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Spatial heterogeneity in the plankton community of an ice covered reservoir.

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SPATIAL HETEROGENEITY IN THE PLANKTON COMMUNITY OF AN ICE COVERED RESERVOIR

A Thesis

Presented to the

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In Partial Fulfillment of the

Requirements for the Degree Master of Arts

University of Nebraska at Omaha

by

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THESIS ACCEPTANCE

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30 July 1981
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INTRODUCTION

Types and Significance of Spatial Pattern

Spatial pattern is of significance to many aspects of ecological investigations, so that ecologists are concerned both with the structure and dynamics of a population, as well as population distribution in space. With the exception of very small bodies of water, most aquatic habitats present the ecologist with unique and difficult sampling problems (UNESCO, 1968). He does not have direct access to the organisms of his study and thus cannot make direct observations on their reaction to his surface operated sampling gear. Because of this, striking a balance between the adequacy and the cost of the sampling methods becomes somewhat of a problem. The problem is intensified when in the design of a sampling program, the investigator must consider the spatial distribution of the population, with regards to minimizing errors due to sampling areas not representative of the population or to taking too few a number of samples to adequately describe a spatially variable population.

Small scale distributions are of interest to investigators concerned with the effects of the physical and biological environment on individuals and populations. This would include the effects of competition, the interpretation of population dynamics, and the modeling of relationships between population densities and factors of mortality (ex. predator-prey, host-parasite, etc.). Furthermore, spatial heterogeneity is becoming increasingly recognized as an important factor in

maintaining the stability of populations and communities (Huffaker, 1958; May, 1973; Steele, 1974).

The spatial patterns of populations can be categorized into three basic types of distributions; uniform, random, and aggregated. These categories are not static and should be thought of as forming a continuum from the uniform to the aggregated pattern. In a random distribution, the location of one individual does not affect the probability of finding another individual nearby, while in an aggregated distribution, the location of one individual increases the probability of finding another nearby. Aggregated populations are often referred to as being clumped, patchy, contagious, or overdispersed.

To describe the position of populations on the above continuum, statistical methods involving the variance in a group of samples are used. Using these methods, it has been shown that many populations tend to be aggregated, and that uniform and random populations are less frequently found (Kershaw, 1964).

Previous Investigations

Discontinuity in the vertical profile of plankton has long been recognized by aquatic ecologists. This situation is not surprising, considering that the vertical dimensions of lakes and oceans are marked by variations in temperature, light extinction, density gradients, and nutrient concentrations. However, horizontal distributions are harder to explain and many limnologists have assumed the surface mixed layers of lakes to be homogeneous and the plankton random in distribution (Hutchinson, 1961). This has been the case even though some early

studies have shown a substantial degree of variability in replicate plankton samples drawn over small distances.

"Swarms" or aggregates of plankton and an avoidance of shore by Cladocera were noticed by several investigators at the turn of the century (Ward, 1896; Huitfeldt-Kaas, 1898; Reighard, 1898; Burckhardt, 1910), although little attention was given them because of their supposed infrequent occurrence. One of the earliest studies to specifically concentrate on the horizontal variability in plankton was that of Moberg (1918) on Devils Lake (North Dakota). He found that from stations located 100-200 meters apart, the average variability in density of crustacea was $\pm$ 50 percent of the mean. This variability was thought to be a constant phenomena because of reoccurrence in samples taken during three consecutive summers.

Other studies on the variability between successive net hauls were performed in the marine environment which gave basically the same results as Moberg (Herdman, 1922; Gardiner and Graham, 1925; Gardiner, 1931; Winsor and Walford, 1936). The results of these studies were suspect because the variance in sample densities may have been due to the plankton net sampling different quantities of water. Because of this, Barnes (1949) used a pump in his study which accurately gave samples of equal volume. His results were similar to the above and so gave definite evidence of an aggregated population.

Several studies were made on fresh-water habitats that compared the variance in a set of samples to the mean of the set (Ricker, 1937; Langford, 1938; Tonolli, 1949). In all the studies, there were instances found where the variance was significantly larger than the mean, giving evidence to an aggregation of individuals.

Barnes and Marshall (1951) were the first investigators to obtain a large enough set of samples to produce a frequency distribution from their data. They found that when densities were low, the distributions closely approached the Poisson distribution, indicating randomness. At higher densities the Neyman Type A and Thomas series gave a better fit, indicating an aggregated population. They suggested that the variable populations were associated with different water masses that had maintained their identity over a period of time during which the populations developed.

Cassie (1959a) used frequency distributions in investigating the small scale pattern of plankton and found that when densities were high, the populations were significantly aggregated. But in the 18 sets of samples that had densities below 3 per sample, only 6 gave evidence of aggregation. He showed that at low densities both random and aggregated frequency distributions were quite similar in shape, and at densities below unity it may take several hundred samples before significant departures from randomness can be detected. In another set of experiments (Cassie, 1959b; Cassie, 1960), Cassie sampled a mixing zone from harbor to ocean waters. Using regression and covariance analysis, he found plankton densities to be correlated to temperature and salinity, and that there is reason to believe that physical inhomogeneities in the open ocean may be of sufficient magnitude to influence the small scale spatial pattern of plankton.

Weibe (1970) used an empirical method in analyzing his data on the spatial pattern of marine zooplankton. His approach was to quantitatively assess patchiness in terms of its structural components. His

approach was to quantitatively assess patchiness in terms of its structural components. His results indicated that patches were roughly circular in dimension with an average radius of 38-73 meters. The patches were distributed randomly with an average patch density of 2.6-5.1 times the background density. Other examples of this approach can be found in the work of Ziemann (1970) and Fasham et al. (1974).

Early work in the small-scale distribution of phytoplankton was hindered by the errors associated with laboratory methods of sub-sampling and counting samples. Because of these errors, only generalized statements on the phytoplankton appearing to have a more uniform distribution than the zooplankton could be made (Moberg, 1918; Welch, 1935).

Later investigations correlated accumulations of phytoplankton with wind induced water currents (Sverdrup and Allen, 1939; Neess, 1949; Verduin, 1951; Wohlschla and Hasler, 1951; Oliver, 1952; Loeffler, 1954). George and Heaney (1978) found that during periods of calm winds (below 50 Km day^{-1}) the motile dinoflagelate Ceratium, produced extreme small scale variations in density. Wind speeds above 100 Km day^{-1} were sufficient to break down these patches.

The small-scale distribution of phytoplankton has been investigated by several authors (McAlice, 1970; Harris and Smith, 1977; Richards and Happey-Wood, 1979). These studies have reported aggregation of phytoplankton on scales ranging from 10 centimeters to 10 meters. Some of these studies have been criticized by Richerson et al. (1978) on the basis that the sub-sampling and counting error may be large relative to the in situ variance, requiring analysis of variance techniques to separate the error terms. Richerson suggested that small-scale patchi-

ness in small basins is likely to occur only where those basins are subjected to a strong external source of variation, as in the investigation of Harris and Smith (1977).

The above investigations were limited in the range of variability that could be studied by the available techniques used in processing data. With new methods of continuous *in vivo* flurometric measurements of chlorophyll, and the data handling techniques of spectral analysis, this range has been expanded considerably. These techniques have been applied to the phytoplankton of oceans by Platt *et al.* (1970), Platt (1972), Platt and Denman (1975), Denman (1975), and Denman (1976), and to the phytoplankton of lakes by Powell *et al.* (1975), Richerson *et al.* (1975), Abbott and Coil (1978), and Abbott *et al.* (1980). The investigations have shown that the largest variability occur on the largest scales. At scales between 40 and 1000 meters, the coherence between the temperature and chlorophyll spectra was found to be high, indicating that the phytoplankton behave as a passive contaminant of fluid motion.

Aims of the Present Investigation

By definition, the plankton community floats passively, or exhibits limited locomotion in the water column. This would imply that the density of the plankton at any one point is as much a consequence of drifting on turbulent water currents, as it is on their own productivity and mortality. The pattern of plankton then is controlled through the interaction of the physical transport processes of water motion and the environmental factors promoting growth under various physical, chemical, and biological conditions. The importance of water currents and turbulance has been substantiated by past investigations.

During winter conditions, basins with an ice cover exhibit reduced turbulance and current flows, which is primarily due to the absence of wind stress on the basin. Under these conditions the magnitude of the small-scale spatial pattern away from randomness may be great, with the biological and environmental factors predominating over the physical transport system.

This study will investigate the small-scale horizontal distribution of the plankton community in an ice covered reservoir at a single point in time. Populations of both the phytoplankton and zooplankton will be considered. The basin under study is Papio Creek Site 16. It is a small, shallow, eutrophic reservoir, constructed by the Army Corps of Engineers in 1973 for the multi-purpose of flood control and recreation (Table I). The objectives of the investigation are:

1. Describe the small-scale pattern of the plankton community with respect to any departure from randomness.
2. Quantify any aggregated populations with respect to patch size, patch density, background density, and patch frequency.
3. Correlate the occurrence of individuals interspecifically and with environmental factors.

Table I

Morphometric features of Papio Creek Site 16.

This table was obtained from the Army Corps of Engineers, 1977.

Dimension	Value
Maximum depth	10.4 m
Mean depth	3.4 m
Maximum length	1,432 m
Mean width	381 m
Shorelength	8,047 m
Shoreline development	3.07
Surface area	5.46×10^5 m^2
Volume	1.86×10^6 m^3
Watershed drainage area	1.55×10^7 m^2

MATERIALS AND METHODS

Sampling Procedure

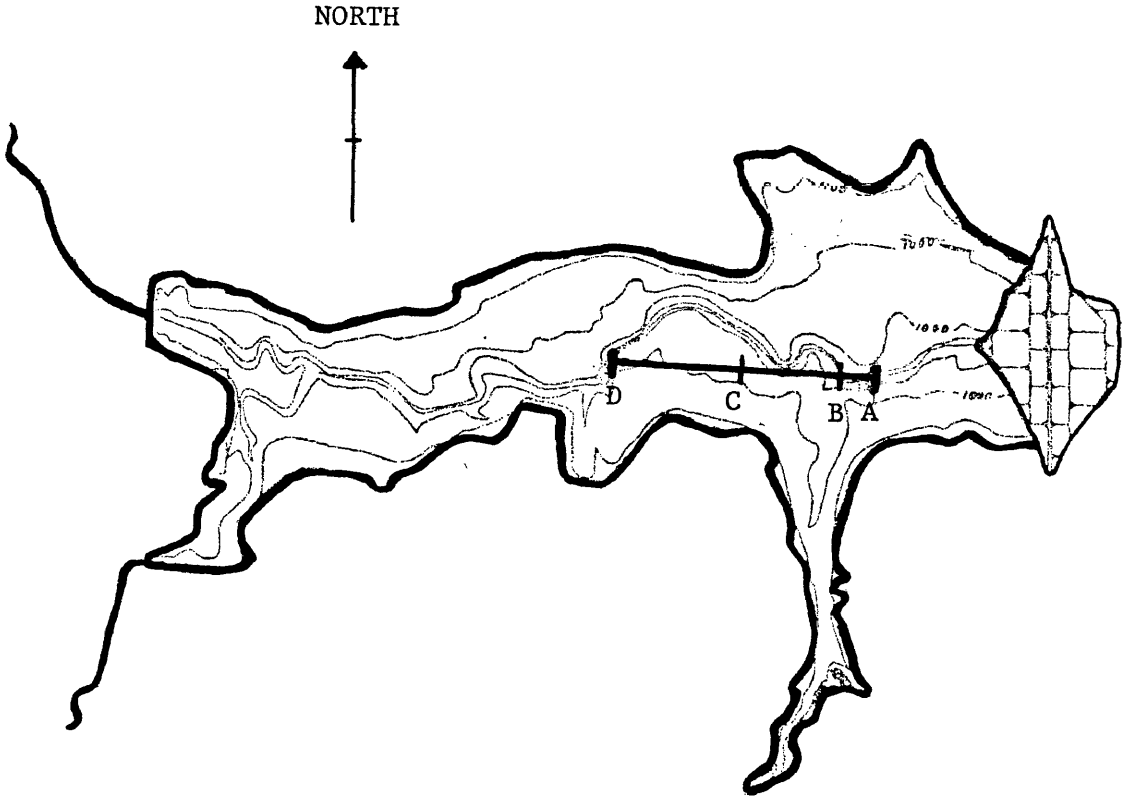
Plankton samples were collected from 10:00 A.M. to 2:00 P.M. on February 15, 1981 along a transect running roughly parallel to the main axis of the reservoir, Figure 1. The samples were taken at a depth of 2 meters below the ice, over water ranging from 4.2 to 8.5 meters in depth. The transect line was broken into three subtransects, each of which were analyzed separately for spatial patterns. Transect A-B consisted of 40 stations located at 1 meter intervals. Transect A-C consisted of 40 stations at 5 meter intervals, giving a sampling distance of 195 meters. The length of transect A-D was shortened because of unsafe ice conditions and consisted of 28 stations at 15 meter intervals, for a total sampling distance of 405 meters.

Holes were cut in the ice with a hand powered Swedish ice auger, which allowed the passage of a 3 liter Van Dorn sampling bottle. Since the bottle was closed at a 2 meter depth, there should have been no disturbance in the water column at that depth caused by cutting the holes through the ice. Similarly, the 1 meter sampling interval of transect A-B was thought to be the minimum distance at which the operation of the sampling bottle would not disturb the water parcels at adjacent stations.

The samples were filtered through a number 12 (119 micron) plankton net and preserved with 5 percent formalin for zooplankton enumeration.

Figure 1

Position of sampling transect and stations
in Papio Creek Site 16.



TRANSECT	LENGTH	SAMPLE INTERVAL	STATION NUMBER
A-B	40 M	1 M	1-40
A-C	195 M	5 M	41-71
A-D	405 M	15 M	72-85

Four hundred milliliters of the filtrate passing through the net were collected, preserved with 4 milliliters of Lugol's solution, and transferred to sedimentation jars for the enumeration of the phytoplankton.

The entire 3 liter zooplankton sample was counted, which greatly minimized laboratory sampling error. The phytoplankton were counted in a Sedgwick-Rafter cell using a two stage sampling scheme in order to maximize counting time against counting error (McAlice, 1971). This system consisted of counting the individuals in 30 randomly picked microscope fields in each of 3 separate aliquots of the Sedgwick-Rafter cell for each sample.

Conductivity, pH, and oxygen were recorded at each station with a YSI model 54 oxygen meter, Fisher model 150 Accumet pH meter, and a Chemtrix type 700 conductivity meter. Temperature profiles were also recorded at each station and examined for any indications of currents operating below the ice (Krumholz and Cole, 1959; Stewart, 1972).

Statistical Methods

The initial step in analyzing the data will be to examine the densities of each species along the transect, with the intent of locating any spatial pattern away from randomness. This will require the use of different procedures for the zooplankton and phytoplankton, since the phytoplankton samples were sub-sampled in the laboratory during the counting procedure. This will produce an additional error into the phytoplankton counts that is absent in the zooplankton counts.

I. Zooplankton

There are two standard tests used for the detection of nonran-

domness, the $\chi^2(\bar{x}=s^2)$ test and the $\chi^2(0=E)$ test. The first test is the simplest and most common method and has its origins with R. A. Fisher (Fisher et al. 1922). It compares the sample mean to the sample variance. The sample mean and variance are seldom equal, but if their magnitudes differ greatly, then nonrandomness is suspected. The test statistic is:

$$D = \frac{\Sigma(x-\bar{x})^2}{\bar{x}} = \frac{(n-1)s^2}{\bar{x}} ,$$

where D approximates a chi-square distribution with n-1 degrees of freedom, and where n is the number of observations. This test statistic has often been called the index of dispersion.

The second test, $\chi^2(0=E)$, is one that compares the observed number of individuals in a sample to the expected number if the sample were random, and which are obtained from the Poisson series:

$$P_x = e^{-\bar{x}} \frac{\bar{x}^x}{x!} .$$

The test statistic used for the comparison is given by Fisher (1950):

$$\chi^2 = 2\Sigma 0 \ln (O/E),$$

where 0 is the observed number, E is the expected number obtained from the Poisson series, and with degrees of freedom 2 less than the number of classes used in the frequency distribution.

