ZOOPLANKTON ECOLOGY OF A GREAT PLAINS RESERVOIR

by 6408

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B. S., Colorado State University, 1969

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1971

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INTRODUCTION

Zooplankton inhabit a wide variety of aquatic environments (Hutchinson, 1967). The taxonomic composition of a zooplankton community and the numerical density of each species are affected by environmental conditions. Most investigators agree that temperature, food supply, and predation, acting separately or together, regulate the composition and density of the majority of zooplankton populations (Borecky, 1956; Edmondson, 1965; Frank, Bo11, and Kelley, 1957; Galbraith, 1967; Hall, 1964; Hazelwood and Parker, 1961; and others). The chemical properties of the water may be important in some cases (Hazelwood and Parker, 1962; Hutchinson, 1967). Rapid flushing time depletes zooplankton populations in some lakes (Brook and Woodward, 1956; Cowell, 1967).

Temperature usually affects the reproductive rate and the individual growth characteristics of zooplankton (Coker, 1933; Hall, 1964). For a given species an optimum temperature exists at which the species is most successful, other factors remaining constant. On either side of this optimum is a range of temperatures at which the organism can survive but is less successful than at the optimum.

Food also affects the reproduction and growth of zooplankton. Lower food supplies cause decreased reproduction (Hall, 1964), slower individual growth (Richman, 1958), and in extreme cases starvation (Hutchinson, 1967). The food of herbivorous zooplankton includes algae, bacteria, and detritus. Algae is

considered to be the most important source of food in most lakes, but detritus can be a major food source in the absence of algae (Saunders, 1969). The value of bacteria as an energy source has not been adequately established. Carnivorous zooplankton depend mainly on other zooplankton or protozoans for food, often being quite selective in their diet (Fryer, 1957).

Among the major predators of zooplankton are fish and, as stated above, other zooplankton. In addition to lowering the density, predation may also change the species composition of the zooplankton community (Brooks and Dodson, 1965; Cramer and Marzolf, 1970; Galbraith, 1967; Reif and Tappa, 1966). Cyclopoid copepods are at times predacious on other zooplankton and often cannibalistic, preying on their own species (Fryer, 1957).

In most freshwater environments water chemistry has little direct effect on zooplankton (Hutchinson, 1967). Dissolved oxygen can be limiting in very low concentrations. Correlations between populations and other elements have been shown, but no direct cause and effect was evident (Hazelwood and Parker, 1962).

The effect of rapid flushing time is merely depletion of the populations by loss through the lake outlet. Cowell (1967) found it to be a very effective depletion mechanism in Lewis and Clark Lake, South Dakota. Hall (1964) reported little loss of zooplankton to the outlet of Base Line Lake, Michigan even though the flushing rate was 12 percent of the lake volume per day during portions of the year.

Great Plains Reservoirs are relatively new environments from

which little information regarding zooplankton population regulation has been reported. The species composition has been determined for several reservoirs (Applegate and Murray, 1967; Cowell, 1967; Cramer and Marzolf, 1970; Prather and Prophet, 1969; Tash, Swanson, and Siefert, 1966). Standing crop estimates have been reported by Cowell (1967), Cowell (1970), and Applegate and Mullan (1967). With regard to population regulation, Cowell (1967) studied the effects of rapid flushing time and Cramer and Marzolf (1970) investigated the effects of selective predation by larval gizzard shad.

Great Plains Reservoirs are typically unstratified, high in nutrients, and often turbid, creating a unique environment for the zooplankton. The factors regulating populations in these waters may be different from the limiting factors in relatively clear, stratified lakes where most previous studies of zooplankton ecology have taken place. The turbid conditions may limit algal production, depriving the herbivorous zooplankton of their major food source. If this occurs the possibility exists for the zooplankton to utilize a detritus or bacterial energy source derived mainly from allochthonous organic material (Novak, 1969; Chen, 1968). Can populations of zooplankton survive on a bacterial and allochthonous organic matter diet? Water quality, suspended clay particles, isothermal temperature conditions, and wind mixing almost certainly affect the populations, but how? Most reservoirs of this type support a large population of gizzard shad which impose a major predatory force

on the zooplankton (Cramer and Marzolf, 1970). However, no quantitative predation data has been reported. Nor is the nature of the predatory impact known over the horizontal extent of any reservoir.

Before well defined questions about reservoir zooplankton populations can be formulated, a general survey was needed to establish important possible relationships and aid in designing future reservoir studies. This study was designed to monitor various chemical, physical, and biological variables while following fluctuations of the major zooplankton groups in Tuttle Creek Reservoir, Kansas. The specific objectives of the investigation were: 1) Through periodic measurement, determine the seasonal fluctuations in zooplankton populations in Tuttle Creek Reservoir; 2) Using a relatively large number of random samples on each sampling date, determine the horizontal distribution of zooplankton in the reservoir; 3) Assess the dynamics of various possible food sources by measuring chlorophyll, bacteria, and particulate organic matter on each sampling date at each sampling site; 4) Through measurement of physical, chemical, and food supply parameters concurrent with the sampling of zooplankton populations, determine some of the factors affecting the size and the fluctuations of the zooplankton populations in the reservoir.

The importance of understanding the dynamics of reservoir zooplankton populations is twofold. First, it is an area of zooplankton ecology which has received very little attention,

probably due to the relative newness of the environments. Secondly, zooplankton are a major source of food for the young of many game and forage fishes. The abundance of zooplankton affects the survival and growth of these fishes, and hence affects the sport fishing recreational value of the reservoir.

DESCRIPTION OF STUDY AREA

Tuttle Creek Reservoir is described adequately by Cramer and Marzolf (1970), Dufford (1970), Novak (1969), and Schwartz and Marzolf (1971) who have established the strata used for sampling purposes (Fig. 1). Table 1 lists additional physico-chemical features of the reservoir measured in 1970.

Table 1. Values of some important physico-chemical parameters for Tuttle Creek Reservoir, Kansas during 1970.

Parameter	Minimum	Maximum	Mean
Water temperature, ^{o}C	7.20	27.90	20.90
Extinction coefficient	0.50	20.00	3.46
Secchi disc transparency, cm	3.00	142.00	46.80
Dissolved oxygen, mg/l	3.20	8.90	6.96
Specific conductance, μmhos	250.00	580.00	414.40
pH	7.10	8.70	8.26
Carbonate alkalinity, mg/l	0.00	22.00	3.94
Bicarbonate alkalinity, mg/l	102.00	210.00	148.20
Orthophosphate, mg/l	0.04	1.44	0.21
Nitrate nitrogen, mg/l	0.01	1.49	0.85
Nitrite nitrogen, mg/l	0.01	0.36	0.04
River inflow, m^3/sec	5.66	866.99	45.43
River outflow, m^3/sec	4.24	424.30	59.55

The tributaries of the reservoir are characterized by highly

fluctuating flow rates due to erratic rainfall patterns. Since the drainage basin is mainly cultivated land, high sediment loads are common especially during periods of prolonged rainfall which, once the soils are saturated, causes extensive runoff. Dufford (1970) estimated a total of 5,490,291 metric tons of sediment entered Tuttle Creek Reservoir from 1 February 1969 to 15 October 1969. Due to the high sediment content of inflowing waters, the reservoir is turbid (light extinction coefficient greater than 3) most of the year. The water tends to clear during ice cover in January and February, but heavy spring rains bring high, sediment-rich inflow water causing the upper reaches of the reservoir to become very turbid. The turbid water gradually moves through the reservoir losing part of the sediment as it moves. Hence, strata I-III of the reservoir generally are less turbid than strata IV and VI (Fig. 1). Stratum V collectively refers to the coves which, because they are protected, are less affected by the turbid inflowing waters. The extent of the turbidity gradient is altered by wind, river inflow, river outflow, and the periodicity of the rainfall (Dufford, 1970). The gradient usually persists throughout the summer and fall, its extent dependent mainly on rainfall patterns.

The narrow, shallow basin with long fetch, and the general north-south orientation makes the reservoir particularly susceptible to prevailing winds. The winds, coupled with the periodically high inflows, prevent prolonged thermal stratification in the reservoir.

EXPLANATION OF FIG. 1

Map of Tuttle Creek Reservoir, Kansas with strata and numbered grid shown.

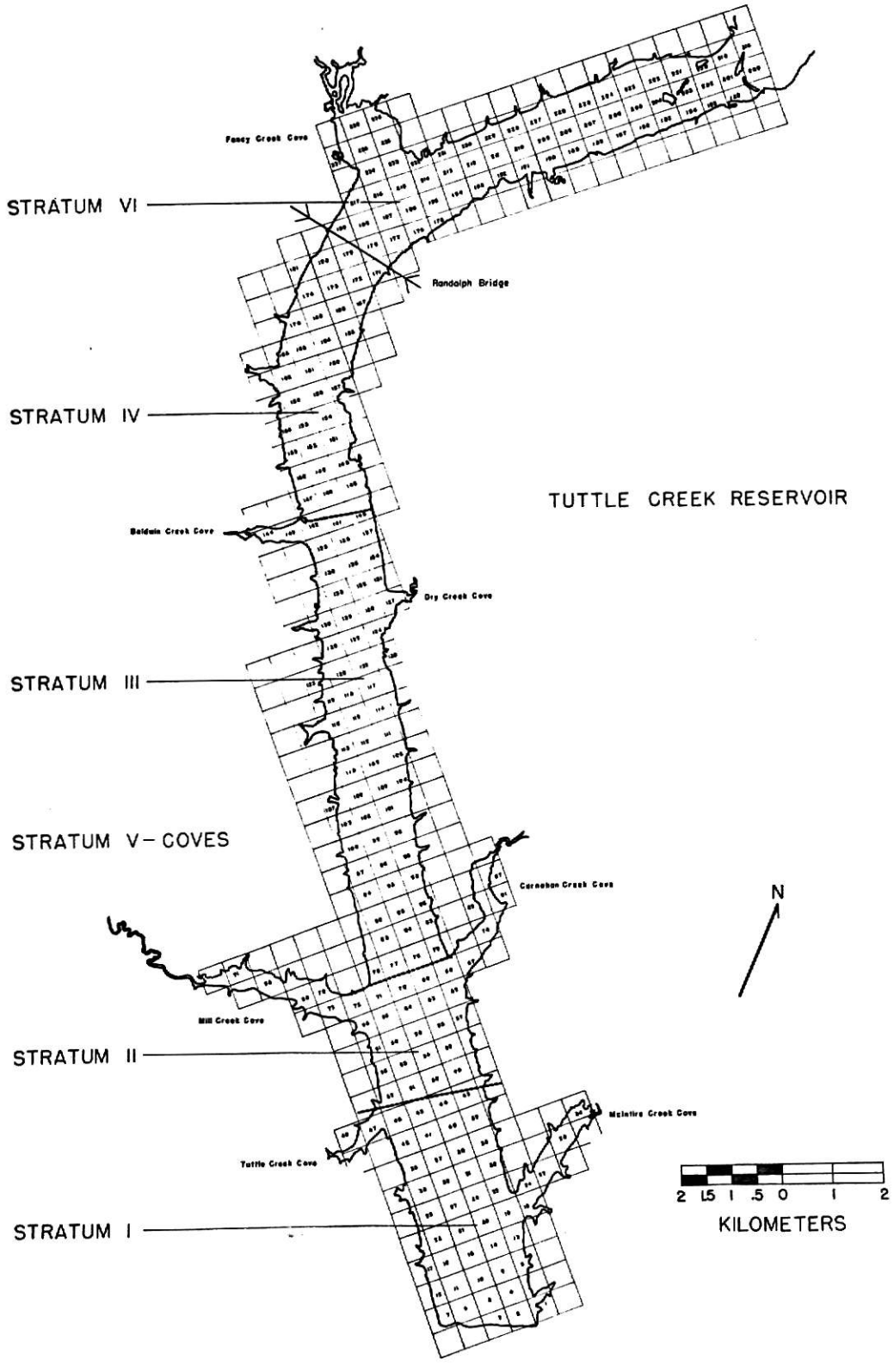
STRATUM VI
STRATUM IV
STRATUM III
STRATUM V – COVES
STRATUM II
STRATUM I
TUTTLE CREEK RESERVOIR
Fancy Creek Cove
Randolph Bridge
Baldwin Creek Cove
Dry Creek Cove
Cannahan Creek Cove
Mill Creek Cove
McIntire Creek Cove
Tuttle Creek Cove
N
2 1.5 1 .5 0 1 2
KILOMETERS

Fig. 1

MATERIALS AND METHODS

Zooplankton populations and presumably important environmental variables were measured on 17 sampling dates from 11 April 1970 to 16 November 1970. A biweekly to monthly sampling interval was followed in April, May, September, October, and November, and a 10-day sampling interval was employed during June, July, and August.

