THE DISTRIBUTION OF ZOOPLANKTON ALONG THE WESTERN SHORE OF LAKE ERIE

Thesis for the Degree of M. S.

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THOMAS F. NALEPA

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ABSTRACT

THE DISTRIBUTION OF ZOOPLANKTON

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OF LAKE ERIE

by

Thomas F. Nalepa

Zooplankton distributions in the near-shore areas of western Lake Erie were studied in relation to six environmental variables - temperature, oxygen, particulate organic carbon, primary productivity, suspended solids, and fish predation. Samples were collected with a Van Dorn water bottle at 2 week intervals from 1 May 1970 to 7 November 1970. Zooplankton density, biomass and composition were compared in four different habitats: near the shore of western Lake Erie, a man-made discharge canal, a shallow creek embayment, and a polluted river.

Distributions were generally uniform within the lake but different from the inshore areas. The lake was intermediate in density but highest in biomass. The discharge canal and the shallow embayment had relatively high densities but were intermediate in biomass. The river was lowest in both density and biomass. Species composition was essentially similar in all the areas but density composition of the major taxa of zooplankton (rotifers, copepods, caldoceran) differed widely. The discharge canal and the shallow embayment had a comparatively high density of rotifers while the discharge canal also had a high density of copepod nauplii. The lake had the highest density of Cladocerans. The river had the lowest density of all major taxa of zooplankton taxa except in June. Mean size of individual plankters was greatest in

the lake, intermediate in the river, and lowest in the discharge canal and the shallow embayment.

These basic differences in zooplankton distributions were attributed mainly to variations in oxygen, food availability, and fish predation. Therefore, where abiotic conditions are tolerable, food availability and predation appeared to be the most influential regulators of zooplankton in the near-shore areas of western Lake Erie.

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OF LAKE ERIE

By

Thomas F. Nalepa

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INTRODUCTION

The purpose of this research was to determine the seasonal variation in the horizontal and vertical distributions of zooplankton along the western shore of Lake Erie in relation to factors that hypothetically regulate their distribution. Much of the resource value of the Great Lakes, including Lake Erie, is derived from the use of its near-shore waters. Any resource use or management program must be based on a sound knowledge of the ecosystem function that influences these resources. Although the zooplankton are not directly utilized as a resource, they are the main trophic link between the algae and the fisheries resource and are likely to have a direct influence on their dynamics. Western Lake Erie is the most thoroughly studied of the Great Lakes, but near-shore variability in the zooplankton, particularly in relation to environmental variation, has not been well-assessed.

The distributions of zooplankton populations are influenced by a complex of chemical, physical, and biological variables. Hypothetically, these variables act in consort upon the plankton and determine any variation in time and space. Of all the variables that could potentially influence zooplankton dynamics, temperature, food, competition and predation are thought to have the most impact. Temperature increases, below critically high levels, enable potential increases in zooplankton densities by reducing maturation time and therefore increasing the production of young animals (Hall, 1964). Considering differential metabolic and reproductive rates, changes in temperature also contribute to the seasonal progression of species through competitive selection. Certainly there are eurythermal and stenothermal species in most large phylogenetic groups with widely differing temperature tolerances and optimums (Odum, 1959). Since the zooplankton differ widely in mean size, variation in species biomass is also potentially important. The larger forms (Cladocera, Copepoda) seem to be positively related to temperature (Hazelwood and Parker, 1961) while the much smaller rotifers can become abundant at various times at greatly differing water temperatures (Davis, 1962). However, attempts to explain large seasonal changes in terms of temperature differences alone have largely met with failure (Davis, 1962).

Two of the more important factors to consider are food and predation. Zooplankton reproductive rates can be highly dependent upon food availability (Hall, 1964; Edmondson, 1964). In general, increased food leads to population increases through increased brood number. Given a moderate, constant supply of food at a moderately low temperature, an increment in the population can be caused by increasing the temperature which, in turn, increases the rate of molting and brood production, or by increasing the food supply which stimulates the production of eggs per brood (Hutchinson, 1967).

The composition and size of available food is also very important. Pennak (1955) suggests that seston is the main source of food for the zooplankton but Davis (1958) found phytoplankton to be more important in western Lake Erie. Total particulate organic carbon is a measure of organic seston and gross primary production is a measure of total phytoplankton availability, as long as phytoplankton respiratory efficiencies are not widely variant.

Competition for food among the zooplankton is very intense (Brooks and Dodson, 1965). Hypothetically, the larger plankters (cladocerans, calanoid copepods) can outcompete the smaller forms (rotifers, small cladocerans) for the same-sized food through increased efficiency of food collecting and greater metabolic efficiency (Brooks and Dodson, 1965). They can also utilize larger particles than the smaller zooplankton. The smaller forms should then be effectively eliminated. However, through size-selective feeding by fish, predation on the larger plankters is much more intense than on the smaller forms (Brooks and Dodson, 1965; Galbraith, 1967; Hall, Cooper and Werner, 1970). In fact, Hall (1964) found that the population size of *Daphnia galeata mendotae*, a relatively large plankter, was probably regulated more by predation than by food supply during the summer. Therefore, when predation is intense, the smaller plankters that escape predation should become dominant.

Oxygen concentrations and inorganic suspended solids can also influence zooplankton distributions. Low oxygen concentrations (1-2 mg/liter) definitely have an adverse effect upon the larger plankters (Pacur, 1939; Hazelwood and Parker, 1961) while rotifers can better withstand low oxygen concentrations (Ruttner, 1952). Inorganic suspended solids should have an indirect effect on the zooplankton by inhibiting the production of food. Turbidity has been found to reduce light penetration and thus reduce algal photosynthesis (Chandler and Weeks, 1945). Also, high concentrations of inorganic suspended solids in western Lake Erie are often indicative of stormy conditions which could also affect zooplankton distributions (Andrews, 1948).

Reduction of all these variables to a minimal number is necessary before any generalities can be made about the planktonic system. This was accomplished by comparing the density, biomass, and composition of zooplankton in near-shore areas that were highly variable in all the above environmental factors purported to regulate zooplankton.

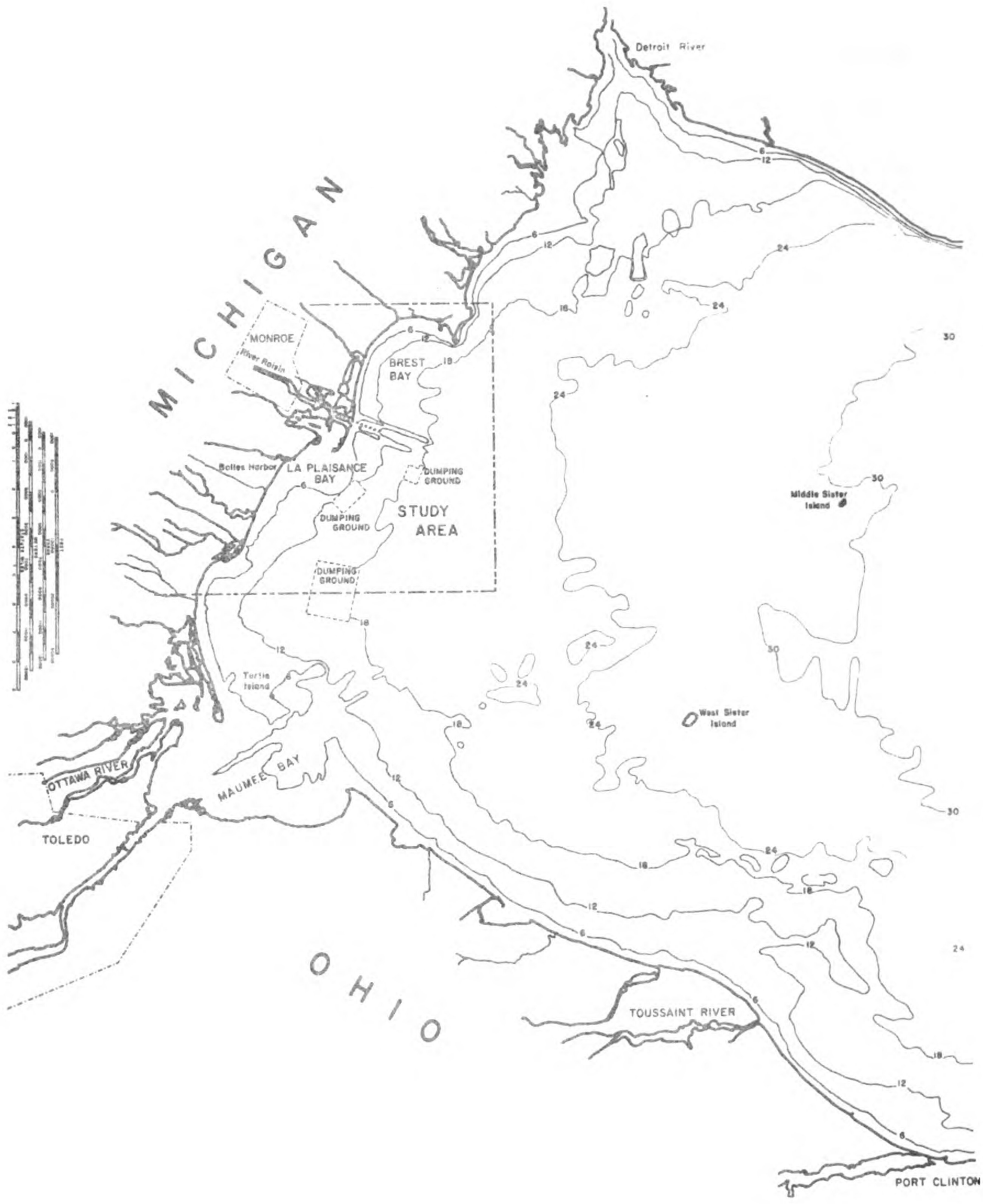
DESCRIPTION OF STUDY AREA

The western basin of Lake Erie receives 95% of all the drainage water entering Lake Erie, yet it comprises only 5% of the total Lake Erie volume. These tributaries carry various industrial, municipal and agricultural wastes into the western basin. The Detroit River, with a mean discharge of 173,000 ft^3/sec, delivers 95% of all water entering the basin. The Maumee River, in the southwest corner of the basin, contributes 3%. The interaction of these two main tributaries, along with the influence of the prevailing southwesterly winds, causes the water along the western shores to circulate counterclockwise (Andrews, 1948). However, circulation patterns can change dramatically during storms.

The western basin averages 8 meters deep. This is particularly true along the western shores where the 6.4 meter contour line extends 8-11 kilometers from the beach (Wright, 1955). Because of this extreme shallowness, the western basin is usually homothermous and thermal stratification occurs only occasionally. However, when stratification does occur, rapid oxygen depletion of bottom waters follows (Carr, et al., 1965). Persistant wind generated mixing permits the resuspension of bottom sediments, which contributes to high turbidities. Large quantities of suspended solids are also contributed by tributaries (Chandler and Weeks, 1945).

The specific near shore region studied centers on the mouth of the Raisin River near Monroe, Michigan (Figure 1). Stations were

Figure 1. Map of western Lake Erie and specific area under study.


Detroit River
MICHIGAN
MONROE
River Raisin
BREST BAY
Bolles Harbor
LA PLAISANCE BAY
DUMPING GROUND
DUMPING GROUND
STUDY AREA
DUMPING GROUND
Middle Sister Island
Turtle Island
West Sister Island
OTTAWA RIVER
MAUMEE BAY
TOLEDO
OHIO
TOUSSAINT RIVER
PORT CLINTON

located as given in Figure 2. Stations positioned in the lake (1-6) were oriented parallel to the prevailing north-easterly currents and north and south of the mouth of the Raisin River. The stations are about 1-2 km offshore and about 1 1/2 km apart except Station 6 which is 3 km offshore and 5.5 km southwest of Station 5. Water depth is 5-6 m at all the lake stations except Station 4 (3-4 m). Bottom sediments are quite variable. Stations 1 and 2 are composed of silt, sand, and gravel, Stations 3, 4, and 5 are predominantly sand and Station 6 is predominantly silt.

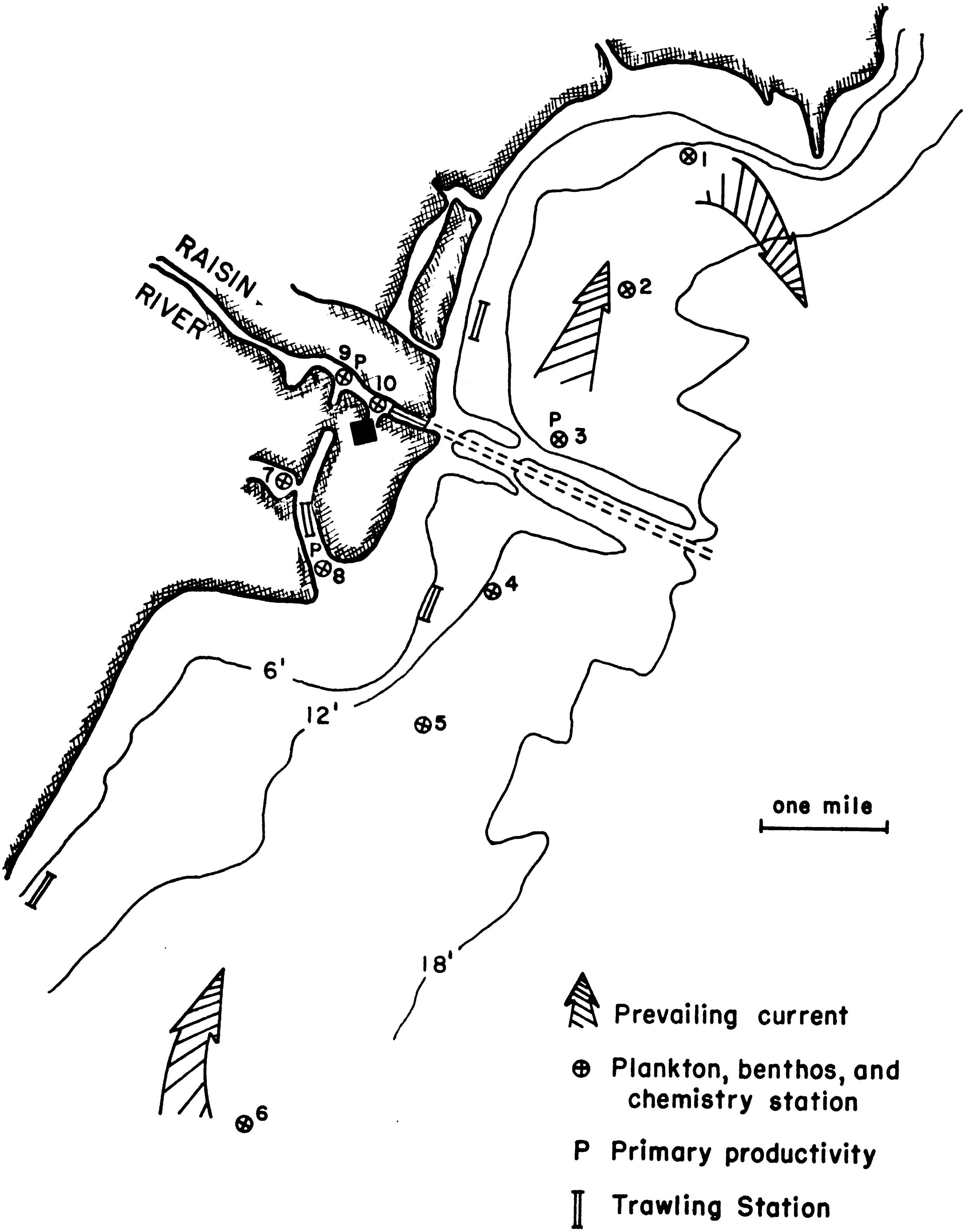
Plum Creek (Station 7) is a relatively shallow (1-2 m), broad (1 km) embayment that fosters the growth of scattered macrophytes. Bottom sediments consist mainly of silt and clay with particulate plant debris. The creek enters into the discharge canal (Station 8) with a discharge that is usually less than 1 m^3/sec.

The discharge canal was recently constructed (1969-1970) to carry the discharged cooling water from a new stream-electric plant. Its waters are influenced by both Plum Creek and Lake Erie. Water depth is 6-7 m (dredged) with a bottom composed of silt, clay, and plant debris. The canal is 2 1/2 km long and 150 m wide.

The polluted River Raisin (Station 9) receives municipal wastes, heavy metals, and paper mill wastes from Monroe, Michigan. Water depth is 6-7 m (dredged) with a bottom of putty-like silt combined with paper fiber and traces of oil. In 1970, the mean discharge into the lake was 17 m^3/sec.

Temperature varied uniformly among the six lake stations, while differences at Plum Creek, the discharge canal and the river were more discernable (Figure 3). In early May, temperatures were 12.8° C to 15° C in the lake, 17° C at Plum Creek and the discharge canal, and

Figure 2. Map of the study area with the location of sampling stations.

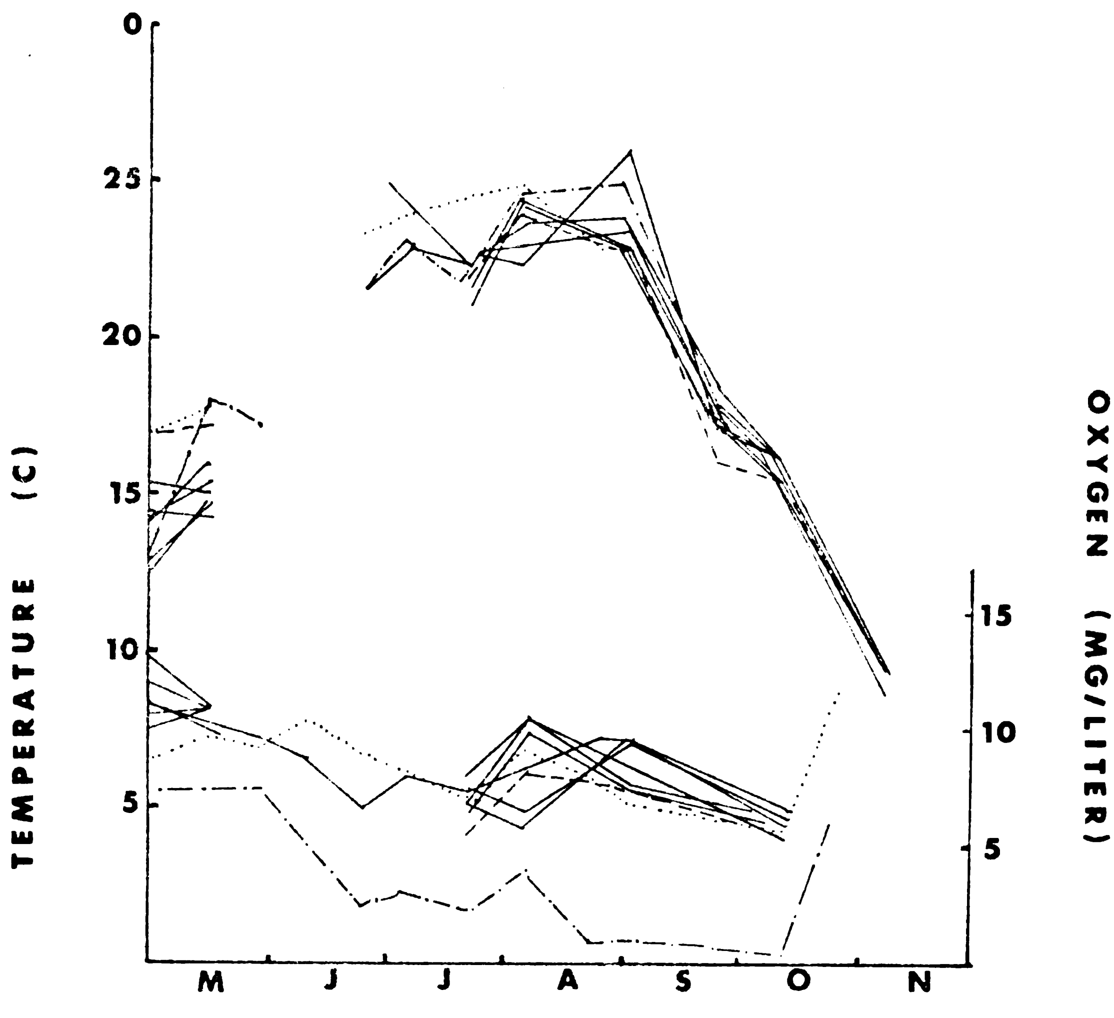

RAISIN RIVER
9 P
10
P 3
1
2
7
P 8
4
5
6
6'
12'
18'
one mile
Prevailing current
Plankton, benthos, and chemistry station
P Primary productivity
Trawling Station

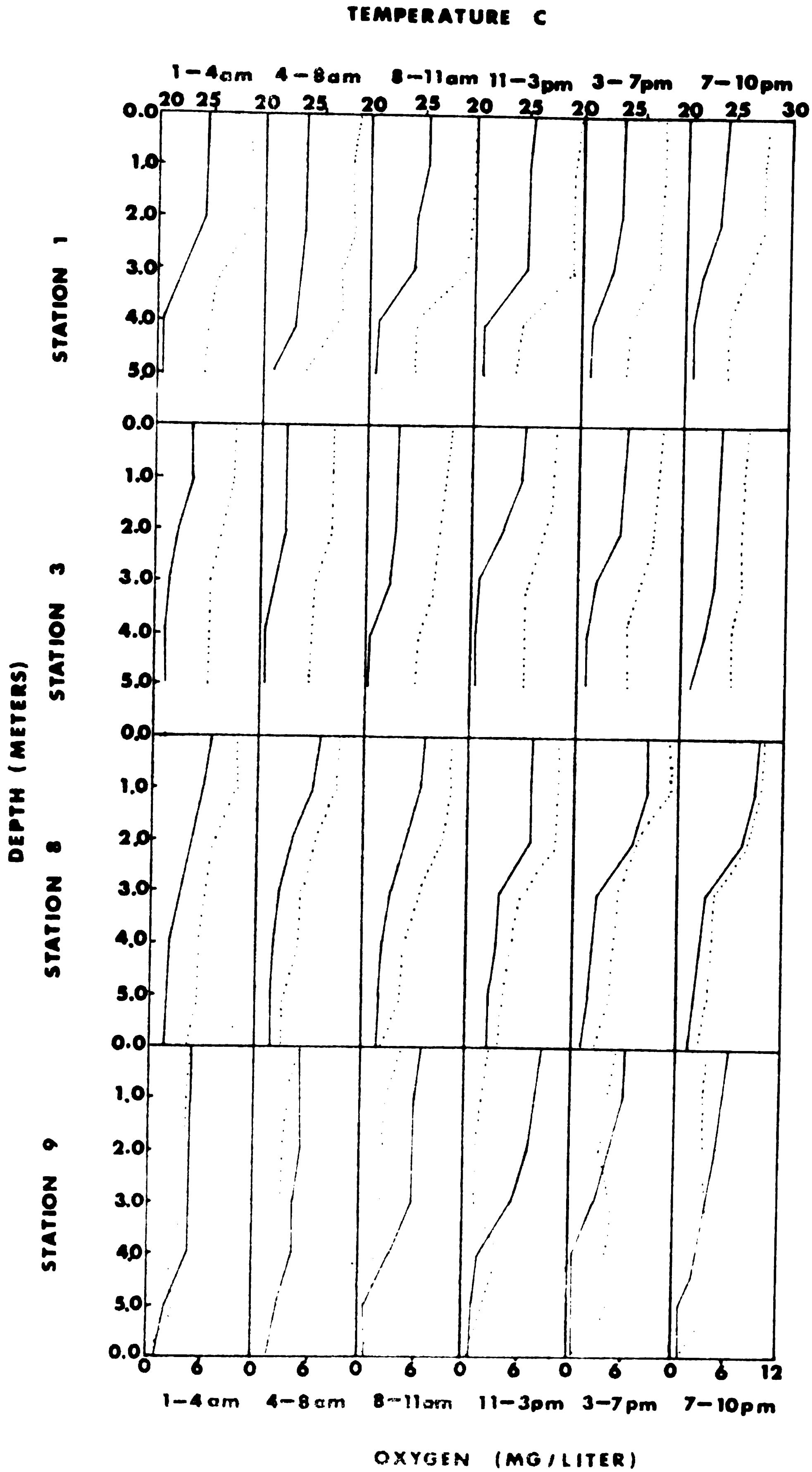
13.9° C in the river. By July 24, all stations reached 22° C other than the discharge canal, where it was slightly warmer at 24.5° C. Peak seasonal temperatures occurred in August and early September. The differences that occurred among the stations at this time were probably due to diurnal variations incurred by sampling over an eight to ten hour period. On July 1, when temperatures were measured throughout a 24-hour period at four of the stations, the diurnal range at each station was similar to the range found among all the stations on each late summer sampling date (Figure 4). After early September, temperatures decreased at all stations until, on November 7, the average was 9.5° C. Ice began to form along shore in early December.