Cassie (1971) stated that where sufficient data are available, the $\chi^2(0=E)$ test is the more critical one, while Cochran (1954) reported that the $\chi^2(\bar{x}=s^2)$ will more often correctly result in the rejection of the null hypothesis than the $\chi^2(0=E)$ test. Although the $\chi^2(\bar{x}=s^2)$ test is sensitive with regards to aggregation, it will not detect certain types of skew distributions (Barnes and Marshal, 1951). Despite these

technicalities, the $\chi^2(\bar{x}=s^2)$ test is a good one in practice, and the ease in which it is applied outweighs any slight inadequacies (Cassie, 1971).

Both tests were run on the present data and the results agreed with Cochran, in that the $\chi^2(\bar{x}=s^w)$ test more often resulted in the rejection of the null hypothesis. This would tend to indicate that there was insufficient data for the more critical test. Because of this, only the $\chi^2(\bar{x}=s^2)$ test will be used in the remainder of the paper.

Since previous studies of spatial patterns in ecology have shown a direction away from randomness $(\bar{x}=s^2)$ towards overdispersion $(\bar{x}<s^2)$, the test of significance used for the above procedure is a one tailed test, H_o: $\bar{x} = s^2$ against H_1: $\bar{x} < s^2$, with the rejection criteria of $P(\chi^2) \leq 0.05$.

The success of all methods used to detect non-randomness are dependent on the size of the sample used (Kershaw, 1964). The variance in a sample from an aggregated population will be the greatest when the size of the samples taken equals the size of the aggregates or clumps of organisms. This effect is built into the methods of block size analysis of variance and is a useful technique where data are too complex or the degree of aggregation is not apparent to the eye. The technique involves the laying out and enumerating a set of samples along a transect line, after which larger samples are made by combining adjacent samples into adjacent pairs of samples, adjacent four samples, adjacent eight samples, etc. An analysis of variance is conducted on the data with the variance partitioned between the different block sizes created. When a graph of mean squares to block size is constructed, peaks in the graph will indi-

cate aggregation with the size of aggregation indicated by the block size corresponding to the peak. Reviews of this methodology can be found in Greig Smith (1961), Kershaw (1964), Hill (1972), and Poole (1974).

A second technique used to quantify the dimensions of aggregation will be the empirical method of Weibe (1970). An aggregation will be defined as a concentration of individuals exceeding a central value in the data set. Since the data are not normally distributed, the median will be used as this central value. When a plot is made of the densities of individuals against distance, it will be possible to estimate the frequency of patches by counting the number of values, or sets of values, above the median with adjacent values below the median. From this graph, the length of each patch can be measured, as can the distance between patches. Finally, patch and background densities were determined from the average number of individuals above and below the median. In order to compare the results between species, the densities were expressed as a ratio, Patch density : background density.

Correlation coefficients were calculated between species in order to find groups of species with like responses to environmental and biological factors. The Pearson product-moment correlation coefficient was used for this comparison.

II. Phytoplankton

Since the phytoplankton densities are mean estimates for each sampling station, the appropriate technique for finding significant differences between them is the analysis of variance. The experimental

design used for this analysis is a one-way hierarchical classification of fields within aliquots within stations. The model being:

$$X_{ijk} = N + A_i + B_{ij} + \varepsilon_{ijk},$$

$$i = 1...a,\ j = 1...b,\ k = 1...n,$$

$$A_i = \mathcal{N}(0, \sigma_A),\ B_{ij} = \mathcal{N}(0, \sigma_B),\ \varepsilon_{ijk} = \mathcal{N}(0, \sigma)$$

where ε is the population mean, A_i refers to the effects of the stations, B_{ij} refers to the effects of the aliquots, and X_{ijk} refers to the error associated with the fields (Snedecor and Cochran, 1937). The test of the null hypothesis of no difference between stations is given by:

$$F = \frac{\text{Station mean square}}{\text{Error mean square}}$$

The raw data were transformed to $\sqrt{x + 1}$ in order to stabilize the variances, and normalize the data (Barnes, 1952).

Where the analysis of variance indicated that a significant difference exists among the station means, Tukey's w-test was used to show which means differed significantly. Tukey's test was chosen because it is more conservative than Duncan's or Student-Newman-Keul's test, and has an error rate that applies on an experimentwise, rather than a per-comparison basis. The procedure requires a single value for judging the significance of the differences between means. This value is computed from:

$$W = q\ (t,f)\ s_x$$

where q is obtained from a table of upper percentage points of the studentized range (Steele and Torrie, 1960, p. 444) for t treatments and f error degrees of freedom, and s_x is estimated from the error mean square.

Summary statistics, the $\chi^2(\bar{x} = s^2)$ test, the block size analysis of variance, and correlation coefficients were determined as in the zooplankton data, with the total collection counts for each sample being used in the calculations. In the empirical determination of the spatial dimensions of the phytoplankton, total collection counts were converted to number per milliliter.

RESULTS

Physical Data

Little variation was found in the pH, oxygen, temperature, and conductivity readings along the sampling transects. Conductivity ranged from 240-250 microhmos/cm, temperature from 2.5-3.0 ^{o}C, pH from 7.8-8.0, and oxygen from 10.4-10.8 mg/l. The sensitivity available in the recording instruments was such that discerning real variations within the above ranges was impossible.

A plot of isotherms, Figure 2, shows a wave like pattern, which may be the result of one or several mechanisms. The reservoir had partially thawed 3 weeks prior to the investigation, with the lower reservoir losing its ice cover and the upper reservoir remaining in ice. The thaw line in the reservoir fell at the 190 meter mark on the sampling transect. The reservoir then refroze 11 days before the study. The pattern may also reflect internal waves operating within the basin which may have been produced during the windy period of the partial thaw.

Zooplankton Distribution

Densities of the zooplankton along the three sampling transects are given in Figure 3. The plots show a high degree of variability in all three transects. A set of summary statistics for the species is presented in Table II, and Fisher's index of dispersion in Table III. All D-values in transect A-D were highly significant, indicating an aggregated distribution. In transect A-C only the males of *Cyclops*

Figure 2

Temperature isotherms along the sampling transect.

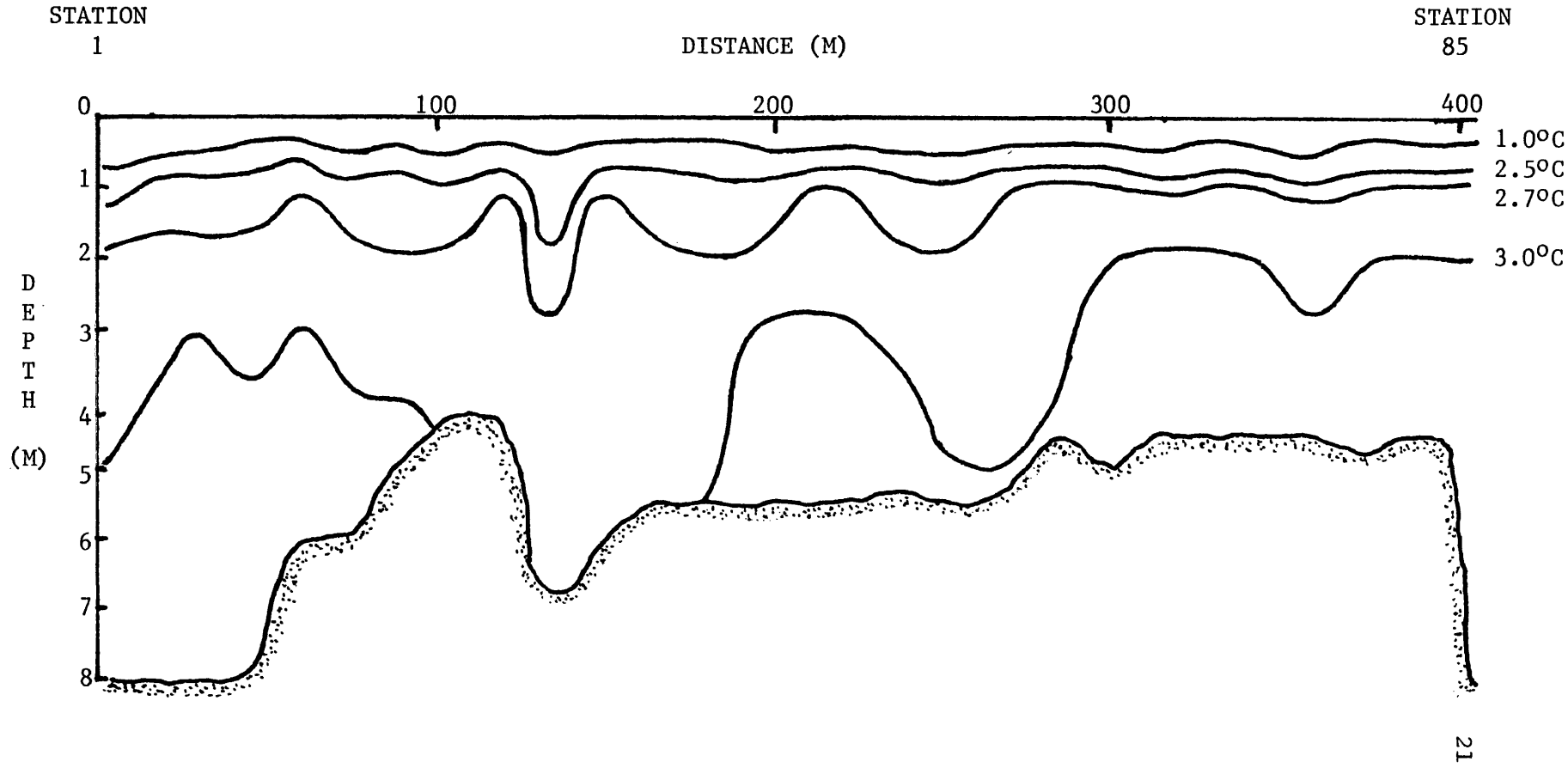
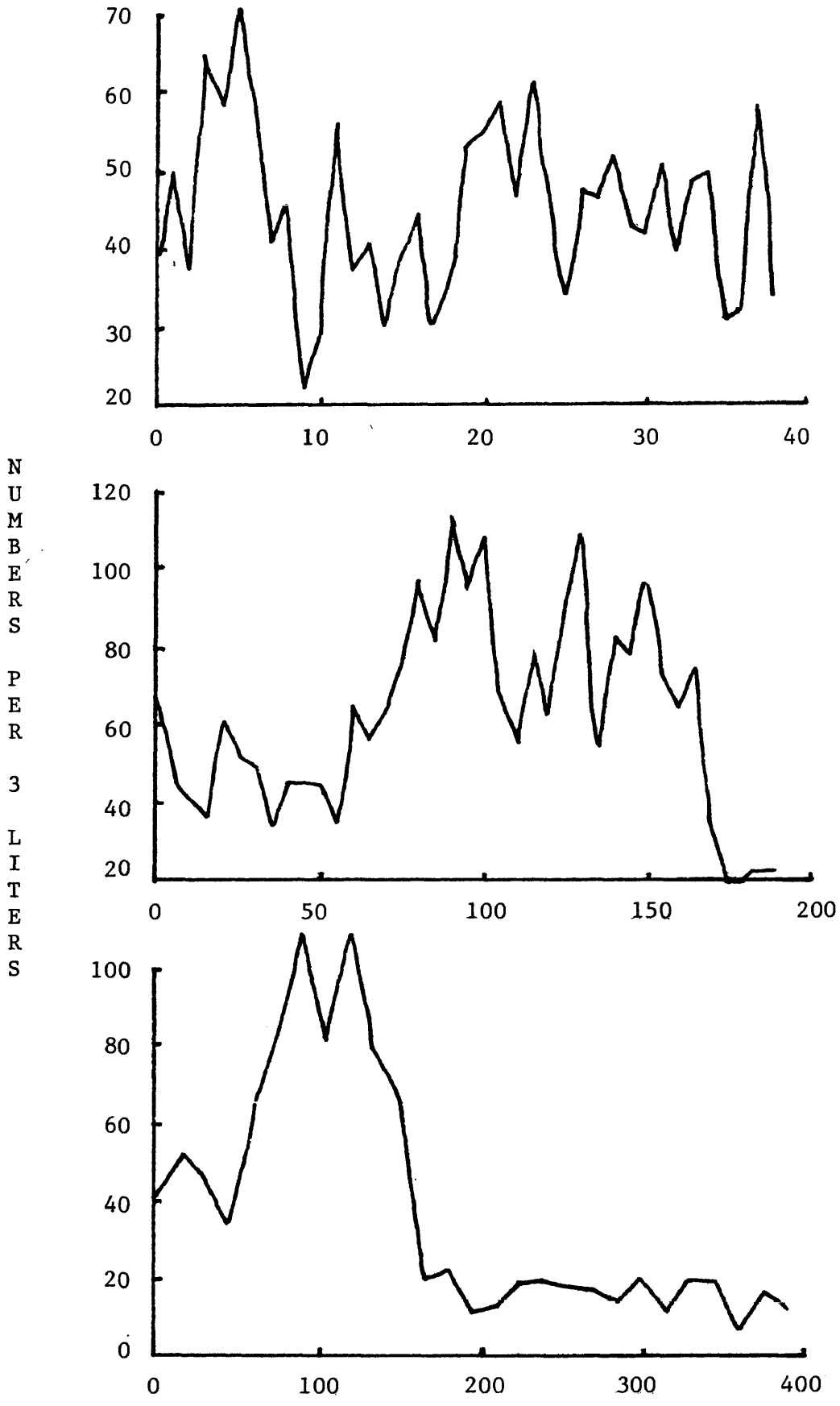

STATION
1
DISTANCE (M)
STATION
85
0
100
200
300
400
1.0°C
2.5°C
2.7°C
3.0°C
DEPTH
(M)
1
2
3
4
5
6
7
8

Figure 3

Densities of Bosmina longirostris in transect A-B (upper), A-C (center), and A-D (lower).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60
50
40
30
20
0
10
20
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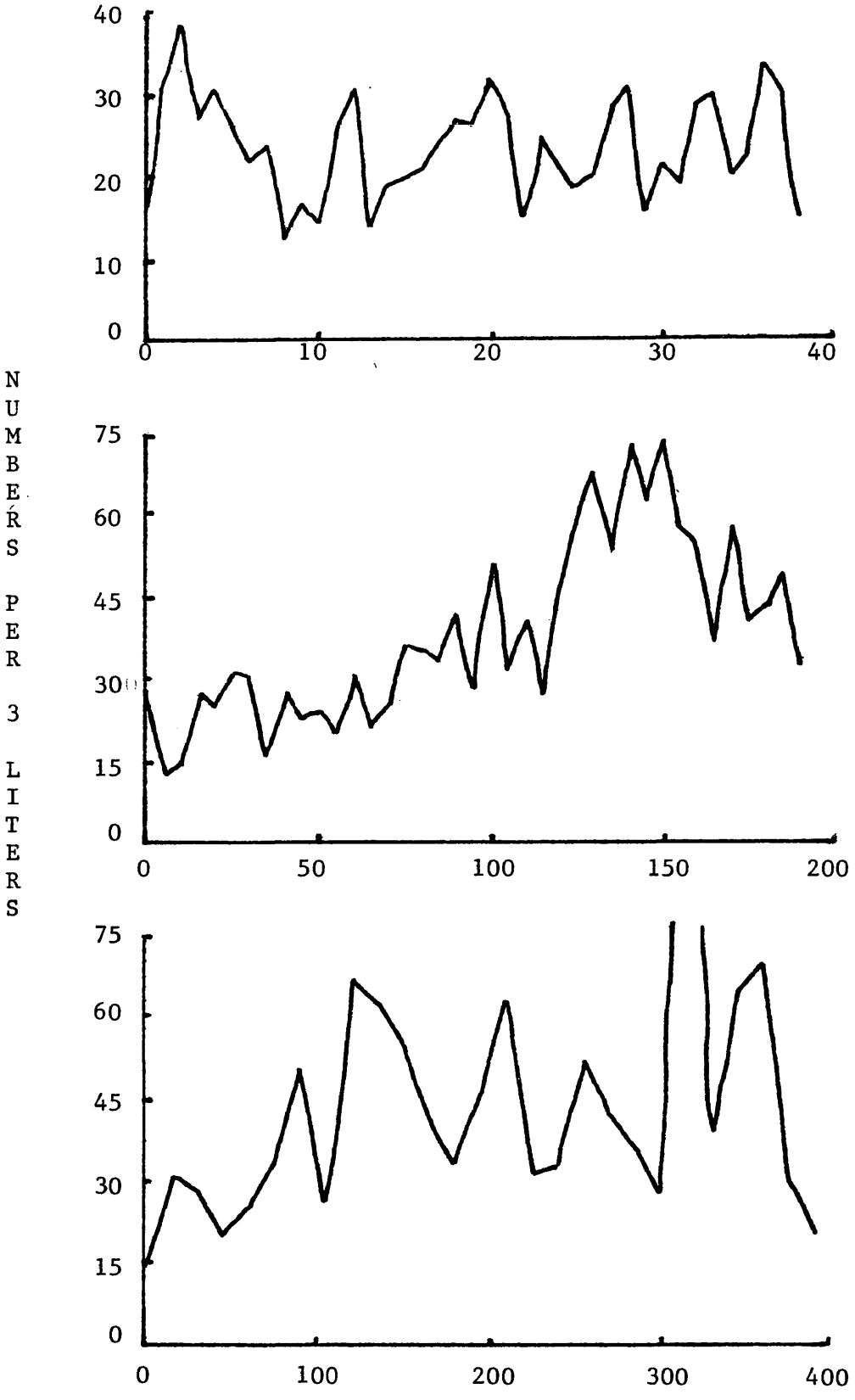
40
120
100
80
60
40
20
0
50
100
150
200
100
80
60
40
20
0
0
100
200
300
400
NUMBERS PER 3 LITERS
DISTANCE (M)

