The population dynamics and production of limnetic crustacean zooplankton in the Tongue River Reservoir, Montana
by Stephen Arthur Leathe

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Botany
Montana State University

Abstract:
An intensive survey of the dynamics and production of the principal limnetic crustacean zooplankton species in the Tongue River Reservoir was conducted during the period 2 October 1976 - 7 October 1977. The goals of the study were to document existing limnological conditions and to provide baseline data needed to monitor potential impacts of current and future surface coal mining activities on lands adjacent to the reservoir.

The species assemblage and dynamics of the crustacean zooplankton community in the reservoir were found to be more typical of nonalkaline Colorado plains lakes and of shallow midwestern water bodies than of lakes and reservoirs in the upper Missouri River basin. Two of the four principal cladoceran species (Bosmina longirostris- and Daphnia galeata mendotae) were perennial whereas Ceviodaphnia reticulata and Daphnia parvula were summer and early fall species which overwintered as ephippial (resting) eggs. Of the three principal copepod species, two (Cyclops bicuspidatus thomasi and Diaptomus siciloides) were perennial whereas Mesocyclops edax was a summer species which overwintered primarily as diapausing fourth-instar copepodites, The life history of Cyclops in the Tongue was distinctly different from other published studies due to the appearance of a large, slow-developing winter cohort. Crustacean zooplankton production averaged 0.49 g m^2 day^-1 dry weight and was similar to published values for mesotrophic and eutrophic lakes. It is suggested that changes in population levels of planktivorus fishes (particularly the white croppie, Pomoxis annularis) would have more noticeable effects on the composition of the limnetic crustacean zooplankton community than would moderate changes in reservoir water quality.

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A thesis submitted in partial fulfillment
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TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

An intensive survey of the dynamics and production of the principal limnetic crustacean zooplankton species in the Tongue River Reservoir was conducted during the period 2 October 1976 - 7 October 1977. The goals of the study were to document existing limnological conditions and to provide baseline data needed to monitor potential impacts of current and future surface coal mining activities on lands adjacent to the reservoir.

The species assemblage and dynamics of the crustacean zooplankton community in the reservoir were found to be more typical of non-alkaline Colorado plains lakes and of shallow midwestern water bodies than of lakes and reservoirs in the upper Missouri River basin. Two of the four principal cladoceran species (*Bosmina longirostris* and *Daphnia galeata mendotae*) were perennial whereas *Ceriodaphnia reticulata* and *Daphnia parvula* were summer and early fall species which overwintered as ephippial (resting) eggs. Of the three principal copepod species, two (*Cyclops bicuspidatus thomasi* and *Diaptomus siciloides*) were perennial whereas *Mesocyclops edax* was a summer species which overwintered primarily as diapausing fourth-instar copepodites. The life history of *Cyclops* in the Tongue was distinctly different from other published studies due to the appearance of a large, slow-developing winter cohort.

Crustacean zooplankton production averaged 0.49 $g \cdot m^{-2} \cdot day^{-1}$ dry weight and was similar to published values for mesotrophic and eutrophic lakes. It is suggested that changes in population levels of planktivorus fishes (particularly the white croppie, *Pomoxis annularis*) would have more noticeable effects on the composition of the limnetic crustacean zooplankton community than would moderate changes in reservoir water quality.

INTRODUCTION

Surface coal mining on lands abutting the southwest shore of the Tongue River Reservoir was initiated in the summer of 1972 by Decker Coal Company. Mining activity was expanded to the southeast shoreline in 1977 and is to extend northward from the West Decker mine site in the near future (Figure 1).

A series of aquatic research projects was initiated in the spring of 1975 by the Montana Cooperative Fishery Research Unit in cooperation with the Montana Department of Fish and Game. The goal of these studies is to describe selected chemical, physical and biological characteristics of the reservoir. Adequate baseline information is essential to the process of identifying and predicting current and future impacts of surface coal mining within the drainage basin.

Virtually no information concerning the limnology of this reservoir existed prior to the initiation of these studies. Whalen (1979) thoroughly investigated the chemical and physical characteristics and primary production in the reservoir during the period June 1975 through November 1976. This study was initiated in April of 1976 to complement Whalen's (1979) investigation and continued until early October of 1977. The purpose of this study is to document the distribution, abundance, population dynamics, and production of each major crustacean zooplankton species in the reservoir and to determine the flushing loss of zooplankton from the reservoir.