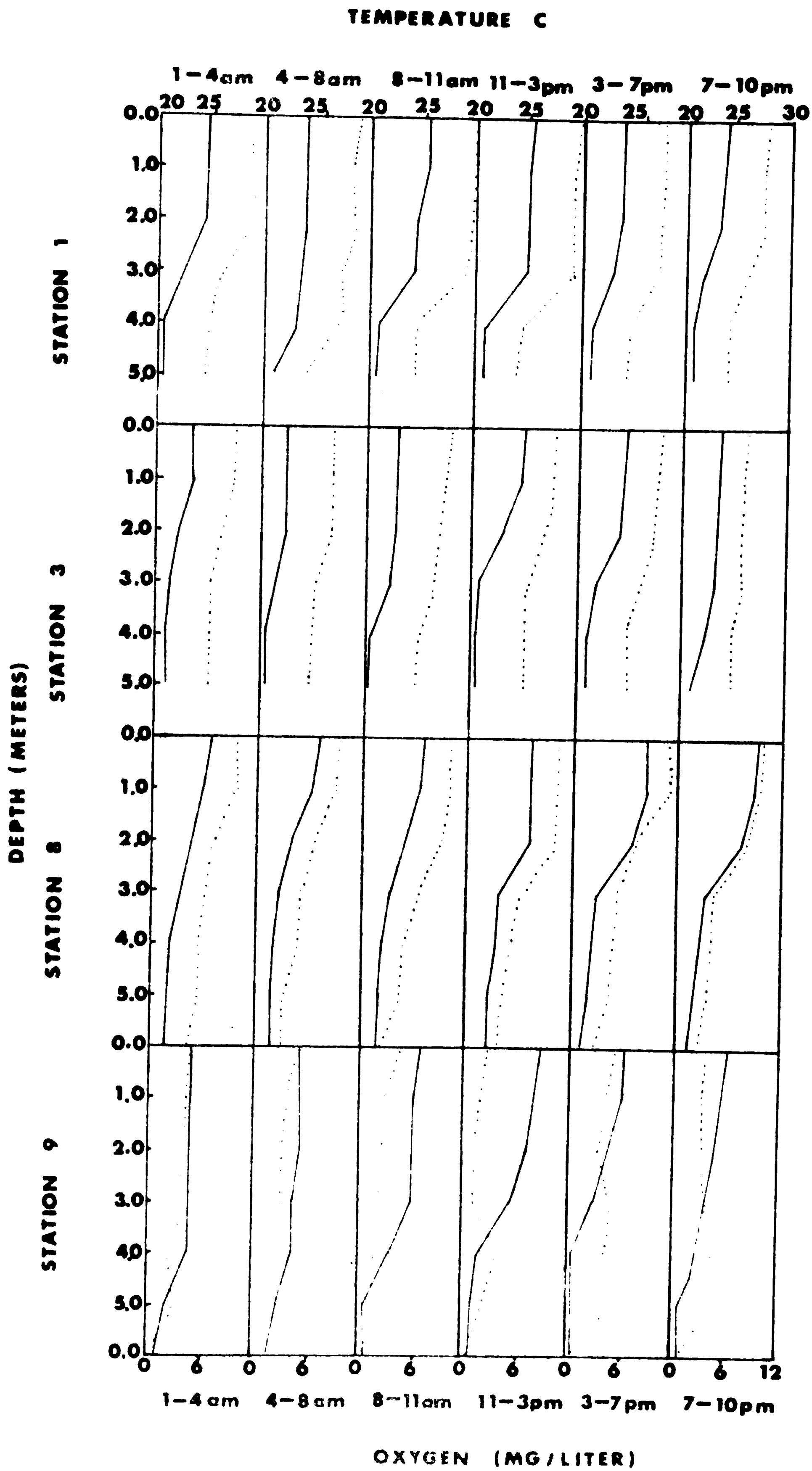
All the stations showed seasonally similar oxygen concentrations except for the river, which was always lower (Figure 3). Highest concentrations occurred in early May and ranged from 9 mg/liter in the lake to 5.5 mg/liter in the river. Concentrations decreased uniformly until early August when some station variation occurred, but, like temperature, part of this variability was due to the different times of day the recordings were made. After August, concentrations generally decreased until, on October 11, the oxygen content was 4 mg/liter at all stations except in the river, where it was only 0.5 mg/liter. Concentrations in the discharge canal and the river began to rise sharply in late October, probably in delayed response to the seasonal cooling.

The diurnal variations in temperature and oxygen profiles for a 24-hour period (July 1, 1970) are given in Figure 4. At the lake stations (1, 3) there was a diurnal temperature variation of 2° C while oxygen concentrations varied between 2-3 mg/liter. Thermal stratification was strongest during the afternoon hours, with the thermocline between 3-4 m deep at Station 1 and 2-3 m deep at Station

Figure 3. Mean seasonal variation of temperature and oxygen. ______Lake; - - - Plum Creek; .... Discharge Canal; _._._. River.


TEMPERATURE (C)
0
25
20
15
10
5
OXYGEN (MG/LITER)
15
10
5
M
J
J
A
S
O
N


TEMPERATURE C
1-4am 4-8am 8-11am 11-3pm 3-7pm 7-10pm
20 25 20 25 20 25 20 25 20 25 20 25 30
DEPTH (METERS)
STATION 1
STATION 3
STATION 8
STATION 9
0.0 1.0 2.0 3.0 4.0 5.0
0 6 0 6 0 6 0 6 0 6 0 6 12
1-4am 4-8am 8-11am 11-3pm 3-7pm 7-10pm
OXYGEN (MG/LITER)



TEMPERATURE C
1-4am 4-8am 8-11am 11-3pm 3-7pm 7-10pm
20 25 20 25 20 25 20 25 20 25 20 25 30
0.0 1.0 2.0 3.0 4.0 5.0
STATION 1
STATION 3
STATION 8
STATION 9
DEPTH (METERS)
0 6 0 6 0 6 0 6 0 6 0 6 12
1-4am 4-8am 8-11am 11-3pm 3-7pm 7-10pm
OXYGEN (MG/LITER)

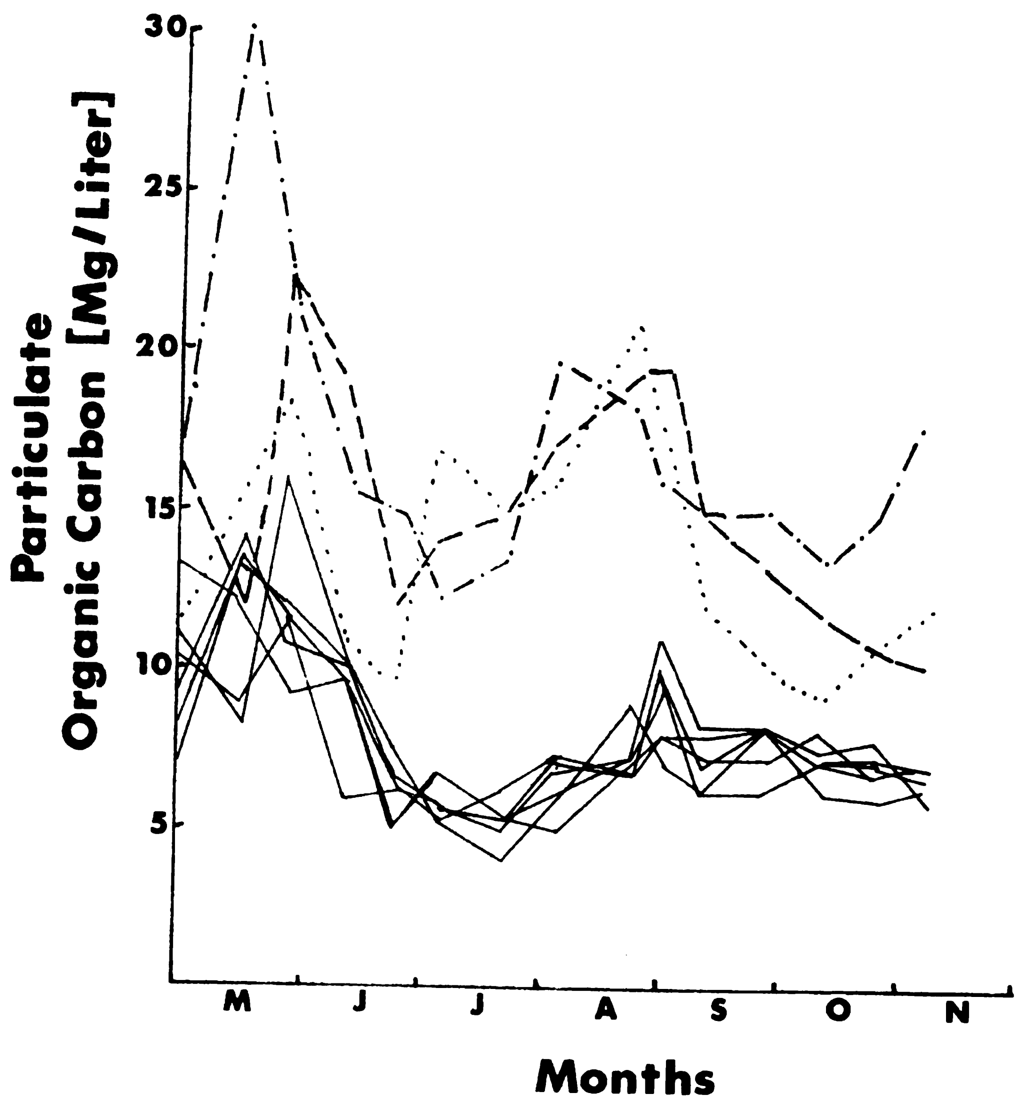
3. The maximum change in one meter was a decrease of 3.5° C in temperature and 6 mg/liter in oxygen at Station 1.

The discharge canal surface temperatures varied from 25.5° C to 28.0° C while oxygen concentrations varied between 8.5 mg/liter to 11.0 mg/liter during the course of the day. A sharp thermocline occurred at 2-3 m during the period of stratification from early afternoon to late evening.

A thermocline occurred in the river at 3-4 m in early afternoon with temperatures dropping from 24.5° C to 21.5° C in 1 m. Oxygen concentrations were nearly uniform at all depths until early afternoon. At that time, oxygen concentrations increased only at the 3-5 m depth and lasted until late evening. Perhaps the best explanation for this phenomena is the upstream movement of oxygenated lake water under a downstream surface flow of river water during a seiche in the lake. Data obtained from the Corps of Engineers indicates a rise of 1.5 ft in the lake from 12 noon to 9 p.m. on this date.

A potential indicator of available food, the seasonal variability of particulate organic carbon (> .45μ) at the 0.5 m depth is summarized in Figure 5. Concentrations of particulate matter at 2.5 m were usually similar (within 10%) to concentrations at 0.5 m at all stations. The lake stations showed similar seasonal concentrations but averaged consistently lower than Plum Creek, the discharge canal, and the river. Highest concentrations in the lake occurred in late May with a maximum of 12 mg/liter. Concentrations then decreased and remained low until early August with another peak on September 1, 1971. This peak, however, was lower than that in the spring, with a maximum of 11 mg/liter. All the lake stations recorded stable concentrations of 6-8 mg/liter during the fall months.

Figure 5. Mean seasonal variation of particulate organic carbon. ____Lake; --- Plum Creek; ....Discharge Canal; _._._. River.


30
25
20
15
10
5
Particulate
Organic Carbon [Mg/Liter]
M
J
J
A
S
O
N
Months

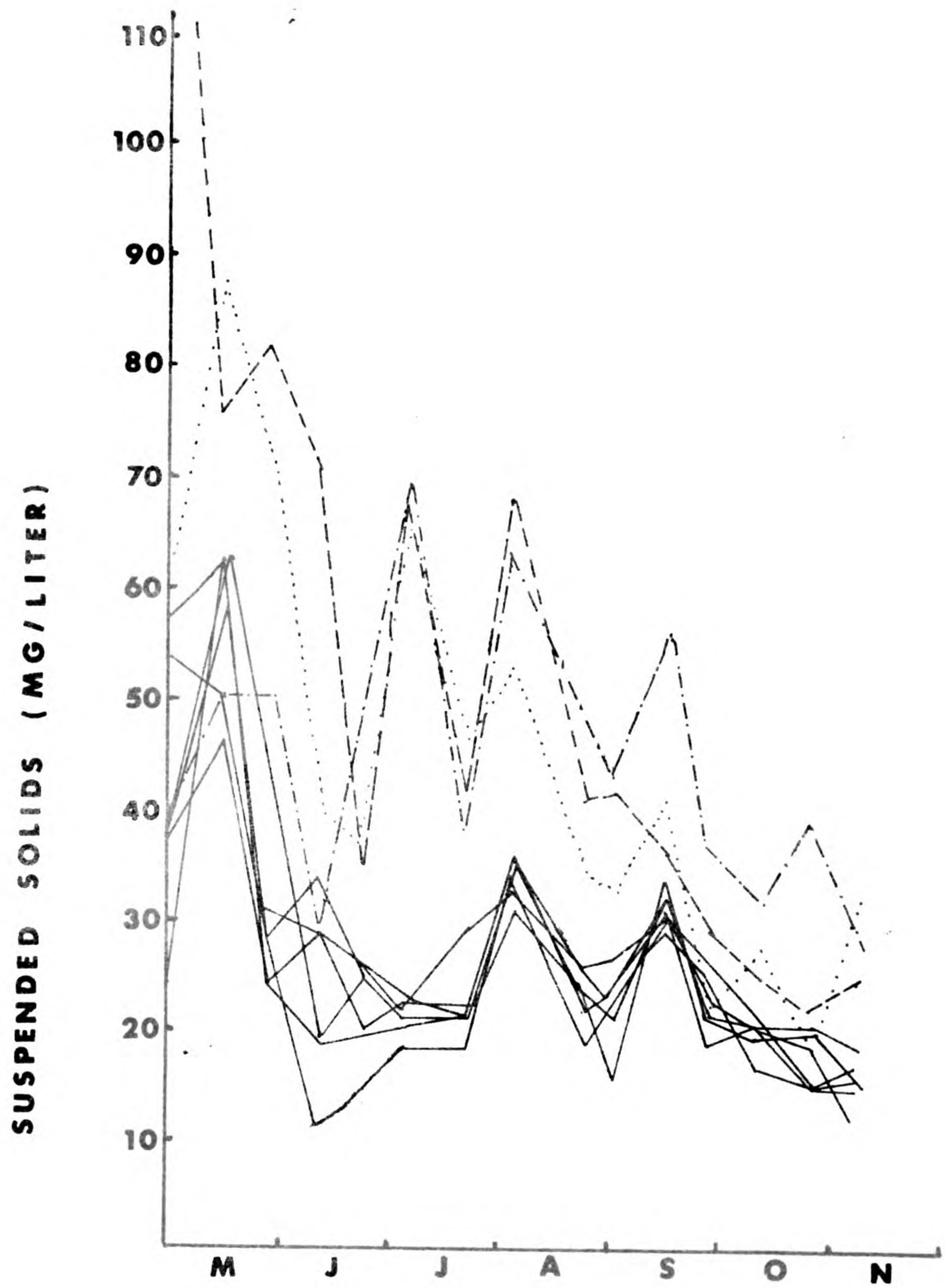
Particulate organic carbon at Plum Creek, the discharge canal, and the river averaged 3-10 mg/liter higher than the lake on any one sampling date. As in the lake, concentrations were high in late May with a maximum of 25 mg/liter at the river. The late summer peak at these three stations began in early August and remained high until September 1. Each of these areas peaked at different times. General decreases in concentrations were recorded during the fall months with the river having significantly higher concentrations than the other areas.

Suspended solids (seston) consist mainly of plankton, detritus, and resuspended bottom sediments and is an indicator of total particulate material in the water. Seasonally, three definite peaks occurred at the lake stations: May 15 - maximum of 63 mg/liter; August 4 - maximum of 36 mg/liter; and September 15 - maximum of 33 mg/liter (Figure 6). The lake concentrations varied very little among stations except in early June. At this time, stations north of the river (Stations 1-3) were significantly lower than those south (Stations 4-6).

Except for an additional peak on July 7, Plum Creek, the discharge canal, and the river showed seasonal trends comparable to the lake. However, levels were usually twice as high, with a maximum of 111.3 mg/liter at Plum Creek on May 15 and a minimum of 18 mg/liter at the discharge canal on October 25. The river had significantly higher concentrations during the fall months.

During 1970, Parkhurst (1971) demonstrated that fish were unevenly distributed throughout the study area. Fish numbers and biomass were highest in the discharge canal, intermediate in the lake, and low in the river. Total values for numbers and biomass (kg) were: 2423 and 143.6 in the discharge canal; 2058 and 85.0 in the lake; and 173 and 3.3 in the river. The river was devoid of most fish species throughout

Figure 6. Mean seasonal variation in suspended solids.
____Lake; ----Plum Creek; ....Discharge Canal;
_._._._. River.


SUSPENDED SOLIDS (MG/LITER)
110
100
90
80
70
60
50
40
30
20
10
M
J
J
A
S
O
N

the sampling period except in late fall when oxygen concentrations approached saturation. The more important species included: yellow perch (*Perca flavescens*), white bass (*Roccus chrysops*), carp (*Cyprinus carpio*), goldfish (*Crassius auratus*) and gizzard shad (*Dorosoma cepedianum*).

As an indicator of available algal food, gross primary productivity measurements were taken at two week intervals throughout the sampling period (M. Marcus, unpublished data). The discharge canal had significantly higher values ($p < .05$) than the lake or river, which were similar although the lake averaged slightly higher. The seasonal means (spring, summer, fall), given as $mgC/m^2/day$, for the three areas were: 2447, 3302, 2636 in the discharge canal; 1031, 2097, 828 in the lake; and 935, 1860, and 839 in the river. Species composition was uniform at the three areas.

METHODS AND MATERIALS

Experimental Design and Analysis

Zooplankton samples were taken at two-week intervals from May 1, 1970 to November 7, 1970. Incomplete sets of samples were taken on April 18, 1970 and February 18, 1970. Triplicate samples were taken from all the stations at each of two depths, 0.5 and 2.5 meters, except the shallow Plum Creek station which was only sampled at 0.5 m. From July 7 to October 11 a single sample from each station at 5.5 meters was added. The various stations were marked by buoys and the replicate samples were taken about 500 ft. east and west of this buoy. At Plum Creek (Station 7), the discharge canal (Station 8) and the river (Station 9) replicate samples were taken about 100 ft. apart.

The extent of vertical day-night movement was measured by taking night samples on 6 dates and continuous 24-hour sampling on one date (1 July 1970). The night samples consisted of one sample each from 0.5 and 2.5 m depths at 3 stations (1, 3, 9) while the 24-hour analysis consisted of taking one sample from 0.5, 2.5 and 5.5 m depths at 4 stations (1, 3, 8, 9) every 4 hours.