Figure 3 (continued)

Densities of Diaptomus siciloides in transect A-B (upper), A-C (center), and A-D (lower).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20
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0
0
10
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30
40
NUMBERS PER 3 LITERS
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60
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30
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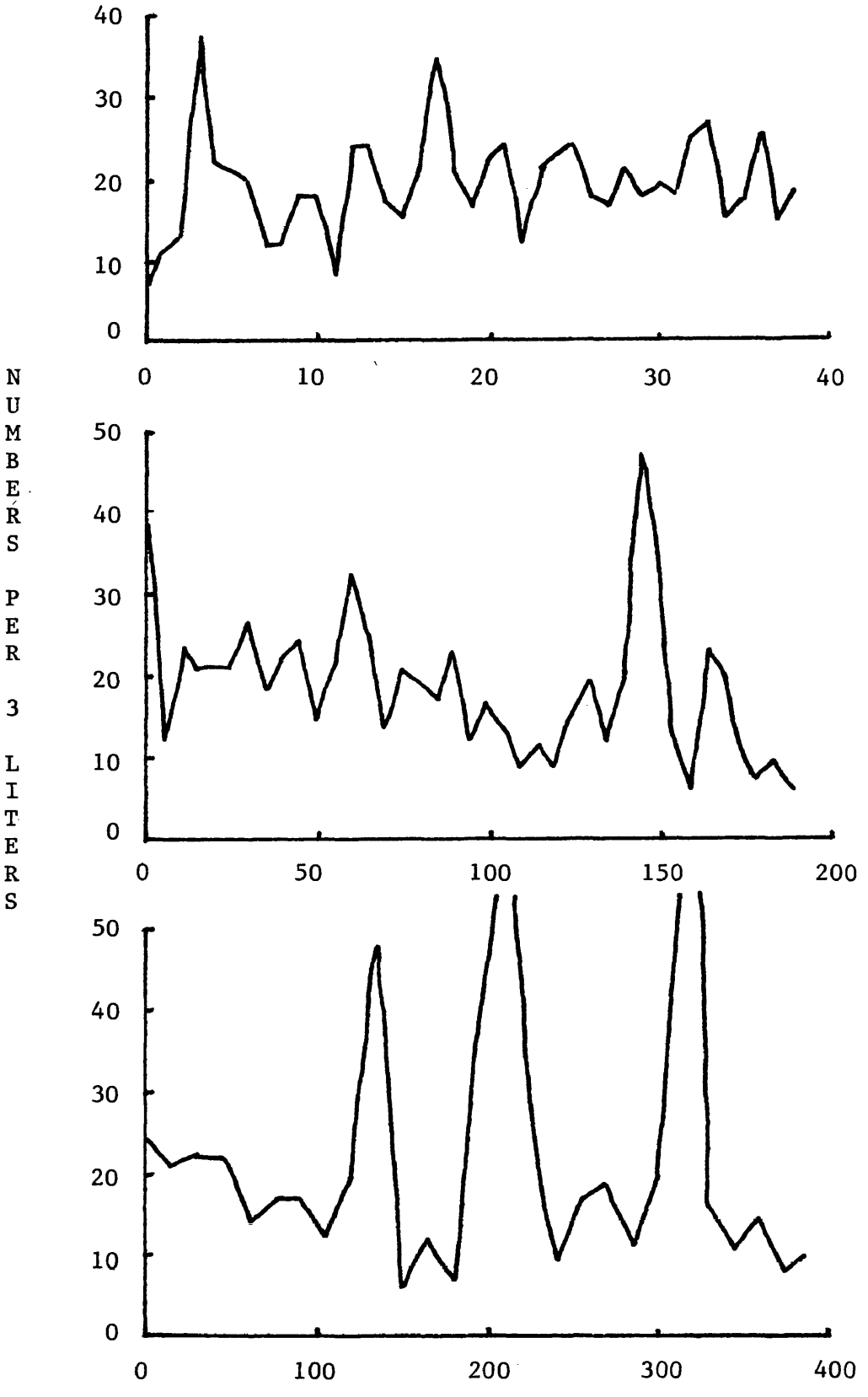
0
0
50
100
150
200
75
60
45
30
15
0
0
100
200
300
400
DISTANCE (M)

Figure 3 (continued)

Densities of *Cyclops vernalis* in transect A-B (upper), A-C (center), and A-D (lower).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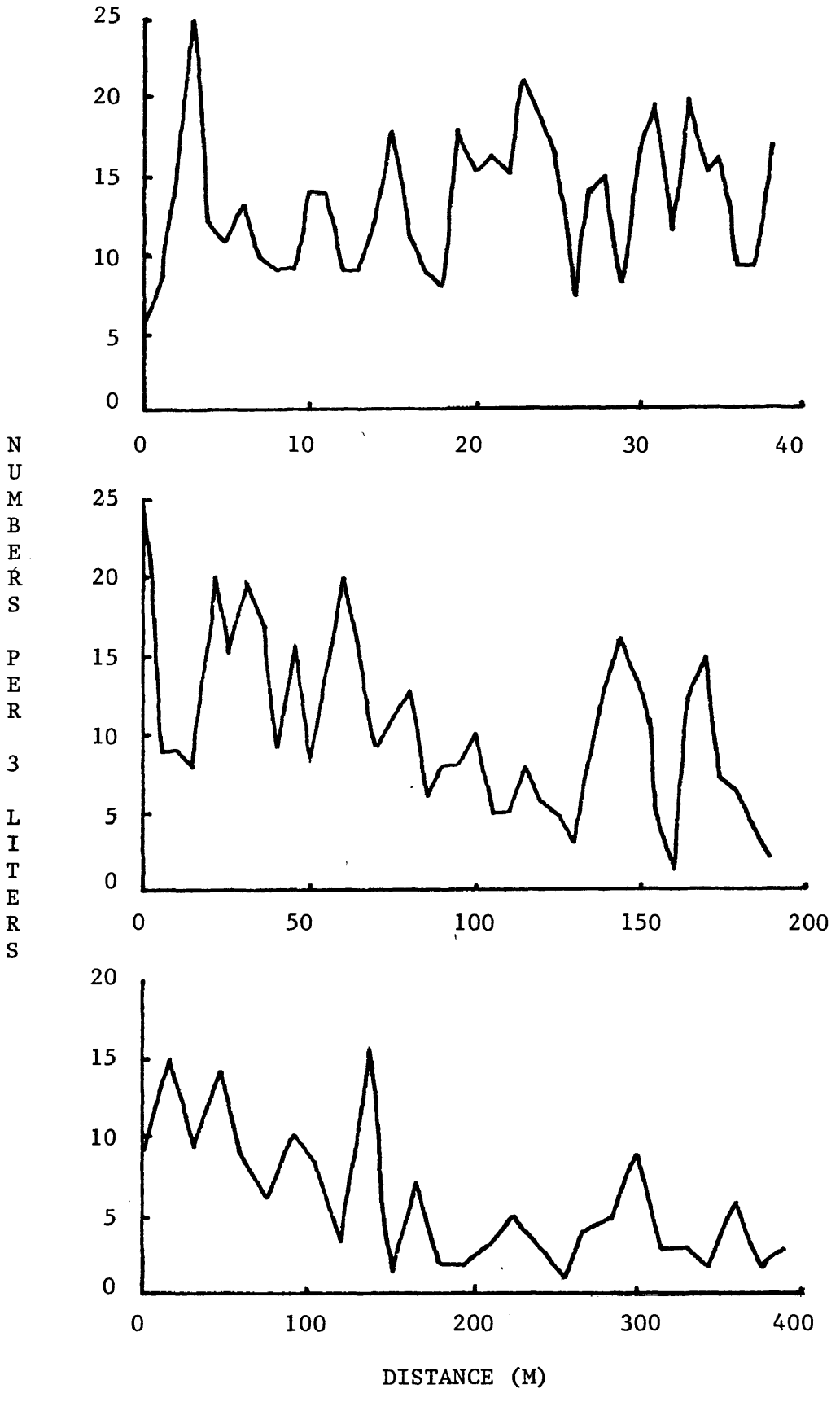
0
0
10
20
30
40
NUMBERS PER 3 LITERS
50
40
30
20
10
0
0
50
100
150
200
50
40
30
20
10
0
0
100
200
300
400
DISTANCE (M)

Figure 3 (continued)

Densities of Asplanchna sp. in transect A-B (upper), A-C (center), and A-D (lower).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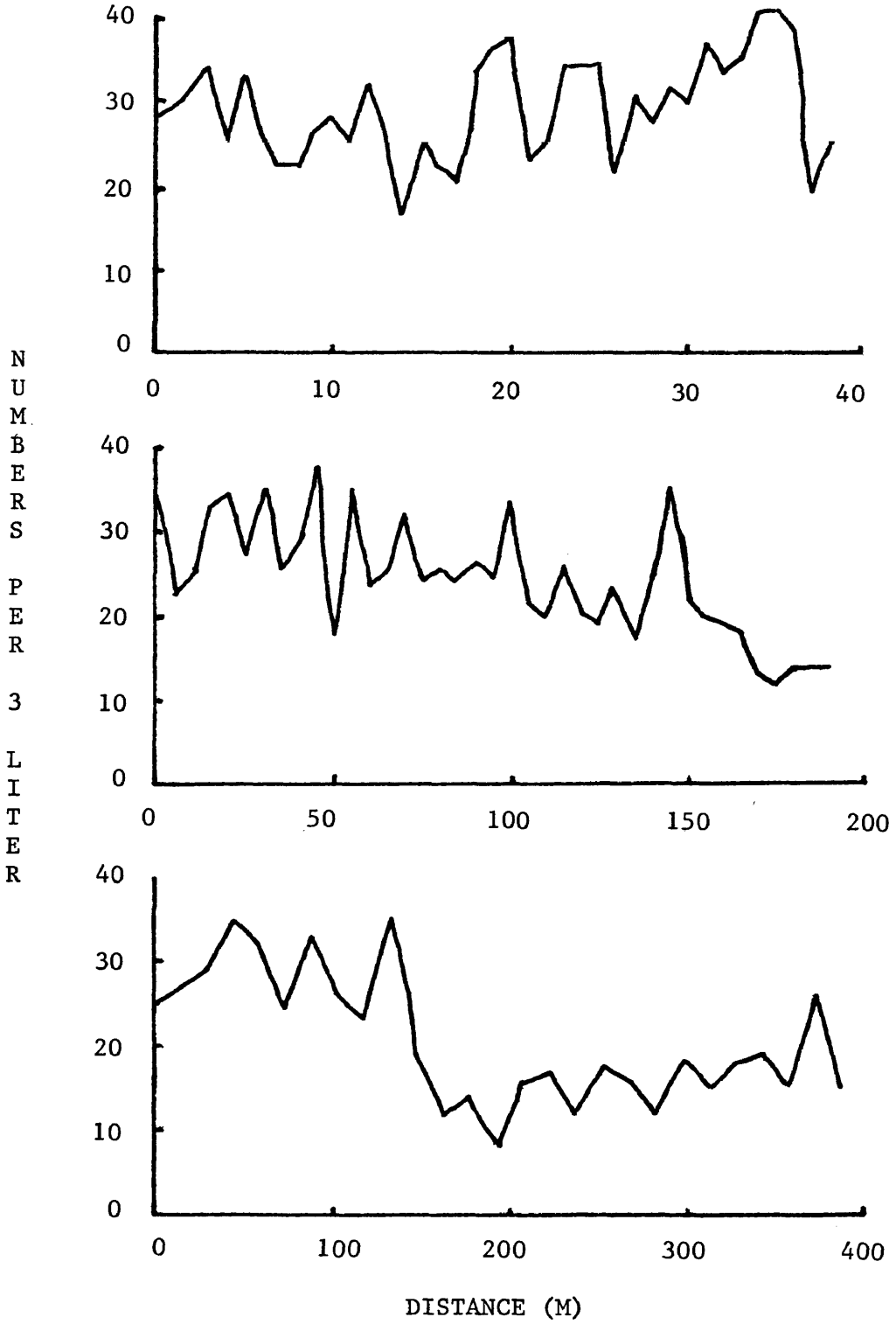
50
100
150
200
20
15
10
5
0
0
100
200
300
400
NUMBERS PER 3 LITERS
DISTANCE (M)

Figure 3 (continued)

Densities of nauplis larva in transect A-B (upper), A-C (center), and A-D (lower).


40
30
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0
0
10
20
30
40
NUMBERS PER 3 LITER
40
30
20
10
0
0
50
100
150
200
40
30
20
10
0
0
100
200
300
400
DISTANCE (M)

Table II

Mean ($\bar{x}$), variance (s^2), range, standard error (SE), and the coefficient of variability (CV) for the zooplankton of transects A-B, A-C, and A-D.

		$\bar{x}$	s^2	Min.-Max.	SE	CV (%)
Transect A-B						
Bosmina	longirostris	44.4	173.2	22- 71	2.2	29.6
Diaptomus	sicilaides	23.7	42.3	12- 34	1.1	27.4
	Male	6.1	13.1	1- 20	0.6	59.8
	Female	13.1	24.9	0- 22	0.8	38.2
	Copepodid	4.1	5.5	1- 12	0.4	57.6
Cyclops	Vernalis	19.2	40.2	7- 38	1.0	33.2
	Male	0.6	0.7	0- 3	0.1	134.4
	Female	7.6	10.7	2- 14	0.5	42.9
	Copepodid	10.9	21.5	3- 28	0.7	42.3
Asplanchna sp.		13.2	19.3	6- 25	0.7	33.4
nauphis llaivae		28.9	37.7	16- 40	1.0	21.3
Transect A-C						
Bosmina	longirostris	61.9	659.1	20-114	4.1	41.4
Diaptomus	sicilaides	38.0	266.6	12- 73	2.6	42.9
	male	13.2	72.6	1- 32	1.4	64.6
	female	20.0	72.2	9- 38	1.4	42.4
	Copepodid	4.4	9.3	0- 12	0.5	69.4
Cyclops	Vernalis	18.9	77.5	6- 48	1.4	46.4
	male	1.1	1.5	0- 5	0.2	110.0
	female	9.1	21.3	2- 23	0.7	50.9
	Copepodid	8.8	20.6	2- 21	0.7	51.6
Asplanchna sp.		10.3	31.3	1- 25	0.9	54.1
nauplis larvae		24.1	48.6	12- 38	1.2	28.9
Transect A-D						
Bosmina	longirostris	37.7	958.5	6-109	5.9	82.1
Diaptomus	sicilaides	45.2	1036.1	14-186	6.2	71.2
	male	11.4	77.8	1- 38	1.7	77.1
	female	25.7	329.8	9-105	3.5	70.5
	Copepodid	8.2	69.5	1- 43	1.6	101.3
Cyclops	Vernalis	25.6	400.2	6- 93	3.8	78.2
	male	1.0	2.7	0- 6	0.3	164.0
	female	12.0	178.8	2- 58	2.6	111.4
	Copepodid	9.9	38.6	3- 30	1.2	62.4
Asplanchna sp.		5.9	18.3	1- 16	0.8	72.3
nauplis larvae		20.7	56.9	9- 35	1.4	36.4

Table III

Fisher's index of dispersion for the zooplankton of transects A-B, A-C, and A-D.

