Spatial and Temporal Heterogeneity in Phytoplankton Communities

By

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For My Wife, Often Neglected But Always Loved.

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Table of Contents

Table of Contents cont'd.

List of Figures

List of Figures cont'd.

List of Figures cont'd. Page

List of Tables

List of Tables cont'd.

NOTATIONS

N_s	Block Size
ps	Power Spectral
C.C.I.W.	Canada Centre for Inland Waters
FREQ	Frequency
FFREQ	log frequency
η	Wavelength (2 x patch size)
MS	Mean Square
Sd	Standard Deviation
FRP	Filtered Reactive Phosphorous
FRS	Filtered Reactive Silica
NO_3	Nitrate
NO_2	Nitrite
s	second
a	year
m	metre
km	kilometre
cm	centimetre
mm	millimetre
KPa	Kilopascals
IMSL	International Mathematical and Statistical Library
C. erosa	Cryptomonas erosa Ehrenberg

Notations cont'd.

R. minuta	Rhodomonas minuta Skuja
Cyclotella men.	Cyclotella meneghiniana Kützing
O. borgei	Oocystis borgei Snow
C. sphagnicola	Chlamydomonas sphagnicola Fritsch & Takeda
Chlorella vulg.	Chlorella vulgaris Bujerinck
Stephanodiscus ast.	Stephanodiscus astrea Grun.
O.M.E.	Ontario Ministry of the Environment

Abstract

Simultaneous discrete volume samples and synoptic continuous transect samples were taken in Hamilton Harbour during stratified and unstratified conditions in order to look for small scale pattern in the phytoplankton community.

Continuous transect data collected from the measurement of fluorometric chlorophyll a, spectrophotometric chlorophyll a, nitrate+ nitrite, nitrite, filtered reactive phosphorous, total phosphate, filtered reactive silica and some species enumerations were examined using mean square pattern analysis and power spectral analysis.

The excessive spatial variability encountered precluded the use of pooled variance analysis techniques.

Power spectral analysis was much more sensitive to small scale variations than mean square pattern analysis although the latter may be more indicative of larger scale structure.

Cross comparisons (covariance, correlation, cross-spectra) could not be performed because of peak shift phenomena and because of large differences in the estimates of parameter values.

The fluorometric determinations of chlorophyll a smoothed out structure revealed by the more precise spectrophotometric determinations. The spectrophotometric chlorophyll a estimates, in most cases, did not reflect the distributions of the numerically dominant species.

The spectral analyses for most parameters displayed structure predominately at scales less than 25 m which are a reflection of the fundamental periodicities present in the harbour at all times of the year. Parameter distributions at length scales beyond 25 m tend to be randomized under the influence of increased wind speed. Parameter distribution at basin scales appears to be a function of the wind driven circulation.

1.0 Introduction

A general characteristic of all ecosystems is that they are patchy. Factors influencing the physiological condition, behavioural state or ultimate fitness of individuals exhibit discontinuities on many scales in time and space. The patterns of these discontinuities influence the interaction and adaptations of organisms, which ultimately dictate their distribution. Spatial and temporal heterogeneity of the biotic and abiotic environment has been proposed as the basis for such phenomena as the maintenance of genetic polymorphisms and the regulation of community diversity (Wiens, 1976; Levin, 1976). A community may be defined as an assemblage of populations of all the living organisms in an area which potentially interact with one another. Heterogeneity has been cited further as the single most important factor ensuring the stability of ecosystems (Huffaker, 1958; MacArthur and Wilson, 1967; Simberloff and Wilson, 1969; May, 1973).

Phytoplankton population dynamics and community structure were traditionally assumed to be governed by temperature, light and a few major nutrients such as nitrogen, phosphorous and silica. The aquatic planktonic environment was assumed to be relatively isotropic with respect to these parameters, and local patches were regarded as anomalous (Hutchinson, 1961). Hutchinson (1961) questioned the persistence of multispecies phytoplankton assemblages in this homogeneous environment since their coexistence appeared to violate the competitive

exclusion principle (Hardin, 1960). This principle essentially states that in an environment where more than one species utilizes a given resource, only one species will survive. Hutchinson referred to this apparent violation as the "paradox of the plankton" (Hutchinson, 1961). He suggested that the principle was not violated but that temporal fluctuations in the environment allowed coexistence. This implies that the necessary criterion of equilibrium conditions for competitive exclusion is never attained. Richerson et al. (1970) also proposed a non-equilibrium theory of coexistence which was however based on contemporaneous rather than temporal heterogeneity. They suggested that the vertically mixed portion of a lake is probably not homogeneous on a time scale of a few hours, a feature which provides a number of unique niches These are however, quite unstable and are destroyed and reconstituted at frequent random intervals. Some investigators have suggested the answer to the coexistence paradox is that the species do not interact with one another strongly (Hulburt and Horton, 1973).

The non-equilibrium theories stress the importance of turbulence for the maintenance of species diversity. Margalef (1967) has stated that the spectrum of species diversity is related to the spectrum of turbulence. In a stable environment where turbulent dispersion is small (e.g. pycnoclines), numerical dominance by one or a few species can be expected (Margalef, 1967; Pingree et al., 1975; Fee, 1976). Conditions of environmental complexity promote increased diversity (Margalef, 1963, 1967; Richerson et al., 1970). However, strong turbulent mixing reduces diversity and therefore spatial variability (Margalef, 1967; Therriault, 1977; Small, 1963).

The detailed investigation of these spatial and temporal inhomogeneities of phytoplankton is important for a number of reasons. Steele (1974) has demonstrated the critical need for this information to be incorporated into our modelling of oceanic productivity and Lasker (1975, 1977) has related the effects that phytoplankton spatial heterogeneity has on the survival of anchovy and sardine larvae. Most aquatic data are gathered by discrete sampling at preselected stations. The representative nature of these data and the validity of the results, clearly depends on the space and time scales of the physical, chemical and biological processes.

The phenomenon of plankton patchiness is not a new observation. Early records of visual sightings include those of Captain James Cook in 1773 on his first round the world voyage and Darwin in 1839 in his account of the voyage of the Beagle. They both made several references to bands, lanes or streams of coloured water. These observations were, until the 1930's, confined to a visual assessment of the surface waters which documented both streaks, and ellipsoidal configurations. Phytoplankton "patches" in this sense are therefore surface water masses containing a concentration of a single species which is several times the background (Bainbridge, 1957). In the 1930's more intensive sampling techniques were used and new instrumentation was developed in an attempt to quantify the extent of patches and describe their composition (Hardy, 1935, 1936a, 1936b). These investigations demonstrated the ubiquitous nature of plankton patchiness but did not disclose all of the scales or explain their causes. The results did show the potential difficulties

of evaluating data from conventional point sample surveys, but the warnings went unheeded.

McEwen (1930) first described the spatial inhomogeneities of plankton in a statistical sense using Poisson criteria of randomness. Winsor and Walford (1936) described the phenomenon using χ^2 tests on paired replicate samples as another method of examining this phemonenon. This early work was followed by the use of more intense sampling networks of data collection which used Poisson criteria (i.e. variance = mean) and Fisher's coefficient of dispersion in an attempt to describe the non-randomness observed (Cassie, 1959, 1962, 1963). Platt, Dickie and Trites (1970) using a grid arrangement of discrete chlorophyll samples and also periodic samples along a straight line transect found a series of discrete scales of variability, rather than a continuous spectrum of variability. They suggested that the scale-sizes probably vary from mm to km and that the sampling design used will restrict the range of variability that can be studied. They also stated the need to distinguish those scales which are strictly due to physical action from those scales with biological origin. The discreteness of these sampling techniques has imposed severe restrictions in the range of scales of variability that could be studied. In order to obtain a more complete statistical analysis, one requires a continuous sample record which extends from the smallest resolvable scale up to the largest scale feasible.

In vivo fluorescence of chlorophyll is frequently used to measure biomass and temperature is used as a physical marker for water masses (Platt, 1972; Denman and Platt, 1975; Powell et al., 1975; Denman, 1976;

Fasham and Pugh, 1976). Measurements are taken in either a Eulerian or a Lagrangian frame of reference. The adjective "Lagrangian" is used to indicate that it relates to moving points ("fluid particles") and the adjective "Eulerian" is used whenever correlations between two fixed points in a fixed frame of reference are considered (Okubo, 1971a). In addition to chlorophyll a and temperature other parameters such as current speed, salinity, species distributions and some nutrient information, have been measured (Powell et al., 1975; McAlice, 1970; Fasham and Pugh, 1976; Richerson et al., 1977; Estrada and Wagensberg, 1977; Harris and Smith, 1977). Experimental one-dimensional spectra are obtained by moving a sampler so rapidly through the turbulence that the velocity field does not change appreciably during the time of measurement. The sampler "sees" a fluctuating velocity, which is a function of time; if the traversing speed (u) of the sampler is large enough, the velocity signal u(t) may be identified with u(x/u), where x is distance. This approximation is known as Taylor's hypothesis. It is also referred to as the frozen turbulence approximation (Taylor, 1938).

Power spectral analysis is a form of an analysis of variance of a one-dimensional series, although a two-dimensional analysis may be employed (Bartlett, 1964), in which the variance of the series of numbers about their mean is partitioned into contributions at frequencies which are harmonics of the length of the data set. Spectral analysis takes a statistical approach and assumes that the series is just a single realization of a stochastic process (i.e. a random or non-deterministic result whose future behaviour can be predicted only in a statistical sense). The power spectrum is the Fourier cosine transform of the

autocovariance function. The autocovariance function is the result of sliding the data set along beside a copy of itself and summing products of adjacent data points. This provides information about how neighbouring points are correlated (Platt and Denman, 1975a). The spectrum plot is therefore a simutaneous least squares fit of a finite number of sine and cosine functions of different frequencies to a series of a fixed length where the error in the approximation to the original series has attempted to be minimized. An error estimate or confidence interval can be evaluated knowing the spectral window and assuming a χ^2 distribution of the estimates (Blackman and Tukey, 1958; Jenkins and Watts, 1968; Rayner, 1971). Spectral analysis is particularly suited to analysing small scale patterns and it is also particularly sensitive to any genuine periodicities (Usher 1975). It is therefore a good indicator of the "grain" or spatial pattern (Pielou, 1969). It is however very insensitive to pattern with long wavelengths and is also restricted in the maximum wavelength that it can examine (Usher, 1975). The maximum data window practical is n/4 (where n is the number of unit samples), since the power spectral values represent smoothed estimates which are a result of the averaged specific wave number values for the quartered data series (Platt and Denman, 1975a).

Spectral analysis is not necessarily the best form of variance analysis for all ecological situations, as Hill has stated.

"Unfortunately, spectral analysis has been obscured by its use in electronic engineering and control systems. There is for example, a baffling concern with smoothing techniques (spectral windows) which has been deplored by Bartlett (1967). The connection between spectral analysis and electronic engineering is accounted for by the fact that it is a natural way of dealing with linear and quasi-linear systems. However,

anyone who has examined a population of organisms will be aware that their responses to each other and to the environment are not in the least linear. In ecological contexts, therefore, spectral analysis bears no particularly important relation to any presumed underlying structure of the data and must be regarded as merely another method of pattern analysis." (Hill, 1973)

Another technique of pattern analysis which has not been utilized in aquatic studies, is mean square pattern analysis. It has been used for a number of years by terrestrial plant ecologists for the detection of pattern in plant communities.

Initially, pattern or non-randomness was detected by enumerating the contents of a number of arbitrarily sized unit samples (quadrats) placed at random throughout a sample area. This method was extensively used since various workers (Blackman, 1935; Clapham, 1936; and Archibald, 1948) made it evident that individuals are rarely distributed at random. It was however, limited in the interpretation of the results to an indication only of the degree and perhaps the type of non-randomness present and gave no clues to the nature of more complex patterns (Thompson, 1958). Interpretation of the results was further hampered as a consequence of using a fixed size sample unit in non-randomly distributed vegetation. As a result, measures of aggregation based on quadrat data will not as a rule be unique so that different values will be obtained with different quadrat sizes (Greig-Smith, 1964; Kershaw, 1973).

Greig-Smith (1952) first introduced the method of mean square pattern analysis. The technique examines the densities of individuals contained in a grid of contiguous unit quadrats. The data from the unit blocks were then adjacently summed into successively larger blocks.

The mean square or variance (assuming the null hypothesis is that of a Poisson distribution) when plotted against the block size should then show a peak (or a sharp point of inflection) at the block size which corresponds to the mean size of the patch or mosiac unit. Kershaw (1957) developed an important modification of this method which avoided the previous implicit assumption that the areas of heterogeneity were isodiametric and allowed enumeration of pattern along gradients. This method employs a series of straight line transects divided into a preselected series (2^n) of unit sample quadrats. The transects are treated as replicates of one another which allows the measures of abundance to be pooled for each successive 2^n block size. The mean square is then calculated for each successive block size and plotted against this grouping. The determination of the significance of any apparent peak presents a problem since once non-randomness has been established, the classical variance ratio test cannot be used. Thompson (1955) discussed this problem in detail and demonstrated the lack of any valid test under the non-randomness condition existing in most communities. Mead (1974) introduced what he describes as a fully valid, distribution free test. This test however, basically skirts the problem of the dependent nature of the adjacent unit samples which tend to show high autocorrelation (Richerson et al., 1977; Fasham, private communication). If these basic units are then combined into larger blocks and used to give mean square estimates, then these estimates are not independent of one another and cannot be tested. In the absence of a valid test for the significance of a particular peak, a subjective assessment of the graphs is employed

using the criterion of the reappearance of a particular scale of pattern in the series of replicate transects (Kershaw, 1973). This has always precluded a clear interpretation of peaks occurring at the maximum block size. The fundamental test requires at least a doubling of sample size and a re-examination of the data unless some *a priori* information about the causal nature of this scale is available (Kershaw and Rouse, 1971a, 1971b). The initial study of the transect pattern analysis (Kershaw, 1957) showed that the peak in variance occurred at the mean diameter of the clump and that peak drift to the right might be encountered at low population densities. Usher (1969) showed that peak drift to the left is also possible and emphasized the importance of the start position in a pattern analysis. Errington (1973) using models of regularly and randomly distributed clumps demonstrated the importance of the space size (i.e. distance between clumps) in influencing the position of peaks. The peak position is indicative of the clump size, the space size, or one half the total unit of pattern. In general, for any given clump size, if the mean space size is less than the mean patch size there will be a peak drift to the left, and if the mean space size is larger then the mean clump size there will be a drift to the right. Usher (1975) has also pointed out another type of behaviour during peak drift which he refers to as peak interference. If for example, two peaks are present, at $N_s 4$ and at $N_s 16$, the $N_s 4$ peak may completely disappear if the peak at $N_s 16$ shifts to $N_s 8$. The amplitude of the peak was also shown to be influenced by a number of factors. As the clump and block sizes become equal a maximum amplitude is reached which is a function of this tendency of the analysis to peak

at the clump size, the space size and often at an average between these two values. At a cover of 50%, the clump, space and half the total unit of pattern are identical confining the peak to only one position thereby giving it a maximum amplitude. High amplitudes also suddenly appear when the sum of the clump size plus space size lies exactly on the series 2^n. Errington (1973) has suggested that, "the fact that the method of analysis relies on the series 2^n is largely responsible for these anomalies".

In comparing spectral analysis with mean square pattern analysis, Usher (1975) suggested that with spectral analysis it is sometimes difficult to sort out the actual peaks from harmonics and spurious peaks which arise owing to the discrete nature of some botanical data and because of the square-wave nature of artificial data. He further states that there are advantages and disadvantages in both of these methods and that a more complete analysis of pattern should include both methods.

Except for a study by Fasham and Pugh (1976) the majority of marine research using spectral analysis on continuous sample records has taken place in the upper ten metres of coastal and estuarine waters. The results of these investigations are explained on the basis of turbulence theory through the KISS model (Kierstead and Slobodkin, 1953; Skellam, 1951).

Kierstead and Slobodkin (1953) proposed a mathematical model dealing with the blooming of dinoflagellates under the adverse influence of turbulence which tends to transport cells from a favourable to a less favourable environment (Strickland, 1965; Ragotzkie et al.,

1957). This model is similar in its formulation to one proposed by Skellam (1951) and the models are now collectively referred to as the KISS model (Okubo, 1977; Denman et al., 1977). The KISS model attempts to predict the minimum size possible for a-water mass containing a single species phytoplankton increasing exponentially which can maintain its integrity against the dispersive forces of turbulent diffusion. The proposed relationship was:

$$L_c = \pi (D/K)^{\frac{1}{2}}$$

for a spherical water mass, where L_c is the critical length, D is the turbulent diffusion rate derived from the fundamental equations of turbulence theory, and K is the rate of increase of the population.

Wroblewski, O'Brien and Platt further developed the theoretical concept of a critical length scale of phytoplankton patchiness by incorporating the effect of losses due to herbivore predation into the KISS model (Wroblewski et al., 1975).

The equation they proposed was:

$$L_c = \pi \left(\frac{D}{K - R_m \lambda} \right)^{\frac{1}{2}}$$

where R_m is the herbivore maximum grazing rate and λ is the Ivlev constant, an empirically determined value to account for feeding rate dependence upon the food concentration (Parsons et al., 1967).

Wroblewski and O'Brien (1976) further developed their grazing model to include nutrient limitation of phytoplankton growth in order to achieve realistic solutions for the oceanic regime.

The original KISS model was developed for a single species population growing in a particular location and in order to apply it

in general circumstances parameters of the model should be examined in more detail. This will be done in the following section.

The constant K represents a net population growth rate. The doubling time for communities may range from 0.25 to 1.0 per day. Eppley (1972) and Beers et al. (1971) note that the accuracy of these estimates is only within a factor of two. In addition to the gross rate of increase one must consider losses due to sinking and increases due to vertical redistribution. Sinking rates vary with the plankton species from 0.1 to 6.8 m per day (Smayda, 1970, 1974; Smayda and Boleyn, 1965, 1966; Eppley et al., 1967). The rate depends on physiological state and shows nutrient dependance (Titman, 1975; Titman and Kilham, 1976). The importance of vertical redistribution to the biomass and the primary productivity measured at any given point has been shown by Feé (1976) and Denman (1977). The major physical force of vertical transport is via internal waves (Kamikowski, 1974; Fasham and Pugh, 1976). The precise influence of internal waves on the estimates of biomass made in previous studies has been difficult to quantify (Denman, 1976).

The variance spectrum of a turbulent flow field that is isotropic in three dimensions and for which the turbulence is generated at large scales only, contains a range of wave numbers, called the inertial subrange, 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. We can denote the one-dimensional turbulent energy spectrum as E(k). The value of this function depends only upon the wave number k and on the

rate of kinetic energy transfer within the inertial subrange. Since this cascade is conservative, the transfer rate must be constant and equal to the rate of viscous dissipation, ε, at small scales. A dimensional analysis based on these assumptions leads to the relationship:

$$E(k) = A\, \varepsilon^{2/3}\, k^{-5/3}$$

where A is a dimensionless constant. Therefore, the turbulent energy spectrum and any passive scalar within the flow field will show a -5/3 slope within the inertial subrange (Denman and Platt, 1976).

The turbulent diffusion rate, D, depends on those factors causing a random change in the concentration of a parameter within the water mass under consideration. The value is scale dependent and therefore a constant cannot be used (Okubo, 1971b; Boyce and Lam, private communication). The rate of turbulent diffusion is greatly affected by the basin size (Boyce, 1974). The largest eddies (i.e. stirring processes) are dictated by the smallest cross-basin length scale (Boyce and Hamblin, 1975; Murthy, 1977). The depth of the water body, to a solid bottom or a density surface, also affects turbulent diffusion. Wind speed is another factor affecting rate of turbulent diffusion (George and Edwards, 1976). The turbulent diffusion rate changes as a function of density and therefore can be related to salinity or temperature. Another factor, which should be considered when applying D to local plankton blooms, is the potential modification of the turbulent diffusion rate as a result of the particulate matter suspended in it (Okubo, 1968, 1974). There are at present no data available on this effect in aquatic media (Boyce and Murthy, private

communication). All these factors demonstrate that D is locally modified.

Incorporation of the effects of zooplankton grazing is definitely desirable in that it improves the realism of the model. It does however present the added difficulties of dealing with the grazers and the grazing. Zooplankton feeding is selective for both filter and raptorial feeders (Conover, 1960; Gauld, 1966; Hargrave and Geen, 1970; Wilson, 1973; Porter, 1973; Boyd, 1976). The animals are themselves patchily distributed (Hutchinson, 1953; Cassie, 1959; Wiebe, 1970). Brooks (1969) and Dodson (1970) have shown that changes in the phytoplankton species composition are as important to the zooplankton species composition and total biomass as an increase in the abundance of the phytoplankton. These factors must also be locally determined and appear as functions rather than constants in the model in order to improve its realism.

The inclusion of a limiting nutrient effect on phytoplankton growth prevents the severe population density fluctuations for both the phytoplankton and the zooplankton populations which were present in the Wroblewski, O'Brien and Platt model. The concept of a single limiting nutrient for a mixed species assemlage appears to be untenable in view of the "Competitive Exclusion Principle" (Hardin, 1960; Hutchinson, 1961). The necessary result of a single limiting nutrient for a number of species, given the constant physical and biological conditions imposed by all of the models, is the persistence of only one species. The inclusion of a single limiting nutrient concentration must further assume that this concentration has an effect on all of the phytoplankton

present. Allen (1977) suggested that there is a great disparity between the measured nutrient levels in the environment and the levels actually experienced by the phytoplankton since their immediate neighbourhood is governed by molecular processes rather than turbulent ones. Wiens (1977) and Grenny et al. (1973) have postulated that the fluctuations of various parameters in the environment are as important or more important than an average value for survival and growth of the organisms.

In summary, the KISS model and its modified versions may be able to relate phytoplankton patchiness to growth and turbulent dissipation but the terms in the model need to be functions rather than constants for general applications.

The applications of the predictions of the KISS model to the critical length scale or minimum patch size of field results have been accomplished as follows.

The spectral analysis of data from some of the marine studies shows a high degree of correlation between temperature and chlorophyll over a wide range of scales. This is taken to mean that the chlorophyll behaves, like temperature, as a passive scalar in a turbulent field. However the chlorophyll spectral plots tend to show a change in the slope of the variance versus distance plots after length scales that bracket 1 km (.2 to 20 km). The point at which this change in slope takes place is postulated to be the length scale at which phytoplankton growth dominates over the physical transport processes to produce a patch of phytoplankton (Platt, 1972; Platt and Denman, 1975a, 1975b). This point is suggested by Platt and Denmann (1975a) as being

equivalent to the critical length scale (Lc) of the KISS model. The point of inflection of the spectral plots of chlorophyll does not necessarily occur at the same position and may in fact be totally absent, which suggests that it is probably locally determined (Fasham and Pugh, 1976; Horwood, 1976). Temperature also diverges from the anticipated -5/3 power relationship predicted from turbulence theory which indicates local modifications to the physical regime (Fasham and Pugh, 1976).

A short discussion of the parameters measured in these studies and the method of analysis used on the data, relative to the theoretical models, is essential for an interpretation of the current state of knowledge with respect to phytoplankton patchiness.

Temperature measured via a sensor implanted at a fixed depth cannot be used as a passive marker in a turbulent field. Woods and Fosberry (1966) have shown that the vertical structure likely consists of uniform layers of water separated by thin sheets of high temperature and density gradients. Phillips (1971) has subsequently shown that the observations obtained from a temperature sensor fixed at one depth in such a situation will produce a -2 power relationship (i.e. very nearly -5/3) irrespective of the underlying motions of the water. Therefore, little information can be deduced from the slope of the temperature spectra (Fasham and Pugh, 1976).

Chlorophyll a as an indicator of population density change may produce a large error in the estimate of phytoplankton biomass since the per cell chlorophyll content varies as a function of species and physiological response to nutrient and light changes (Yentsch and

Scagel, 1958; Ballester, 1966). These changes may be extremely rapid. As Margaleff has stated:

> "Chlorophyll is more quickly synthesized and decomposed than other pigments and responds more rapidly than other pigments to changes in opportunity for growth. Such changes can be detected even on an hour basis, in circadian rhythms."
>
> (Margaleff, 1967)

In vivo fluorescence using the standard filter combinations will reasonably estimate the ambient chlorophyll a concentration providing there is little interference from phaeophytin or suspended solids (Lorenzen, 1966a, 1966b; Lincoln, 1976; Oppenheimer, 1966; Carter, 1974). Phaeophytin is a chlorophyll degradation product which is often correlated with zooplankton grazing. The suspended solids are a particular problem in the coastal zone and result from extraneous silt and detritus. Fluorescence also gives physiological information since the fluorescence yield shows rapid changes with nutrient stress, light and temperature changes (Kiefer, 1973b; Blasco, 1973; Lorenzen, 1966b). Some species of phytoplankton do not show a maximum fluorescence induction/response with the standard excitation/measurement wave lengths of light used (Kiefer, 1973a; Heany, 1978). The difficulties encountered in estimating the spatial variability of phytoplankton communities by fluorescence are further compounded by the problems of estimating the net growth rate of the phytoplankton. These problems were discussed previously in connection with estimating the K term in the KISS model.

In summary, studies using the above techniques do not have adequate information regarding the relationship between the physical environment and the biological response to it. In fact, they may have

some erroneous information about these relationships.

Intensive studies, similar to those just described for marine systems, have been done in freshwater (Powell et al., 1975; Richerson et al., 1975). Powell et al. (1975) working in Lake Tahoe, a large deep oligotrophic lake, discovered a significant change in the distribution of variance of chlorophyll at a length-scale of 100 m (Goldman and Armstrong, 1969). Richerson et al. (1975) found a similar variance peak at 220 m for the dominant plankter Cyclotella stelligera. They suggested that the chlorophyll peak was due to biological variations in cell growth rate, sinking and grazing at these scales. The variance distribution beyond this 100 m peak continued to rise to the limits of resolution, probably as a result of stream inflows at basin scales. At scales below 100 m the chlorophyll appeared as a passive contaminant in a turbulent field. Harris and Smith (1977) working in Cootes Paradise, a shallow highly eutrophic marsh (Bacchus, 1974; Harris and Bacchus, 1974), using periodic discrete volume samples found considerable variance in the chlorophyll and species distributions over scales of one metre. The fresh water results suggested potential links between basin morphometry and patch size, and between trophic states and patch size.

The purpose of this study was to examine the spatial variability in the phytoplankton communities of a small eutrophic body of water in pursuit of a basin size and/or trophic state relationship with the scale of heterogeneity. The programme was designed to study scales of heterogeneity less than 200 m in size, of biomass, species and nutrients during different conditions of water column stability. The results

should show smaller scale distributions than Lake Tahoe but larger scale distributions than Cootes Paradise. The sampling technique was to collect replicate transect samples from the surface metre of water and to examine the variance distributions of the various parameters measured both through spectral analysis and through mean square pattern analysis.

2.0 Materials and Methods

2.1 Description of Sample Site

Hamilton Harbour is a partially open body of water located at the western tip of Lake Ontario. It has a maximum length of 8 km in an east-west direction and a maximum width of 4.8 km, in a north-south direction. At its eastern end, the harbour is connected to Lake Ontario via a ship canal (732 m long, 107 m wide and 9 m deep). At its western end, the Desjardins Canal joins the harbour to a polytrophic marsh (Cootes Paradise). The canal is approximately 240 m long, 24 m wide and 2 m deep (Figure 1).

The harbour contains approximately 2.8×10^8 m^3 of water with a maximum depth of 24 m. The watershed (about 500 km^3) supplies a total annual flow of 1.27×10^8 m^3 via several small creeks. This provides a natural throughput of approximately 45% a^{-1}. The harbour is also used as a receiving water for about 3.2 m^3 s^{-1} of treated municipal wastes and for an estimated 0.1 m^3 s^{-1} of untreated storm sewer overflows during overflow periods. All of these contributions result in an approximate throughput of 80% a^{-1}. There are in addition, a number of industries located along the south shore which utilize some 27 m^3 s^{-1} in a steady state exchange.

The shoreline has been extensively developed, and a great deal of landfilling has taken place for many years. These shoreline changes

have probably led to complex changes in the current flow patterns. The bottom topography is quite variable due to filling, dredging and heavy sedimentation from various sources. The sediment density and composition show marked differences across the basin (OME, 1974-1977).

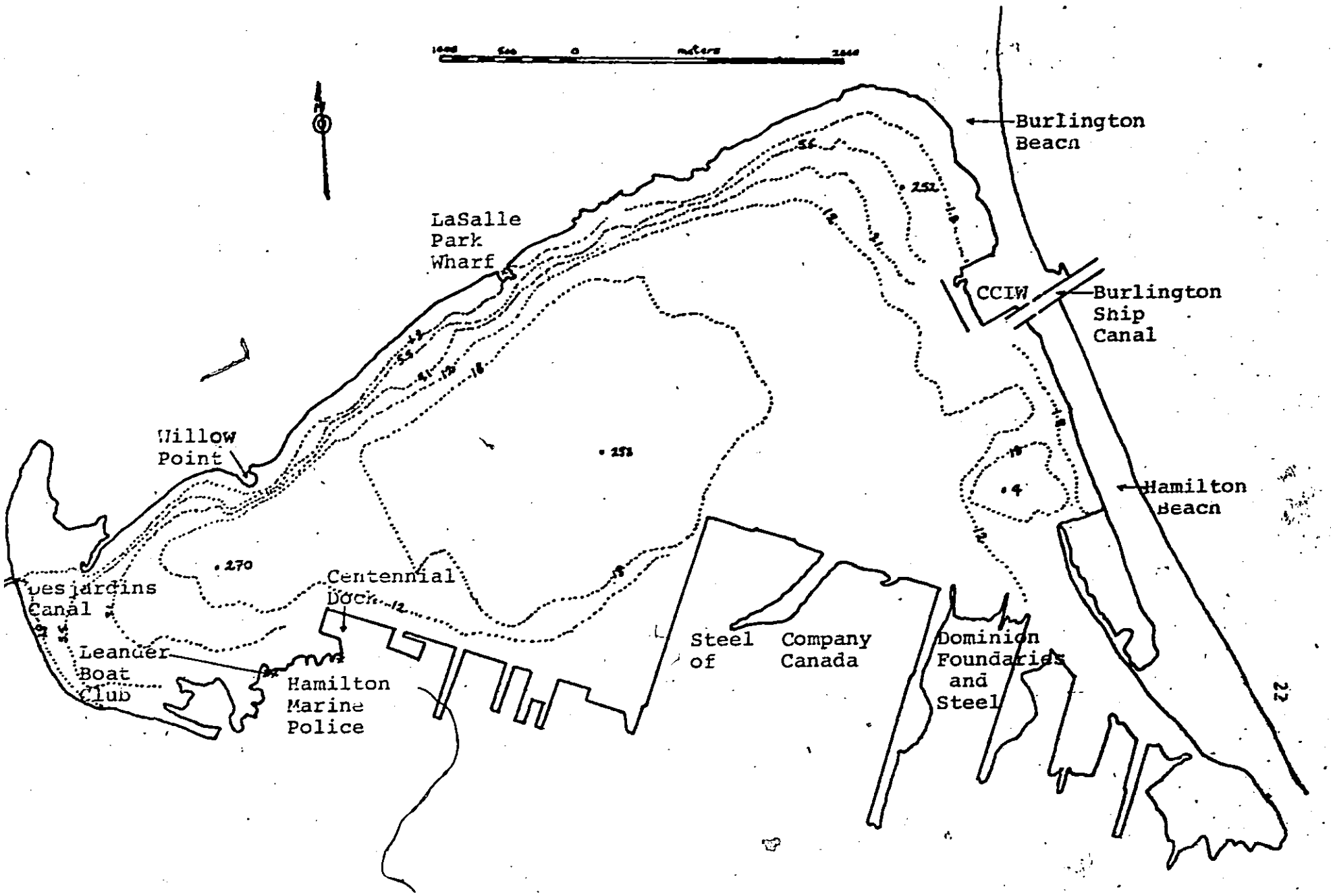
The surrounding relief varies considerably, from bluffs some 30 m above water level along the eastern and north eastern shores, to large industrial warehouses, factories and coal piles along the southern shore. This highly irregular relief promotes complex wind phenomenon over the harbour. This overall basin morphometry suggests that very complex current fields and irregular mixing events should occur.

The harbour is a dimictic body of water, with winter ice cover and summer stratification. The stratified period is characterized by rapid and large deviations of the thermocline of up to 7 m (Harris, 1976; Piccinin, 1977). The water body is eutrophic, with high organic loading and predictably suffers from severe hypolimnial oxygen depletion during the stratified period with bottom dissolved oxygen levels declining to 0 $mg \cdot l^{-1}$ (OME, 1974-1977; Harris, 1976; Piccinin, 1977). Soluble nitrogen and phosphorus concentrations remain high throughout the whole of the water column all year (Harris, 1976; Piccinin, 1977). The total phosphorous loadings for the harbour are in excess of 17 $g \cdot m^{-2} a^{-1}$. The total nitrogen loadings for the harbour are in excess of 348 $g \cdot m^{-2} a^{-1}$ (Snodgrass, private communication). The photic zone is shallow and varies from 4.5 to 9 m due to a high vertical extinction coefficient of the photosynthetically available incident radiation (.5-1.5 m^{-1}).

Figure 1

Hamilton Harbour

Hamilton Harbour with accompanying survey station locations and bathymetry in m. Survey stations are numbered 4, 252, 258 and 270.


Burlington Beacn
LaSalle Park Wharf
CCIW
Burlington Ship Canal
Willow Point
Hamilton Beacn
Centennial Dock
Desjardins Canal
Leander Boat Club
Hamilton Marine Police
Steel Company of Canada
Dominion Foundaries and Steel
22

More specific and detailed descriptions of the harbour's physical, chemical and biological relations can be found in Palmer and Poulton (1976), Snodgrass (1976), Chan et al. (1977), James and Eid (1978) and Polak and Haffner (1978).

2.2 Preface

Continuous samples were obtained from eight straight line transects on three separate occasions (Figures 37, 38 and 39, Appendix I). The transects were arranged such that four of the eight were aligned parallel to the wind direction. The remaining four transects were aligned at right angles to the first set. This design was tested for existing wind or wind-induced current flow effects on phytoplankton patchiness. The number of transects for each occasion and the number of samples per transect were determined by the constraints of mean square pattern analysis (Kershaw, 1973). This series of transects taken synoptically would allow a pooled variance analysis for all the samples using both methods of variance analysis. The length of an individual transect was 660 m with samples being taken continuously at 5 m intervals. The total number of samples per transect was 132. The mean square pattern analysis required only 128 (i.e. 2^7) samples for analysis. This number was analysed from each transect and the remaining four samples per transect were used to test the effect of the start position on the mean square pattern analysis. The length of each transect gave a spectral window from 5 m to 165 m and mean square pattern results from 5 m to 320 m for individual transects. The pooled variance analysis (see section

3.5) will increase the limits of analytical observation for the mean square pattern analysis to 660 m but will not affect the spectral window.

Samples were taken on September 16, 1975; July 20, 1976; and November 3, 1976. The cruises were planned for these dates to compare spatial heterogeneity during different limnological conditions.

The July sample was taken during a period of surface heating in a bilayered system of warmer epilimnial water overlying colder hypolimnial water. Under these conditions vertical exchange between surface and bottom waters will be limited. Biological activities should be more intense during this period of warmer temperatures and limited vertical circulation leading to intense small scale pattern.

The September sample was taken during a period of surface cooling with some sporadic vertical exchange. Vertical exchange causes a deepening of the mixed layer and an increase in the nutrient levels in the epilimnion. These changes should result in the rapid growth of some species and the rapid decline of others.

The November sample was taken during a period of vertically isothermal conditions with much reduced water temperatures. Autumn turnover causes higher nutrient concentrations in the surface waters but an increase in the mixed layer depth. These conditions should result in a dramatic change in the phytoplankton assemblage present and reduced growth rates. The result should be larger scales of heterogeneity in the community.

The wind direction was determined at CCIW (Figure 1) immediately before each cruise. Wind speed data were later collected from various

sources (Tables 13 and 14, Appendix) in order to assess the effect of wind on phytoplankton structure (patches). Structure is used here to refer in a general sense to patches.

The vertical thermal gradient of the water column was measured prior to each sample collection using either a portable electronic bathythermograph or a temperature and dissolved oxygen meter. The former has an accuracy in excess of 0.05°C and the latter has an accuracy of 0.25°C.

The zooplankton present in the harbour are mostly cladocerans (Bosmina and Eubosmina), rotifers and a very few cyclopoid copepods. The community composition changes radically throughout the year (Piccinin, 1977; Wade, private communication). It was assumed that these animals had no significant effects on phytoplankton biomass or their distribution because approximately 80% of the particulate carbon present in the system is bacterial or detrital (Harris, 1976; Piccinin, 1977; OME, 1977; Gliwicz, 1969; Gliwicz and Hillbricht-Ilkowska, 1972).

An initial sample scheme based on the simultaneous collection of discrete samples along a transect was investigated. A sampling apparatus composed of five, clear, cast plexiglass, van Dorn-type samplers (Figure 2) was constructed to allow simultaneous water samples to be taken within one cubic m of water. Each sampler was about 62.5 cm long and had an inside diameter of 6.3 cm. This gave a total volume sample slightly in excess of 2 ℓ. The sampling apparatus covered 1 m^2 of water with one axis oriented in the vertical and the other axis in the horizontal plane. A series of samples were taken both parallel to

and at right angles to the observed current direction. After each sample the sampling apparatus was withdrawn and the contents of each sampler decanted into separate 2 L plastic containers which were then capped and stored in the shade. A total of four such samples were taken. Upon returning to the laboratory, the containers were vigorously shaken and 500 ml from each was immediately filtered under a vacuum of not more than 69 kPa through Whatman 4.25 cm GF/C filters. A volume of the filtrate from each sample was removed and analysed for filtered reactive phosphorous (FRP) and nitrate + nitrite (NO_3+NO_2). The particulate material was analysed for chlorophyll *a* (section 2.4a). Three replicates of each of the above parameters were analysed for each sample. Duncan's multiple range test was used to ascertain the significance of the differences between mean parameter values. The analysis used a set of significant ranges with each range depending upon the number of means in the comparison. Therefore, this takes into account the number of samples involved which the least significance difference does not. It is also not necessary to compute an F value and proceed only if it is significant since the procedure may be used regardless of the significance of F (Steel and Torrie, 1960; Winer, 1962; Bliss, 1967).

The results (Table 1) show no obvious trends for the individual simultaneous samples. Chlorophyll *a* appears to have greater variation in samples taken in a cross-wind orientation. No such generalization seems possible for the FRP or NO_3+NO_2 determinations. Also, there would appear to be no simple correlations between the parameters measured.

Figure 2

Discrete Volume Sampler

An end view of the simultaneous, discrete volume sampling apparatus showing the arrangement and separation of the individual 2 ℓ samplers arranged to sample in the horizontal plane. The labels (A, B, C, D, E) allow reference to be made to a particular van Dorn bottle.

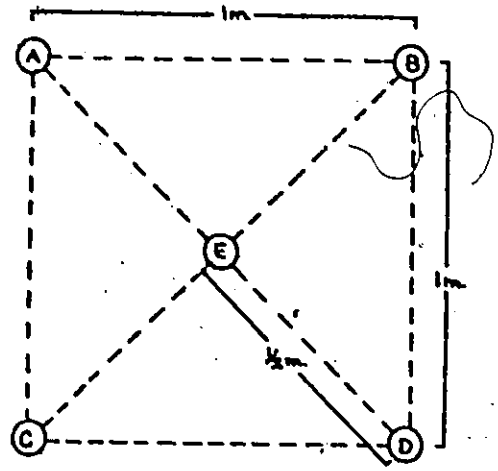
Table 1

Significant Differences (95% level) Between Discrete Volume Samples

Sample *	Chlorophyll a	Orthophosphate	Nitrate + Nitrite
1 (cross current)	(C-A), (C-E) (C-B)	(A-C), (A-D) (A-E), (A-B)	none
2 (with current)	(E-C), (D-C)	(C-B), (C-E)	(A-C), (A-E) (A-D), (B-C)
3 (cross current)	(B-E), (B-C) (D-E)	none	(D-C)

* 1,2,3 represents samples taken at stn. 270 approximately 20 minutes apart.

Figure 2



These findings suggest parameter values are significantly different over horizontal and vertical distances as small as 0.5m to 1m when discrete samples are taken. The significance of these estimates is further illustrated by examining Table 16 (Appendix I) which displays the values for the same parameters measured for two weeks prior to the sample period (Harris, 1976). The chlorophyll a for both surface and depth integrated values appears not to be significantly different from each other. Significance is determined by ±2 standard deviations of the measured value. The FRP and the NO_3+NO_2 concentrations show similar results with differences which appear to be of the same order as those observed from the discrete volume sample programme. A few anomalous values do however appear during the survey period.