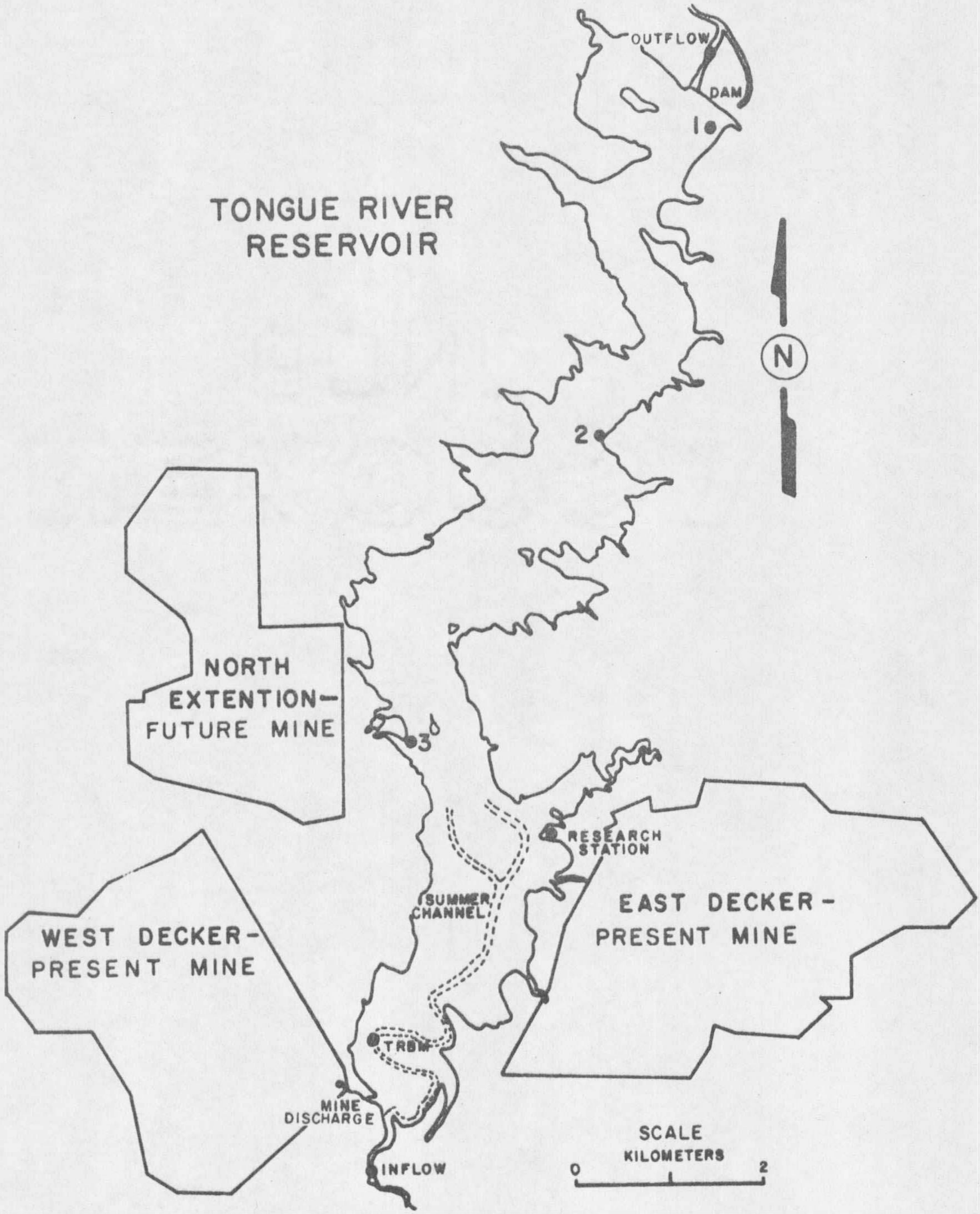

Figure 1. Map of the Tongue River Reservoir detailing the study area.

This report summarizes data collected between 2 October 1976 and 7 October 1977. Information obtained between April and October 1976 are summarized elsewhere (Leathe 1977). The methods and frequency of plankton sampling were significantly altered in October 1976 in order to more effectively address study aims.

DESCRIPTION OF STUDY AREA

The Tongue River Reservoir is located in Big Horn County, Montana and is situated approximately 32 kilometers north of Sheridan, Wyoming (Figure 2). The climate of this region is semiarid, average annual precipitation is approximately 30 centimeters (USGS and Mont. Dept. State Lands 1977). Vegetation is primarily comprised of sagebrush-steppe and grassland-sagebrush community types (USGS and Mont. Dept. State Lands 1977).