		Transect A-B		Transect A-C		Transect A-D	
		C	P(χ^2 38)	D	P(χ^2 39)	D	P(χ^2 27)
Bosmina	longirostris	144.3	0.001	404.3	0.001	661.1	<0.001
Diaptomus	sicilaides	65.9	0.01	266.6	0.001	595.7	<0.001
	male	80.3	0.001	209.2	0.001	176.8	<0.001
	female	70.8	0.001	137.1	0.001	373.1	<0.001
	Copepodid	50.1	0.07	80.6	0.001	219.8	<0.001
Cyclops	vernalis	77.9	0.001	155.3	0.001	406.7	<0.001
	male	41.2	0.30	50.4	0.10	69.9	<0.001
	female	52.2	0.05	89.4	0.001	387.5	<0.001
	Copepodid	72.6	0.001	87.3	0.001	100.9	<0.001
Asplanchna sp.		54.2	0.04	115.3	0.001	80.4	<0.001
nauplis	larvae	48.4	0.10	76.5	0.001	71.3	<0.001

vernalis had a nonsignificant D-value. Although the D-value was non-significant, the coefficient of variation was high, 110 percent. As pointed out in the introduction, there is an inability of this test to detect non-randomness in populations with low mean densities (ex. male C. vernalis $\bar{x}$=1.1). This situation is the same for the males of C. vernalis in transect A-B. Altogether, transect A-B contained three non-significant, two moderately significant, and six highly significant D-values.

The results suggest that as the length of the transect and sampling interval is increased, the number of non-random populations, and the degree of departure from randomness increases. This increase in variability can be seen when the sample variance is plotted against the sample mean (Figure 4). The straight line in the plot is unity and describes a random distribution. The lines for the sampling were fitted by eye. It is seen that transect A-B has the least variability, while transect A-D has the greatest. Further, only at low means (below 5) do the points not depart significantly from randomness.

The results of the pattern analysis are presented in Figure 5. In some of the graphs there is a steady rise in the variance at the larger block sizes. This rise is sometimes due to a trend in abundance of the individuals along the transect which masks some scales of pattern. Thus, they are not always indicative of aggregation at that block size. This effect may be reduced by deducting terms for covariance with position from the sum of squares for the larger block sizes (Greig-Smith, 1961). This was not performed in the analysis. Instead, the totals for the largest block sizes were examined for a trend and taken into consideration when interpreting the results.

Figure 4

Sample variance vs. sample mean. Straight line indicates Poisson randomness. · indicates data points from transect A-B, ⊙ from transect A-C, and x from transect A-D.

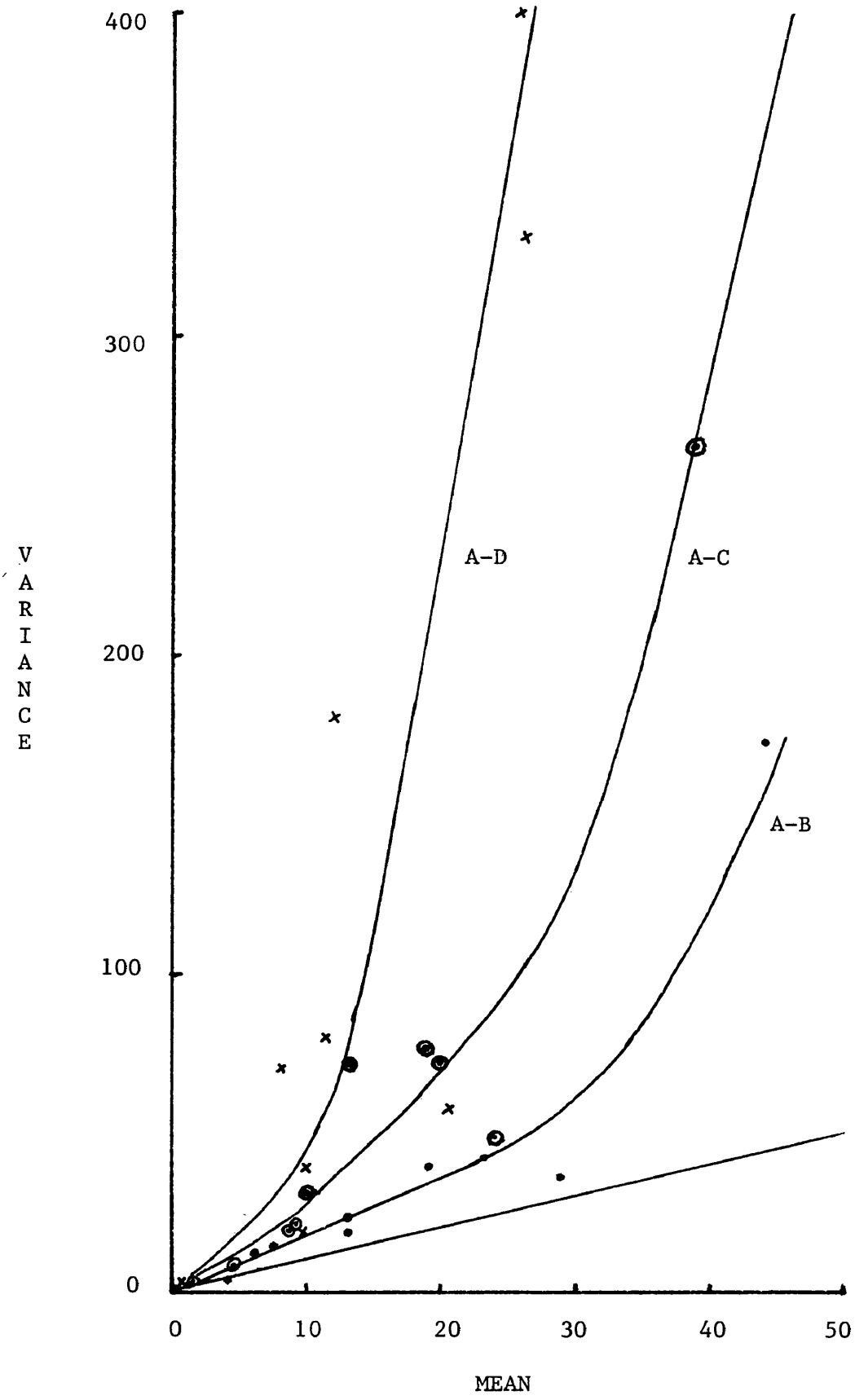

400
300
200
100
0
VARIANCE
A-D
A-C
A-B
0
10
20
30
40
50
MEAN

Figure 5

Block size analysis of variance of zooplankton densities in transect A-B.

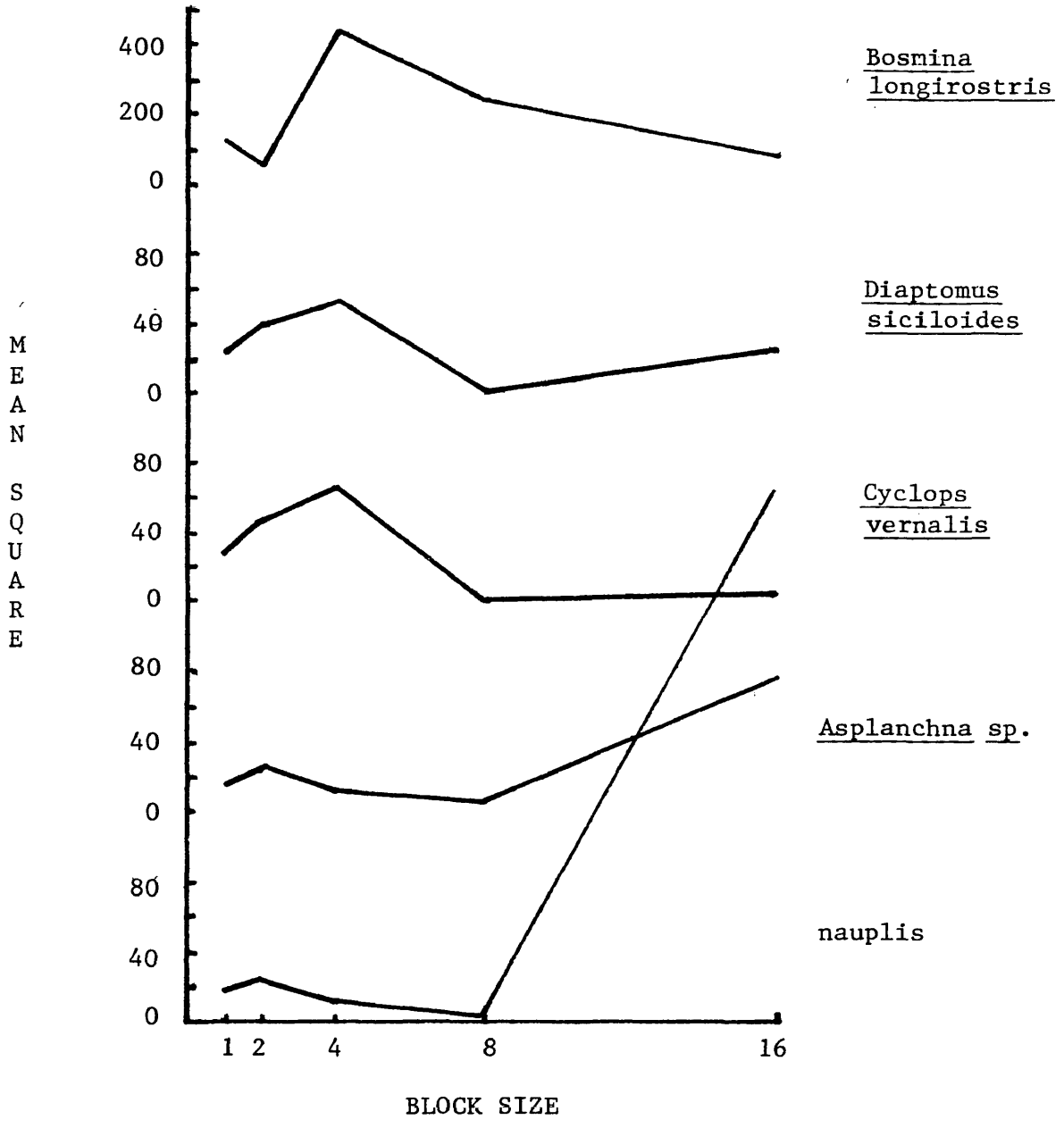

400
200
0
80
40
0
80
40
0
80
40
0
80
40
0
1 2 4 8 16
BLOCK SIZE
MEAN SQUARE
Bosmina longirostris
Diaptomus siciloides
Cyclops vernalis
Asplanchna sp.
nauplis

Figure 5 (continued)

Block size analysis of variance of zooplankton densities in transect A-C.

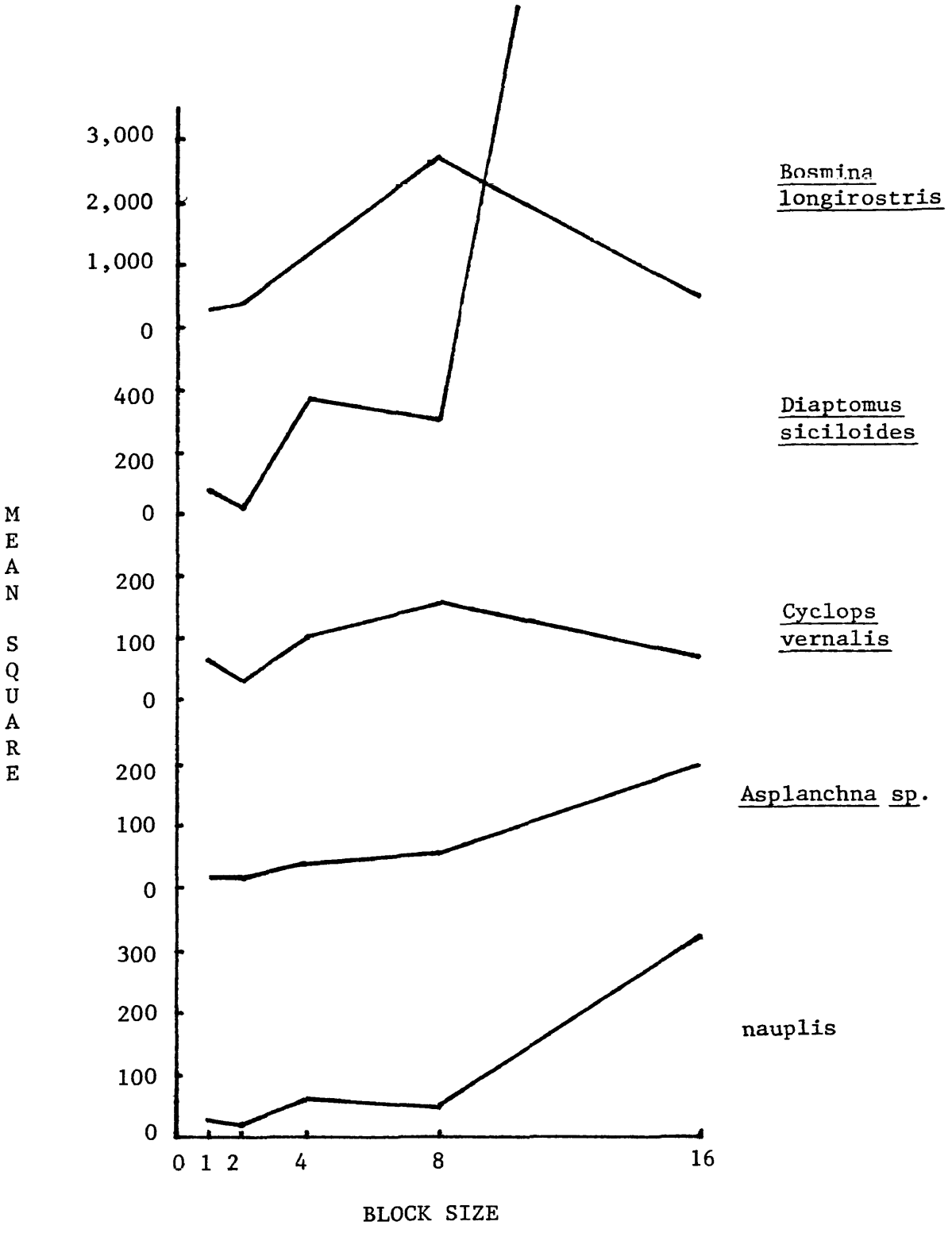
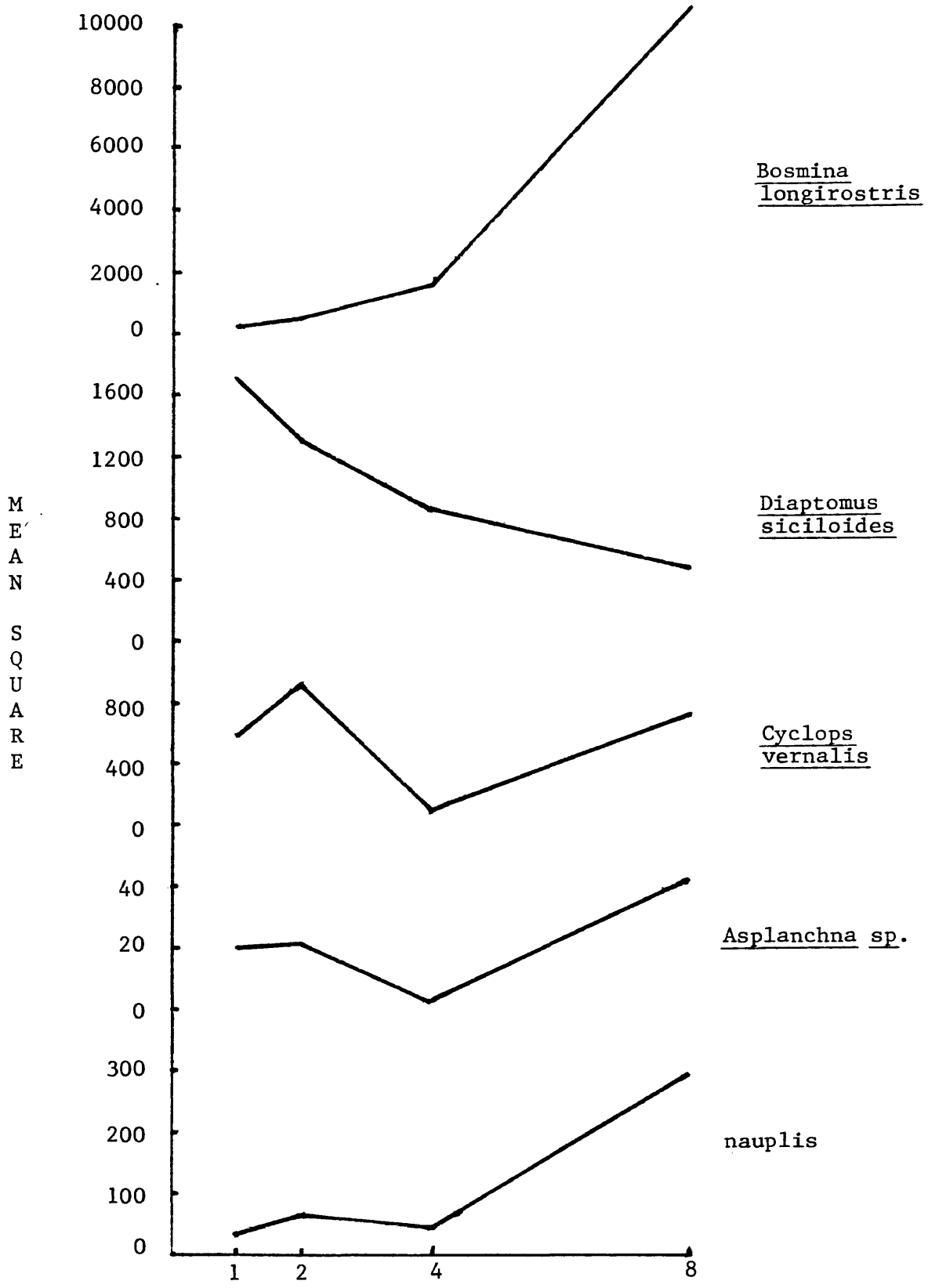