Since no simple correlations between biomass and the major nutrient parameters were observed, the biomass variance might reasonably be attributed to physical forces. The nature of this variance cannot be examined in more detail using this type of sampling. The method cannot be used due to sample aliasing which occurs when the variance at scales smaller than those actually being measured appears erroneously at larger scales which is an especially serious problem for periodic discrete samples. Also, there may be interference from larger scales of pattern. The sample number must be augmented in order that more sophisticated techniques of analysis may be employed to reveal any systematic differences and correlations. Therefore, the continuous transect sampling technique outlined in the next section was employed.

2.3 Continuous Transect Sampling

A 3.7 m, 5 cm by 10 cm wooden beam was fastened to the deck of a launch and a small submersible pump (model 2E-38N, Little Giant Pump Company) was fixed to the beam so as to be suspended approximately 0.5 m below the surface while sampling. This arrangement assured that the sampling occurred away from the influence of the bow shock. Water was pumped inboard from this depth at a fixed rate through a 6 m length of plastic hose into a Turner model III fluorometer fitted with a fast flow door. The cuvette had an inside diameter of 1.7 cm. The fluorometer was equipped with a primary blue filter (Corning CS 5-60, maximum transmission 430 nm) and a red secondary filter (Corning CS 2-64 with a cut-off at 645 nm and a maximum transmission at 650 nm) in order to measure chlorophyll a (Lorenzen, 1966a, 1966b). The range selector of the fluorometer was set to measure the ambient chlorophyll concentration and the machine was zeroed with distilled water in the cuvette. The measured response time of this Turner fluorometer is 5 s, with 1.2 s being necessary for cuvette clearance and an additional 3.8 s to reach 95% of its stable response for a constant input at a scale range of 10 mv. The machine has a measured accuracy of ± 3%.

The water, after leaving the fluorometer, passed into a plastic temperature measuring chamber, in which was imbedded a Rosemount temperature sensor (linear bridge model 414L and sensor 176 LC). The sensor calibration was determined to be 1 mv^{o}c from 0^{o}C to 30^{o}C with a normal accuracy of less than 0.02 ^{o}C or 20 μ volts and a time constant of .25 s. The temperature sensor and fluorometer were connected to a two channel Hewlett-Packard chart recorder model 7100B, at a full scale

reading of 10 mv. The recorder had a time constant of 0.5 seconds to full scale with an accuracy of 0.5%.

After leaving the temperature chamber, the water was collected in white plastic 940 ml capacity bottles after clearing. Each bottle was capped and placed in wooden storage cases. The cases were covered to avoid light damage to the samples.

Each sampling cruise was comprised of a series of eight straight line transects. Four transects were taken parallel to the wind and four more perpendicular to the wind. Each transect was 660 m long and was partitioned into 132 samples. The speed of the launch reflected the volume sampled and the volume of water encountered by the pump as follows:

length scale resolution per unit sample = 5 m

inside diameter of pump opening = 1.27 cm

sample volume encountered in 5 m = 633 ml

pump rate at 0.5 m (with head) = 180 ml s^{-1}

time to collect 633 ml = 3.51 s

time to travel 5 m = 1.42 m s^{-1}

= 5.13 km hr^{-1}

= 3.2 knots

Radar fixes were made at the beginning and end of each transect. The total sample time did not exceed 2.5 hours.

The samples were immediately transported to McMaster University and stored in a cold room (8°C) in the dark. Within two days they were removed and partitioned for various analyses.

Each sample was shaken vigorously and a 20 ml aliquot was poured into a plastic scintilation vial containing approximately 1 ml of Lugol's solution as a preservative. An additional 20 ml were removed from each sample and fast frozen in a plastic scintillation vial for analysis of total phosphorous at a later date. A 450 ml subsample was filtered under a vacuum not exceeding 69 kPa through a Whatman 4.25cm GF/C filter, labelled and frozen (-23°C). Two 20 ml aliquots of filtrate were placed in scintillation vials containing a few drops of concentrated HCL or chloroform (Golterman, 1971) as preservatives, and placed in the freezer for subsequent chemical analysis (section 2.4). The former was to be analysed for FRP and FRS and the latter, for NO_3+NO_2 and NO_2 when necessary.

Chlorophyll samples were corrected for degradation. The following precedure was used to check for the correction. A large volume sample was collected after each excursion and 450 ml aliquots were filtered. Time zero determinations of chlorophyll a concentration were made on five aliquots and the rest were frozen. The frozen samples, three at a time, were withdrawn periodically and analysed. This gave a chlorophyll degradation curve and allowed corrections to the sample chlorophyll concentrations to be made. A test for the potential preservative effects of $MgCO_3$ was carried out. $MgCO_3$ solution was added to 12 aliquots which were filtered as described above for chlorophyll analysis (Strickland and Parsons, 1968). These were then frozen along with some untreated samples taken from the same initial sample and analysed at a later date.

The data were subjected to a power spectral analysis using the IMSL subroutine FTFREQ and the results plotted using USPLOT. The spectral window employed in this analysis approximates that of the Parzen window, which for a given number of lags, achieves a smaller variance than either the Bartlett or the Tukey window since it is wider and and flatter than the other two windows. A larger bandwidth implies that the number of degrees of freedom of the smoothed estimator is large and the variance is small giving rise to a larger bias (i.e. averaging out real peaks and valleys; Jenkins and Watts, 1968). The spectral estimates seen, have been smoothed by an averaging process (a low pass filter) which removes the higher and, in part the medium-scale-disturbances (frequencies or inverse wavelengths) while allowing the low frequencies through (Rayner, 1971). This implies that the spectral estimates represent much reduced variance values for the high and medium-scale frequencies (inverse wavelengths). This procedure has very likely eliminated some of the small-scale structure but has ensured that any surviving small-scale structure is significant. The data were further analysed for blocked pattern, covariance and correlations (Kershaw, 1961).

2.4 Parameter Analysis

2.4a Biological Parameters

Fluorometer

Each fluorometer trace was divided into 132 equal sections. The geometric mid-point of each section was measured and this value was used as reading for that sample. The data were analysed in relative

units and no attempt was made to convert the readings into actual chlorophyll a values. No information on pheophytin was obtained.

Chlorophyll a

The frozen, filtered samples were ground in 90% aqueous acetone using a pyrex tissue grinder which was attached to an electric Eberbach Con-Torque grinder assembly. The volume was made up to 12 ml and the samples were left in the refrigerator, in the dark for two hours (Strickland and Parsons, 1968; IFYGL chlorophyll working group, 1972). They were then centrifuged at 7000 rpm in an International Clinical Centrifuge, model CL for 10 minutes. The supernatant was carefully decanted into 5 cm path length optical grade cuvettes and measurements of absorbance at 750, 663, 645 and 630 nm were taken using a Zeiss PMQ II spectrophotometer. The chlorophyll a concentration for each sample was calculated using the SCOR UNESCO equations (Strickland and Parsons, 1968). No corrections for pheophytin were done. The accuracy (±2 sd) of the estimates of concentration are ± 12%. This was determined by examining five replicates from each sample period.

Species Enumerations

The preserved samples were shaken vigorously and poured into specially designed 10 ml settling chambers and allowed to stand for at least 12 hr. This would allow time for all the cells to settle to the bottom plate (Utermohl, 1958; Lund et al., 1958). For each sample, four or five of the commonest species were counted over 40 random fields (Table 19) through the 40 x objective on the Zeiss Invertescope D. The

total magnification being 400 x.

The above figure of 40 fields per sample was decided upon after an analysis of variance was done on sets of cell counts for one very common species and one much less common. The change in the level of accuracy, after 20, 30, 40 and 50 fields were enumerated, was recorded and then tested for significance. The results show significant reductions in variance up to counts of 40 fields per sample (Table 2). The anticipated error in estimates for these many fields are: for cells with a density of the order of one per field the counts are accurate to about ± 20%(i.e. 2 standard errors for five samples and 3 subsamples each); for cells with a density of the order of one per two or three fields, the counts are accurate to about ± 50%.

No attempt was made to convert these density measurements to a concentration measurement, however, simple multiplication by a constant factor of 32.3 will yield the number of cells ml^{-1} if one assumes a Poisson distribution of the cells (Lund et al., 1958).

2.4b Chemical Analysis

All chemical parameters were measured using the Auto Analyser II system, manufactured by the Technicon Corporation. The coefficient of variation (standard deviation/mean) was determined using 10 replicate samples for each parameter.

Standards were measured for each method every 10 or 20 samples in order that corrections for system drift might be made. FRP was determined using the molybdate hydrazine, stannous chloride method (Kramer et al., 1972). Total phosphorous was measured in a similar fashion

after persulfate digestion for 30 minutes at 82°C and 101 KPa in an autoclave. The coefficient of variation for FRP analysis is 5% at 25 $\mu g l^{-1}$ orthophosphate. Filtered reactive silica was measured using a method based on the reduction of silicomolybdate in an acidic solution to 'molybdenum blue' by ascorbic acid (Technicon Corporation, 1973). The coefficient of variation of the method was quoted as 0.36% at 5 $mg l^{-1}$ and measured as 1.61% at 1 $mg l^{-1}$. NO_3+NO_2 concentrations were determined using a copper cadmium reduction system (Technicon Corporation, 1971) which reduces NO_3 to NO_2. The individual NO_2 concentrations were measured by circumventing the copper cadmium column. The coefficient of variation for the NO_3 method is 0.62% at 1 $mg l^{-1}$ NO_3. The measured coefficient of variation was 2.04% for NO_3 + NO_2 at 1 $mg l^{-1}$ NO_3 and 4.25% for NO_2 at .7 $mg l^{-1}$ NO_2.

3.0 Results and Discussion

3.1 Chlorophyll Degradation Studies

The September 1975 study (Figure 3) indicates a decrease in the mean value of chlorophyll *a* by approximately 25% after 20-30 days, after which no further decline (i.e. degradation) is observed. The November 1976 results (Figure 3) show no such discernible changes, since the mean values lie within the limits of error of estimation which are defined as plus or minus twice the standard deviation. In July 1976 the potential effects of cold room storage (i.e. a delay in sample filtering and preservation) were examined. The results (Figure 3) clearly show no effect of a delay of up to two days for samples stored according to the conditions described. In July a study was also conducted to examine the effects of using $MgCO_3$ to prevent chlorophyll degradation (Strickland and Parsons, 1968). The results (Figure 3) indicate no increase in preservation with the addition of $MgCO_3$. Therefore, $MgCO_3$ was not added to samples taken for the purposes of determining the chlorophyll *a* concentration.

The degradation observed in the September 1975 study was probably a result of the storage temperature. The September 1975 samples were stored in a refrigerator-top freezer at approximately $-12^{o}C$ whereas, all the other samples were kept in a chest freezer at approximately $-23^{o}C$.

Figure 3

Chlorophyll Degradation Studies

a The mean value ± 2 standard deviations for samples not treated with $MgCO_3$ and stored at -23°C for up to 23 days after filtration.

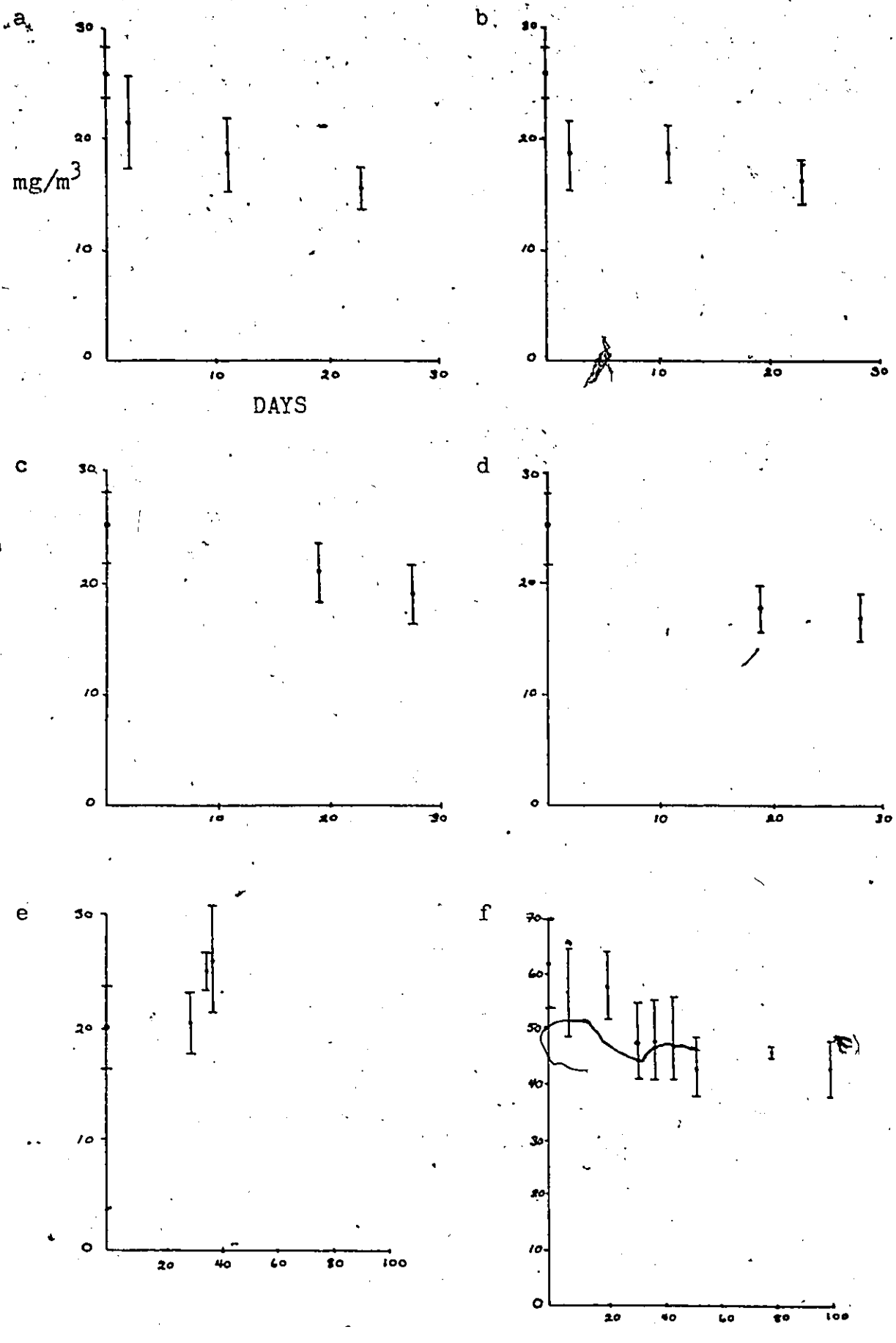
b The mean value ± 2 standard deviations for samples treated with $MgCO_3$ and stored at -23°C for up to 23 days after filtration.

c The mean ± 2 standard deviations for samples collected on July 20, 1976, filtered one day later and stored at -23°C for up to 28 days.

d The mean ± 2 standard deviations for samples collected on July 20, 1976, filtered two days later and stored at -23°C for up to 28 days.

e The mean ± 2 standard deviations for samples collected November 3, 1976 and stored at -23°C for up to 39 days.

f The mean ± 2 standard deviations for samples collected September 2, 1975 and stored at -12°C for up to 100 days.


a
b
c
d
e
f
mg/m3
DAYS
0
10
20
30
40
50
60
70
80
100

3.2 Species Enumeration ANOVA

The results (Table 2) show that for both C. erosa and Cyclotella men. there is an oscillation of the accuracy of the estimate with an increasing number of fields counted. There appears to be a significant increase in the level of accuracy of the estimate of the mean when enumerating 40 rather than 30 fields. There was however, no corresponding increase in the accuracy when 50 rather than 40 fields are enumerated. Therefore the greatest accuracy for a unit effort is available by enumerating 40 fields per sample.

The oscillatory behaviour of the accuracy is a regular phenomenon of the counting procedure and a significant improvement in the level of accuracy may not be realized until quite a large number of additional fields are enumerated. Lund et al. (1958) showed that the counting accuracy varies inversely with the square root of the number of units counted. Therefore, to doubly improve the accuracy requires a quadrupled unit effort.

3.3 Transect Data

In order to give a general impression of the raw data, plots of some of the parameters measured are presented in figures 40 through 47 (Appendix I). These represent sequential values taken from only two of the 24 transects (transect A, September 16, 1975 and transect A, July 20, 1976).

In general, the data fluctuate a great deal over short distances (1-5 samples) with the possible exception of the fluorometer and NO_2 plots.

Table 2

Analysis of Variance for Species Enumerations

Species	Number of Fields Compared	F Ratio	Probability of F >
Cryptomonas erosa [1]	20 x 30	1.6364	.225003
	30 x 40	3.12498	.102495
	40 x 50	1.18785	.297166
Cyclotella sp. [2]	20 x 30	.198409	.663937
	30 x 40	.45455	.512961
	40 x 50	.281245	.605561

F ratio here tests $S_1^2 = S_2^2$ (where $S_1 > S_2$); therefore, the closer the ratio to unity, the higher the probability that this is true (i.e. that they are from the same sample).

1 greater than one per field.
2 less than one per field.

There appears to be no long term trends in any of the plots with the possible exception of O. borgei (Figure 44). However, an examination of this plot (Figure 44) shows that the higher values are found in less than 15% of the transect. Within this subset, there are extremely large fluctuations in the values over 3-5 samples. These fluctuations would give rise to a high variance in the estimate of the subset mean value which suggests that the subset mean is not significantly different from that of the rest of the data set. Therefore all the parameters would appear to satisfy the stationary series requirement for power spectral analysis; that is, no long term trends were observed in the data series. This hypothesis was not statistically tested as outlined by Estrada and Wagensburg (1977) since the short length of the total series prohibitively restricts the number of subsets available for purposes of statistical comparisons (Kennett, private communication). The large differences in values over short sections would also give rise to excessively large variances in the estimation of subset means. No attempt was made therefore to apply any data detrending algorithm, which in the absence of the correctly identified trend would give rise to spurious results.

In contrast to the other parameters measured, the temperature traces show no fluctuations over the 660 m distance covered for each transect. A sample trace can be found in figure 47 (Appendix I). Another trace, taken at the end of the September 1975 cruise is also presented (Figure 47, Appendix I). It represents a transect of some 1200 m taken across the width of the harbour. Very slight end point effects can be seen with temperatures dropping by less than $1^{o}C$ near the shores. No

further analysis of temperature data was made because of the lack of variation.

3.4 Mean Square Pattern Analysis and Spectral Analysis of Some Test Data

In order to gain a better understanding of the limitations of the methods of data analysis used, six data series were tested. Two random number sequences were obtained from a table of random numbers and these values were sequentially added or subtracted from a constant value. This was done to insure stationarity of the data series (Figure 9). The other four number sequences were from data supplied by Dr. K. A. Kershaw. These data came from four transects of contiguous quadrat samples for a lichen, Cladonia rangiferina and a shrub, Ledum groenlandicum. The samples were obtained using a 5 cm square sampling device in an area of spruce-lichen woodland near Hawley Lake Ontario. The complete study can be found in Kershaw and Rouse (1971a, 1971b). The first two data sequences were taken from the recorded values of transect number one. The remaining two data sequences were obtained by summing the four transects of that study, one quadrat at a time.

Figures 4a and 4b show that the mean square pattern analysis of the two random number series generally displays peaking rather than a gradual increase in the variance to the end of the resolvable information which is block size (N_s) 64. None of these peaks are significant using the variance ratio test. However, peaks as large as that appearing at $N_s 32$ in figure 4a demonstrate the difficulty in an objective assessment of peaks appearing in the analysis.

Figure 4

Mean Square Pattern Analysis of Some Test Data

a Random number series 1

b Random number series 2

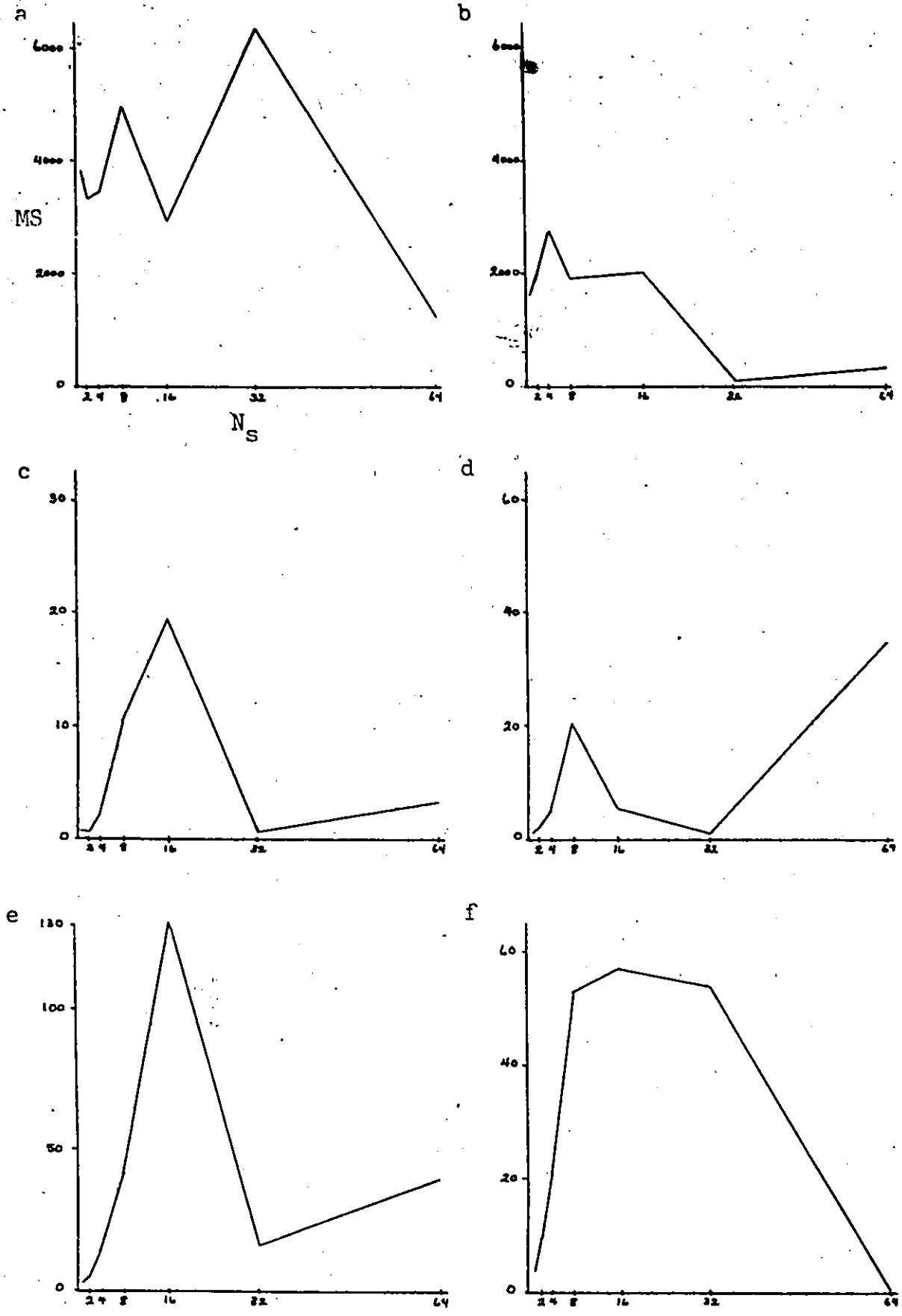
c Hawley Lake Transect 1 *L. groenlandicum*

d Hawley Lake Transect 1 *C. rangiferina*

e Hawley Lake Summed Transects *L. groenlandicum*

f Hawley Lake Summed Transects *C. rangiferina*

Figure 4



The spectral analyses of the random number sequences show scale independent variance (Figures 5 and 6). There are slight oscillations in the plotted values but no points fall outside the 95% confidence limits. These results agree with the theoretical expectations for a random number series.

The mean square analysis of the Hawley Lake data taken from transect number one (Figures 4c and 4d) shows a slight drop in the variance from N_s1 to N_s2 and also a sharp peak at N_s16 for L. groenlandicum. These results agree with the analysis by Kershaw and Rouse (1971a, 1971b). However the results for C. rangiferina do not agree with the original analysis (Kershaw and Rouse, 1971b) in that there is a significant variance peak at N_s8 rather than N_s16.

The spectral analyses for both of these species (Figures 7 and 8) show random fluctuations at short wavelengths with no identifiable peak in the variance which corresponds to N_s16 (Table 3). However, the variance does drop after this point is reached, but more points would be needed to clearly show a peak. This is termed an end-window effect. The N_s and wavelength transforms to length scales can be obtained from Table 3.

The mean square analysis for the four summed transects shows the disappearance of the slight variance drop at N_s1-N_s2, but maintains the peak at N_s16 for L. groenlandicum (Figure 4d). The results from C. rangiferina show a broad peak at N_s16 which ranges over N_s8-16-32 and then plummets to N_s64. This peak, although in general agreement with the standard mean square pattern analysis of Kershaw and Rouse (1971b) does

Table 3

Mean Square and Spectral Analysis Length-Scale Conversions

FFREQ (-ve)	FREQ	Period	Distance (m)	Batch Size (m)	MS
.30103	.50000	2.00	10.0	5	1
.31482	.48438	2.06	10.3	5	1
.32906	.46875	2.13	10.7	5	1
.34378	.45313	2.21	11.0	5	1
.35902	.43750	2.29	11.4	5	1
.37482	.42188	2.37	11.9	5	1
.39121	.40625	2.46	12.3	5	1
.40824	.39063	2.56	12.8	5	1
.42597	.37500	2.67	13.3	5	1
.44445	.35938	2.75	13.9	5	1
.46376	.34375	2.91	14.5	5	1
.48396	.32813	3.05	15.2	10	2
.50515	.31250	3.20	16.0	10	2
.52743	.29688	3.37	16.8	10	2
.55091	.28125	3.56	17.8	10	2
.57573	.26563	3.76	18.8	10	2
.60206	.25000	4.00	20.0	10	2
.63009	.23438	4.27	21.3	10	2
.66005	.21875	4.57	22.9	10	2
.69224	.20313	4.92	24.6	10	2
.72700	.18750	5.33	26.7	15	2 or 4
.76479	.17188	5.82	29.1	15	2 or 4
.80618	.15625	6.40	32.0	15	2 or 4
.85194	.14063	7.11	35.6	20	4
.90309	.12500	8.00	40.0	20	4
.96108	.10938	9.14	45.7	25	4 or 8
1.02803	.09375	10.67	53.3	25	4 or 8
1.10721	.07813	12.80	64.0	30	4 or 8
1.20412	.06250	16.00	80.0	40	8
1.32906	.04888	21.33	106.7	55	8 or 16
1.50515	.03125	32.00	160.0	80	16
1.80618	.01563	63.98	319.90	160	32

Figure 5

Spectral Analysis of Random Number Series 1

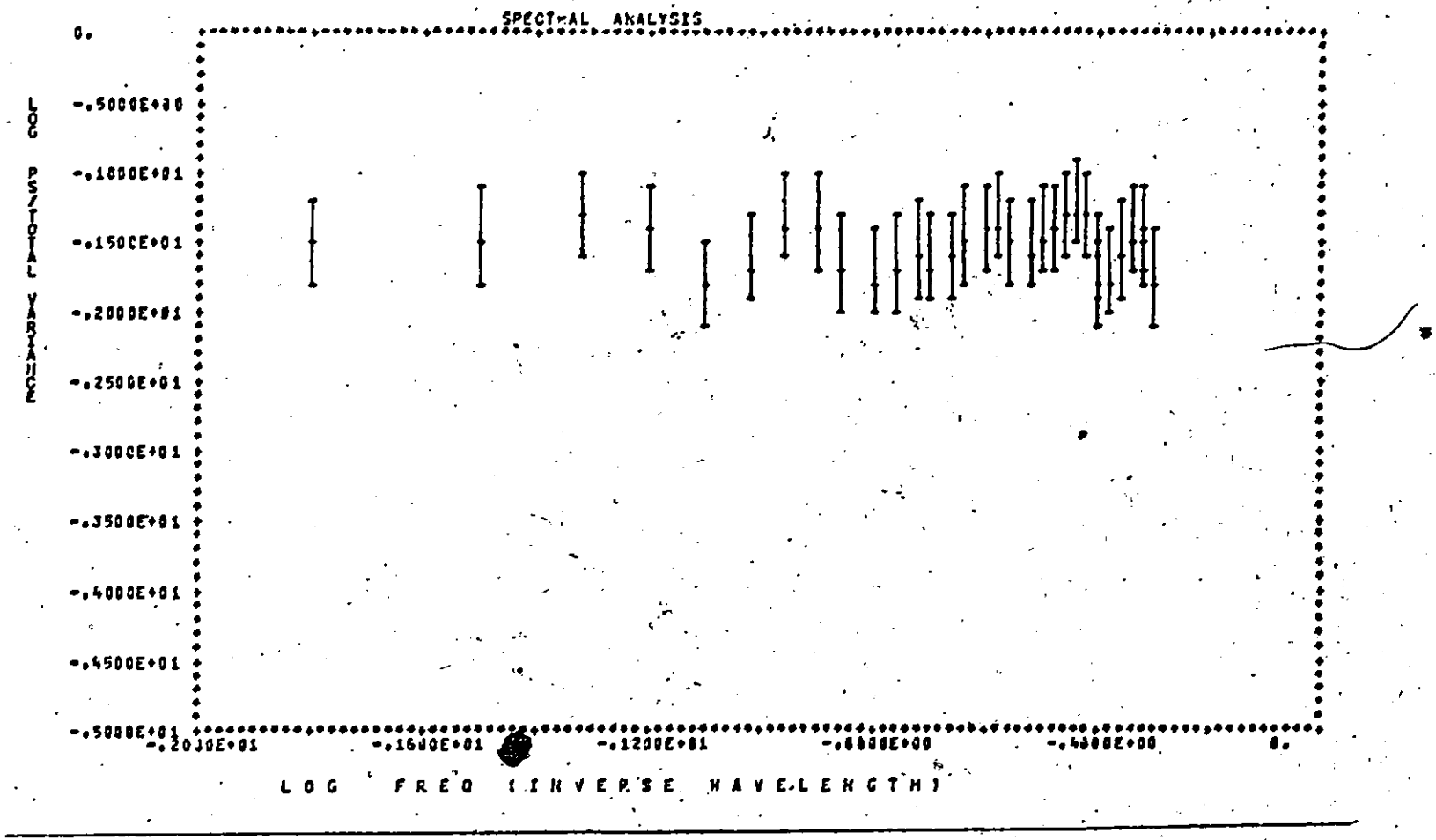

SPECTRAL ANALYSIS
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 6

Spectral Analysis of Random Number Series 2

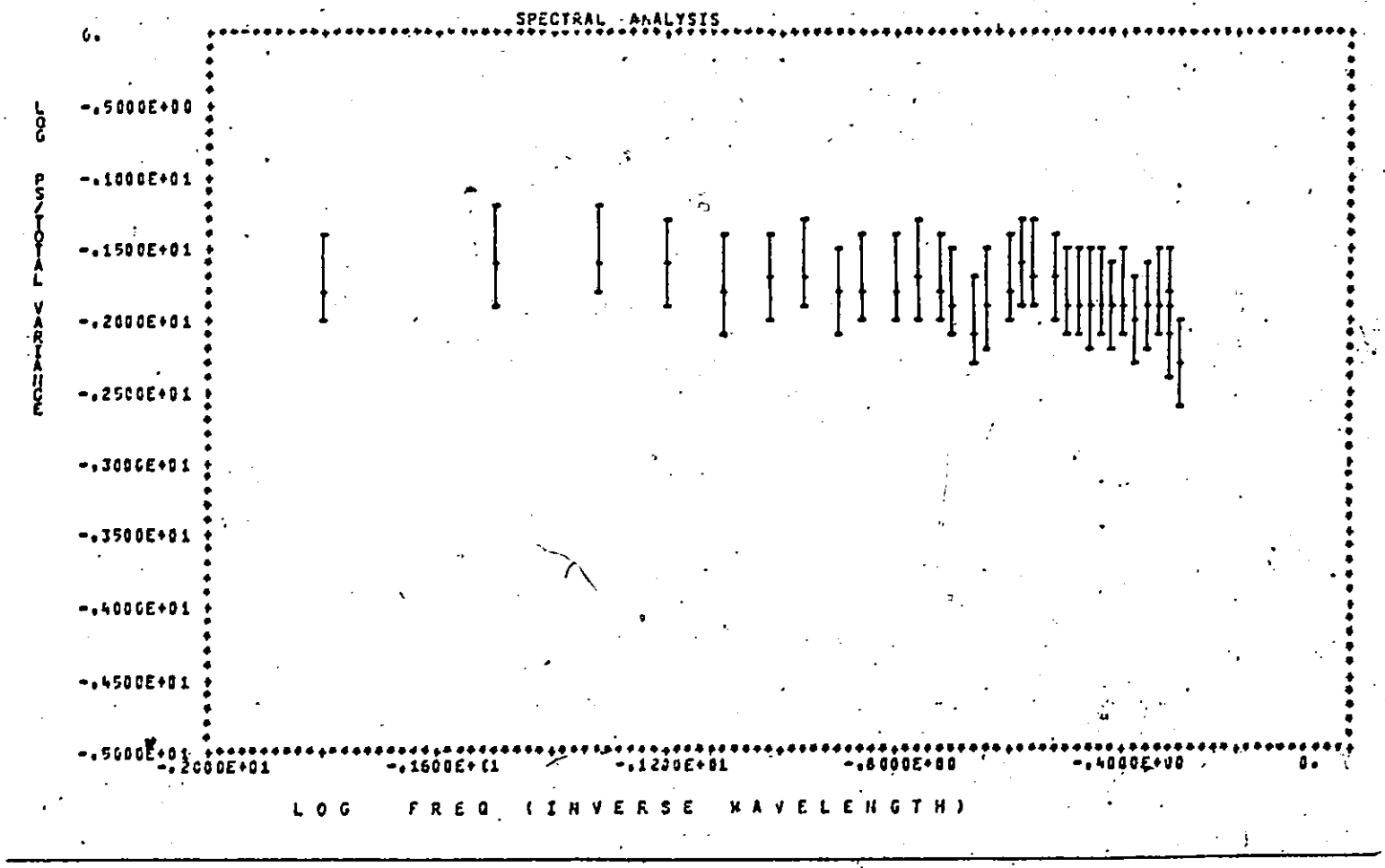

SPECTRAL ANALYSIS
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 7

Spectral Analysis of L. groenlandicum at Hawley Lake

The data are taken from Transect 1. This figure should be compared with its corresponding mean square pattern analysis (Figure 4c) and the slight drop in variance after the length scale corresponding to Ns16 (second point from left-hand side) noted.

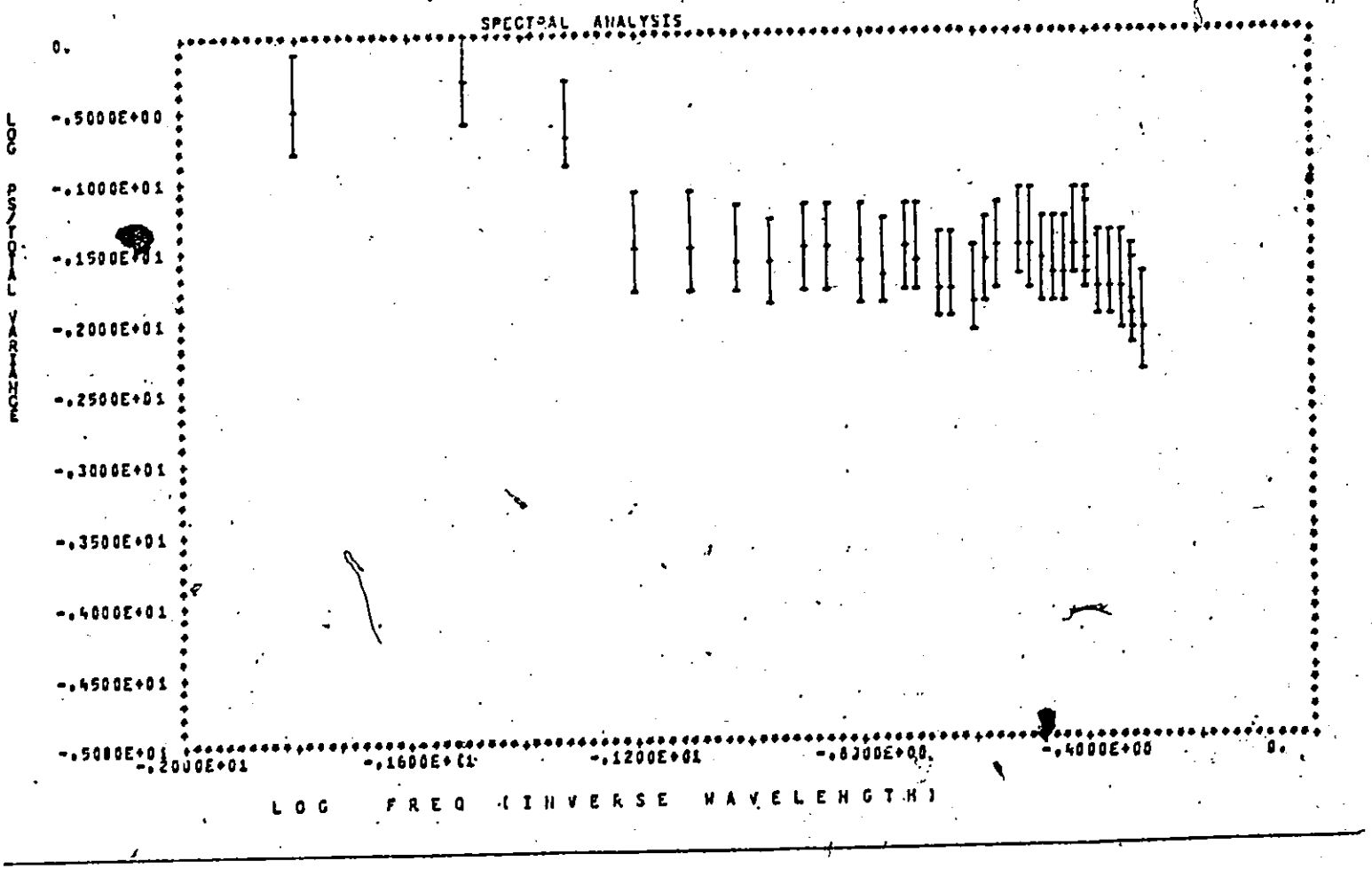

SPECTRAL ANALYSIS
LOG PS/TOTAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 8

Spectral Analysis of C. rangiferina at Hawley Lake

The data are taken from transect 1. This figure should be compared with its corresponding mean square pattern analysis (Figure 4 d) and the slight drop in variance after the length-scale corresponding to Ns16 (second point from left-hand side) noted.

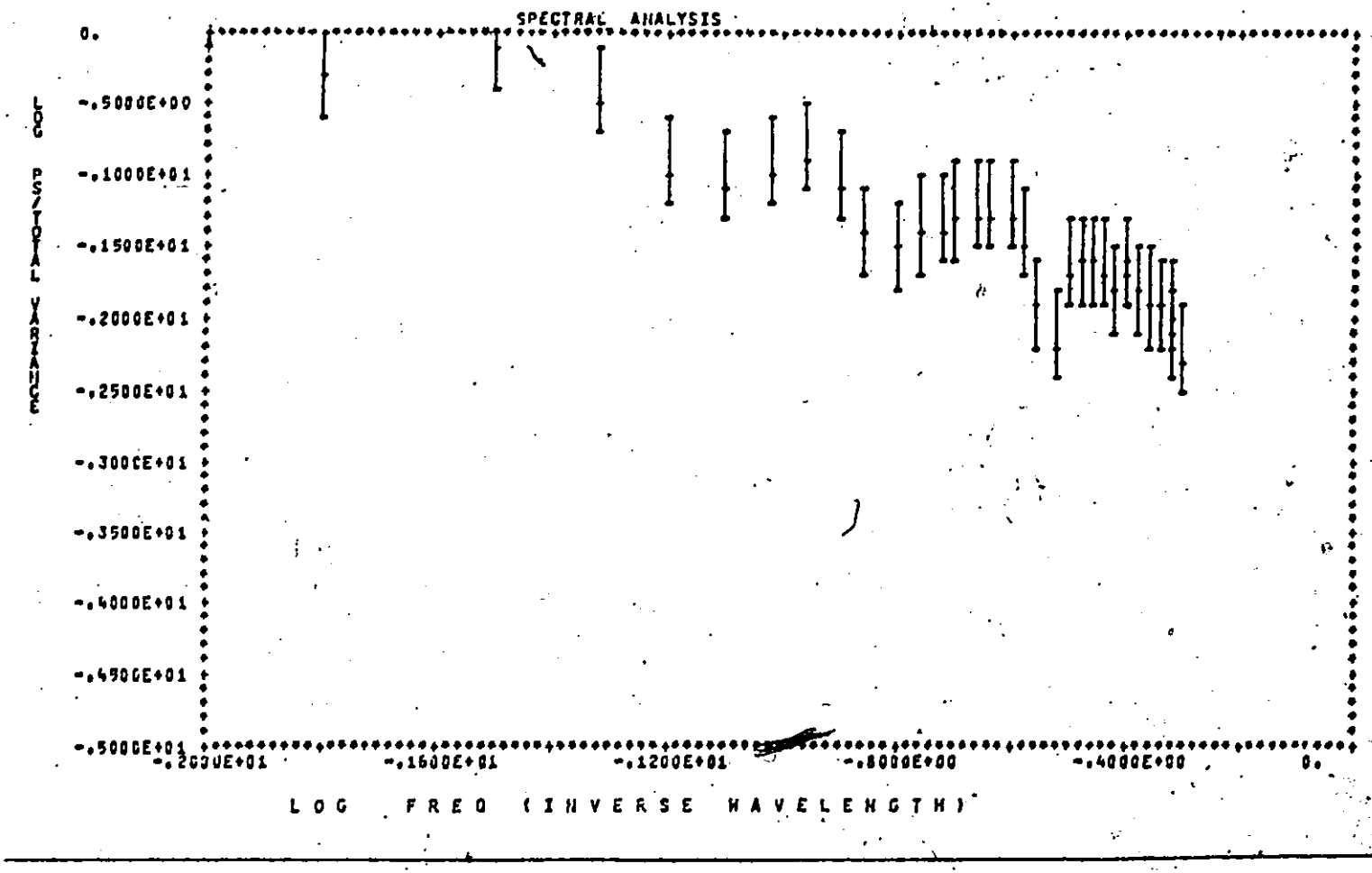

SPECTRAL ANALYSIS
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 9

Spectral Analysis of L. groenlandicum at Hawley lake

The data are taken from the four summed transects. This figure should be compared with its corresponding mean square pattern analysis (Figure 4e) and the slight drop in variance after the length-scale corresponding to Ns16 (second point from the left-hand side) noted.