Samples were collected according to a stratified random sampling technique taken from Cochran (1953) and developed for Tuttle Creek Reservoir by Heltshe (1969). The reservoir was divided into six strata. The strata were selected in such a manner as to try to minimize sampling variation within each stratum and increase the power of detecting differences among strata. A grid system superimposed on a reservoir map was used to select random sampling sites within each stratum (Fig. 1). Since a new random sample was selected for each sampling date, the sampling sites on two sampling dates could be the same only by chance. The number of samples per stratum was constant and weighted according to the surface area of the stratum except for stratum VI which contained only one sampling site added after the design was completed. The total number of samples desired per sampling date was originally 15, therefore Heltshe (1969) recommended the following apportionment of samples for strata I-V:

Stratum	No. of samples
I	3
II	2

III 5
IV 3
V 2

The design readily lended itself to a one-way analysis of variance to determine differences among parameter means of the strata, therefore testing for horizontal variation in the parameter being considered. It also divided the reservoir into six sections which, if desired, could be considered separately when evaluating the effects of various factors on zooplankton populations.

Zooplankton were collected using a #20 (.076 mm mesh size) weighted nylon tow net with a mouth diameter of .31 m. One vertical tow was made at each station by allowing the net to settle on the bottom then bringing it slowly straight up to the surface. Each sample was labeled and preserved in 95 percent alcohol for later analysis.

Later each sample was divided into two equal parts by drawing the sample down to 100 ml, mixing well, and pouring 50 ml into another container. One portion of the sample was used for enumeration; the other was used for determining biomass.

The biomass of the zooplankton was determined by filtering a sample onto an oven dry, previously weighed circular piece (61 mm dia.) of #20 nylon bolting cloth. A filtering apparatus was constructed by placing the net filter on a 61 mm diameter circular, perforated plexiglass disc and clamping a regular 2-inch Millipore filtering funnel onto the filter and disc.

Filtering was accomplished by simply pouring the sample in the funnel, the plankton being retained by the net filter. The filter and zooplankton were dried at 50 C for 24 hours, then weighed to the nearest .1 mg. The biomass of the zooplankton was obtained by subtraction. The biomass per m^3 was then calculated from the total biomass using:

$$Z = (B \times 2) / (D \times R^2 \times \pi)$$

where: Z = biomass of zooplankton, mg/m^3

B = total mass of zooplankton in the sample, mg

R = radius of the mouth of the plankton net, .155 m

D = depth of water at the sampling site, m

Most of the zooplankton found in the samples were members of one of the three groups: Daphnia spp., Diaptomus spp., or cyclopoid copepods. Hence, only six categories, the juveniles and adults of each of the above groups, were considered in this study. Identification was made with the keys of Brooks (1957) and Edmondson (1959). When counting, identifications were made to the generic level for Daphnia and Diaptomus and to ordinal level for the cyclopoid copepods. The general nature of the study did not allow specific identification. Table 2 lists the species within each of these groups known to be in Tuttle Creek Reservoir (Cramer and Marzolf, 1970).

The remaining one-half sample was diluted to 100 ml and three 1 ml subsamples were removed with a Hensen-Stempel piston pipette. One subsample at a time was placed in a rotary type counting chamber (Ward, 1955). By revolving the chamber the

the plankters passed single file under the scope and were easily counted without duplication. After enumeration the data from each subsample were punched on data cards, and a computer program was written to calculate the number of individuals in each group per liter of water using the formula:

$$N_i = ((C_{i1} + C_{i2} + C_{i3}) / 3) / (5 \times D \times R^2 \times \pi)$$

where: N_i = number of individuals of ith group per liter

C_{i1}, C_{i2}, C_{i3} = number of individuals in ith group in each respective subsample

D = depth of the water at the sampling site, m

R = radius of the mouth of the plankton net, .155 m

Table 2. Species of the groups considered known to be in Tuttle Creek Reservoir, Kansas.

Group	Species included
Daphnia spp.	*Daphnia ambigua*
	D. pulex
	D. schødleri
	D. parvula
Diaptomus spp.	*Diaptomus pallidus*
	D. oregonensis
	D. siciloides
	D. clavipes
Cyclopoida	*Cyclops bicuspidatus*
	Mesocyclops edax

Water temperature in degrees C was measured at depth intervals of 1 m using a model TC5 Whitney underwater thermometer.

Water transparency was determined to the nearest cm using a 20 cm diameter Secchi disc with black and white quadrants. The methods of Dufford (1970) using an underwater photometer were utilized in finding the light extinction coefficient of the water.

A 3 liter Kemmerer water bottle was used to collect a 1 liter water sample from the top meter of water for the determination of nitrate nitrogen, nitrite nitrogen, orthophosphate, chlorophyll, particulate organic matter, pH, carbonate alkalinity, bicarbonate alkalinity and specific conductance. A 300 ml BOD bottle for dissolved oxygen determination and a sterile 30 ml bottle for bacterial analysis were also filled from the same bottle.

The bacterial samples were kept in an ice chest until reaching the laboratory. Two suitable dilutions of each sample (usually 1:100 and 1:500 depending upon the expected number of bacteria) were made with lake water which had been sterilized for 30 minutes at 20 psi. A 1 ml sample from each dilution was then pipetted into a sterile 100 mm x 15 mm disposable Petri dish. Approximately 20 ml of one-half strength nutrient agar, sterilized for 30 minutes at 20 psi and then kept in a water bath at 50 C, was then poured in each plate. The agar was allowed to solidify, and the plates were inverted and cultured in the dark for 96 hours at 25 C (Harris, personal communication).

A Quebec Colony Counter was utilized in counting the number of colonies per plate. The most probable number of cells per ml of water was calculated by multiplying the number of colonies on the plate by the dilution factor (Carpenter, 1967). Whenever possible, the plate with 30 to 300 colonies was used in calculating the most probable number (Carpenter, 1967), or if both plates fell in the above range the average was used. If neither plate count fell within this range, the one nearest 30 was used.

Particulate organic matter in mg glucose carbon per m^3 was determined using a modification of the dichromate oxidation-spectrophotometric method of Strickland and Parsons (1960). The modified method included all organic matter trapped by a filter equivalent to an HA Millipore filter (pore size = .45 microns). Novak (1969) gives a complete discussion of various methods of organic matter measurement and lists the advantages of the dichromate oxidation method. See Appendix 1 for a detailed description of the modified method. Organic matter samples are missing for April and May due to delayed equipment delivery.

The concentration of dissolved oxygen in mg per liter was determined by the PKA Modification of the Winkler Method (APHA, 1961). Due to the homogeniety of the reservoir with respect to dissolved oxygen (Osborne, personal communication), only one sample per stratum was obtained.

Specific conductance was measured in μmhos with a model 2300 Hach Dissolved Solids Meter.

A model PBL Sargent-Welch pH Meter was used to determine

the hydrogen ion concentration in the water.

Carbonate and bicarbonate alkalinities were determined in mg per liter using the change in pH method of APHA (1961).

The spectrophotometric method of Richards and Thompson (1952) was utilized in the measurement of chlorophyll concentration in mg per m^3.

Orthophosphate, nitrite nitrogen, and nitrate nitrogen were measured in mg per liter using the methods described by Golterman (1969).

All spectrophotometric methods utilized a Beckman model 2400 DU Spectrophotometer.

The U. S. Army Corps of Engineers kindly provided copies of reservoir data collected daily including river inflow, river outflow, and wind velocity. These data were converted to 7-day means by averaging the values for the sampling date and six days prior to sampling. These means partially accounted for the lag effects of inflow, outflow, and wind.

For some organisms a juvenile to adult ratio is a good index of the immediate reproductive history of a population (Gross, 1969). This parameter was calculated for each of the three zooplankton groups in an effort to detect changes in the reproductive state of the populations. Juvenile populations alone were not considered.

Variables included in the analysis described subsequently are listed in Table 3 as abbreviations. Measurements of these variables were recorded for subsequent analysis on an IBM

Systems 360/50 computer.

Table 3. Description of variables considered in the study. These variable names are used hereafter in the text.

Variable Abbreviation	Description
TEMP	water temperature, ^{o}C
EXTCOEF	extinction coefficient of the water
SECCHI	Secchi disc transparency, cm
DEPTH	water depth, m
O2	dissolved oxygen, mg/l
SPCOND	conductance of the water, μmhos
PH	$\log_{10}$ hydrogen ion concentration in the water
CO3	carbonate ion, mg/l
HCO3	bicarbonate ion, mg/l
PO4	orthophosphate ion, mg/l
NO3	nitrate nitrogen, mg/l
NO2	nitrite nitrogen, mg/l
CHLORO	chlorophyll, mg/m^3
POM	particulate organic matter, mg/m^3
BACTERIA	bacterial cells, number/ml
ZBIOM	zooplankton biomass, mg/m^3
DAPHNIA	adult Daphnia, number/l
JA-DAPH	juvenile-adult ratio for Daphnia
CYCLPOID	adult Cyclopoida, number/l
JA-CYCL	juvenile-adult ratio for Cyclopoida

Table 3. (continued)

Variable Abbreviation	Description
DIAPTMUS	adult Diaptomus, number/l
JA-DIAP	juvenile-adult ratio for Diaptomus
INFLOW	7-day mean river inflow, cfs
OUTFLOW	7-day mean river outflow, cfs
WIND	7-day mean wind velocity, mph
% OUT 30	percentage of water in the reservoir replaced in the 30 days previous to sampling
% OUT 60	percentage of water in the reservoir replaced in the 60 days previous to sampling
TEMP2	the square of water temperature

A two-way analysis of variance was performed to assess significant seasonal changes in zooplankton densities and differences in numerical densities among strata. A computer program was written by the author specifically for the analyses desired using the methods of Snedecor and Cochran (1967).

Pearson's product moment correlation coefficients were computed between each pair of parameters to assess possible relationships and as a preliminary screening process prior to regression analysis. The Missing Data Correlations Program of the Kansas State University Statistical Laboratory was used.

Multiple regression analysis was employed to assess possible effects of environmental variables on zooplankton populations.

Three main criteria were used in assessing the significance of environmental variables affecting zooplankton. First, the T-test for significance of the regression coefficient, b, was used to determine statistical significance of the variables in the model. Second, if the coefficient was statistically significant at a reasonable alpha level such as .10, a biological explanation for the relationship was sought. If no valid explanation could be suggested, the variable was not considered further. Thirdly, the effect of adding a variable to the model on the coefficient of multiple determination, R^2, was considered. R^2 x 100 is the percentage of the variation observed in the dependent variable which can be "accounted for" by the independent variables in the model (Draper and Smith, 1968). In Table 5 and Tables 8-14, b for each independent variable and R^2 and n, the number of observations, are given for each analysis.

The square of water temperature, TEMP2, was introduced into several analyses since the relationship between temperature and some zooplankton groups appeared parabolic on a scatter diagram. In those cases a quadratic model fit the data better than a linear model and the quadratic model was, therefore, used. If TEMP2 was significant and possessed a negative coefficient, it implied that a population possessed a temperature preference and the population reacted negatively to temperatures higher or lower than the preferred temperature.

Rapid flushing rates in some lakes can deplete zooplankton and phytoplankton populations (Cowell, 1967; Brook and Woodward,

1956). To relate the flushing time of Tuttle Creek Reservoir to its populations, two terms were created, % OUT 30 and % OUT 60. The terms supplied an index to the time that the water from which the sample was taken had been in the reservoir. It was assumed that all portions of the reservoir were equally affected by the flushing time. This assumption was not necessarily valid, but it was the best approximation since very little is known about the currents in the reservoir.

RESULTS

The mean number of zooplankton in each group per liter for each stratum on each sampling date are listed in Appendix 2.

The seasonal variations in each of the three adult groups of zooplankton are shown in Fig. 2 as means for the reservoir on each sampling date. Peaks in Daphnia numbers occurred in May and August. Statistical analysis showed the spring (May and April) population of Daphnia to be significantly ($p \leq .05$) larger than either the summer (June, July, August) or the fall (September, October, November) populations. No difference was evident between the number of Daphnia in the summer and fall. Cyclopoida were abundant during the spring, but few were present thereafter. A significant ($p \leq .05$) difference existed between the populations of the spring and the summer, and between the spring and fall populations. The numerical density of cyclopoids in the summer was not shown to be different than that in the fall. Diaptomus populations in the reservoir were low during the study except for a slight peak in late August lasting through September. Analysis of variance and multiple comparisons (Snedecor and Cochran, 1967) showed the summer and fall populations to be significantly larger ($p \leq .05$) than the spring population. Summer and fall populations were not significantly ($p > .05$) different from one another.

Analysis of variance of Daphnia distribution provided the basis for detecting differences among densities of each stratum.

EXPLANATION OF FIG. 2

Mean number of *Daphnia*, *Diaptomus*, and Cyclopoida for the reservoir on each sampling date.