Variance among stations and depths was analyzed on each sampling date for numbers, biomass and percent composition of the major taxa of zooplankton. This was followed by Tukey's multiple range comparison of stations and the least significant difference between depths. Plum Creek was excluded from the analysis of variance (only 1 depth) but included in the multiple range comparisons. Single samples taken from

5.5 m depths were not included in the analysis. All calculations were made on the raw data before conversions to numbers /liter or mg/liter. Day-night comparisons were made with the Chi-square test. Arcsin transformations were performed on all data expressed as percentages before statistical tests were applied.

Field and Lab Techniques

Samples were collected with an 8-liter Van Dorn water bottle. The animals in four liters of the sample were concentrated in a #25 Wisconsin plankton bucket and immediately preserved in 5% formalin. Water from the remaining four liters was analyzed for particulate organic carbon and total suspended solids (seston).

In the laboratory, each sample was adjusted to a known volume of concentrate. This ranged from .05 to .015 of the total sample size, depending upon the plankter abundance. Two 1-ml aliquots from each sample were placed in a Sedgewick-rafter counting cell where, under a binocular zoom scope, the plankters were counted and identified to species. When possible, life-history stage, sex, and number of eggs per individual were also recorded. No attempt was made to identify the nauplii or copepedites.

The length of each plankter other than rotifers and nauplii was measured with a Whipple micrometer. The Cladoceran species were placed into .25 mm size categories, including the carapace and helmet, with the exception of *Bosmina* sp. and *Chydorus sphaericus* (0.1 mm intervals) and *Leptodora kindtii* (immature or mature). The calanoid and cyclopoid juveniles were also categorized according to length (1 mm intervals). The size of maturity of *Daphnia* sp. was set at 1.00 mm (Hall, 1964).

Volume measurements were made by randomly choosing 20 individuals of each species size category throughout the sampling dates and measuring their individual areas. Volume was then calculated by assuming the plankters to be either a cone, cylinder, sphere, or ellipsoid (Davis, 1958). Proportions between the body volume of one species and a similar one (Ravera, 1969) were used as a guideline.

Total volume was calculated by summing the products of the mean volume and the number of each species (Naucerk, 1964). Dry weight was assumed to be 15% of wet weight and constant with a specific gravity of 1.00 (Ravera, 1969). The species list and their corresponding dry weights are given in Table 1.

The stomach contents of yellow perch (Perca flavescens) and white bass (Roccus chrysops) were analyzed by taking 1-ml aliquots from the entire contents and calculating th percentage each species made of the total.

Methods employed for the determination of suspended solids and particulate organic carbon were basically those outlined by the EPA (1969).

Temperature and oxygen profile readings were made with a YSl oxygen meter which was periodically standardized against Winkler determinations of oxygen. Duplicate readings were usually made for each depth at each station.

TABLE 1: Estimated Dry Weights (μg.) and Lengths (mm) of Zooplankton Species

Rotifera (14 species)	Length	Weight
Asplanchna sp.		2.1
Brachionus calyciflorus		.06
Brachionus diversicornis		.01
Brachionus spp.		.01
Conochilus unicornis		.01
Euchlanis sp.		.05
Filinia longiseta		.005
Keratella cochlearis		.005
Keratella quadrata		.01
Kellicottia longicornis		.005
Polyarthra spp.		.01
Pompholyx sulcata		.005
Synchaeta stylata		.03
Trichocera sp.		.01
Cladocera (7 species)		
Bosmina spp.	.25	1.35
Bosmina spp.	.35	1.95
Bosmina spp.	.50	3.90
Ceriodaphnia sp.	.50	4.2
Ceriodaphnia sp.	.75	25.3
Ceriodaphnia sp.	>1.0	40.5
Chydorus sphaericus		1.35
Daphnia galeata mendotae	.5	2.8
Daphnia galeata mendotae	.75	4.3
Daphnia galeata mendotae	1.00	10.8
Daphnia galeata mendotae	1.25	16.5
Daphnia galeata mendotae	1.50	35.0
Daphnia galeata mendotae	1.75	50.0
Daphnia galeata mendotae	>2.00	55.0
Daphnia retrocurva	.5	2.8
Daphnia retrocurva	.75	4.3
Daphnia retrocurva	1.00	10.8
Daphnia retrocurva	1.25	16.5
Daphnia retrocurva	1.50	27.0
Daphnia retrocurva	1.75	42.1
Daphnia retrocurva	>2.00	44.0
Diaphanosoma leuchtenbergiana	.50	8.4
Diaphanosoma leuchtenbergiana	.75	11.2
Diaphanosoma leuchtenbergiana	>1.00	16.4
Leptodora kindtii		
Copepoda (10 species)		
Nauplii		.01
Juvenile cyclopoid	.25	1.0
Juvenile cyclopoid	.35	1.9
Juvenile cyclopoid	.50	3.0

TABLE 1: (con't.)

	Length	Weight
Juvenile diaptomid	.25	1.0
Juvenile diaptomid	.35	1.9
Juvenile diaptomid	.50	3.0
Canthocamptus robertcokeri		1.9
Cyclops vernalis		8.6
Cyclops bicuspidatus		8.6
Diaptomus ashlandi (female)		8.5
Diaptomus ashlandi (male)		7.0
Diaptomus minutus (female)		5.5
Diaptomus minutus (male)		5.0
Diaptomus oregonensis (female)		8.5
Diaptomus oregonensis (male)		7.0
Diaptomus sicilis (female)		8.5
Diaptomus sicilis (male)		7.0
Diaptomus siciloides (female)		8.5
Diaptomus siciloides (male)		7.0
Eurytremora affinis		8.5
Tropocyclops prasinus		3.0

RESULTS

Horizontal Distributions

Zooplankton Density

Inconsistent and relatively minor differences in density occurred among the lake stations throughout the sampling period but densities at inshore stations were consistently and often greatly different from densities in the lake (Figure 7). Lake densities were usually less than in the discharge canal and Plum Creek but more than in the river. Most lake stations clearly exhibited two density peaks, a relatively minor peak in late spring and a major one in late summer. The greatest mean density, 1,330/liter, occurred at Station 1 on September 1.

Plum Creek and the discharge canal had significantly ($p < .05$) higher densities than all or most of the other stations from May 1 to August 23, excluding May 27 (Table 2). Differences were not detected in the fall. Throughout the sampling period, the discharge canal usually had higher densities than Plum Creek, being significantly so on four dates. The greatest difference, 1,470/liter, occurred on June 24 when the discharge canal had a density of 3,150/liter. This was the highest density recorded for any station on any one sampling date.

Zooplankton in the river were consistently less dense than in any other station. Multiple range tests indicated that the river was significantly ($p < .05$) lower than all or most of the other stations on about half of the dates sampled. Only on June 23 and October 25 were plankters at any stations lower in density than in the river. Densities

Figure 7. Mean seasonal variation of total zooplankton density. ____ .5m; .... 2.5m.

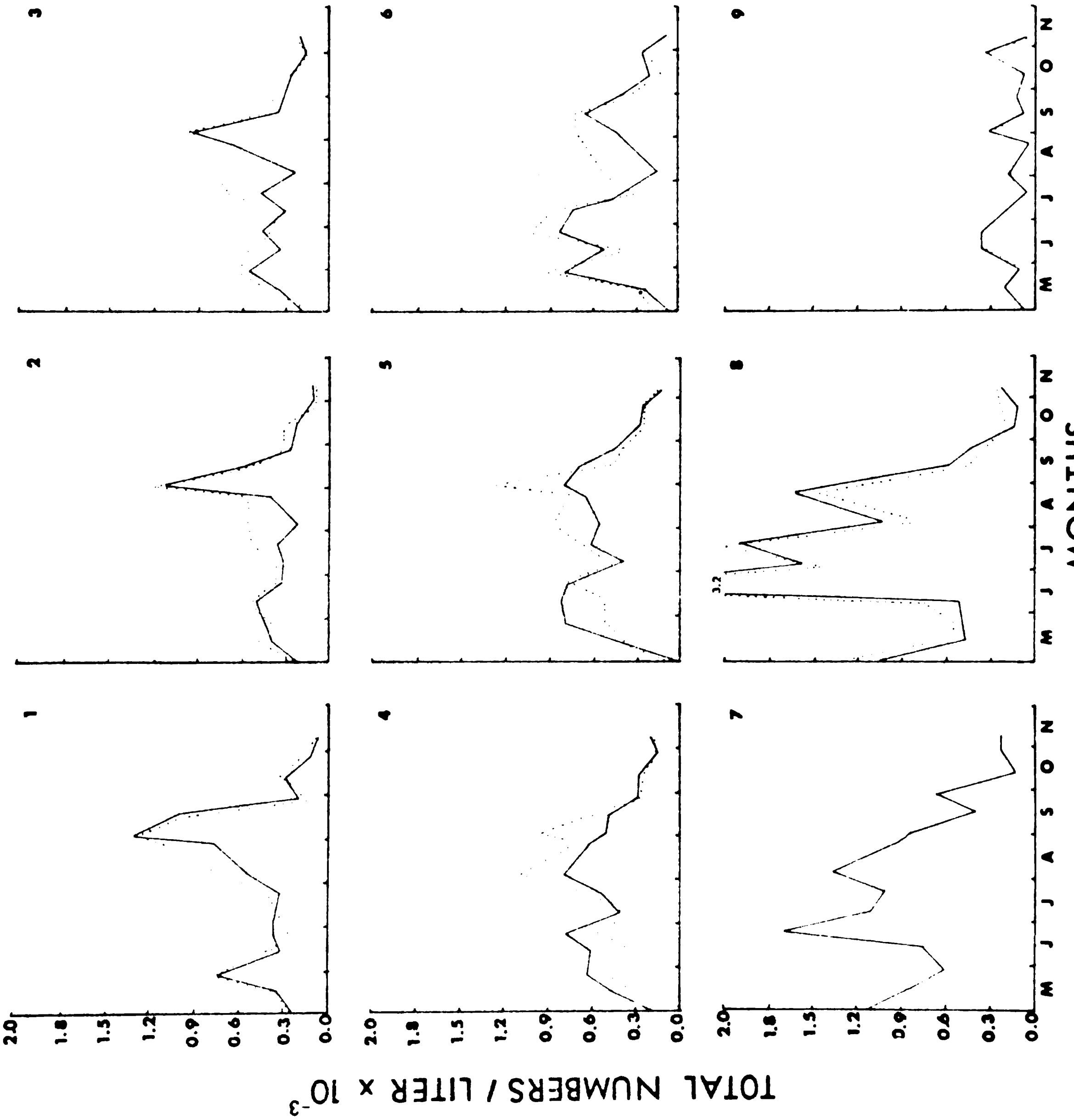

TOTAL NUMBERS / LITER x 10-3
MONTHS
1
2
3
4
5
6
7
8
9
2.0 1.8 1.5 1.2 0.9 0.6 0.3 0.0
M J J A S O N
3.2

Table 2: Numbers of zooplankton per liter arranged in increasing order of abundance at the sampling stations.

2 May 1970

Station	9	5	6	3	2	1	4	7	8
Mean	88	144	168	195	241	249	304	1122	1149
Multiple Range									

15 May 1970

Station	9	6	1	5	3	4	2	8	7
Mean	179	262	363	409	414	420	427	693	855
Multiple Range									

27 May 1970

Station	9	2	8	5	3	4	7	1	6
Mean	87	422	504	555	577	598	613	751	849
Multiple Range									

10 June 1970

Station	9	1	6	3	4	2	5	8	7
Mean	342	359	435	459	480	585	667	728	771
Multiple Range									

23 June 1970

Station	1	2	9	3	4	5	6	7	8
Mean	326	348	352	454	684	738	912	1680	3150
Multiple Range									

Table 2 : (con't.)

7 July 1970

Station	9	1	3	2	4	5	6	7	8
Mean	286	333	334	334	391	429	777	1080	1530
Multiple Range									

21 July 1970

Station	9	6	1	2	3	4	5	7	8
Mean	97	354	387	453	582	588	628	1011	2032
Multiple Range									

4 August 1970

Station	9	6	2	3	1	5	8	4	7
Mean	174	336	394	504	657	714	925	949	1372
Multiple[1] Range									

23 August 1970

Station	9	2	4	3	5	1	7	8
Mean	54	483	663	705	708	915	927	1575
Multiple Range								

1 September 1970

Station	9	6	4	7	3	5	2	8	1
Mean	321	571	736	825	960	1023	1159	1248	1309
Multiple[1] Range									

Table 2 : (con't.)

15 September 1970

Station	9	3	7	2	8	4	5	6	1
Mean	66	392	417	561	523	511	582	678	990
Multiple Range									

27 September 1970

Station	9	1	2	4	3	6	8	5	7
Mean	105	181	288	321	342	394	405	438	660
Multiple Range									

10 October 1970

Station	9	7	6	8	4	3	5	2	1
Mean	63	138	156	174	264	264	271	274	288
Multiple Range									

25 October 1970

Station	2	8	1	4	3	7	5	6	9
Mean	120	135	148	157	168	232	235	237	262
Multiple Range									

7 November 1970

Station	9	1	6	2	5	4	3	7	8
Mean	55	67	90	120	141	193	202	241	255
Multiple Range									

1. Interaction (p <.05) exists between depths and stations.

were significantly lower than the discharge canal on all dates and lower than Plum Creek on all but two dates (October 11 and 27).

The mean (± .95 confidence) density in numbers per liter throughout the sampling period was 464 ± 135 in the lake, 797 ± 222 at Plum Creek, 1005 ± 360 in the discharge canal, and 170 ± 57 in the river. In summary, Plum Creek and the discharge canal had relatively dense concentrations of zooplankton, the lake was intermediate, and the river was lowest.

Zooplankton Biomass

No obvious trends or differences appeared to exist in zooplankton biomass at the lake stations (Figure 8). However, subtle differences indicate that all stations did not change uniformly in biomass over the sampling period. Only 3 of the 6 lake stations were ever significantly different from the majority (3 of 5) of the remaining stations. Of the seven dates when these stations were higher, Station 4 was significantly higher on three dates, Station 6 on three dates, and Station 1 on one date. Only Stations 1 and 6 were ever significantly lower than the remaining stations, both on four dates each (Table 3). This indicates that Stations 2, 3, 4, and 5 tended to change in phase, with Station 4 having inconsistently greater concentrations than all the other lake stations; that Station 6 was the most out of phase (Station 6 was about 5 km from the closest station while all the other lake stations were within 3 km of each other); and that Station 1 was somewhat out of phase, with tendencies toward lower concentrations.

Zooplankton biomass in Plum Creek and the discharge canal was lower than in the lake but higher than in the river. In the spring, biomass here was highest of all areas. Significant biomass differences between Plum Creek and the discharge canal occurred on only two dates,

Figure 8. Mean seasonal variation of total zooplankton biomass. ____ .5m; .... 2.5m.

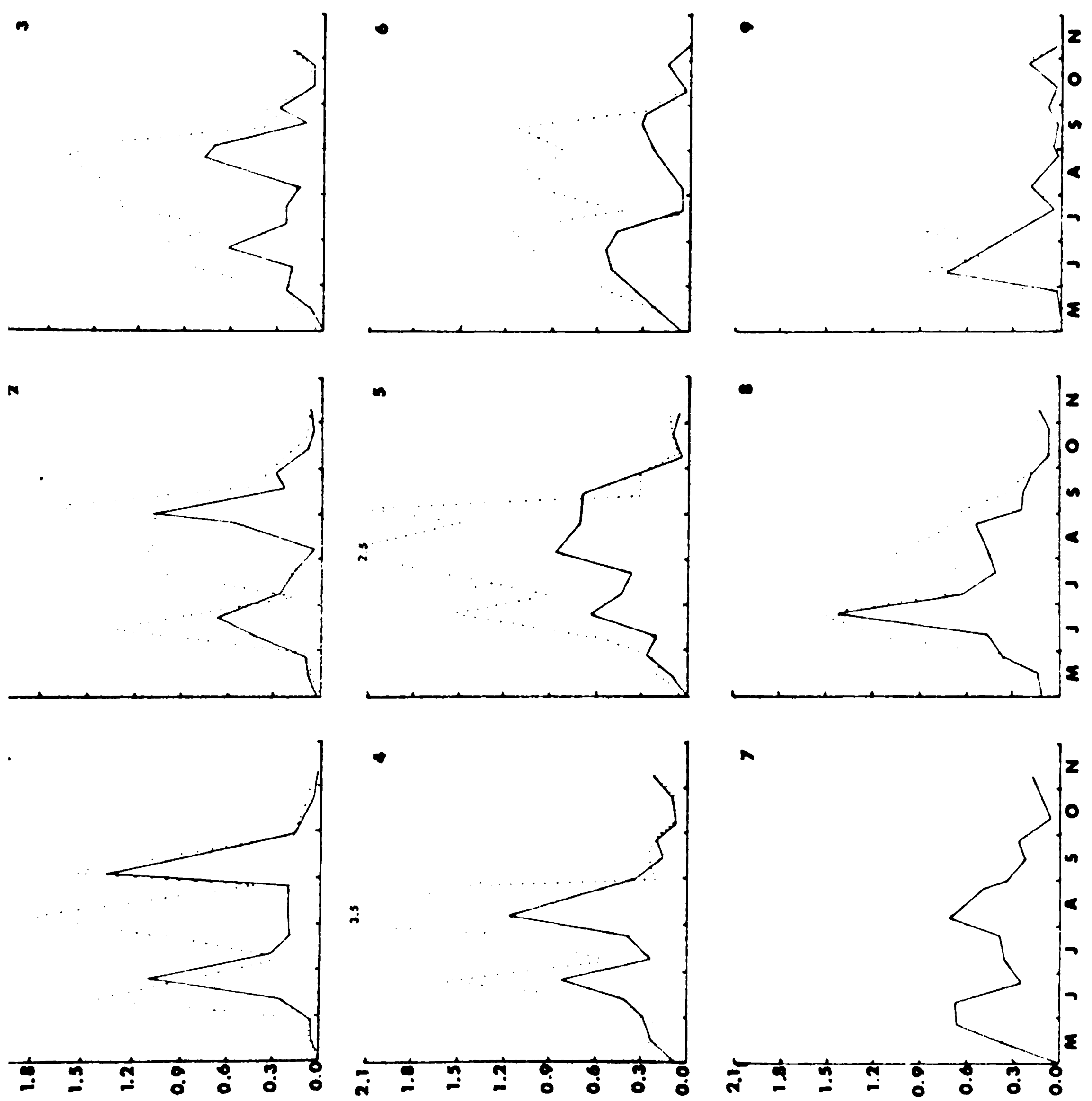

MG/LITER
MONTHS
M J J A S O N
1.8 1.5 1.2 0.9 0.6 0.3 0.0
2.1 1.8 1.5 1.2 0.9 0.6 0.3 0.0
3.5
2.5
2
3
4
5
6
7
8
9

Table 3 : Biomass (mg/liter) of zooplankton arranged in increasing order of abundance at the sampling stations.

2 May 1970

Station	3	6	9	2	1	5	4	7	8
Mean	.02	.02	.02	.03	.03	.03	.08	.10	.12
Multiple Range	—	—	—	—	—	—			
							—	—	
								—	—

15 May 1970

Station	9	1	2	3	5	6	8	4	7
Mean	.03	.05	.06	.15	.16	.20	.20	.24	.37
Multiple Range	—	—	—	—	—				
				—	—	—	—	—	
						—	—	—	—

27 May 1970

Station	9	1	2	5	4	3	8	6	7
Mean	.03	.06	.08	.22	.25	.27	.37	.44	.65
Multiple Range	—	—	—	—					
		—	—	—	—				
			—	—	—	—			
				—	—	—	—		
					—	—	—	—	
									—

10 June 1970

Station	5	3	4	7	6	9	8	1	2
Mean	.42	.51	.53	.66	.68	.81	.82	.84	.96
Multiple[1] Range	—	—	—	—	—	—	—	—	
			—	—	—	—	—	—	—

23 June 1970

Station	7	9	2	6	3	1	5	4	8
Mean	.25	.45	.70	.82	.88	.93	1.09	1.22	1.49
Multiple Range	—	—	—	—	—	—			
		—	—	—	—	—	—		
				—	—	—	—	—	—

Table 3: (con't.)

7 July 1970

Station	2	1	7	4	3	9	5	8	6
Mean	.23	.30	.40	.42	.45	.61	.68	.70	.85
Multiple Range									

21 July 1970

Station	9	6	7	8	1	2	3	4	5
Mean	.05	.29	.39	.49	.57	.70	.79	.81	1.07
Multiple Range									

4 August 1970

Station	9	6	2	7	8	3	1	5	4
Mean	.18	.58	.58	.74	.75	.78	1.00	1.57	2.36
Multiple[1] Range									

23 August 1970

Station	9	1	7	8	4	2	5	3
Mean	.02	.38	.51	.63	.73	.83	1.11	1.24
Multiple Range								

1 September 1970

Station	9	7	8	6	4	3	2	5	1
Mean	.03	.32	.44	.56	.92	1.17	1.39	1.41	1.54
Multiple[1] Range									

Table 3 : (con't.)

15 September 1970

Station	9	3	4	7	2	8	5	1	6
Mean	.02	.17	.21	.22	.35	.36	.52	.76	.77
Multiple[1] Range	———	———	———	———	———	———			
		———	———	———	———	———	———		
						———	———	———	———

27 September 1970

Station	9	1	8	4	7	2	6	5	3
Mean	.10	.17	.21	.21	.26	.32	.32	.34	.34
Multiple Range	———	———	———	———	———				
		———	———	———	———	———	———	———	———

10 October 1970

Station	9	7	6	3	4	8	5	2	1
Mean	.02	.05	.05	.06	.07	.07	.08	.14	.14
Multiple Range	———	———	———	———	———	———			
		———	———	———	———	———	———		
								———	———

25 October 1970

Station	2	1	3	8	4	7	5	6	9
Mean	.06	.07	.08	.08	.09	.12	.14	.18	.25
Multiple Range	———	———	———	———	———	———	———		
						———	———	———	
								———	———

7 November 1970

Station	1	9	6	2	5	7	8	3	4
Mean	.02	.03	.03	.05	.10	.14	.14	.20	.24
Multiple Range	———	———	———	———					
			———	———	———				
					———	———	———		
						———	———	———	
								———	———

1. Interaction exists between depths and stations.

May 27 and June 24. Biomass in the river was lowest of all the stations except during the late spring peak (June 10 to July 7) and in late fall (October 27).

