). The high specific migration activities of floating colonies of Microcystis (August 5) and Gomphosphaeria (August 12 and August 19) and of Lyngbya filaments (July 30, August 5 and August 12) at 10m (Table 8) suggested that in Guelph Lake a fair number of filaments and colonies were recruited from the sediments. The high rates of accumulation of TP in the downward trap at

10m (Figure 25) provided further evidence that resuspension of material from the sediments occurred at this time. If the trap recoveries at 10m were merely due to chance trappings of colonies or filaments dislodged from and sinking back to the mud, the specific migration activities would not be expected to be > 1 . A specific migration activity > 1 of either floating or sinking colonies or filaments implies that daily migration to higher or lower depths was in excess of the biomass of that species present at those depths. To fully quantify the contribution of overwintering colonies or filaments to the summer populations it would have been necessary to examine changes in the sediment areal concentrations of these species. It would also have been necessary to examine fluxes and areal concentrations in shallower areas of the lake.

The appearance of these three species of blue-green algae (Figure 22, 46) coincided with high $N^2(0-10)_m$ (Figures 23, 42) and the development of anoxia, high NH_3 , low pH and increases in temperature at 10m (Figure 24, 47) which would be expected to stimulate the formation of new infective colonies or filaments (Reynolds et al., 1981). Significant negative cross-correlations between residuals of DO at 10m and residuals of the abundance of Microcystis at a lag of 11 days and Gomphosphaeria at a lag of 4 days were observed (Table 9). The relationship between $N^2(0-10)_m$ and the abundances of these species was not clear. High $N^2(0-10)_m$ appeared to be necessary for the recruitment of these species but not necessary for their continued growth.

Aphanizomenon appeared in mid-May and reached its peak

spring-early summer abundance on May 23 (Figure 22, 46). Growth or recruitment of this blue-green algal species was initiated under different environmental conditions than for Microcystis, Gomphosphaeria and Lyngbya. The pattern observed in the sedimentation trap catches was consistent with the earlier suggestion that growth or recruitment of Aphanizomenon occurred preferentially near station 3 in Guelph Lake and that filaments were then transported towards station 1 (where the sedimentation traps were suspended). The fact that filaments showed up in the downward trap at 2m approximately 1 week before dispersal to the lower traps suggests that filaments were transported from station 3 to station 1 at a depth of 2-3m.

Use of sedimentation traps-

The problems involved in using traps of this design have been discussed by Reynolds (1975). In general, traps operate most efficiently under non-turbulent conditions. Some unexpected results were seen with the traps at 4m on May 19 and May 26 (Figures 26, 27, 28 and 29). On these dates, the downward facing traps caught more diatoms than the upward facing traps suggesting that the traps were twisted on these occasions. Despite possible problems of underestimation and overestimation the trap catch data was useful in explaining the loss of spring diatom species and the recruitment of summer blue-green algal species.

Relationship between physical variables and vertical heterogeneity-

Vertical heterogeneity and surface concentrations of Lyngbya, TP, SRP and chlorophyll (July 30 to August 19, 1981) were most highly cross-correlated to the Richardson number from the day before (Table 13). Lower, but still significant cross-correlations were seen when vertical heterogeneity and surface concentrations were compared to the wind speed from the day before (Table 12). Some significant cross-correlations were also seen between N^2 and vertical heterogeneity or surface concentrations on the same day and the day before (Table 11). In general, a high Richardson number, rather than a low wind speed or a high N^2 value alone, was the best predictor of high vertical heterogeneity and high surface concentrations during this sampling period.

Higher cross-correlations between environmental variables and vertical heterogeneity or surface concentrations occurred in subsamples of the daily time series taken from the later part of the summer. For example, low wind speeds in late June-early July (Set A) did not necessarily result in high surface chlorophyll concentrations (Table 12). This suggests that positively buoyant algae were not abundant at this time. Low wind speed may be a resource which is not exploited unless buoyancy regulating or motile algal species are present.

The vertical heterogeneity of SRP responded to increased Richardson number with a longer time lag than for TP or chl (Table 13).

Significant cross-correlations were observed when the vertical heterogeneity of SRP was compared to the Richardson number 4 days earlier. In an earlier section it was shown that the horizontal transport of SRP differed from that of TP and chlorophyll. A less than 1-day lag from station 3 to station 1 for TP (Figure 13a) and chlorophyll (Figure 15a, 15b) was observed, whereas a 3-day lag from station 3 to station 1 for SRP (Figure 12a, 12b) was observed. This suggested that the vertical distribution of SRP differed from that of TP and chl. The results obtained from the cross-correlations and auto-correlations of SRP at different depths (Table 2 and Figure 20) suggested that on average over the 105 days the top 2m was distinct from the rest of the water column with regards to SRP concentrations. In contrast, when TP values from 0, 5 and 10m were cross-correlated all combinations had simultaneous maximal values (Table 3).

The intensity of a surface bloom is influenced by the extent and duration of calm conditions, the size of the buoyant population, the average population flotation rate and the extent of the vertical heterogeneity immediately before the onset of calm conditions (Reynolds and Walsby, 1975). An important factor in determining buoyancy is the relationship of z_{eu}/z_m (Reynolds and Walsby, 1975). If z_{eu} is much less than z_m , the average light intensity which is received by the algae is sub-optimal and the relative gas-vacuolation is high. Organisms which could migrate to the surface layers under calm conditions would have a competitive advantage. The z_{eu}/z_m ratios in Guelph Lake were consistently low ($< .7$) throughout late July and August (Figure 24).