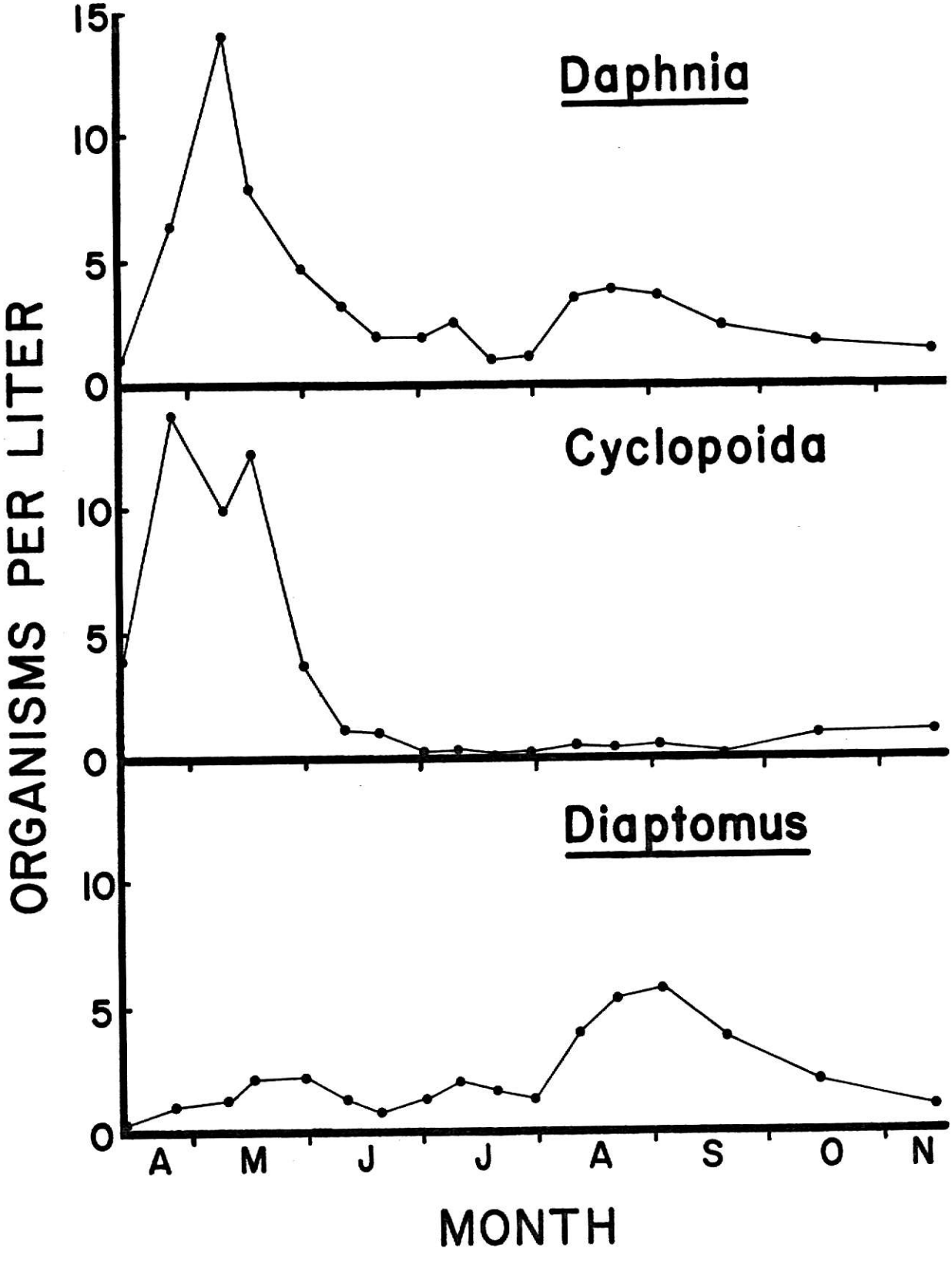
Daphnia
Cyclopoida
Diaptomus
ORGANISMS PER LITER
15
10
5
0
A
M
J
J
A
S
O
N
MONTH

Fig. 2

The analysis indicated a significant ($p \leq .05$) difference among the densities in each stratum (Fig. 3). Average standing crops of Daphnia were significantly ($p \leq .05$) larger in strata III, IV, and VI than in strata I and II. No difference was evident between the populations of strata III and IV, or IV and VI. No significant ($p > .05$) difference was found between the Daphnia numbers in the coves (stratum V) and the main reservoir, nor between stratum V and strata I and II, the main reservoir strata from which all but one of the coves extends (Fig. 1). These analyses indicate that Daphnia were not distributed evenly throughout the reservoir. Larger populations per liter were present in the upper, shallower portions of the reservoir than in the lower portions.

Cyclopoid copepods were distributed similarly to Daphnia (Fig. 4). There was a significant ($p \leq .05$) difference between strata III, IV, and VI and strata I and II, with greater numbers in the upstream strata. Cove populations were not different from lake populations, except that stratum I contained slightly lower densities than the coves.

Although seasonally different Diaptomus was distributed similarly to Daphnia and the cyclopoid copepods (Fig. 5). Their density was significantly ($p \leq .05$) higher in strata III, IV, and VI than in strata I and II. Cove populations were similar to the main reservoir. Stratum I produced significantly ($p \leq .05$) smaller numbers than the coves and stratum IV produced more. Comparison of cove population density to the mean

EXPLANATION OF FIG. 3

Mean number of Daphnia per liter in each stratum for entire sampling period with standard error.

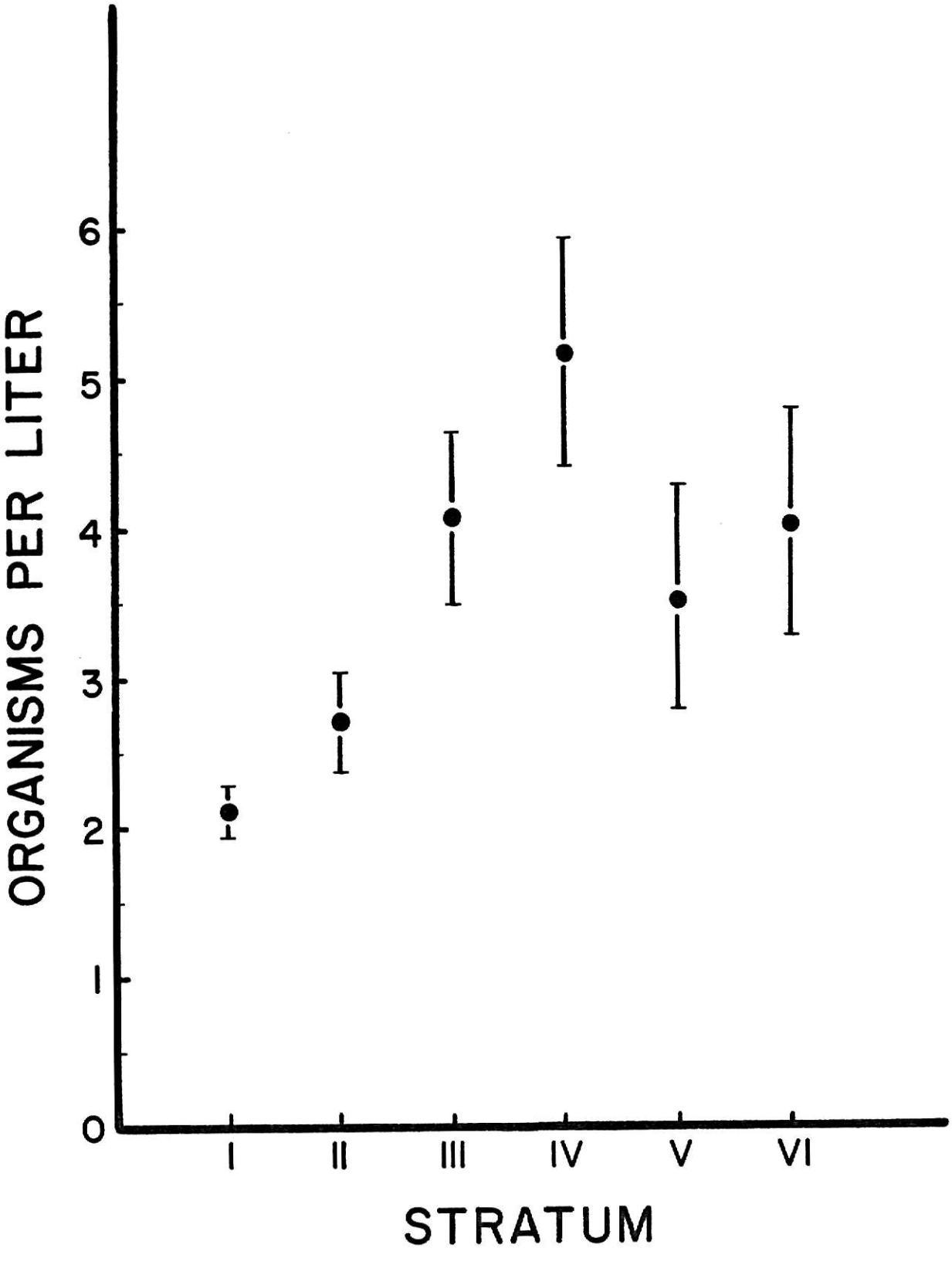

Fig. 3

EXPLANATION OF FIG. 4

Mean number of Cyclopoida per liter for each stratum for entire sampling period with standard error.

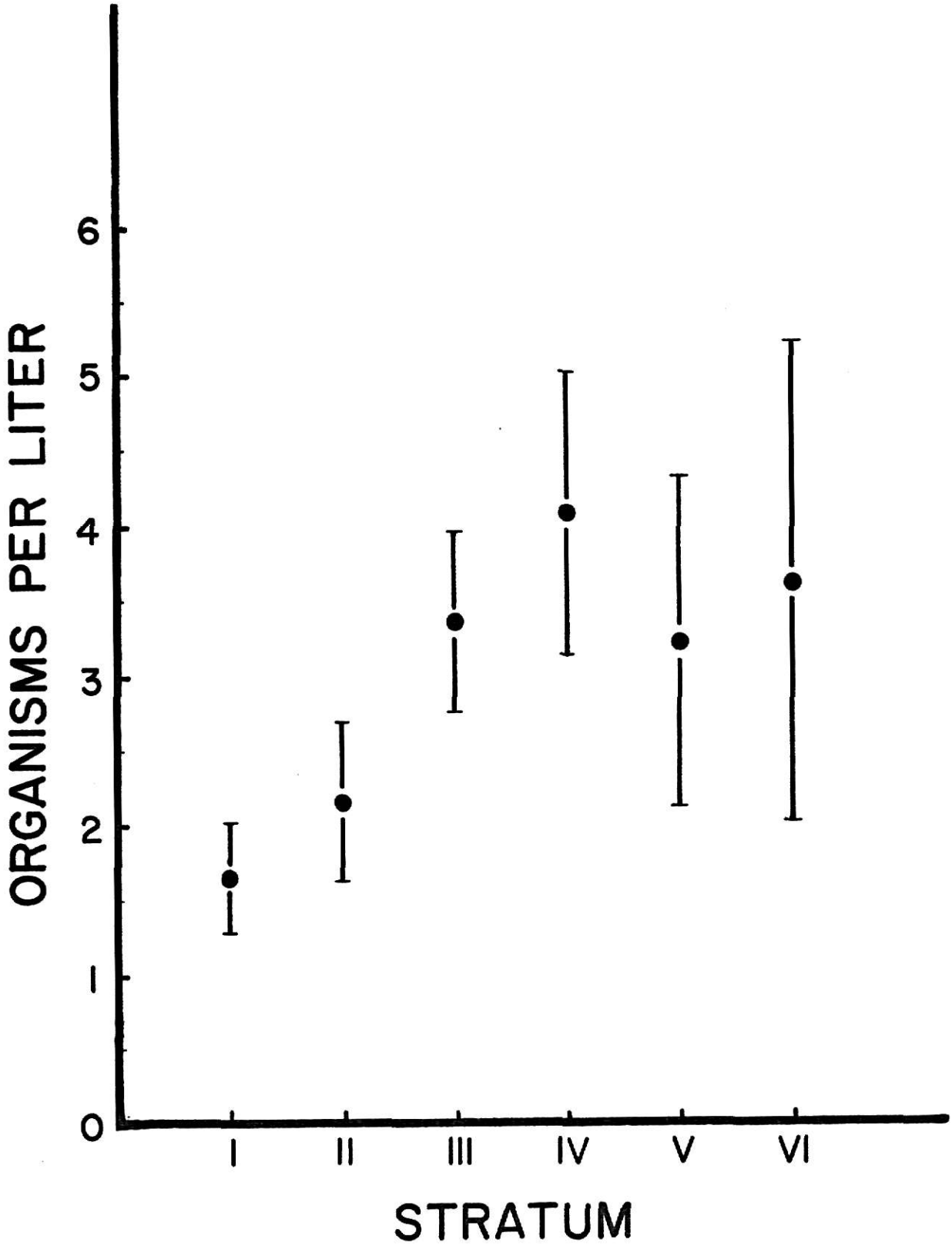

Fig. 4

EXPLANATION OF FIG. 5

Mean number of *Diaptomus* per liter in each stratum for entire sampling period with standard error.