The mean (± .95 confidence) biomass (mg/liter) throughout the sampling period was .49 ± .23 in the lake, .43 ± .22 in the discharge canal, .34 ± .12 in Plum Creek, and .18 ± .14 in the river. Seasonal shifts in mean lake biomass are given in Figure 9.

In summary, area differences in biomass were more difficult to detect than differences in density simply because of the greater variability in biomass throughout the sampling period and within the station replicates. However, it is apparent from the relative values of biomass and density that mean biomass per individual differed considerable among stations. Individuals in the lake averaged twice the biomass of those in the discharge canal or Plum Creek (Table 4). The river was intermediate. Why these differences exist is partly revealed by a detailed examination of the distribution of the major taxonomic zooplankton groups i.e., rotifers, cladocerans, and copepods.

Zooplankton Composition

Rotifers: Little variation occurred in rotifer densities or species composition among the lake stations. However, the temporal variability in density appeared greatest at Station 1 and Station 6. At Station 1, spring densities of *B. calyciflorus* and *K. cochlearis* reached maximums that were respectively 12 and 3 times greater than the average of the other lake stations (Figure 10). During the summer, *P. sulcata* and *Polyarthra* spp. reached densities three times greater at Station 6 than the other lake stations (Figure 11). Peak densities occurred in late May and in mid-September at all stations.

Figure 9. Mean seasonal variation of total zooplankton biomass in the lake.

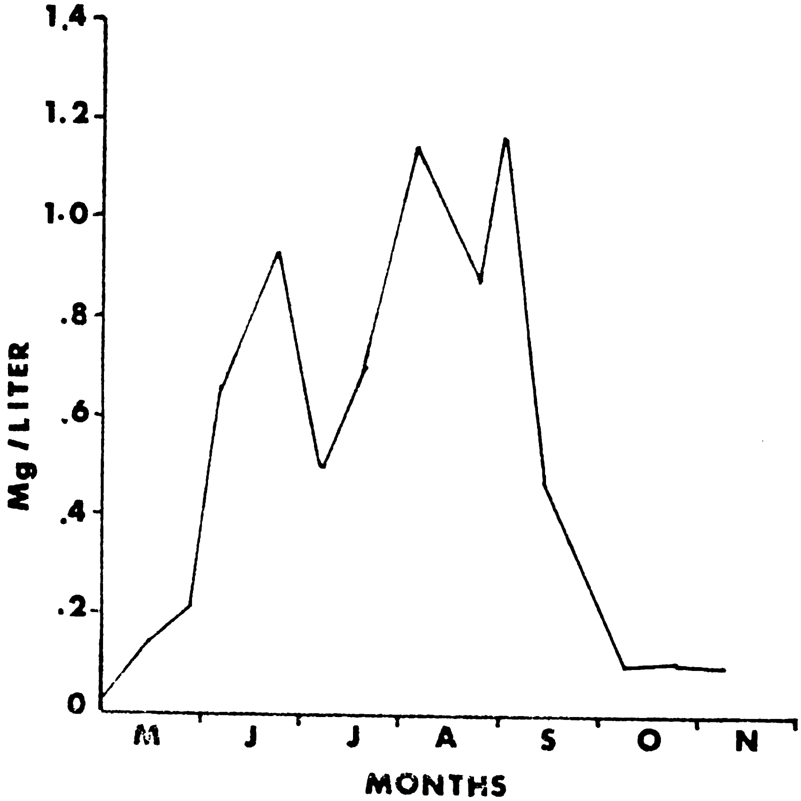

1.4
1.2
1.0
.8
.6
.4
.2
0
Mg /LITER
M
J
J
A
S
O
N
MONTHS

Table 4: Average biomass per individual (µg/individual) at the various stations.

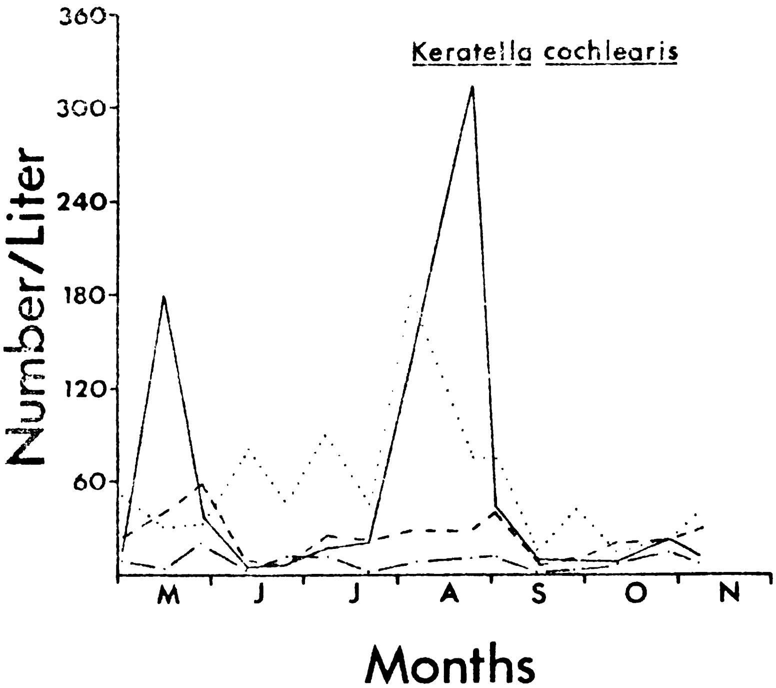
DATE	STATION 1	2	3	4	5	6	7	8	9
1 May 70	.11	.10	.10	.26	.20	.14	.08	.10	.27
15 May 70	.15	.14	.35	.59	.38	.77	.42	.35	.17
27 May 70	.07	.18	.45	.42	.37	.51	1.06	.72	.46
10 June 70	2.40	1.92	1.09	1.27	.67	1.56	.86	1.21	2.37
24 June 70	3.17	2.01	1.93	1.77	1.47	.90	.15	.47	1.27
7 July 70	.89	.67	1.35	1.06	1.61	1.09	.37	.45	2.12
21 July 70	1.48	1.55	1.36	1.38	1.70	.87	.38	.25	.53
4 August 70	1.52	1.47	1.55	2.48	2.19	1.72	.53	.80	1.01
24 August 70	.41	1.68	1.88	1.09	1.57	-	.56	.39	.30
1 September 70	1.20	1.19	1.22	1.24	1.37	.98	.38	.34	.12
15 September 70	.76	.58	.44	.41	.86	1.09	.52	.67	.25
27 September 70	.97	1.11	1.08	.65	.77	.82	.39	.45	.94
10 October 70	.53	.49	.22	.27	.27	.26	.33	.38	.24
25 October 70	.46	.47	.45	.55	.59	.75	.50	.56	.96
7 November 70	.27	.42	1.00	1.19	.70	.36	.59	.56	.51
$\bar{x}$	.90	.87	.90	.91	.92	.79	.45	.48	.72

Plum Creek and the discharge canal had the highest rotifer densities of all the areas (Figure 12). Spring densities peaked two weeks earlier than in the lake, with _B_. _calyciflorus_ peaking at densities two times greater than Station 1 and 24 times greater than the rest of the lake. Also contributing to high spring densities (Figure 13) were _K_. _quadrata_ (twice as high as the lake) and _S_. _stylata_ (3 times greater than the lake). During the summer, total densities remained, in contrast to the lake, relatively high. At that time _Polyarthra_ sp. maintained densities that were 5-8 times greater at Plum Creek and the discharge canal than in the lake. Also, two additional species peaked here but not in the lake during the summer, _Brachionus_ sp. and _Keratella_ sp.

Individual species densities were always lowest in the river, but composition was similar to the other areas. Increases of _S_. _stylata_ are primarily responsible for the peaks that occurred in the river during May and late October. In summary, rotifer densities were highest in Plum Creek and the discharge canal, intermediate in the lake, and lowest in the river.

Cladocerans: The lake stations exhibited little difference in density as well as in composition. The two peaks that occurred (during June and late August) can be attributed mainly to increases of 2 species; _D_. _retrocurva_ in the spring and _C_. _sphaericus_ and _D_. _retrocurva_ (to a lesser extent) in the fall (Figure 14). The pulses of _D_. _retrocurva_ consisted mainly of immature individuals (Figure 15). The dramatic rise and subsequent peaking of _C_. _sphaericus_ in late August was most evident in the lake. On August 4 it was virtually non-existent yet on September 1 densities of 300/liter were observed. Seasonal densities of some other cladoceran species are given in Figure 16.

Figure 10. Mean seasonal variation of the total density of Brachionus calyciflorus and Keratella cochlearis. ____ Station 1; ---- mean of the other 5 lake stations; .... mean of Plum Creek and the discharge canal; _._._._. River.


Keratella cochlearis
Number/Liter
360
300
240
180
120
60
M J J A S O N
Months

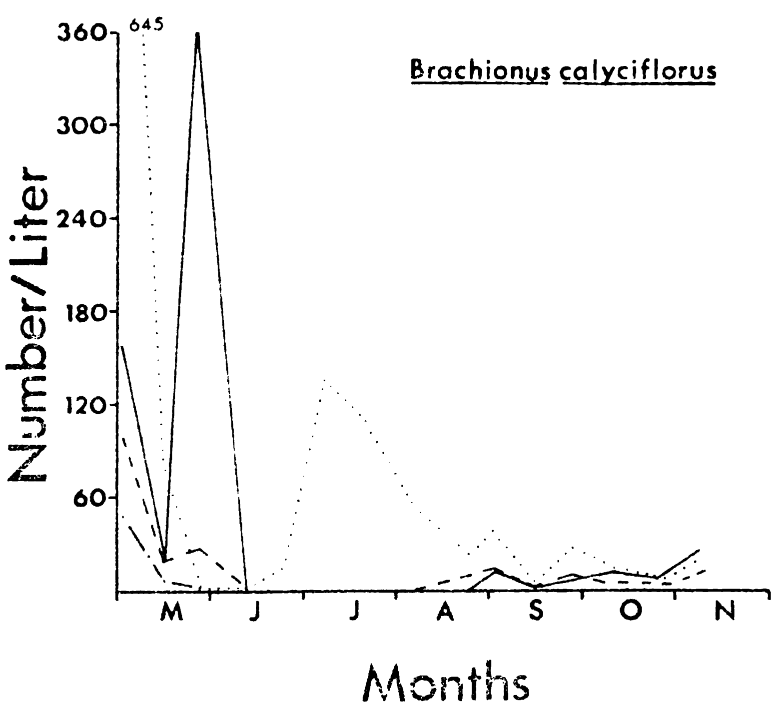
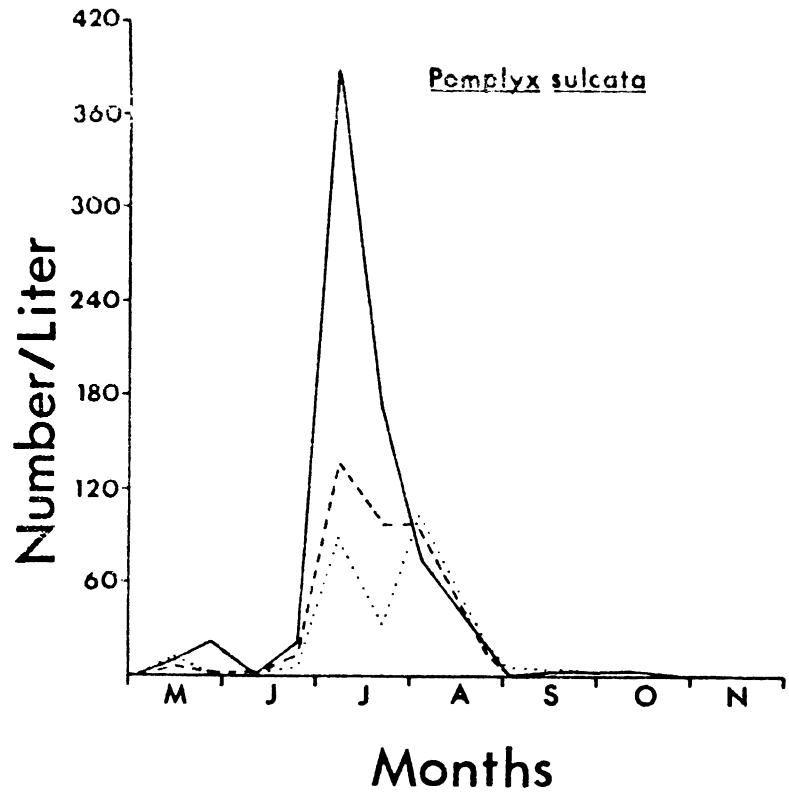

Brachionus calyciflorus
645
Number/Liter
360
300
240
180
120
60
M J J A S O N
Months

Figure 11. Mean seasonal variation of the total density of Pomplyx sulcata and Polyarthra spp. ____Station 6; ----mean of the other 5 lake stations; ....mean of Plum Creek and the discharge canal; _._._._. River.


420
360
300
240
180
120
60
Number/Liter
Pomplyx sulcata
M
J
J
A
S
O
N
Months

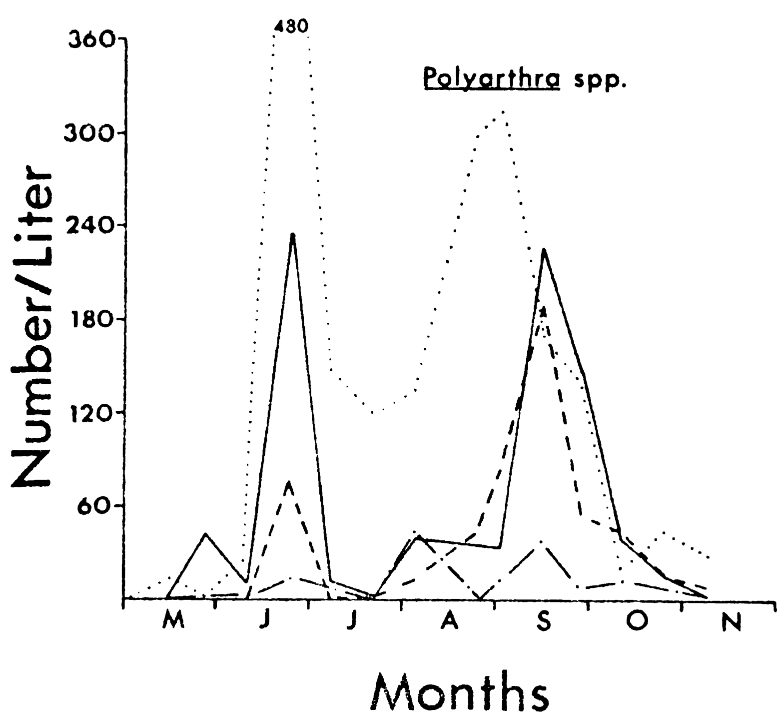

360
300
240
180
120
60
Number/Liter
480
Polyarthra spp.
M
J
J
A
S
O
N
Months

Figure 12. Mean seasonal variation of the total density of rotifers. ____mean of lake stations; ----Plum Creek; ....Discharge Canal; _._._._. River.

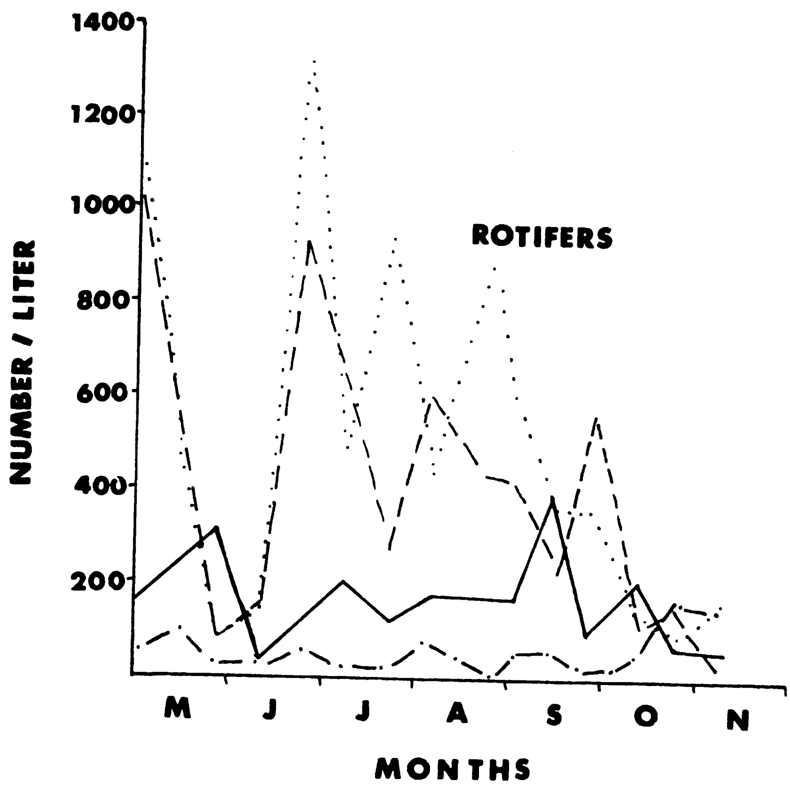
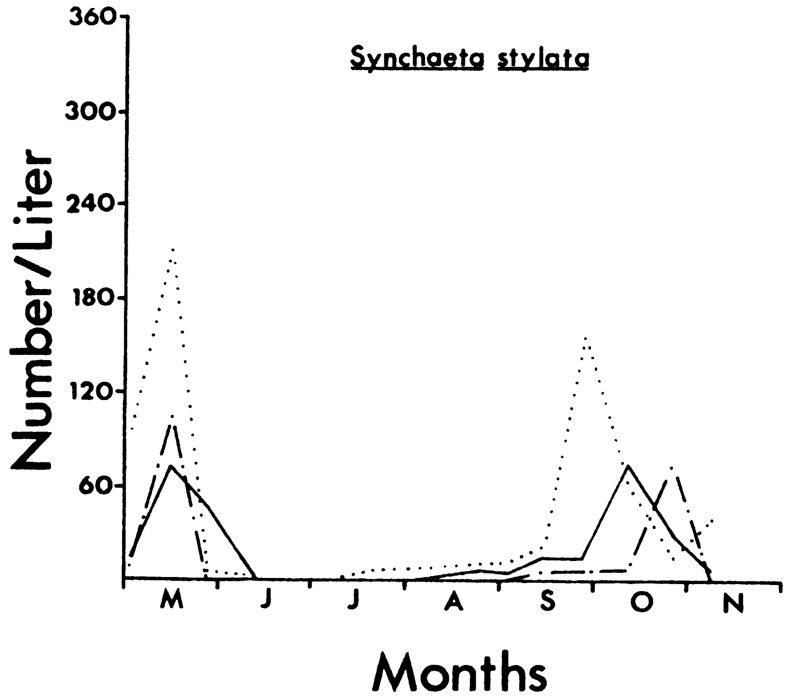

ROTIFERS
NUMBER / LITER
1400
1200
1000
800
600
400
200
M
J
J
A
S
O
N
MONTHS

Figure 13. Mean seasonal variation of the total density of Keratella quadrata and Synchaeta stylata. For the former species: ____Station 1; ----mean of 5 other lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River. For the latter species: ____mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.