Significant cross-correlations between Richardson numbers and the vertical heterogeneity and / or surface concentrations of blue-green algae present in August, other than Lyngbya, such as Gomphosphaeria and Microcystis were not observed. At this time, the surface abundance of Lyngbya was significantly correlated to surface chlorophyll and TP concentrations (Table 14). The surface accumulations of chlorophyll were mainly due to the accumulation of Lyngbya filaments. The fact that calm conditions (high Richardson numbers) consistently resulted in surface blooms suggests that throughout this time period a stock of positively buoyant Lyngbya filaments with sufficient flotation rates to respond on a daily basis must have been available. Positively buoyant colonies of Microcystis and Gomphosphaeria must not have been available in sufficient amounts or must not have had sufficient flotation rates to cause surface blooms under these environmental conditions. The average flotation rate is affected by the colony or filament size and the relative gas-vacuolation. The difference in relative gas-vacuolation may be related to the stage of population development. Increases in relative gas-vacuolation have been associated with the onset of growth limitation in lab cultures and bloom forming natural populations of blue-green algae (Klemer et al., 1982). Lyngbya increased and declined in abundance throughout this time period whereas Microcystis and Gomphosphaeria increased in abundance throughout (Figure 22).

IV-2-2- WEEKLY TIME SERIES (fall/1980-fall/1982)

The delayed onset of the spring bloom in 1982 (Figure 45) was a

result of the later date of lake level restoration in 1982 (Figure 48). The decline of the spring diatom bloom in 1982 occurred under similar environmental conditions as in 1981. Cyclotella declined (Figure 45) as the surface pH increased (Figure 47). Asterionella, Stephanodiscus and Melosira declined (Figure 45) as water column stability ($N^2(0-6)m$) increased (Figure 42). Unlike in 1981, these diatoms were present in measurable quantities throughout most of the summer in 1982 due to periods of intermittent mixing (Figure 45).

The increased abundance of Aphanizomenon observed in 1982 as compared to 1981 (Figure 46) may have been a result of the different physical conditions (Figure 42), the later date of lake level restoration (Figure 48), the difference in the spring-early summer $NO_3-N + NO^2-N/SRP$ ratios (Table 16) or more likely a combination of these factors. The recruitment of Aphanizomenon flakes is favored when the bottom waters are oxygenated (Lynch, 1979). Lynch and Shapiro (1981) have suggested that the sediments provide a refuge which allows new Aphanizomenon colonies to grow to an ungrazeable size before they enter the water column. In their study, flakes of Aphanizomenon never appeared in the presence of Daphnia pulex when the bottom waters were anoxic or when the water column was artificially separated from the bottom sediments. Anoxia at 10m only occurred for a short period of time in Guelph Lake in 1982 as compared to most of the summer in 1981 (Figure 47). This difference was due to the increased frequency of mixing events in 1982, as compared to 1981 (Figure 42). Aphanizomenon occurred in flake form and Daphnia pulex was present in Guelph Lake in

both summers. It may be that growth of flakes at the bottom was only possible during late May and late August of 1981 as compared to most of the summer in 1982. The effect of mixed versus stratified conditions on the growth of Aphanizomenon in the surface waters is not as clear. The major increase in Aphanizomenon abundance in 1982 (Figure 46) coincided with an increase in $N^2(0-10)m$ and a decrease in $N^2(0-6)m$ (Figure 42). A decrease in $N^2(0-10)m$ in mid-August, 1982, resulted in an initial decrease of Aphanizomenon in the (0-7)m sample, but abundances were quickly restored even though $N^2(0-10)$ continued to decline. The initial decrease in abundance may have resulted from a redistribution of flakes to a greater depth. Growth of Aphanizomenon appeared to be favored by a high $N^2(0-10)m$ and a low $N^2(0-6)m$. Some observations from the literature suggest that blue-green such as Aphanizomenon become dominant under stratified conditions (Shapiro, 1973, Konopka et al., 1978). Others (Hammer, 1970, Barica, 1975 and Haertel, 1976) reported that Aphanizomenon is often found in shallow lakes which tend to circulate continuously so that nutrients are recirculated from bottom decomposition. Reynolds (1980) suggested that Aphanizomenon is found under both stratified and non-stratified conditions. 8

The date of lake level restoration may also influence the recruitment of Aphanizomenon by affecting the germination of akinetes. The conditions favoring the germination of akinetes are poorly understood but it is believed that temperature, light and nutrients are of importance (Wildman et al., 1975). Since the majority of the Aphanizomenon akinetes probably overwintered on the sediments of the

shallower areas of Guelph Lake, the later date of lake level restoration in 1982 (Figure 48) may have altered the environment to favor germination of these akinetes.

Low N/P ratios favor gas-vacuolate, N_2 fixing blue-green algae such as Aphanizomenon (Schindler, 1977, Leonardson and Bengtsson, 1978). Similarly, shifts in dominance from N_2 fixing blue-greens to non N_2 fixing blue-greens or greens by adding N to limnocorrals before the N_2 fixing blue-greens are very abundant have been observed (Barica et al., 1980). Leonardson and Ripl (1980) observed that the addition of nitrate to ponds was followed by die-offs of the Aphanizomenon populations present. Although the fluxes of N and P in Guelph Lake are not known, it is not unreasonable to suggest that the significantly ($p < .05$) lower $NO_3-N + NO_2-N/SRP$ ratios in the spring-early summer of 1982 (Table 16) favored the development of N_2 fixing blue-greens such as Aphanizomenon.