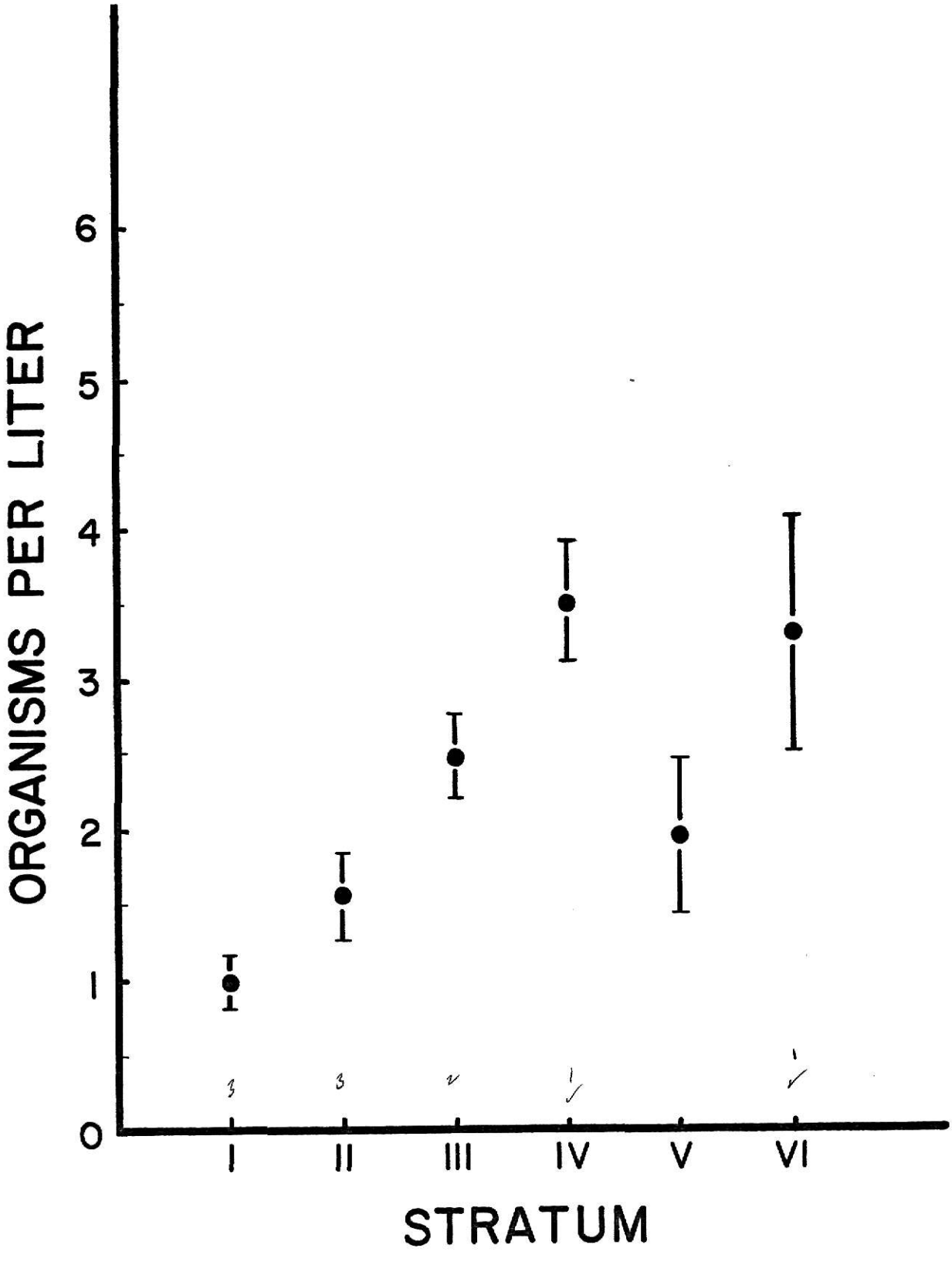

Fig. 5

of the remaining strata revealed no significant difference ($p > .05$).

The seasonal distribution of bacteria, particulate organic matter, and chlorophyll is shown in Fig. 6. Bacteria and particulate organic matter were not collected in April and May.

The mean values of each potential food source for each stratum for the entire sampling period are shown in Table 4. Food was more abundant in the upstream strata.

Table 4. Mean values with standard error for BACTERIA, POM, and CHLORO for each stratum for the entire sampling period. The number of observations is shown in parentheses.

Stratum		BACTERIA (cells/ml)	POM (mg/m^3)	CHLORO (mg/m^3)
I	Mean	9611(36)	660(29)	7.67(48)
	Std. Err.	2502	64	0.81
II	Mean	9860(24)	678(20)	11.82(32)
	Std. Err.	4366	53	2.60
III	Mean	9368(60)	785(48)	11.71(80)
	Std. Err.	2033	53	1.75
IV	Mean	13093(34)	926(28)	13.41(46)
	Std. Err.	3199	80	2.30
V	Mean	18570(24)	966(20)	14.90(32)
	Std. Err.	5480	94	2.50
VI	Mean	25283(12)	1710(13)	16.70(16)
	Std. Err.	8009	373	4.20

Regression analyses revealed some possible relationships between the abundance of various food types and other reservoir

EXPLANATION OF FIG. 6

Mean values for reservoir on each sampling date for chlorophyll, particulate organic matter, and bacteria.

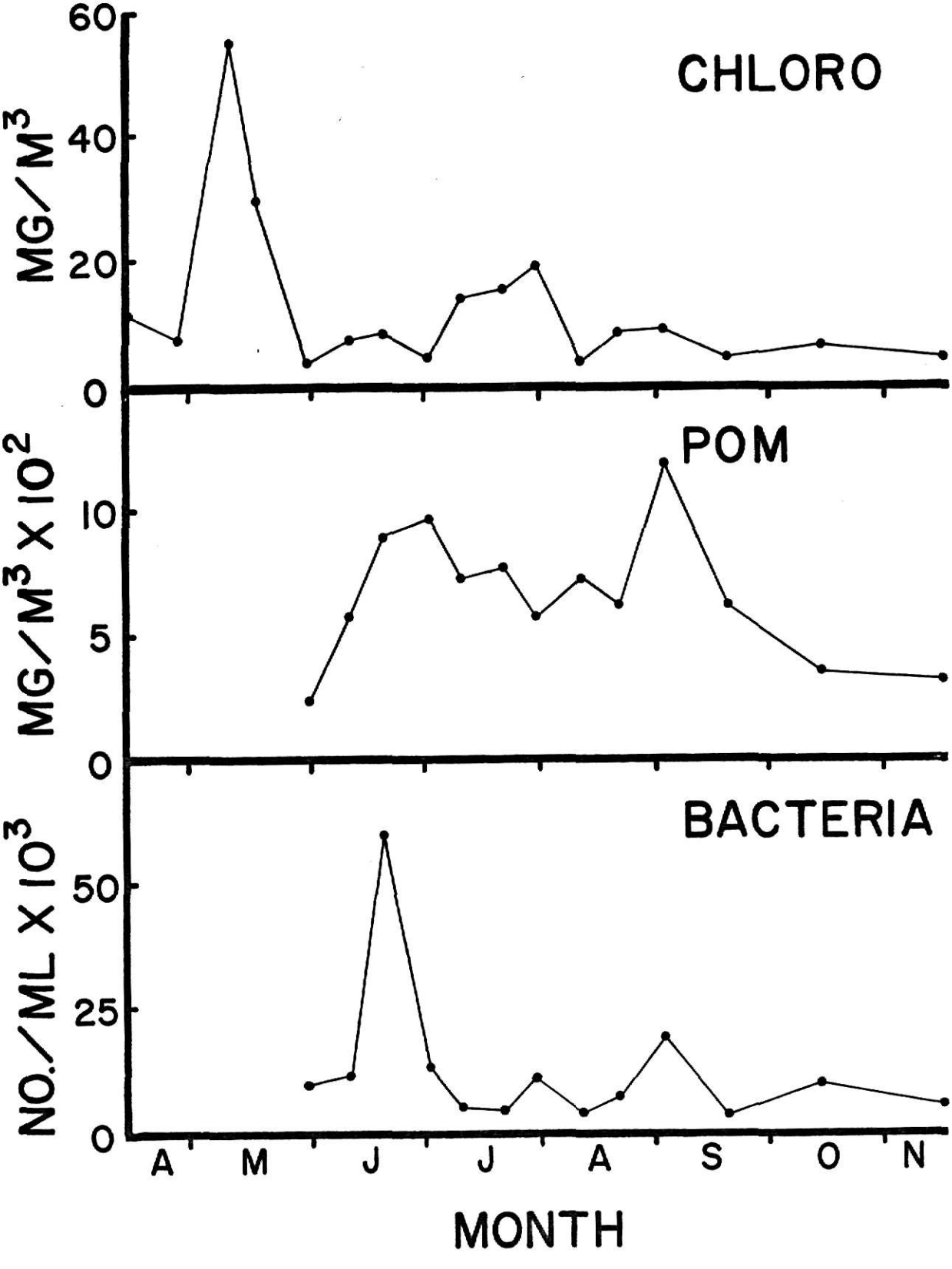
CHLORO
MG/M3
60
40
20
0
POM
MG/M3 X 10^2
10
5
0
BACTERIA
NO./ML X 10^3
50
25
0
A
M
J
J
A
S
O
N
MONTH

Fig. 6

variables. These are presented in Table 5.

Table 5. Analyses used in explaining the variation in the abundance of potential food.

Dependent Variable	Analysis No.	Independent Variable	b	n	R^2
CHLORO	1	HCO3	0.4538**	270	.2298*
		INFLOW	-0.0012**		
		EXTCOEF	1.0178**		
		TEMP	0.1596		
		% OUT 30	-3.7439		
	2	HCO3	0.4520**	270	.2279*
		INFLOW	-0.0014**		
		EXTCOEF	0.8553		
		TEMP	0.1353		
	3	HCO3	0.4400**	270	.2247*
		INFLOW	-0.0014**		
		EXTCOEF	0.9579*		
POM	1	BACTERIA	0.0118**	142	.4314**
		OUTFLOW	0.1433		
		CHLORO	9.2553		
		INFLOW	-0.0438		
	2	BACTERIA	0.0117**	142	.4308**
		OUTFLOW	0.1118**		
		CHLORO	9.7466		
	3	BACTERIA	0.0124**	142	.4165**
		OUTFLOW	0.1031**		
BACTERIA	1	POM	9.0318**	142	.4132**
		INFLOW	2.0695		
		OUTFLOW	1.1693		
	2	POM	9.2261**	142	.4122**
		INFLOW	3.5674**		

** significant at .01 level
* significant at .05 level

Correlation and multiple linear regression were employed to identify the major factors affecting the zooplankton distribution and density. The correlations between zooplankton and environmental variables in each stratum were generally similar, hence it was reasoned that any particular factor had essentially the same effect on the populations regardless of reservoir location. The similar correlations in all strata allowed pooling of these data for further analysis. Using the pooled data more extensive and thorough analyses could be undertaken than with several smaller data sets. Correlation coefficients for the pooled data between zooplankton variables and the measured environmental variables are shown in Tables 6 and 7.

Dissolved oxygen showed little relationship with the zooplankton (Table 6). This was expected since the reservoir is well mixed by wind, maintaining the oxygen high above limiting levels. Therefore, dissolved oxygen was not considered limiting in any stratum or at any time.

Since POM and BACTERIA were not measured during April and May, they were not included in the regression analyses. Instead, the effects of these variables were evaluated separately on the basis of correlations and discussions in the literature.

The remaining variables were used as independent variables in regression analyses with zooplankton densities as the dependent variables. These analyses, combined with data plots, were used to delineate the most important factors affecting the

zooplankton densities and in what season each factor was most important. Results of the regression analyses for each group are shown in Tables 8-13.

The seasonal variation of total zooplankton biomass is shown in Fig. 7. Table 14 lists regression analyses used to determine the factors affecting the amount of biomass.

Table 6. Correlation coefficients for DAPHNIA, CYCLPOID, and DIAPTMUS with environmental variables.

Variable	n	DAPHNIA	CYCLPOID	DIAPTMUS
TEMP	270	-.0815	-.3614**	.2940**
EXTCOEF	270	-.1538*	-.1901**	-.0288
SECCHI	270	.0511	.0971	-.1482
DEPTH	270	-.2088**	-.1457*	-.3072**
O2	114	-.0275	.0718	-.1183
SPCOND	270	.4088**	.5170**	.0128
PH	270	.0651	.1298*	.0167
CO3	270	.0372	.2656**	.0055
HCO3	270	.4694**	.4345**	.0064
PO4	270	-.0490	-.0738	.0715
NO3	270	-.4585**	-.5452**	.0203
NO2	270	.0731	.0428	-.0026
CHLORO	270	.5621**	.3747**	-.0697
POM	158	.0717	.1881*	-.0310
BACTERIA	190	-.0268	.0742	-.1693*
INFLOW	270	-.0827	-.0806	-.1850**
OUTFLOW	270	.0282	.1313*	-.1790**
WIND	270	.1065	.0001	-.2397**

** significant at .05 level
* significant at .10 level

Table 7. Correlation coefficients for JA-DAPH, JA-CYCL, and JA-DIAP with environmental variables.