Synchaeta stylata
Number/Liter
360
300
240
180
120
60
M
J
J
A
S
O
N
Months

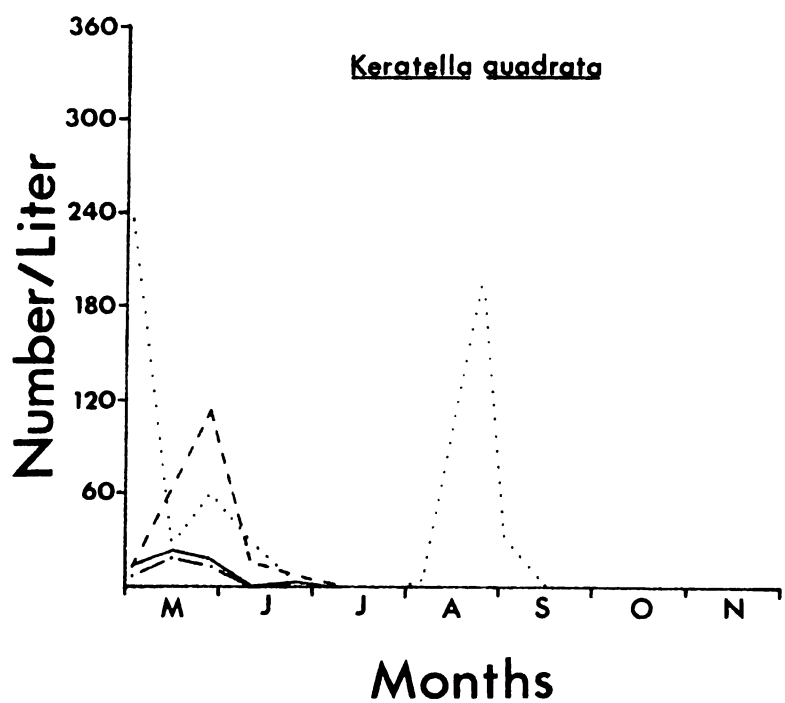
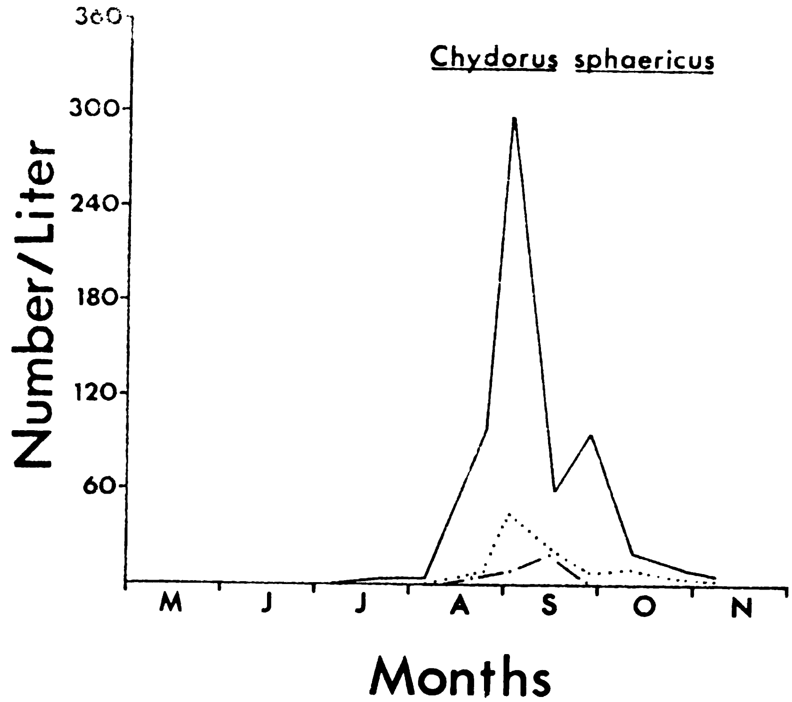
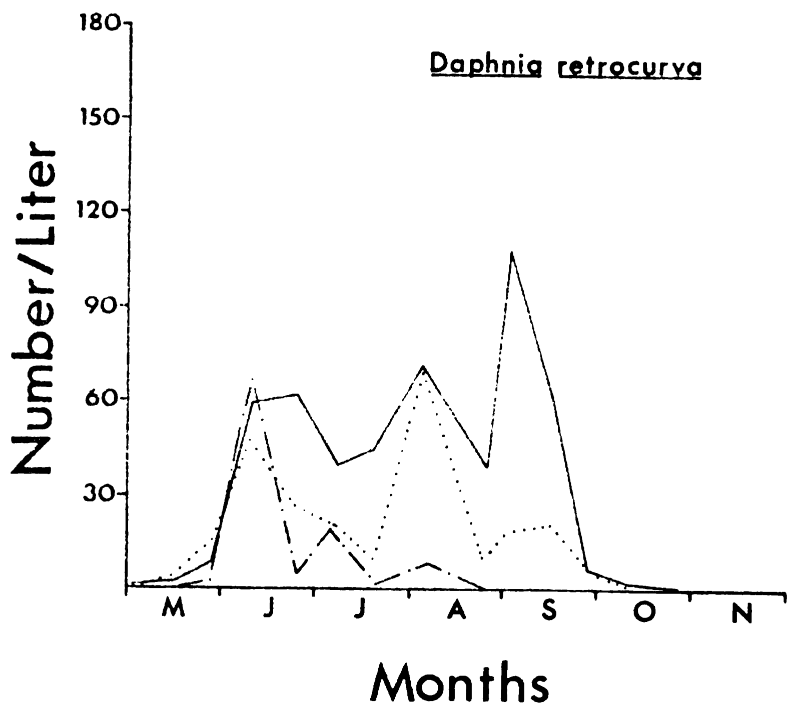

Keratella quadrata
Number/Liter
360
300
240
180
120
60
M
J
J
A
S
O
N
Months

Figure 14. Mean seasonal variation of the total density of Daphnia retrocurva and Chydorus sphaericus. ____mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.



Chydorus sphaericus
Number/Liter
360
300
240
180
120
60
M
J
J
A
S
O
N
Months



Daphnia retrocurva
Number/Liter
180
150
120
90
60
30
M
J
J
A
S
O
N
Months

Figure 15. Mean seasonal variation of the total density of mature and immature *Daphnia retrocurva* in the lake (upper graph) and in the discharge canal (lower graph). ____mature *Daphnia retrocurva*; ....immature *Daphnia retrocurva*.

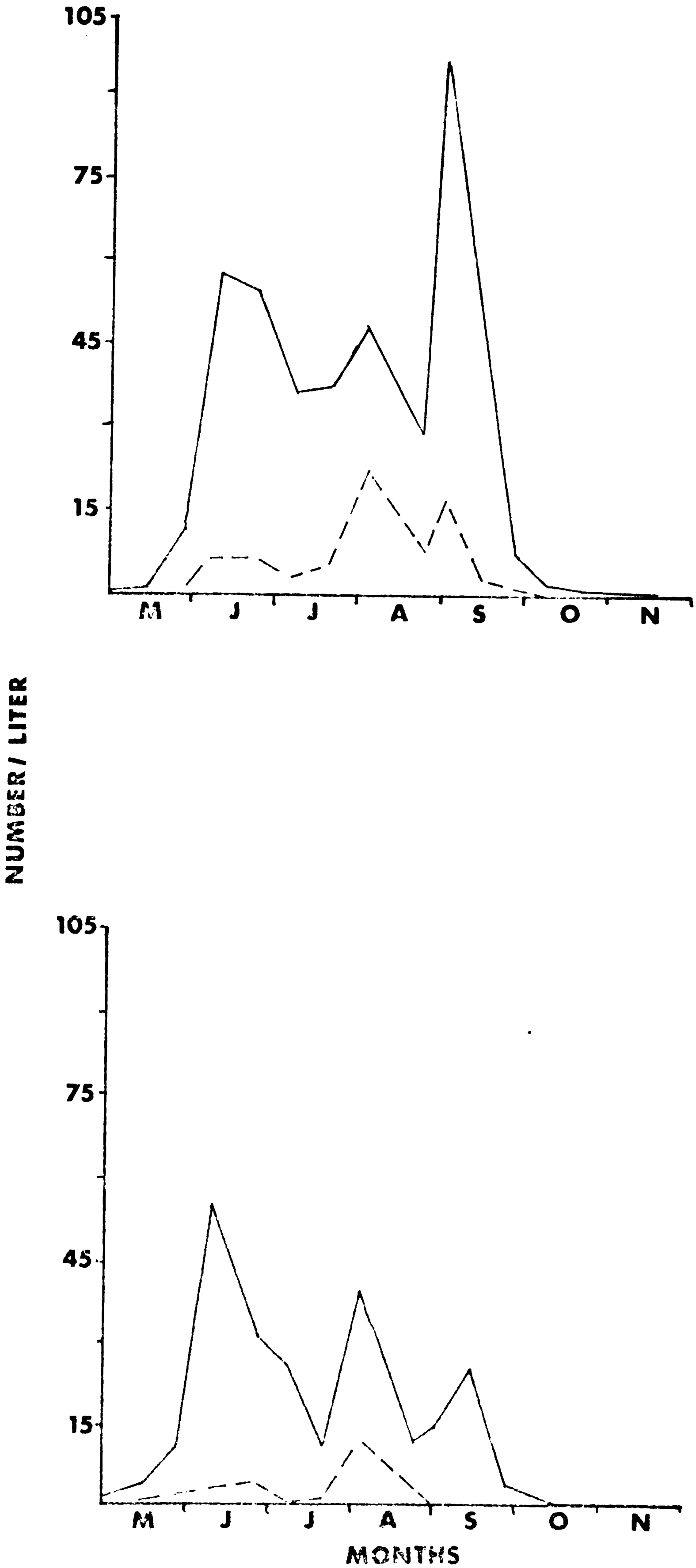
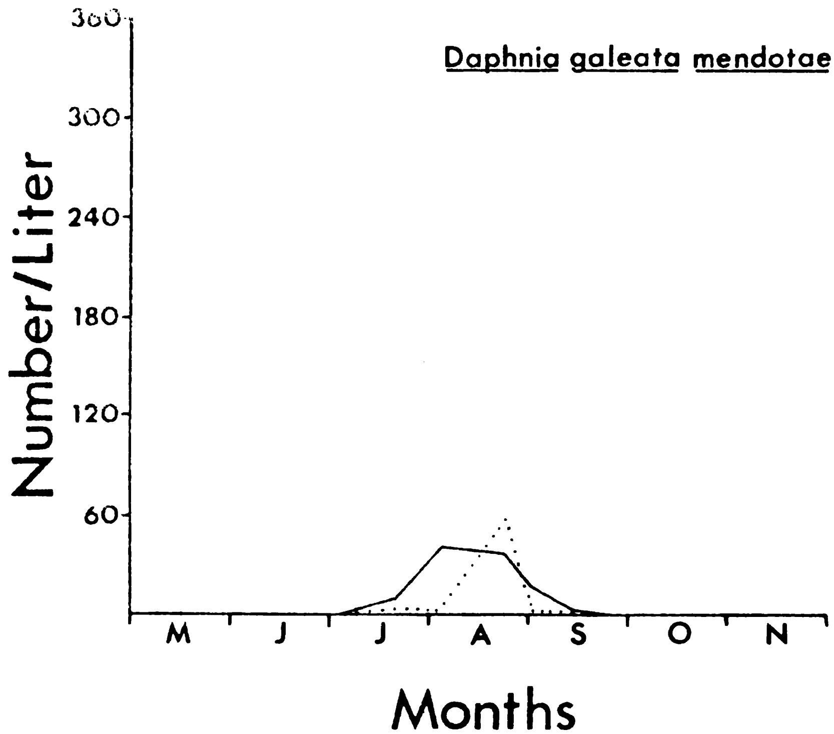
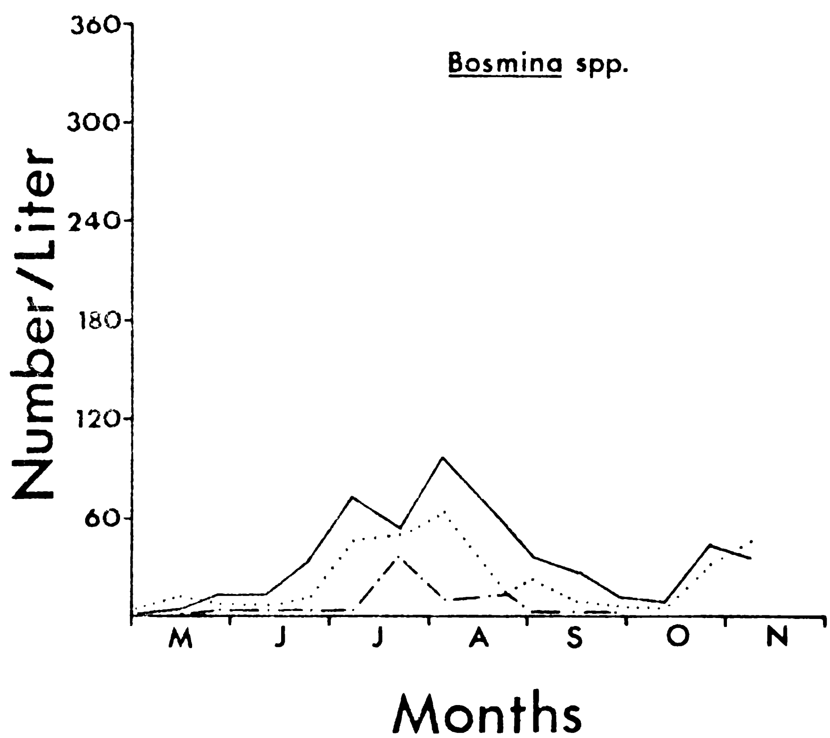

105
75
45
15
M
J
J
A
S
O
N
NUMBER / LITER
105
75
45
15
M
J
J
A
S
O
N
MONTHS

Figure 16. Mean seasonal variation of the total density of Bosmina sp. and Daphnia galeata mendotae. ____mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.


Daphnia galeata mendotae
360
300
240
180
120
60
Number/Liter
M
J
J
A
S
O
N
Months


Bosmina spp.
360
300
240
180
120
60
Number/Liter
M
J
J
A
S
O
N
Months

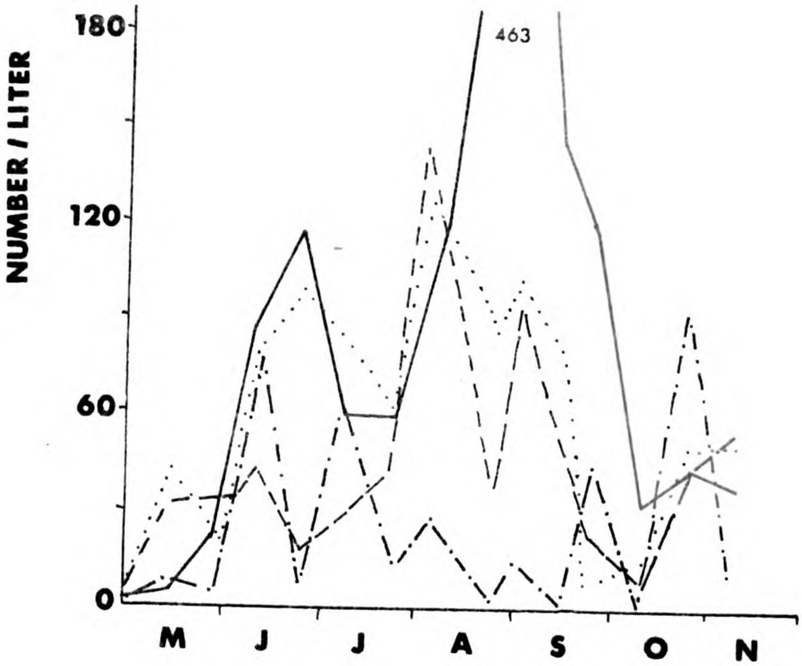
The discharge canal and Plum Creek had densities comparable to the lake except during the fall when densities of _C. sphaericus_ were six times lower. Plum Creek had lower densities than the discharge canal during spring. The most variation in cladoceran densities occurred in the river where the lowest densities also occurred from late July to September (Figure 17).

Except in the spring and fall when concentrations were comparable, Cladoceran biomass was greatest in the lake, intermediate in the discharge canal and Plum Creek, and lowest in the river (Figure 17).

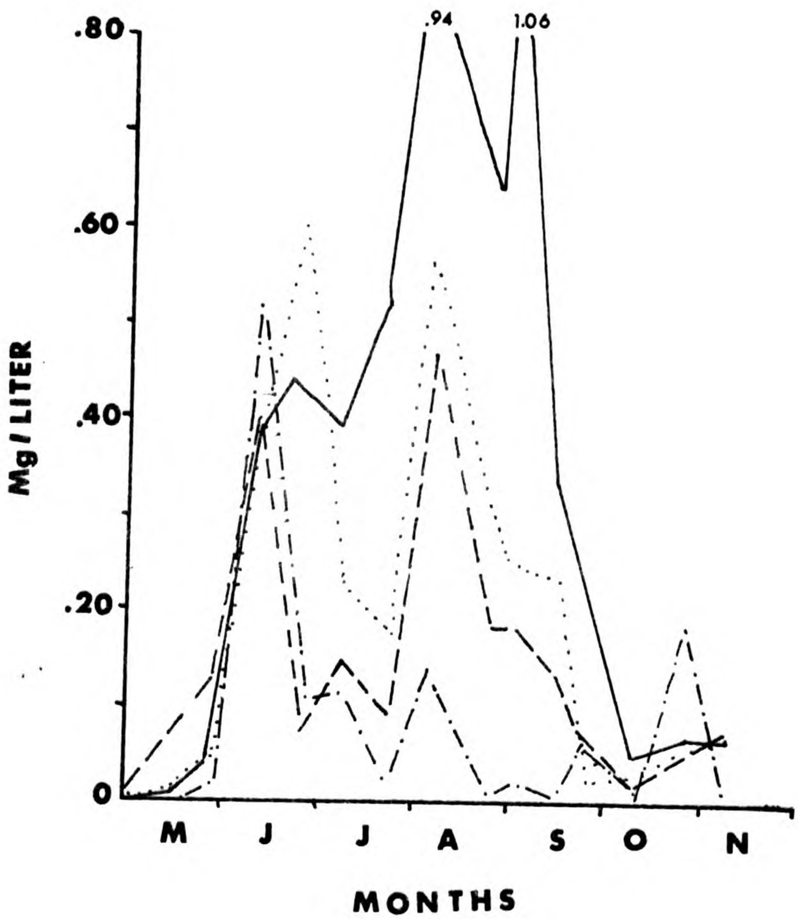
Copepods: Total densities of copepods (nauplii, juveniles, adults) were highest in the discharge canal followed in decreasing abundance by Plum Creek, the lake, and then the river (Figure 18). At both the discharge canal and Plum Creek, densities peaked in early summer while the lake and river peaked during June and early September. The density differences between the various areas can be attributed to the nauplii and juveniles, since the adults had similar abundances at all the stations. The two extreme cases were the discharge canal and the river. The former area had a disproportionately larger number of nauplii and juveniles to adults and the latter a higher proportion of adults to nauplii and juveniles (Figures 19, 20, 21).

Compositional Variation: The relative densities and biomass (expressed as per-cent) of the major zooplankton taxa varied little within the lake (Figures 22 and 23). Stations 1 and 6 tended to exhibit minor differences from the rest of the lake stations just as they did for biomass. At Station 1, rotifers comprised a higher proportion of both density and biomass in late May and October. At Station 6, a higher proportion of copepods occurred in the fall (mainly nauplii). Since mean size of the members of each taxa differ considerably, these

Figure 17. Mean seasonal variation of total density (upper graph) and total biomass (lower graph) of cladocerans. ____mean of lake stations; ---- Plum Creek; ....Discharge Canal, _._._._.River.

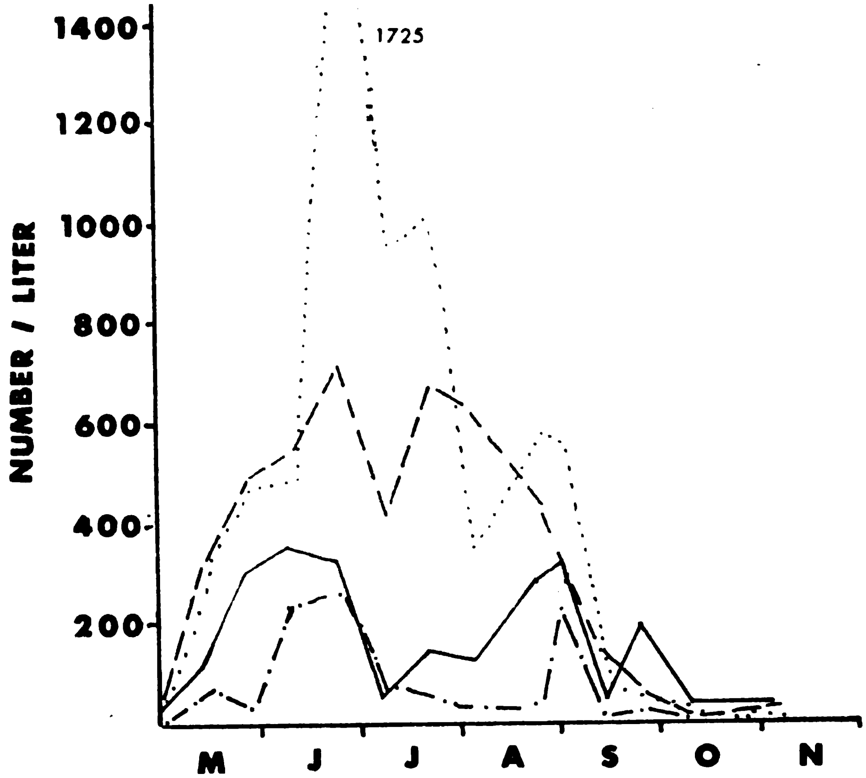


NUMBER / LITER
180
120
60
0
463
M
J
J
A
S
O
N



Mg / LITER
.80
.60
.40
.20
0
.94
1.06
M
J
J
A
S
O
N
MONTHS

Figure 18. Mean seasonal variation of total density (upper graph) and total biomass (lower graph) of copepods. ____mean of lake stations; ---- Plum Creek; ....Discharge Canal; _._._._.River.


1725
1400
1200
1000
800
600
400
200
NUMBER / LITER
M
J
J
A
S
O
N

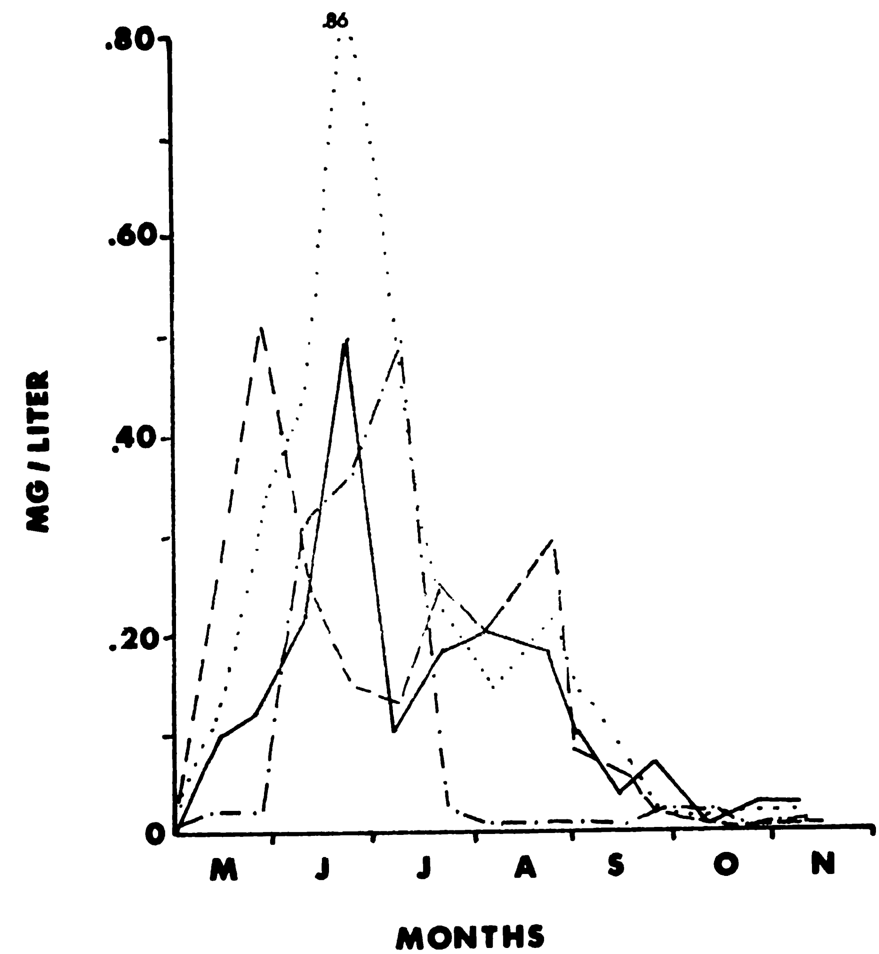

.86
.80
.60
.40
.20
0
MG / LITER
M
J
J
A
S
O
N
MONTHS

Figure 19. Mean seasonal variation of the total density of copepod nauplii and juvenile cyclopoids. ____ mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.