The recruitment of blue-green algae such as Microcystis, Gomphosphaeria and Lyngbya was favored by stable or stratified conditions. These blue-green algae do not fix N_2 but rather use primarily ammonium as a nitrogen source (Leonardson and Ripl, 1980, Liao and Lean, 1978, Kappers, 1980). Consequently, the abundances of these algae were much higher in 1981 than in 1982 (Figure 46).

The phytoplankton dynamics observed in Guelph Lake in the spring and summer of 1982 did not follow the typical progression from spring diatoms to summer species better adapted to survive under stratified

conditions as seen in 1981. Decreases in $N^2(0-10)m$ occurred several times throughout the summer in 1982 (Figure 42). In limnocorrals, which were intermittently mixed, Reynolds et al. (1983) found that at each mixing event the competitive advantage shifted from r-selected species back to diatoms and that the effect of mixing on the more K-selected species was to temporarily arrest their increase and delay their eventual attainment of a dominant biomass through the intervening periods of stable conditions. The patterns observed for the rate of community change in the spring through summer of 1981 and 1982 differed greatly (Figure 43). In 1981, rates of community change increased in late May, mid-June, early July and late July and remained low throughout August and September. The increase in late May coincided with the loss of diatoms as a result of the initial onset of thermal stratification. The increase in mid-June coincided with the emergence of Cryptomonads and lagged an increase in the z_{eu}/z_m ratio. The increase in early July coincided with the emergence of summer blue-green algae and the development of anoxic conditions at 10m. The increase in late July coincided with the loss of some species (Merismopedia and Ceratium) favored under stratified conditions and an increase in some of the diatoms (Melosira) as a result of a decrease in $N^2(0-10)m$. In contrast, in 1982, rates of community change were low in May and June and increases were observed in mid-July, early August, late August and late September. Increases in rate of community change coincided with changes in water column stability. Under stratified conditions, Aphanizomenon may be considered as having a more r-selected strategy. Other blue-green algae such as Microcystis, Gomphosphaeria and Lyngbya may

have a more K-selected strategy.

IV-3- General Discussion

IV-3-1- The interpretation of field data

The results of this study suggest that strong basin scale mixing effects cause events observed at a single station to be a function of events at the station plus advective effects from populations washed in from elsewhere. Estimation of such parameters as productivity/biomass (P/B) ratios and growth rates will depend heavily on physical processes within the basin and the characteristic depth profile of each variable. Such estimates may change drastically for reasons due more to shifts in species composition than to physiological adaptation. Previously published productivity data for Hamilton Harbour which showed week to week fluctuations in physiological parameters in response to mixed layer depth changes (Harris et al., 1980a) has recently been examined. Physiological changes were shown to be due to changes in the phytoplankton assemblages rather than to physiological adaptation (Harris et al., 1982).

Thus the use of chlorophyll as a measure of biomass hides much important information about the changing species composition of the assemblage. The species composition is an important determinant of many physiological processes (Harris et al., 1982) and cannot be ignored. The pattern observed for the advection of chlorophyll is the result of

the advection patterns of the individual species which may be moving in different directions at the same time. The 2-3 day horizontal mixing events and the 10-20 day vertical mixing events will influence results obtained from weekly sampling making them difficult to interpret. The vertical distribution of algae affects the patterns of horizontal advection and vertical distribution is, itself, a function of the water column stability. Even in this small basin, therefore, there are some complex interactions between the time scales of vertical and horizontal mixing. The characterization of these important mixing scales is a necessary preliminary step in both the design of field sampling schemes and the understanding of phytoplankton dynamics.

IV-3-2- Non-equilibrium versus Equilibrium

Significant environmental variability in Guelph Lake has been detected at time scales of days to weeks, as in Hamilton Harbour (Sephton, 1980, Harris, 1982). The majority of the increases observed in phytoplankton succession rate occurred in response to allogenic factors. Several episodes were initiated in the spring through fall periods of 1981 and 1982. This does not suggest that autogenic succession or competition did not occur, but merely that the environment changed with sufficient rapidity that progression to competitive exclusion was disrupted. Experimental work (Titman, 1976, Tilman, 1977, Tilman et. al., 1981) has shown that up to 50 days are required for competitive exclusion to occur in phytoplankton cultures. Time lags between changes in environmental variables and changes in algal

abundances occurred. Available resources, for example, calm conditions, were not necessarily exploited. These results suggest that the phytoplankton community of Guelph Lake, like Hamilton Harbour, is a non-equilibrium system.

IV-3-3- Use of Bivariate Time Series Analysis in Phytoplankton Ecology

In this study, cross-correlations and/or cross-spectral analysis were used in 2 ways:

- 1) in station-to-station comparisons of the same variable to determine the time scales for horizontal and vertical mixing,
- 2) to compare an input or x time series (environmental variable) to an output or y time series (biological variable). The purpose of such comparisons was to determine if x was a leading factor of y.

There are 4 possibilities which may occur when the input stationary residuals and output stationary residuals are cross-correlated (Haugh and Box, 1977):

- i) the 2 series are uncorrelated at all lags and the x series will not aid in the forecasting of y,
- ii) the 2 series are only correlated on the same day,
- iii) there is at least one significant cross-correlation for $k > 0$ and there are no significant cross-correlations at -ve lags. It would then be possible to build a dynamic regression model for y on x and

thereby improve the forecastability of y .

iv) there exists significant cross-correlations for some +ve as well as -ve lags. This would indicate a feedback from y to x and it would not be possible to build a dynamic regression of y on present and past x .