3,000
2,000
1,000
0
400
200
0
200
100
0
200
100
0
300
200
100
0
0 1 2 4 8 16
BLOCK SIZE
MEAN SQUARE
Bosmina longirostris
Diaptomus siciloides
Cyclops vernalis
Asplanchna sp.
nauplis

Figure 5 (continued)

Block size analysis of variance of zooplankton densities in transect A-D.


10000
8000
6000
4000
2000
0
1600
1200
800
400
0
800
400
0
40
20
0
300
200
100
0
MEAN SQUARE
Bosmina longirostris
Diaptomus siciloides
Cyclops vernalis
Asplanchna sp.
nauplis
1
2
4
8
BLOCK SIZE

In transect A-B, Bosmina longirostris, Diaptomus siciloides, and Cyclops vernalis show a maximum pattern intensity at block size 4, indicating an aggregated distribution with a distance of 4 meters coinciding or missing patches of the species. Pattern intensity for Asplanchna sp. and nauplis larva were greatest at block size 2, but were small in intensity. The small change in intensity indicate that these two groups are less aggregated than the above species, with their distribution being closer to randomness. The rise in intensity at block size 16 for Asplanchna, and especially nauplis larva, reflect a trend in abundance along the transect which is not very apparent from a visual inspection of the density vs. distance graphs.

In transect A-C, B. longirostris, D. siciloides, and C. vernalis have high values of pattern intensity at block sizes 4 and 8, indicating aggregation on a scale between 20-40 meters. The extreme increase in the variance of D. siciloides at block size 16 is the result of a quite apparent rise in abundance along the transect. The graphs for Asplanchna and the nauplis larva are similar again in being of less intensity and and rising sharply at block size 16. Relatively high variance values start at block size 4, indicating a distance of 20 meters for the aggregations.

In transect A-D, only 16 of the 28 stations were available for use in the pattern analysis. Because of this, interpretation of the results is made somewhat more difficult. B. longirostris, Asplanchna, and the nauplis larva all have high values at block size 8 (120 meters). This is attributable to high densities found in the first part of the transect for Asplanchna and the nauplis larva. Asplanchna and the

nauplis larva also have a smaller peak at block size 2 (30 meters). D. siciloides is seen to be aggregated at block size 1 and 2, and thus at a scale between 15-30 meters, C. vernalis has an aggregated pattern on the scale of 30 meters (block size 2).

Table IV compares the dimensions obtained from the pattern analysis for the zooplankton along the three transects. Again, it is seen that pattern intensity increases with increased transect length and sampling interval, with the greatest variability occurring at the largest distances. The pattern intensities also indicate that B. longirostris consistently had the highest organized spatial pattern, followed by C. vernalis and D. siciloides. Nauplis larva were considerably less organized than the above, and Asplanchna seem to be only marginally organized.

To further investigate the dimensions of spatial pattern, an empirical method of analysis was performed and is summarized in Table V. The results show that with an increase in transect length and sample interval the number of patches per transect decreases, the size of the patches increases, and the ratio of patch density to background density increases. It was also found that as the density increases within transects the ratio of patch to background densities tended to decrease.

Tables IV and V show a similarity in some of the spatial dimensions between species within transects. To investigate the interspecific relationships and the possibility that the patches are multispecies structures, Pearson's correlation coefficients were determined (Table VI). The results show that out of the 30 possible pairs of species for the 3 transects, 10 had a significant positive r-value while one had a signi-

Table IV

Block size, size of aggregation, and pattern intensity for the zooplankton of transect A-B, A-C, and A-D.

	Transect A-B			Transect A-C			Transect A-D		
	Block Size	Size of Aggregation (m)	Pattern Intensity	Block Size	Size of Aggregation (m)	Pattern Intensity	Block Size	Size of Aggregation (m)	Pattern Intensity
Bosmina longirostris	4	4	455	4-8	20-40	1120-2761	16	120	10,000
Diaptomus Siciloides	4	4	56	4	20	371	1	15-30	1,736
Cyclops Vernalis	4	4	66	4-8	20-40	107-152	2	30	927
Asplanchna sp.	2	2	23	4-8	20-40	37- 56	2	30	21
							8	120	42
nauplis larvae	2	2	46	4	20	62	2	30	55
							8	120	289

Table V

Spatial dimensions of the zooplankton distributions.

	No. patches per transect	Median length transect across patch (m)	Patch density (No./3d)	Background density (No./3d)	Ratio: Patch density / Background Density
Transect A-B					
Bosmina longirostris	8	1.4	55.1	35.8	1.539
Diaptomus siciloides	7	2.0	29.4	16.8	1.750
Cyclops vernalis	9	2.2	24.2	13.3	1.890
Asplanchna sp.	7	2.0	16.8	8.9	1.888
nauplis larvae	7	3.0	34.1	22.5	1.515
mean	7.6	2.1			1.716
Transect A-C					
Bosmina longirostris	4	27.0	79.2	42.7	1.855
Diaptomus siciloides	4	14.5	50.6	24.3	2.082
Cyclops vernalis	7	13.0	25.7	12.2	2.106
Asplanchna sp.	7	13.0	16.5	5.7	2.895
nauplis larvae	8	9.5	30.4	16.9	1.799
mean	6	15.4			2.133
Transect A-D					
Bosmina longirostris	1	166	65.2	14.7	4.435
Diaptomus siciloides	5	42	64.3	26.8	2.399
Cyclops vernalis	5	37	39.0	10.8	3.611
Asplanchna sp.	5	24	9.8	2.5	3.920
nauplis larvae	3	22	27.1	13.9	1.949
mean	3.8	58.2			3.263

Table VI

Correlations among the zooplankton species.

		D.S.	C.V.	A. Sp.	Nauplis
Transect A-B					
Bosmina	longirostris	.2967	.0619	.3401	.0827
Diaptomus	sicioloides		.2490	.0943	.2804
Cyclops	vernalis			.2563	.1792
Asplanchna sp.					.3986*
Transect A-C					
Bosmina	longirostris	.4037*	.0384	-.0257	.2319
Diaptomus	siciloides		.0481	-.2891	-.3283*
Cyclops	vernalis			.7305**	.5724**
Asplanchna sp.					.5836**
Transect A-D					
Bosmina	longirostris	-.0878	-.1328	.4139*	.6787**
Diaptomus	siciloides		.7239**	-.2412	-.2082
Cyclops	vernalis			.0544	-.0476
Asplanchna sp.					.7241**

*significant at the 0.05 level
**significant at the 0.01 level

ficant negative r-value ($P \leq 0.05$). The degree and direction of association between species pairs was not constant between transects. The only species pair that was significantly associated in all three transects was Asplanchna-nauplis larva. Even so, only 8 out of the 30 coefficients were negative, which would indicate that individuals have high and low concentrations that tend to occur together, and that patches are multispecies structures. Disregarding the direction of association, it was found that the average degree of association between species increased from transect A-B to A-D (transect A-B, r=0.2239; transect A-C, r=0.3251; transect A-D, r=0.3313).

Phytoplankton Distribution

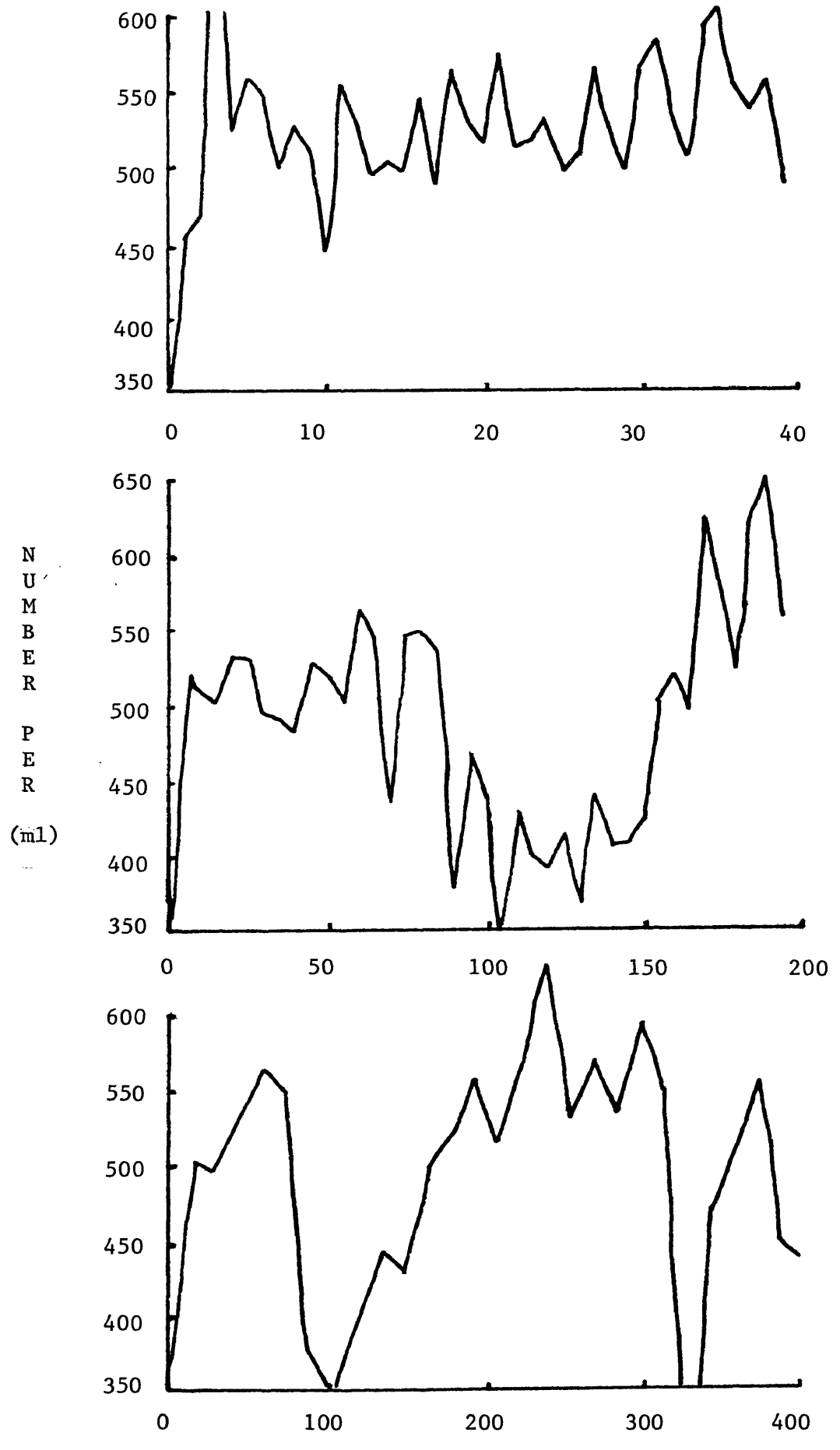
The dominant phytoplankters in the reservoir were Mallomonas caudata, and two cryptomonads (Cryptomona ovata, Chroomonas Nordstedii). In this investigation, the two cryptomonads were counted together with their total being used in the analysis.

The densities of the phytoplankton are presented in Figure 6. The results of the analysis of variance on station means are presented in Table VII. In every case, the null hypothesis of no difference between stations is rejected. Tukey's w-test is presented in Table VIII, where any pair of means not connected by the same line differ significantly at the 0.05 level.

The low mean square for fields within aliquots and the nonsignificant F value for aliquots within stations indicate that the laboratory subsampling and counting procedure was accurate enough, relative to the degree of variation in the population, to discern real differences in over 82 percent of the means.

Figure 6

Densities of *Mallomonas caudata* along transect A-B (upper), A-C (center), and A-D (lower).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550
500
450
400
350
0
10
20
30
40
650
600
550
500
450
400
350
0
50
100
150
200
600
550
500
450
400
350
0
100
200
300
400
NUMBER PER (ml)
DISTANCE (M)

Figure 6 (continued)

Densities of Crytomonadaceae along transect A-B (upper), A-C (center), and A-D (lower).