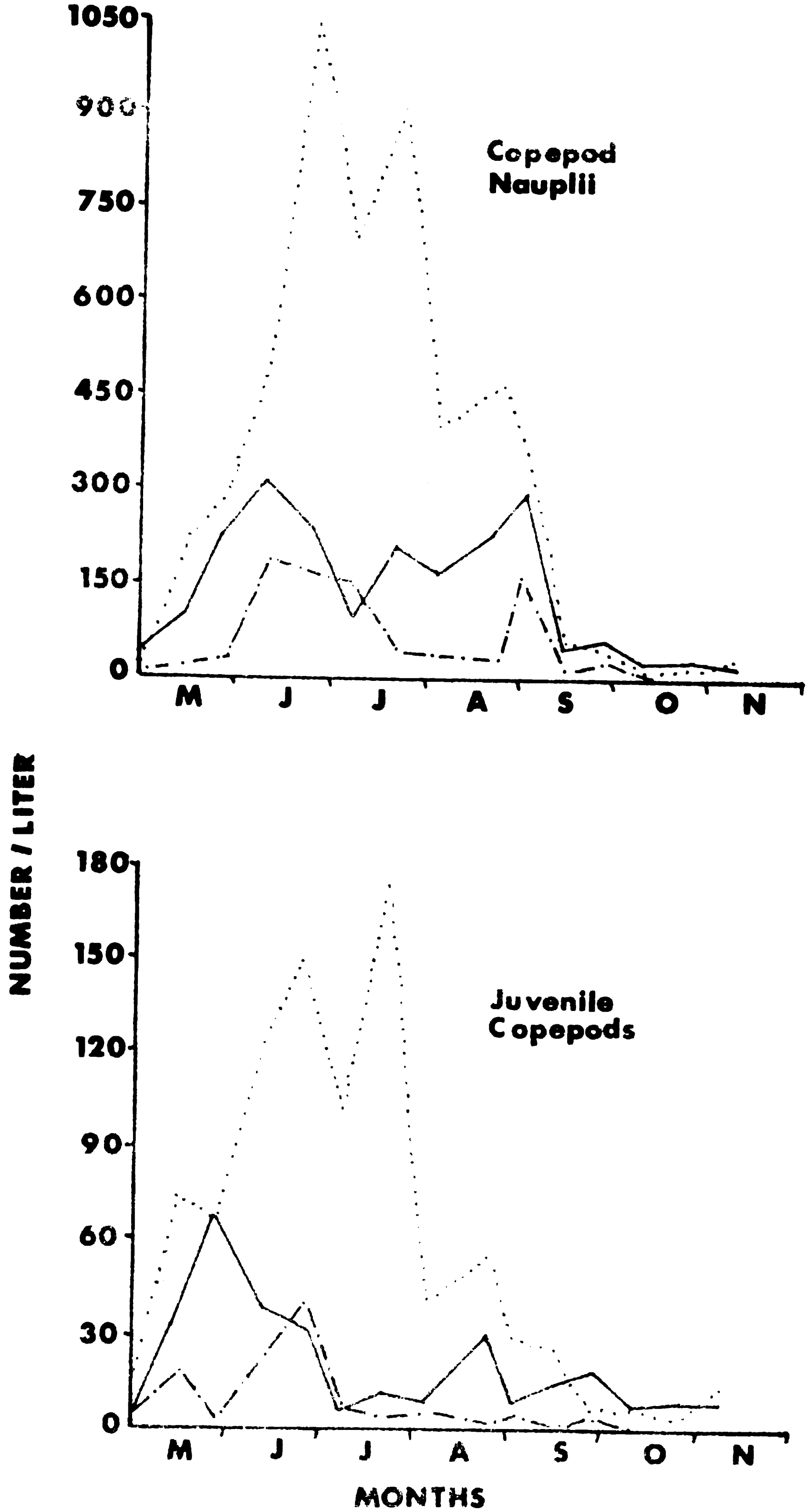
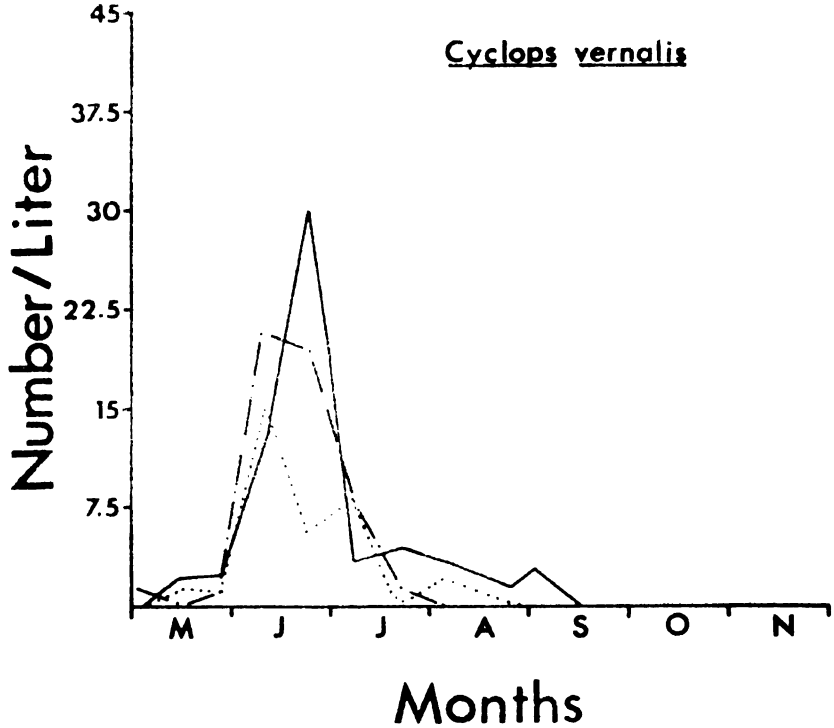

Copepod Nauplii
Juvenile Copepods
NUMBER / LITER
1050
900
750
600
450
300
150
0
180
150
120
90
60
30
M
J
J
A
S
O
N
MONTHS

Figure 20. Mean seasonal variation of the total density of _Cyclops vernalis_ and _Tropocyclops prasinus_. ____mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.


Cyclops vernalis
Number/Liter
45
37.5
30
22.5
15
7.5
M
J
J
A
S
O
N
Months

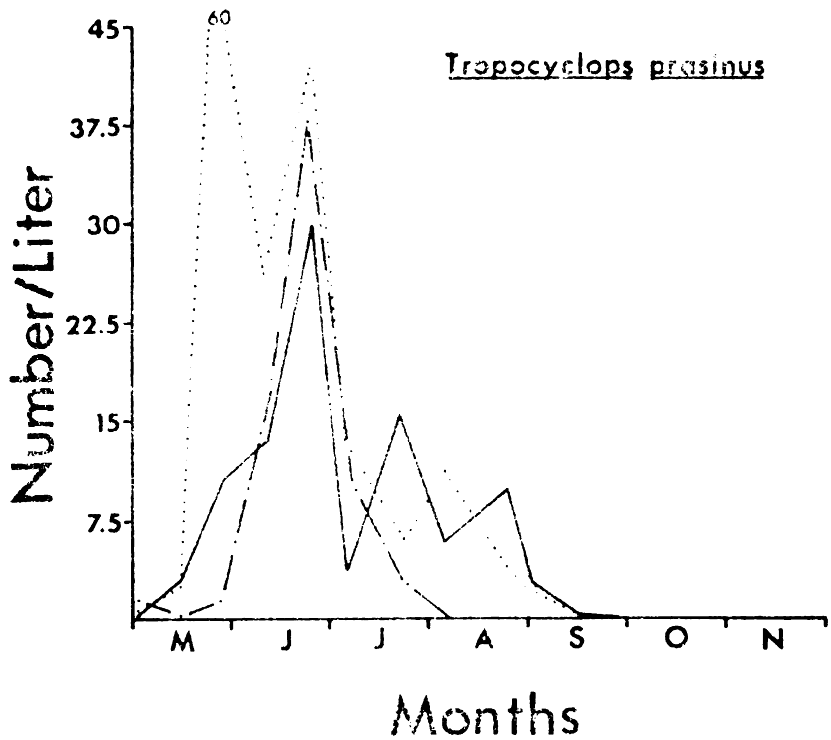

Tropocyclops prasinus
60
Number/Liter
45
37.5
30
22.5
15
7.5
M
J
J
A
S
O
N
Months

Figure 21. Mean seasonal variation of the total density of juvenile calanoids and Diaptomus siciloides. ____mean of lake stations; ....mean of Plum Creek and the discharge canal; _._._._.River.

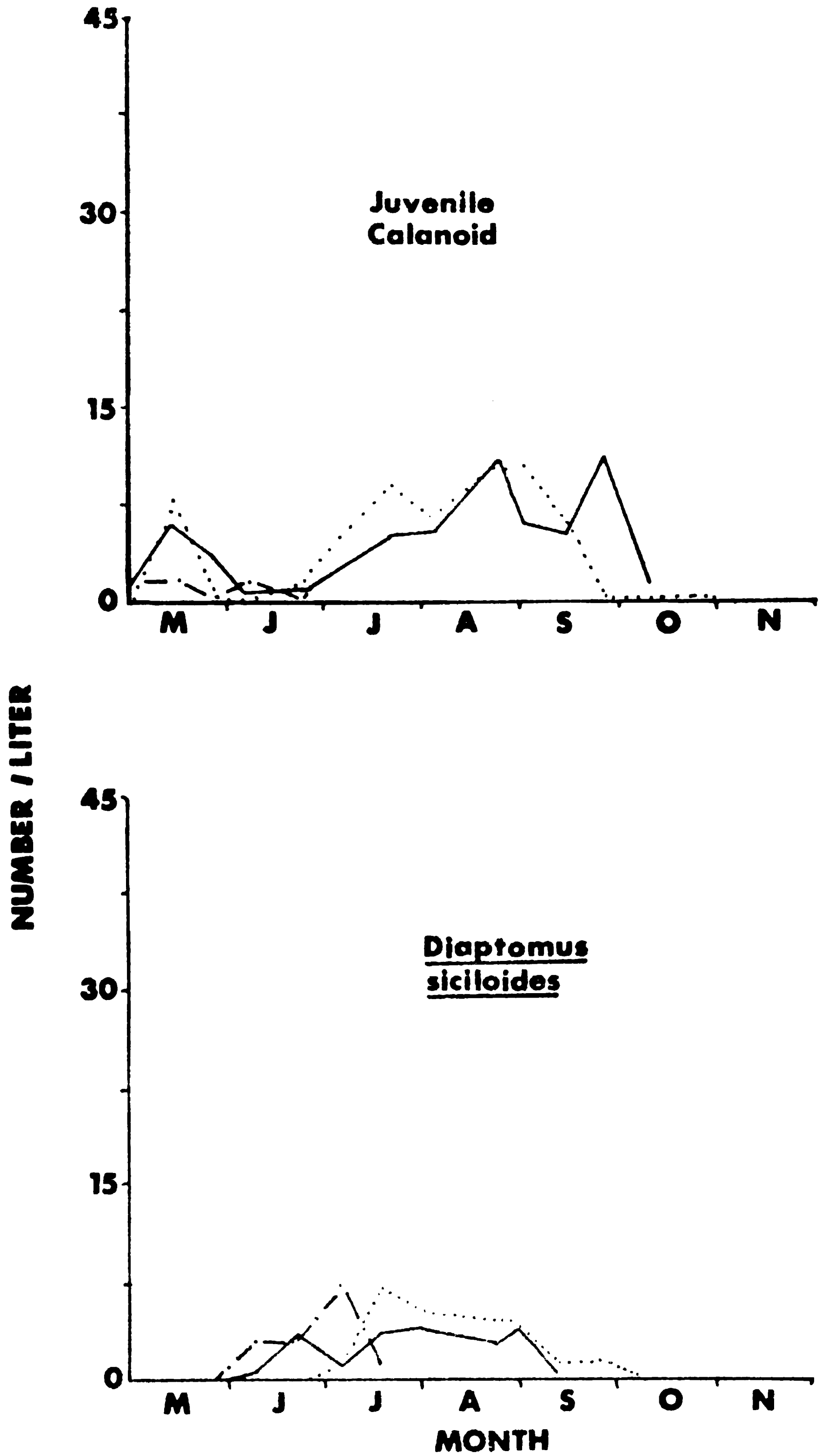

45
30
15
0
Juvenile
Calanoid
M
J
J
A
S
O
N
NUMBER / LITER
45
30
15
0
Diaptomus
siciloides
M
J
J
A
S
O
N
MONTH

Figure 22. Mean seasonal variation in the composition of density of the major zooplankton groups. Top stipling - rotifers; middle clear area - copepods; bottom stipling - cladocerans.

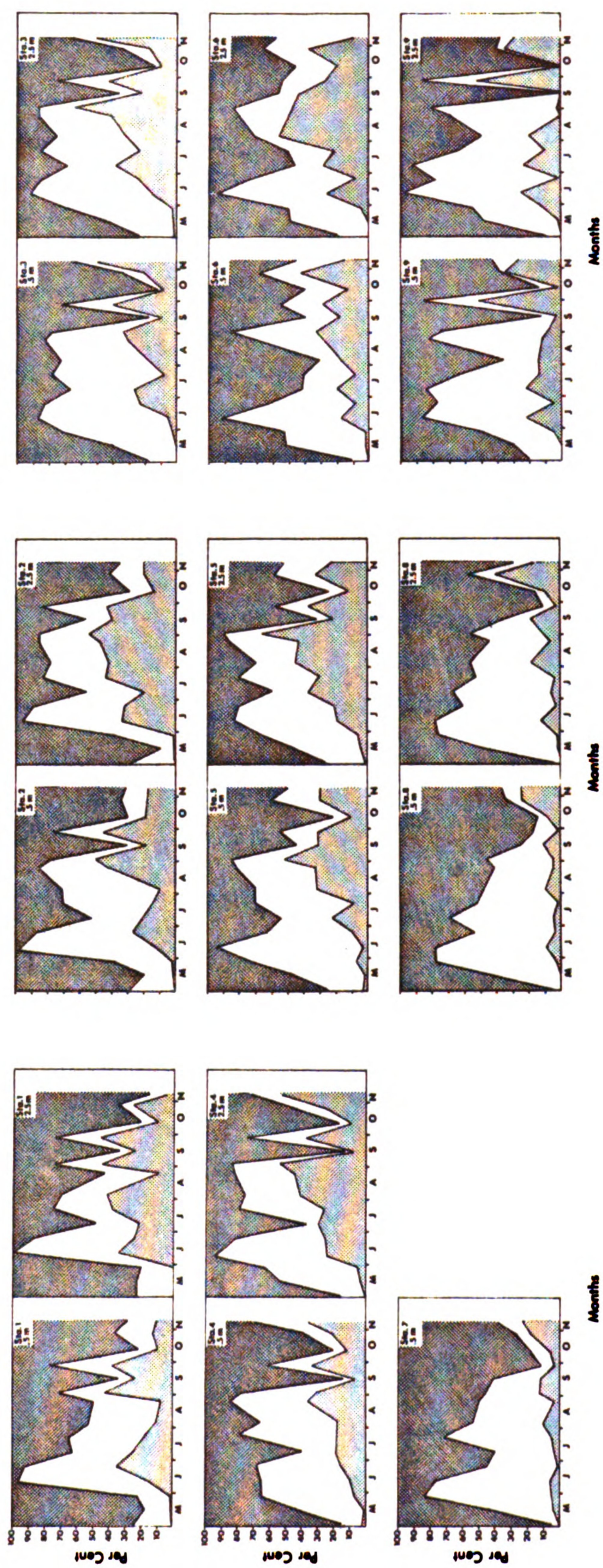

Per Cent
Per Cent
Per Cent
Months
Months
Months

Figure 23. Mean seasonal variation in the composition of biomass of the major zooplankton groups. Top stipling - rotifers; middle clear area - copepods; bottom stipling - cladocerans.

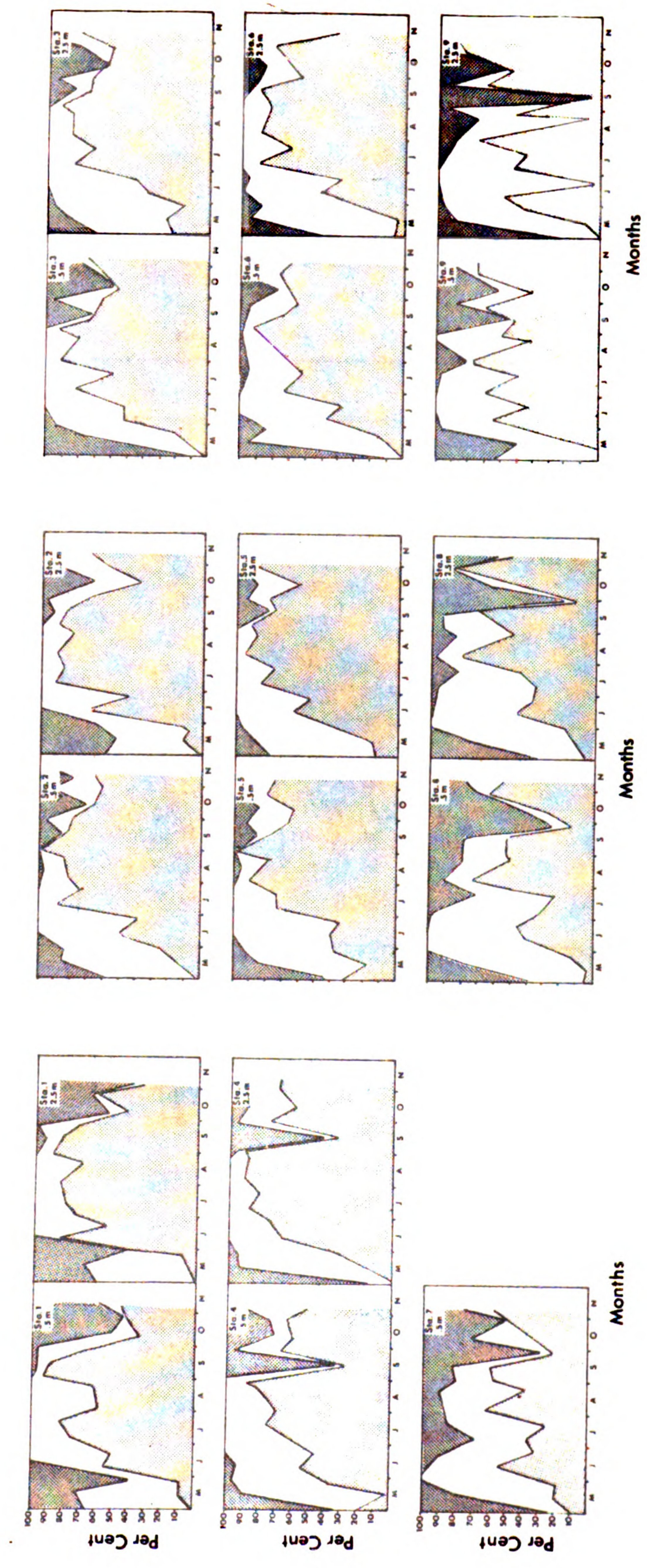

Sta. 1 .5 m
Sta. 1 2.5 m
Sta. 2 .5 m
Sta. 2 2.5 m
Sta. 3 .5 m
Sta. 3 2.5 m
Sta. 4 .5 m
Sta. 4 2.5 m
Sta. 5 .5 m
Sta. 5 2.5 m
Sta. 6 .5 m
Sta. 6 2.5 m
Sta. 7 .5 m
Sta. 8 .5 m
Sta. 8 2.5 m
Sta. 9 .5 m
Sta. 9 2.5 m
Per Cent
100 90 80 70 60 50 40 30 20 10
M J J A S O N
Months

Table 7 : Number and Lengths of the Two Fish Species Used for Stomach Analysis

	Perch		White Bass	
Date	Number of Stomachs	Mean (cm.) Length	Number of Stomachs	Mean (cm.) Length
21 May 70	5	9.6	-	-
12 June 70	10	11.8	-	-
25 June 70	6	3.4	-	-
7 July 70	23	3.8	-	-
22 July 70	11	4.9	7	4.2
4 August 70	5	6.7	5	4.4
16 September 70	6	8.6	14	7.2

compositional differences contributed to the variations in total biomass and density observed at these stations.

During the summer, cladocerans dominated the biomass in the lake (70-90%) but comprised only 30% of the total lake density. In turn, rotifers comprised <1% of the biomass yet 20-30% of the total density. This contrasted greatly with the inshore areas where cladocerans comprised a significantly lower percentage of the density and biomass and both rotifers and copepods were consistently more important. Copepods were consistently more common than rotifers in the river during the summer. Cladocerans were virtually non-existent.

It is apparent that the distributions of total density and biomass are greatly affected by composition of the major taxa. This, in turn, is assumed to be influenced by the major physical or biological characteristics of the area.