In station-to-station comparisons of the same variable, a Δt but the first possibility occurred in the cross-correlations. Short term lags and leads between stations were interpreted as being due to horizontal advection. Long term (10-20 day) cross-correlations were attributed to periodicities in vertical mixing.

In input to output comparisons of different variables, the first possibility frequently occurred when the stationary residuals from each time series were cross-correlated even though cross-correlation estimates between the non-stationary time series were high. No attempts were made to develop distributed lag models relating the input to the output.

The use of cross-correlations and cross-spectral analysis assumes there is a linear relationship between the input and the output. Is this a reasonable assumption to make for example, between N^2 and the abundance of diatoms such as Stephanodiscus? Results from this study have shown that most of the accountable Stephanodiscus cells were eventually removed to the sediments (Table 7), therefore grazing was unlikely of importance in the loss of this algae. Increases in the

sinking rate of Stephanodiscus coincided with an increase in N^2 . However, if an equivalent decrease in N^2 were to then occur the abundance of Stephanodiscus would not necessarily return to its original level. This may explain why significant cross-correlations between the stationary residuals of N^2 and the stationary residuals of Stephanodiscus on a daily basis were not observed (Figure 37). Another reason for the lack of a clear relationship between N^2 and the abundance of Stephanodiscus is that N^2 is not the only factor affecting the sinking rate. The population stage of growth is also important.

It is not reasonable to assume that the abundance of a particular alga will respond the same way to an environmental variable over all stages of population growth. The recruitment of blue-green algae such as Microcystis, Gomphosphaeria and Lyngbya was favored by the development of stratified conditions, that is, high N^2 (0-10)m and the development of anoxic conditions at 10m. Further increases in the abundances of these algae were observed even though water column stability decreased. Environmental factors favoring the recruitment of an algal species may not necessarily have to be maintained for further increases to occur. The population may react differently, for example, in response to N^2 or Richardson number, depending on the stage of growth. For example, for surface blooms to occur, sufficient stocks of positively buoyant blue-green filaments or colonies must be present. However, relative gas-vacuolation and size and thereby relative buoyancy may vary with the stage of population growth. A restriction on the length of the data set is thus imposed by the nature of the time series

itself (Koopman, 1974). Koopman (1974) suggests that the complete data set should be divided into epochs, within which the generating mechanism for the time series is invariant. An epoch could then refer to a stage in population growth.

V) Summary

V-1- Temporal and Spatial Variability

Significant environmental variability was detected at time scales of days to weeks. Time-series analysis of daily data from the 3 stations demonstrated the existence of a) strong horizontal advection within the basin at a time-scale of 2-3 days and b) longer term periodicities (10-20) days associated with the passage of atmospheric weather systems. Different rates and directions of horizontal advection were observed for different variables.

The 2-3 day horizontal mixing events and the 10-20 day vertical mixing events will influence results obtained through weekly sampling making them difficult to interpret. The vertical distribution of the algae affects the patterns of horizontal advection and this vertical distribution, is itself, a function of water column stability. Even in this small basin, there are some interactions between the time scales of horizontal and vertical mixing. The characterization of these important mixing scales is a necessary preliminary step in both the design of field sampling schemes and the understanding of phytoplankton dynamics.

V-2- Relationship between environmental variables and phytoplankton dynamics

V-2-1- Daily time-series

The phytoplankton dynamics observed in Guelph Lake in the spring and summer of 1981 showed a typical progression where spring diatoms gave way to summer species better adapted to survive in stratified lakes. Chlorophyll-a concentrations were higher when water column stability was low. Phytoplankton diversity was higher under stratified conditions. Increases in the rate of phytoplankton community change on a daily basis occurred in late May (loss of diatoms coincident with the onset of thermal stratification), mid-June (emergence of Cryptomonads lagging an increase in z_{eu}/z_m) and early July (emergence of summer blue-greens coincident with development of anoxia at 10m).

Information from sedimentation traps was used to examine the loss of diatoms in the spring. Increased sinking rates for Cyclotella coincided with an increase in surface pH whereas increased sinking rates for Stephanodiscus, Asterionella and Melosira coincided with increases in surface water temperature and the onset of summer stratification. The results showed good agreement between the proposed sedimentary fluxes of diatoms and the corresponding maximal standing crop.

Information from the sedimentation traps was also useful in determining the origin of summer blue-greens such as Microcystis, Gomphosphaeria and Lyngbya. The high specific migration activities of floating colonies or filaments of these algae at 10m in late July and August suggested that in Guelph Lake, a fair number of colonies and filaments were recruited from the sediments. The high rates of accumulation of TP in the downward facing traps at 10m provided further evidence that resuspension of material from the bottom sediments was occurring at this time. The appearance of these three blue-green algae coincided with high $N^2(0-10)m$ and the development of anoxic conditions, high NH_3 , low pH and an increase in temperature which would be expected to stimulate the formation of new infective colonies or filaments.

High Richardson numbers were better predictors of high vertical heterogeneity than low wind speed or high N^2 alone. Higher correlations between environmental variables and vertical heterogeneity were obtained later in the summer. For example, low wind speeds in late June-early July did not necessarily result in high surface chlorophyll concentrations, whereas low wind speeds in August did.