The reservoir was formed in 1939 by the impoundment of the Tongue River which originates in the Big Horn Mountains of Wyoming, located 105 river kilometers to the southwest. It was established for the purposes of downstream irrigation and flood control.

The Tongue River Reservoir is of moderate size when compared to other Montana impoundments (Appendix Table 16). The reservoir has maximum dimensions of 12.5 kilometers by 1.4 kilometers and averages 5.9 meters in depth with a maximum depth of 18.0 meters at maximum pool elevation (1044 meters; Table 1). It is a deepwater withdrawal reservoir, the bottom of the outlet is 15.2 meters below the spillway crest. The Tongue River contributes 97.7% of the mean annual discharge into the reservoir; ground water, ephemeral streams, and other tributaries are of minor importance (USGS and Mont. Dept. State Lands 1977).

According to Whalen (1979) the Tongue River Reservoir is a mildly eutrophic, hardwater lake. Calcium and magnesium are the dominant

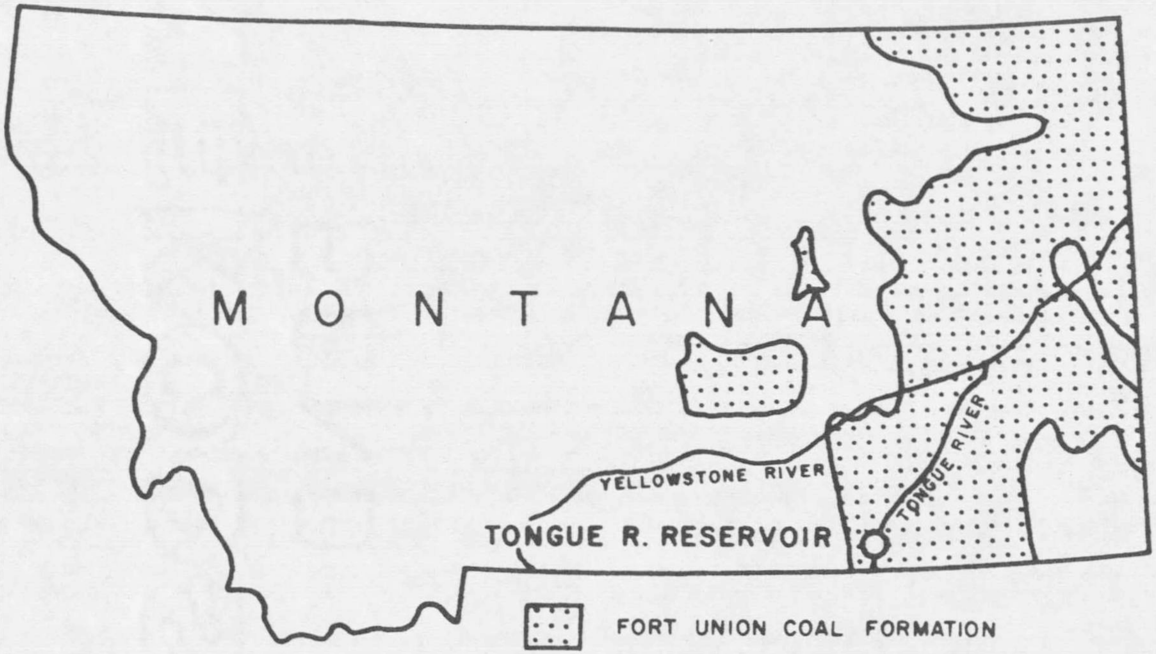

Figure 2. Location map.

Table 1. Morphometric data for the Tongue River Reservoir at maximum pool elevation (1043.7 m).[1]

Maximum depth [2]	18.0 m (59.1 ft)
Mean depth	5.9 m (19.5 ft)
Depth of outlet [3]	15.2 m (49.9 ft)
Maximum length [2]	12.5 km (7.8 mi)
Maximum breadth [2]	1.4 km (0.9 mi)
Surface area [3]	1277 ha (3156 acres)
Usable capacity [4]	740×10^5 m^3 (6.0×10^4 acre-ft)
Volume [5]	757×10^5 m^3 (6.14×10^4 acre-ft)
Length of shoreline [3]	60 km (37.3 mi)
Shoreline development [3]	4.74

[1] Definition and discussion of these parameters can be found in Ried and Wood (1976) or Welch (1948).

[2] Garrison, *et al.* (1975).

[3] Penkal (1976).

[4] U.S.G.S. and Mt. Dept. of State Lands (1977).