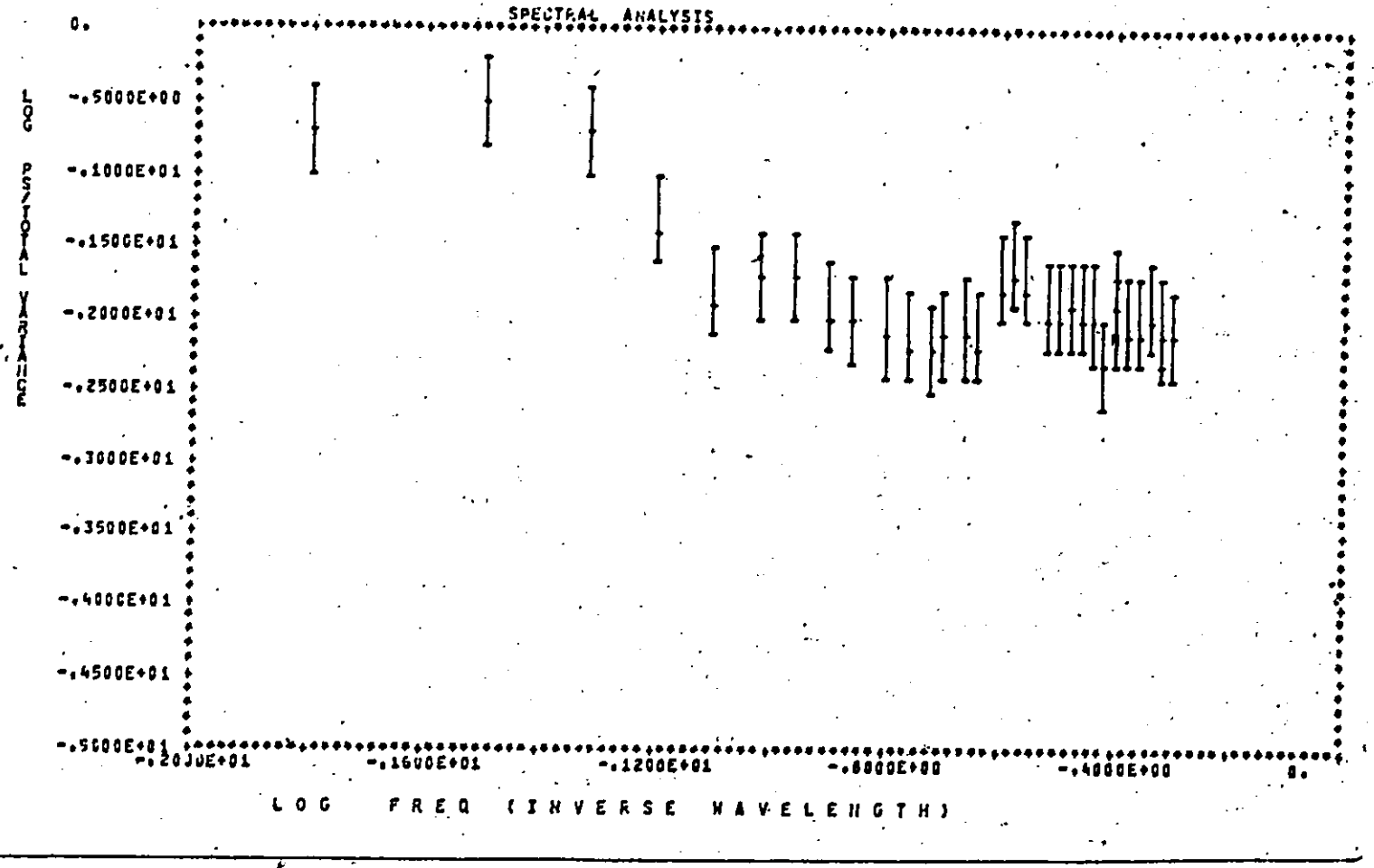
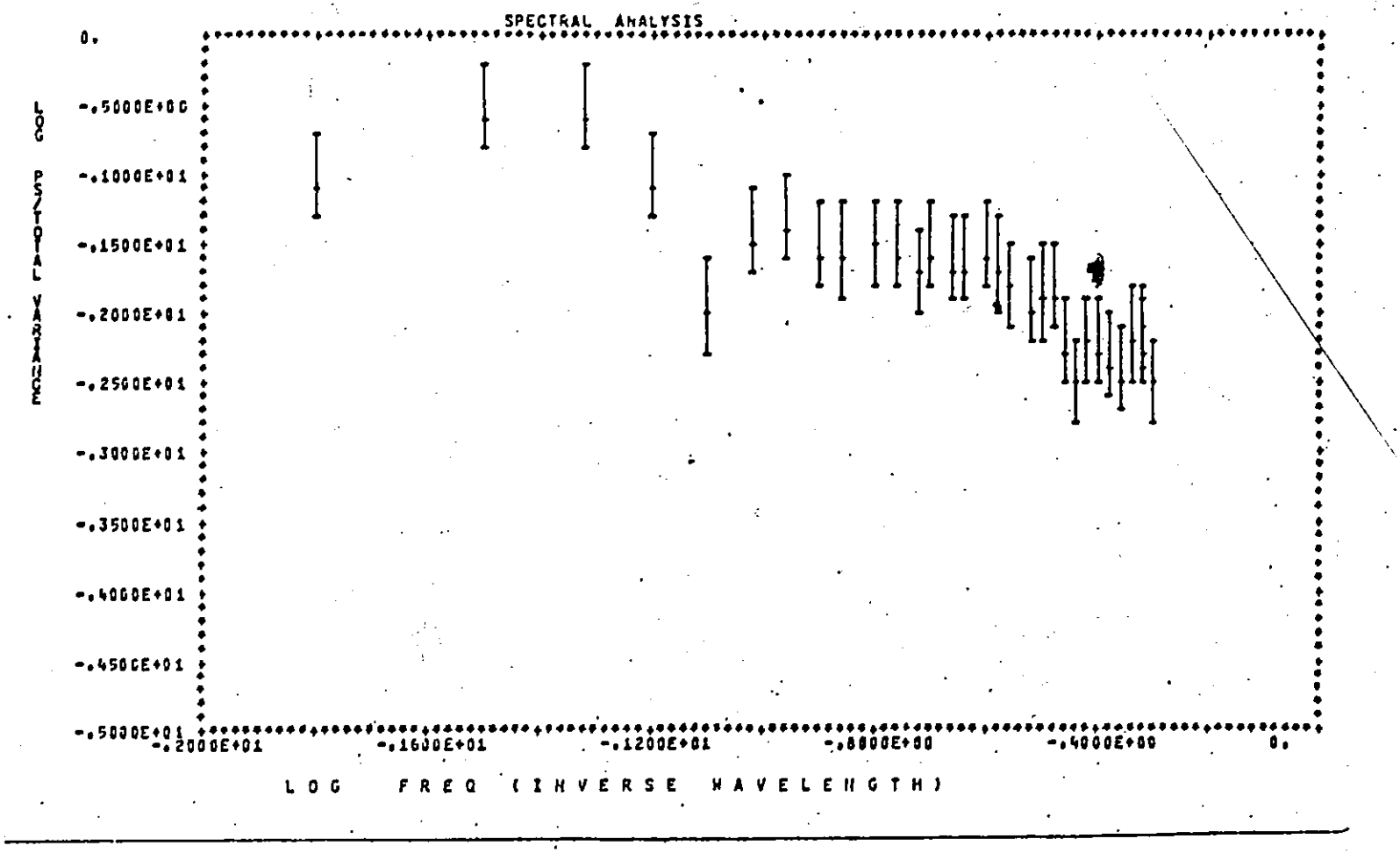

SPECTRAL ANALYSIS
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 10

Spectral Analysis of C. rangiferina at Hawley Lake

The data are taken from the summed transects (4). This figure should be compared with its corresponding mean square pattern analysis (Figure 4f) and the slight drop in variance after the length-scale corresponding to Ns8-Ns16 (second and third points from the left-hand side) noted.


SPECTRAL ANALYSIS
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

not have as sharp a peak at N_s16. The peak shift seen in the two analyses of the C. rangiferina data shows the averaging effect of the standard mean square pattern analysis which was a pooled variance analysis of the four replicate transects. The patch and/or space size for each individual transect does not exactly correspond to N_s16 but appears when a pooled variance analysis is used.

The spectral analyses for the summed data series (Figures 9 and 10) are similar to the single transect results with the same non-significant drop in variance after a point corresponding to N_s16 for L. groenlandicum is reached. The plot for C. rangiferina also shows the averaging effect of the summed transects by displaying a drop in the variance after a point corresponding to N_s8-16 is reached.

In summary, an objective assessment of the peaks appearing in a mean square pattern analysis may be difficult or even erroneous since peaks appear in the analyses of random numbers. Therefore, for the purposes of this study, peaks appearing at length-scales of up to one half the spectral window will be judged significant if and only if they also appear in the spectral analysis. Spectral analysis may not reveal patterns at scales between one quarter and one half the spectral window used. This problem is illustrated in the analyses of both C. rangiferina and L. groenlandicum.

3.5 Pooled Variance Analysis of Continuous Transect Data

Some representative plots for a pooled variance analysis using both a standard mean square pattern analysis and ensemble averaged spectral

analysis are presented in figures 11 through 25. The data for these plots were taken from transects E, F, G and H from July 20, 1976. Similar analyses were performed for each set of four transects having parallel orientations during sampling cruises. This method of grouping the transects required that the pooled variance analyses techniques be performed on two separate sets or groups of transects for each sampling cruise. This arrangement of grouped transects was necessary to test any wind direction and spatial patchiness relationships.

The standard mean square pattern analysis treats the separate transects as replicates of one another and pools the data for each N_s examined in a 2^n series. In the pooled analysis of these data, the range of n is 0 to 7.

The mean square pattern plots for the pooled variance technique (Figures 11 to 14) when compared to the results obtained from a mean square pattern analysis of each of the individual transects comprising the pooled set shows the potentially misleading information which may be obtained through the pooled variance analysis. Table 5 presents a summary of the pattern peaks encountered when each parameter from each transect was analysed. Peaks at $N_s 8$ in transect G and $N_s 2$ in transect H are entirely missed in the pooled chlorophyll a analysis. The pooled analysis flattens the peak at $N_s 1$ which is present in all transects except H. The same general results of flattened and missed variance peaks are seen for all the parameters except for NO_3+NO_2 and FRS which did not show any structure in the individual transect analyses. There is in general a rise in the variance to the end of the plots.

Peaks at the maximum block size or a sharp rise in the variance to the end of the resolvable information are of doubtful significance. They can be a reflection of real pattern at this scale or an indication of pattern of the next smallest block size overlapping into the larger scale (peak shift). They may also be result of inter-transect variance. If the length of the transect can be doubled, then the peak may become apparent (Kershaw, 1973).

The simplest way to pool the variance estimates from power spectral analyses is to first analyse each transect separately according to its wavelength components and then, assuming that each is a replicate of the other, add or average the variance estimates over each wavelength to give a composite periodogram (Woods, private communication).

The results of the ensemble average analysis (Figures 15 through 25) when compared to the analyses for each transect show that the assumption of replication is not true. Table 5 presents the significant peaks for each parameter from each transect which was analysed. For the sake of brevity, only three figures will be presented here (15-17) and the remainder can be found in Appendix II. There is a general flattening of the ensemble outputs resulting in missed significant peaks in several of the parameters in most of the transects.

These results show that the harbour is so spatially variable at any point in time that the individual transects can not be regarded as replicates of one another. Therefore, the pooling of variance at various length scales cannot be done.

These results also support the decision of the initial sample design which was to obtain a series of short transects rather than a single long one. The analysis of a single long transect would likely have been grossly misleading about the extreme horizontal heterogeneity present.

Figure 11

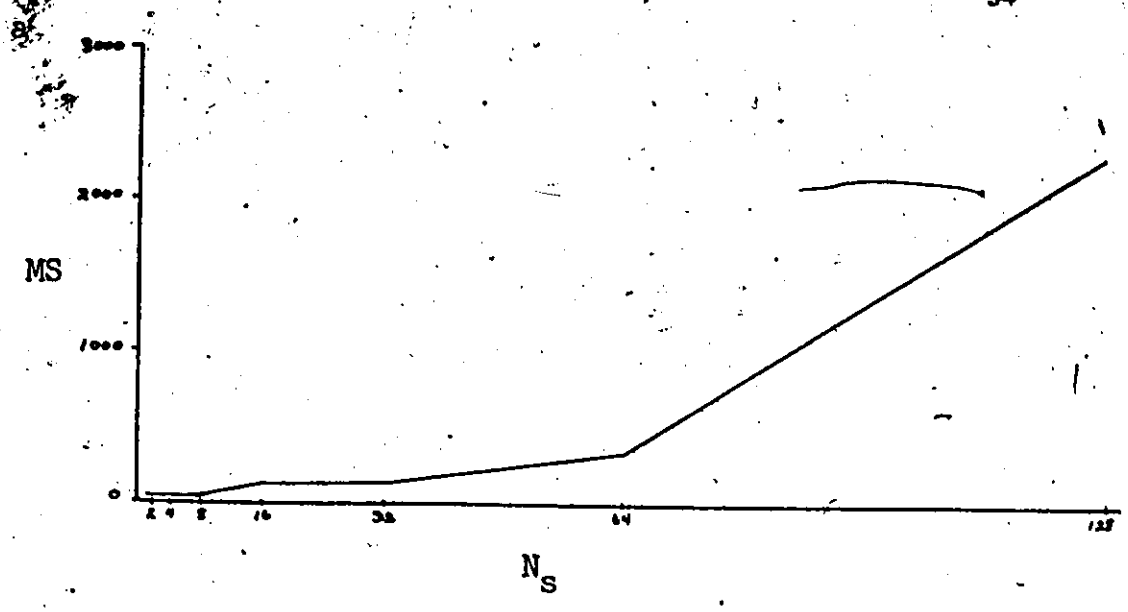
Mean Square Pooled Variance Analysis

Plots of the MS versus Ns for the pooled variance analysis from July 20, 1976, transects E-H for the following parameters:

a Chlorophyll a

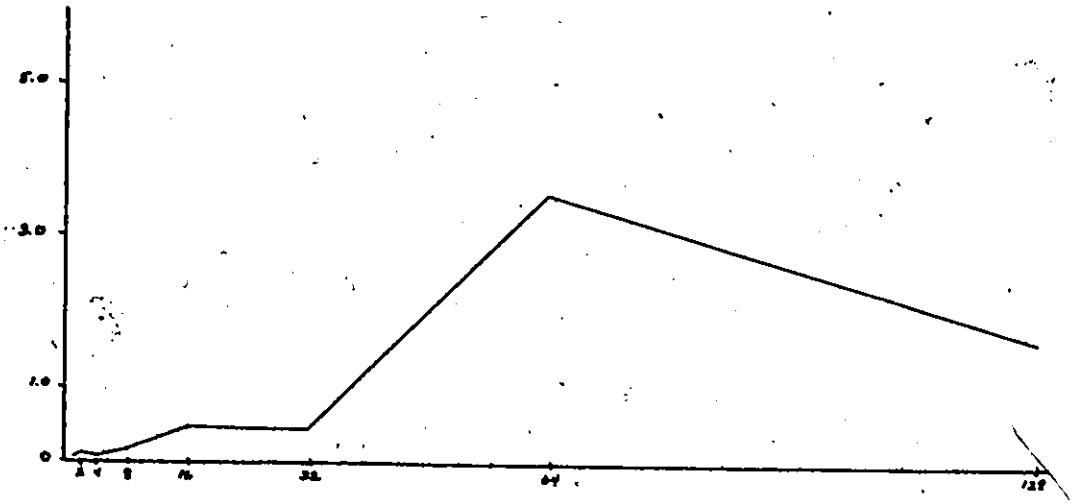
b $NO_3 + NO_2$

c NO_2


MS
2000
1000
0
2
4
8
16
32
64
128

N_S

b


3.0
2.0
1.0
0
2
4
8
16
32
64
128

c

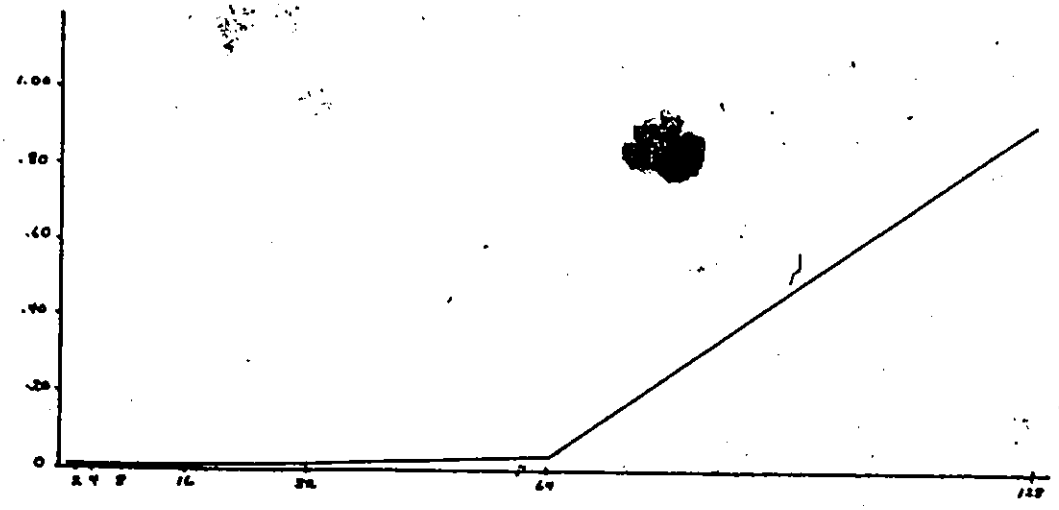

.80
.60
.40
.20
0
2
4
8
16
32
64
128

Figure 12

Mean Square Pooled Variance Analysis

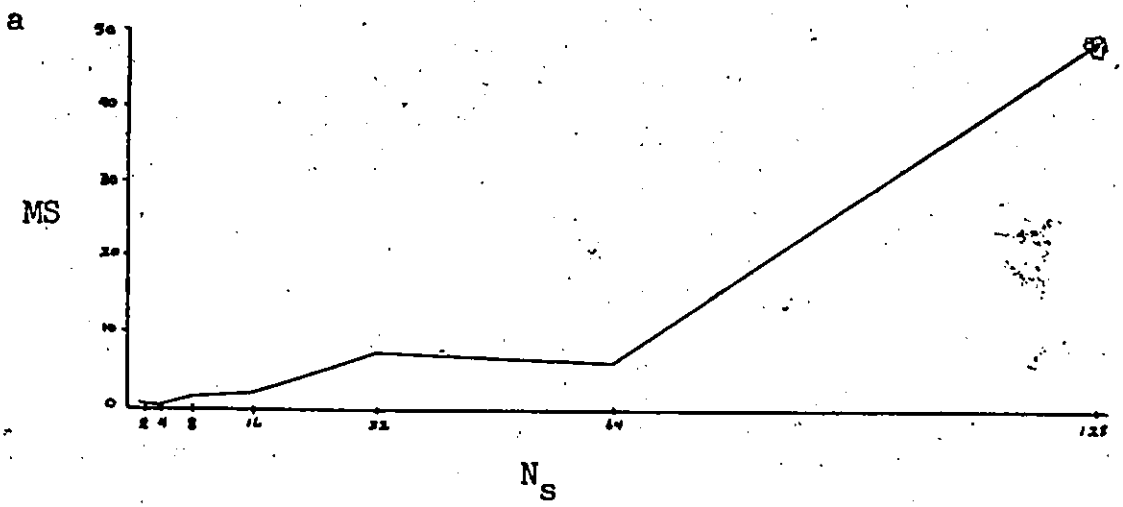
Plots of the MS versus Ns for the pooled variance analysis from July 30, 1976, transects E-H for the following parameters:

a Filtered Reactive Phosphorous

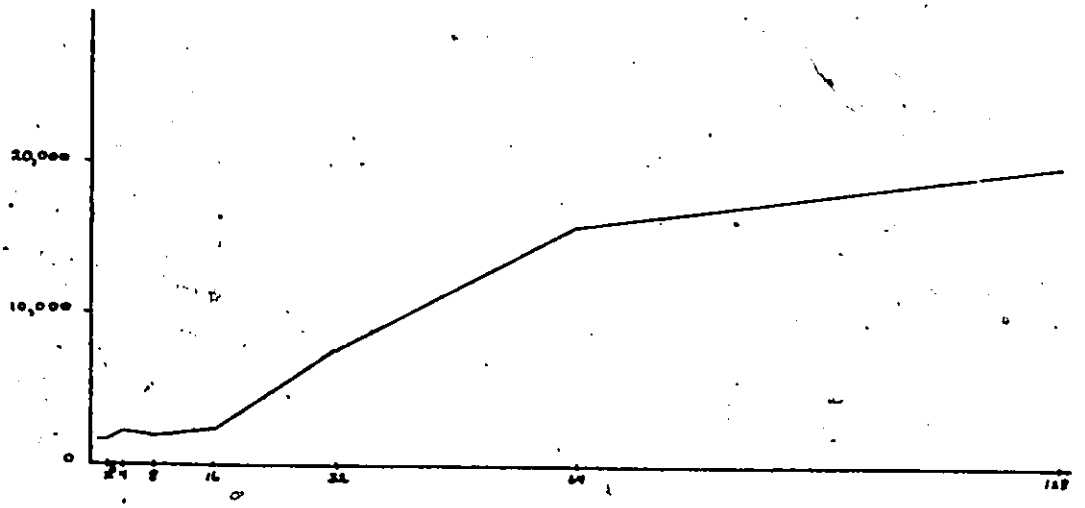
b Total phosphorous

c Soluble Reactive Silica

a


MS
0
10
20
30
40
50
2
4
8
16
32
64
128
N_S

b


20,000
10,000
0
2
4
8
16
32
64
128

c

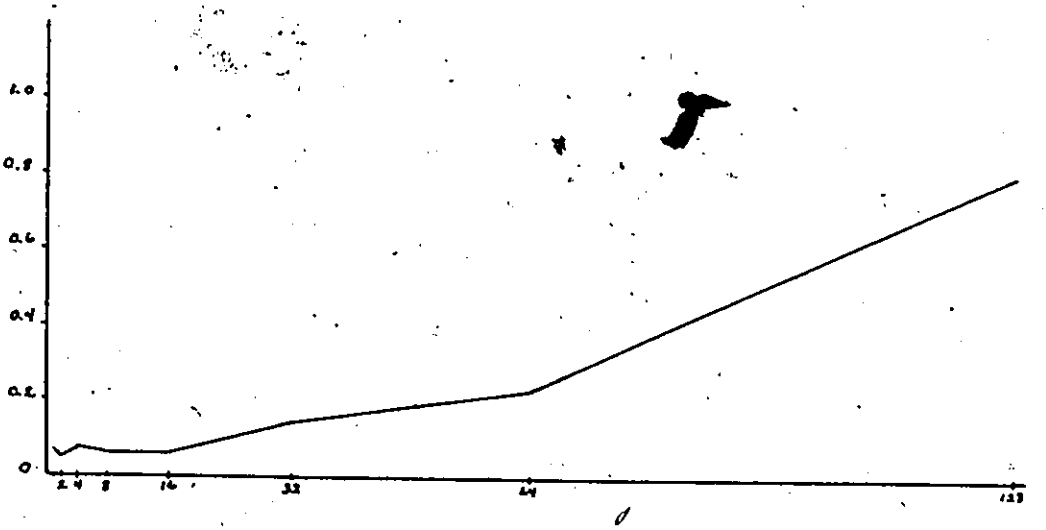

1.0
0.8
0.6
0.4
0.2
0
2
4
8
16
32
64
128

Figure 13

Mean Square Pooled Variance Analysis

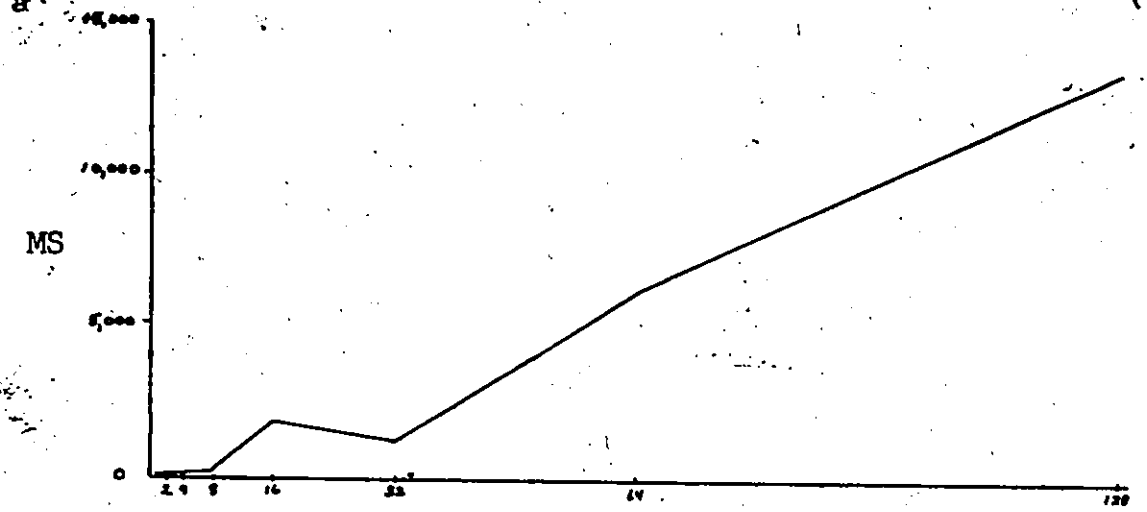
Plots of the MS versus Ns for the pooled variance analysis from July 20, 1976, transects E-H for the following parameters:

a *R. minutum*

b *Mougeotia* sp.

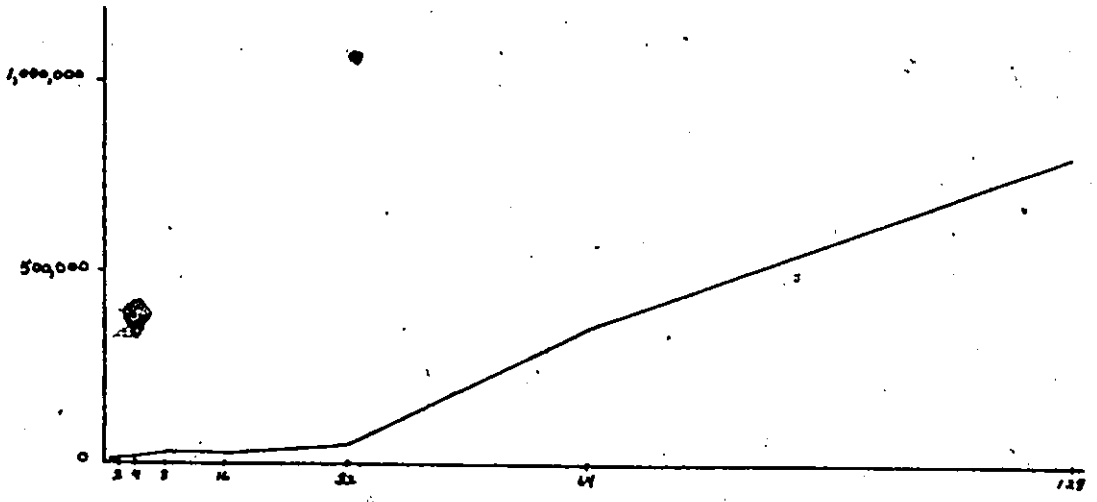
c *C. sphagnicola*

a

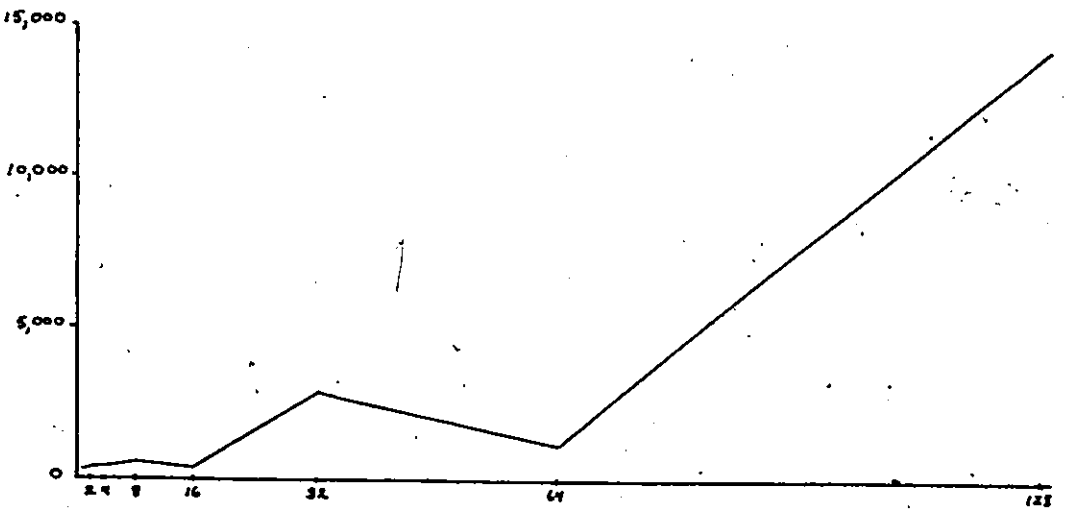

MS
0
5,000
10,000
15,000
2
4
8
16
32
64
128

N_S

b


0
500,000
1,000,000
2
4
8
16
32
64
128

c


0
5,000
10,000
15,000
2
4
8
16
32
64
128

b

Figure 14

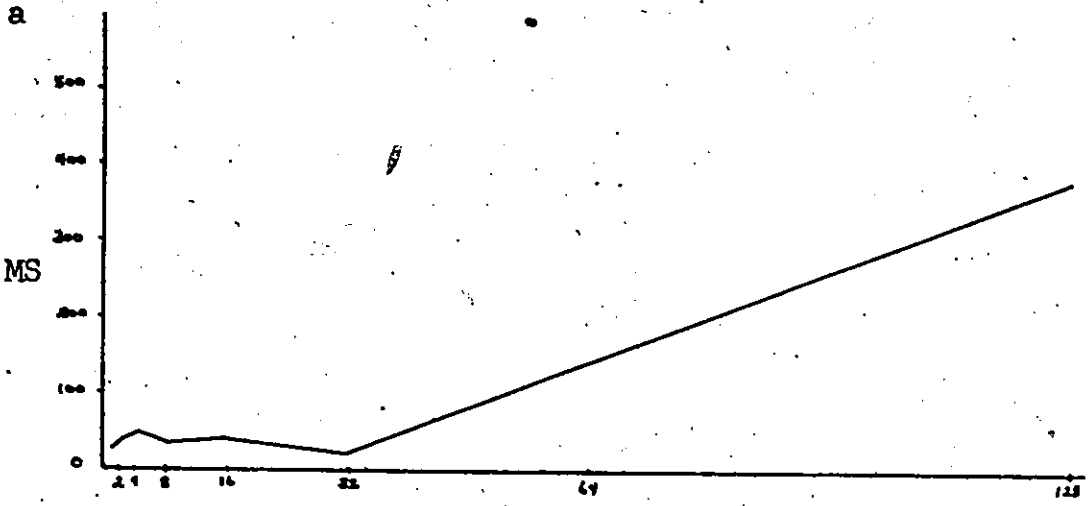
Mean Square Pooled Variance Analysis

Plots of the MS versus Ns for the pooled variance analysis from July 20, 1976, transects E-H for the following parameters:

a *Chlorella vulgaris*

b *O. borgei*

a



N_S

b

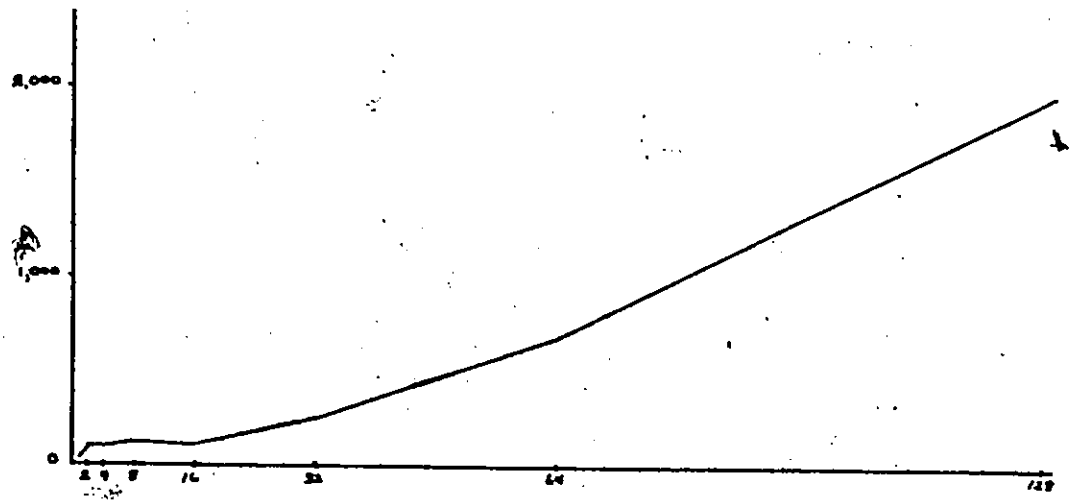


Figure 15

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) for July 20, 1976 transects E-H Chlorophyll a

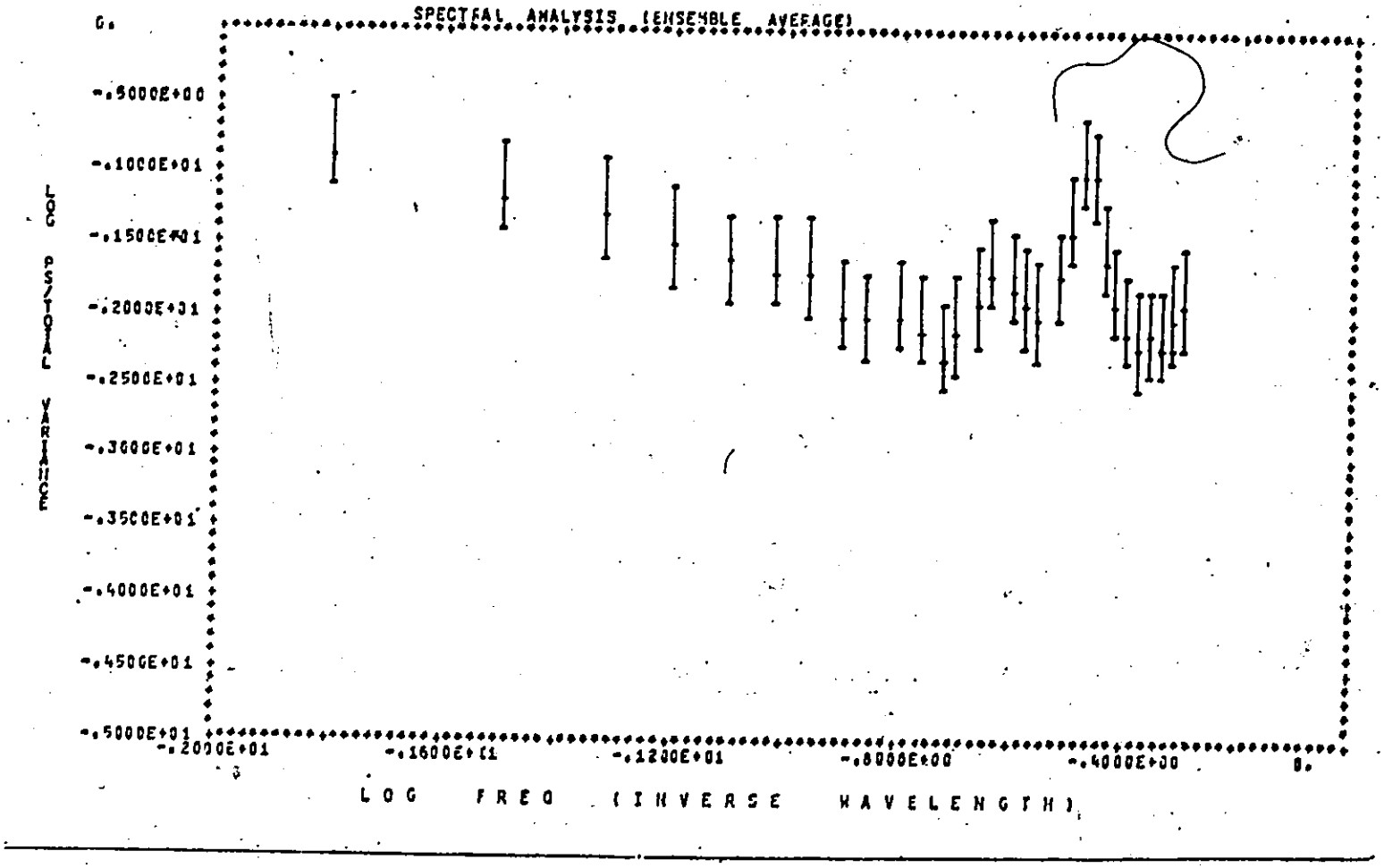

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
LOG SPECTRAL VARIANCE
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 16

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H Filtered Reactive Phosphorous

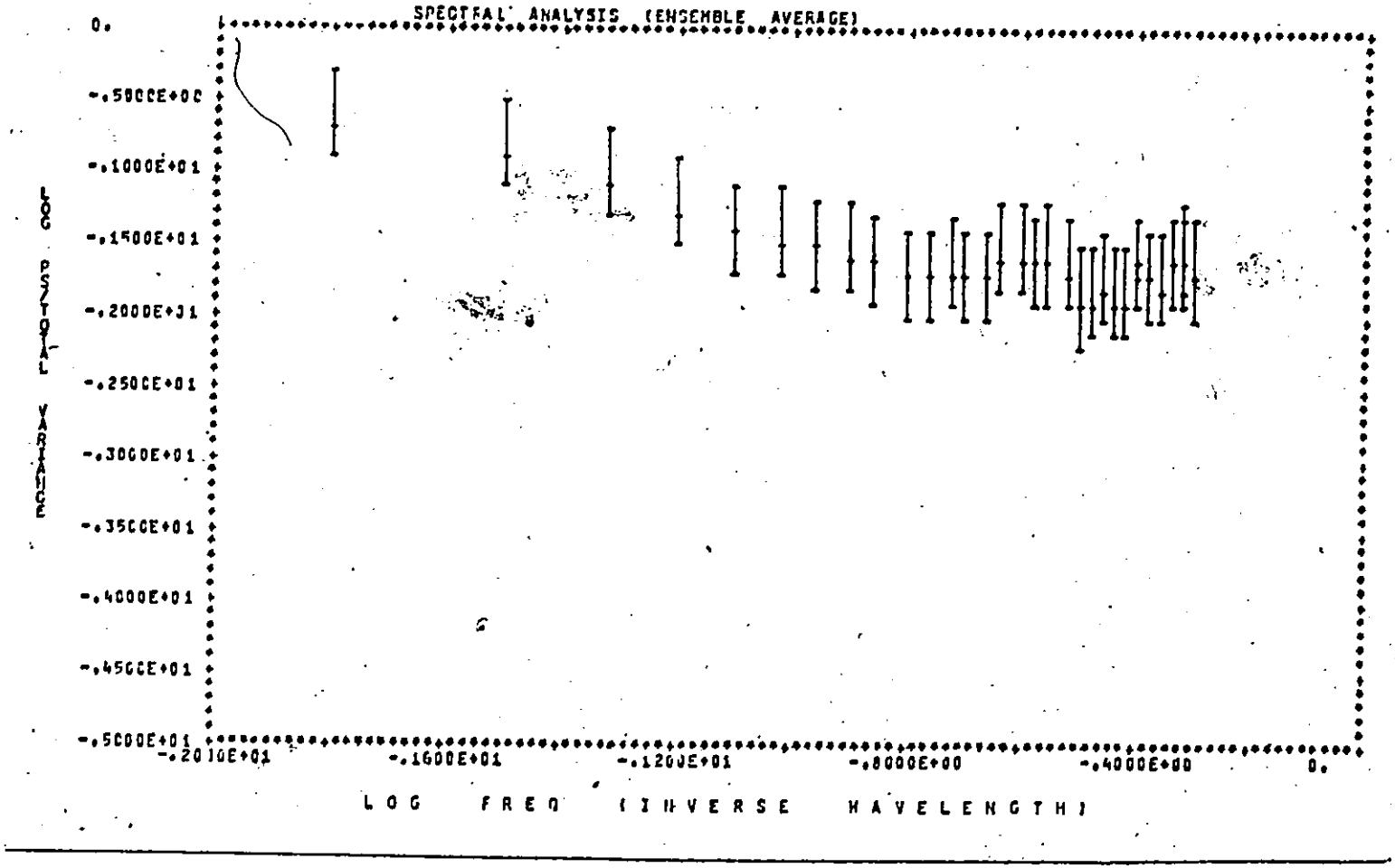
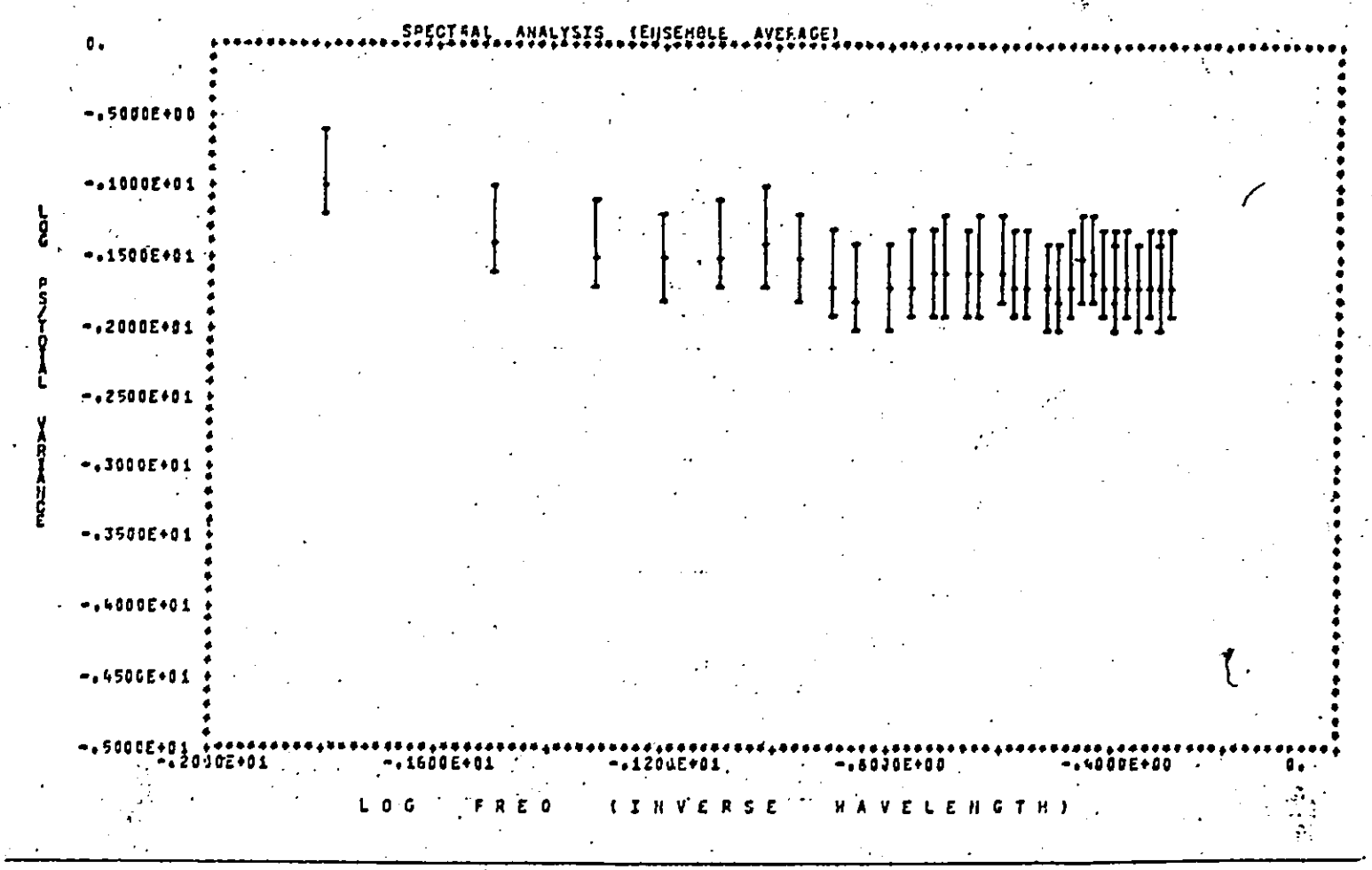

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
LOG SPECTRAL VARIANCE
-.2010E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 17

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H Mougeotia sp.


SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
LOG SPECTRAL VARIANCE
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

These results further suggest that a great deal more caution should be exercised in the use of pooled variance analyses in terrestrial applications. They also suggest that a loss of information at small scales may result from smoothing the spectral estimates via an averaging technique. The data collected from a long transect may be so heterogeneous at the smaller scales that the smoothed spectral estimates will not resolve it.

In summary, no composite picture of the variance distribution for any parameter is possible due to the extreme spatial variability present in the harbour. Information about the spatial pattern of parameters must be obtained through the variance analysis of individual transects.

3.6 Comparison of Spectral Analysis and Mean Square Pattern Analysis of the Individual Transect Data

The significant spectral peaks and all of the mean square pattern peaks for all 32 transects are summarized in tables 4, 5 and 6. The comparison between pattern peaks and significant spectral peaks, at first glance, appears relatively poor. However, considering problems outlined in section 1 for an analysis of variance using a 2^n series, the agreement between the results from the two forms of analysis can be reconciled. The pattern peaks reported in tables 4, 5 and 6 are encoded to indicate the most probable explanation for the disparity between themselves and the spectral peaks.

Table 4

Mean Square and Spectral Analysis Patterns for the September 16,1975 Cruise

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block Size (N_s)	Pattern Peak (m)	Pattern Peak Code
A	Chlorophyll a	5, 10	1	5	+
	fluorometer	none	8	40	NS
	NO_3	none (r)	none		
	PO_4	none (r)	16	80	NS
	Cerosa	none (r)	32	160	NS
	R. minutum	5	8, 32	40, 160	NS
	Cyclotella sp.	5	1, 4, 32	5, 20, 160	-, NS, NS
	O. borgei	5, 10	4	20	NS
	SRS	none (r)	32	160	#
B	Chlorophyll a	none	1	5	NS
	fluorometer	none	16	80	NS
	NO_3	none	32	160	#
	PO_4	5, 15	2, 8	10, 40	**
	Cerosa	none (r)	none		
	R. minutum	none (r)	4, 32	20, 160	NS, NS
	Cyclotella sp.	none (r)	1, 32	5, 160	NS, #
	O. borgei	none (r)	2, 16	10, 80	NS, #
	SRS	none (r)	2, 32	10, 160	NS, #
	Tot. Phosphorus	none	16	80	#
C	Chlorophyll a	none	none		
	fluorometer	none	16	80	#
	NO_3	5, 10 (r)	1, 8	5, 40	-, # *
	PO_4	none (r)	4	20	NS
	Cerosa	5, 10, 15	1, 8	5, 40	-, *
	R. minutum	none	none		
	Cyclotella sp.	none (r)	4	20	NS
	O. borgei	5	1, 4, 16	5, 20, 80	-, NS, #
	SRS	5 (r)	8, 32	40, 160	NS, #
	Tot. Phosphorus	none (r)	8, 32	40, 160	NS, NS
D	Chlorophyll a	none (r)	4	20	NS
	fluorometer	none	4	20	NS
	NO_3	5, (r)	4	20	NS
	PO_4	none (r)	2, 32	10, 160	NS, NS
	Cerosa	none	4, 32	20, 160	NS, NS
	R. minutum	25	4	20	-
	Cyclotella sp.	5	1, 4	5, 20	-, NS
	O. borgei	10	8, 32	40, 160	NS, #
	SRS	20	4	20	-
	Tot. Phosphorus	5 (r)	1, 4	5, 20	-, NS

Footnote

NS → not significant
\+ → peak interference
→ non-discriminatory
* → peak shift
\# → not detectable by PS
r → random
\- → O.K.

Table 4 cont'd

September 16, 1975

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block Size (N_B)	Pattern Peak (m)	Pattern Peak Code
E	Chlorophyll a	5, 10	2, 8	10, 40	+, NS
	NO_3	none (r)	2, 8	10, 40	NS, NS
	PO_4	5, 10, 25	4, 32	20, 160	-, NS
	Cafosa	none (r)	2, 32	10, 160	NS, ∅
	R. minutum	10 (r)	4, 32	20, 160	*, ∅
	Cyclotella sp.	none (r)	2, 8	10, 40	NS, NS
	O. borgei	5, 10 (r)	8	40	*, ∅
	SRS	none (r)	1, 8, 32	5, 40, 160	NS, *, ∅, ∅
	Tot. Phosphorus	5 (r)	2, 16	10, 80	*, ∅
F	Chlorophyll a	none	1, 4	5, 20	NS, NS
	NO_3	none	4	20	NS
	PO_4	none	none		
	Cafosa	15	2, 16	10, 80	-, NS
	R. minutum	5, 10	4, 32	20, 160	*, ∅
	Cyclotella sp.	none (r)	2, 16	10, 80	NS, NS
	O. borgei	none (r)	1, 16	5, 80	NS, NS
	SRS	none (r)	8, 32	40, 160	NS, NS
	Tot. Phosphorus	none	4, 32	20, 160	NS, ∅
G	Chlorophyll a	5	1, 8	5, 40	-, NS
	fluorometer	none	none		
	NO_3	none (r)	16	80	∅
	PO_4	10	1	5	*
	Cafosa	5, 15	1, 8, 32	5, 40, 160	-, *, NS
	R. minutum	none (r)	1, 4, 32	5, 20, 160	NS, NS, *
	Cyclotella sp.	10, (r)	8, 32	40, 160	NS, NS
	O. borgei	5, 10 (r)	1, 8, 32	5, 40, 160	-, NS, NS
	SRS	5, (r)	1, 4, 16	5, 20, 80	-, NS, NS
	Tot. Phosphorus	5, 10 (r)	1, 4	5, 20	-, *
H	Chlorophyll a	5, 15 (r)	2, 32	10, 160	+, NS
	fluorometer	5	16	80	NS
	NO_3	none	4, 32	20, 160	NS, ∅
	PO_4	none	none		
	Cafosa	none (r)	2, 8	10, 40	NS, NS
	R. minutum	none (r)	1, 4, 32	5, 30, 160	NS, NS, NS
	Cyclotella sp.	none (r)	2, 8, 32	10, 40, 160	NS, ?, NS
	O. borgei	10 (r)	1, 8	5, 40	*, NS
	SRS	5, 10 (r)	16	80	∅
	Tot. Phosphorus	none (r)	4, 32	20, 160	NS, NS

Footnote

NS → not significant
\+ → peak interference
→ non-discriminatory
* → peak shift
∅ → not detectable by PS
r → rAndom
\- → O.K.

Table 5

Mean Square and Spectral Analysis Patterns for the July 20,1976 Cruise

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block Size (N_B)	Pattern Peak (m)	Pattern Peak Code
A	Chlorophyll a	none	2	10	NS
	NO_3	none (r)	4, 16	20, 80	NS, NS
	NO_2	none	4, 32	20, 160	NS, #
	PO_4	10	2, 32	10, 160	-, #
	Tot. Phosphorus	10, (r)	4	20	*
	SRS	5, 10, 30 (r)	1, 32	5, 160	-, NS
	Mougeotia sp.	5, (r)	1, 4, 32	5, 20, 160	-, NS, NS
	C. sphagnicola	5, (r)	4, 32	20, 160	NS, #
	R. minutum	none (r)	4, 32	20, 160	NS, NS
	Chlorella vul.	5, (r)	4, 16	20, 80	NS, #
	O. horsei	none (r)	8, 32	40, 160	NS, NS
B	Chlorophyll a	none (r)	1, 4	5, 20	NS, NS
	NO_3	none (r)	2, 16	10, 80	NS, NS
	NO_2	none	16	80	NS
	PO_4	none	2, 32	10, 160	NS, NS
	Tot. Phosphorus	none (r)	2, 16	10, 80	NS, NS
	SRS	5, 15	1, 32	5, 160	-, NS
	Mougeotia sp.	5, 10	1, 8	5, 40	-, NS
	C. sphagnicola	none (r)	2, 32	10, 160	NS, #
	R. minutum	none (r)	4, 32	20, 160	NS, #
	Chlorella vul.	none (r)	2, 8	10, 40	NS, NS
	O. horsei	5, 10	1, 4, 16	5, 20, 80	-, *, NS
C	Chlorophyll a	10	16	80	#
	NO_3	5	4	20	NS
	NO_2	none	1, 16	5, 80	NS, #
	PO_4	5	1, 8	5, 40	-, NS
	Tot. Phosphorus	none (r)	2, 8	10, 40	NS, NS
	SRS	10, (r)	1, 32	5, 160	-, #
	Mougeotia sp.	none (r)	4, 16	20, 80	NS, NS
	C. sphagnicola	5	16	80	NS
	R. minutum	none (r)	1, 16	5, 80	NS, NS
	Chlorella vul.	10	1, 8	5, 40	*, NS
	O. horsei	none (r)	1, 32	5, 160	NS, NS
D	Chlorophyll a	5, 10 (r)	2	10	+
	NO_3	25	1, 32	5, 160	NS, #
	NO_2	none	32	160	#
	PO_4	5, 10	2	10	+
	Tot. Phosphorus	5, 10	1, 8, 32	5, 40, 160	+, NS, #
	SRS	5	1, 4	5, 20	-, NS
	Mougeotia sp.	10	2, 8, 32	10, 40, 160	-, NS, NS
	C. sphagnicola	10	2, 16	10, 80	-, #
	R. minutum	none (r)	1, 4, 16	5, 20, 160	NS, NS, NS
	Chlorella vul.	15 (r)	2, 16	10, 80	-, NS
	O. horsei	none (r)	2, 16	10, 80	NS, NS

Footnote

NS → not significant
\+ → peak interference
→ non-discriminatory
* → peak shift
\# → not detectable by PS
r → random
\- → O.K.

Table 5 cont'd

July 20, 1976

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block Size (N_B)	Pattern Peak (m)	Pattern Peak Code
K	Chlorophyll a	5	1, 16	5, 80	-, ∅
	NO_3	5	2, 16	10, 80	*, NS
	NO_2	25 (r)	4, 16	20, 80	-, NS
	PO_4	10 (r)	8, 32	40, 160	NS, ∅
	Tot. Phosphorus	10	8, 32	40, 160	NS, NS
	SRS	5	1	5	-
	Mougeotia sp.	none	8	40	NS
	C. sphagnicola	none (r)	1, 8	5, 40	NS, NS
	R. minutum	none (r)	16	80	NS
	Chlorella vul.	none (r)	4, 16	20, 80	NS, NS
	O. borgei	none (r)	8	40	NS
F	Chlorphyll a	10 (r)	1, 8, 32	5, 40, 160	-, NS, ∅
	NO_3	15, (r)	2, 32	10, 160	-, NS
	NO_2	none	16	80	NS
	PO_4	5 (r)	32	160	∅
	Tot. Phosphorus	5 (r)	4, 16	20, 160	?, NS
	SRS	5 (r)	1, 4	5, 20	-, NS
	Mougeotia sp.	none (r)	1, 4, 16	5, 20, 80	NS, NS, ∅
	C. sphagnicola	none (r)	2, 8	10, 40	NS, ?
	R. minutum	10 (r)	4, 16	20, 80	*, ∅
	Chlorella vul.	none(r)	2, 8	10, 40	NS, NS
	O. borgei	none (r)	2, 8, 32	10, 40, 160	NS, NS, NS
G	Chlorophyll a	10, 40	1, 4	5, 20	*, *
	NO_3	none	2, 16	10, 80	?, NS
	NO_2	10 (r)	16	80	NS
	PO_4	5, 10	1, 8	5, 40	+, NS
	Tot. Phosphorus	5, 20	1, 16	5, 80	-, NS
	SRS	none (r)	1, 4	5, 20	NS, NS
	Mougeotia sp.	5, 10 (r)	1, 32	5, 160	+, ∅
	C. sphagnicola	10 (r)	2, 8, 32	10, 40, 160	-, NS, NS
	R. minutum	none (r)	2	10	NS
	Chlorella vul.	none (r)	2	10	NS
	O. borgei	none (r)	2	10	NS
H	Chlorophyll a	10	2, 32	10, 160	-, ∅
	NO_3	none	4	20	NS
	NO_2	10, 25(r)	4, 16	20, 80	+, ∅
	PO_4	5	none		
	Tot. Phosphorus	5	1, 4	5, 20	-, NS
	SRS	none (r)	16	80	NS
	Mougeotia sp.	none (r)	2	10	NS
	C. sphagnicola	5	2, 32	10, 160	*, NS
	R. minutum	15 (r)	4, 16	20, 80	-, NS
	Chlorella vul.	none (r)	1, 4	5, 20	NS, NS
	O. borgei	none (r)	2	10	NS

Footnote

NS → not significant
\+ → peak interference
→ non-discriminatory
* → peak shift
∅ → not detectable by TS
r → random
\- → O.K.

Table 6

Mean Square and Spectral Analysis Patterns for the November 3, 1976 Cruise

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block Size (N_B)	Pattern Peak (m)	Pattern Peak Code
A	Chlorophyll a	none (r)	8	40	NS
	NO_3	10, 25	2, 16	10, 80	-, NS
	NO_2	none (r)	16	80	NS
	PO_4	5 (r)	1, 4, 32	5, 20, 160	-, NS, NS
	Tot. Phosphorus	none	4, 32	20, 160	NS, NS
	C. erosa	5, (r)	2, 8, 32	10, 40, 160	^, ?, ∅
	C. sphagnicola	none (r)	8	40	NS
	R. minutum	none	none		
	Stephanodiscus sp.	5, 10	2, 32	10, 160	+, ∅
B	Chlorophyll a	5, 15	16	80	?
	NO_3	none	1, 16	5, 80	NS, NS
	NO_2	none (r)	8	40	NS
	PO_4	5, 10	2	10	+
	Tot. Phosphorus	10	16	80	NS
	SRS	none (r)	4, 32	20, 160	NS, NS
	C. erosa	10, 20	1, 32	5, 160	^, ∅
	C. sphagnicola	10 (r)	8, 32	40, 160	NS, NS
	R. minutum	none (r)	2, 8, 32	10, 40, 160	NS, ?, NS
	Stephanodiscus sp.	none (r)	2, 8	10, 40	NS, ?
C	Chlorophyll a	none (r)	1, 8, 32	5, 40, 160	NS, NS, NS
	NO_3	none (r)	1, 8, 32	5, 40, 160	NS, NS, NS
	NO_2	5, 10 (r)	8, 32	40, 160	NS, NS
	PO_4	15 (r)	2, 32	10, 160	-, NS
	Tot. Phosphorus	5, 10 (r)	4	20	^
	SRS	none (r)	1, 8	5, 40	NS, NS
	C. erosa	10 (r)	1, 16	5, 80	^, NS
	C. sphagnicola	none (r)	4, 32	20, 160	NS, ∅
	R. minutum	none (r)	1, 32	5, 160	NS, NS
	Stephanodiscus sp.	5 (r)	4, 32	20, 160	NS, ∅
D	Chlorophyll a	5 (r)	4, 32	20, 160	NS, ∅
	NO_3	none	8, 32	40, 160	?, NS
	NO_2	none (r)	4, 16	20, 80	NS, NS
	PO_4	5, 10	1, 32	5, 160	-, NS
	Tot. Phosphorus	10 (r)	none		
	SRS	none (r)	16	80	NS
	C. erosa	5 (r)	1, 4	5, 20	-, NS
	C. sphagnicola	15 (r)	2, 16	10, 80	-, NS
	R. minutum	none (r)	1, 16	5, 80	NS, NS
	Stephanodiscus sp.	5, 10 (r)	1, 4, 16	5, 20, 80	-, NS, NS

Footnote

NS → not significant
\+ → peak interference
? → non-discriminatory
^ → peak shift
∅ → not detectable by PS
r → random
\- → O.K.

Table 6 cont'd

November 3, 1976

Transect	Parameter	Significant Spectral $\lambda/_2$ (m)	Pattern Block-Size (N_B)	Pattern Peak (m)	Pattern Peak Code
K	Chlorophyll a	none (r)	8	40	NS
	NO_3	none	8	40	NS
	NO_2	10, 25 (r)	4	20	+
	PO_4	none (1)	1, 16	5, 80	NS, NS
	Tot. Phosphorus	none (r)	1, 8	5, 40	NS, NS
	SRS	15 (r)	32	160	NS
	C. arosa	none (r)	1, 8	5, 40	NS, NS
	C. sphagnicola	none (r)	1, 8	5, 40	NS, NS
	R. minutum	none	1	5	NS
	Stephanodiscus sp.	none (r)	2	10	NS
F	Chlorophyll a	5 (r)	none		
	NO_3	none (1)	1, 4, 32	5, 20, 160	NS, NS, NS
	NO_2	none	32	160	∅
	PO_4	none (1)	4	20	NS
	Tot. Phosphorus	none (1)	8, 32	40, 160	NS, ∅
	SRS	none (r)	2, 8, 32	10, 40, 160	NS, NS, NS
	C. arosa	5	4, 32	40, 160	NS, ∅
	C. sphagnicola	none (r)	16	80	NS
	R. minutum	none (r)	8	40	NS
	Stephanodiscus sp.	none (r)	2, 8, 32	10, 40, 160	NS, NS, NS
G	Chlorophyll a	none	8	40	NS
	NO_3	5 (r)	2, 8	10, 40	*, NS
	NO_2	none	32	160	∅
	PO_4	5 (r)	1, 4, 16	5, 20, 80	-, NS, NS
	Tot. Phosphorus	5 (r)	1, 8, 32	5, 40, 160	-, NS, NS
	SRS	none (r)	8, 32	40, 160	NS, NS
	C. arosa	none (r)	2, 32	10, 160	NS, NS
	R. sphagnicola	none (r)	2, 32	10, 160	NS, ∅
	R. minutum	5 (r)	4, 32	20, 160	NS, NS
	Stephanodiscus sp.	none (r)	1, 16	5, 80	NS, NS
H	Chlorophyll a	5 (r)	1, 8, 32	5, 40, 160	-, NS, NS
	NO_3	5, 15 (r)	8	40	NS
	NO_2	none (r)	4, 16	20, 80	NS, ∅
	PO_4	5 (r)	1, 16	5, 80	-, NS
	Tot. Phosphorus	none (r)	1, 16	NS, NS	
	SRS	none (r)	none		
	C. arosa	5 (r)	1, 4, 32	5, 20, 160	-, NS, ∅
	C. sphagnicola	5 (r)	2, 8, 32	10, 40, 160	*, NS, NS
	R. minutum	5 (r)	2, 32	10, 160	*, ∅
	Stephanodiscus sp.	10	2, 16	10, 80	-, ∅

Footnote

NS → not significant
\+ → peak interference
→ non-discriminatory
* → peak shift
∅ → not detectable by PS
r → random
\- → O.K.

Two chronic problems of the mean square pattern analysis are peak shifts and its general insensitivity to pattern at small block sizes. The analysis is also incapable of indicating peaks in the variance which occur in adjacent block sizes.

The problem of peak shifting was investigated through the use of the four additional samples collected for each transect. The additional samples allowed an examination of the effects of five different start positions on the mean square peaks. The results for two parameters, chlorophyll a and C. sphagnicola for transect G July 20, 1976 are presented in figures 26 and 27. The peak shift response to the changed start positions are summarized in Table 7.

Peak shifts in both parameters are readily observable. The final start sequence for chlorophyll a shows complete agreement with the spectral analysis. However, the results for C. sphagnicola change from initial agreement to a loss of significance for the peak appearing at 10 m which was present in both the initial mean square and the spectral analysis. The peak at $N_s 2$, which is also indicated in the spectral analysis, is diminished in amplitude but remains fixed over the five varied start positions. Most of the results from the analyses of other parameters were similar, however, some were not. These are too few additional samples (i.e. too few additional start positions) to perform a detailed analysis for all block sizes. Usher (1969, 1975) recommends an additional 20-25% of the 2^n series of samples to be taken and the average or modal peak from the changed start position analyses be used as the true pattern peak.

Figure 26

Mean Square Pattern Peak Shifts

Plots of MS versus Ns for chlorophyll a from July 20, 1976 transect G, showing the effect of shifting the start position through five consecutive samples (a-e).

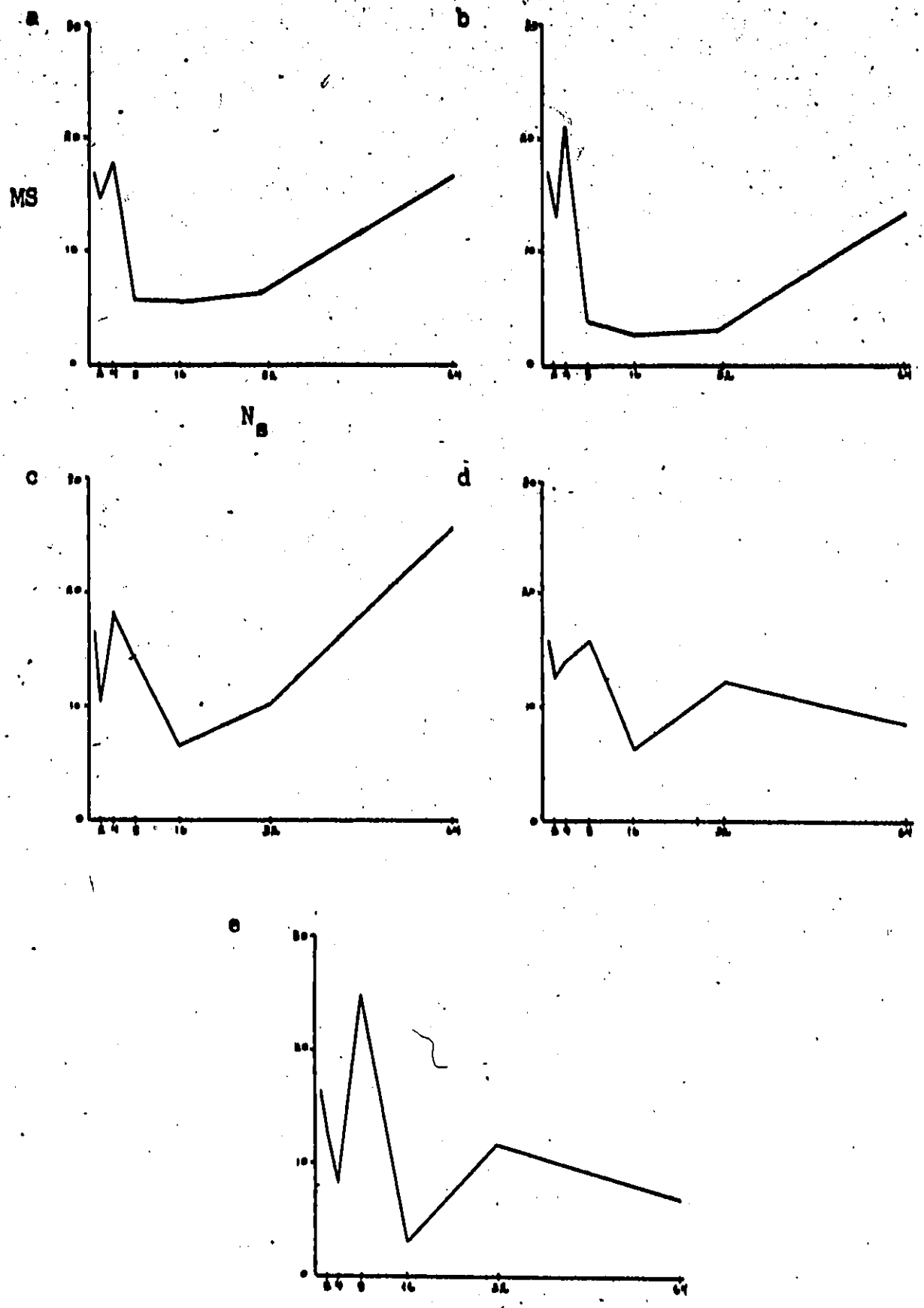

a
b
MS
N_B
c
d
e

Figure 27

Mean Square Pattern Peak Shifts

Plots of MS versus Ns for C. sphagnicola from July 20, 1976 transect G, showing the effect of shifting the start position through five consecutive samples (a-e).

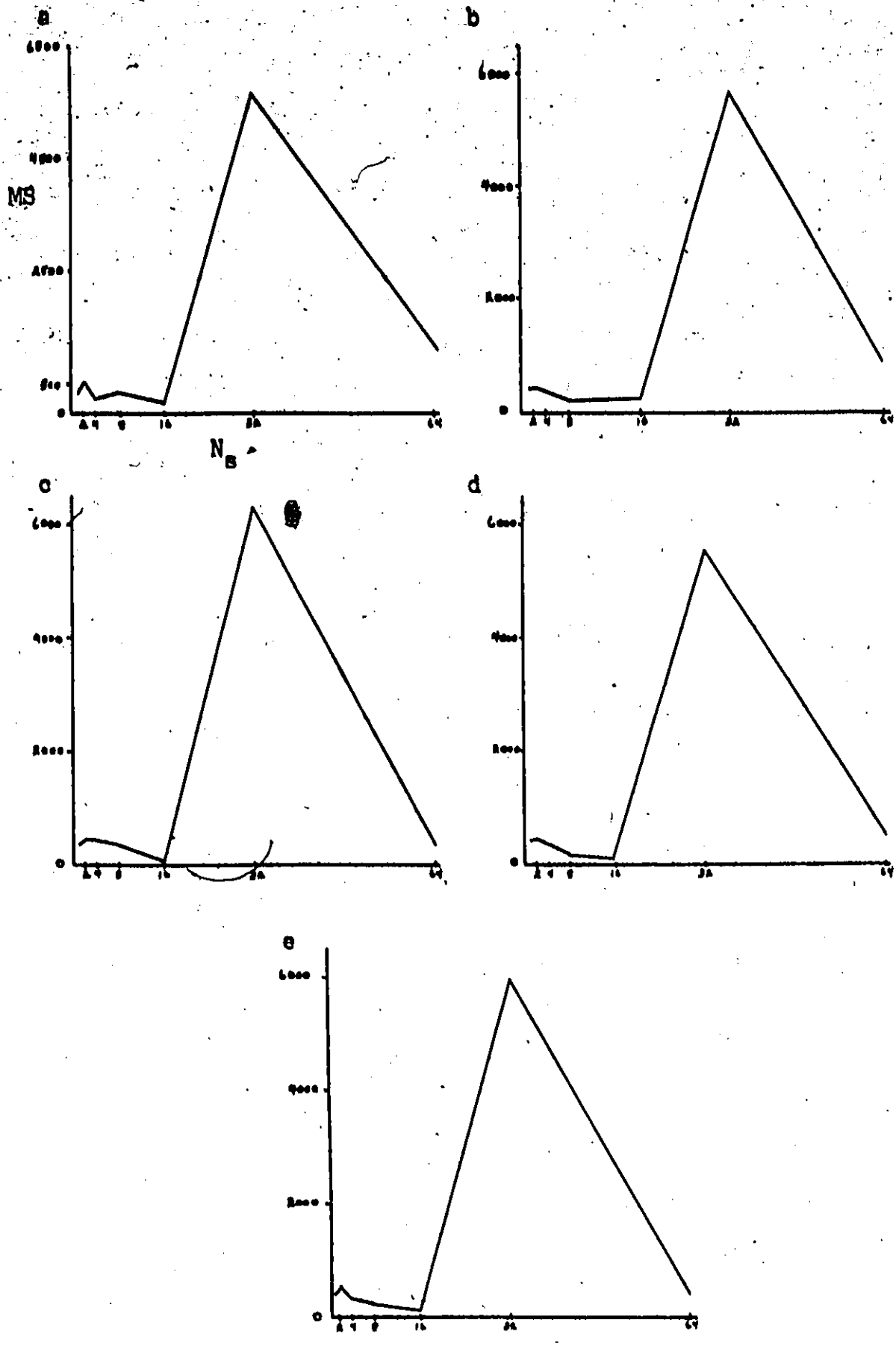

a
b
c
d
e
MS
N_S

Table 7 a and b

a Altered Start Position MS Pattern Analysis Chlorophyll a
July 20/76 Transect G

Block Size (Ms)	Position 1	Position 2	Position 3	Position 4	Position 5
1	NS	NS	NS	NS	*
2					
4	*	*	NS		
8				NS	*
16					
32				NS	
64					

b Altered Start Position MS Pattern Analysis Chlorophyll a
July 20/76 Transect G

Block Size (Ms)	Position 1	Position 2	Position 3	Position 4	Position 5
1					
2	*	NS	NS	NS	NS
4					
8	NS				
16					
32	NS	NS	NS	NS	NS
64					

* Significant by Variance Ratio

NS Not Significant by Variance Ratio

No more than four additional samples per transect could be taken due to handling considerations both in the field and in the laboratory.

No covariance or correlation analysis using the 2^n series can be employed due to the peak shift phenomenon and the lack of resolution at small scales shown by the mean square pattern analysis. In addition, no cross covariance or cross spectral analysis are to be reported here for two basic reasons. The individual parameters are subject to different magnitudes of error surrounding the estimates of their values. These errors are constant for any given parameter but only through careful normalization procedures could cross comparisons be accurately made (Richerson et al., 1977). Also, there is an a priori reason not to examine cross comparisons between the parameters of greatest interest which are the species, biomass and nutrients. Recent investigations have shown that phytoplankton productivity and growth are not nutrient limited in the harbour (Piccinin, 1977).

In summary, the compared results of mean square pattern analysis and power spectral analysis for individual transects show that the mean square variance analysis is an inadequate description of the predominantely small scale variability present in the harbour since it does not indicate all of the small scale variance that spectral analysis does and because numerous peak shifts occur. The analysis has however indicated that larger scale pattern is present in some of the parameters in some of the transects. However, this could not be thoroughly investigated due to sample size limitations. In view of these findings, only the variance results from spectral analysis will be used in further discussions.

3.7 Fluorometric and Spectrophotometric Chlorophyll a Spectral Analysis

An examination of the spectral outputs from the coincident fluorometric and spectrophotometric chlorophyll a analyses shows them to be quite different at short wavelengths (Figures 28 and 29). The short period structures appearing in the spectrophotometric analysis of transects A and G have no counter part in the fluorometric spectra. The fluorometric analysis indicates structure only at one scale in transect H which is also indicated in the spectrophotometric output. There is however, another variance peak present not revealed in the fluorometer analysis. The numerical value of the slope cannot be used to imply anything about the cause of the observed distribution of the variance (Fasham and Pugh, 1976; Fasham, 1977) but qualitatively it can be used to compare the two methods of analysis. The fluorometric spectral analyses all show a rapid rise in the variance from short periods to long periods (i.e. variance increases with distance) but the spectrophotometric graphs show a significant increase in the slope of the variance only after 80 to 100 m. Transect H shows no increase in the variance with increasing wavelength after an initial short wavelength peak. The distribution of the variance in transect D is very nearly length scale independent (random).

These results were to some degree anticipated for a number of reasons. The response time of this instrument to a constant input signal is in excess of the time taken to collect a unit sample and it is therefore averaging unit samples. Turner 111 fluorometer results also show differences in output as compared to electronic signal input for both identical,

Figure 28

Spectral Analysis of Chlorophyll a Determinations

The fluorometic analyses show entirely different shaped spectral plots and omit some high frequency information.

A Spectrophotmetric Determination for Transect A September 16, 1975

B Fluorometric Determination for Transect A September 16, 1975

C Spectrophotometric Determination for Transect B September 16, 1975

D Fluorometric Determination for Transect B September 16, 1975

E Spectrophotometric Determination for Transect C September 16, 1975

F Fluorometric Determination for Transect C September 16, 1975

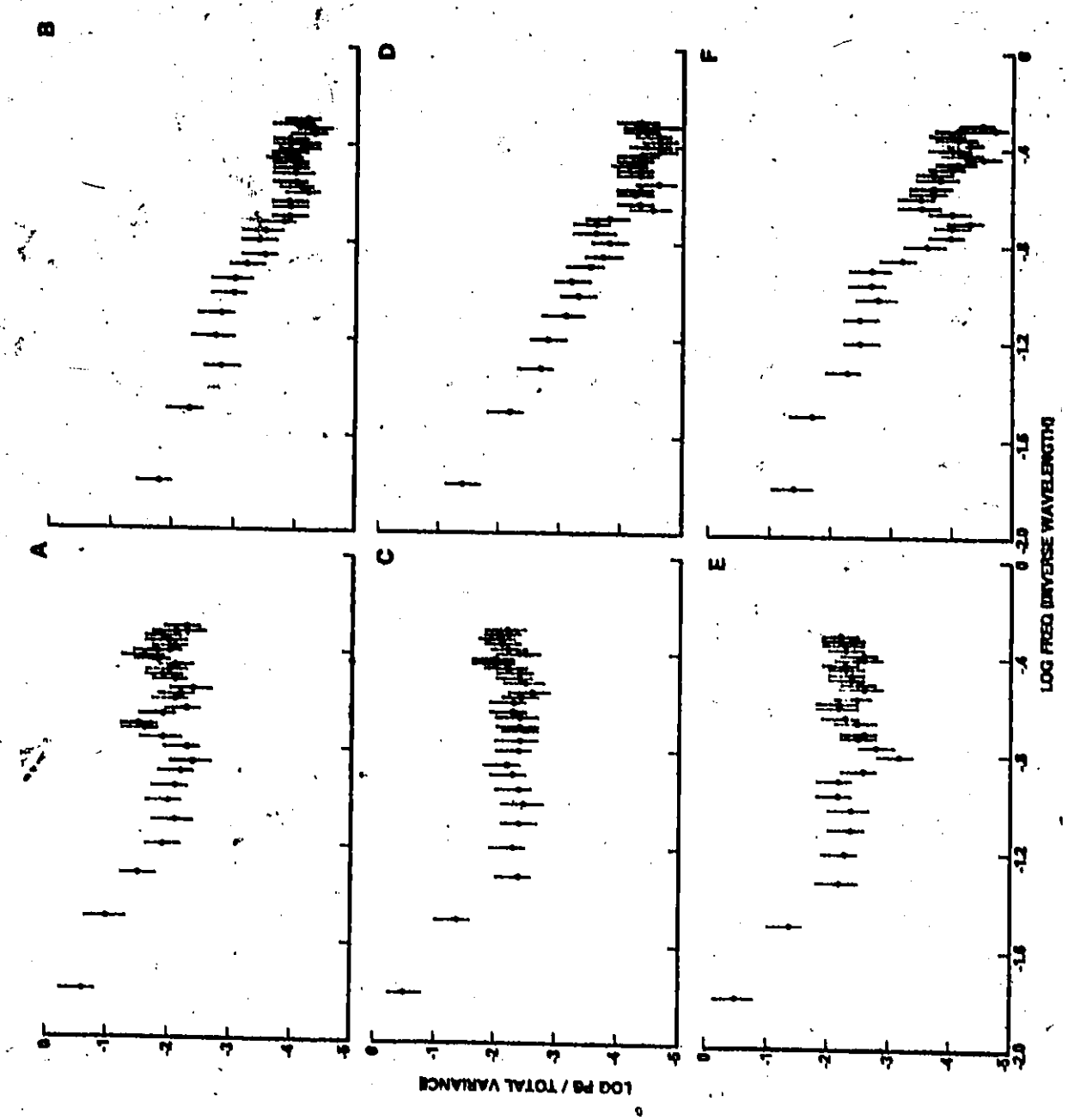

A
B
C
D
E
F
LOG PS / TOTAL VARIANCE
LOG FREQ (INVERSE WAVELENGTH)

Figure 29

Spectral Analysis of Chlorophyll a Determinations

The fluorometric analyses show entirely different shaped spectral plots and omit some high frequency information.