V-2-2- Weekly time-series

The phytoplankton dynamics observed in the spring and summer of 1982 did not follow the typical progression from spring diatoms

to summer species as in 1981. The decline of the spring bloom in 1982 occurred under similar environmental conditions as in 1981. However, unlike in 1981, diatoms were present in measurable quantities throughout most of the summer. The most obvious difference in the phytoplankton communities in the two years was the much increased abundance of Aphanizomenon in 1982. Blue-green algae such as Microcystis, Gomphosphaeria and Lyngbya were less abundant in the summer of 1982 than in 1981. Phytoplankton diversity was lower in mid-summer of 1982 than of 1981.

The physical conditions were very different in the two summers. In 1981, $N^2(0-6)m$ fluctuated from high to low back to high values approximately every 20-30 days throughout the spring and summer. In 1982, $N^2(0-6)m$ remained relatively low throughout July and August. In 1981, $N^2(0-10)m$ increased in mid-May, reached a maximum in late July and declined to a low value again in October. In 1982, $N^2(0-10)m$ increased in mid-May but decreased to low values in mid-July and again in mid-August. Consequently, the conditions at 10m were very different for the two summers. In 1981, the water at 10m became anoxic at the beginning of July and remained anoxic until mid-September. NH_3 concentrations at 10m were high from July 4 to October 22 in 1981. In contrast, the water at 10m became anoxic for only two weeks in late July and NH_3 concentrations were high only from August 3 to August 24 in 1982.

The increased abundance of Aphanizomenon observed in 1982 as

compared to 1981 may have been a result of the different physical conditions, the later date of lake level restoration in 1982, the lower $\text{NO}_3\text{-N} + \text{NO}_2\text{-N}/\text{SRP}$ ratios in the spring to early summer of 1982, or more likely, a combination of these factors.

V-3-1 Non-Equilibrium versus Equilibrium

Results suggested that non-equilibrium conditions prevail in the phytoplankton community of Guelph Lake. Significant environmental variability was detected at time scales of days to weeks, time lags were observed to occur between changes in environmental variables and algal abundances and the majority of the increases in phytoplankton succession rate occurred in response to allogenic factors.

V-3-2 Use of Bivariate Time Series Analysis

In input to output comparisons of different environmental variables to biological variables, cross-correlations were frequently non-significant when the stationary residuals of each data set were used even though cross-correlation estimates between the non-stationary data sets were high. The use of cross-correlations and cross-spectral analysis assumes there is a linear relationship between the input and the output. This is not a reasonable assumption to make, for example, between N^2 and the abundance of Stephanodiscus. It is also not reasonable to assume

that the abundance of a particular alga will respond the same way to an environmental variable over all stages of population growth. This limits the lengths of the data sets available for analysis.

VI) REFERENCES

- Allen, T.F.H. 1977. Scale in microscopic algal ecology: a neglected dimension. *Phycologia* 16: 253-257.
- Barica, J. 1975. Collapses of algal blooms in midwestern pothole lakes: their mechanism and ecological impact. *Verh. internat. Verein. Limnol.* 19: 606-615.
- Barica, J., H. Kling and J. Gibson. 1980. Experimental manipulation of algal bloom composition by nitrogen addition. *Can. J. Fish. Aquat. Sci.* 37: 1175-1183.
- Bowden, K.F. 1970. Turbulence II. *Oceanogr. Mar. Biol. Ann. Rev.* 8: 11-32.
- Boyce, F.M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. *J. Fish. Res. Board Can.* 31: 689-730.
- Rox, G.E.P. and G.M. Jenkins. 1976. Time series analysis, forecasting and control. (rev.ed). Holden Day, San Francisco. 575p.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Demers, S., P.E. Lafleur, L. Legendre and C.L. Trump. 1979. Short-term covariability of chlorophyll and temperature

- in the St. Lawrence Estuary. J. Fish. Res. Board Can. 36: 568-573.
- Denman, K.L. and T. Platt. 1976. The variance spectrum of phytoplankton in the ocean. J. Mar. Res. 34: 593-601.
- Dixon, W.J., ed. 1969. BMD Biomedical computer programs, X series, Suppl., Univ. Calif. Press, Berkeley.
- Fallon, R.D. and T.D. Brock. 1981. Overwintering of Microcystis in Lake Mendota. Freshwater Biology 11: 217-226.
- Fischer, H.B., E.J. List, R.C.Y. Koh, J. Imberger and N.H. Brooks, N.H. 1979. Mixing in Inland and Coastal Waters, Academic Press, New York.
- Ganf, G.G. 1974. Diurnal mixing and the vertical distribution in a shallow equatorial lake (Lake George, Uganda). J. Ecol. 62:611-629.
- George, D.G. and R.W. Edwards. 1976. The effect of wind on the distribution of chlorophyll a and crustacean plankton in a shallow eutrophic reservoir. J. Appl. Ecol. 13: 667-690.
- Gliwicz, Z.M. and A. Hillbricht-Ilkowska. 1975. Ecosystems of the Mikolajskie Lake. Elimination of phytoplankton biomass and its subsequent fate in lake through the year. Polskie Archivum Hydrobiologii 22:39-52.
- Haertel, L. 1976. Nutrient limitation of algal standing crops in shallow prairie lakes. Ecology 57:664-678.