Vertical Distributions

Zooplankton Density

In the lake, significant density differences ($p < .05$) between depths (0.5 m and 2.5m) occurred on two dates, August 4 and September 1 (Table 5). A difference of at least 30% between the depth means was usually required to detect a significant difference ($p < .05$). Nearly every lake station had a greater density at the lower depth during late summer but the difference was usually too small to detect with any confidence. The inshore stations did not have any significant depth differences.

When compared to .5m, there was a strong tendency for higher densities at 5.5m in the lake during July and August but this was not apparent during the fall. The discharge canal had lower densities

Table 5: Numbers of zooplankton per liter at different depths and stations in the study area.

Station	2 May 1970			15 May 1970			27 May 1970			10 June 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	249	249	-	352	376	-	736	766	-	327	391	-
2	228	256	-	390	472	-	432	412	-	501	676	-
3	210	180	-	368	459	-	561	637	-	355	562	-
4	252	357	-	490	349	-	633	562	-	609	334	-
5	136	151	-	454	366	-	789	519	-	816	519	-
6	127	210	-	240	285	-	787	910	-	472	396	-
7	1122	-	-	855	-	-	613	-	-	771	-	-
8	1059	1239*	-	516	627	-	480	526	-	670	187	-
9	84	93	-	199	159	-	84	90	-	345	339	-

Table 5: (con't.)

Station	23 June 1970			7 July 1970			21 July 1970			4 August 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	358	294	-	348	337	840	330	442	427	555	780*	784
2	331	364	-	321	348	435	367	538	577	225	562*	804
3	472	436	-	304	363	660	468	694	610	241	766*	1215
4	793	576	-	408	372	355	540	636	715	796	1102*	705
5	747	727	-	387	471	429	609	646	697	555	873*	985
6	801	1024	-	711	843	934	379	330	385	159	513*	379
7	1680	-	-	1080	-	-	1011	-	-	1372	-	-
8	3135	3165	-	1575	1477	1140	2007	2070	1084	1023	828	694
9	361	345	-	226	348	375	70	123	67	183	166	244

Table 5: (con't.)

Station	23 August 1970			1 September 1970			15 September 1970			27 September 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	769	1059	805	1326	1293	1237	990	988	418	205	169	210
2	417	549	930	1107	1209	949	586	528	540	280	297	214
3	670	739	799	969	951	885	376	397	255	300	384	304
4	627	699	675	517	954*	889	481	541	570	307	337	379
5	654	760	700	790	1254*	895	685	478	817	477	399	517
6	-	-	-	427	714*	619	654	702	543	409	379	483
7	927	-	-	825	-	-	417	-	-	660	-	-
8	1687	1494	1485	1323	1173	1159	592	454	309	445	364	439
9	37	72	325	319	322	150	75	55	30	135	75	154

Table 5 : (con't.)

Station	10 October 1970			25 October 1970			7 November 1970		
	Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	300	277	285	142	154	-	72	60	-
2	249	300	300	127	114	-	145	94	-
3	270	255	300	162	171	-	184	220	-
4	288	241	135	154	159	-	196	189	-
5	279	262	172	249	232	-	129	153	-
6	183	130	235	246	225	-	102	78	-
7	138	-	-	235	-	-	241	-	-
8	154	195	135	138	132	-	226	261	-
9	63	63	63	337	240	-	63	48	-

*Significant differences ($p < .05$) between 0.5 and 2.5m depths.

at 5.5m on all eight dates this depth was sampled. Although sampling was not replicated at the 5.5m depth, the values obtained were more than 30% less than the means at .5m on four dates. When compared to 2.5m, 5.5m densities were inconsistently different in the lake and river. However, again the discharge canal showed a strong tendency for lower densities at 5.5m.

Zooplankton Biomass

When significant differences between .5m and 2.5m occurred, the lower depth always had greater biomass concentrations. A difference of at least 30% was usually enough to detect significance. At the majority ($\geq$ 4) of the lake stations, 2.5m had significantly greater concentrations from June 11 to September 15 with the greatest difference occurring on August 4. At Plum Creek and the discharge canal, significant depth differences occurred less frequently than in the lake (only 4 dates) and in the river it was negligiable (1 date) (Table 6).

When compared to .5m, biomass concentrations were greater at 5.5m for the majority of the lake stations (4 of 6) on all the eight dates the latter depth was sampled. The discharge canal had trends similar to the lake and the river had inconsistent but usually higher concentrations at 5.5m. When compared to 2.5m, biomass concentrations in the lake were greater at 5.5m in the summer but not in the fall and the discharge canal and the river were inconsistent.

The fact that significant differences in biomass between depths (.5m and 2.5m) was much more common than differences in density (9 dates to 2 dates), indicates that differences in the vertical distribution of a few large species were primarily responsible for the depth differences encountered. Indeed, *D. retrocurva* accounted for 60-100% of the biomass

Table 6: Biomass (mg/liter) of zooplankton at different depths and stations in the study area.

Station	2 May 1970			15 May 1970			27 May 1970			10 June 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	.03	.03	-	.03	.07	-	.05	.07	-	.27	1.41	-
2	.02	.03	-	.07	.05	-	.10	.06	-	.45	1.36	-
3	.01	.03	-	.12	.18	-	.22	.31	-	.21	.86*	-
4	.07	.09	-	.22	.27	-	.27	.23	-	.45	.65*	-
5	.02	.03	-	.12	.20	-	.27	.18	-	.21	.64*	-
6	.02	.03	-	.20	.20	-	.38	.50	-	.54	.82*	-
7	.10	-	-	.37	-	-	.65	-	-	.66	-	-
8	.12	.11	-	.12	.28*	-	.37	.37	-	.48	1.16*	-
9	.03	.02	-	.02	.04	-	.04	.03	-	.76	.87	-

Table 6: (con't.)

Station	23 June 1970			7 July 1970			21 July 1970			4 August 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	1.12	.75*	-	.34	.25	1.60	.20	.94*	1.57	.21	1.79*	1.90
2	.70	.70	-	.28	.18	.77	.20	1.21*	2.10	.05	1.12*	1.04
3	.63	1.13*	-	.26	.65*	.93	.26	1.33*	1.56	.17	1.40*	2.29
4	.84	1.60*	-	.27	.51*	.90	.42	1.21*	1.33	1.19	3.54*	.85
5	.65	1.52*	-	.44	.91*	1.23	.39	1.76*	1.09	.87	2.27*	1.79
6	.59	1.06*	-	.49	1.21	2.35	.10	.49*	1.59	.10	1.06*	.64
7	.25	-	-	.40	-	-	.39	-	-	.74	-	-
8	1.45	1.52	-	.65	.74	1.09	.41	.56	1.01	.45	1.04*	1.59
9	.52	.38	-	.30	.91*	.91	.04	.06	.08	.20	.15	.19

Table 6: (con't.)

Station	23 August 1970			1 September 1970			15 September 1970			27 September 1970		
	Depths			Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	.21	.54*	.34	1.43	1.66*	1.88	.64	.81*	.96	.18	.17	.21
2	.58	1.08*	3.05	1.12	1.68*	1.02	.24	.51*	.81	.27	.37	.19
3	.79	1.70*	1.78	.72	1.63*	1.41	.11	.25	.23	.31	.37	.18
4	.51	.94*	1.70	.33	1.50*	2.51	.18	.25	.66	.21	.21	.30
5	.73	1.49*	1.24	.72	2.09*	1.24	.70	.33*	2.01	.34	.34	.44
6	-	-	-	.27	.86*	1.00	.35	1.18*	1.47	.31	.34	.71
7	.51	-	-	.32	-	-	.22	-	-	.26	-	-
8	.53	.69	.59	.25	.63*	1.83	.38	.33	.31	.19	.22	.24
9	.02	.01	.28	.03	.03	.05	.03	.01	.02	.10	.10	.06

Table 6: (con't.)

Station	10 October 1970			25 October 1970			7 November 1970		
	Depths			Depths			Depths		
	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m	0.5m	2.5m	5.5m
1	.12	.17	.16	.05	.10	-	.02	.02	-
2	.10	.18	.17	.06	.06	-	.06	.03	-
3	.06	.06	.10	.07	.08	-	.18	.22	-
4	.08	.06	.08	.09	.09	-	.26	.22	-
5	.07	.09	.02	.14	.14	-	.08	.12	-
6	.05	.05	.08	.19	.17	-	.03	.03	-
7	.05	-	-	.12	-	-	.14	-	-
8	.07	.08	.06	.07	.10	-	.14	.14	-
9	.03	.01	.02	.21	.28	-	.03	.02	-

*Significant differences ($p < .05$) between 0.5 and 2.5m depths.

difference on 6 of the 9 dates when depth significance occurred. On two of the remaining dates it comprised 30-50%. Also contributing somewhat were C. vernalis in late spring and C. sphaericus in the late summer.

Diurnal Change in Vertical Distribution

Depth differences between day and night determined by a single set of samples at three stations suggest that limited migration occurs in the shallow waters of the study area (Figure 24). The most obvious changes in vertical distribution from day to night occurred in June when the larger species, such as D. retrocurva and C. vernalis were most abundant. The tendency was for movement from the lower depths to the upper depths in the evening. If anything, rotifers and copepod nauplii tended to move downward (or disperse) at night.

Predation

Fish predation on zooplankton has been accorded to be an important regulator of zooplankton composition. To appraise the potential effect of fish predation upon the zooplankton, the stomach contents of two common species (young of the year) were examined (Perca flavescens, Roccus chrysops) (Table 7). Table 8 consists of ratios computed as the percent each species made of the total stomach contents divided by the percent that it made up in the water, considering only the species found in the stomach. Therefore, a ratio of >1 indicates species selectivity by the fish and a ratio of <1 indicates the opposite.

Analysis of these fish feeding habits indicates a selection for zooplankton that is dependent upon the relative density and size of the organisms. Comparisons between species density graphs and percentage of stomach contents (Figure 25) reveals that the highest stomach

Figure 24. Comparison of day - night vertical distributions at three representative stations. Light bar - day samples; dark bars - night samples; top pair of light-dark bars - night samples; top pair of light-dark bars - .5m; middle pair of light-dark bars - 2.5m; bottom pair of light-dark bars - 5.5m.

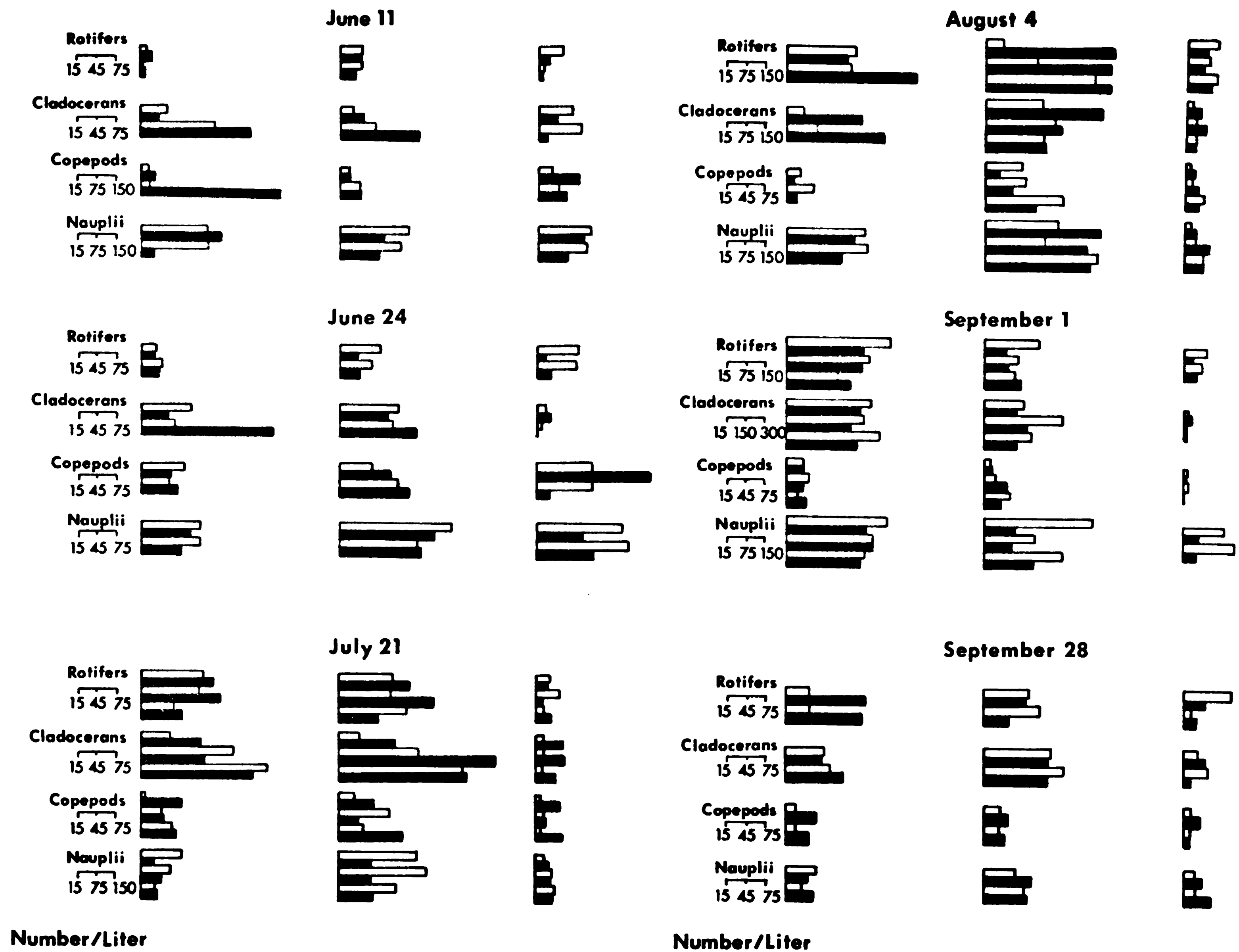

June 11
Rotifers
15 45 75
Cladocerans
15 45 75
Copepods
15 75 150
Nauplii
15 75 150
June 24
Rotifers
15 45 75
Cladocerans
15 45 75
Copepods
15 45 75
Nauplii
15 45 75
July 21
Rotifers
15 45 75
Cladocerans
15 45 75
Copepods
15 45 75
Nauplii
15 75 150
Number/Liter
August 4
Rotifers
15 75 150
Cladocerans
15 75 150
Copepods
15 45 75
Nauplii
15 75 150
September 1
Rotifers
15 75 150
Cladocerans
15 150 300
Copepods
15 45 75
Nauplii
15 75 150
September 28
Rotifers
15 45 75
Cladocerans
15 45 75
Copepods
15 45 75
Nauplii
15 45 75
Number/Liter

Table 7: Number and Lengths of the Two Fish Species Used for Stomach Analysis

	Perch		White Bass	
Date	Number of Stomachs	Mean (cm.) Length	Number of Stomachs	Mean (cm.) Length
21 May 70	5	9.6	-	-
12 June 70	10	11.8	-	-
25 June 70	6	3.4	-	-
7 July 70	23	3.8	-	-
22 July 70	11	4.9	7	4.2
4 August 70	5	6.7	5	4.4
16 September 70	6	8.6	14	7.2

Table 8: Selectivity of Certain Zooplankton Species Expressed as the Ratio Between the Per Cent Each Species Made of the Total Stomach Contents and the Per Cent of the Total Density it Comprised in the Water.

	Perch Stomachs				
	Zooplankton Species				
Date	D. retrocurva	D. g. medotae	C. Vernalis	D. Siciloides	Bosmina sp.
May 21	16.0	1	.2	1,000	<.001
June 12	4.3	1,000	.2	.5	.03
June 25	2.5	>1,000	.9	3	.06
July 7	.3	>1,000	17	9	.2
July 22	.7	2	.8	15	.1
August 5	.3	9	.6	.5	.1
September 16	<.001	1	>1,000	<.001	<.001
	White Bass				
22 July	.2	1	.7	21	.02
5 August	.05	2	2	31	.01
16 September	.1	1	>1,000	1	.03

percentages of particular prey species are associated with peak densities in the water. However, species size is also a factor. Selectivity ratios indicate a high preference for D. g. mendotae (large size) and low for Bosmina sp. (small size). No rotifers were found in any of the stomachs. Leptodora kindtii was the most selected of all zooplankton species. Preference for the other species was dependent upon each of their seasonal densities, although D. siciloides appeared to be differentially selected; especially by the White Bass.

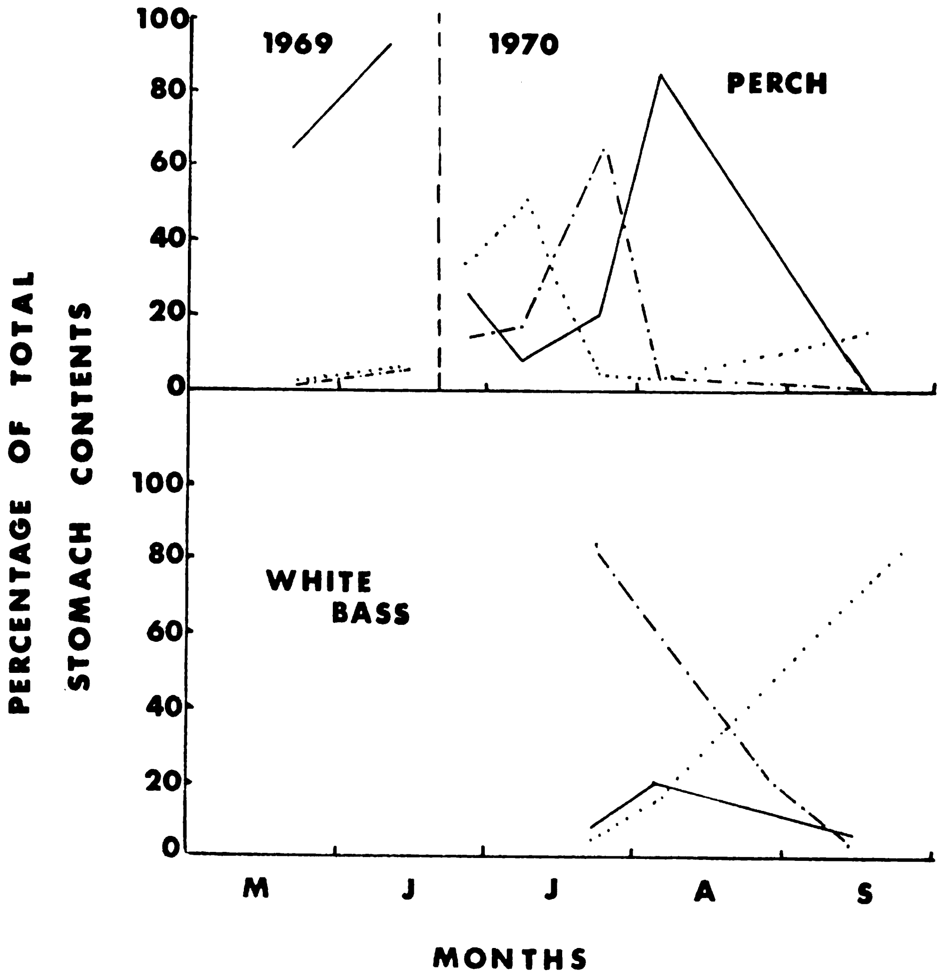
In the fall, age 0 perch were 8.6 m long and fed almost exclusively from the bottom (chironomids). In the spring of the following year, age I fish were feeding heavily on D. retrocurva (90%). This suggests shifts in feeding habits that are not entirely based on fish size alone but also upon the density of preferred prey species.

Other predators upon the zooplankton are zooplankton themselves; Leptodora kindtii, Cyclops vernalis, and Asplanchna sp. The first species was heavily selected by the fish thus probably reducing its effect on the zooplankton. Little is known of the feeding habits of C. vernalis, but since it had similar densities at all stations it is unlikely to be responsible for any major station differences in total biomass or density. The large rotifer, Asplanchna sp., preys on the smaller rotifers, but ratios between the densities of the two (Asplanchna sp./total rotifers) were similar at all areas, therefore, it was not responsible for any compositional differences between the areas.

Chemical and Physical Regulators of Zooplankton Density

Multiple regression was employed to estimate the relationship between various variables and zooplankton densities. Dependent variables were expressed as total number per liter of either rotifers,

Figure 25. Mean seasonal variation in the composition of zooplankton in the stomachs of young perch and white bass. ___ *Daphnia* spp.; ....*Cyclops vernalis*; _._._._.*Diaptomus siciloides*.



100
80
60
40
20
0
1969
1970
PERCH
100
80
60
40
20
0
WHITE
BASS
PERCENTAGE OF TOTAL
STOMACH CONTENTS
M
J
J
A
S
MONTHS

cladocerans, copepods, or total zooplankton. Independent variables included temperature, oxygen, particulate organic carbon, and inorganic suspended solids. Regression coefficients for each dependent variable were significantly different from zero ($p < .001$). However, the contribution of all four independent variables to the regulation of zooplankton densities accounted for less than half of the variation encountered. Partial regression coefficients suggest which factors were more important to the total relationship within each dependent variable (Table 9).

Densities of cladocerans, copepods and total zooplankton were highly correlated with temperature but not rotifers. However, the differences in temperature among stations at any particular time were negligible so that the spatial variation noted in these groups should not be caused by thermally regulated processes. The relationship between rotifers and inorganic suspended solids appears coincidental. Rotifers happened to be most abundant in the spring and fall when inorganic seston had high concentrations. Also, when utilizing this relationship to explain spatial differences, inconsistencies arise. The river had high inorganic seston concentrations but low rotifer densities.

Particulate carbon contributed little to the total relationship in any of the dependent variables. Some relationship would be expected simply because the zooplankton themselves contribute to particulate carbon values. Either particulate carbon is a poor estimator of food availability or food is relatively unimportant in regulating the zooplankton distributions in the study area.