A Spectrophotometric Determination for Transect D September 16, 1975

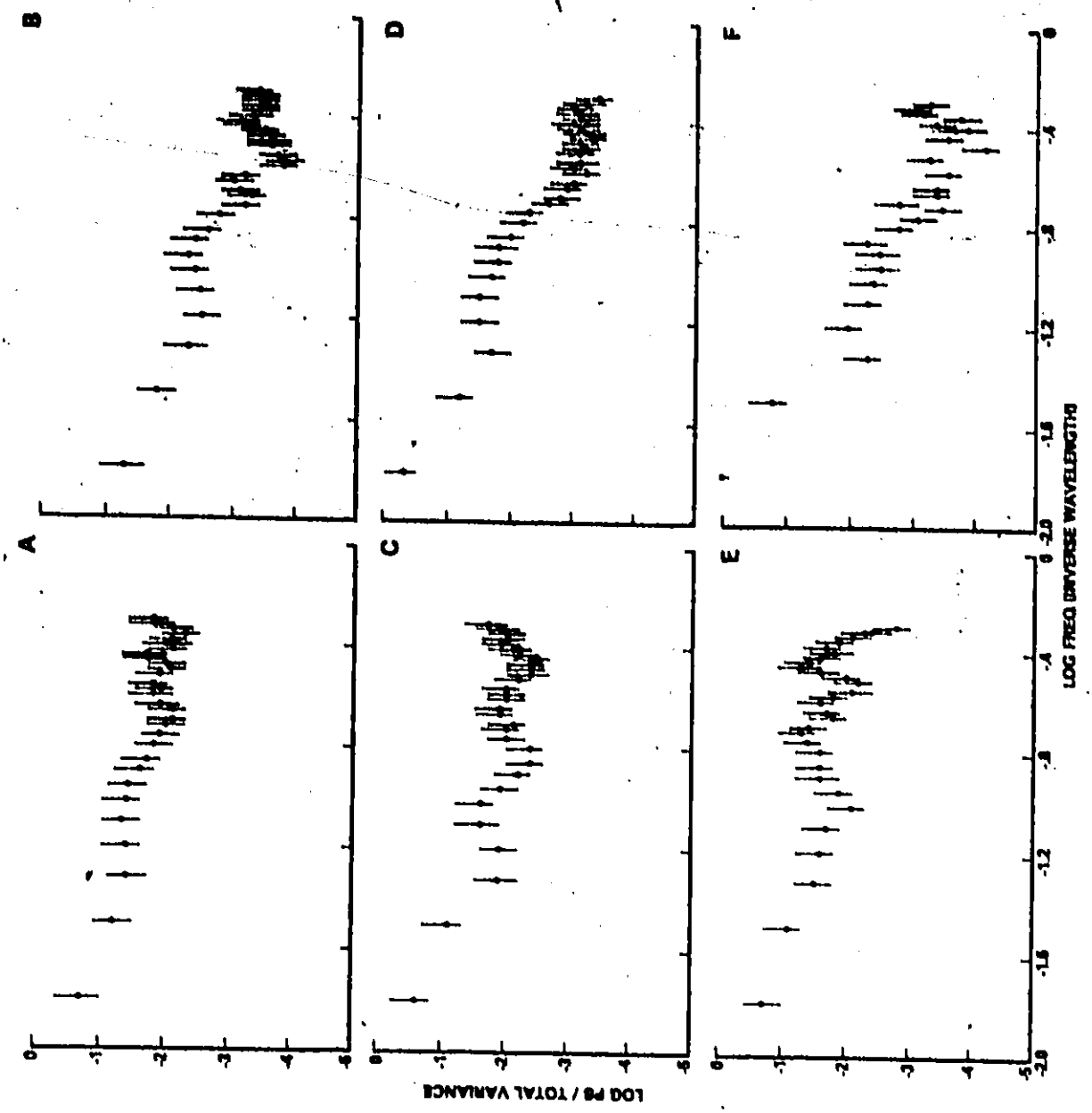
B Fluorometric determination for Transect D September 16, 1975

C Spectrophotometric Determination for Transect G September 16, 1985

D Fluorometric Determination for Transect G September 16, 1975

E Spectrophotometric Determination for Transect H September 16, 1975

F Fluorometric Determination for Transect H September 16, 1975


A
B
C
D
E
F
LOG Pθ / TOTAL VARIANCE
LOG FREQ (INVERSE WAVELENGTH)

fluctuating signals and non-identical fluctuating signals, administered over periods longer than the response time (K. Miners, private communication). The fluorometric analysis will also be less sensitive to actual chlorophyll a concentration changes (as determined by spectrophotometric analysis) for the reasons previously outlined (section 1). The electronic damping, the slow response time and the in situ interference prevent the resolution of the small scale pattern present in the biomass.

3.8 Distribution of Chlorophyll a and Phytoplankton Cells

Comparison of the power spectral analyses for spectrophotometrically determined chlorophyll a (hereinafter referred to simply as chlorophyll a) and the species enumerated for each transect indicates that the biomass pattern is not necessarily the same as the species pattern. The relationship between the distribution of the biomass indicator and the major species distributions (Table 8) appears to fall within three broad categories. In some instances, an apparent absence of significant structure can be observed in the chlorophyll a distribution while significant peaks are present in most of the species of the same transect. Transect D from September 16, 1975 exemplifies this behaviour (Figure 30). The chlorophyll a spectral output shows random variance until approximately 20 m (-.83) after which there is a gradual increase in the variance to the end of the resolvable wavelengths. The species, R. minuta Cyclotella mon. and O. borgei each show a significant variance peak which indicates a patch size of 25 (-.96), 5 (-.40), and 10 m (-.69) respectively. C. crosa however, shows scale independent (random) distribution of variance.

On occasions, structure may be observed in the chlorophyll a with no corresponding structure in any of the species distributions. Transect G from July 20, 1976 illustrates this phenomenon (Figure 31). The analysis of chlorophyll a indicates peaks at 10 m and 40 m (-.48 and -1.2). The 10 m peak is accounted for by its similar appearance in the distributions of C. sphagnicola and Mougeotia sp., with the latter showing an additional peak at 5 m (-.46). The other species (R. minutum, Chlorella vulg. and O. borgei) all show random distributions of variance.

In a few instances, the structure observed in the chlorophyll a analysis is accounted for entirely with coincident structure in some or all of the species. Transect D from July 20, 1976 clearly shows that the peaks at 5 m and 10 m (-.30 and -.46) observed in the chlorophyll a are present in R. minutum (5 m, -.30), C. vulg. (5 m, -.40), Mougeotia sp. and C. sphagnicola (having 10 m peaks around -.55), while O. borgei displays scale independent variance (Figure 32).

These results point out the potential problems of utilizing biomass estimates to investigate ecological phenomena. Cassie (1968) previously criticized the use of biomass estimates and showed that they lump together too many sources of error.

3.9 Seasonal and Wind Related Length Scales for Nutrients, Species and Biomass

The effects of seasonal weather changes and wind speeds on the variance distribution of the various parameters will be examined in a statistical sense. This is done by relating the proportion of the

Table 8

Species Enumerated for Each Sampling Cruise.

SPECIES	Proportion of Biomass (%) * Sept. 16/75	July 20/76	Nov. 3/76
C. eroso	8		22.8
R. minuta	17.2	4.2	19.3
Cyclotella mon	7.7		
O. borgei	8.2	2.9	
Mougeotia sp.		48.2	
C. sphagnicola		12.6	11.1
Chlorella vulg.		4.1	
Stephanodiscus nst.			22.6
Total	41.1%	72.0%	75.8%
No. Species Counted	27	31	27

* it was estimated that 38.5% of biomass was Fragillaria sp.

Figure 30

Spectral Analysis of Species and Biomass

Comparative spectral analysis of chlorophyll a and the major species from transect D September 16, 1975

A *O. borgei*

B Chlorophyll *a*

C *Cyclotella men.*

D *C. erosa*

E *R. minutum*

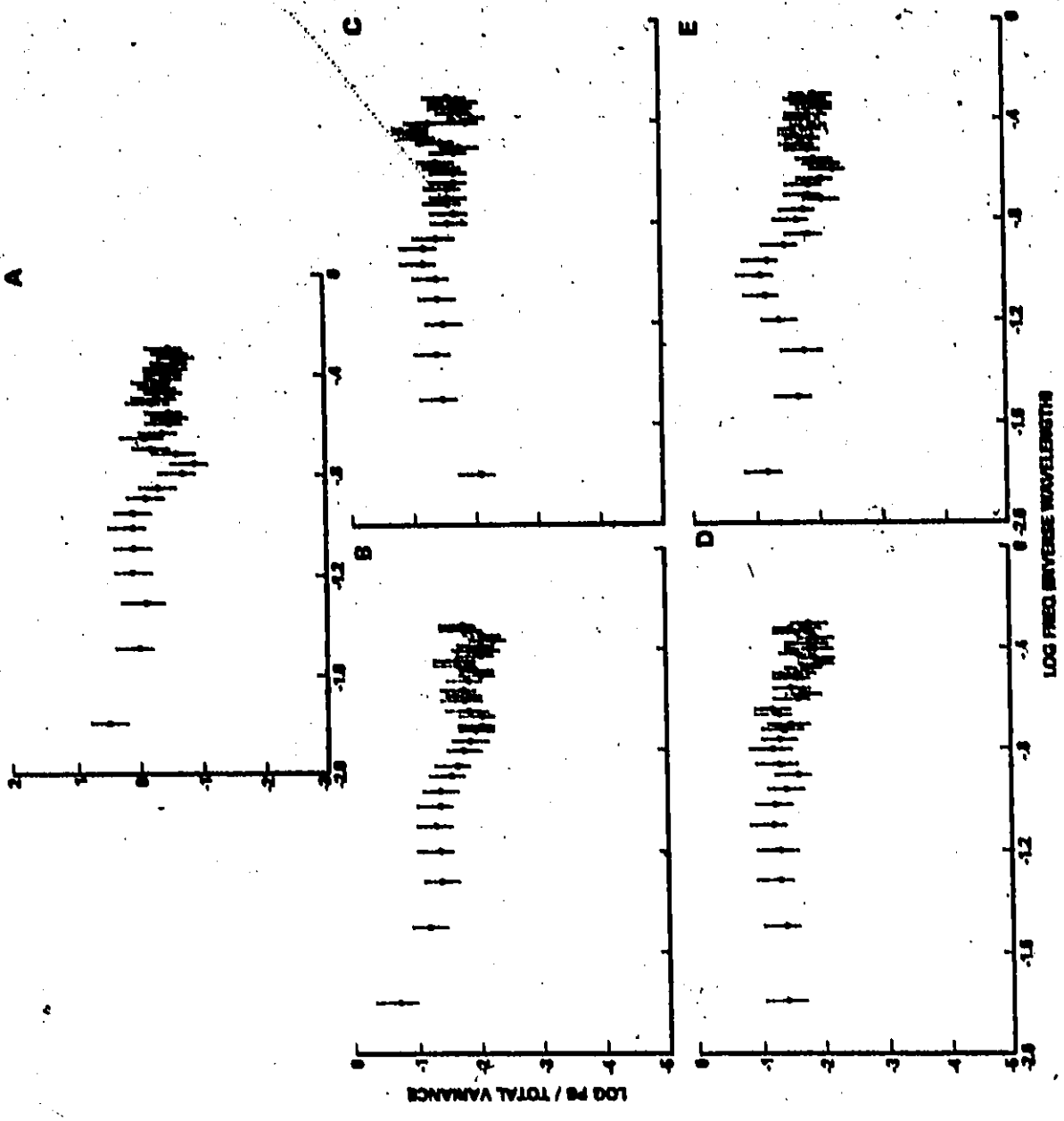

A
B
C
D
E
LOG PS / TOTAL VARIANCE
LOG FREQUENCY/CYCLES/MONTH

Figure 31

Spectral Analysis of Species and Biomass

Comparative spectral analysis of chlorophyll *a* and the major species for transect G July 20, 1976

A	Chlorophyll *a*
B	*R. minutum*
C	*Mougeotia* sp.
D	*C. sphagnicola*
E	*Chlorella vulgaris*
F	*O. borgei*

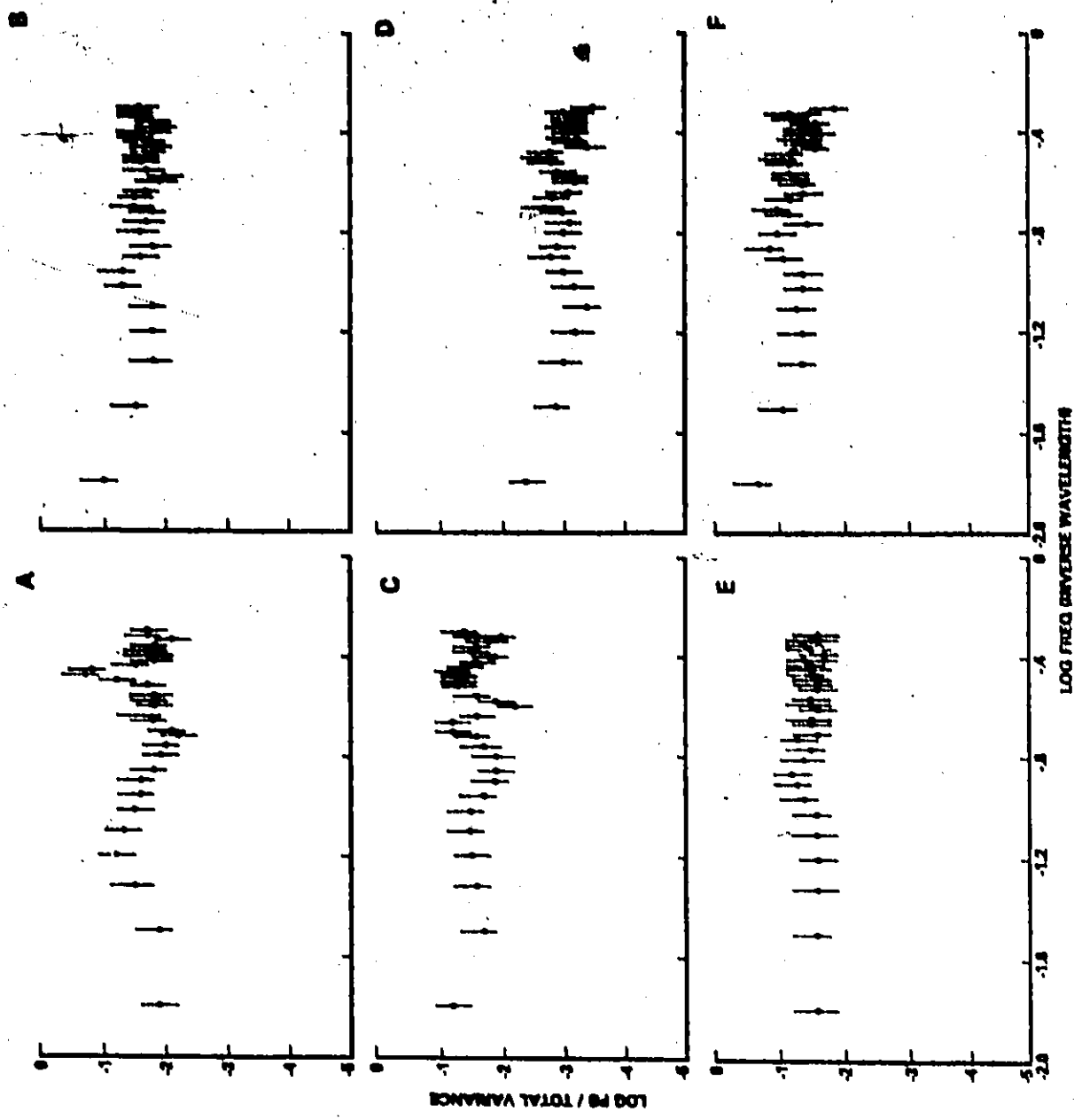

A
B
C
D
E
F
LOG PS / TOTAL VARIANCE
LOG FREQUENCY/SCALE WAVELENGTH

Figure 32

Spectral Analysis of Species and Biomass

Comparative spectral analysis of chlorophyll *a* and the major species for transect D' July 20, 1976

A Chlorophyll *a*

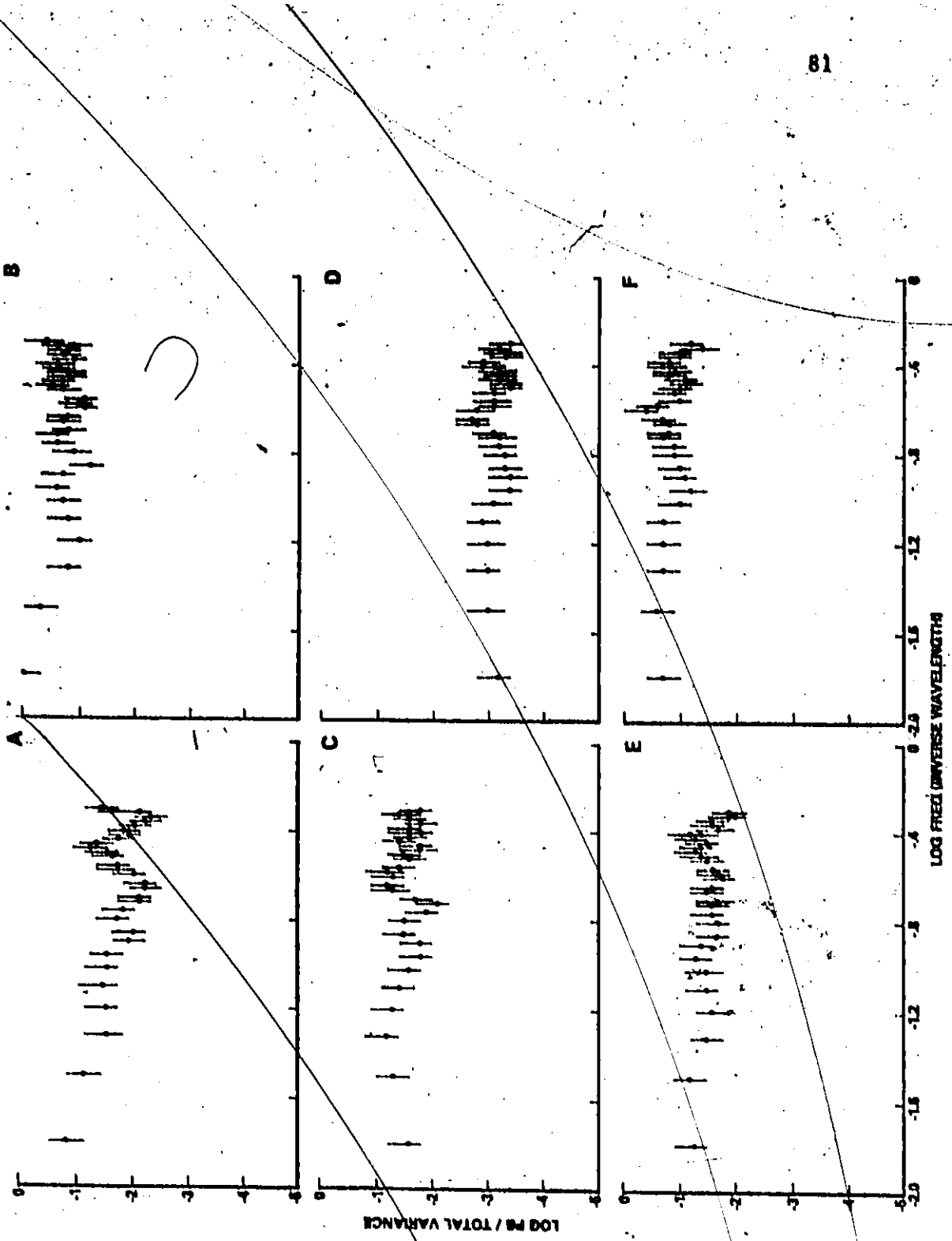
B *R. minutum*

C *Mougeotia* sp.

D *C. sphagnicola*

E *Chlorella vulgaris*

F *O. borgei*


A
B
C
D
E
F
LOG PR / TOTAL VARIANCE
LOG FREQ (INVERSE WAVELENGTH)

total number of transects displaying structure for a given parameter. Structure, implying density pattern, is ascertained by the appearance of significant peaks in the power spectral analysis (Tables 4, 5, and 6). In some cases, an assessment of trend is not possible because of the small number of transects (8 per cruise) analysed.

The wind regimes are recorded as daily summaries in Table 12 (Appendix) and by hourly analysis over a thirty hour period prior to the completion of sampling for each cruise (Table 13, Appendix I). These records show the September 16, 1975 sample period to be a time of little or no wind (the velocity dropping to zero during the sample period), also a feature of the two preceeding days. July 20, 1976 in sharp contrast displays wind speeds of around 20 km hr^{-1} during the period of study and similarly for at least two days prior to the excursion. On November 3, 1976 there were a more moderate wind speed of around 12 km hr^{-1}, with the two days preceeding it having slightly higher wind velocities. The vertical temperature profiles (Table 9) show a 4°C stratification appearing around 6 m for the July cruise. The September profile shows a similar thermal gradient while the November profile shows a gradual temperature change of less than 2°C over the 20 m depth measured.

The results of the spectral analysis for chlorophyll a have a tendency to display more structure in a cross wind orientation for all dates. The greatest number of significant peaks appears during the July sample. Also, more transects show at least one significant peak. This is followed by the September results which show a greater total

Table 9

Vertical Temperature (°C) Profiles

Depth (m)	Sept. 16/75	July 20/76	Nov. 3/76
.2	16.4	20.5	9.8
3	16.4	20.5	9.4
6	16.4	18.4	9.3
12	13.4	14.5	8.9
20	8.7	12.8	8.1

number of peaks than the November results. However, the November results are the same as the September ones with respect to the number of transects which do not show any significant peaks. This would suggest that the structure seen in not a simple function of wind speed since the November 3, 1976 wind velocity far exceeded that of September 16, 1975. In general, all the transects for September show a rise in the variance plot to the end of the spectral window either directly or after some initial short wavelength peak. Whereas, most of the plots from July and November show no change in slope (i.e. are random) or else a slight increase in the variance, after an initial short wavelength peak to a value no greater than that of the largest short wavelength peak.

The NO_3 + NO_2 results are characterized by a flat variance response regardless of wind direction, speed, or time of the year. The actual concentrations vary little from season to season (Harris, 1976; Piccinin, 1977). There is structure present in some transects for each of the cruises. Spectral plots of the July 1976 results for NO_3 + NO_2 in general show significant peaks in those transects where there are significant chlorophyll a peaks. The results although not coincident in length scales, are positively related. The September and November results show that significant peaks do not appear in NO_3 + NO_2 plots for transects in which chlorophyll a peaks appear. Significant peaks do however appear in a number of those transects which show no structure with respect to chlorophyll a.

The FRP results show a greater number of significant peaks and fewer totally random distributions for the July 1976 results, as

did chlorophyll a. However, the November results show a greater number of significant peaks and fewer totally random distributions than did the September results. Therefore, the FRP results show positive relationships throughout all excursions with chlorophyll a. The end point trends are rather different than those for chlorophyll a with a highly variable response in September 1975, a flattening tendency for November 1976 and a general increase in the slope for July 1976. The appearance of structure would seem to be indifferent to the trends in the concentration over the two or three weeks prior to each excursion (Tables 14, 15 and 16, Appendix I).

The total phosphorous analyses display more cross wind structure for July and September (stratified periods) but less during the November sample period. The largest wavelengths generally have flattened slopes during July and September but a high percentage of the total number of transects rise in slope (from right to left) for November 1976. The total structure exhibited is greatest in July 1976 and approximately the same for the other periods. There is in general no discernable relationship with chlorophyll a. The general lack in structure and flattened variance is probably a result of the high constant basin wide loadings which result from large bacterial populations and high dissolved organic and colloidal organic carbon (OME, 1977).

The FRS results for total structure show sharp contrasts between sample periods. July 1976 has peaks in 75% of its transects while November 1976 has only a single peak. September 1975 shows structure in about 50% of its transects. The average FRS concentration is higher

during the summer months when there are only few diatoms present (Harris, 1976; Piccinin, 1977). There appears to be no relationship between structure and wind orientation. The spectral slopes tend to be completely flat or else become flat after an initial peak(s).

The NO_2 analysis, conducted only for July 20, 1976 and November 3, 1976 shows somewhat more total structure in July with a definite cross wind maximum. The November results are almost entirely flat but the downwind transects of July show a definite rise in slope to the end of the spectral window. The concentrations of NO_2 are roughly constant throughout the year (Piccinin, 1977).

The survey data of Harris (1976) and Piccinin (1977) from Hamilton Harbour from 1975 through to 1976, (Table 10) for the above mentioned parameters, also shows no trends or correlations in terms of station or basin differences for different parameters and wind regimes. There are periods prior to each cruise in which there are no numerical differences in the parameters between any of the stations. There are on other occasions quite noticeable station differences. Sometimes, a dish effect is seen whereby the values at either end of the harbour are very nearly identical while the middle of the basin shows lower values. On other occasions definite gradients appear with values increasing or decreasing from one end of the harbour to the other.

It is instructive to compare (Tables 10 and 11) the maximum differences for a given parameter between stations for a particular day to some of the typical differences displayed by the synoptic transect data. These values are all reported for the same day and are for the most part the maximum differences ever observed for that parameter

Table 10

Maximum Parameter Variability for Estimates Between Stations

Date	Parameter	Stations Compared	% Difference
Sept. 15/75	Chlorophyll a	252 - 270	38.9
	NO_3	4 - 258	5.4
	PO_4	4 - 270	86.6
	SRS	4 - 270	21.9
July 19/76	Chlorophyll a	4 - 270	58.0
	NO_3	4 - 258	21.7
	PO_4	252 - 258	29.9
	SRS	4 - 270	37.6
	NO_2	4 - 270	36.0
Nov. 1/76	Chlorophyll a	252 - 270	37.6
	NO_3	4 - 252	9.7
	PO_4	252 - 258	72.6
	SRS	4 - 258	45.5
	NO_2	4 - 270	16.0

Parameter Variance Estimates Between Samples Along a Transect

Date	Parameter	Distance (m)	% Difference
Sept. 16/75	Chlorophyll a	60	41.0
	NO_3	20	6.0
	PO_4	40	7.0
	SRS	20	73.0
July 20/76	Chlorophyll a	40	40.0 - 50.0
	NO_3	40	60.0
	PO_4	20	60.0 - 200.0
	SRS	40	70.0
	NO_2	40	50.0
Nov. 3/76	Chlorophyll a	30	25.0 - 35.0
	NO_3	70	30.0 - 35.0
	PO_4	25	65.0
	SRS	20	50.0 - 60.0
	NO_2	25	60.0

Table 11

during the one month period of survey prior to an excursion. In all cases, the differences observed between samples for any single parameter usually taken 50 m apart or less, are as great or greater than those maximum differences between the stations which are at least 2.4 km apart. These results show that there are no consistent relationships between structure and wind speed or direction as have been found in some previous studies (Small, 1963; George and Edwards, 1976). The lack of consistent trend found in this study is similar to the results of Billington and Jones (1976). The transect analysis for all parameters in general shows a tendency toward the flattening of spectral slopes to the end of the window with increased wind speeds.

The species spectral analyses appear to show more consistent relationships with wind (Table 12). The September 1975 distributions exhibit structure for all species in at least two transects, with no structure at all in only one transect.

It is convenient to collectively examine the significant peaks from the spectral analyses for each of the major species present in any single cruise. The results from each transect can show structure for all of the species enumerated. Since there always are eight transects per cruise, the total number of possible transect/species permutations of structure will be n x 8, where n is the number of species enumerated for each cruise.

Forty percent of the transect/species analyses in September (ie. 4x8 paired permutations possible) show flattened spectral slopes toward the end of the window, while 22% (of the transect/species paired permutations)

Table 12 a,b,c.

Significant Length-Scale Variance Peaks for each Transect; September 16,1975, July 20,1976, and November 3,1976.

12 a

Species	A	B	C	D	E	F	G	H
				— September 16, 1975				
C. eros	none	none	5, 10, 15	none	none	15(random)	5,15(random)	none
R. minutus	5	none	none	25	10(random)	5, 10	none	none
Cyclotella	5	none(random)	none(random)	5	none(random)	none(random)	10(random)	none(random)
O. borgei	5, 10	none(random)	5	10	5, 10	none(random)	5,10(random)	10 (random)

12 b

					— July 20, 1976			
R. minutus	none	none	none(r)	none(r)	none(r)	10	none (r)	15 (r)
Mougeotia	5 (r)	5, 10 (r)	none(r)	10 (r)	none(r)	none(r)	5, 10(r)	none(r)
C. sphagnicola	5 (r)	none (r)	5 (r)	10 (r)	none(r)	none(r)	10 (r)	5 (r)
Chlorella	5	none (r)	10 (r)	15	none(r)	none(r)	none (r)	none(r)
O. borgei	none(r)	5, 10 (r)	none(r)	none(r)	none	none(r)	none (r)	none(r)

12 c

					— November 3, 1976			
C. eros	5 (r)	10, 15 (r)	10 (r)	5	none(r)	5	none (r)	5 (r)
C. sphagnicola	none	10 (r)	none(r)	15 (r)	none(r)	none(r)	none(r)	5 (r)
R. minutus	none	none (r)	none(r)	none(r)	none	none(r)	5 (r)	5 (r)
Stephanodiscus	5, 10 (r)	none (r)	5 (r)	5,10 (r)	none(r)	none(r)	none(r)	10

(r) random (if preceded by a number this means that the variance peaks where indicated and is then random to the end of the window).

display entirely random distributions. In July 1976 all species show structure in at least one transect, and only one transect has no structure whatsoever. An examination of the possible transect/species paired permutations (5 x 8), indicates that 58% show entirely random distributions while some 88% show the flattened spectral slopes to the end of the spectral window. November 1976 shows structure for all the species in at least two transects, and has only one transect with no structure. The flattening of spectral slopes at longer wavelengths is exhibited by 81% of the possible paired permutations, with 40% of the total being entirely randomly distributed. These results show that increasing wind speeds reduce the total amount of structure and flatten the variance at longer wavelengths (i.e. implies a reduction in basin effects). There appears to be more downwind structure during July and November only, for those species present in the greatest numbers (e.g. Mougeotia sp. during July, Stephanodiscus ast. during November) and wind orientation indifference for the species which are present as a small fraction of the total cell number.

An examination of the cell densities of the species concerned from the survey periods prior to the cruises (Tables 17, 18 and 19, Appendix I) in general indicates that those species present in the greatest densities immediately before a sample excursion exhibit the greatest amount of structure in their transect variance analyses (Tables 8 and 12). There are no reasonable estimates for species specific growth rates available other than using the change in the cell density over time. The particulate organic carbon of the harbour is up to 80% bacterial

and colloidal (OME, 1977). There is a great deal of error surrounding single discrete volume station samples of chlorophyll and the best conversion value to estimate carbon contents from chlorophyll concentrations is difficult to assess due to rapid changes in the species assemblage and because of facultative heterotrophy by some of the higher density species (Harris, 1976). Therefore, carbon fixation rates as measured by C^{14} uptake cannot be readily converted to growth rates. There are some exceptions to the relationship between high cell densities and the intensity of structure.

Haffner, D. (private communication) has suggested that these exceptions are a result of vertical dilution and redistribution. The basic vertical thermal instability and leaky nature of the harbour thermocline has been well documented and commented upon by numerous other workers (Harris, 1976; Piccinin, 1977; OME, 1974, 1975, 1977). Further evidence for this being the most likely explanation to these exceptions lies in the disparity of both the cell density and the relative assemblage composition between the station survey samples and the continuous track transect samples taken 24 to 48 hours apart (Tables 16-19, Appendix I). These disparities could not be explained on the basis of cell growth, grazing or sinking. The same explanation is likely true of the observed variance distribution of nutrients as a result of the physical forces operating in the vertical and horizontal dimensions.

In summary, there is a general lack of structure in the nutrients which is probably a result of the continuous high loadings. The

greatest intensity of structure can be found in those species present in the greatest densities. Increases in wind speed tend to reduce variance at scales greater than 160 m.

3.10 Hamilton Harbour Periodicities and Circulation

The Ontario Ministry of the Environment conducted a study in 1972-1973 to examine the periodic variations of water chemistry and movement in Hamilton Harbour, and to examine the mass exchange and lake influence via the ships' canal (OME, 1974). The lake exchange phenomenon was found to be very complex and to have a potentially great influence on the harbour as a whole. The offshore region of the harbour, unlike the canal, is influenced by both changing geometry and bottom friction. A series of lake-induced motions which are semi-diurnal and diurnal in nature were observed. In addition to these there are a number of higher frequency oscillations which can be associated with harbour motions. These observed motions were categorized through theoretical comparisons of motion for Lake Ontario (Rockwell, 1966). These motions produce temporary displacements of the thermocline up to several metres from some average value. This causes severe difficulties in obtaining synoptic survey data through conventional discrete volume sampling methods, and implies that at any point in the harbour, currents and water quality are a function of waste discharges as well as lake-induced motions. The water motion and quality are also influenced by very high frequency harbour oscillations either due to higher longitudinal or transverse modes of oscillation. The periods identified occurred at

Figure 33

Numerical Circulation Model for Hamilton Harbour

Vector plots of the results of a numerical model, from Hamilton Harbour Report, 1974 Ontario Ministry of the Environment (1974) showing the wind induced current field for Hamilton Harbour. As indicated, these are the results for winds south to south-east at a mean speed of 4.9 ms^{-1} for 40 hours.

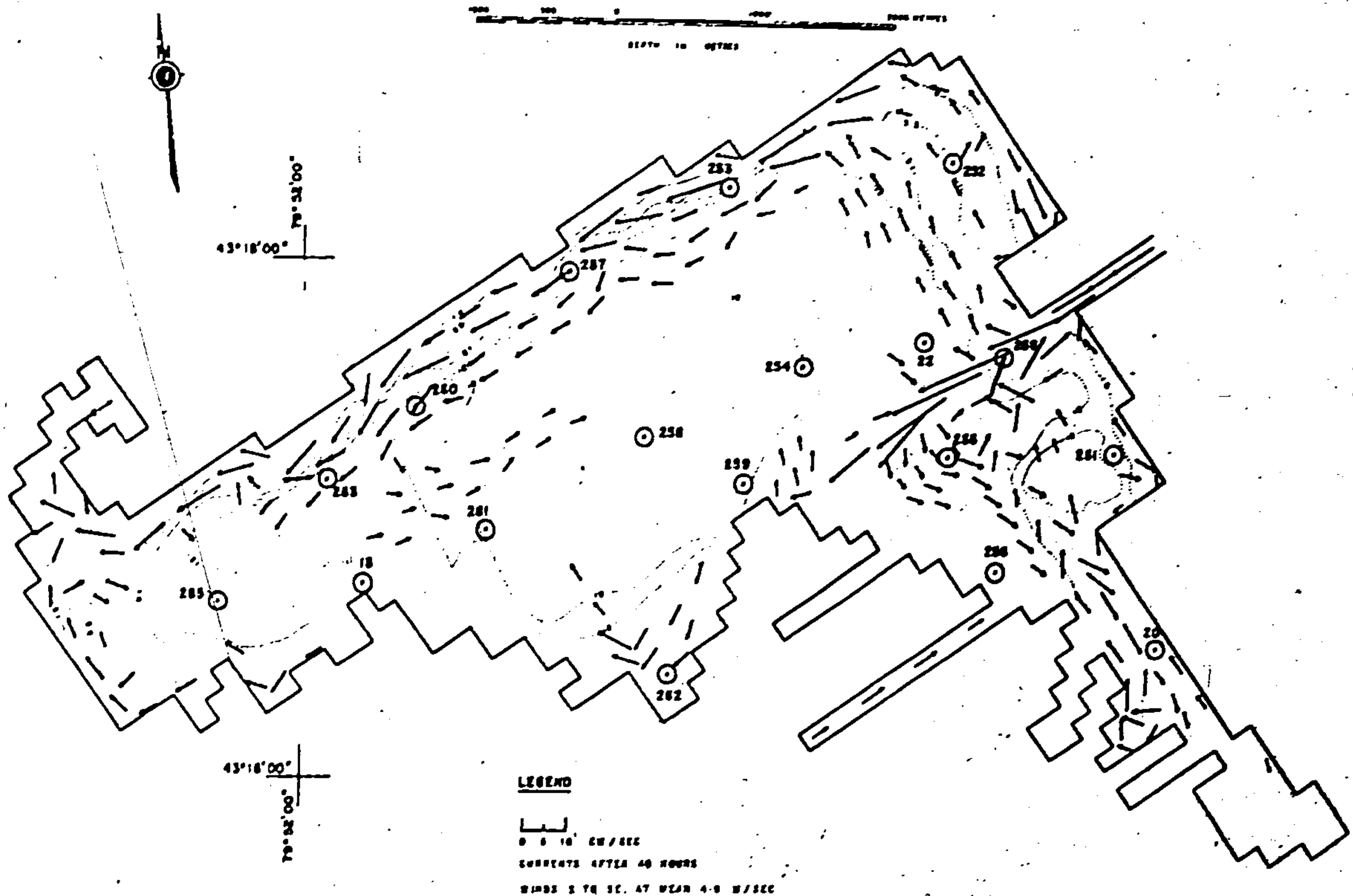
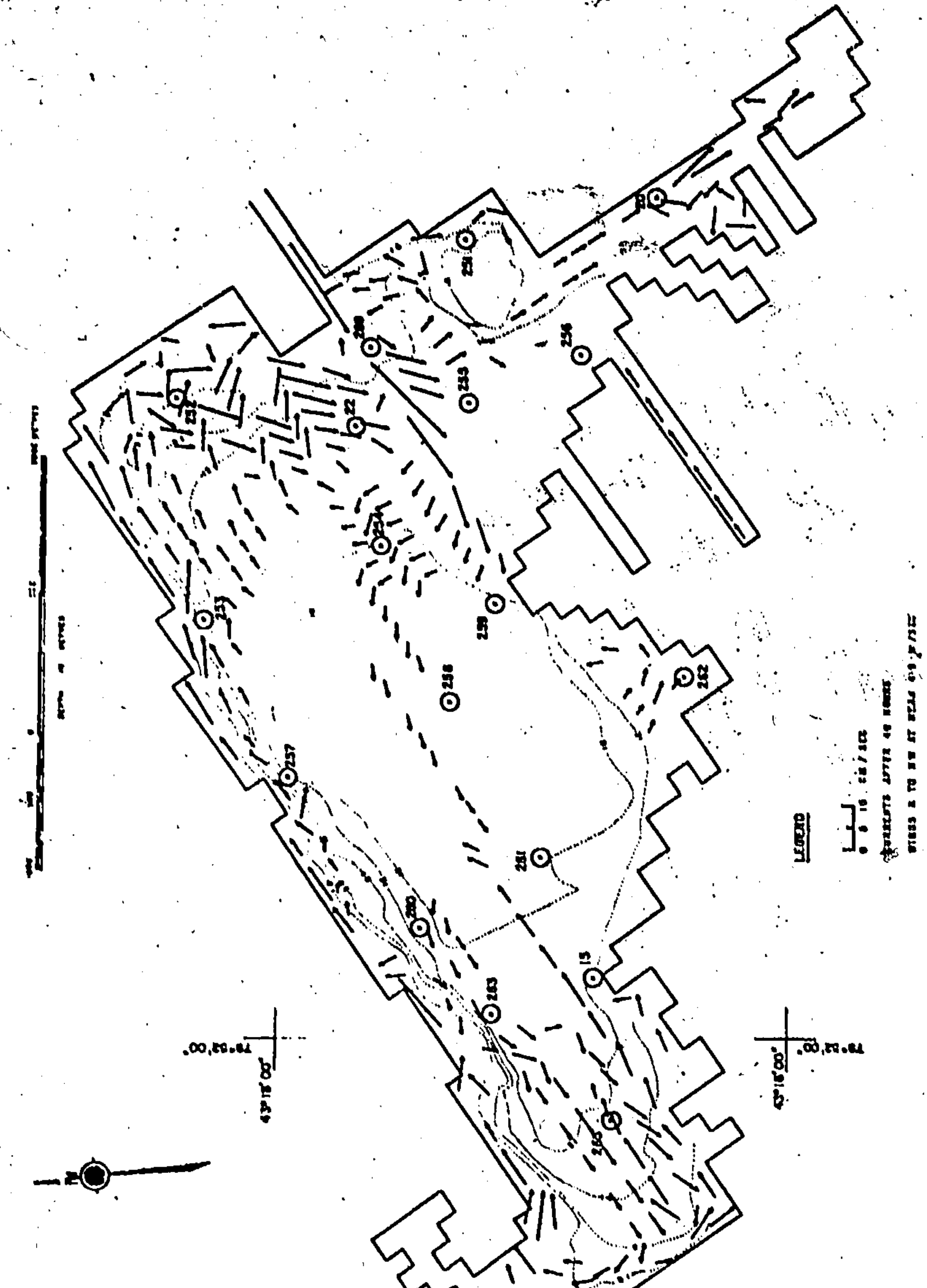

43°18'00"
43°18'00"
LEGEND
232
233
287
260
283
285
18
281
258
254
22
259
262
286
256
261

Figure 34

Numerical Circulation Model for Hamilton Harbour

Vector plots of the results of a numerical model, from the Hamilton Harbour Report 1974, Ontario Ministry of the Environment (1974) showing the wind induced current field fro Hamilton Harbour after a wind direction reversal (from Figure 43). As indicated, these are the results for winds north to north-west at a mean speed of 4.9 ms^{-1} for 40 hours.