- Haffner, G.D., G.P. Harris and M.K. Jarai. 1980. Physical variability and phytoplankton communities. III. Vertical structure in phytoplankton populations. Arch. Hydrobiol. 89: 363-381.
- Hammer, V.T. 1969. Blue-green algal blooms in Saskatchewan lakes. Verh. Internat. Verein. Limnol. 17:116-125.
- Harris, G.P. 1978. Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. Ergeb. Limnol. Beih. Arch. Hydrobiol. 10: 1-171.
- Harris, G.P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models and management. Can. J. Fish. Aquat. Sci. 37: 877-890.
- Harris, G.P. 1982. Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. In Progress in Phycological Research. Vol.2. (eds.) F.E.Round and D.J. Chapman. Elsevier Biomedical Press.
- Harris, G.P. and R.E.H. Smith. 1977. Observations of small-scale spatial patterns in phytoplankton populations. Limnol. and Oceanogr. 22: 887-899.
- Harris, G.P. and B.B. Piccinin. 1980. Physical variability and phytoplankton communities: IV. Temporal changes in the phytoplankton community of a physically variable lake. Arch. Hydrobiol. 89: 447-473.
- Harris, G.P., S.I. Heaney and J.F. Talling. 1979. Physiological and environmental constraints in the ecology of the

planktonic dinoflagellate Ceratium hirundinella.
Freshwater Biology 9: 413-428.

- Harris, G.P., G.D. Haffner and B.B. Piccinin. 1980a. Physical variability and phytoplankton communities: II. Primary productivity by phytoplankton in a physically variable environment. Arch. Hydrobiol. 89: 393-425.
- Harris, G.P., B.B. Piccinin, G.D. Haffner, W. Snodgrass and J. Polak. 1980b. Physical variability and phytoplankton communities: I. The descriptive limnology of Hamilton Harbour. Arch. Hydrobiol. 88: 303-327.
- Harris, G.P., B.B. Piccinin, J. VanRyn. 1982. Physical variability and phytoplankton communities: V. Cell size, niche diversification and the role of competition. Arch. Hydrobiol. (in press).
- Haugh, L.D. and G.E.P. Box. 1977. Identification of dynamic regression (distributed lag) models connecting 2 time series. Journal of the American Statistical Association Vol. 72 No.357 Theory and Methods Section: 121-130.
- Heaney, S.I. 1976. Temporal and spatial distribution of the dinoflagellate Ceratium hirundinella O.F. Muller within a small productive lake. Freshwater Biology 6: 531-542.
- Heaney, S.I. and J.F. Talling. 1980. Dynamic aspects of dinoflagellate distribution patterns in a small productive lake. Journal of Ecology 68: 75-94.
- Hutchinson, G.E. 1941. Ecological aspects of succession in natural populations. Am. Nat. 75: 406-418.

- Hutchinson, G.E. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. Philadelphia 105:1-11.
- Hutchinson, G.E. 1961. The paradox of the plankton. Am. Nat. 95:137-145.
- Hutchinson, G.E. 1965. The Ecological Theatre and the Evolutionary Play. Yale University Press. 139 pp.
- Hutchinson, G.E. 1967. A Treatise on Limnology, Vol. 1, Wiley, New York.
- Jassby, A.D. and C.R. Goldman. 1974. A quantitative measure of succession rate and its application to the phytoplankton of lakes. Am. Nat. 108: 688-693.
- Jaworski, G.H.M., J.F. Talling and S.I. Heaney. 1981. The influence of carbon dioxide-depletion on growth and sinking rate of two planktonic diatoms in culture. Br. Phycol. J. 16: 395-410.
- Jenkins, G.M. and Watts, D.G. 1968. Spectral analysis and its applications. San-Francisco: Holden-Day Inc.
- Jones, R.I. 1979. Notes on the growth and sporulation of a natural population of Aphanizomenon flos-aquae. Hydrobiologia 62: 55-58.
- Kamykowski, D. and S.J. Zentara. 1977. The diurnal vertical migration of motile phytoplankton through temperature gradients. Limnol. and Oceanogr. 22: 148-151.
- Kappers, F.I. 1980. The cyanobacterium Microcystis aeruginosa

kg. and the nitrogen cycle of the hypertrophic Lake Brielle (The Netherlands). In : Developments in Hydrobiology. (ed) by J. Barica and L.R. Mur. 2: 37-45.

Kemp, W.M. and W.J. Mitsch. 1979. Turbulence and phytoplankton diversity: a general model of the "paradox of the plankton". Ecol. Modell. 7: 201-222.

Klemer, A.R., J. Feillade and M. Feillade. 1982. Cyanobacterial blooms: carbon and nitrogen limitation have opposite effects on the buoyancy of Oscillatoria. Science 215: 1629-1631.

Kolmogoroff, A.N. 1941. The local structure of turbulence in compressible viscous fluid for very large Reynolds number. (trans.) Doklady Akad. Nauk. U.S.S.R. 30:301.

Konopka, A. 1982. Buoyancy regulation and vertical migration by Oscillatoria rubescens in Crooked Lake, Indiana. Br. Phycol. J. 17: 427-442.

Konopka, A., T.D. Brock and A.E. Walsby. 1978. Buoyancy regulation by planktonic blue-green algae in Lake Mendota, Wisconsin. Arch. Hydrobiol. 83: 524-537.

Koopman, L.H. 1974. The Spectral Analysis of Time Series. In: Probability and Mathematical Statistics. Academic Press.

Kramer, J.R., S.E. Herbes and H.E. Allen. 1972. Phosphorus, analysis of water, biomass and sediment. 51-100. In:

Allen, H.E. and J.R. Kramer (Eds). Nutrients in natural waters. Wiley Intersciences.

Leonardson, L. and L. Bengtsson. 1978. Effects of sewage diversion in Lake Sodra Bergundasjon. 11. Phytoplankton changes and the role of nitrogen fixation. Verh. Internat. Verein. Limnol. 20:2701-2707.