Variable	n	JA-DAPH	JA-CYCL	JA-DIAP
TEMP	270	-.0284	-.1265*	.3770**
EXTCOEF	270	.0309	-.0572	.0832
SECCHI	270	-.1386*	.0391	-.1418*
DEPTH	270	-.2068**	-.0398	-.0519
O2	114	-.0068	-.0317	-.1416
SPCOND	270	.0863	.1687**	-.2931**
PH	270	-.0091	.0275	.0920
CO3	270	.0468	.1189	-.0990
HCO3	270	.0217	.2248**	-.1398*
PO4	270	-.1276*	-.0452	-.0936
NO3	270	.0982	-.1944**	.3307**
NO2	270	-.0344	-.0467	-.0639
CHLORO	270	.0657	.1382*	-.0842
POM	158	-.0683	.1294	-.0828
BACTERIA	190	-.1931**	.2234**	-.0710
INFLOW	270	-.2439**	-.2310**	-.1042
OUTFLOW	270	-.1892**	.2204**	-.1771**
WIND	270	.1191	.1063	.0492

** significant at .05 level
* significant at .10 level

Table 8. Results of multiple linear regression analyses with DAPHNIA as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	TEMP	0.1179**	270	.5069**
	CHLORO	0.0988**		
	NO3	-3.3601**		
	HCO3	0.0544**		
	SPCOND	0.0105		
	INFLOW	-0.0003		
	EXTCOEF	-0.1186		
	SECCHI	-0.0066		
	DEPTH	-0.0976		
	PH	-0.1988		
	CO3	-0.0146		
	PO4	-0.4454		
	NO2	4.3451		
	OUTFLOW	0.0001		
2	TEMP	0.1540**	270	.4933**
	CHLORO	0.1045**		
	NO3	-3.4798**		
	HCO3	0.0472**		
	SPCOND	0.0157**		
3	% OUT 60	-2.7534**	270	.4211**
	CHLORO	0.1520**		
	TEMP	0.7881**		
	TEMP2	-0.0209**		
	INFLOW	0.0002		
4	% OUT 60	-2.3063**	270	.4158**
	CHLORO	0.1455**		
	TEMP	0.8922**		
	TEMP2	-0.0240**		
5	CHLORO	0.1435**	270	.3905**
	TEMP	1.0917**		
	TEMP2	-0.0318**		
6	% OUT 60	-3.1714**	270	.3866**
	CHLORO	0.1648**		
	TEMP	0.0753		
7	% OUT 60	-2.4558**	270	.3777**
	CHLORO	0.1647**		

** significant at .01 level

Table 9. Results of multiple linear regression analyses with JA-DAPH as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	INFLOW	-0.0001**	270	.1127
	DEPTH	-0.0325**		
	EXTCOEF	0.0648*		
	TEMP	-0.0019		
	SPCOND	0.0005		
	PH	-0.3243		
	CO3	0.0153		
	HCO3	-0.0004		
	NO3	0.0666		
	OUTFLOW	-0.0000		
2	INFLOW	-0.0001**	270	.1360
	SECCHI	-0.0078**		
	PO4	-0.9812**		
	TEMP	-0.0149*		
	DEPTH	-0.0255*		
3	INFLOW	-0.0001**	270	.1255
	SECCHI	-0.0099**		
	PO4	-1.0095**		
	TEMP	-0.0161**		
4	INFLOW	-0.0001**	270	.1126
	SECCHI	-0.0080**		
	PO4	-0.8643**		
5	INFLOW	-0.0001**	270	.0970
	SECCHI	-0.0082**		

** significant at .01 level
* significant at .05 level

Table 10. Results of multiple linear regression analyses with CYCLPOID as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	TEMP	-0.1384**	270	.5971**
	SECCHI	-0.0618**		
	CO3	0.2968**		
	HCO3	0.0857**		
	INFLOW	-0.0014**		
	OUTFLOW	0.0010**		
	NO3	-4.0042**		
	CHLORO	0.0492*		
	PH	-1.5902		
	EXTCOEF	-0.2935		
	DEPTH	0.0214		
	SPCOND	0.0032		
	PO4	-3.0504		
	NO2	7.5123		
2	TEMP	-0.1100**	270	.5811**
	SECCHI	-0.1462**		
	CO3	0.3254**		
	HCO3	0.1010**		
	NO3	-4.7435**		
	INFLOW	-0.0014**		
	OUTFLOW	0.0009**		
	CHLORO	0.0432*		
	PH	-2.2250*		
3	TEMP	1.5093**	270	.4037**
	TEMP2	-0.0502**		
	CHLORO	0.1064**		
	% OUT 60	-0.3699		
4	TEMP	1.5413**	270	.4032**
	TEMP2	-0.0515**		
	CHLORO	0.1060**		
5	TEMP	-0.1975**	270	.3180**
	CHLORO	0.1465**		
	% OUT 60	-2.1774**		
6	TEMP	-0.2690**	270	.3007**
	CHLORO	0.1510**		

** significant at .01 level
* significant at .05 level

Table 11. Results of multiple linear regression analyses with JA-CYCL as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	HCO3	0.0289**	270	.1688
	CO3	0.0540*		
	OUTFLOW	0.0001*		
	TEMP	-0.0169		
	EXTCOEF	0.0652		
	DEPTH	0.0216		
	SPCOND	0.0022		
	PH	-0.3227		
	NO3	0.0594		
	INFLOW	0.0001		
2	HCO3	0.0198**	270	.1780
	INFLOW	0.0004**		
	WIND	0.1427**		
	% OUT 60	-0.7643**		
	CO3	0.0476**		
3	HCO3	0.0241**	270	.1628
	INFLOW	0.0004**		
	WIND	0.1312**		
	% OUT 60	-0.8240**		
4	HCO3	0.0308**	270	.1437
	INFLOW	0.0003**		
	WIND	0.0825**		
5	HCO3	0.0335**	270	.1288
	INFLOW	0.0003**		

** significant at .01 level
* significant at .05 level

Table 12. Results of multiple linear regression analyses with DIAPTMUS as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	TEMP	0.2124**	270	.3242**
	DEPTH	-0.1377**		
	PO4	3.6808**		
	NO3	-1.7995**		
	CHLORO	-0.0422**		
	INFLOW	-0.0003		
	SPCOND	0.0063		
	EXTCOEF	-0.1104		
	SECCHI	-0.0153		
	PH	-0.9658		
	CO3	0.0499		
	HCO3	0.0084		
	NO2	-2.6263		
	OUTFLOW	-0.0001		
2	TEMP	0.2080**	270	.3051**
	DEPTH	-0.1573**		
	PO4	3.3137**		
	NO3	-1.4722**		
	CHLORO	-0.0434**		
	INFLOW	-0.0004**		
	SPCOND	0.0092**		
3	% OUT 60	-2.7047**	270	.4019**
	TEMP	0.2027**		
	DEPTH	-0.1777**		
	WIND	-0.1609**		
	INFLOW	-0.0002**		
	CHLORO	-0.0094		
4	% OUT 60	-2.5941**	270	.3998**
	TEMP	0.2011**		
	DEPTH	-0.1738**		
	WIND	-0.1854**		
	INFLOW	-0.0002**		
5	% OUT 60	-3.1103**	270	.3818**
	TEMP	0.2085**		
	DEPTH	-0.1755**		
	WIND	-0.1395**		
6	% OUT 60	-3.5291**	270	.3601**
	TEMP	0.2190**		
	DEPTH	-0.1740**		

** significant at .01 level

Table 13. Results of multiple linear regression analyses with JA-DIAP as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	TEMP	0.0530**	270	.2014
	NO3	0.5394**		
	EXTCOEF	-0.0082		
	DEPTH	-0.0094		
	SPCOND	-0.0014		
	PH	0.5842		
	CO3	-0.0346		
	HCO3	-0.0012		
	INFLOW	0.0000		
	OUTFLOW	-0.0001		
2	TEMP	0.0610**	270	.1772**
	NO3	0.7804**		

** significant at .01 level

EXPLANATION OF FIG. 7

Mean biomass of zooplankton for the reservoir on each sampling date.

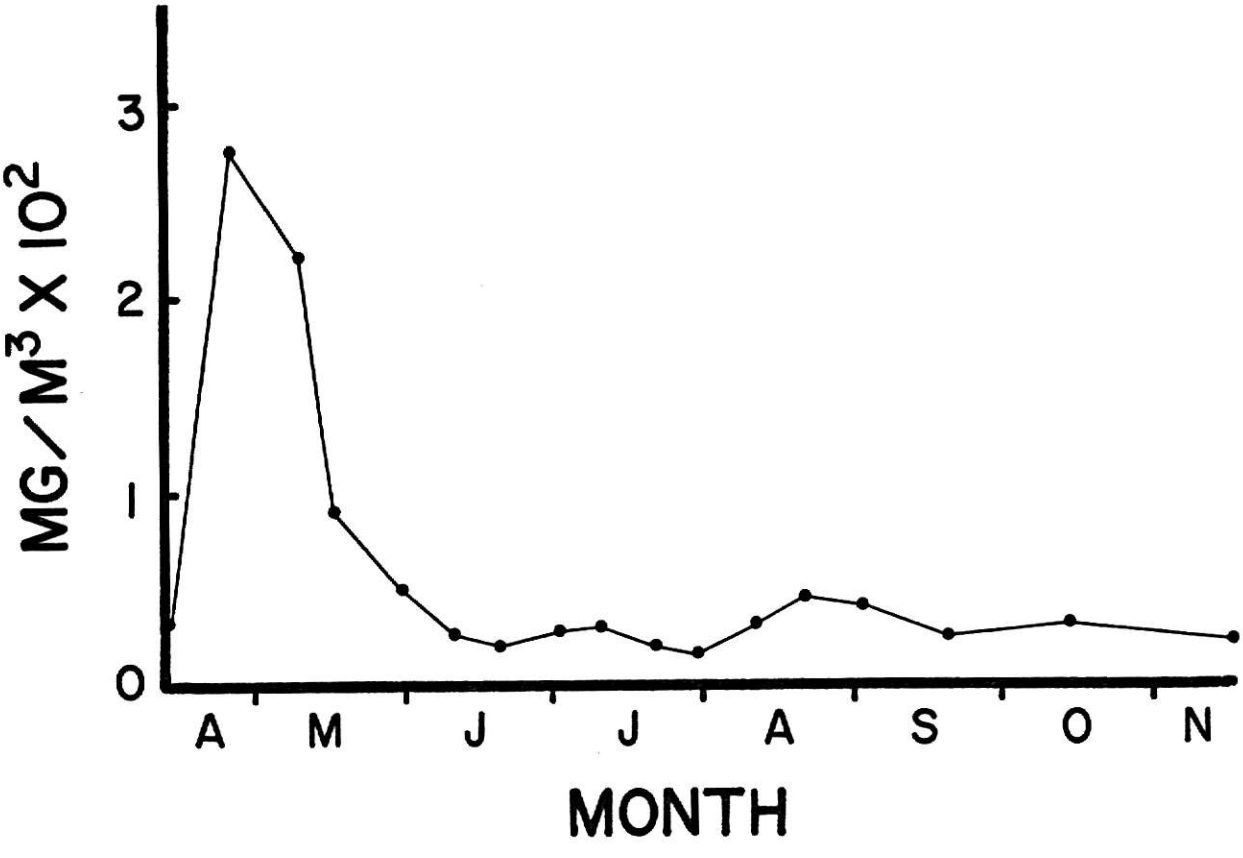

Fig. 7

Table 14. Results of multiple linear regression analyses with ZBIOM as the dependent variable.

Analysis No.	Independent Variable	b	n	R^2
1	CHLORO	1.0481**	270	.5064**
	SECCHI	0.9510**		
	CO3	4.8942**		
	HCO3	1.5102**		
	NO3	-79.0130**		
	EXTCOEF	-6.6899*		
	TEMP	0.0790		
	DEPTH	-1.3045		
	INFLOW	-0.0015		
	% OUT 60	3.1745		
	SPCOND	0.1431		
	PH	-15.9495		
	PO4	-63.9468		
	NO2	-97.5637		
2	CHLORO	2.3746**	270	.3301**
	EXTCOEF	-13.1516**		
	TEMP	-2.7094**		
	DEPTH	-6.9459**		
	INFLOW	0.0077**		

** significant at .01 level
* significant at .05 level

DISCUSSION

Analysis of Data

The multiple linear regression methods used in this investigation are explained adequately in other biological and statistical literature (Borecky, 1956; Cook, 1960; Draper and Smith, 1968; Edmondson, 1965; Hazelwood and Parker, 1961 and others). It is a powerful tool when used correctly, but one must remember that correlation does not mean cause and effect in biological systems. Neither does lack of correlation imply the absence of a cause and effect. The joint actions of two or more factors on a variable may be offset by one another, therefore eliminating the simple correlation but not the cause and effect. Multiple linear regression and correlation analysis is useful in determining the coefficients for predetermined relationships or suggesting possible relationships or critical experiments for future studies. In this study the emphasis was on the latter.

Analyses are given (Tables 8-14) which include physico-chemical variables as independent variables whose direct effects on zooplankton cannot be explained adequately on the basis of present literature. They are included as a reference for investigators who are studying the effects of chemical or physical parameters on zooplankton and need field correlations to support their findings, and as a guide in designing future studies of the effects of physico-chemical parameters on zooplankton in

Tuttle Creek Reservoir.

The juvenile to adult ratios showed few significant relationships with environmental variables as indicated by low R^2 values. The lack of relationships was probably due to the presence of several species in each group considered. If one species was reproducing rapidly, resulting in many young, and the others were not, then the index to the reproductive history of that species would be altered by the presence of adults of other species. Since reproduction is a species centered phenomenon, the juvenile-adult ratio for a multispecies group cannot give an accurate index to the reproductive history of the group as a whole unless all of the species in the group reproduce simultaneously under identical conditions. The juvenile-adult ratio is a widely used concept in unispecies populations, especially those with a longer generation time than most zooplankton (Gross, 1969). But its usefulness in interspecific studies is doubtful due the above reasons. Because of these drawbacks, little emphasis was placed on the analyses of the effects of environmental factors on the juvenile-adult ratio.