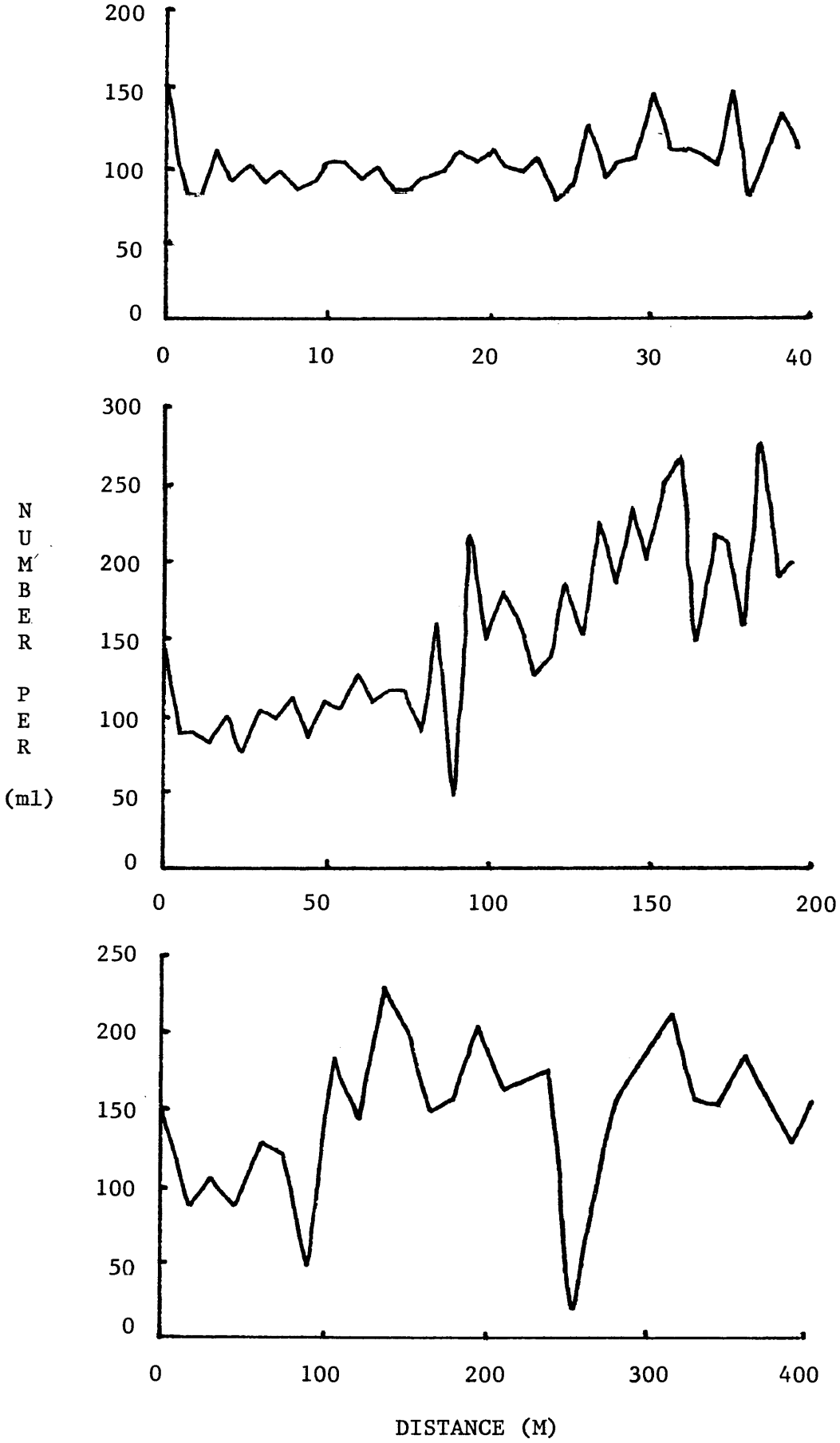

200
150
100
50
0
0
10
20
30
40
300
250
200
150
100
50
0
0
50
100
150
200
N
U
M
B
E
R
P
E
R
(ml)
250
200
150
100
50
0
0
100
200
300
400
DISTANCE (M)

Table VII

Analysis of variance for *Mallomonas caudata*.

Transect A-B:

Source of Variation	df	SS	ms	F
Stations	39	39.586	1.015	2.909**
Aliquots within stations	80	27.913	0.349	1.199
Fields within aliquots	2880	837.684	0.291	
Total	2999	405.183		

Transect A-C:

Source of Variation	df	SS	ms	F
Stations	39	102.584	2.630	9.513**
Aliquots within stations	80	22.122	0.276	1.033
Fields within aliquots	2880	770.717	0.267	
Total	2999	895.423		

Transect A-D:

Source of Variation	df	SS	ms	F
Stations	27	103.167	3.821	13.483**
Aliquots within stations	56	15.868	0.283	1.105
Fields within aliquots	2016	516.892	0.256	
Total	2099	635.927		

**significant at 0.01 level

Table VII (continued)

Analysis of variance for Crytomonadaceae.

Transect A-B:

Source of Variation	df	SS	ms	f
Stations	39	15.256	0.391	2.724**
Aliquots within stations	80	11.468	0.144	1.009
Fields within aliquots	2880	409.629	0.142	
Total	2999	436.353		

Transect A-C:

Source of Variation	df	SS	ms	f
Stations	39	138.976	3.563	24.074**
Aliquots within stations	80	11.831	0.148	0.841
Fields within aliquots	2880	505.989	0.176	
Total	2999			

Transect A-D:

Source of Variation	df	SS	ms	f
Stations	27	74.932	2.7753	17.378**
Aliquots within stations	56	8.943	0.1597	0.924
Fields within aliquots	2016	348.554	0.1729	
Total	2099			

**significant at 0.01 level

Table VIII

Tukey's w-test for the phytoplankton of transect A-B.

Mallomonas caudata

Station	Ranked Mean
4	2.9868
36	2.9235
32	2.8842
22	2.8789
28	2.8673
19	2.8491
31	2.8444
6	2.8317
12	2.8259
39	2.8239
37	2.8176
7	2.8038
17	2.7993
38	2.7798
33	2.7761
9	2.7738
20	2.7727
25	2.7672
29	2.7619
13	2.7574
5	2.7560
24	2.7509
21	2.7451
23	2.7364
10	2.7306
15	2.7125
34	2.7071
27	2.7065
8	2.7033
30	2.6931
35	2.6883
14	2.6863
16	2.6859
26	2.6827
18	2.6682
40	2.6555
11	2.5579
3	2.5571
2	2.5546
1	2.3156

W = 5.24 (0.0045)
= 0.0236

Cryptomonadaceae

Station	Ranked Mean
1	1.6716
31	1.6543
36	1.6385
39	1.6033
27	1.5792
40	1.5239
4	1.5169
21	1.5129
33	1.5128
32	1.5116
38	1.5107
19	1.4985
24	1.4894
29	1.4878
6	1.4872
34	1.4872
12	1.4848
30	1.4828
20	1.4765
11	1.4754
14	1.4656
22	1.4626
35	1.4569
8	1.4564
23	1.4500
18	1.4406
28	1.4391
5	1.4344
13	1.4311
10	1.4305
17	1.4299
7	1.4151
26	1.4124
15	1.4032
16	1.4029
9	1.3996
3	1.3894
2	1.3894
37	1.3869
25	1.3744

W = 5.24 (0.0018)
= 0.0094

Table VIII (continued)

Tukey's w-test for the phytoplankton of transect A-C.

Mallomonas caudata

Station	Ranked Mean
70	3.0418
69	2.9918
66	2.9905
67	2.8774
44	2.8567
71	2.8436
47	2.8275
49	2.7931
48	2.7894
20	2.7727
41	2.7721
45	2.7700
25	2.7672
5	2.7560
64	2.7448
68	2.7418
62	2.7395
10	2.7306
43	2.7166
15	2.7125
65	2.6941
30	2.6931
35	2.6883
63	2.6757
40	2.6555
51	2.6356
46	2.5404
52	2.5370
59	2.5338
54	2.5264
62	2.5186
57	2.5008
61	2.4604
55	2.4558
60	2.4452
56	2.4243
50	2.3822
58	2.3352
1	2.3156
53	2.2979

W = 5.24 (0.0034)

= 0.0181

Cryptomonadaceae

Station	Ranked Mean
69	2.1185
64	2.0846
63	2.0388
61	1.9810
59	1.9332
66	1.9078
51	1.9077
67	1.8944
71	1.8730
62	1.8475
70	1.8100
57	1.8052
53	1.7885
60	1.7791
49	1.7157
54	1.7096
68	1.6967
58	1.6797
1	1.6716
52	1.6581
65	1.6558
56	1.6290
44	1.5865
55	1.5708
46	1.5395
47	1.5365
40	1.5239
42	1.5142
45	1.5043
30	1.4828
20	1.4765
43	1.4740
35	1.4569
5	1.4344
10	1.4305
48	1.4186
15	1.4032
41	1.4012
25	1.3744
50	1.2399

W = 5.24 (0.0018)

= 0.0097

Table VIII (continued)

Tukey's w-test for the phytoplankton of transect A-D.

Mallomonas caudata

Station	Ranked Mean
74	3.0300
78	2.9084
76	2.8623
73	2.8593
44	2.8567
71	2.8436
83	2.8379
47	2.8275
79	2.7861
41	2.7721
77	2.7569
75	2.7519
68	2.7418
82	2.7396
72	2.7155
15	2.7125
65	2.6941
30	2.6931
81	2.6260
84	2.5602
85	2.5410
59	2.5338
62	2.5186
56	2.4243
50	2.3822
1	2.3156
53	2.2979
80	1.9860

W = 5.24 (0.0051)

= 0.0265

Cryptomonadaceae

Station	Ranked Mean
59	1.9332
71	1.8730
79	1.8676
62	1.8475
78	1.8027
53	1.7885
83	1.7862
74	1.7598
85	1.7558
73	1.7549
82	1.7281
77	1.7226
72	1.7181
68	1.6967
80	1.6861
1	1.6716
81	1.6621
65	1.6558
56	1.6290
44	1.5865
84	1.5803
47	1.5365
76	1.5214
30	1.4828
15	1.4032
41	1.4012
50	1.2399
75	1.0936

W = 5.24 (0.0028)

= 0.0149

Fisher's index of dispersion and summary statistics for the phytoplankton are given in Table IX. The statistics in this table were calculated from the total collection counts for each station. The D-values are large enough that they would not have been expected by chance alone ($P<0.001$), indicating that the variance is larger than that of a random distribution and the individuals are aggregated to some degree.

Pattern analysis was applied to the total collection counts for each station with the results presented in Figure 7. The results for transect A-B indicate that M. caudata is aggregated on a scale from 1-2 meters, while the cryptomonads are aggregated on a scale of 4 meters. Both groups have a high pattern intensity at block size 16, resulting from a gradual increase in density along the transect. In transect A-C, this high variance at block size 16 is very pronounced. Considering the density vs. distance graph for M. caudata, it is apparent that this species is aggregated on a scale of approximately 80 meters (block size 16), and while the pattern analysis agrees with this description, the pattern was clear enough that the analysis was not really needed. The same is true for the cryptomonads of transect A-C. In the density vs. distance graph, this group has a low population for the first half of the transect, with a higher density during the last half of the transect. Thus, it would seem that this group was aggregated on a scale of approximately 100 meters, which is in agreement with the pattern analysis. Because the spatial scale of the phytoplankton in transect A-D is readily apparent from the density vs. distance graphs, and only 16 of the 28 stations are available for the analysis, pattern analysis was not carried out.

Table IX

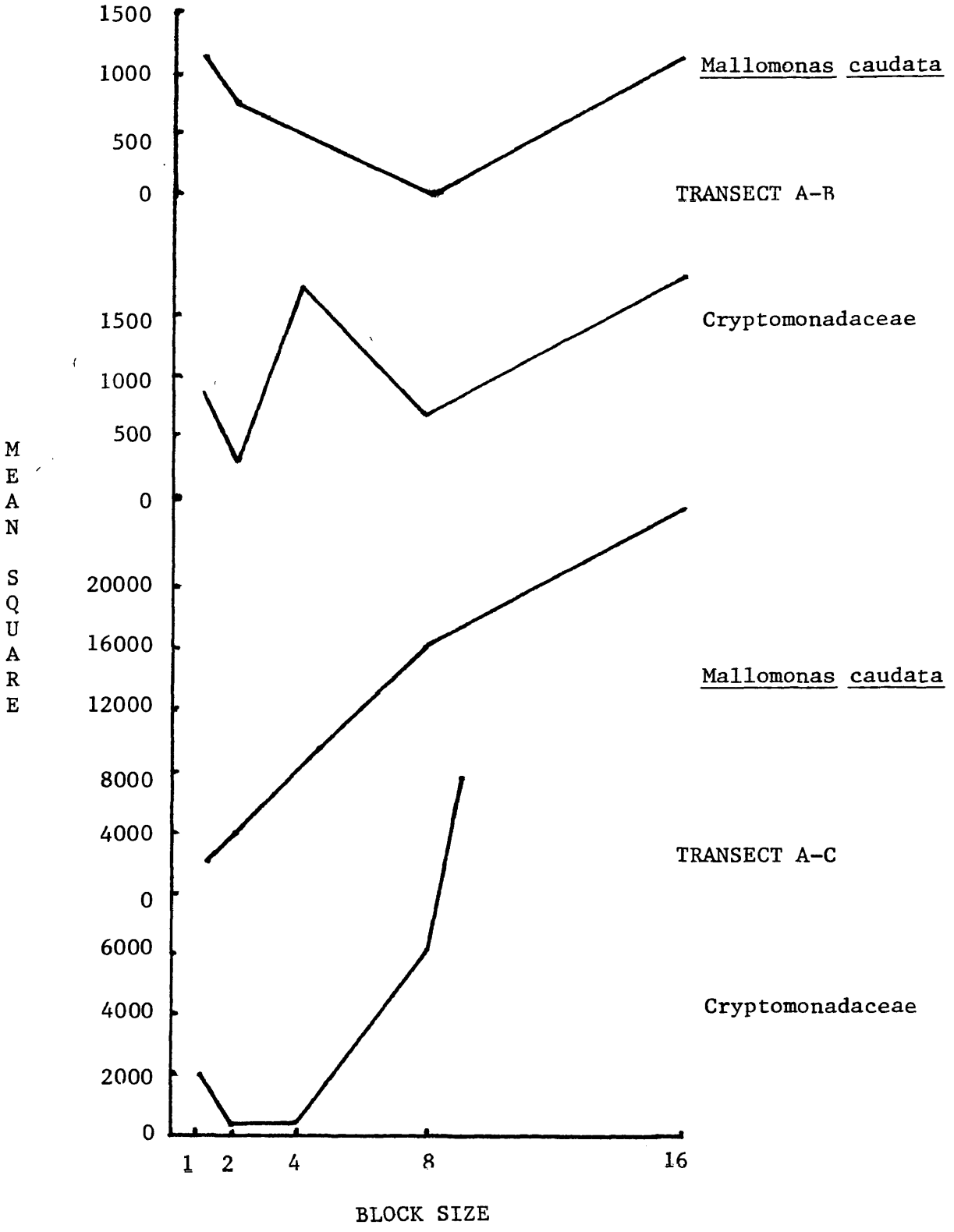
Summary statistics and fisher's index of dispersion for the phytoplankton.

Calculations based on total collection counts of each sample.

		$\bar{x}$	s^2	SE	CV	D	$P(\chi^2 39)$
Transect A-B							
Mallomonas	caudata	512.9	2524.0	8.0	9.8	191.9	<0.001
	Cryptomonadaceae	99.5	319.2	2.9	17.9	125.2	<0.001
Transect A-C							
Mallomonas	caudata	479.6	5556.2	11.9	15.5	451.8	<0.001
	Cryptomonadaceae	146.5	4016.7	10.3	43.3	1041.9	<0.001
Transect A-D							
Mallomonas	caudata	479.7	7437.9	13.8	17.9	604.4	<0.001
	Cryptomonadaceae	149.2	1688.5	8.1	27.5	305.6	<0.001

Figure 7.

Block size analysis of variance of phytoplankton densities in transect A-B (upper) and A-C (lower).


1500
1000
500
0
Mallomonas caudata
TRANSECT A-B
1500
1000
500
0
Cryptomonadaceae
MEAN SQUARE
20000
16000
12000
Mallomonas caudata
8000
4000
0
TRANSECT A-C
6000
4000
2000
0
Cryptomonadaceae
1 2 4 8 16
BLOCK SIZE

The results of the empirical method of analyzing spatial pattern (Weibe, 1970) are presented in Table X. The data show an increase in patch size with increased transect length and sample interval. This increase was much larger between transect A-B and transect A-C than between transect A-C and transect A-D. The number of patches per transect decreased from transect A-B to A-C, and then increased from transect A-D. The ratio of patch density to background density increased from transect A-B to A-C, and then decreased from transect A-C to A-D in the cryptomonads, and increased only slightly in M. caudata.

The results would indicate that the phytoplankton are aggregated on a number of spatial scales which increase in patch size and intensity with the distance of observation, or the increase in sample interval, or both. This increase in patch dimensions was then found to level off at a scale found somewhere between transect A-C and A-D where the number of patches started to increase.

Correlation coefficients were determined for M. caudata and the cryptomonads and found to be positive and non-significant in all three transects (Table XI). Although the density vs. distance graphs show a similar pattern in transect A-D, the patterns are out of phase with one another, thus giving the low correlation coefficient.

Correlation between the total zooplankton and phytoplankton counts was significant only in transect A-D (Table XI). To further investigate the association between the phytoplankton and zooplankton, coefficients were determined for each zooplankton species in transect A-D (Table XI). While none of the zooplankton species show a significant correlation value when considered separately, all values were nega-

Table X

Spatial dimensions of the phytoplankton distributions.

	No. patches per transect	Median length transect across patch (m)	Patch density (No./ml)	Background density (No./ml)	Ratio: Patch density / Background density
Transect A-B					
Mallomonas caudata	9	1.8	511	531	0.963
Cryptomonadaceae	9	1.4	114	86	1.325
Transect A-C					
Mallomonas caudata	2	65	536	406	1.320
Cryptomonadaceae	1	100	200	103	1.937
Transect A-D					
Mallomonas caudata	3	100	541	392	1.381
Cryptomonadaceae	2	120	179	101	1.780

Table XI

Correlation coefficients between phytoplankton groups (upper), total phytoplankton and zooplankton (center), and the phytoplankton and individual zooplankton species of transect A-D (lower).