0.1 and 0.2 hrs with an additional component at 0.33 hrs. These fundamental and persistent high frequency periodicities further complicate convential sampling.

The harbour is therefore an active internal wave region with reflections. Thermal and chemical stratification are both time variant during various wind climates and are not necessarily coincident (Palmer and Poulton, 1976).

A two dimensional estuarine type water quality simulation model, originally developed and verified by Leendertse (1970, 1971), was constructed to assess the changes in water quality resulting from changes in harbour geometry, water withdrawals and waste discharges for various meteorological conditions (OME, 1974).

The simplifying assumptions necessary to keep development and computational costs reasonable (e.g. basin geometric approximation; constant wind velocity; size of grid spacings and therefore time-scale increments; vertical homogeneity; etc.) preclude the specific use of the model in analysing the results of this thesis work. The model does however show that even under the large number of simplifying assumptions about the harbour physics, the circulation field is exceedingly complex (Figures 33 and 34) in space and in time. Average current speeds in the upper few metres range from 1.75 cm s^{-1} to about 2.5 cm s^{-1} with ranges of 0.08 cm s^{-1} to 1.33 cm s^{-1} for the resultant currents. The disparity between resultant and average is some indication of net movement relative to average instantaneous inputs.

3.11 Harbour Motions and Length-Scale Variance Distributions

The fundamental high frequency periodicities of water motions observed in the harbour are reflected in the length-scale variance distributions of most of the parameters measured which show small scale structure (Figures 35 and 36). These motions are the result of surface and internal stationary and travelling oscillations. Direct comparisons between the physical periodicities measured and the biological or chemical parameters measured in terms of length-scale agreement cannot be made with any degree of accuracy. The Eulerian measurements of the recording current meters are only convertable approximations to the Lagrangian dispersion field when the Reynolds number is very large and when the velocity field is spatially homogeneous (Palmer and Izatt, 1971; Franz, 1974). These assumptions are invalid for the harbour. However, using the range of average current speeds available it can be seen that the fundamental high frequency periods of harbour oscillation correspond reasonably to the most frequently encountered length scale structures of 10, 20 and 30 m periods (Figures 35 and 36). The spatial complexity of this activity is expressed in the appearance of structure in identical measurements taken synoptically over the harbour. If we ignore the anomalous appearance of a few structures at longer wavelengths, the results show basin scale variance predominating during periods of low wind speed (e.g. September 1975). However, since the harbour is readily mixed by wind induced motions on basin or half-basin scales, there is an increase in the number of totally random and end window flattened distributions seen during increased wind speeds.

Figure 35

Frequency Histograms of Significant Spectral Peaks

Frequency histograms of spectral peaks (n/2) obtained from all the data (cf. Tables 4, 5 and 6). Note the complete absence of structure at larger scales. The clear portions of the zero class bars indicate the number of completely random distributions observed.

a Filtered Reactive Silica

b Chlorophyll a

c Species (all those enumerated)

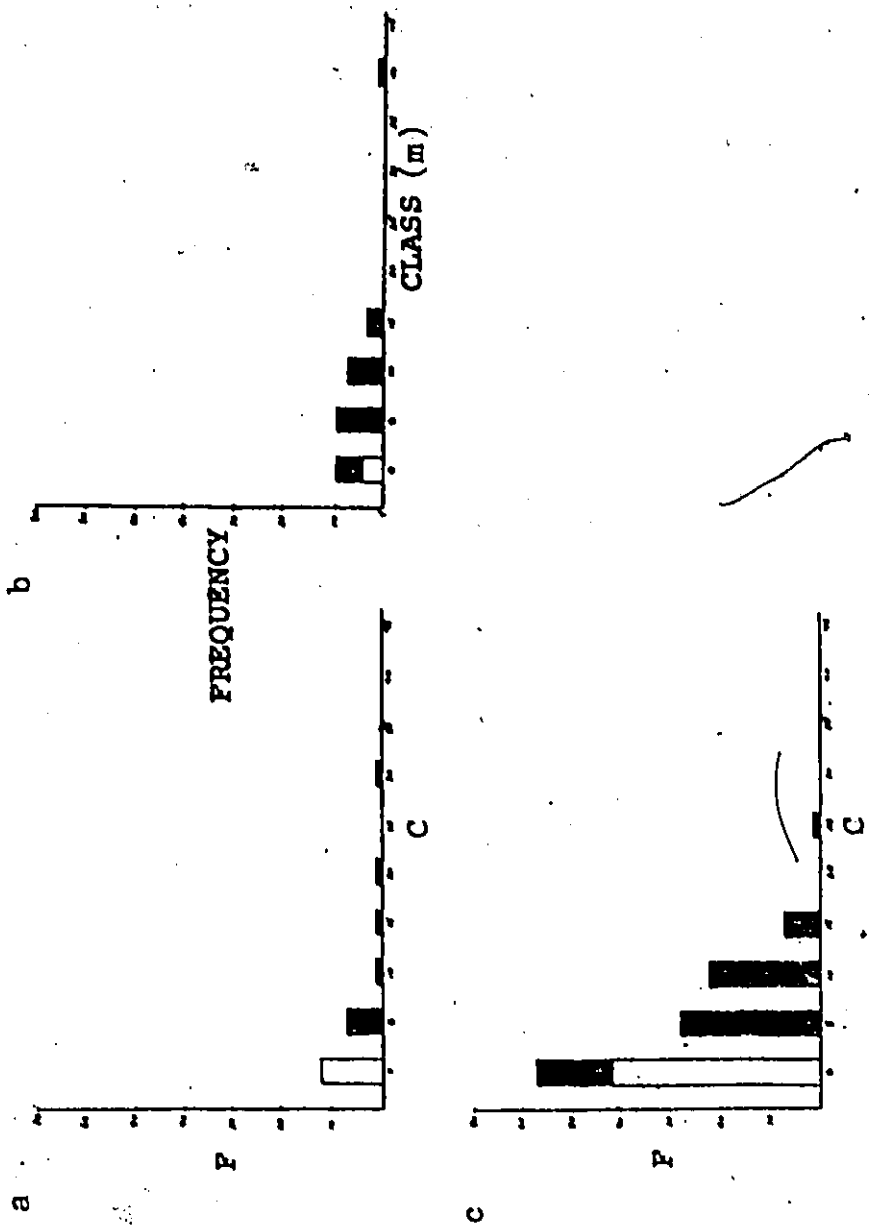

a
P
C
b
FREQUENCY
CLASS (m)
c
P
C

Figure 36

Frequency Histograms of Significant Spectral Peaks

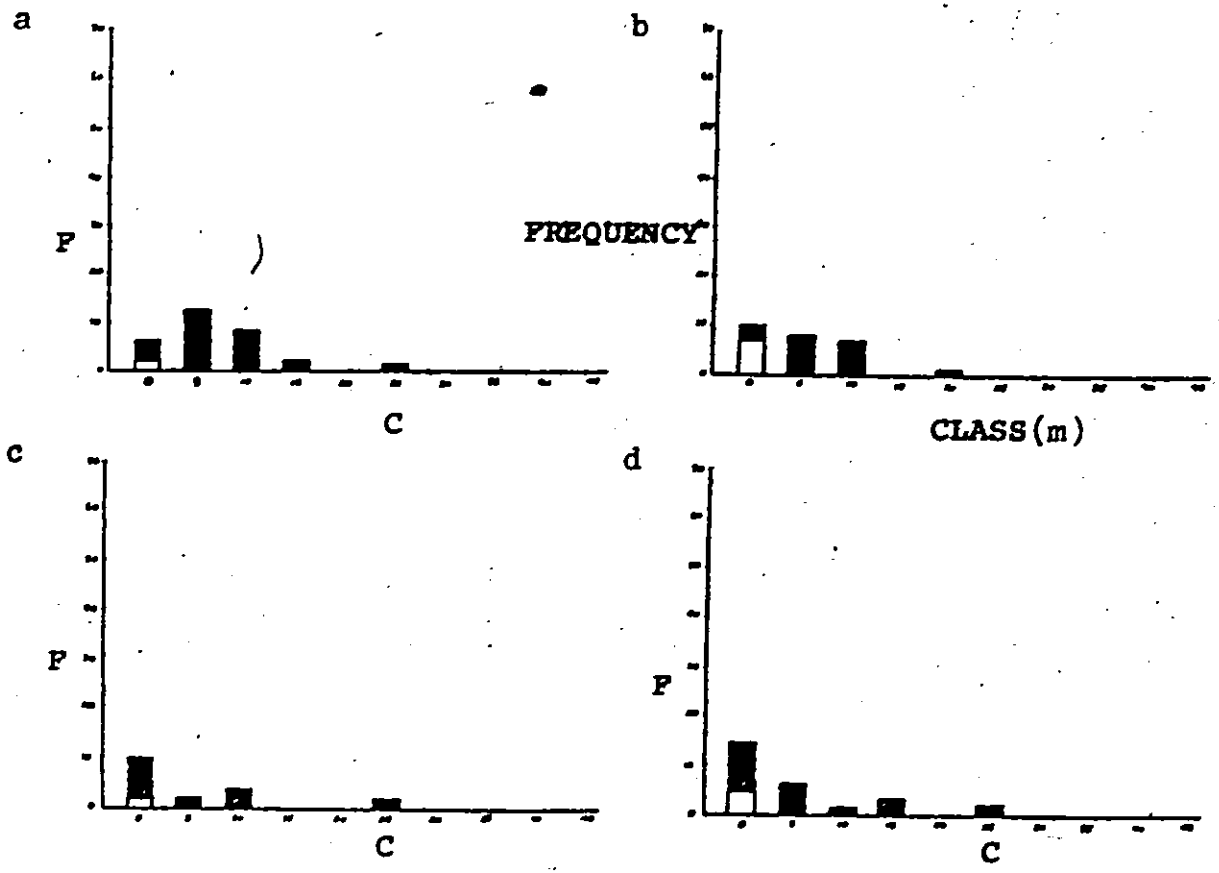
Frequency histograms of spectral peaks (n/2) obtained from all the data (refer Tables 4, 5, and 6). Note the complete absence of structure at larger scales. The clear portions of the zero class bars indicate the number of completely random distributions observed.

a Filtered Reactive Phosphorous

b Total Phosphorous

c NO_2

d $NO_3 + NO_2$


a
b
F
FREQUENCY
C
CLASS(m)
c
d
F
F
C
C

The only results from this study which show any agreement with the KISS model and previous observations by other researchers are those of the fluorometer. This sampling situation is perhaps the worst possible for this method and it is not surprising therefore, that the results bear no resemblance to any of the other simultaneous parameter measurements. It therefore suggests that other fluorometric analyses may be averaging out heterogeneity present.

In summary, the high frequency periodicities of harbour motions can be seen in the small scale variability of most of the parameters measured in this study. These findings reinforce previous hypotheses concerning the difficulty in obtaining synoptic survey information on the harbour. They also demonstrate the absolute necessity for specific information about the length and time scales of the physical environment when designing a survey programme.

4.0 Conclusions

Richerson et al. (1977) have stated that "... the existence of ecologically significant heterogeneity of phytoplankton on very small scales (10 m) is unexpected under most circumstances and is seldom found by more sophisticated techniques". It can be seen however, that in some special cases extreme small-scale variability is common (Harris and Smith, 1977). Indeed, the results of this study show that in Hamilton Harbour the horizontal variability is completely contained at small scales (Figures 35 and 36) rather than at basin wide scales (Tables 10 and 11). Discrete-volume simultaneous sampling has shown that in Hamilton Harbour there is significant variance or patchiness in the environment at or below scales of 1 m (Table 1). The preliminary sampling also pointed out the difficulties encountered in the precise measurement of patchiness using discrete volume sampling techniques. The major difficulty encountered is data aliasing (section I) and the common occurence of this problem at small scales leads one to question the representativeness of discrete volume survey data gathered from a few stations which are used to describe large areas. It was the results of these preliminary studies that led to the use of a continuous sampling program to investigate patchiness in the phytoplankton community of Hamilton Harbour. The continuous sampling results revealed extreme horizontal variations in both biological and chemical parameters which were not evident in conventional survey sampling programs (c.f. Tables 10 and 11).

Although the results obtained from any single transect are generally similar to those of the other seven transects which comprise a single sampling period, they are not identical, showing phase shifts in the length scales observed. These shifts lead to erroneous interpretations of the scales of variance present when ensemble averages are used to represent patchiness in any single dimension. Ensemble averages using both mean square pattern analysis (Figures 11-14) and power spectral analysis (Figures 15-25) were computed for a single synoptic data set comprised of four transects oriented in the same direction. These results which show no significant peaks, when compared with the results from the individual transects presented in Tables 4, 5 and 6 which record only the statistically significant peaks, demonstrate the smoothing effect obtained by averaging out variance (section 3.5).

Previous investigators have used a one-dimensional analysis, or a quasi two-dimensional analysis which has attempted to include vertical information, to investigate phytoplankton patchiness (Platt, 1972; Powell et al., 1975; Denman, 1976). The data records, while not simultaneous, were deemed to be synoptic according to Taylor's frozen turbulence hypothesis (Taylor, 1938). The spatial records collected were then related to time records under this hypothesis.

These results not only show differences between transects oriented in two dimensions of the same plane, but also differences between transects oriented in the same dimension which are separated by a few hundred metres and a few minutes (c.f. Tables 4, 5 and 6). The results show that the frozen turbulence hypothesis (refer to section I) is violated for scales below 100 m. These findings lead one to

question the correctness of previous interpretations concerning small scale variance imbedded in data records some 10-20 km long which are collected over two hours or more.

Examination of the transect data using two statistical techniques which describe patchiness revealed several interesting points. Power spectral analysis is indeed more sensitive to small scale variation than mean square pattern analysis as Usher (1975) suggested. A comparison of the scales of variance or patchiness revealed by the two methods is presented in Tables 4, 5 and 6. It can be seen that the mean square analysis is less sensitive to the small scale information which is conveyed in the power spectral results. However, analysis of the transect data as well as some test data (Figures 4, 7, 8, 9 and 10) demonstrated the inadequate resolution of spectral analysis for variance scales which approximate the maximum length of record available for this type of analysis. This has been termed the end-window effect. Mean square pattern analysis also showed peak shift or peak drift. This problem was investigated in some detail by sequentially changing the data start positions for two parameters and comparing the results for each subsequent analysis (Figures 26 and 27, Tables 7a and 7b). A comparison of the scales of patchiness estimated by mean square analysis with the scales of patchiness estimated by spectral analysis (Tables 4, 5 and 6) showed that peak shifts in the mean square pattern analysis were a commonly occuring problem and were a function of the start position of analysis (refer to section I). As a result of this and the predominance of small scale variance, mean

square pattern analysis was not used in a detailed investigation of patchiness.

The most commonly used parameter for the investigation of phytoplankton patchiness is in vivo fluorescence. Under certain circumstances fluorescence may be a good indicator of chlorophyll a concentrations, but it should not be used to study phytoplankton patchiness for numerous reasons which were outlined in section I (Introduction). Figures 28 and 29 show that fluorescence, using the Turner 111, underestimates the actual variance present in chlorophyll a which is revealed in point by point spectrophotometric determinations. However chlorophyll a, whether spectrophotometrically determined or not, is an inadequate measure of the spatial variation exhibited by the individual species of phytoplankton. The spectral plots of chlorophyll a are a composite picture of the spatial patterns of the major species present (Figures 30, 31 and 32). These species patterns are a result of their individual interactions with the environment.

Temperature is commonly used in patchiness studies as a marker for different water masses. It is deemed to be a passive contaminant which follows the energy cascade observed during energy dissipation due to viscosity (Denman and Platt, 1975). Fasham and Pugh (1976) have argued that temperature cannot be used as a water mass marker and the results from this thesis support this argument. The temperature traces, of which only two are presented (Figure 47), show no appreciable variance along either a single transect or across the harbour. Although, significant patchiness was seen in other parameters which were measured simultaneously.

The spectral analysis results of the various parameters are completely different from those found by previous workers in both freshwater and marine environments. The results are not only unique in their concentration of variance at small scales, but also in their general variance distribution. Scales of patchiness when present, are entirely contained below 100 m. The shape of the spectral plots, for all parameters except fluorescence, deviates from the previously reported -5/3 slope for length scales less than 100 m. Previous workers have been unable to resolve smaller scale patchiness because of the methods of measurement and the method of analysis used. Fluorescence, or for that matter any biomass measure, cannot be used to examine the general occurrence, persistence or ecological importance of phytoplankton patchiness. One-dimensional sampling routines cannot be used since the planktonic environment is unequivocally three-dimensional and physically non-isotropic. Long data records probably violate the frozen turbulence hypothesis for small scales. In addition, the probability of traversing areas which differ significantly over short scales according to their chemistry, physics or biology increases with the length of record. The power spectral analysis technique used compounds the problems outlined above by segmentally averaging the variance present. The result of this averaging process on unphased variance was demonstrated in section 3.5. The averaging effect is most serious at small scales since so many measurements are made here.

The length-scales of patchiness in Hamilton Harbour could not have been predicted on the basis of existing theory, nor can they be explained using the KISS model. The patchiness present in the phytoplankton

communities is a direct result of the physical environment in which the communities are found and the interactions of the individual species with that environment. The KISS model is not however applicable to small scale patchiness because of its assumptions of constant growth and diffusion rates, and three-dimensional isotropy. The application of the model as an explanatory mechanism for patchiness in the aquatic environment has imposed the further requirement of analagous behaviour of chlorophyll with energy. Although for turbulent energy a cascading process is necessary for kinetic energy to be dissipated by viscosity as heat, there is no substatiated reason for chlorophyll to cascade to smaller and smaller scales. The -5/3 slope of this energy cascade does not consistently appear in the chlorophyll spectra. The breakpoint of these chlorophyll spectral plots, which is purported to identify the point at which growth sustains patch integrity in the presence of the dissipative process, not only shows dramatic length-scale shifts but may be entirely absent. The analogy of the behaviour of chlorophyll with the behaviour of turbulent energy is therefore a poor one.

Recent studies of phytoplankton patchiness have not yielded consistent results. Some studies have demonstrated that biomass variance increases with distance at a constant rate until scales of 0.1-10 km are reached. The breakpoint in the variance distribution plots which occurs at this scale defines a stable patch. The casual mechanisms which are purported to underly patch formation are the antithetical processes of growth and turb ulent dissipation. These processes are related to the empirical results through the KISS model.

The disparity of patch sizes in marine and freshwater environments is thought to be due to the smaller scales of motion present in lakes. Other studies have not found a breakpoint in the variance distribution of biomass. Although these studies show that variance generally increases with distance, they also show that the rates of variance increase with distance are not constant. Studies in Hamilton Harbour and other small basins have found small scale patches (Harris and Smith, 1977). The longevity of an individual patch cannot be ascertained due to our lack of knowledge of the physical environment at these scales. One can conclude from these studies that phytoplankton are not strictly passive contaminants in a turbulent environment. Phytoplankton must actively exploit their turbulent environment by utilizing their repertoire of adapted physiological responses (Harris, 1978).

The diversity of species present in a community and the successional sequences observed are not only the result of gross changes in light, temperature and nutrients which take place over several division cycles, but are also the result of environmental changes which are experienced in less than one division cycle (Harris, 1978). We are, as Pingree et al. (1975) have stated, limited in our understanding of primary production (and for that matter all of phytoplankton ecology) by an inadequate knowledge of the turbulent nature of the physical environment in which the phytoplankton exist. Future work must seek to integrate and improve our knowledge of physiological responses of phytoplankton and the physical environment in which they occur.

5.0 Summary

1. Hamilton Harbour is a highly spatially variable body of water, a consequence of basin morphometry and Lake Ontario influences.

2. Significant differences in discrete-volume, simultaneous samples exist for chlorophyll a, filtered reactive phosphorous and nitrate + nitrite within dimensions of 1 m^3.

3. Coincident scale-structure was not present in all of the transects, or even all of the parallel transects, as a result of the extreme spatial heterogeneity of the harbour. This precluded the use of pooled variance analyses and forced the treatment of each transect as an individual sample in a spatial frame of reference. These results reinforced the validity of the original multi-transect sampling design.

4. Power spectral analysis was much more sensitive to small-scale variations than mean square pattern analysis although the former may be less indicative of larger-scale structure.

5. Cross comparisons (covariance, correlation, cross-spectral) could not be performed because of peak shift phenomena and because of large differences in the estimates of parameter values.

6. Parameter distributions at length-scales, beyond 25 m tend to be randomized under the influence of increased wind speed.

7. Significant structure, as determined by spectral variance peaks, in all parameters at small scales is a constant feature of this body of water which is unlike observations from studies conducted elsewhere.

8. The variance observed at small scales often exceeds that observed at basin scales under conditions of wind-induced basin circulation.

9. In vivo fluorescence (as measured by a Turner III fluorometer) was found not to be the same as spectrophotometrically determined chlorophyll a. The fluorometric analysis, in sharp contrast to the spectrophotometric analysis, showed a smooth increase in variance with distance. These results although in agreement with results from other researchers, were atypical for all the other parameters measured during this study.

10. The variance distribution of chlorophyll a (spectrophotometrically determined) was often found to be different from the variance distributions of the numerically dominant species. On occasion, structure can be seen in the chlorophyll periodograms without corresponding structure in any of the species enumerated. On other occasions, structure present in the species distributions is not reflected in the chlorophyll analysis.

11. The spectral distributions for nitrate + nitrite, nitrite and total phosphorous are characterized by a general lack of structure accompanied by scale-independent variance due to the presence of exceedingly high loadings throughout the basin.

12. Structure in filtered reactive silica, when present, is almost entirely at small scales. The intensity of this structure appears to diminish with the appearance of significant densities of diatoms in the community.

13. The intensity of structure, and length-scales of variance for filtered reactive phosphorous approximate those for chlorophyll a.

APPENDIX I

Figure 37

Continuous Transect Sampling

Transect locations (A-H) for September 16, 1975 Map also indicates bathymetry (M) and survey stations from ONE, 1974.

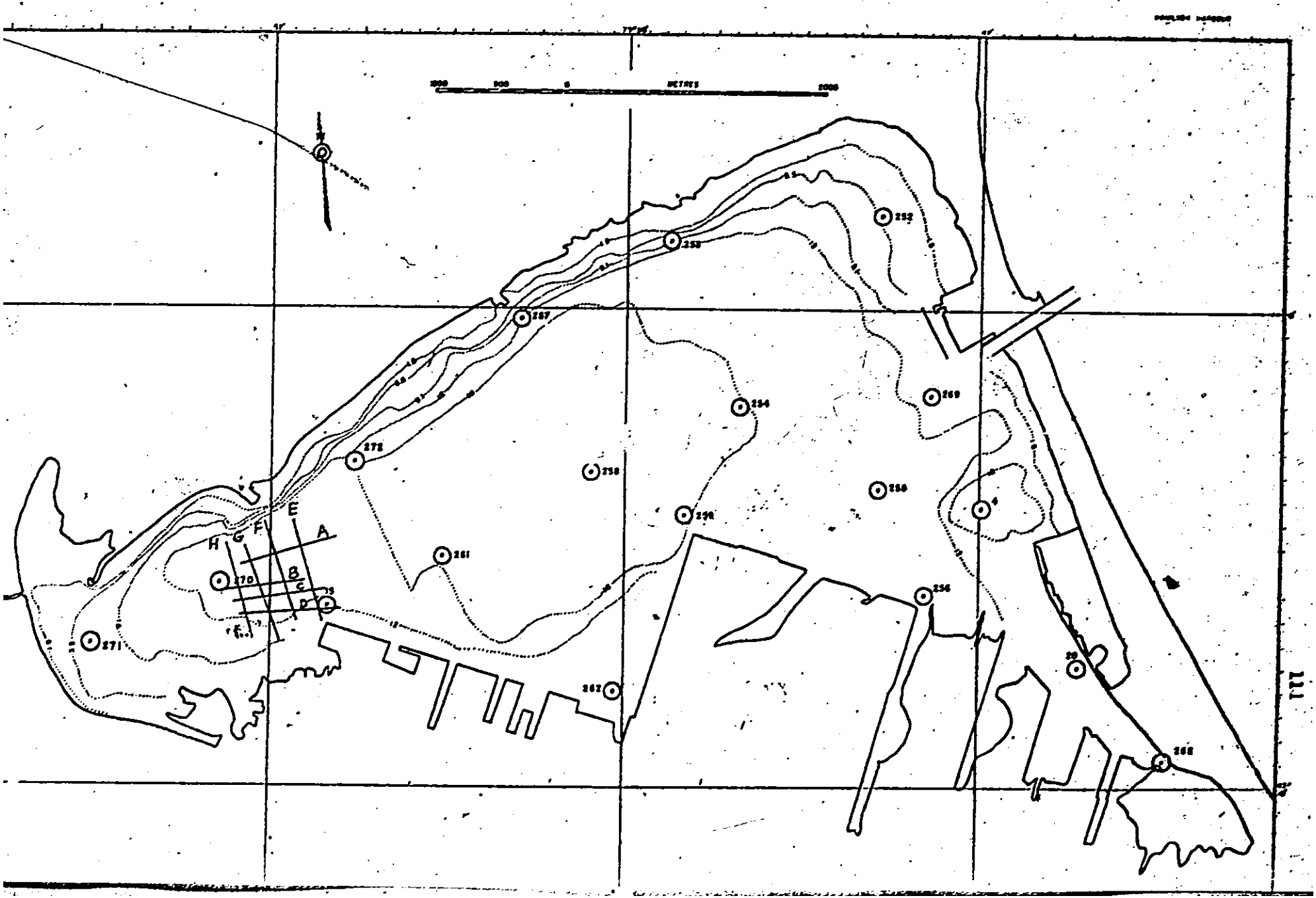

METRES
252
253
257
254
269
272
258
256
259
261
270
A
B
C
D
E
F
G
H
271
262
266
111

Figure 38

Continuous Transect Sampling

Transect locations (A-H) for July 20, 1976. Map also indicates bathymetry (M) and survey stations from OME, 1974.

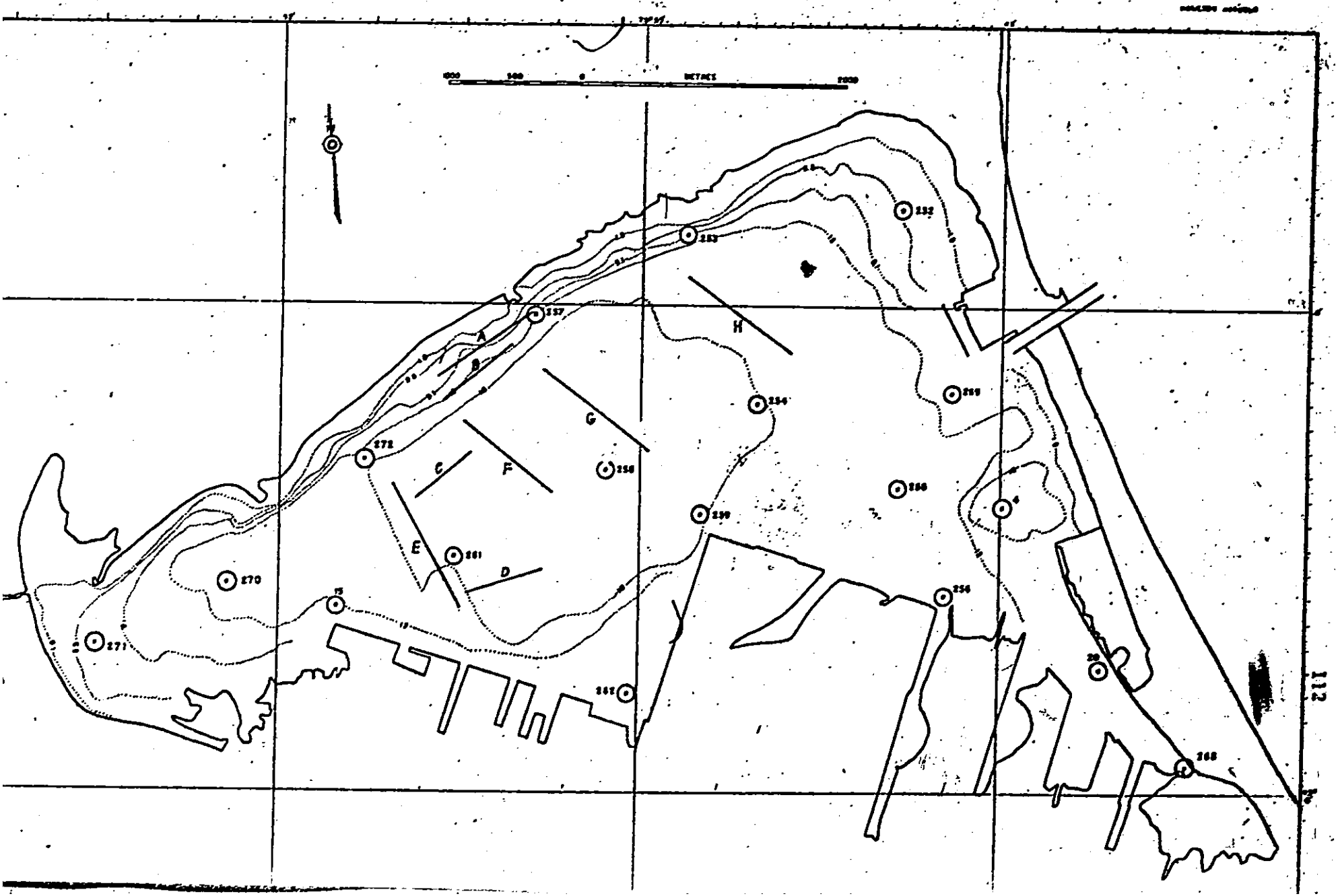

METRES
A
B
C
D
E
F
G
H
112

Figure 39

Continuous Transect Sampling

Transect locations (A-H) for November 3, 1976. Map also indicates bathymetry (M) and survey stations from OME, 1974.

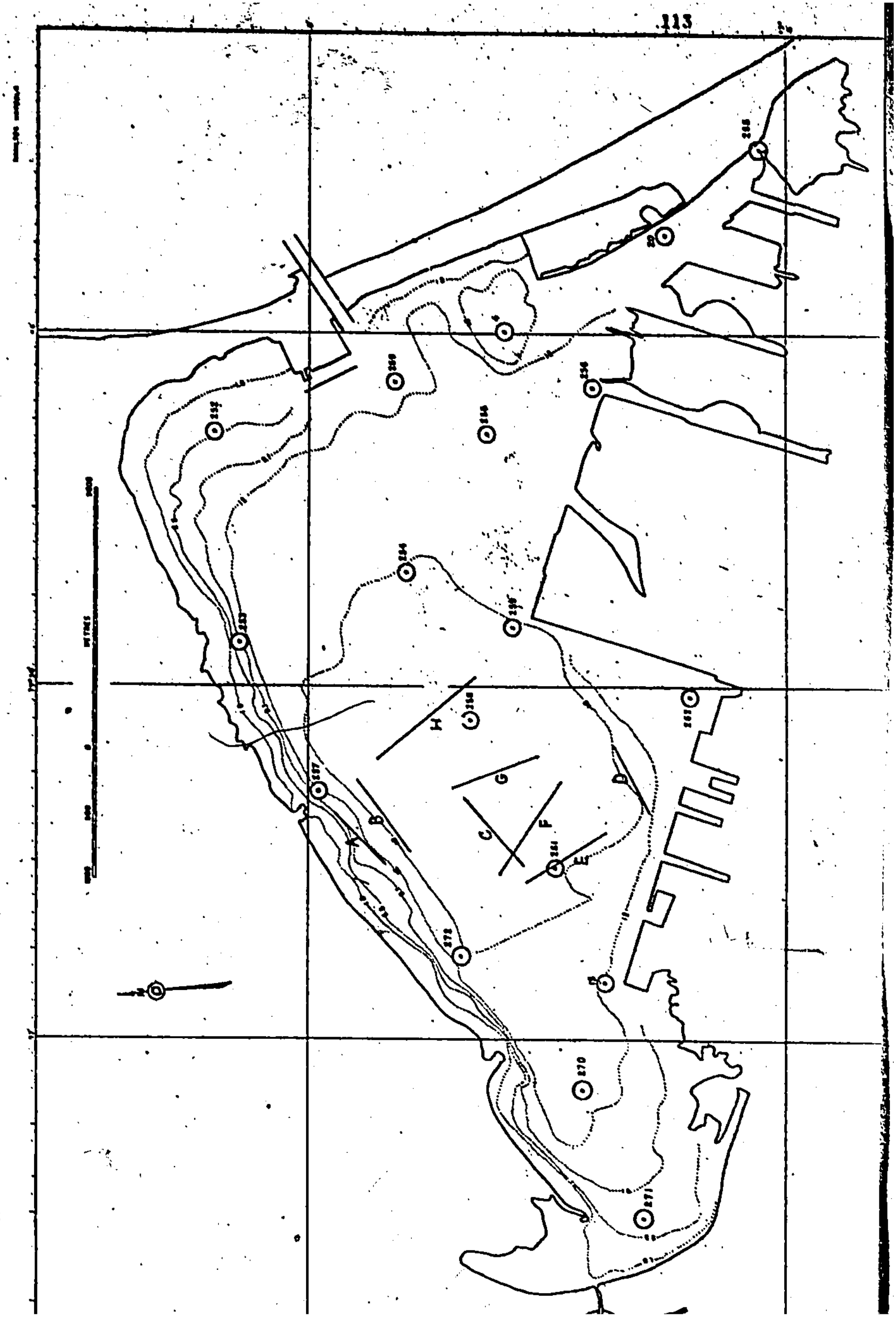

A
B
C
D
E
F
G
H

Table 13

Wind Data from the Royal Botanical Gardens Headquarters;
(1) Plains Road West, Burlington and
(2) Hamilton Marine Police.