Food Supply Dynamics

Chlorophyll measurements were used as an index to the availability of an algal food source. Analyses proposing conditions possibly affecting this food source are shown in Table 5. HCO3 was an important variable probably altering the photosynthetic rate of the algae (Ruttner, 1964), hence affecting chlorophyll production. The turbidity of the water

caused by high inflow and outflow rates (Dufford, 1970), likely limited photosynthetic activity through lack of light. Although the term % OUT 30 was not significant ($p > .10$), the possibility of depletion of algae populations by losses through the outlet still existed (Brook and Woodward, 1956). The increased turbidity associated with the rapid flow rates then may have hampered the recovery of algae populations. An R^2 of only .2298 indicated that there were other factors affecting the chlorophyll which were not considered. A more complete analysis of the photosynthetic energy base of the reservoir will be available soon (Osborne, personal communication).

The pour plate method of bacterial enumeration (Carpenter, 1966) was used to obtain an index of the number of bacteria available as food for zooplankton. The method was partially selective, not including all groups of microorganisms. Direct microscopic counts tend to give more accurate estimates of the actual number of bacterial cells present, both living and dead (Sorokin, 1970). But direct counts are time consuming and distinguishing live bacteria from dead bacteria and detritus in turbid water is difficult. McCoy and Sarles (1969) present data indicating that plate counts are directly proportional to direct counts. Therefore, the faster plate count method was used to obtain an index of the number of bacteria in the water.

The factors governing bacterial numbers were not well defined, but it is clear from Table 5 that bacteria were highly related to particulate organic matter and inflowing waters.

Whether the bacteria were brought in by inflowing water or simply used the abundant allochthonous detritus from the inflowing waters as a nutrient substrate is unknown. Most of the bacterial types in the reservoir are typically found in soil (Harris, personal communication). Therefore, it is more likely that many of the bacteria in the reservoir were brought in by inflowing waters. Once in the reservoir the particulate organic matter may have promoted the growth of the populations. Novak (1969) and Chen (1968), who collected their data together, also showed a strong relationship between the two parameters.

Particulate organic matter was used as an index of the detrital material available as food for zooplankton. The measurement used included microorganisms, phytoplankton, and all other organic detritus. Analyses in Table 5 indicated, as did Novak (1969), that the inflow-outflow regime greatly affected the variation in particulate organic matter. The distribution of particulate organic matter within the reservoir showed higher concentrations in the strata nearer the areas of inflowing waters (Table 4). These data tended to support Novak's conclusion that much of the organic matter in the reservoir is allochthonous, at least during periods of high inflow and outflow. Inflow likely affected particulate organic matter and bacteria separately and the POM-BACTERIA relationship was not as strong as the correlation suggested.

Combined, the three possible food sources offered an abundant organic biomass from April through August. After the

initial peak in May, phytoplankton populations remained relatively low. Therefore, if the organisms were dependent mainly on an algal diet, food may have been limiting. The bacteria and detritus levels were relatively high, but the question of their utilization and nutritive value to the zooplankton remains unanswered.

The distribution of these food sources within the reservoir indicated a greater abundance of available food in strata IV-VI, the supply gradually decreasing nearer the dam. The reasons for this distribution are obvious for bacteria and particulate organic matter. On the average chlorophyll concentrations were higher in the upper strata, possibly due to incoming river periphyton, more available nutrients, or an increased production of chlorophyll to more efficiently use the limited available light.

From the above discussion and analysis, it appears that the food availability was primarily dependent on the inflow-outflow rates in the reservoir. Inflowing waters brought both a possible energy source in detritus or bacteria, and turbidity which may have limited the production of another known source of energy, phytoplankton. Outflow depleted all sources of food, but it also may have depleted the zooplankton populations at a similar rate. No consideration was given to the possible depletion of food resources by the zooplankton.

Zooplankton Standing Crop Estimates

A comparison of the standing crop of Daphnia, Diaptomus, and Cyclopoida in Tuttle Creek Reservoir and a variety of other waters is shown in Table 15. Tuttle Creek Reservoir had a larger average annual standing crop of Daphnia than other Great Plains Reservoirs and oligotrophic lakes such as Lake Michigan, and much smaller populations than eutrophic lakes such as Base Line Lake, Michigan and Pymatuning Reservoir, Pennsylvania. Cyclopoid copepod densities were similar to other reservoirs on the plains, but greater than Lake Michigan and much less than the population of cyclopoids in Canyon Ferry Reservoir, Montana. Diaptomus populations were relatively large compared to other reservoirs and Lake Michigan. Corbett Lake, British Columbia, a small eutrophic lake, contains somewhat larger populations of Diaptomus than Tuttle Creek Reservoir. The comparisons indicate that Tuttle Creek Reservoir has a standing crop of zooplankton per unit volume of water similar to or slightly higher than other waters of its type. From this, and the general physical and chemical features of the environment, it was concluded that Tuttle Creek Reservoir is at least partially representative of Great Plains Reservoirs in general.

Seasonal Variations and Their Possible Causes

The seasonal variation in Daphnia was affected by several factors as shown by Analyses 1-3 of Table 8. Of the significant ($p \leq .10$) factors only the effects of TEMP, TEMP2, CHLORO, and % OUT 60 were biologically reasonable. Analyses 3-5 of Table

Table 15. Standing crop estimates of Daphnia, Diaptomus, and Cyclopoida for Tuttle Creek Reservoir for 1970 compared with a variety of other lakes.

Zooplankton Group	Investigator and Lake	Number Per Liter Min	Max	Mean
Daphnia	Author Tuttle Creek Reservoir, Kansas	1.07	13.90	3.68
	Cowell (1967) Lewis and Clark Lake, South Dakota	0.00	3.99	0.65
	Cowell (1970) Lake Francis Case, South Dakota	0.04	4.22	0.98
	Applegate and Mullan (1967) Beaver Reservoir, Arkansas	0.00	7.10	2.70
	Applegate and Mullan (1967) Bull Shoals Reservoir, Arkansas	0.10	10.20	2.20
	Wells (1970) Lake Michigan	0.00	1.40	----
	Hall (1964) Base Line Lake, Michigan	0.60	43.00	----
	Borecky (1956) Pymatuning Reservoir, Pennsylvania	6.00	52.30	24.40
Cyclopoida	Author Tuttle Creek Reservoir, Kansas	0.05	13.90	3.01
	Cowell (1967) Lewis and Clark Lake, South Dakota	0.00	2.01	0.57
	Cowell (1970) Lake Francis Case, South Dakota	0.53	30.13	6.92

Table 15. (continued)

Zooplankton Group	Investigator and Lake	Number Per Liter Min	Max	Mean
Cyclopoida	Applegate and Mullan (1967) Beaver Reservoir, Arkansas	0.10	13.90	2.33
	Applegate and Mullan (1967) Bull Shoals Reservoir, Arkansas	0.50	10.00	3.70
	Wells (1970) Lake Michigan	0.50	1.90	----
	Wright (1965) Canyon Ferry Reservoir, Montana	0.00	250.00	----
Diaptomus	Author Tuttle Creek Reservoir, Kansas	0.34	5.70	2.30
	Cowell (1967) Lewis and Clark Lake, South Dakota	0.01	4.30	0.84
	Cowell (1970) Lake Francis Case, South Dakota	0.13	1.64	0.54
	Applegate and Mullan (1967) Beaver Reservoir, Arkansas	0.20	20.80	5.80
	Applegate and Mullan (1967) Bull Shoals Reservoir, Arkansas	0.10	4.40	1.40
	Wells (1970) Lake Michigan	0.30	1.60	----
	Healey (1967) Corbett Lake, British Columbia	0.23	9.30	3.70

9 show that the juvenile-adult ratio was significantly ($p \leq .10$) affected by SECCHI and INFLOW. Analyses 5-7 of Table 8 show the effect on R^2 of removing % OUT 60, TEMP2, or TEMP2 and TEMP from Analysis 4. Little decrease was noticed in each case, indicating that CHLORO was the most important variable and each of the other variables accounted for only a small but significant ($p \leq .01$) amount of the variation in the Daphnia population.

The positive relationship between Daphnia and CHLORO and TEMP suggested that the significant spring population peak was caused by these factors which were high during the same period or shortly preceding. Increasing temperature and food resources promotes a higher reproductive rate in Daphnia (Hall, 1964).

The analyses and previous work implied that the crash in mid-May was caused by one or more of four factors: high temperatures, lack of algal food, high outflows and predation.

The initial high inflows of the year followed by high discharges occurred on 10 May. The excessive outflow may have depleted the Daphnia population (Cowell, 1967; Brook and Woodward, 1956), as indicated by the significance of % OUT 60.

The algal food supply may have been lowered in the same manner and turbid waters possibly limited its recovery. Daphnia depend chiefly on phytoplankton for food (Saunders, 1969). The significance of CHLORO indicated that Daphnia in Tuttle Creek Reservoir also were dependent on an algal food source. Hence, the decrease in their main food source, which occurred in mid-May (Fig. 6), possibly caused the decline in numbers (Slobodkin,

1954).

During this period POM and BACTERIA concentrations were high (Fig. 6), offering a possible alternative food source. But simple correlations between Daphnia and the two food source variables revealed no significant ($p > .10$) relationships (Table 6). Detrital or bacterial feeding possibly existed, but the effects may have been masked by other variables such as % OUT 60 or predation. It is possible that the reproductive rate increased or at least remained stable after high inflow and the depletion of phytoplankton populations. The increase may have been more than offset by depletion by outflow or possibly predation.

A decreased filtering rate due to high food concentrations was described by Burns and Rigler (1967). If the high concentrations of suspended material other than food in Tuttle Creek Reservoir had the same inhibitory effect, then the energy intake of the Daphnia was lowered, decreasing their reproductive capacity. This suggests consideration of the reproductive rate as a function of the ratio of food particles to non-food particles in the water.

The importance of the TEMP2 term indicated that high temperatures may have inhibited the populations, the optimum temperature being reached in May. Burns and Rigler (1967) showed that the filtering rate of Daphnia decreased when temperatures exceeded 20 C, therefore slowing the rate of energy intake. This may have been the mechanism of the effects of high

temperatures.

The reproductive success of the populations was in some way affected by the turbidity of the water as evidenced by the juvenile-adult ratio analysis. The negative effects may have been mediated through lack of food, inhibition of feeding, or possibly mortality of the young.

The gizzard shad population in the reservoir should have spawned when the water reached 15-15.5 C, which was in early May in 1970 (Cramer and Marzolf, 1970). Their larvae, which are numerous after spawning, feed exclusively on zooplankton (Cramer and Marzolf, 1970). They are selective predators, Daphnia being a "selected for" organism (Cramer and Marzolf, 1970). Predation by the shad could have depleted the populations and changed the species composition of the zooplankton community (Cramer and Marzolf, 1970; Brooks and Dodson, 1965; Wells, 1970; Galbraith, 1967; Reif and Tappa, 1966).

A small increase in the population occurred in August (Fig. 2). The peak was likely due to increased chlorophyll concentrations resulting from clearing water and increased flushing time allowing phytoplankton populations to rebuild. Predation by gizzard shad probably subsided about the same time as they should have been large enough to switch to a pure algal diet (Cramer and Marzolf, 1970). The subsequent decline in numbers was probably due to below optimum temperatures and relatively high outflows and turbid waters in October and November.

Analyses 3-6 of Table 10 showed TEMP, CHLORO, TEMP2, and

% OUT 60 to be the biologically and statistically significant variables which affected the cyclopoid copepod populations. The variables were very similar to those affecting the Daphnia, but the mechanisms were likely different. Relationships of the juvenile-adult ratio in Table 11 indicated that the success of the cyclopoids was positively related to INFLOW and WIND.

The sharp population increase in the spring followed the Daphnia closely and was probably due to rising temperatures and an abundant food supply, both algal and other zooplankton since cyclopoids are often predacious (Fryer, 1957). Rotifers, a possible food source, were much more abundant at this time than during the remainder of the sampling period.

The crash in May could have been due to temperature increases, depletion of food supply, predation, or simply depletion of the population through the outlet. Of these factors, temperature seemed to be the most likely limiting factor. Armitage (1961) reported that Cyclops bicuspidatus, the dominant cyclopoid in Tuttle Creek Reservoir, generally reaches peak populations at temperatures of 15-18 C, and quickly disappears at higher temperatures. The temperatures in May ranged from 15-20 C, therefore the crash was probably due to temperature. Lack of food may have been mediated as described for Daphnia. The elimination of the food of the filter feeding organisms may have limited many of the organisms that cyclopoids prey upon. Predation by shad again was probably important in assisting temperature in reducing the populations.

The population remained low and did not increase again until October when a slight increase was noted. More favorable temperatures, lack of predation by shad, and fewer competitors were possible factors likely responsible for the increase.

Cyclopoida seemed to be more successful in a current laden environment as indicated by the significance of the INFLOW and WIND terms in the juvenile-adult ratio analysis. The exact reason for this is unknown, but Swain, Olson, and Odlaug (1970) discovered a similar phenomenon in the Great Lakes. Cyclopoids were found in littoral areas in shallow, wind mixed areas and not in the open pelagic waters.