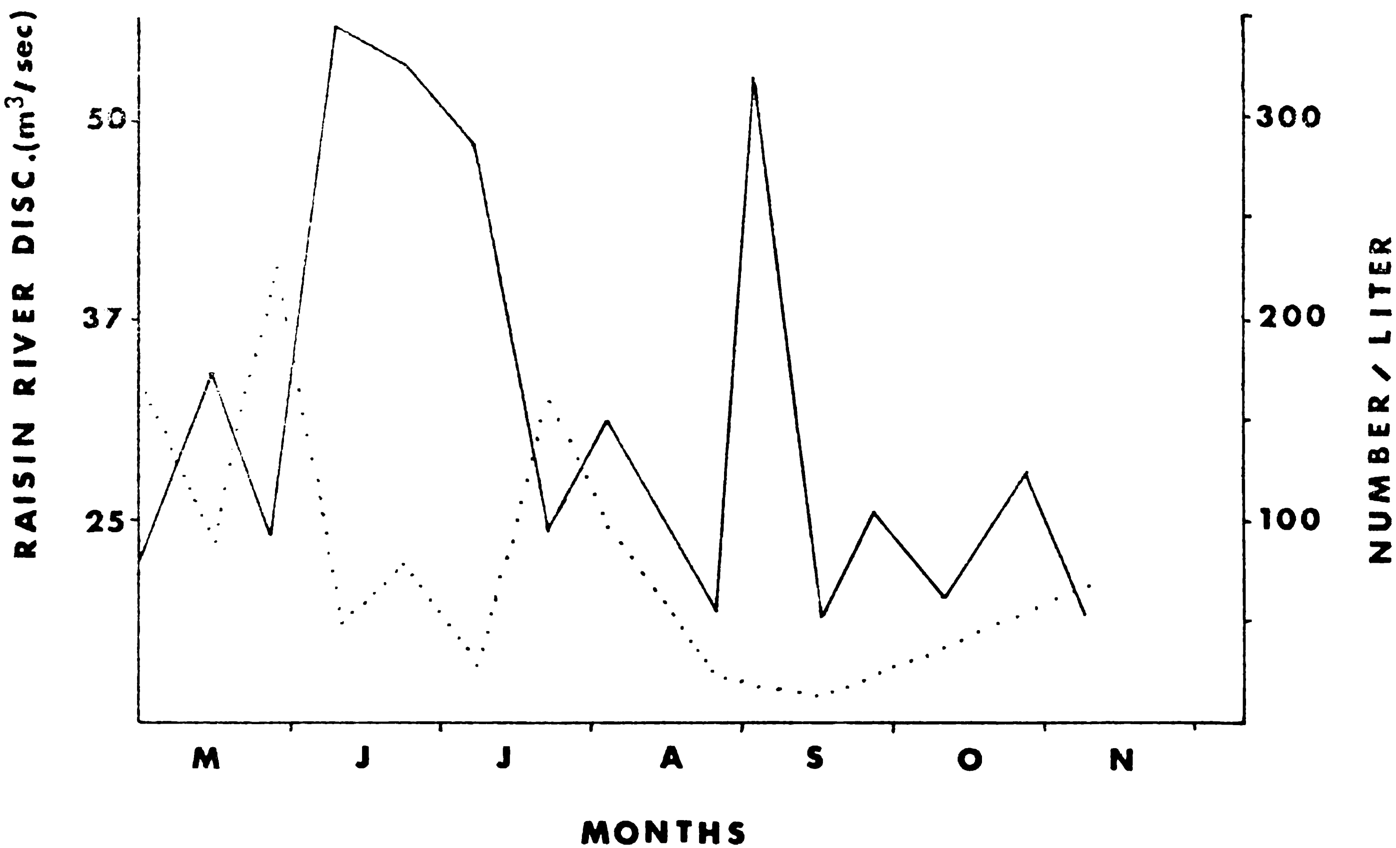
Oxygen concentrations were correlated more with Cladoceran densities than with the other dependent variables. Oxygen concentrations were lowest in the river, particularly during the summer and early fall. Cladoceran

Table 9: Partial regression coefficients associated with the various dependent and independent variables.

	INDEPENDENT VARIABLES				
DEPENDENT VARIABLES	TOTAL	TEMPERATURE	OXYGEN	PARTICULATE ORGANIC CARBON	INORGANIC SUSPENDED SOLIDS
Rotifers	.322	.252	.145	.169	.503
Cladocerans	.290	.498	.327	-.162	-.226
Copepods	.265	.496	.209	.113	-.002
Total Zooplankton	.308	.501	.257	.118	.225

densities were also low in the river at this time while they were abundant at the other areas where oxygen was plentiful. Although densities of rotifers and copepods were also low in the river at this time, the overall difference in their densities was less than that of the Cladocerans. River discharge could also conceivably be the cause of low river densities by washing individuals out of the area. Indeed, in the spring, there is an inverse relation between river discharge and densities (Figure 26). However, during the summer, discharge rates were similar to water movement in the lake and should be discounted as a cause of low densities at that time.

Figure 26. Seasonal relationship between the density of zooplankton in the river and river discharge. ____total zooplankton density; ....river discharge.


RAISIN RIVER DISC.(m3/sec)
50
37
25
NUMBER / LITER
300
200
100
M
J
J
A
S
O
N
MONTHS

DISCUSSION

Regulation of Zooplankton Distributions

Variation in the density and biomass of zooplankton along the western shore of Lake Erie can be related to the variation in three parameters particularly; primary productivity, fish biomass and density, and oxygen concentrations. Relatively subtle and inconsistent distributional patterns occurred in the lake but the inshore areas; a newly dug discharge canal, a shallow creek embayment, and a polluted river all varied from the lake and from each other.

Hypothetically, zooplankton biomass is linearly dependent upon food supply (Slobodkin, 1954; Hall, Cooper and Werner, 1970). The discharge canal had the greatest potential source of food while the river and lake had lower food potentials. However, zooplankton biomass in the discharge canal was lower than in the lake (but higher than in the river) except in the spring when rotifers were dominant throughout the study area. Also, although the river had food potentials similar to the lake, it had much lower biomass concentration except in June and late October. Apparently, food is a regulator of zooplankton biomass only in conjunction with other regulators. Other potential regulators include temperature, predation and oxygen.

Temperatures changed uniformly throughout the study area. Therefore, the spatial differences in density and biomass encountered cannot be explained by any differential species response to thermal variation. However, seasonal changes in the zooplankton were definitely related to thermal changes. Densities of cladocerans and copepods particularly appear to be temperature dependent as indicated by Hazelwood and Parker (1961). Rotifer densities, on the other hand, were much less related to thermal change which agrees with the observations of Davis (1962). But even in the larger forms, seasonal relations to temperature could explain less than half of the variation found in the study area.

Size-selective fish predation can have a substantial effect on zooplankton densities and biomass (Brooks and Dodson, 1965; Hall, Cooper and Werner, 1970). Assuming that the larger zooplankton are more efficient at converting food to biomass (Odum, 1959) intense predation on the larger forms should decrease total biomass. Removal of large, efficient zooplankton would allow the small, less efficient forms to become more dense and perhaps increase the total density, but they would realize a smaller biomass than zooplankton standing crops dominated by the larger forms. Since predation, as indicated by fish abundances, was greatest in the discharge canal, intermediate in the lake, and negligible in the river, observed differences between these areas fit this pattern well. Mean size of zooplankton was lowest in the discharge canal where fish predation was high and greatest in the lake where fish predation was lower. However, these predator-prey relationships do not fit the expected pattern in the river. If no other environmental factor is of consequence, mean size of zooplankton in the river should have been the highest of all areas, for fish predation was negligible, and total biomass should have been equal to the lake, for food availability was similar in the two areas. This variation from the expected could potentially result from: (1) proportionately more zooplankton predation in the river, (2) differences in the quality of food produced, (3) differences in habitat quality which includes

oxygen concentrations, water velocities and toxins.

Differences in zooplankton predators are not likely to be responsible. With the exception of *C. vernalis*, none of the potentially important zooplankton predators were disproportionately more abundant in the river. *C. vernalis* was relatively more abundant only in June.

Compositional data on phytoplankton are unavailable but although food quality may contribute to the distributional pattern observed, it is likely that the river environment alone can account for much of the variation. In the spring, when river discharges were relatively high and unstable, zooplankton densities were negatively related to the discharge. However, during the summer and early fall, no correlation of river discharge and density was noted, yet the river had the lowest biomass of all areas. Also, the fact that biomass concentrations were comparable to the discharge canal and the lake in late spring and late October suggests a factor operating only during the summer months. This factor is very likely low oxygen concentrations directly or some toxic by-products associated with anaerobic conditions. Low oxygen concentrations do inhibit the larger plankters, cladocerans and copepods (Hazelwood and Parker, 1961). Although nothing is known about the relation of size to oxygen requirements in zooplankton it is conceivable that larger plankters are more susceptible to low oxygen concentrations than the smaller ones. This could explain why the mean size was less than in the lake even though predation was much lower.

Differences in the structure of particular zooplankton populations can also be explained by variations in food, predation and oxygen. The densities of copepod nauplii and juveniles, in relation to the densities of adults, was disproportionately high in the discharge canal and low in the river when compared to the lake. Less obviously but similarly, the ratio of immature and mature _D. retrocurva_ was lowest in the river. For the copepods, this phenomena could be attributed to: (1) selective predation on the adults in the discharge canal but not in the river, (2) higher reproductive rates in the discharge canal than in the river. Selective predation by fish on copepod adults probably was density dependent. In June and early July, when the greatest difference in population structure was noted between the two areas, adult copepods were very abundant. Since predation was relatively great in the discharge canal and low in the river, the obvious conclusion is that predation is the primary factor for the differential population structure. However, this does not account for the tremendous density of nauplii found in the discharge canal or low numbers found in the river (when compared to the lake). Edmondson, _et al._ (1962) found that copepod reproductive rates were positively related to food supply. This accounts for the high number of nauplii in the discharge canal. However, since nauplii densities were lower in the river than in the lake although both had similar food supplies, this would indicate that reproductive capacities in the river were reduced by some abiotic factor, such as oxygen availability.

The subtle variations in the vertical distribution of zooplankton in the study area also seem to be related to the mean plankter size. Larger species accounted for most of the difference in biomass found at the different depths. If fish predation strongly selects larger forms of zooplankton, the evolutionary advantage would be for the large plankters to avoid the illuminated surface waters and thus avoid sight-feeding fish (McLaren, 1965).

In summary, in western Lake Erie, except where abiotic conditions are intolerable, the distribution of zooplankton appears to be regulated by the variation in food availability and predation as hypothesized by Brooks and Dodson (1965).

Changes in Western Lake Erie

Data comparisons between this study and previous ones on western Lake Erie are assumed valid since similar netting was employed. Several significant changes have apparently occurred within the last several decades. The peak of C. sphaericus in late summer can be associated with a tremendous bloom of blue-green algae (Microcystis, Aphanozomenon) that occurred at the same time. Historically, this is not unusual (Hutchinson, 1967). However, peak densities of C. sphaericus found in this study were the highest ever reported for Lake Erie. Chandler (1940) did not even record this species from the western basin while maximums during this study were six times greater than those reported by David (1962) in the central basin.

Other zooplankton have shown various degrees of increase throughout the years. Most data is summarized from Bradshaw (1964). The trend for density increases in cladocerans and copepods is quite obvious (Figures 27, 28), but not in rotifers (Figure 29). Also, the spring and fall peaks of all these major groups has increased in intensity. Comparisons of biomass to Davis' (1958) data were made by converting his volume measurements to mg/liter. Indications are that zooplankton biomass, from June to August, have increased 5-fold in 14 years. Although his study was conducted on the east end of the basin, it is unlikely that there is much difference in phytoplankton between the two areas (Hartley and Potos, 1971) and therefore zooplankton densities are likely to be similar. In summary, the western basin has increased in standing crop of zooplankton with apparently most of this production

Figure 27. Changes in the total number of cladocerans in Lake Erie from 1939 to 1970. ....Chandler (1940); ----Verduin (1949), Hubschman (1960); _.._.._.._.. Davis (1962); ____this study.

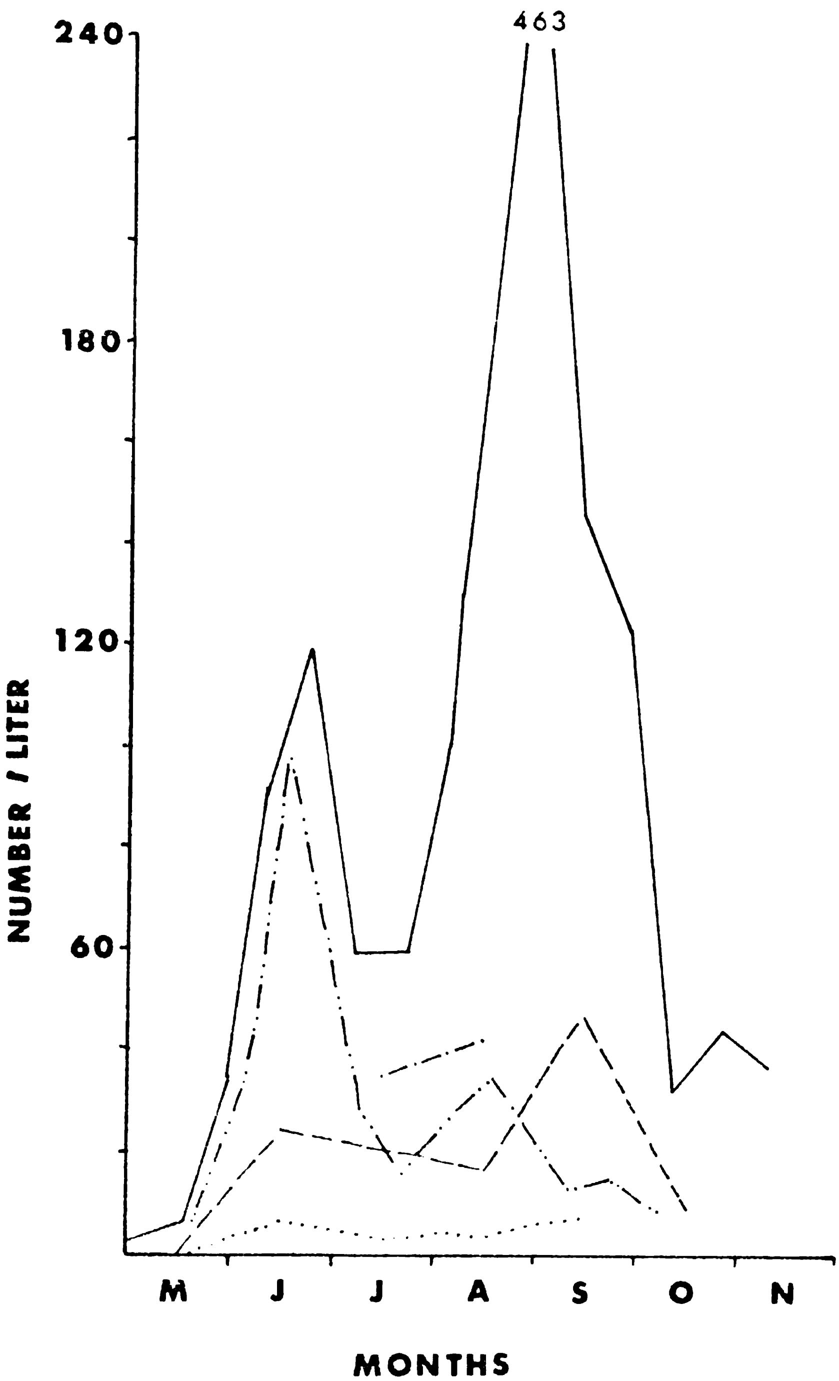

463
240
180
120
60
NUMBER / LITER
M
J
J
A
S
O
N
MONTHS

Figure 28. Changes in the total number of copepods in Lake Erie from 1939 to 1970. ....Chandler (1940); ----Verduin (1949); _._._._. Davis (1962); ____this study.

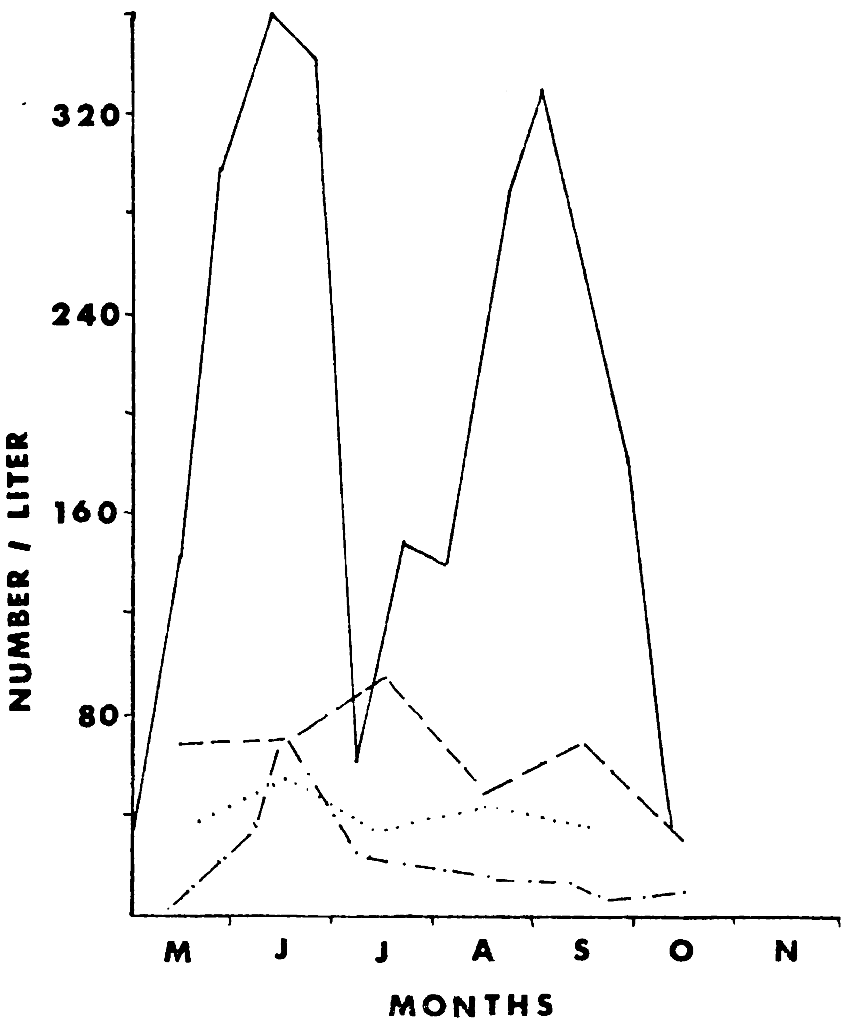
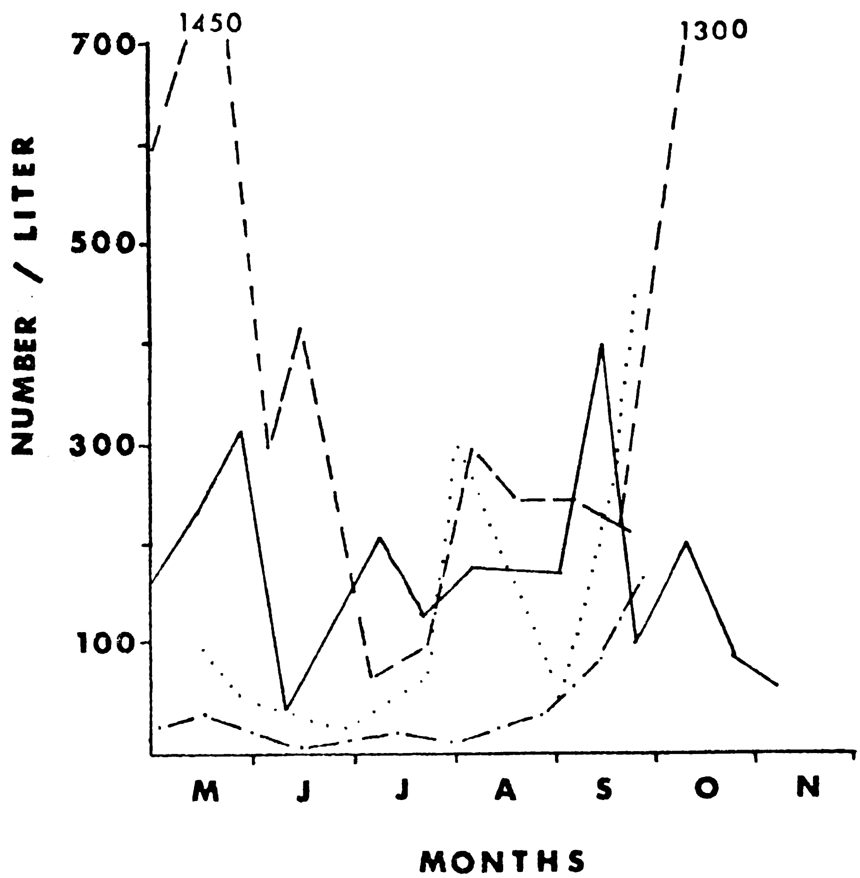

320
240
160
80
NUMBER / LITER
M
J
J
A
S
O
N
MONTHS

Figure 29. Changes in the total number of rotifers in Lake Erie from 1939 to 1970. ._._._._Chandler (1940); ....Davis (1954); ----Davis (1962); ____this study.


1450
1300
700
500
300
100
NUMBER / LITER
M
J
J
A
S
O
N
MONTHS

being channeled through the larger forms (cladocerans and copepods).

Most studies of the diet of young perch in the Great Lakes have been concerned with samples taken during a limited period in the summer (Ewers, 1933; Turner, 1920; Tharatt, 1959). Only Price (1963) has followed the seasonal changes in perch feeding habits. However, his data on young-of-the-year fish is very limited. This study is unique in following age 0 perch from spring to fall.

As found in previous studies, the young perch in this study fed heavily upon the entomostraca, cladocerans and copepods. However, in addition, species composition of the diet changed dramatically during the sampling period, shifting to the particular species most abundant at the time. Therefore, species preference tables, such as those given by Ewers (1933), are not meaningful unless prey densities are also given. This is especially true in areas where seasonal composition is quite variable, as in western Lake Erie.

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