Leonardson, L. and W. Ripl. 1980. Control of undesirable algae and induction of algal successions in hypereutrophic lake ecosystems. In: Developments in Hydrobiology. (ed) by J. Barica and L.R. Mur. 2: 57-67.

Levins, R. 1979. Coexistence in a variable environment. Am. Nat. 114: 765-783.

Lewis, W.M.Jr. 1978a. Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Phillipines. Journal of Ecology 66:849-880.

Lewis, W.J.Jr. 1978b. Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. Am. Nat. 112: 401-414.

Liao, C.F.H and D.R.S. Lean. 1978. Nitrogen transformations within the trophogenic zone of lakes. J. Fish. Res. Board Can. 35: 1102-1108.

Livingstone, D. and G.H.M. Jaworski. 1980. The viability of akinetes of blue-green algae recovered from sediments of Rosetherne Mere. Br. Phycol. J. 15: 357-364.

Livingstone, D., and C.S. Reynolds. 1981. Algal sedimentation

in relation to phytoplankton periodicity in Rosetherne Mere. Br. Phycol. J. 16: 195-206.

Lund, J.W.G., C. Kipling and E.D. LeCren. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia, 11:143-170.

Lund, J.W.G. and C.S. Reynolds. 1982. The development and operation of large limnetic enclosures in Blelham Tarn, English lake district, and their contribution to phytoplankton ecology. Prog. Phyc. Res. 1: 1-65. Eds. F.E. Round and D.J. Chapman, Elsevier, Amsterdam.

Lynch, M. 1979. Aphanizomenon blooms: alternate control and cultivation by Daphnia pulex, in: W.C. Kerfoot, (ed.) Evolution and ecology of zooplankton communities. ASLO Special Symposium 3: 299-305.

Lynch, M. and J. Shapiro. 1981. Predation, enrichment and phytoplankton community structure. Limnol. and Oceanogr. 26: 86-102.

Mackie, G.L., J.C. Roff, J.F. Gerrath, R.C. Mahon, K. Counsell, L. Newman. 1976. Effects of impoundment on water quality parameters in Guelph Reservoir. Experience '76 Project Report Univ. of Guelph, Department of Zoology.

Margalef, R. 1967. Some concepts relative to the organization of plankton. Oceanogr. Marine Biol. Annu. Rev. 5:257-289.

Margalef, R. 1978. Life forms of phytoplankton as survival

alternates in an unstable environment. *Oceanologica Acta* 1: 493-509.

Marra, J and K. Heinemann. 1982. Photosynthesis response by phytoplankton to sunlight variability. *Limnol. and Oceanogr.* 27: 1141-1153.

Nalewajko, C., G. Bryant and M. Sreenivasa. 1981. Limnology of Heart Lake, Ontario. *Hydrobiologia* 79: 245-253.

Odum, E.P. 1971. Fundamentals of Ecology. W.B. Saunders Cpy.

Okubo, A. 1971. Horizontal and vertical mixing in the sea. p. 89-168. In D.W. Hood (ed.) *The impingement of man on the oceans*. Wiley, N.Y.

Palmer, M.V. and D.J. Poulton. 1976. Hamilton Harbour: periodicities of the physico-chemical process. *Limnol. Oceanogr.* 21: 118-127.

Peterson, R. 1975. The paradox of the plankton: an equilibrium hypothesis. *Am. Nat.* 109:35-49.

Platt, T. 1978. Spectral analysis of spatial structure in phytoplankton populations. In : Spatial Pattern in Plankton Communities. (ed.) J.H. Steele , Plenum Press, New York, 470 pages.

Platt, T. and K.L. Denman. 1975. Spectral analysis in ecology. *Ann. Rev. Eol. Syst.* 6: 189-210.

Powell, T.M., P.J. Richerson, T.M. Dillon, B.A. Agee, B.J. Dozier, D.A. Godden and L.O. Myrup. 1975. *Spatial*

scales of current speed and phytoplankton biomass
fluctuations in Lake Tahoe. Science 189: 1088-1090.

Preston, T., W.D.P. Stewart and C.S. Reynolds. 1980. Bloom-
forming cyanobacterium Microcystis aeruginosa overwinters
on a sediment surface. Nature 288: 365-367.

Reynolds, C.S. 1973. The seasonal periodicity of planktonic
diatoms in a shallow eutrophic lake. Freshwater
Biology 3: 89-110.

Reynolds, C.S. 1975. Interrelations of photosynthetic behaviour
and buoyancy regulation in a natural population of a
blue-green alga. Freshwat. Biol. 5: 323-338.

Reynolds, C.S. 1976a. Sinking movements of phytoplankton
indicated by a simple trapping method. I. A Fragilaria
population. Br. Phycol. J. 11: 279-291.

Reynolds, C.S. 1976b. Sinking movements of phytoplankton
indicated by a simple trapping method. II. Vertical
activity ranges in a stratified lake. Br. Phycol. J.
11: 293-303.

Reynolds, C.S. 1980. Phytoplankton assemblages and their
periodicity in stratifying lake systems. Holarctic
Ecol. 3: 141-159.

Reynolds, C.S. and A.E. Walsby. 1975. Water-blooms. Biol. Rev.
50: 437-481.

Reynolds, C.S. and Rogers, D.A. 1976. Seasonal interactions
in the vertical distribution and buoyancy of

Microcystis aeruginosa Kutz. emend. Elenkin. in
Rosetherne Mere, England. *Hydrobiologia* 48: 17-24.