	Cryptomonadaceae		
	transect A-B	transect A-C	transect A-D
Mallomonas caudata	0.0161	0.0899	0.0259

	Total Zooplankton		
	transect A-B	transect A-C	transect A-D
Total Phytoplankton	0.2042	-0.1385	-0.5078**

	Bosmina longirostris	*Diaptomus siciloides*	nauplis larva	*Cyclops vernalis*	*Asplanchna* sp.
Total Phytoplankton	-0.3743	-0.3548	-0.2809	-0.2301	-0.0816
	-0.5247**				
	-0.5646**				
	-0.5078**				

**significant at the 0.01 level

tive. When the densities of the zooplankton species were pooled and correlated with the phytoplankton, the values were significant at the 0.01 probability level. It was found that the filter feeding species (B. longirostris, D. siciloides, and nauplis larva) had higher correlations with total phytoplankton than did the raptoral and predaceous species (C. vernalis and Asplanchna).

DISCUSSION AND CONCLUSION

The present investigation has found an aggregation of the plankton populations on all observed scales and for all species where the total collection count was used in the calculations. An increase in size and intensity of patches was found as the sampling interval and transect length was increased. It would be expected that the minimum patch size detectable would increase as the sampling interval was increased, so that even though the smaller scale aggregations could not be detected in the transects with a larger sampling interval, it is likely that they were present. These smaller and less intense aggregations are then superimposed on the larger variations and act as a "noise level" over which signals of the larger, more intense, pattern can be detected as the distance of observation is increased. These smaller, less intense, variations are probably due to the ambit of individuals over periods of hours and although they may be of short duration, their ecological significance is not necessarily lessened by this.

The dimensions of aggregation found in this study are similar to those observed by other investigators who have conducted their studies on a similar scale. Weibe's (1970) results from a transect similar to the present transect A-D found oceanic zooplankton patches with a median length of 25 meters and a mean patch to background density ratio of 3.6. The dimensions for the present study are 37 meters and a ratio of 3.3. On a night tow, which was increased in length by 6x (to 3 Km) and 2x in sample interval (to 39 m), Weibe observed patches which were

approximately 100 meters in length and had a patch to background ratio of 3.2. This does not necessarily indicate a diurnal change in spatial structure, since as Weibe pointed out, the increased sampling size of the night tow could not discriminate smaller scale structures. In other words, his samples were collected on a larger scale which provided information on spatial structure for that scale. McNaught (1979) reported aggregation of fresh-water zooplankton on scales of 4.5, 8, and 30 meters, with a maximum to mean density ratio that ranged from 3.6 to 6.3. The present study found a maximum to mean density ratio ranging from 1.4 to 4.1.

In studying the spatial pattern of phytoplankton, Richards and Happey-Wood (1979) sampled a 128 meter transect at 2 meter intervals and found Asterionella formosa to be aggregated on a scale of 8, 24, and 48 meters, with an average maximum to mean density ratio of 1.45. This ratio in the present study was 1.37 in transect A-B, 1.61 in transect A-C, and 1.40 in transect A-D. Denman and Platt (1975) averaged chlorophyll readings over 3.2 meter intervals for distances up to 80 kilometers, and found aggregates on an order of 100 meters and a maximum to mean density ratio of 5. Richerson's et al. (1975) study, with a large sampling interval of 68.5 meters and a transect length of 6.85 kilometers, found phytoplankton patches on a scale of 225 to 450 meters.

The factors affecting the generation, maintenance, and observation of plankton patterns can be grouped under observational, biological, and physical influences. Observational influences include factors such as aliasing and sampling design. Error due to aliasing is from using a sample interval which is too large to resolve the shortest fluctuations

present in the data. Platt et al. (1975) suggested using a sampling rate of at least four samples per cycle of fluctuation, or using a sampling device that would integrate or average samples over a distance. In this study, point samples were collected, and thus some of the calculated spatial dimensions, particularly the smaller patches of transect A-B, may be affected by aliasing.

Platt et al. (1977) suggested that patches on the 10 meter scale would persist for 10 minutes, and on the 100 meter scale for 1.5 hours before being destroyed by diffusion. Patches larger than 100 meters would be stable against diffusion. These suggestions refer to the open ocean and are not entirely relevant to the reduced turbulances found in ice covered basins. Even so, they point to a shorter life expectancy for smaller patches. If this is the situation, then the patterns found in transect A-B may be due more to a sampling error on a time factor than to what is the actual pattern. The length of time involved in drilling the sampling holes and obtaining the samples was in the order of two hours. During this time the zooplankton movements may have been significant enough to affect the observed pattern. There is no way of detecting to what extent this error may be present, but it is worth noting that the fine scale patterns of transect A-B are similar to investigations where the length of time in taking the samples is not an error factor. One way of avoiding the error would have been to obtain all samples simultaneously, as done by Cassie (1959) and Harris and Smith (1977). These experiments found a similar pattern which persisted on a number of occasions. Clutter (1969) and Emery (1968) give further evidence for their persistance of fine scale pattern with their observance

of patches of copepods and mysids that remained intact in swash over reefs and near surf zones.

Other observational factors that may affect spatial pattern through acting as a filter that may increase or decrease this pattern are avoidance of sampler, sample size, and laboratory analysis. Avoidance of the sampler is to some degree common to all sampling devices. If this avoidance is not excessive and remains constant in all samples, the error involved will be minimal. Sample size may affect the observation of pattern through interaction with the method of analysis, such as discussed with Fisher's index of dispersion. A desirable sample size would be large enough to be within the power range of the analytical method, but not of such size that would make data handling unwieldy. Length of the sampling interval is also of importance because of the effects of aliasing. Laboratory treatment of the data may affect observed patterns through the precision of the counts or measurements, the type of count or measure, and the choice of analytical methods to use on the data. The choice of species counts or biomass measurements, such as chlorophyll, will give different pictures of spatial pattern. Biomass measurements lose much ecologically important information, though in terms of economics, they allow the gathering of large data sets, and thus the use of powerful analytical methods such as spectral analysis. Though the type of analytical method used effects the observed spatial patterns, little has been reported on the comparability of the various methods. This experiment compared the results of pattern analysis and an empirical method of analysis. The results obtained found good agreement between the two methods.

Biological factors affecting pattern can be grouped into reproductive, social, and coactive factors. Reproduction, through the release

of the brood close to the parent, and social factors would tend to aggregate populations. Coactive processes involve competition, predation, and parasitism. Although one can conceptualize how predator-prey interactions, grazing, and interspecific competition can create heterogeneity, it is not known what the relative importance of these processes are to the development and maintenance of patches. In the present study, association between the zooplankton species was predominantly positive, which would tend to indicate that the patches were multispecies structures whose abundances increase and decrease together. The association between the phytoplankton and zooplankton ranged from a statistically insignificant positive correlation in transect A-B, to a statistically significant negative correlation in transect A-D. On a larger spatial scale, it is not uncommon to find a negative correlation between the zooplankton and phytoplankton. This has led to theories of animal exclusion (Hardy et al., 1935), grazing (Harvey et al., 1935), and models of plankton patchiness (Riley, 1976). Steeman Nielsen (1937) suggested that this negative association was not a direct relationship, but was caused by a time lag between rates of development of the phytoplankton. Experimental work in the laboratory has shown both positive (Bainbridge, 1953) and negative (Lucus, 1938) relationships. There is little doubt that the phytoplankton and zooplankton interact in a way that affects spatial pattern, but to interpret patterns found in the present study raises difficulties because there are equal grounds for suspecting both positive and negative associations, and these two conditions may alternate with time.

The physical factors affecting pattern consist of the physical transport system, bottom topography, and nutrient inputs. In the study

reservoir, nutrient input by feeder streams is significant only during periods of high runoff in the spring season, when the reservoir inlets are not dried up. Both advection and diffusion operate in the physical transport system. Advection is a vectoral process that transports the organisms with the currents, while diffusion may produce a spatial exchange of organisms without an overall transport of water. In a reservoir with an ice cover and with no major current inflows, advection is minimal. The plot of isotherms from the present investigation suggest the possibility of currents operating, which may have been set in motion during a break in the ice cover prior to the investigation. It may be that currents larger than those in other ice covered basins were operating, but to a substantially less degree than in ice free water. Similarly, turbulent diffusion is reduced under an ice cover. It has been theorized that 100 meters would be the minimum patch size in which growth could offset turbulent diffusion in the open ocean (Platt et al., 1977). Since mixing processes scale with size, mixing in lakes is diminished as compared to oceans, and is further diminished by an ice cover. This would mean that the critical length scale for patches should be less for ice covered basins, resulting in more intense and longer lasting patches. This may be likened to George and Heaney's (1978) finding of an increased spatial heterogeneity during periods of light winds, and thus low turbulance. This did not seem to be the case in the present investigation. As discussed earlier, the intensity and dimensions of pattern were similar to that of studies done in open basins and the oceans, where turbulance is much greater.

Since this and previous studies have reported an aggregation of plankton populations in the majority of cases, it is likely that

aggregation is a common phenomena of plankton which can be observed over a wide range of scales and habitats. Considering this, the main questions left unanswered are those dealing with the causes and ecological significance of aggregation. If these questions are to be answered, information on the dimensions of aggregations from a wide variety of habitats will be of value.

SUMMARY

1. The zooplankton were found to be aggregated on all observed scales. When the species were differentiated as to sex and juvenile stage, three groups in transect A-B and one group in transect A-C were found to be randomly distributed.

2. Estimates of patch size, patch density, background density, and patch frequency are given for the zooplankton and phytoplankton.

3. Bosmina longirostris was found to have the highest organized spatial pattern, followed by Cyclops vernalis and Diaptomus siciloides. Nauplis larva and Asplanchna were considerably less organized than the above. Mallomonas caudata had greater variability than the cryptomonads, although this may have been due to the pooling of the counts from two species of cryptomonads.

4. The largest variability was found to occur on the largest scale. When the distance of observation and sampling interval were increased, the intensity of aggregation increased.

5. The degree or intensity of the aggregations and the size of patches examined in this investigation are similar to those of previous investigations. This was an unexpected result, as previous theoretical and experimental work has shown that the degree of aggregation is inversely related to the degree of turbulance in the water column. Under winter conditions with minimal turbulance, the degree of aggregation in populations should be higher than that found under ice-free waters.

6. Out of the 30 possible pairs of zooplankton in the three transects, 10 had a significant positive correlation, while 1 pair had a significant negative correlation. Asplanchna sp. and the nauplis larva were the only pair found to have a significant correlation in all three transects. The degree and direction of association between the remaining zooplankton pairs were not constant between transects.

Correlation coefficients between the phytoplankton were positive and non-significant in all three transects.

Correlation between the total zooplankton and phytoplankton count was significant only in transect A-D. The direction of the relationship was negative. When the individual zooplankton species of transect A-D were considered against total phytoplankton, all correlations were negative and non-significant.

LITERATURE CITED

Abbott, M. R., and J. A. Coil. 1978. Effects of a coastal front on the distribution of chlorophyll in Lake Tahoe, California-Nevada. J. Geoph. Res. 83:4668-4672.

Abbott, M. R., T. M. Powell, and P. J. Richerson. 1980. The effects of transect direction on observed spatial patterns of chlorophyll in Lake Tahoe. Limnol. Oceanog. 25:534-537.

Bainbridge, R. 1953. Studies on the interrelationships of zooplankton and phytoplankton. J. Mar. Biol. Assoc. 32:385-440.

Barnes, H. 1949. Statistical study of the variation in the vertical plankton hauls, with special reference to the loss of catch with divided hauls. Journ. Mar. Biol. Ass. 29:324-345.

Barnes, H. 1952. The use of transformations in marine biological statistics. J. Cons., Cons. Perm. Int. Explor. Mer. 18:61-71.

Baines, H. and S. M. Marshall. 1951. On the variability of replicate plankton samples and some applications of 'contagious' series to the statistical distribution of catches over restricted periods. Journ. Mar. Biol. Ass. 30:233-263.

Burckhardt, G. 1910. Hypothesen und Beobochtungen uber dic Bedeutung der vertikalen planktonwanderung. Int. Rev. ges. Hydrobiol. Hydrogr. 3:156-172.

Cassie, R. M. 1959a. Micro-distribution of plankton. New Zeal. J. Sci. 2:398-409.

Cassie, R. M. 1959b. An experimental study of factors inducing aggregation in marine plankton. New Zeal. J. Sci. 2:339-365.

Cassie, R. M. 1960. Factors influencing the distribution pattern of plankton in the mixing zone between oceanic and harbour waters. New Zeal. J. Sci. 3:26-50.

Cassie, R. M. 1971. Sampling and statistics. p. 174-209. In W. T. Edmondson and G. G. Winberg (eds.), A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Blackwell Scientific Publications.

Clutter, R. I. 1969. The microdistribution and social behavior of some pelagic mysid shrimps. J. Exp. Mar. Biol. Ecol. 3:125-155.

Cochian, W. G. 1954. Some methods for strengthening the common χ^2 tests. Biometrics, 10:417-451.

Denman, K. L. 1976. Covariability of chlorophyll and temperature in the sea. Deep Sea Res. 23:539-550.

Denman, K. L. and T. Platt. 1975. Coherence in the horizontal distributions of phytoplankton and temperature in the upper ocean. Mem. Soc. Roy. Sci. de Liege. 7:19-30.

Emery, A. R. 1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13:383-387.

Fasham, M. J. R., M. V. Angel, and H. S. J. Roe. 1974. An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy-plankton recorder. J. Exp. Mar. Biol. Ecol. 16:93-112.

Fasham, M. J. R., and P. R. Pugh. 1976. Observations on the horizontal coherance of chlorophyll a and temperature. Deep Sea Res. 23:527-538.

Fisher, R. A. 1950. The significance of the deviation from expectation in a Poisson series. Biometrics. 6:17-24.

Fisher, R. A., H. G. Thornton, and W. A. MacKenzie. 1922. The accuracy of the plating method of estimating the density of bacterial populations. Ann. Appl. Biol. 9:325-359.

Gardiner, A. C. 1931. The validity of single vertical hauls of the International Net in the study of the distribution of the plankton. J. Mar. Biol. Ass. U. K. 17:449-472.

Gardiner, A. C., and M. Graham. 1925. The working error of Peterson's Young fish trawl. Fishery Investigations (England). Series II. 8:1-8.

George, D. G., and S. I. Heaney. 1978. Factors influencing the spatial distribution of phytoplankton in a small productive lake. J. Ecol. 66:133-155.

Greig-Smith, P. 1961. Data on pattern within plant communities. I. The analysis of pattern. J. Ecol. 49:695-702.

Greig-Smith, P. 1964. Quantitative Plant Ecology. Butterworths. 256 pp.

Hardy, A. C., and E. R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-27. Discovery Rep. 11:1-456.

Harris, G. P., and R. E. H. Smith. 1977. Observations of small scale spatial patterns in phytoplankton populations. Limnol. Oceonogr. 22: 887-899.

Harvey, H. W., L. H. N. Cooper, M. V. Lebour, and F. S. Russell. 1935. The control of production. J. Mar. Biol. Ass. 20:407-441.

Heaney, S. I. 1976. Temperal and spatial distribution of the dinoflagellate Ceratium hirundinella. O. F. Müller within a small productive lake. Freshw. Biol. 6:531-542.

Herdman, W. A. 1922. Spolia Runiana, V. Journ. Limn. Soc. Bot. XLVI: 141-170.

Hill, M. O. 1973. The intensity of spatial pattern in plant communities. J. Ecol. 61:225-235.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia. 27:343-383.

Huitfeldt-Kaas. 1898. Plankton in Norwegischen Binnenseen. Biol. Centrolblatt. 18:625.

Hutchinson, G. E. 1961. The paradox of plankton. Am. Nat. 95:137-145.

Kershaw, K. A. 1964. Quantitative and Dynamic Ecology. Edward Ainold. 183 pp.

Kierstead, H., and L. B. Slobodkin. 1953. The size of water masses containing plankton blooms. J. Mar. Res. 12:141-147.