	Date	1 Average Speed (mph)	1 Max Speed (mph) & Direction	1 Prevailing Direction	2 Prevailing Direction	2 Mean Speed (mph)	2 Maximum Velocity (mph)
	July 14/75	8.0	SW 15	SW	SE	8.7	14
	July 21/75	8.3	NW 13	SW	E	10.9	15
a	July 26/75	5.5	SW 8	SW	W	6.1	8
	Aug. 25/75	8.5	SW 16	SW	*	*	*
	Sept. 2/75	8.3	NW 15	SW	NW	10.0	17
	Sept. 9/75	7.2	NW 11	NW	SUL	9.8	14
	Sept. 15/75	3.6	SW 8	SW	W	4.5	8
a	Sept. 16/75	2.1	NW 4	W	W	3.1	5
	June 29/76	4.6	NE 8	NE	*	*	*
	July 5/76	4.1	W 5	SW	W	4.8	8
	July 13/76	10.6	NW 17	NW	NW	11.3	18
	July 19/76	8.4	SW 11	SW	SW	8.7	12
a	July 20/76	9.8	SW 16	SW	SW	9.6	15
	Sept. 30/76	2.8	E 10	NE	*	*	*
	Oct. 4/76	4	E 10	NE	*	*	*
	Nov. 1/76	5.3	NW 12	W	SE	6.2	15
a	Nov. 3/76	5.9	SW 12	SW	SE	6.6	12

a Sampling excursion

* not obtained

SUL several

Table 14

Wind Speed (mph) and Direction Data for 30 hr. Period Prior to Completion of Each Excursion

1 Hamilton Marine Police and

2 CCIW

Time (Local)	September '75' 15-16		July '76' 19-20		November '76' 2-3	
	1	2	1	2	1	2
9	W 2	NE 4	W 9	W 7	S 6	W 9
10	NE 4	NE 6	W 8	W 7	SE 7	SW 10
11	NE 6	NE 6	SW 8	W 7	SE 8	SW 15
12	S 6	NE 6	SW 9	W 7	SE 10	SW 16
13	SW 8	SW 7	NW 12	W 8	SE 10	SW 15
14	SW 8	SW 11	SW 10	SW 9	SE 10	SW 16
15	SW 8	SW 9	SW 11	W 8	SE 12	SW 16
16	SW 8	SW 10	SW 10	SW 7	SE 12	SW 18
17	SW 7	SW 10	SW 11	SW 11	SE 11	SW 17
18	SW 6	SW 11	SW 11	SW 10	SE 9	SW 16
19	SW 4	S 7	SW 9	SW 11	SE 9	SW 15
20	W 3	W 3	SW 9	SW 9	SW 8	SW 12
21	W 4	NW 3	SW 9	SW 7	SE 8	SW 8
22	W 2	S 1	SW 8	W 7	SW 12	SW 8
23	W 3	00	SW 7	W 7	SE 11	W 10
24	W 5	00	SW 6	W 6	SE 6	W 8
1	W 3	N 1	SW 5	NW 6	SE 5	W 5
2	S 4	S 4	SW 4	W 6	SE 4	W 5
3	W 3	N 2	W 6	NW 6	SE 7	SW 6
4	W 1	N 2	SW 8	W 6	SE 8	W 6
5	W 3	N 2	SW 7	W 5	SE 6	NW 6
6	W 4	W 2	SW 6	SW 6	SE 6	W 6
7	W 4	W 3	SW 6	SW 9	SE 5	W 7
8	W 4	NW 4	SW 8	SW 11	SE 6	SW 6
9	W 4	NW 3	SW 10	SW 14	SE 7	W 5
10	W 4	NW 4	SW 12	SW 14	SE 9	W 8
* 11	W 5	NW 7	SW 12	SW 17	SE 8	W 7
* 12	NW 3	NW 5	SW 12	SW 17	SE 11	SW 9
* 13	NW 3	NW 3	SW 12	SW 16	SE 11	SW 12
* 14	NW 1	00	SW 13	SW 16	SE 12	SW 10

* periods during excursion

Table 15

Survey Results for Surface Water Samples, Station 270, July 1975. (after Harris 1976)

Date	Depth *	Chlorophyll a (mg/m³)	Temperature (°C)	FRP (µg/l)	$NO_3 + NO_2$ (mg/l)
July 19	T	53.	23.5	5.5	1.64
	M	28	19.0	7.2	1.66
	B	7.6	12.7	7.4	1.40
July 21	T	49	20.9	7.3	0.28
	M	28	18.4	7.0	0.0
	B	8.6	11.9	57.0	1.10

* T – top
M – middle
B – bottom

Figure 40

Parameter Data Plots

September 16, 1975 Transect A

a Fluorometer

b Spectrophotometric Chlorophyll a

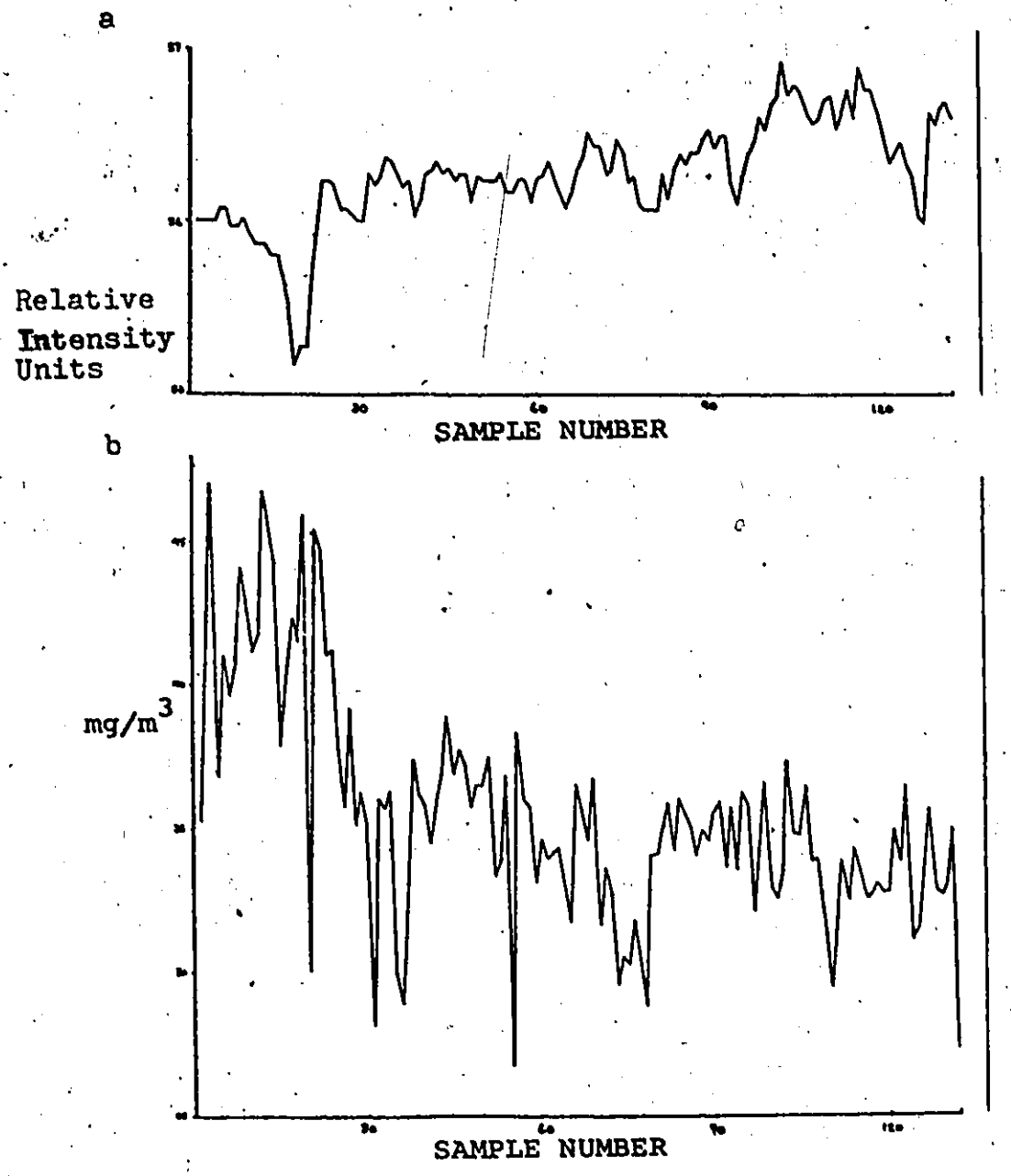

a
Relative
Intensity
Units
SAMPLE NUMBER
b
mg/m3
SAMPLE NUMBER

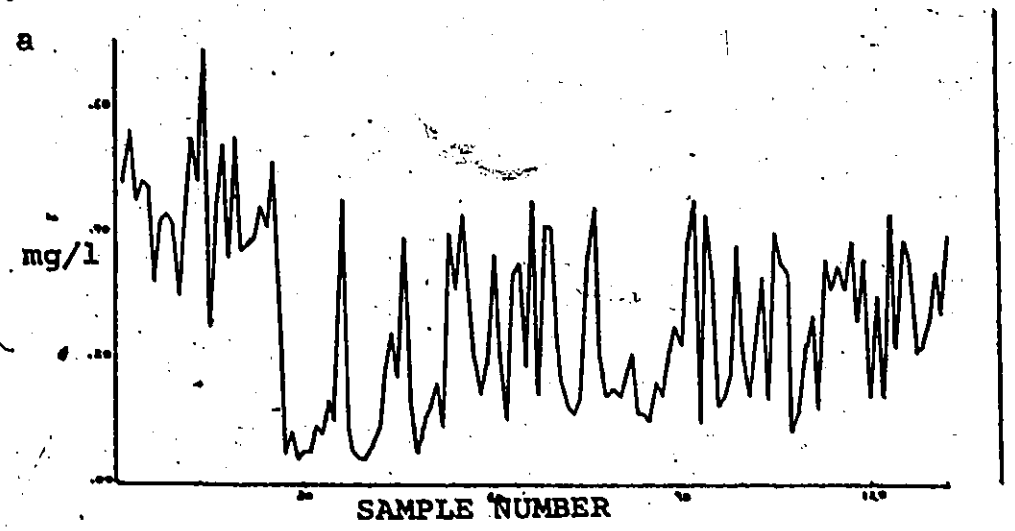
Figure 41

Parameter Data Plots

September 16, 1975 Transect A

a Filtered Reactive Silica

b Filtered Reactive Phosphorous


a
mg/l
SAMPLE NUMBER

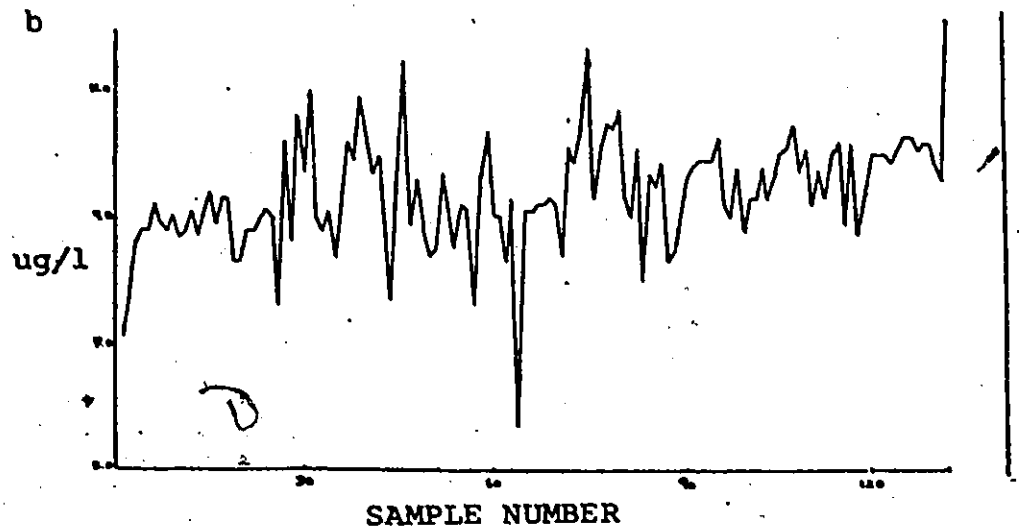

b
ug/l
SAMPLE NUMBER

Figure 42

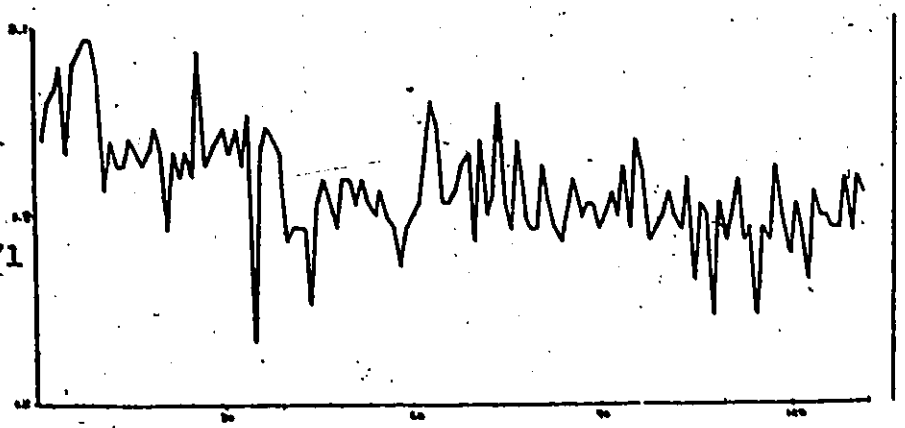
Parameter Data Plots

September 16, 1975 Transect A

a $NO_3 + NO_2$

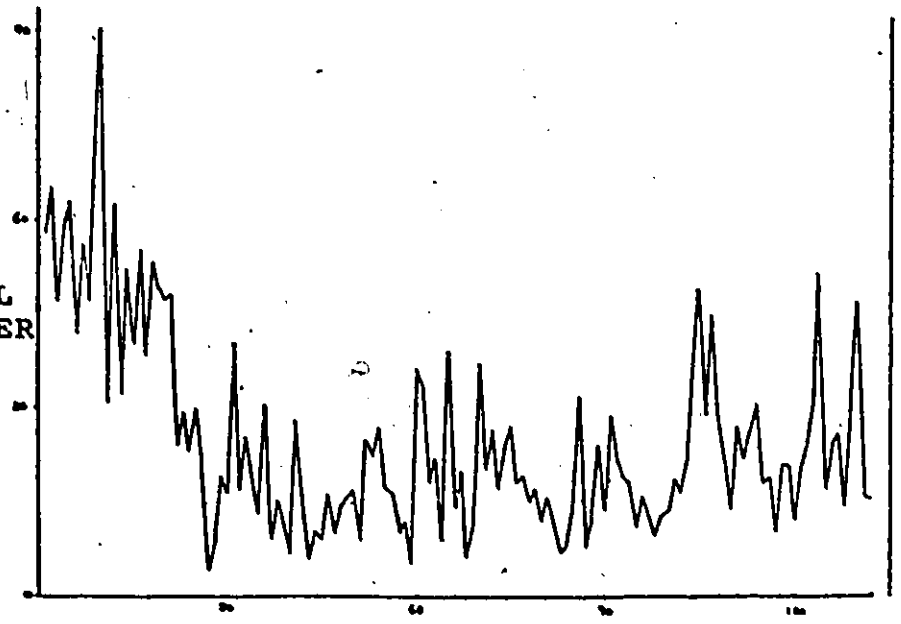
b C. erosa

a



SAMPLE NUMBER

b



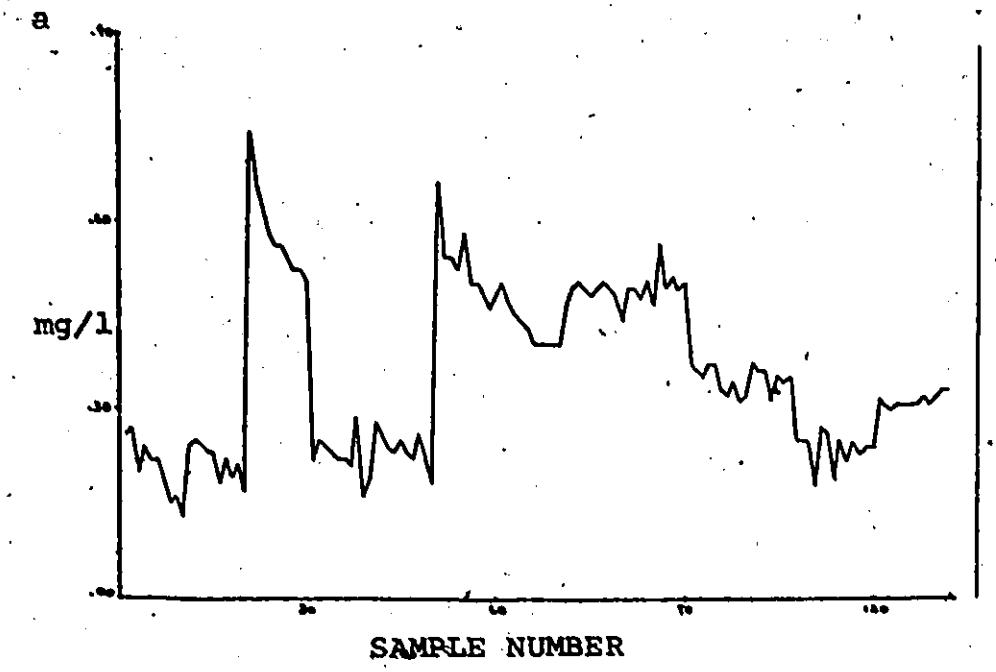
SAMPLE NUMBER

Figure 43

Parameter Data Plots

a NO_2 July 20, 1976 Transect A

b Cyclotella men. September 16, 1975 Transect A


a
mg/l
SAMPLE NUMBER

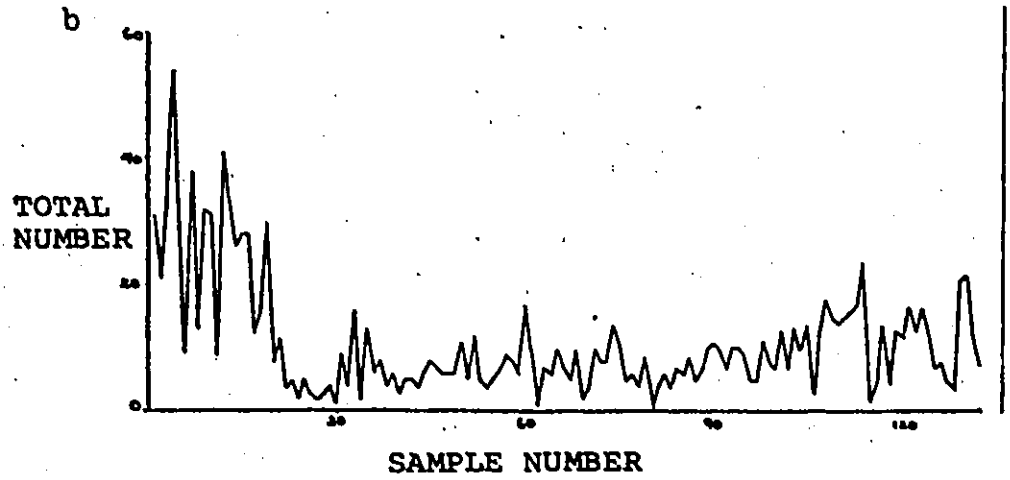

b
TOTAL
NUMBER
SAMPLE NUMBER

Figure 44

Parameter Data Plots

O. borgei September 16, 1975 Transect A

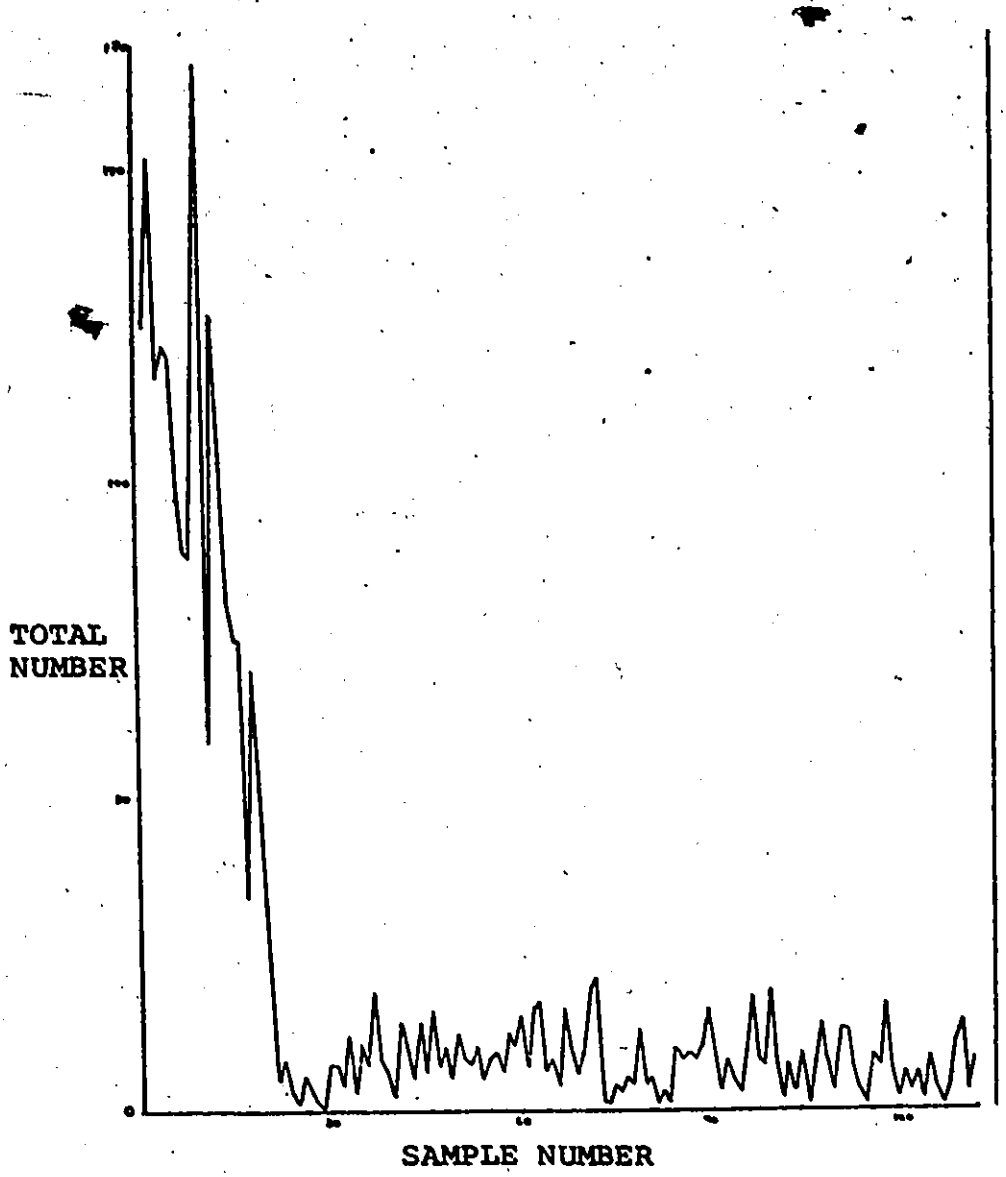

TOTAL
NUMBER
SAMPLE NUMBER

Figure 45

Parameter Data Plots

R. minutum September 16, 1975 Transect A

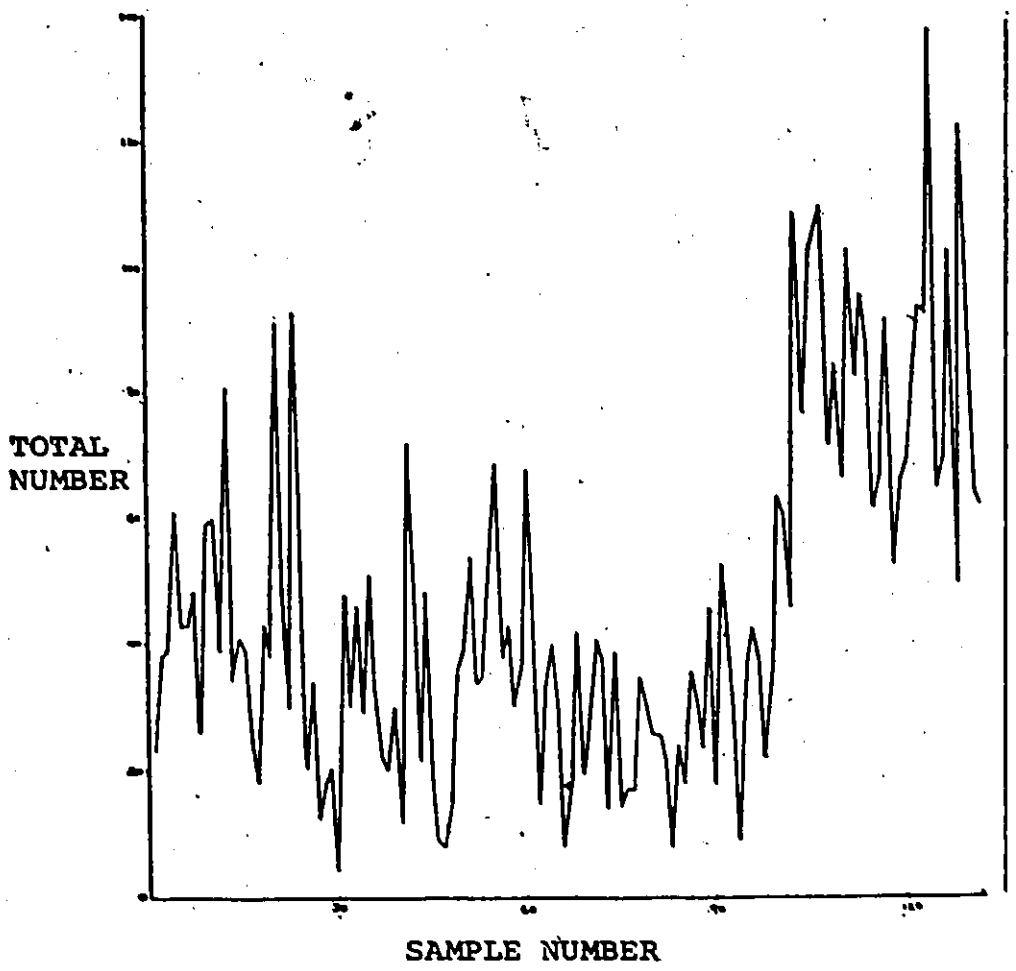

TOTAL
NUMBER
SAMPLE NUMBER

Figure 46

Parameter Data Plots

Total Phosphorous September 16, 1975

Transect A

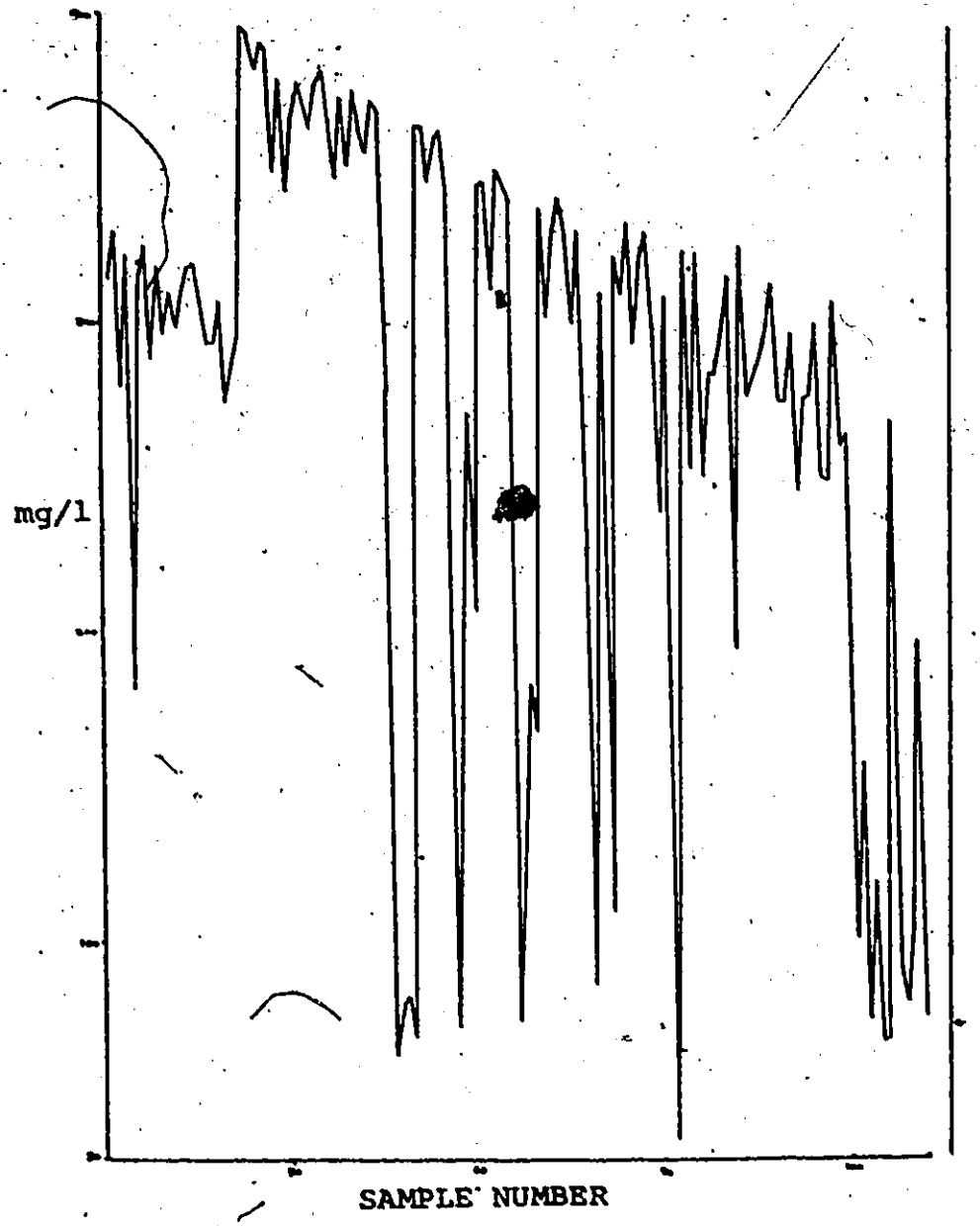

mg/l
SAMPLE NUMBER

Figure 47

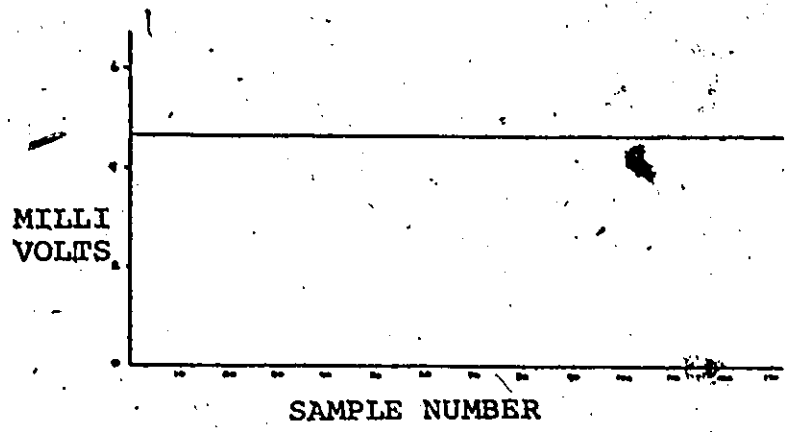
Parameter Data Plots

a Temperature Trace November 3, 1976

Transect H

B Temperature Trace September 16, 1975

Willow Point to Leander Boat Club


MILLI
VOLTS
SAMPLE NUMBER

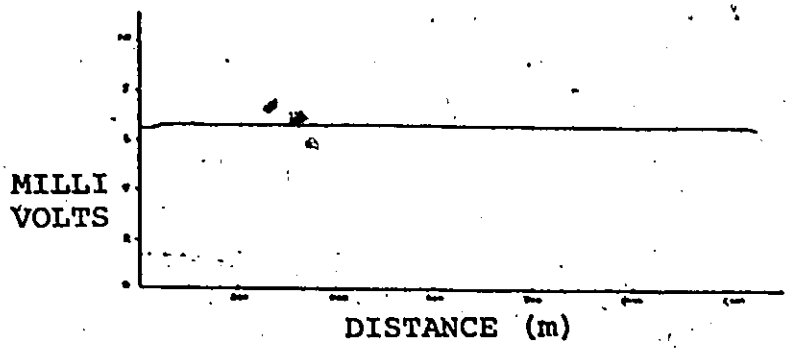

MILLI
VOLTS
DISTANCE (m)

Table 16

Hamilton Harbour Survey Data 1975 for One Month Prior to (most recent date first) the September 16,1975 excursion (after Harris, 1975).

Date	Station No. (maximum depth meters)	Depth	Chloro A (mg/m³)	Temp. (°C)	ph	D.O. (mg.l)	NO_3+NO_2 (mg/l)	PO (ug/l)	STS (mg/l)
Sept. 15/75	#4 (18)	T	32.56	19.3	7.6	7.13	1.84	15.4	0.32
		M	13.61	16.2	7.45	4.52	1.50	9.4	0.21
		B	15.22	13.2	7.3	0.59	0.92	3.6	0.10
	#252 (6)	T	35.02	17.7	7.95	8.62	1.82	16.9	0.26
		M	28.60	17.4	7.8	7.31	2.02	42.9	0.16
		B	27.91	17.6	7.75	7.94	1.74	20.1	0.26
	#258 (20)	T	30.43	17.3	7.75	7.99	1.74	20.1	0.26
		M	16.16	17.2	7.5	5.62	1.72	41.6	0.28
		B	8.47	12.2	7.35	0.82	0.88	16.9	0.15
	#270 (12)	T	21.38	16.50	7.35	6.75	1.76	115.0	0.25
		M	24.36	17.2	7.65	6.91	1.60	42.5	0.26
		B	33.29	15.2	7.50	3.88	1.48	31.6	0.11
Sept. 9/75	#4 (18)	T	40.5	18.8	8.0	8.25	1.70	1.5	.25
		M	35.0	19.1	7.85	7.83	1.96	2.3	.33
		B	10.1	11.9	7.30	-	1.14	1.5	.18
	#252 (6)	T	42.4	18.9	8.00	8.78	1.94	7.9	.21
		M	43.0	18.8	8.05	8.73	1.94	1.6	.24
		B	39.5	18.8	7.90	8.45	2.02	7.3	.33
	#258 (20)	T	40.2	18.5	8.15	8.16	1.96	2.7	0.23
		M	25.4	15.7	7.60	4.39	1.66	2.3	.24
		B	12.9	11.7	7.30	0.65	0.78	0.6	.10
	#270 (12)	T	31.7	17.5	7.75	7.29	1.96	18.8	0.30
		M	24.3	16.9	7.60	5.12	1.82	2.9	0.20
		B	12.8	12.8	7.35	0.64	1.20	2.7	0.15

Table 16 cont'd

Hamilton Habour Survey Data 1975
(after Harris, 1975)

Date	Station No. (maximum depth meters)	Depth	Chloro.a (mg/m^3)	Temp. (°C)	pH	D.O. (mg/l)	NO_2+NO_3 (µg/l)	PO (µg/l)	SPS (mg/l)
Sept. 2/75	#4 (18)	T	22.1	19.4	7.8	7.0	2.08	8.8	0.52
		M	16.1	18.0	7.5	3.9	2.22	78.2	0.84
		B	7.5	11.8	7.4	0.7	1.16	13.7	0.63
	#252 (6)	T	25.8	19.6	7.8	7.5	2.20	12.9	0.52
		M	26.9	19.6	7.8	7.3	2.18	9.9	0.56
		B	25.7	18.3	7.8	7.2	2.26	8.3	0.55
	#258 (20)	T	24.6	19.4	7.6	7.0	1.88	9.10	.57
		M	9.8	14.4	7.4	1.94	1.44	8.70	.55
		B	7.5	11.3	7.3	0.80	0.92	13.00	.67
	#270 (12)	T	23.1	19.4	7.7	7.5	2.00	14.3	0.61
		M	18.6	16.6	7.5	3.4	1.84	11.3	0.58
		B	9.4	12.5	7.3	1.6	1.52	17.6	0.78
Aug. 25/75	#4 (18)	T	61.5	22.5	8.1	7.6	2.56	4.5	.39
		M	23.6	14.3	7.4	2.1	1.88	10.6	.32
		B	18.1	11.2	7.4	0.6	1.20	14.3	.25
	#252 (6)	T	64.2	21.4	8.1	8.1	2.42	6.7	.33
		M	64.8	21.5	8.2	8.1	2.52	6.4	.38
		B	60.3	21.4	8.0	7.5	2.66	79.4	.48
	#258 (20)	T	67.4	21.0	8.0	7.2	2.32	5.33	.34
		M	15.1	14.2	7.4	3.1	1.50	6.6	.24
		B	13.4	11.2	7.4	0.6	1.20	6.7	.22
	#270 (12)	T	66.5	20.3	7.9	7.4	2.00	12.80	.43
		M	46.1	17.6	7.5	3.4	1.90	10.00	.36
		B	21.7	11.9	7.2	0.8	1.22	8.51	.25

Hamilton Harbour Survey Data 1976 for One Month Prior to (most recent date first) the July 20,1976 Excursion (after Piccinin, 1976)

Date	Station No.	Depth (m)	Chloro a (mg/m³)	Temp. (°C)	ph	D.O. (mg/l)	NO_3+NO_2 (mg/l)[2]	NO_2 (mg/l)	PO (ug/l)	SRP (mg/l)
July 19/76	4	.2	67.73	23.6	7.8	9.9	2.58	.36	26.4	1.33
		3	61.53	24.6	7.9	10.1	2.50	.37	25.6	1.40
		6	32.10	22.2	8.2	8.8	2.48	.32	24.6	1.06
		12	6.32	14.9	7.4	2.5	1.66	.22	20.6	0.85
		18	10.02	12.6	7.5	7.5	0.90	.19	19.8	0.59
	252	.2	52.94	21.4	8.4	9.4	2.28	.22	19.3	1.10
		3	47.79	22.6	8.1	9.2	2.04	.23	25.7	0.44
		6	32.15	21.5	7.7	10.2	2.39	.25	25.6	0.66
	258	.2	53.84	20.5	8.5	10.2	2.02	.29	27.5	0.99
		3	41.78	20.5	8.3	10.9	2.20	.28	27.1	0.83
		6	15.48	18.4	7.8	9.8	2.26	.25	24.8	0.98
		12	4.56	15.5	7.5	4.1	2.16	.17	26.1	0.71
		20	6.97	12.8	7.6	4.0	1.33	.20	26.4	0.90
	270	.2	28.37	18.2	7.9	6.6	2.29	.23	23.2	0.83
		3	20.90	18.4	7.8	6.8	2.26	.21	23.6	0.92
		6	13.87	17.1	7.6	7.2	1.96	.17	24.1	0.48
		12	7.61	13.6	7.4	5.4	1.67	.14	24.6	0.99

Table 17 cont'd

Date	Station No.	Depth (m)	Chloro a (mg/m^3)	Temp. (°C)	ph	D.O. (mg/l)	NO_3+NO_2 (mg/l)	NO_2 (mg/l)	PO_4 (µg/l)	SRS (mg/l)
July 13/76	4	.2	24.20	22.0	7.8	8.8	2.74	.19	30.7	0.76
		3	24.89	21.8	7.8	9.2	2.84	.19	24.4	0.74
		6	24.82	21.0	7.8	8.9	2.08	.21	22.5	0.84
		12	8.59	11.2	7.5	6.0	2.66	.12	25.2	0.73
		18	4.39	5.3	7.5	6.0	1.76	.07	25.1	0.65
	252	.2	27.72	21.8	7.7	7.9	2.68	.12	27.2	0.56
		3	29.86	20.9	7.8	9.9	2.70	.13	24.7	0.67
		6	16.42	18.0	7.5	11.1	2.44	.11	26.8	0.59
	258	.2	23.10	19.0	7.8	8.8	3.04	.12	47.3	0.76
		3	25.00	19.0	7.9	9.4	3.08	.14	40.2	0.78
		6	25.57	16.9	7.7	9.6	2.70	.12	48.7	0.37
		12	4.30	6.6	7.5	6.1	2.28	.10	40.0	0.35
		20	2.45	5.5	7.4	4.9	1.84	.07	49.2	0.37
	270	.2	10.78	19.0	7.5	3.9	2.74	.13	56.7	0.56
		3	14.56	18.3	7.5	5.4	2.54	.10	57.2	0.30
		6	10.74	13.5	7.5	6.4	2.56	.09	57.7	0.51
		12	4.75	4.8	7.4	5.5	2.06	.07	53.4	0.28

Table 17 cont'd

Date	Station No./	Depth (m)	Chloro a (mg/m^3)	Temp. (°C)	ph	D.O. (mg/1)	NO_3+NO_2 ($mg/1)^2$	NO_2 (mg/1)	PO_4 (µg/1)	SRS (mg/1)
July 5/76	4	.2	19.55	21.3	7.6	7.1	2.48	.18	10.2	.51
		3	18.29	20.9	7.6	6.4	3.14	.19	11.9	.56
		6	13.14	18.9	7.5	6.4	3.22	.14	13.9	.38
		12	11.20	13.5	7.5	3.7	2.86	.08	15.2	.40
		18	6.35	10.5	7.5	5.1	1.86	.06	10.1	.23
	252	.2	17.13	23.5	7.7	8.4	3.50	.19	7.6	.40
		3	16.77	19.9	7.6	6.1	3.28	.15	10.8	.35
		6	13.06	17.0	7.4	2.7	2.70	.12	17.3	.29
	258	.2	12.27	21.7	7.6	7.0	3.30	.17	10.9	.41
		3	10.96	20.0	7.5	6.4	3.42	.17	16.4	.27
		6	11.80	18.0	7.5	5.6	3.16	.11	10.6	.51
		12	5.11	12.2	7.4	1.8	2.90	.06	18.5	.29
		20	5.68	9.9	7.4	1.0	2.02	.06	25.0	.38
	270	.2	17.30	23.0	7.6	8.2	2.56	.17	11.8	.44
		3	10.72	20.5	7.7	6.1	2.44	.12	11.5	.29
		6	11.18	18.1	7.6	5.0	3.14	.14	9.7	.38
		12	7.98	10.1	7.4	1.7	2.62	.06	8.4	.18

Table 17 cont'd.