The growth of Diaptomus populations seemed quite dependent on temperature as shown by the positive relationship of temperature with the adult population and the juvenile-adult ratio (Analyses 1-6, Table 12 and Analysis 2, Table 13). Other important variables included INFLOW, % OUT 60, DEPTH, and WIND.

Chlorophyll, reported to be important in Diaptomus reproductive rates by Edmondson, Comita, and Anderson (1962), was not significantly ($p > .10$) related to the Diaptomus population density. This may have been due to the failure to account for the lag effect of food since diaptomids possess a relatively long generation time.

Diaptomus numbers remained relatively low and stable throughout the spring and summer until August. The low populations were attributed to several factors on the basis of analyses and the literature. Low temperatures, competition,

high outflows and inflows, higher than average winds, and predation could each have been responsible for limitations.

Other studies have shown that the various species of Diaptomus exhibit extremely variable seasonal cycles, possibly as a coexistence mechanism (Hammer and Sawchyn, 1968). Therefore, the effects of temperature in retaining the population in the spring and early summer is not well documented. But extremely good relationships existed between Diaptomus adults and juvenile-adult ratios and temperature, therefore suggesting that the major Diaptomus species in Tuttle Creek Reservoir depends in part on higher temperatures for successful reproduction.

Again the inflow and outflow effects were likely mediated through population losses and depleted food supply as described for Daphnia.

As shown by the significance of DEPTH, Diaptomus seemed to prefer shallower water. This was in contrast to the results of Swain, et al. (1970) who found Diaptomus in the open, deeper areas of the Great Lakes. Applegate and Mullan (1967), however, found calanoid copepods to prefer shallower waters in two Ozark reservoirs. Although they preferred shallower waters, Diaptomus were negatively related to the wind velocity, showing a possible inhibitory effect of wind caused currents or other factors associated with strong winds. This does agree with Swain, et al. (1970).

Cyclopoid copepods competing with the Diaptomus may have been a factor in the low spring population (Pennak, 1957).

When the water warmed enough to limit the cyclopoids and enough food became available, then the Diaptomus were able to reproduce and become more abundant.

Predation pressure from shad was likely much lighter than on the other groups because shad select against Diaptomus when other prey is available (Cramer and Marzolf, 1970). However, cyclopoid copepods do prey upon Diaptomus (Fryer, 1957) and may have been a definite factor in the relatively low spring population.

The main population peak in August can probably be attributed to favorable temperatures, an adequate food supply, low winds creating a calmer environment, and low cyclopoid populations. The return of temperatures more favorable for cyclopoids, lower food supply, and lower than optimum temperatures probably caused the fall decline in numbers.

Horizontal Distribution and Possible Causes

All groups of zooplankton studied exhibited a similar horizontal distribution in the reservoir (Figs. 3-5). The populations in the upper strata and coves were greater than in the lower strata, indicating some environmental condition which was more favorable in the shallower waters. Applegate and Mullan (1967) found a similar situation in two Ozark reservoirs, but they did not give reasons for the distribution. In Tuttle Creek Reservoir the most obvious reason for the distribution was a more abundant source of food (Table 4). At times chlorophyll

was low in the upper strata, but detrital food was abundant. No relationship was evident to support the theory of detrital or bacterial feeding in Daphnia or Diaptomus, but a slightly significant ($p \leq .10$) correlation existed between POM and CYCLPOID. Also, literature strongly supports the possibility of detrital feeding (Saunders, 1969). The horizontal distribution suggests further investigation into the feeding habits of the three groups, and the relationship of birth rates to the amount and type of available food.

Zooplankton Biomass

The biomass estimates were made to obtain an indication of the energy contained in zooplankton in the reservoir. No measurement was made of the actual rate of biomass production. Biomass estimates shown in Fig. 7 are compatible with those found by Applegate and Mullan (1967). Factors affecting the amount of biomass present were similar to those factors affecting the numerical density of the populations (Analyses 1 and 2, Table 14).

Regulation of Zooplankton Populations

Previously, the factors normally affecting zooplankton populations were discussed. Temperature, predation, and food are considered the most important in most lakes with chemical factors and depletion by physical means significant in a few lakes.

During periods of low inflow and outflow, zooplankton in

Tuttle Creek Reservoir seemed to respond as expected to the well documented factors of population control such as temperature and food supply. During periods of favorable temperatures and light, the reservoir became turbid and current laden due to high wind velocities and excessive inflow-outflow rates. This imposed further limitations on the populations, both directly through losses to the outlet and the effects of turbidity, and indirectly through the limitation of an algal food source. Reductions were also likely due to fish predation. In general, the populations were regulated by factors independent of population density during most of the year. A possible exception would have been during the winter months when no samples were collected.

Suggestions for Further Work

The R^2 values obtained in all zooplankton analyses were relatively low, but statistically significant ($p \leq .10$) in most cases due partially to the large sample size. Much of the variation which was unaccounted for was likely due to sampling, since the volume filtered per sample was in many cases small. Subsequent studies would likely show less variability due to sampling if a larger volume of water was filtered over a vertical and horizontal transect. This could be accomplished with a metered tow net or a pump. More time would be required per sample, but fewer samples could be taken, and the larger integrated samples may eliminate some of the error due to sampling and make clearer the effects of the environmental variables.

Birth rates for each species of zooplankton need to be determined and related to the environmental factors of temperature and food supply. Birth rates would be much more valuable than standing crop estimates in evaluating the effects of environmental parameters, but their consideration requires a significant amount of time consuming taxonomic work, hence limiting the scope of any birth rate study to a relatively small number of samples and one or two species. Nevertheless, studies of this nature on the major species would be very valuable in understanding the regulation of zooplankton populations in the reservoir.

Zooplankton feeding studies are needed to establish the feeding patterns and food sources of the zooplankton. Phytoplankton is a known source of adequate food, but the value of detritus, especially allochthonous detritus, and bacteria in a turbid reservoir would be an interesting question. The effects of very turbid water and the ratio of food particles to non-food particles on the feeding and general activities of the zooplankton should be investigated.

More consideration needs to be given the inflow-outflow regime and the currents within the reservoir. Plankton samples from the outlet would indicate the extent of losses through river outflow. Extensive transect sampling during initial periods of high inflow and outflow would offer answers to the question of movement of zooplankton with relation to the currents through the reservoir.

Quantitative data concerning predation by all species of

fish is needed to evaluate their dependence on zooplankton as an energy source and to determine their impact on the zooplankton populations over the horizontal extent of the reservoir. Some of this data would be very difficult to obtain due to the difficulties involved in estimating the density of fish populations in a large body of water.

The effects of various chemicals need further study. Nutrients such as nitrates, phosphates, and bicarbonates are relatively high in the reservoir, and some are highly correlated with the zooplankton populations. But without further study, one must assume that these correlations are mediated through changes in an algal food source rather than a direct cause and effect.

SUMMARY

1. The standing crops of Daphnia, Diaptomus, and Cyclopoida plus several important environmental variables were monitored at 10-30 day intervals from April to November, 1970. Among the variables considered were the food sources of zooplankton: phytoplankton, bacteria, and particulate organic matter.

2. A stratified random sampling design was used with six strata chosen to minimize within stratum variation. A total of 16 random samples were collected per sampling date.

3. Analysis of variance was used to determine differences in the horizontal distribution of the zooplankton. Multiple linear regression and correlation was utilized to delineate the factors affecting the zooplankton populations.

4. The availability of food was primarily related to the inflow-outflow regime. Rapid flushing time brought influxes of allochthonous bacteria and particulate organic matter, but also brought suspended matter which increased turbidity, limiting phytoplankton production.

5. All zooplankton groups exhibited ligher average standing crops in the shallower, upstream portions of the reservoir. A more abundant food supply was hypothesized as the reason for the higher populations.

6. Daphnia populations were related to the reservoir flushing time, water temperature, and the availability of an

algal food source.

7. Cyclopoida appeared to be limited by temperature, reservoir flushing time, and lack of food.

8. Diaptomus populations preferred warmer, shallower waters and were negatively affected by wind currents and the inflow-outflow regime of the reservoir.

9. Predation by gizzard shad and other young fish was considered but not measured in this study.

10. Suggestions for further study included zooplankton feeding habits, quantitative predation data, birth rate studies on individual species, effects of various chemicals, and consideration of energy losses through the reservoir outlet.

ACKNOWLEDGEMENTS

The author's most heartfelt appreciation goes to Dr. G. R. Marzolf without whose guidance and assistance this study would not have been possible. Thanks also go to Dr. Stephen Fretwell and Dr. K. E. Kemp for reading and criticizing the manuscript. The author wishes to express a special thanks to Mr. John Osborne who performed the chemical analyses, assisted in the field work, and prepared a major portion of Fig. 1.

Last, but certainly not least, appreciation goes to my wife Lee for her encouragement and lasting endurance during the course of the study.

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APPENDICES

APPENDIX 1

Strickland and Parsons (1960) present a method for the determination of particulate organic matter in the form of glucose carbon in water using dichromate oxidation and subsequent spectrophotometry. However, their method requires the use of regular HA Millipore filters which interfere with dichromate oxidation. To eliminate this problem, they coated the filters with magnesium carbonate powder, filtered the water sample, then washed the filtrate from the filter into a beaker. The filtrate was refiltered onto an ultra-fine scintered glass filter which was used in the oxidation procedures. This filtering procedure is time consuming and contains possibilities for error, but it was the best solution at the time since filtering a reasonable volume of water directly onto a scintered glass filter is nearly impossible. But, a new filter now on the market is made of pure glass fibers and costs less than regular Millipore filters. Laboratory tests have shown that the filters do not interfere with dichromate oxidation and their efficiency is comparable to a Millipore HA filter (pore size = .45 microns). The filters are available from Gelman Instrument Co., Ann Arbor, Michigan. Therefore, the method of Strickland and Parsons (1960) was modified to use the glass fiber filters.

MODIFIED METHOD

Materials

30 ml beakers with covers
100 ml volumetric flasks
filtering apparatus(1" heads)
glass fiber filters
sulfuric acid(s. g. 1.82)
potassium dichromate
glucose
spectrophotometer

Chemical Preparations

Dichromate oxidant. Dissolve 4.84 g of potassium dichromate in 20 ml of distilled water (heating may be necessary). Add a little at a time to about 500 ml of concentrated sulfuric acid in a 1 liter volumetric flask. Cool to room temperature and make to volume. Store in a glass stoppered bottle.

Glucose standard solution. Dissolve 7.5 g of glucose in distilled water and make to volume of 100 ml. Store in a refrigerator. The solution is stable indefinitely. For use, dilute 10 ml to 1 liter and use within a day of preparation. One ml of the dilute solution contains 300 μg of carbon. This solution is used for calibration.

Cleaning of Glassware

Before initial use, all beakers and flasks must be washed with hot sulfuric acid-dichromate oxidant. After use it is sufficient to rinse the glassware several times with distilled water and store in a dust free container such as a desiccator. As a safety precaution periodic acid rewashing is recommended.

Calibration

Make the following glucose solutions using acid washed glassware:

Solution	Dilute Glucose, ml	Water, ml	µgC/ml
1	1000	0	300
2	250	750	75
3	100	900	30
4	30	970	9

Place glass filters in nine clean 30 ml beakers and add the following:

Beaker	Solution	Amount, ml	Water, ml	Oxidant, ml	µgC
1	1	2	0	2	600
2	1	1	1	2	300
3	2	2	0	2	150
4	2	1	1	2	75
5	3	2	0	2	60
6	3	1	1	2	30
7	4	1	1	2	9
b_1	0	0	2	2	0
b_2	0	0	2	2	0

Cover the beakers and place in an oven at 100-110 C for 1 hour. Remove from oven and cool to room temperature. Pour each solution in a separate 100 ml volumetric flask and make to volume, rinsing the beaker thoroughly. Fill half of a spectrophotometer cuvette with each of the blank solutions (beakers b_1 and b_2) and read the extinction of each standard solution against the blank and record the extinction, E. Multiply E by 1.1 to correct for the extinction of trivalent chromium to obtain E_c. Prepare a graph of µgC in each sample versus E_c for the sample. The line should be linear up to about 300 µgC. Fit a linear

regression to the line and obtain an equation:

$$\mu gC = a + b \cdot E_c$$

where a and b are constants. The value of a should be near 0 and b should be about 4550. Use this equation to calculate the μgC present in a sample after determining E_c for the sample by the procedure given below.

Analytical Procedure

Water samples should be collected and analyzed immediately or frozen to minimize error due to bacterial activity.