Krumholz, L. A., and G. A. Cole. 1959. Studies on a Kentucky Knob Lake. IV. Some Limnological conditions during an unusually cold winter. Limnol. Oceanogr. 4:367-385.

Langford, R. R. 1938. Diurnal and seasonal changes in the distribution of the limnetic crustacea of Lake Nipissing, Ontario. Publ. Ontario Fish. Res. Lab. 56:1-142.

Likens, G. E., and R. A. Regotzkie. 1965. Vertical water motions in a small ice covered lake. J. Geophys. Res. 70:2333-2344.

Loeffler, R. J. 1954. A new method of evaluating the distribution of planktonic algae in freshwater lakes. Ph.D. thesis. Univ. of Wisc. 205 pp.

Lucus, C. E. 1938. Some aspects of integration in animal communities. J. Du. Cons. 13:309-322.

May, R. M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press. 235 pp.

McAlice, B. J. 1970. Observations on the small-scale distribution of estuarine phytoplankton. Mar. Biol. 7:100-111.

McAlice, B. J. 1971. Phytoplankton sampling with the Sedgwick Rafter Cell. Limnol. Oceanogr. 16:14-27.

McNaught, D. C. 1979. Considerations of scale in modeling large aquatic ecosystems. p. 3-24. In O. Savia and A. Robertson (eds.), Lake Ecosystem Modeling. Ann Arbor Science.

Moberg, E. G. 1918. Variation in the horizontal distribution of plankton in Devils Lake, North Dakota. Trans. Am. Microsp. Soc. 37: 239-267.

Neess, J. C. 1949. A contribution to aquatic population dynamics. Ph.D. thesis. University of Wisc.

Oliver, S. P. 1952. Horizontal distribution of plankton in Lake Salada Grande. Rev. Brazil Biol. 12:161-180.

Platt, T. 1972. Local phytoplankton abundance and turbulence. Deep Sea Res. 19:183-187.

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

Platt, T., K. L. Denman and A. D. Jassby. 1977. Modelling the productivity of phytoplankton. p. 807-856. In E. D. Goldberg, I. N. McCave, J. J. O'Brian, and J. H. Steele (eds.), The Sea, vol. 6, Marine Modelling, Wiley and Sons.

Platt, T., L. M. Dickie, and R. W. Trites. 1970. Spatial heterogeneity of phytoplankton in a nearshore environment. J. Fish. Res. Bd. Canada. 27:1453-1473.

Poole, R. W. 1974. An Introduction to Quantitative Ecology. McGraw-Hill, 532 pp.

Powell, T. M., P. J. Richerson, T. M. Dillon, B. A. Agee, B. J. Dozier, D. A. Godden, and L. O. Myrup. 1975. Spatial scale of current speed and phytoplankton biomass fluctuations in Lake Tahoe. Science. 189:1088-1090.

Reighard. 1898. Plankton in Norwegischen Bennewseen. Biol. Centralblott. 18:32.

Richards, M. C. and C. M. Happey-Wood. 1979. The application of pattern analysis to freshwater phytoplankton communities. Limnol. Oceanogr. 24:950-956.

Richerson, P. J., B. J. Dozier, and B. T. Maeda. 1975. The structure of phytoplankton associations in Lake Tahoe (California-Nevada). Verh. Inteinat. Verein. Limnol. 19:843-849.

Richerson, P. J., T. M. Powell, M. R. Abbott, and J. A. Coil. 1978. Spatial heterogeneity in closed basins, p. 239-276. In J. H. Steele (ed.), Spatial Pattern in Plankton Communities. Plenum.

Ricker, W. E. 1937. Statistical treatment of sampling processes useful in the enumeration of plankton organisms. Arch. Hydrobiol. 31: 68-84.

Riley, G. A. 1976. A model of plankton patchiness. Limnol. Oceanogr. 21:873-879.

Snedecor, G. W. and W. G. Cochran. 1937. Statistical Methods. Iowa State Press, 593 pp.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, 481 pp.

Steele, J. H. 1974. Spatial heterogeneity and population stability. Nature. 248:83.

Steeman Nielsen, E. 1937. On the relation between quantities of phytoplankton and zooplankton in the sea. J. Du. Cons. 12:147-154.

Stewart, K. M. 1972. Isotherms under Ice. Verh. Internat. Verien. Limnol. 18:303-311.

Sverdrup, H. V. and W. E. Allen. 1939. Distribution of diatoms in relation to the character of water masses and currents off Southern California in 1938. J. Mar. Res. 2:131-144.

Tonolli, V. 1949. Struttura spaziale del popolamento meso-plankctico. Eterogeneita delle densita dei popolamenti olizzontal: e sue variazione in funzione della quota. Mem. Ist. Ital. Idrobiol. 5:191-208.

UNESCO. 1968. Zooplankton sampling. Monographs in Oceanographic Methodology. 2. Imprimeries Populaires, Geneva. 174 pp.

Verduin, J. 1951. A comparison of phytoplankton data obtained by a motile sampling method with those obtained from a single station. Amer. J. Bot. 38:5-11.

Ward, H. B. 1896. A biological examination of Lake Michigan. Bulletin of the Michigan Fish Commission. No. 6:62-64.

Weibe, P. H. 1970. Small scale spatial distribution in oceanic zooplankton. Limnol. Oceanogr. 15:205-217.

Welch, P. S. 1935. Limnology. McGraw-Hill. 471 pp.

Winsor, C. P. and L. A. Wolford. 1936. Sampling variations in the use of plankton nets. Journ. Cons. Int. Explor. Mer. 2:190-204.

Wohlschlag, D. E. and A. D. Hasler. 1951. Some quantitative aspects of algal growth in Lake Mendota. Ecol. 32:581-593.

Ziemann, D. A. 1970. The horizontal distribution of zooplankton in Kaneohe Bay, Oahu, Hawaii. Masters Thesis, Univ. Hawaii, 56 pp.

APPENDIX

APPENDIX A

Zooplankton Densities (No. per 3 liters)

Station	Bosmina longirostris	Asplanchna sp.	Nauplis	Diaptomus Siciloides	Cyclops Vernalis
2	38	6	28	16	7
3	50	9	29	31	11
4	37	14	31	39	13
5	65	25	34	27	38
6	58	12	25	31	22
7	71	11	33	26	21
8	60	13	26	22	20
9	41	10	22	24	12
10	46	9	22	12	12
11	22	9	26	17	18
12	29	14	28	14	18
13	56	14	25	25	8
14	37	9	32	31	24
15	41	9	25	14	24
16	30	12	16	19	17
17	39	18	25	20	15
18	45	11	22	21	21
19	30	9	20	24	35
20	36	8	33	27	21
21	53	18	36	26	16
22	55	15	37	32	22
23	59	16	23	28	24
24	47	15	25	15	12
25	61	21	34	25	21
26	lost sample (inadequate fixitive)				
27	34	16	34	19	24
28	48	7	21	20	18
29	47	14	31	28	16
30	52	15	27	31	21
31	43	8	31	16	18
32	42	16	29	22	19
33	51	20	37	19	18
34	40	11	33	29	25
35	49	20	35	30	27
36	50	15	40	20	15
37	31	16	40	23	17
38	32	9	30	34	26
39	59	9	19	30	15
40	34	17	25	15	18
41	46	9	29	28	22
42	45	16	38	23	25
43	45	8	17	24	14

APPENDIX A (continued)

Station	Bosmina longirostris	Asplanchna sp.	Nauplis	Diaptomus Siciloides	Cyclops Vernalis
44	34	14	35	20	22
45	65	20	23	31	33
46	56	15	25	21	25
47	64	9	32	25	14
48	75	11	24	36	21
49	98	13	25	35	19
50	81	6	24	33	17
51	114	8	26	42	23
52	94	8	24	27	12
53	109	10	33	51	17
54	68	5	21	31	14
55	54	5	20	41	9
56	80	8	26	26	12
57	58	6	20	46	9
58	92	5	19	59	15
59	109	3	23	67	20
60	53	8	17	52	12
61	83	12	24	73	20
62	79	16	35	62	48
63	97	12	22	73	34
64	73	5	20	58	14
65	64	1	19	55	6
66	75	12	18	36	24
67	35	15	13	59	20
68	20	7	12	41	12
69	20	6	14	44	8
70	23	4	14	50	10
71	23	2	14	32	7
72	12	2	9	46	39
73	13	3	16	63	74
74	19	5	17	31	26
75	19	3	12	32	9
76	18	1	18	52	17
77	17	4	16	42	19
78	14	5	12	36	11
79	20	9	18	27	21
80	11	3	15	186	93
81	20	3	18	38	16
82	19	2	19	64	11
83	6	6	15	69	14
84	16	2	26	30	8
85	12	3	15	20	10

APPENDIX B

Densities of Copepod Sexes and Copepodids (No. per 3 liters)

Station	Diaptomus siciloides ♂	Diaptomus siciloides ♀	Diaptomus siciloides Copepodid	Cyclops vernalis ♂	Cyclops vernalis ♀	Cyclops vernalis Copepodid
2	4	6	6	0	4	3
3	10	19	2	1	6	4
4	20	17	2	1	5	7
5	8	15	4	3	14	21
6	5	20	6	0	7	15
7	9	16	1	0	7	14
8	6	12	4	1	9	10
9	6	13	5	1	6	5
10	1	10	1	1	3	8
11	3	9	5	1	5	12
12	5	7	2	0	8	10
13	6	15	4	0	2	6
14	13	13	5	0	11	13
15	4	9	1	0	11	13
16	6	8	5	0	9	8
17	8	7	5	0	5	10
18	3	13	5	1	6	14
19	8	8	8	3	4	28
20	6	0	1	0	9	12
21	7	18	1	0	8	8
22	13	15	4	1	13	8
23	9	16	3	2	6	16
24	3	8	4	0	3	9
25	2	18	5	1	11	9
26	lost sample (inadequate fixitive)					
27	2	10	7	0	10	14
28	5	13	2	0	8	10
29	7	18	3	0	10	6
30	4	20	7	0	12	9
31	2	11	3	0	4	14
32	8	9	5	1	9	9
33	5	11	3	0	6	12
34	3	22	4	0	13	12
35	5	13	12	1	10	16
36	5	14	1	0	7	8
37	6	12	5	0	3	14
38	4	22	8	1	14	11
39	6	20	4	1	5	9
40	3	9	3	2	6	10
41	10	16	2	1	12	9
42	7	13	3	1	12	12
43	5	15	4	1	7	6

APPENDIX B (continued)

Station	Diaptomus siciloides ♂	Diaptomus siciloides ♀	Diaptomus siciloides Copepodid	Cyclops vernalis ♂	Cyclops vernalis ♀	Cyclops vernalis Copepodid
44	7	13	0	1	10	11
45	10	15	6	1	16	16
46	7	11	3	0	13	12
47	11	12	2	0	5	9
48	13	20	3	5	7	9
49	12	20	3	0	8	11
50	17	12	4	1	8	8
51	13	25	4	3	9	11
52	10	15	2	0	6	6
53	22	21	8	0	11	6
54	11	19	1	1	8	5
55	17	21	3	0	3	6
56	16	12	3	0	5	7
57	19	22	5	3	2	4
58	32	26	1	0	10	5
59	28	28	11	2	15	3
60	25	23	4	1	9	2
61	33	32	8	2	8	10
62	27	27	8	4	23	21
63	24	38	11	2	20	12
64	23	28	7	1	9	4
65	18	33	4	0	3	3
66	6	27	3	2	13	9
67	19	32	8	1	9	10
68	14	25	2	1	5	6
69	7	28	9	0	4	4
70	10	37	3	1	4	5
71	8	21	3	0	4	3
72	6	29	11	3	20	16
73	11	38	14	6	51	17
74	6	18	7	1	15	20
75	5	17	10	0	4	5
76	10	32	10	0	9	8
77	6	31	5	0	8	11
78	4	22	10	0	2	9
79	3	18	6	1	11	9
80	38	105	43	5	58	30
81	5	28	5	1	4	11
82	13	37	14	0	3	8
83	8	41	20	0	8	6
84	7	18	5	0	3	5
85	1	12	7	0	4	6

APPENDIX C

Phytoplankton Densities

Station	*Mallomonas caudata* Total Count	*Mallomonas caudata* $\bar{x}$ per Field	*Mallomonas caudata* No. per ml	Cryptomonadaceae Total Count	Cryptomonadaceae $\bar{x}$ per Field	Cryptomonadaceae No. per ml
1	340	4.57	348	146	1.95	149
2	443	5.91	451	79	1.05	80
3	456	6.08	464	78	1.04	79
4	661	8.81	672	108	1.44	110
5	512	6.83	521	88	1.17	89
6	550	7.33	559	98	1.31	100
7	537	7.16	546	86	1.14	87
8	488	6.51	496	95	1.26	96
9	519	6.92	528	82	1.09	83
10	501	6.68	509	88	1.17	89
11	433	5.77	440	98	1.30	99
12	545	7.27	554	100	1.33	101
13	518	6.91	527	89	1.18	90
14	486	6.48	494	97	1.29	98
15	493	6.57	501	82	1.09	83
16	487	6.49	495	82	1.09	83
17	535	7.13	544	89	1.19	91
18	479	6.39	487	92	1.23	94
19	553	7.37	562	105	1.40	107
20	524	6.99	533	98	1.31	100
21	504	6.72	512	106	1.41	108
22	564	7.52	573	96	1.28	97
23	503	6.71	512	93	1.24	95
24	508	6.77	516	102	1.36	104
25	523	6.97	531	75	1.00	76
26	486	6.48	494	85	1.13	86
27	497	6.63	506	122	1.63	124
28	557	7.43	567	88	1.17	89
29	517	6.89	525	99	1.32	101
30	486	6.48	494	101	1.36	104
31	555	7.40	564	144	1.92	146
32	572	7.63	582	107	1.43	109
33	526	7.01	535	107	1.43	109
34	495	6.60	503	103	1.37	104
35	483	6.44	491	97	1.29	98
36	591	7.88	601	146	1.94	148
37	544	7.25	553	78	1.04	79
38	526	7.01	535	107	1.42	108
39	547	7.29	556	134	1.79	136
40	474	6.32	482	109	1.45	111
41	520	6.93	528	83	1.11	85
42	509	6.97	518	109	1.45	111
43	496	6.61	504	102	1.36	104

APPENDIX C (continued)

Station	Mallomonas caudata			Cryptomonadaceae		
	Total Count	$\bar{x}$ per Field	No. per ml	Total Count	$\bar{x}$ per Field	No. per ml
44	554	7.39	563	127	1.69	129
45	533	7.11	542	107	1.42	108
46	428	5.71	435	115	1.53	117
47	537	7.16	546	116	1.55	118
48	539	7.19	548	87	1.16	88
49	528	7.04	537	165	2.14	163
50	370	4.93	376	46	0.61	46
51	464	6.19	472	214	2.85	217
52	430	5.73	437	145	1.93	147
53	339	4.52	345	179	2.39	182
54	424	5.65	431	158	2.11	161
55	394	5.25	400	123	1.64	125
56	386	5.15	393	138	1.84	138
57	409	5.45	415	183	2.44	186
58	357	4.76	363	149	1.99	152
59	433	5.77	440	225	3.00	229
60	398	5.31	405	180	2.40	183
61	400	5.33	406	235	3.13	239
62	418	5.57	425	196	2.61	199
63	492	6.56	500	248	3.31	252
64	513	6.84	521	266	3.55	271
65	486	6.48	494	144	1.92	146
66	616	8.21	626	216	2.88	220
67	564	7.52	573	209	2.79	213
68	510	6.80	519	153	2.04	156
69	611	8.15	621	275	3.67	280
70	641	8.55	652	186	2.48	189
71	548	7.29	556	199	2.65	202
72	501	6.68	509	160	2.13	162
73	557	7.43	567	165	2.20	168
74	621	8.28	631	170	2.27	173
75	518	6.91	527	18	0.24	18
76	561	7.48	570	110	1.47	112
77	519	6.92	528	158	2.11	161
78	585	7.80	595	181	2.41	184
79	534	7.12	543	207	2.76	210
80	238	3.17	242	152	2.03	155
81	460	6.13	467	150	2.00	153
82	504	6.71	512	165	2.21	168
83	548	7.30	557	182	2.43	185
84	439	5.85	446	126	1.68	128
85	428	5.71	435	167	2.23	170