[5] Usable capacity and dead storage volume.

cations and are present in nearly equal proportions in reservoir waters (Appendix Table 17) presumably because of the presence of large amounts of dolomite in the watershed. Bicarbonate and sulfate comprise the two major anions. High sulfate concentrations in reservoir waters (3.35 $me \cdot l^{-1}$ or 161 $mg \cdot l^{-1}$ on the average at Station 2; Appendix Table 17) apparently stem from the weathering of gypsum, anhydrite, pyrite, and sodium sulfate in the drainage.

Mean annual reservoir storage volume for the 1976 and 1977 water years averaged 488.6 X 10^5 cubic meters which was approximately 7.0% higher than the 1961 through 1975 mean (Appendix Table 18). Except for May 1977, all storage values fell within ranges observed over the previous 15-year period (Figure 3). Average inflow and outflow discharges were less than the 15-year means of 14.0 $m^3 \cdot sec^{-1}$ (496 cfs) and 14.3 $m^3 \cdot sec^{-1}$ (523 cfs) but nearly all monthly values were included within the ranges reported from 1961 to 1975 (Appendix Table 18).

The annual hydrological cycle has been described in detail by Whalen (1979). Reservoir storage usually peaks in June (Figure 3) as a result of snowmelt and consequent runoff from the Bighorn Mountains. Short retention times are common during the summer months because large amounts of water are released through the dam to meet downstream irrigation needs. Storage is lowest in the early fall months after which retention times increase to late winter maxima with a concommitant increase in reservoir volume. The mean retention time

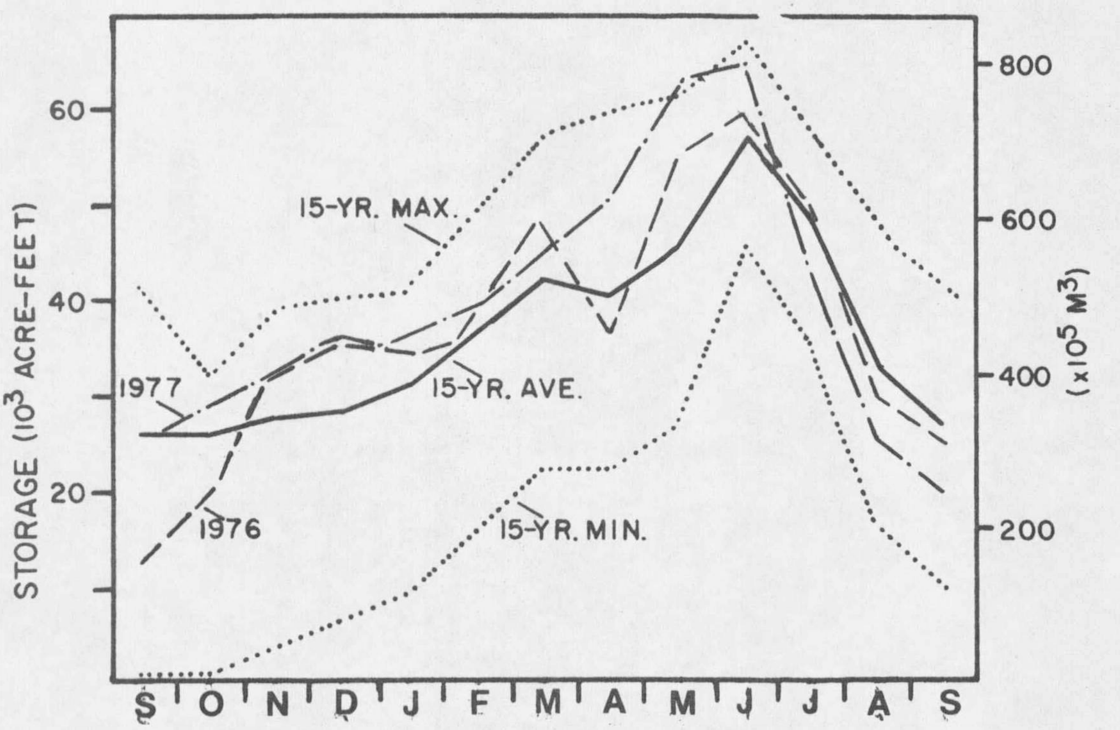

Figure 3. Storage volumes of the Tongue River Reservoir for the 1976 and 1977 water years as compared to the mean and extremes observed over the period 1961-1975.

during the study period was 74 days and the range was 19 to 300 days (Appendix Table 19).