Strain the water sample through a medium mesh plankton net to remove the larger zooplankton. Fit the filtering apparatus with a glass fiber filter and filter a suitable volume of water to obtain between 0 and 300 μgC. This is necessary because the equation derived above is not valid for values outside this range. For most freshwaters 50 to 250 ml is a sufficient volume to filter. After filtering, wash the sides of the filter funnel with distilled water and suck dry. Remove filter with forceps and place in a beaker and cover. Add 2 ml of distilled water and 2 ml of dichromate oxidant to the beaker, cover and place in an oven for 1 hour at 100-110 C. The time is not critical as long as adequate time is allowed for complete oxidation. Remove the beakers from the oven and cool to room temperature. Pour contents of the beakers into separate 100 ml volumetric flasks. Rinse beakers and filter thoroughly and make to volume of 100 ml with distilled water. Two blanks

should be prepared just as in the rest of the procedure except for no filtrate. Fill a cuvette, half from each blank, and read the extinction of the samples against the blank. Multiply the extinction, E, by 1.1 to get E_c. If E_c exceeds .8 repeat the sample filtering a smaller volume of water. It is also advisable to repeat the analysis on samples with a reading less than .1 using a larger volume of water. The value obtained for E_c is entered in the equation derived above to find the μgC in the sample. Divide this value by the volume of water filtered in liters to obtain mgC/m^3 in the water.

APPENDIX 2

Zooplankton densities (mean number per liter) for each stratum on each date. Mean densities with standard error are given for each date.

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
11 April 1970							
Daphnia spp.	0.158	0.693	1.419	2.722	0.068	1.325	1.161(0.34)
Daphnia juv.	0.173	1.389	0.917	0.990	0.049	0.795	0.734(0.23)
Cyclopoida	1.319	4.767	4.898	6.034	0.941	5.300	3.954(0.95)
Cyclopoida juv.	3.874	8.416	6.575	15.258	1.629	10.599	7.560(1.69)
Diaptomus spp.	0.018	1.003	0.332	0.505	0.000	0.265	0.344(0.14)
Diaptomus juv.	0.000	0.000	0.000	0.000	0.000	0.000	0.000(0.00)
25 April 1970							
Daphnia spp.	1.472	5.652	6.091	15.049	7.949	4.122	6.959(1.29)
Daphnia juv.	1.760	5.429	8.996	18.166	7.006	13.544	8.956(1.60)
Cyclopoida	5.832	10.537	14.573	20.624	11.864	24.732	13.860(1.78)
Cyclopoida juv.	28.314	8.369	24.334	62.810	26.217	67.718	33.246(7.23)
Diaptomus spp.	0.091	0.321	2.061	1.341	1.144	0.589	1.133(0.28)
Diaptomus juv.	0.000	0.000	0.000	0.196	0.000	0.000	0.037(0.04)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
9 May 1970							
Daphnia spp.	8.726	8.243	19.757	17.609	9.937	8.833	13.937(1.67)
Daphnia juv.	2.510	5.712	23.805	29.611	5.005	9.893	15.420(3.52)
Cyclopoida	6.634	6.182	9.327	15.478	9.937	15.192	10.025(1.03)
Cyclopoida juv.	13.007	9.951	26.558	78.457	11.703	53.703	31.512(9.55)
Diaptomus spp.	0.045	0.118	0.868	3.281	0.073	7.419	1.382(0.55)
Diaptomus juv.	0.000	0.000	0.000	0.000	0.000	0.000	0.000(0.00)
16 May 1970							
Daphnia spp.	6.664	4.564	8.631	9.891	11.209	1.060	7.839(1.03)
Daphnia juv.	4.158	2.694	9.549	15.247	10.925	4.063	8.579(1.36)
Cyclopoida	6.775	6.742	15.800	13.116	20.599	2.826	12.262(2.06)
Cyclopoida juv.	6.074	29.516	25.066	10.270	15.341	3.886	16.748(3.28)
Diaptomus spp.	0.354	0.162	2.997	3.421	3.585	0.177	2.124(0.57)
Diaptomus juv.	0.000	0.000	0.000	0.000	0.000	0.000	0.000(0.00)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
30 May 1970							
Daphnia spp.	2.105	3.629	6.163	6.464	1.390	10.158	4.795(1.07)
Daphnia juv.	1.567	1.713	4.981	6.039	1.214	15.016	4.287(1.21)
Cyclopoida	3.069	3.292	4.640	1.903	5.861	5.300	3.858(0.50)
Cyclopoida juv.	3.607	4.552	5.961	2.761	4.754	1.325	4.303(0.63)
Diaptomus spp.	0.593	0.719	2.576	3.633	1.061	6.625	2.234(0.53)
Diaptomus juv.	0.263	0.577	1.816	1.600	0.055	0.000	0.996(0.37)
10 June 1970							
Daphnia spp.	0.815	1.566	2.542	7.213	6.320	1.767	3.120(1.22)
Daphnia juv.	0.066	0.321	1.566	5.005	5.358	0.589	2.052(1.02)
Cyclopoida	1.379	0.482	1.133	0.883	1.598	1.767	1.220(0.14)
Cyclopoida juv.	2.636	2.609	3.612	3.239	4.009	5.005	3.417(0.43)
Diaptomus spp.	0.304	0.521	2.035	2.355	2.126	0.294	1.366(0.38)
Diaptomus juv.	0.000	0.441	0.595	0.294	0.864	0.000	0.439(0.15)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
19 June 1970							
Daphnia spp.	1.615	2.120	2.580	1.198	2.764	0.353	1.966(0.24)
Daphnia juv.	0.948	0.936	0.929	0.369	1.403	0.000	0.830(0.15)
Cyclopoida	0.761	0.698	0.718	3.096	0.551	0.530	1.137(0.25)
Cyclopoida juv.	1.918	2.565	1.803	3.626	1.763	1.590	2.243(0.23)
Diaptomus spp.	0.951	1.816	0.496	0.739	1.380	0.177	0.882(0.15)
Diaptomus juv.	0.524	0.809	0.346	0.084	0.368	0.000	0.369(0.07)
1 July 1970							
Daphnia spp.	1.014	1.108	2.430	3.386	0.795	2.208	1.960(0.39)
Daphnia juv.	1.641	1.767	3.061	4.081	2.208	5.300	2.858(0.49)
Cyclopoida	0.000	0.171	0.076	0.450	0.000	0.000	0.130(0.05)
Cyclopoida juv.	0.294	0.208	0.327	0.818	0.176	1.325	0.422(0.11)
Diaptomus spp.	0.166	0.405	1.463	3.452	1.060	0.883	1.374(0.40)
Diaptomus juv.	0.406	0.589	3.661	4.245	0.530	0.442	2.183(0.68)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
10 July 1970							
Daphnia spp.	1.777	2.287	1.677	3.183	1.252	9.422	2.485(0.53)
Daphnia juv.	1.714	1.837	1.636	3.880	1.128	13.249	2.759(0.80)
Cyclopoida	0.022	0.248	0.241	0.279	0.245	2.061	0.322(0.13)
Cyclopoida juv.	0.042	0.248	0.248	1.063	0.147	4.416	0.610(0.29)
Diaptomus spp.	0.280	0.819	1.550	5.292	0.662	5.594	2.064(0.61)
Diaptomus juv.	0.045	0.378	0.783	3.233	0.343	10.010	1.575(0.65)
21 July 1970							
Daphnia spp.	0.779	0.868	0.438	1.918	1.352	2.355	1.067(0.19)
Daphnia juv.	0.427	0.572	0.792	2.295	1.033	3.926	1.204(0.26)
Cyclopoida	0.039	0.000	0.047	0.107	0.046	0.000	0.048(0.02)
Cyclopoida juv.	0.025	0.033	0.190	0.440	0.046	0.000	0.156(0.06)
Diaptomus spp.	0.678	0.503	0.933	4.748	0.313	3.926	1.656(0.48)
Diaptomus juv.	0.472	0.843	2.792	7.490	0.674	9.422	3.144(0.83)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
30 July 1970							
Daphnia spp.	0.761	0.606	0.953	1.182	0.982	5.152	1.182(0.30)
Daphnia juv.	0.533	0.530	0.846	1.531	1.398	4.416	1.168(0.27)
Cyclopoida	0.000	0.000	0.235	0.000	0.000	0.736	0.120(0.05)
Cyclopoida juv.	0.000	0.033	0.340	0.706	0.417	2.944	0.479(0.18)
Diaptomus spp.	0.295	0.900	1.856	1.897	0.883	2.944	1.398(0.44)
Diaptomus juv.	0.332	0.810	2.483	3.960	0.908	3.680	2.026(0.47)
11 August 1970							
Daphnia spp.	5.458	3.787	1.888	1.291	5.528	5.888	3.388(0.55)
Daphnia juv.	9.251	2.490	0.816	3.515	7.852	8.244	4.457(1.19)
Cyclopoida	0.337	1.149	0.699	0.050	1.001	0.000	0.560(0.16)
Cyclopoida juv.	0.254	0.151	0.039	0.271	1.846	0.589	0.397(0.22)
Diaptomus spp.	3.768	5.177	2.404	5.293	5.220	5.300	4.081(0.41)
Diaptomus juv.	4.030	2.159	1.409	4.153	5.074	5.300	3.210(0.60)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
21 August 1970							
Daphnia spp.	2.162	2.885	3.884	6.520	1.887	5.300	3.769(0.62)
Daphnia juv.	1.784	2.210	3.361	6.894	1.255	3.239	3.313(0.73)
Cyclopoida	0.122	0.271	0.473	1.042	0.119	0.589	0.451(0.10)
Cyclopoida juv.	0.450	0.225	0.578	1.003	0.119	0.000	0.496(0.11)
Diaptomus spp.	2.972	1.941	6.672	8.794	2.793	9.422	5.472(0.84)
Diaptomus juv.	2.975	3.925	6.378	3.903	2.481	1.178	4.157(0.68)
2 September 1970							
Daphnia spp.	0.542	3.189	4.841	5.599	2.412	2.677	3.532(0.60)
Daphnia juv.	0.356	0.868	3.209	5.404	2.463	5.353	2.834(0.59)
Cyclopoida	0.082	0.037	1.209	0.669	0.294	0.535	0.593(0.17)
Cyclopoida juv.	0.047	0.056	0.308	0.753	0.391	0.268	0.319(0.10)
Diaptomus spp.	0.897	5.606	8.011	6.289	8.426	2.409	5.755(1.15)
Diaptomus juv.	1.514	3.171	5.141	5.962	3.896	1.071	3.959(0.59)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
19 September 1970							
Daphnia spp.	1.353	1.352	2.081	2.844	1.785	4.416	2.330(0.31)
Daphnia juv.	0.892	0.284	1.831	2.459	1.167	5.830	1.746(0.35)
Cyclopoida	0.091	0.033	0.050	0.132	0.068	0.000	0.070(0.02)
Cyclopoida juv.	0.160	0.137	0.123	0.347	0.039	0.883	0.211(0.06)
Diaptomus spp.	2.552	2.870	4.495	4.697	1.902	8.479	3.890(0.56)
Diaptomus juv.	2.073	1.191	4.298	3.308	2.768	4.946	3.156(0.46)
14 October 1970							
Daphnia spp.	1.548	2.034	1.740	2.448	0.720	0.442	1.665(0.22)
Daphnia juv.	2.050	2.394	1.943	3.396	1.014	0.000	2.054(0.33)
Cyclopoida	0.800	0.825	0.994	2.094	0.657	0.442	1.066(0.19)
Cyclopoida juv.	0.471	0.597	0.746	0.940	0.152	1.104	0.660(0.09)
Diaptomus spp.	2.189	2.175	2.332	2.899	1.051	0.221	2.100(0.24)
Diaptomus juv.	0.000	0.062	0.038	0.040	0.000	0.000	0.027(0.02)

Zooplankton Group	Stratum Means I	II	III	IV	V	VI	Mean(SE)
16 November 1970							
Daphnia spp.	1.111	1.713	0.965	0.603	2.038	2.849	1.270(0.20)
Daphnia juv.	0.827	1.416	0.871	0.553	1.562	1.425	0.992(0.10)
Cyclopoida	0.728	1.155	1.450	1.292	1.819	1.425	1.293(0.15)
Cyclopoida juv.	0.840	1.340	1.120	1.512	1.198	3.704	1.340(0.20)
Diaptomus spp.	0.811	1.415	1.094	0.656	1.486	1.425	1.069(0.12)
Diaptomus juv.	0.000	0.000	0.000	0.000	0.000	0.000	0.000(0.00)

ZOOPLANKTON ECOLOGY OF A GREAT PLAINS RESERVOIR

by

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B. S., Colorado State University, 1969

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1971

The fluctuations of three groups of zooplankton, Daphnia spp., Diaptomus spp., and Cyclopoida, were followed in Tuttle Creek Reservoir, Kansas from April to November 1970 while simultaneously measuring several environmental variables. The dynamics of the potential food sources of zooplankton which are phytoplankton, bacteria, and particulate organic matter were among the variables considered. The average annual standing crops of the three zooplankton groups were similar to the standing crops of other Great Plains Reservoirs. Higher populations were found in the shallower, upstream portions of the reservoir. Multiple linear regression analysis was utilized to determine the probable effects of environmental variables on zooplankton and the potential food sources. Food availability was greatly affected by the inflow-outflow rates of the reservoir. Daphnia were related primarily to the flushing time of the reservoir, water temperature, and the availability of an algal food source. Diaptomus preferred warmer, shallower waters, and were negatively affected by wind currents and the inflow-outflow regime of the reservoir. Cyclopoida seemed limited by temperature, reservoir flushing time, and lack of food. Predation by fish was considered but not measured. Relationships were not found to indicate the existence of detrital or bacterial feeding. Suggestions for further study are discussed.