Date	Station No.	Depth (m)	Chloro a (mg/m^3)	Temp. (°C)	ph	D.O. (mg/l)	NO_3+NO_2 (mg/l)	NO_2 (mg/l)	PO_4 (ug/l)	SRS (mg/l)
June 29/76	4	.2	23.28	22.0	7.5	7.5	2.84	.26	43.8	.44
		3	13.83	20.0	7.4	7.5	2.88	.23	36.6	.30
		6	7.94	18.1	7.3	4.7	2.44	.11	30.6	.29
		12	7.05	13.0	7.5	3.6	2.22	.04	25.6	.19
		18	5.64	8.9	7.2	2.1	2.04	.07	40.2	.27
	252	.2	30.95	21.5	7.7	9.5	2.72	.21	23.8	.57
		3	13.32	19.2	7.5	4.2	2.82	.17	13.6	.45
		6	9.41	16.3	7.4	3.1	2.42	.07	26.8	.46
	258	.2	21.10	21.8	7.9	9.2	2.94	.20	17.0	.38
		3	19.00	21.2	8.0	7.8	2.84	.17	19.0	.55
		6	8.20	17.8	7.4	2.1	2.96	.06	24.4	.47
		12	8.00	13.1	7.3	3.0	2.16	.05	16.6	.28
		20	6.45	9.1	7.1	2.1	2.14	.13	19.8	.22
	270	.2	24.09	22.0	7.8	11.2	2.58	.16	8.8	.49
		3	20.83	4.5	7.5	8.2	2.66	.18	13.0	.40
		6	11.82	18.9	7.3	2.7	2.70	.05	25.4	.30
		12	4.85	11.9	7.3	1.9	2.46	.12	28.0	.21

Table 18

Hamilton Harbour Survey Data 1976 for One Month Period Prior to (most recent date first) the November 3,1976 Excursion (after Piccinin, 1976)

Date	Station No.	Depth (m)	Chloro a (mg/m³)	Temp (°C)	ph	D.O. (mg/l)	NO_3+NO_2[2] (mg/l)	NO_2 (mg/l)	PO$_4$ (µg/l)	SRS (mg/l)
Nov. 1/76	4	.2	17.10	10.6	7.5	8.3	2.33	.21	43.4	0.44
		3	18.13	10.3	7.4	8.4	2.51	.22	21.5	0.42
		6	19.36	9.8	7.4	10.3	2.48	.23	28.7	0.31
		12	23.73	8.9	7.5	12.0	2.53	.23	42.2	0.31
		18	23.16	7.8	10.8	10.8	2.42	.22	24.4	0.33
	252	.2	16.76	9.3	7.2	9.1	2.50	.23	58.0	0.25
		3	25.86	9.1	7.5	9.5	2.63	.24	37.1	0.21
		6	23.46	9.0	7.5	10.5	2.43	.23	325.0	0.26
	258	.2	23.79	9.6	7.4	8.9	2.58	.24	15.9	0.24
		3	24.85	9.4	7.3	8.9	2.62	.24	19.7	0.33
		6	24.81	9.3	7.2	10.4	2.44	.24	5.4	0.24
		12	23.96	8.9	7.2	13.8	2.44	.23	23.3	0.28
		20	23.75	8.1	7.2	11.7	2.38	.23	14.9	0.21
	270	.2	26.87	8.8	7.4	9.8	2.57	.25	29.6	0.25
		3	25.10	8.8	7.4	9.6	2.61	.25	44.7	0.35
		6	27.50	8.8	7.4	10.8	2.54	.26	40.4	0.26
		12	22.59	7.8	7.5	12.6	2.35	.23	12.8	0.19
Oct. 27/76	258	.2	25.17	10.2	7.6	7.6	2.33	.17	6.6	0.34
		3	25.63	10.4	7.6	7.6	2.27	.17	7.7	0.40
		6	25.45	10.4	7.5	7.5	2.44	.18	5.7	0.30
		12	25.26	10.4	8.7	8.7	2.48	.18	9.7	0.37
		20	23.99	10.2	8.7	8.7	2.32	.18	11.3	0.30
Oct. 4/76	4	.2	23.38	16.3	7.5	7.7	2.21	.25	13.7	0.50
		3	21.52	15.4	7.6	7.1	2.24	.18	17.0	0.38
		6	18.34	15.1	7.5	8.2	2.45	.16	10.8	0.34
		12	14.55	13.4	7.5	6.8	2.33	.05	26.1	0.36
		18	15.60	11.0	7.6	7.9	1.68	.07	13.0	0.42
	252	.2	25.75	15.2	7.6	8.4	2.13	.14	33.7	0.35
		3	24.12	15.2	7.6	8.8	2.27	.17	25.0	0.35
		6	24.77	15.0	7.5	8.6	2.30	.17	20.1	0.35

Table 18 cont'd

Date	Station No.	Depth (m)	Chlorp a (mg/m^3)	Temp. (°C)	pH	D.O. (mg/l	NO_3+NO_2 ($\mu g/l$)	NO_2 (mg/l)	PO_4 ($\mu g/l$)	SRS (mg/l)
Oct. 4/76	258	.2	32.51	16.2	7.8	9.3	2.42	.21	19.8	0.38
		3	32.58	15.7	7.8	8.4	2.34	.22	30.9	0.34
		6	34.97	15.3	7.7	8.5	2.38	.21	104.8	0.35
		12	16.17	14.2	7.6	8.6	2.19	.02	19.0	0.43
		20	11.92	11.2	7.5	4.2	1.54	.02	34.4	0.35
	270	.2	50.97	15.4	7.9	9.7	2.31	.16	22.5	0.34
		3	49.28	15.3	8.0	9.9	1.99	.16	12.8	0.31
		6	41.44	15.3	8.0	10.4	2.29	.19	14.9	0.32
		12	21.26	13.5	7.6	5.8	1.83	.06	25.9	0.34
Sept. 30/76	4	.2	25.95	16.5	7.6	6.3	2.19	.22	28.4	0.59
		3	29.19	15.5	7.6	5.5	2.32	.26	15.8	0.50
		6	29.86	15.2	7.7	7.0	2.26	.30	16.6	0.46
		12	26.46	14.4	7.7	8.9	2.18	.28	12.4	0.47
		18	21.12	11.9	7.7	9.3	1.65	.14	14.1	0.49
	252	.2	35.43	14.8	7.7	8.4	2.18	.28	19.9	0.37
		3	32.16	15.1	7.7	6.6	2.24	.26	11.6	0.46
		6	30.97	14.9	7.8	6.4	2.21	.19	13.7	0.46
	258	.2	28.25	15.5	7.4	6.2	2.28	.26	12.5	0.41
		3	28.37	15.1	7.5	5.5	2.35	.20	10.4	0.41
		6	25.75	14.8	7.6	5.2	2.28	.21	10.0	0.44
		12	26.06	14.4	7.6	6.6	2.14	.22	10.1	0.39
		20	14.77	11.2	7.5	2.8	1.55	.07	16.2	0.40
	270	.2	27.84	14.6	7.7	5.7	2.04	.16	10.1	0.41
		3	26.92	14.5	7.7	5.2	2.09	.12	12.4	0.45
		6	25.93	14.3	7.7	4.9	2.09	.08	10.6	0.50
		12	22.28	14.0	7.6	5.3	1.84	.07	13.7	0.38

Table 19

Species Counts (cells/ml(%total))for One Month Prior to (most recent date first) the September 16,1975 Excursion (after Harris, 1975)

Date	Station No.	C. erosa	E. minutum	Cyclotella	O. borgei	Fragillaria	Total
Sept. 15/75	270	172 (6.4)	295 (11.0)	722 (26.8)	681 (25.3)	49 (1.8)	2690
	258	525 (19.1)	558 (20.3)	221 (8.0)	164 (6.0)	33 (1.2)	2760
	4	664 (15.1)	115 (2.6)	82 (1.9)	525 (11.9)	49 (1.1)	4410
	252	344 (7.5)	927 (20.1)	672 (14.6)	779 (16.9)	66 (1.4)	4600
Sept. 9/75	270	312 (10.9)	369 (12.9)	771 (26.9)	541 (18.9)	57 (2.0)	2860
	258	295 (7.7)	492 (12.8)	1648 (42.9)	229 (5.9)	74 (1.9)	3840
	4	238 (6.9)	172 (5.0)	213 (6.2)	721 (26.0)	74 (2.2)	3430
	252	361 (3.6)	804 (8.1)	5986 (60.4)	820 (8.3)	33 (0.3)	9900
Sept. 2/75	270	49 (2.2)	16 (0.7)	623 (28.7)	836 (38.5)	25 (1.2)	2170
	258	90 (4.6)	16 (0.8)	566 (29.0)	607 (31.1)	33 (1.7)	1950
	4	25 (1.0)	49 (2.0)	590 (23.6)	869 (34.8)	41 (1.6)	2500
	252	57 (1.6)	98 (2.7)	1583 (43.4)	1132 (31.1)	8 (0.2)	3650
Aug. 25/75	270	230 (5.4)	49 (1.1)	959 (22.4)	2304 (53.9)	33 (0.8)	4280
	258	74 (2.4)	25 (0.8)	123 (4.0)	2140 (69.1)	16 (0.5)	3100
	4	107 (3.0)	74 (2.1)	90 (2.5)	2288 (63.9)	57 (1.6)	3580
	252	33 (0.7)	33 (0.7)	74 (1.7)	3149 (71.1)	33 (0.7)	4430

Table 20

Species Counts (cells/ml (%total)) for One Month Prior to (most recent date first) the July 20,1976 Excursion (after Piccinin, 1976)

Date	Station No.	R. minutum	Mongastia	C. sphaericola	O. borgei	Total
July 19/76	270	959 (17.7)	1376 (25.4)	295 (5.5)	652 (12.1)	5,410
	258	2116 (30.2)	1181 (16.8)	886 (12.6)	1267 (18.1)	7,011
	4	3063 (69.9)	258 (5.9)	640 (14.6)	296 (14.5)	4,380
	252	6076 (55.6)	615 (5.6)	984 (9.0)	1156 (10.6)	10,936
July 13/76	270	148 (4.6)	1833 (56.5)	74 (2.3)	258 (7.9)	3,246
	258	467 (9.8)	1933 (41.9)	234 (4.9)	972 (20.4)	4,762
	4	640 (13.6)	689 (14.7)	431 (9.2)	689 (14.7)	4,700
	252	923 (12.3)	4477 (60.0)	357 (4.8)	910 (12.2)	7,489
July 5/76	270	677 (13.3)	369 (7.2)	443 (8.7)	628 (12.3)	5,107
	258	234 (11.9)	443 (22.5)	172 (8.7)	382 (19.4)	1,971
	4	185 (7.4)	431 (17.3)	406 (16.3)	664 (26.7)	2,486
	252	258 (12.2)	0	480 (22.7)	578 (27.3)	2,114
June 29/76	270	652 (24.9)	0	123 (4.7)	985 (37.6)	2,622
	258	750 (24.2)	234 (7.5)	185 (6.0)	1044 (33.1)	3,102
	4	455 (15.2)	98 (3.3)	135 (4.5)	886 (29.6)	2,990
	252	640 (24.2)	0	418 (15.8)	750 (28.4)	2,645

Table 21

Species Counts (cells/ml (%total)) for One Month Prior to (most recent date first) the November 3,1976 Excursion (after Piccinin, 1976)

Date	Station No.	C. acrosa	C. sphagnicola	R. minutum	Stephanodiscus	Total
Nov. 1/76	270	677 (27.1)	49 (2.0)	566 (22.6)	492 (19.7)	2498
	258	209 (17.5)	12 (1.0)	209 (17.5)	246 (20.7)	1191
	4	517 (25.3)	49 (2.4)	455 (22.3)	295 (14.5)	2040
	252	135 (11.8?)	62 (5.2)	209 (17.7)	283 (24.0)	1181
Oct. 27/76	270					
	258	185 (12.3)	25 (1.7)	308 (20.5)	48 (3.2)	1502
	4					
	252					
Oct. 4/76	270	2288 (29.9)	25 (.3)	3739 (48.8)	332 (4.3)	7663
	258	775 (17.9)	86 (2.0)	2042 (47.3)	246 (5.7)	4320
	4	640 (20.2)	74 (2.3)	689 (21.8)	204 (6.6)	3161
	252	1144 (26.6)	49 (1.1)	1833 (42.6)	258 (6.0)	4304
Sept. 30/76	270	443 (14.2)	86 (2.8)	677 (21.6)	357 (11.4)	3124
	258	344 (14.2)	111 (4.6)	295 (12.2)	271 (11.2)	2425
	4	394 (16.4)	49 (2.0)	492 (20.5)	197 (8.2)	2397
	258	517 (17.2)	86 (2.9)	861 (28.7)	308 (10.3)	3003

APPENDIX II

Figure 18

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H NO_3 + NO_2

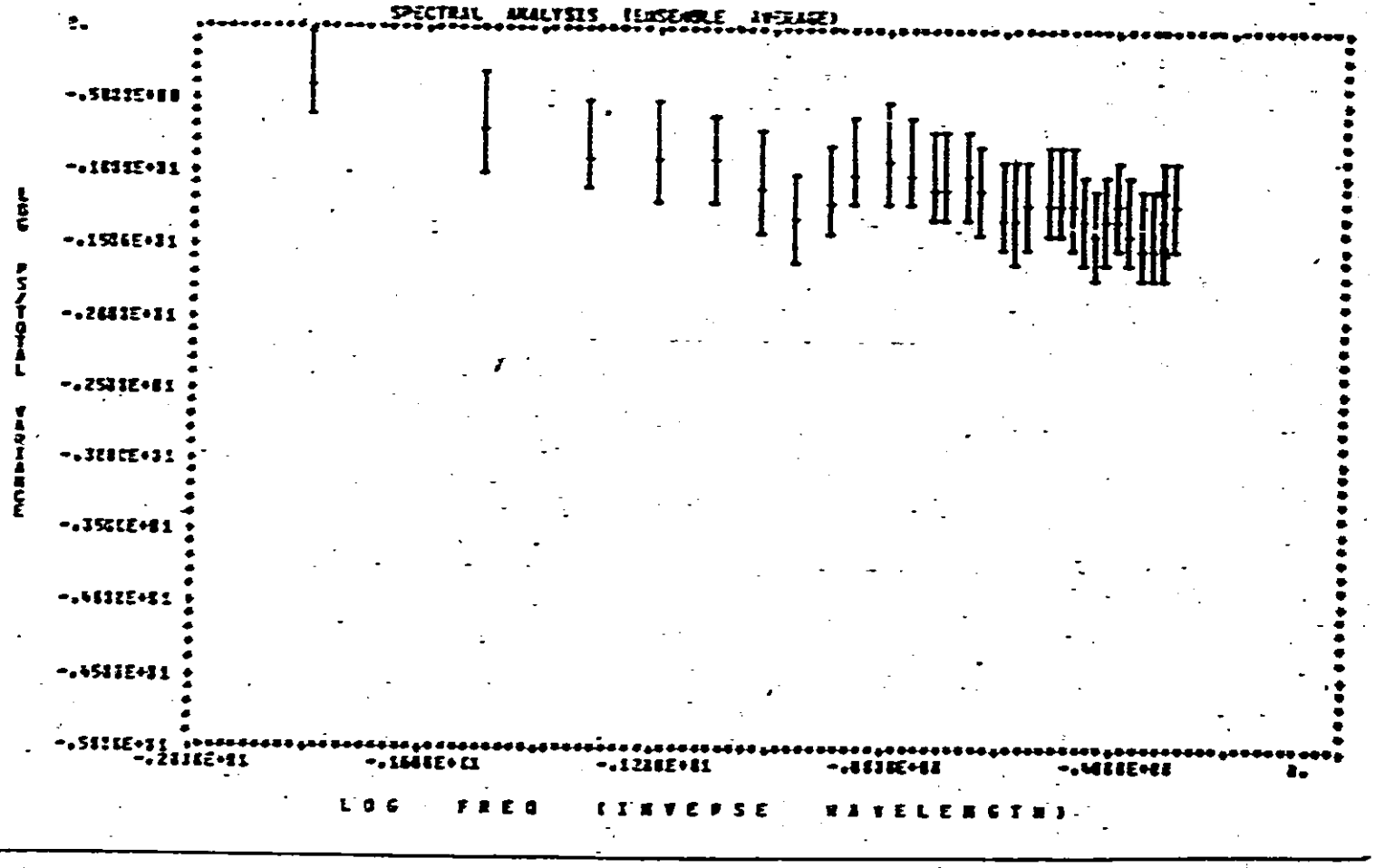

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
LOG FREQ (INVERSE WAVELENGTH)

Figure 19

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects B-H total phosphorous

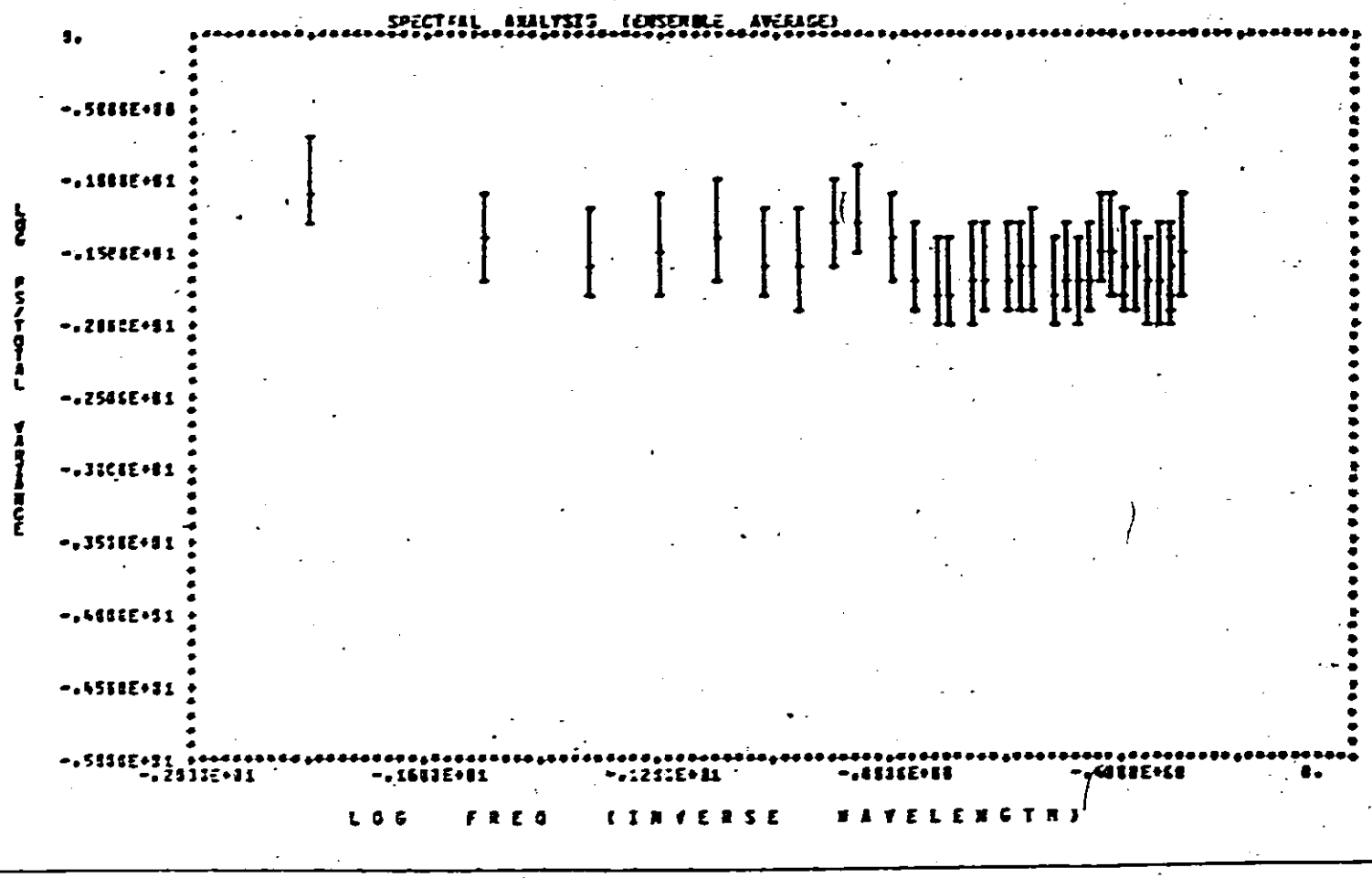

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
9.
-.5888E+88
-.1888E+81
-.1588E+81
-.2888E+81
-.2588E+81
-.3888E+81
-.3588E+81
-.4888E+81
-.4588E+81
-.5888E+81
-.2513E+81
-.1683E+81
-.1233E+81
-.8836E+88
-.6888E+88
8.
LOG FREQ (INVERSE WAVELENGTH)

Figure 20

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H Soluble Reactive Silica (SRS)

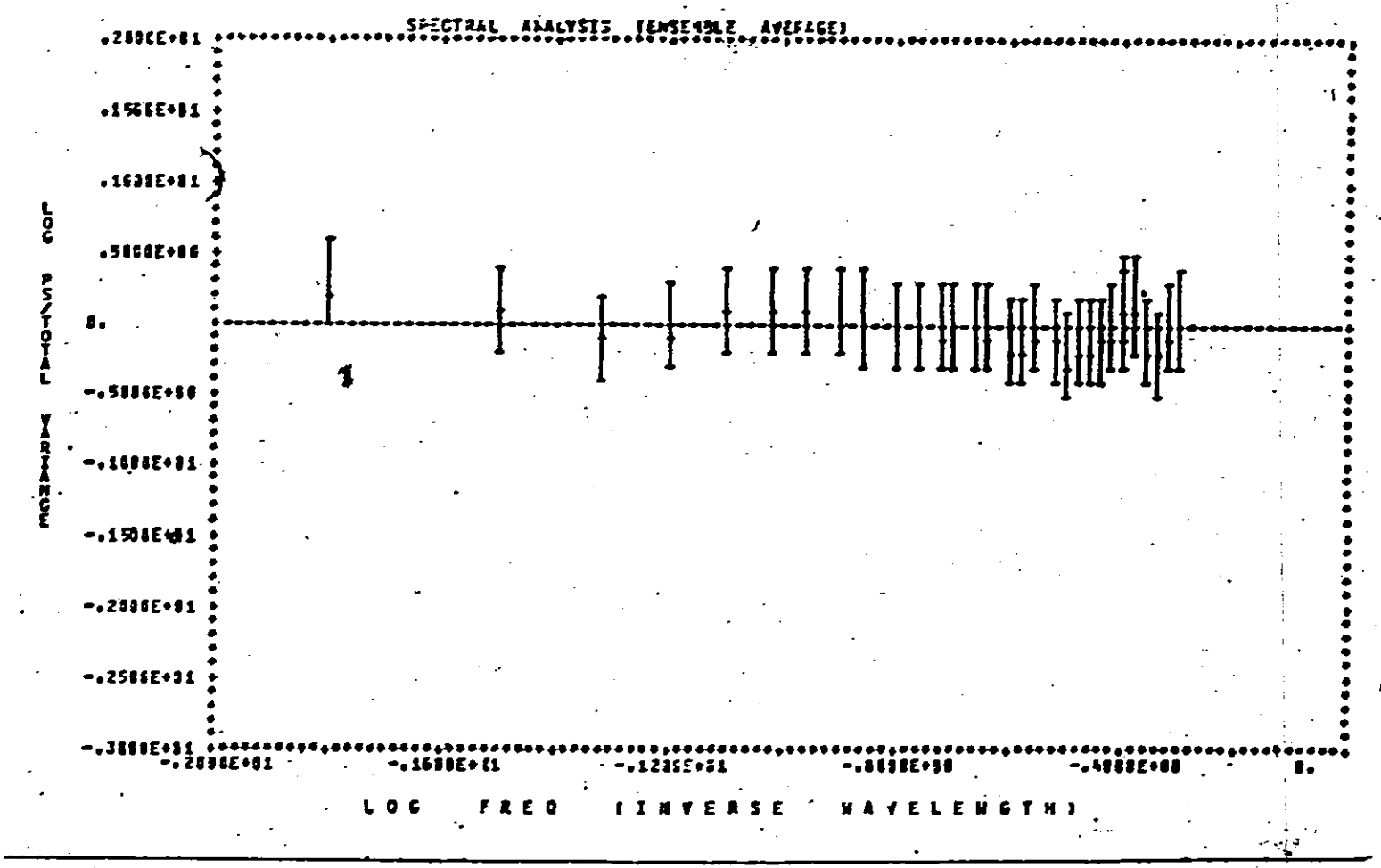
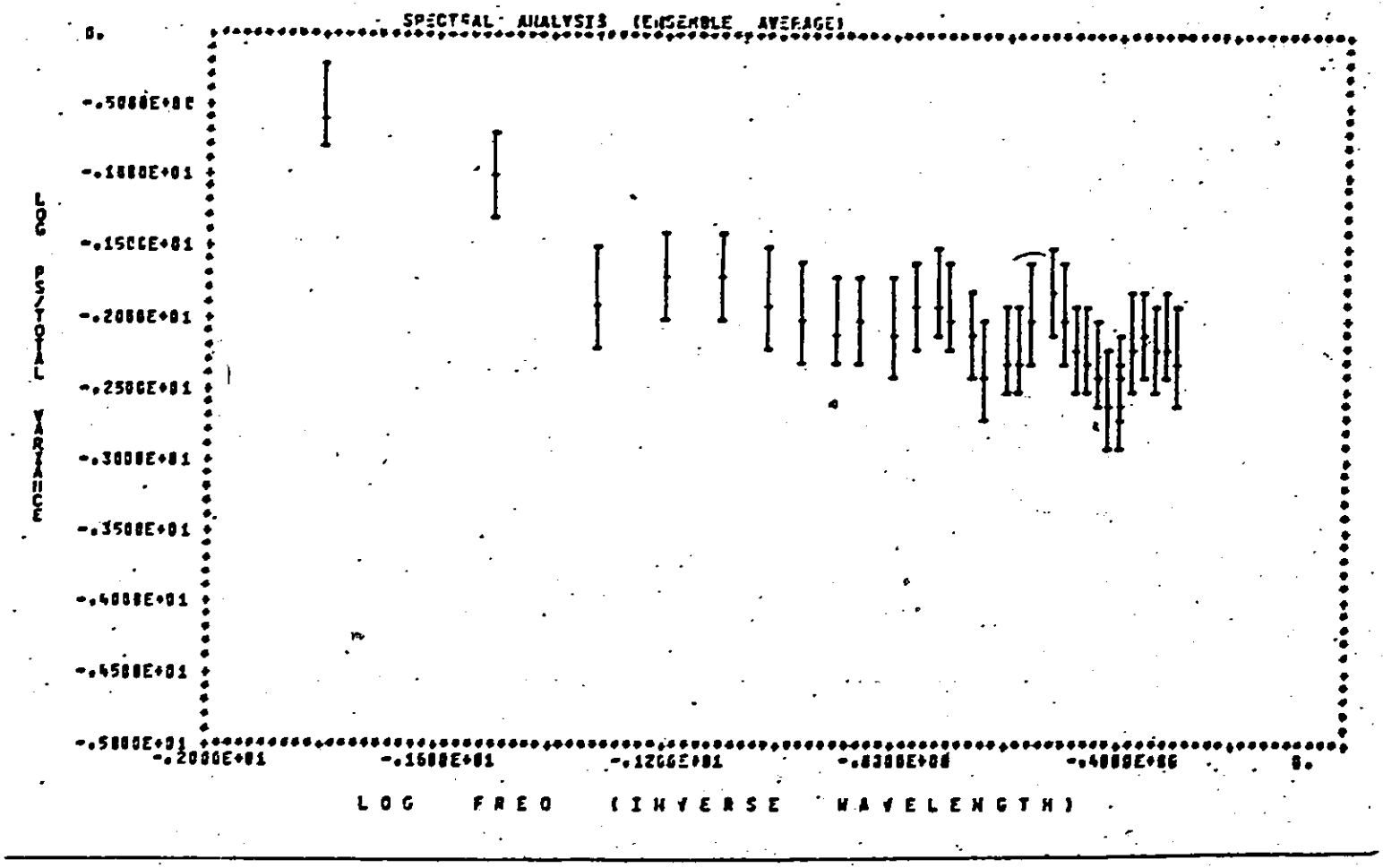

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
.2888E+01
.1568E+01
.1638E+01
.5888E+00
0.
-.5888E+00
-.1688E+01
-.1568E+01
-.2888E+01
-.2568E+01
-.3888E+01
-.2888E+01
-.1688E+01
-.1235E+01
-.8888E+00
-.4888E+00
0.
LOG FREQ (INVERSE WAVELENGTH)
LOG SPECTRAL VARIANCE

Figure 21

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H *R. minutum*


SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
LOG SPECTRAL VARIANCE
0.
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-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1500E+01
-.1000E+01
-.5000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 22

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H NO_2

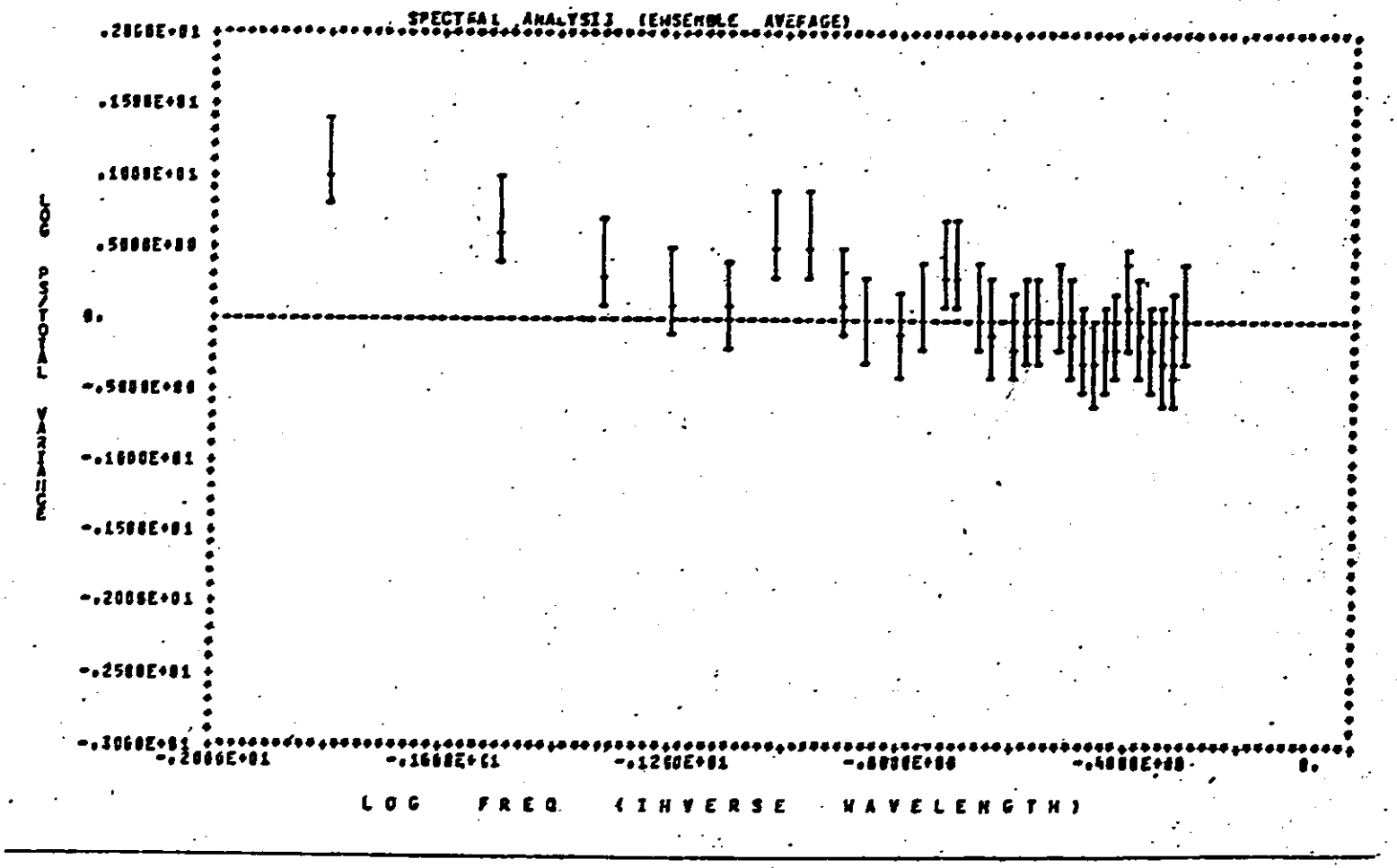

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
.2000E+01
.1500E+01
.1000E+01
.5000E+00
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.2000E+01
-.1500E+01
-.1000E+01
-.5000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)
LOG SPECTRAL VARIANCE

Figure 23

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H *C. sphagnicola*

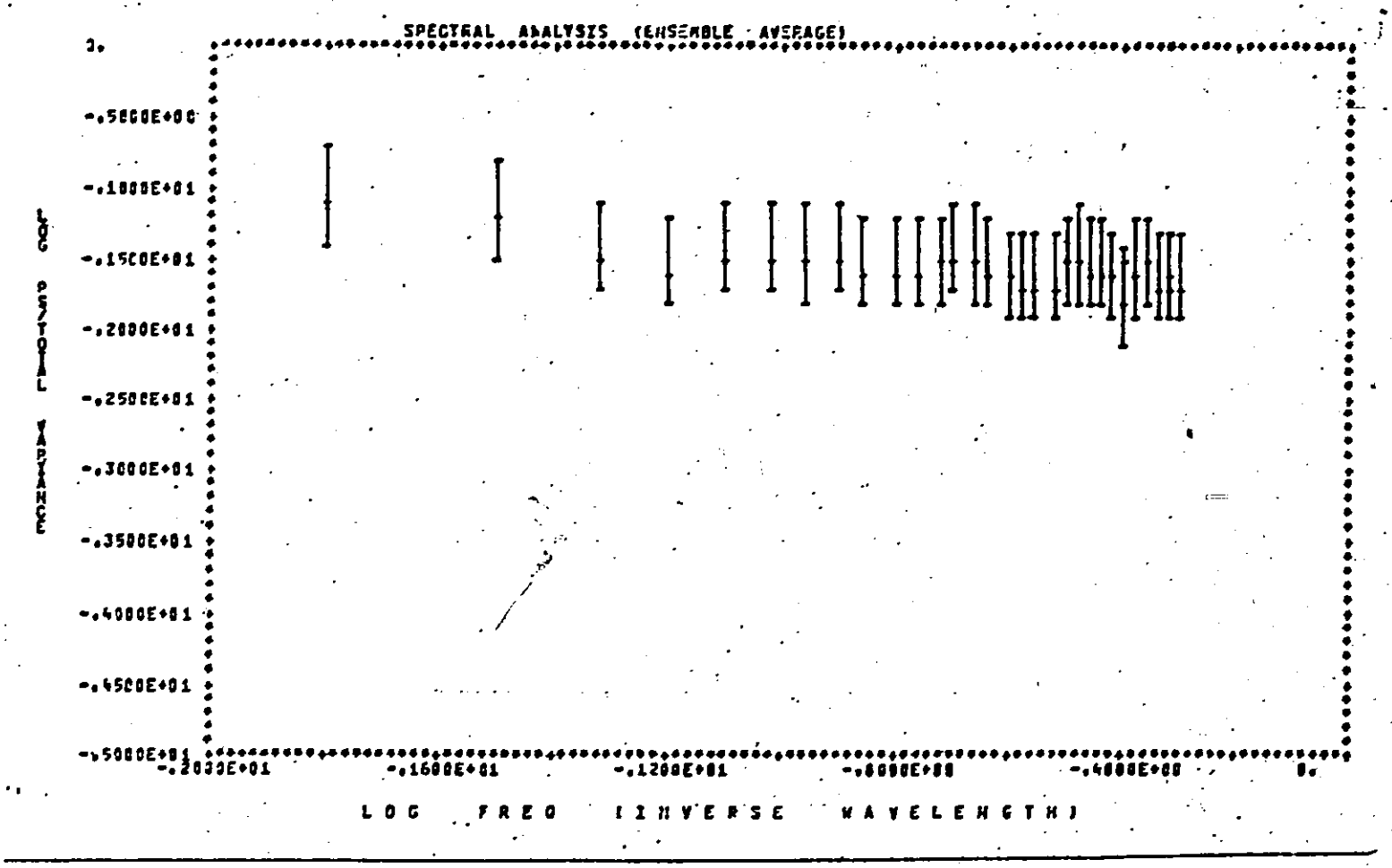

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
LOG SPECTRAL VARIANCE
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 24

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H *Chlorella vulgaris*

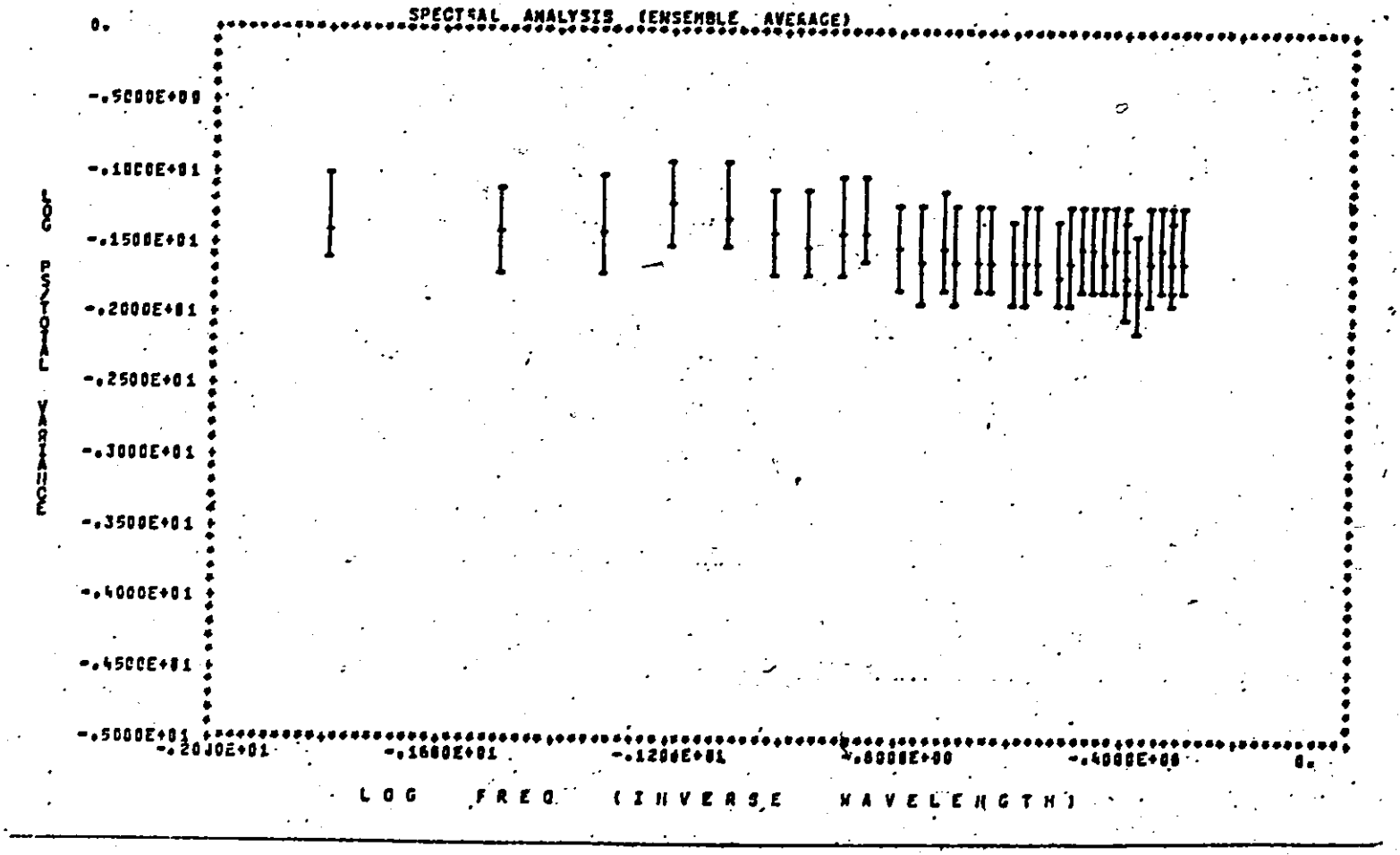
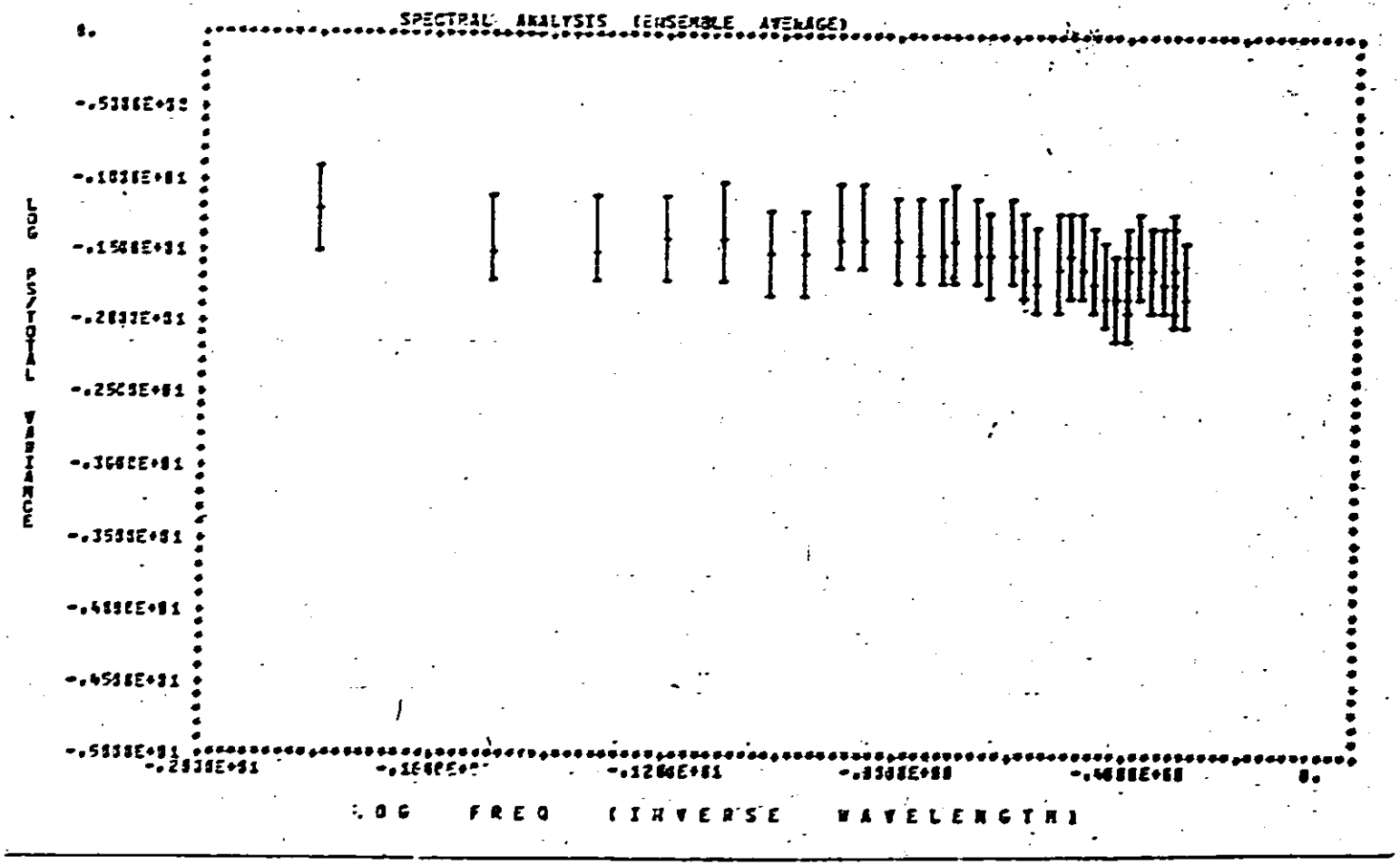

SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
0.
-.5000E+00
-.1000E+01
-.1500E+01
-.2000E+01
-.2500E+01
-.3000E+01
-.3500E+01
-.4000E+01
-.4500E+01
-.5000E+01
LOG SPECTRAL DENSITY
-.2000E+01
-.1600E+01
-.1200E+01
-.8000E+00
-.4000E+00
0.
LOG FREQ (INVERSE WAVELENGTH)

Figure 25

Pooled Spectral Analysis

Pooled variance estimates (with 95% confidence limits) July 20, 1976 transects E-H *O. borgei*


SPECTRAL ANALYSIS (ENSEMBLE AVERAGE)
LOG SPECTRAL VARIANCE
LOG FREQ (INVERSE WAVELENGTH)

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