Reynolds, C.S. and S.W. Wiseman. 1982. Sinking losses of
phytoplankton in closed limnetic systems. *J. Plankton
Res.* 4: 489-522.

Reynolds, C.S., Jaworski, G.H.M., Cmiech, H.A. and Leedale, G.F.
1981. On the annual cycle of the blue-green alga
Microcystis aeruginosa Kutz. emend Elenkin. *Phil. Trans.
R. Soc. Lond. B* 292: 419-477.

Reynolds, C.S., H.R. Morison and C. Butterwick. 1982a. The
sedimentary flux of phytoplankton in the south basin of
Windermere. *Limnol. and Oceanogr.* 27: 1162-1175.

Reynolds, C.S., J.M. Thompson, A.J. Ferguson, and S.W. Wiseman.
1982b. Loss processes in the population dynamics of
phytoplankton in closed limnetic systems. *J. Plankton
Res.* 4: 561-600.

Reynolds, C.S., S.W. Wiseman, B.M. Godfrey and C. Butterwick.
1983. Some effects of artificial mixing on the dynamics
of phytoplankton populations in large limnetic enclosures.
J. Plankton Res. 5: 203-234.

Richerson, P.J., R. Armstrong and C.R. Goldman. 1970.
Contemporaneous disequilibrium: a new hypothesis to
explain the paradox of the plankton. *Proc. Natl. Acad.
Sci.* 67: 1710-1714.

Richerson, P.J., T.M. Powell, M.R. Leigh-Abbott and J.A. Coil.
1978. Spatial heterogeneity in closed basins. In :

- Spatial Pattern in Plankton Communities. (ed.) J.H. Steele
Plenum Press, New York. 470 pages.
- Round, F.E. 1971. The growth and succession of algal
populations in freshwaters. Mitt. Internat. Verein.
Limnol. 19: 70-99.
- Schindler, D.W. 1977. Evidence of phosphorus limitation
in lakes. Science 195: 260-262.
- Shapiro, J. 1973. Blue-green algae: why they become dominant.
Science 179: 382-384.
- Sephton, D.H. 1980. Time series study of phytoplankton ecology.
MSc. thesis, McMaster University, Hamilton, Ont.
- Shannon, C.E. and W. Weaver. 1963. The mathematical theory of
communication. Univ. Illinois Press, Urbana, 117 p.
- Sirenko, L.A., V.M. Chernonsova, V.V. Arendarchuk and
V.N. Kozitskaya. 1969. Factors of mass development
of blue-green algae. Hydrobiol. J. 5: 1-8.
- Smayda, T.J. 1970. The suspension and sinking of phytoplankton
in the sea. Oceanogr. Mar. Biol. Ann. Rev. 8 : 353-414.
- Stauffer, R.E. 1982. Wind stress effects on chlorophyll
distribution in stratified eutrophic lakes. Limnol.
and Oceanogr. 27: 66-74.
- Stewart, F.M. and B.R. Levin. 1973. Partitioning of resources
and the outcome of interspecific competition: a model and
some general considerations. Am. Nat. 107:171-198.

Talling, J.F. 1974. General outline of spectrophotometric methods. p.22-26. In A manual on methods for measuring primary production in aquatic environments. IBP Handbook No 12. (ed.) R.A. Vollenweider. Blackwell Scientific Publications.

Technicon Corporation. 1971a. Nitrate and nitrite in water and wastewater. Industrial method AAll. 100-70 w. Technicon Corp. Tarrytown, New York.

Technicon Corporation. 1971b. Ammonia in water and wastewater. Industrial method AAll. 98-70w. Technicon Corp. Tarrytown, New York.

Technicon Corporation. 1973. Silicates in water and wastewater. Industrial Method AA II 105- 71 w. Technicon Corp. Tarrytown, New York.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338-348.

Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. Am. Nat. 116:362-393.

Tilman, D., M. Mattson and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnol. Oceanogr. 26:1020-1033.

Titman, D. 1976. Ecological competition between algae: experimental confirmation of resources-based competition theory. Science 192: 463-465.

- Titman, D. and P. Kilham. 1976. Sinking in freshwater phytoplankton. Some ecological implications of cell nutrient status and physical mixing processes. *Limnol. and Oceanogr.* 21: 409-417.
- Topachevsky, A.V., L.P. Braginskiy and L.A. Sirenko. 1969. Massive development of blue-green algae as a product of the ecosystem of a reservoir. *Hydrobiol. J.* 5: 1-10.
- Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Verein. Limnol.* 9:1-38.
- Vollenweider, R.A. 1950. Ökologische untersuchungen von planktischen Algen auf experimenteller Grundlage. *Schweiz. Z. Hydrobiol.* 12: 193-262.
- Vollenweider, R.A. 1953. Einige Bemerkungen zur ökologischen Valenzanalyse. *Schweiz. Z. Hydrol.* 15: 190-197.
- Wall, D. and F. Briand. 1980. Spatial and temporal overlap in lake phytoplankton communities. *Arch. Hydrobiol.* 88: 45-57.
- Walsby, A.E. and C.S. Reynolds. 1979. Sinking and floating in phytoplankton ecology. In: The Ecology of Phytoplankton (ed.) by I.G. Morris.
- Wildman, R.B., J.H. Loescher and C.L. Winger. 1975. Development and germination of akinetes of Aphanizomenon flos-aquae. *J. Phycol.* 11: 96-104.
- Zarull, M.A. 1979. Spatial and temporal heterogeneity in

phytoplankton communities. PhD Thesis, McMaster
University, Hamilton.