The three reservoir sampling locations and the single outflow station examined during this study are identical to those investigated by Whalen (1979) and they appear on Figure 1. Average depth of the reservoir stations ranged from a maximum of 15.2 meters at Station 1 (near the dam) to 3.9m at Station 3 at the upper end of the reservoir

(Table 2). Annual reservoir water level fluctuation was approximately 6.5 meters.

Table 2. Depth information for three sampling locations on the Tongue River Reservoir during the period 2 Oct 1976 - 7 Oct 1977.

Station	# Dates	Mean depth (m)	Range (m)	Fluctuation (m)
1	17	15.2	11.5-18.0	6.5
2	38	10.8	7.5-13.5	6.0
3	17	3.9	0-7.0	7.0

METHODS

Chemical and Physical Parameters and Algal Standing Crop

During the first seven months of this study (May-November 1976), chemical and physical parameters and primary production were investigated by Whalen (1979). On each sampling date following this period, water temperature, dissolved oxygen, light attenuation, and chlorophyll *a* concentration were measured by the author using methods identical to those of Whalen (1979).

Zooplankton

Field collection

As has been previously mentioned, the zooplankton sampling program was significantly revised on 2 October 1976. As of this date a 28.1 liter Schindler-Patalas plexiglass plankton trap (Schindler 1969) equipped with a #20 (80 micron) nitex net was employed at the three reservoir stations. The trap was constructed by Montana State University Mechanical Engineering Shop personnel. This device was well-suited to the purposes of this study because it required no calibration, was simple to operate by one person in shallow and ice-covered waters, and is considered to be one of the most efficient zooplankton sampling devices (Schindler 1969; Prepas and Rigler 1978). Zooplankton samples were preserved in 95% ethanol and stored in 125 ml French square bottles.

Sampling was conducted on a biweekly basis at the three reservoir stations and in the outflow from 2 October 1976 until ice-in in late November 1976. Sampling at reservoir stations consisted of duplicate integrated vertical hauls, each a composite of water trapped at one-meter intervals from surface to bottom. Outflow samples were collected by straining water collected with an 8.5ℓ plastic hatchery jar through a #20 plankton net. Duplicate samples each representing 127.5ℓ of filtered discharge water were obtained on each sampling date.

Station 2 was selected for intensive investigation because it was intensively studied by Whalen (1979) and found to be intermediate among the three reservoir stations in terms of chemical, physical, and biological characteristics. Consequently, biweekly plankton collections were obtained solely at this station throughout the iced-in period (late-November 1976 to late-March 1977). Following ice-out in 1977, Station 2 was sampled weekly whereas Stations 1 and 3 and the outflow were sampled biweekly. To increase reliability of results, duplicate sampling at Station 2 was superseded by triplicate sampling as of 5 May 1977. Hillbricht-Ilkowska and Weglenska (1970) observed that a six-day sampling interval gave a reasonable estimate (±20-30%) of midsummer production of crustacean zooplankton. Bottrell et al. (1976) recommended weekly sampling during the summer with longer intervals during other times of the year. Because of the large amount of time involved in thoroughly analyzing weekly collections, standing crop, population dynamics, and production were estimated at Station 2 only.

Enumeration

Replicate samples were combined and concentrated in the laboratory then diluted with 95% ethanol in appropriately sized beakers to volumes ranging between 150 and 1800 mls. Prepared samples were agitated with a flat bladed spatula to assure random distribution of organisms then subsampled using a 1 ml Hensen-Stempel pipette and transferred to a Sedgewick-Rafter counting cell. All organisms contained in the cell were enumerated at 40X under a binocular compound microscope equipped with a mechanical stage. Five 1 ml replicate aliquots were examined, noting the sex and reproductive condition of target organisms. Normally a total of 100-500 individuals of the dominant species were tallied.

For the sole purpose of biomass estimation, copepod nauplii at Station 2 were roughly apportioned between species based on relative density of adult females. Due to difficulty in making specific determinations, early instar cyclopoid copepodite stages at Station 2 were tallied in total and later assigned to species based on species identification resulting from instar analysis counts.

The length of cladocerans in subsamples was measured to the nearest 0.01 mm using an ocular micrometer at 100X total magnification.

When possible, 50 individuals of each of the four important species were measured. Measurements on all crustaceans were made from the anterior margin of the head to the posterior margin of the carapace, excluding terminal spines or setae.

Cladoceran clutch sizes were determined by examination and occasional dissection under a binocular dissecting microscope of 10-40 randomly selected ovigerous females of each species, when obtainable. Clutch sizes of copepod species were based upon dissection of egg masses from 2-10 ovigerous cyclopoid females and 2-25 calanoid females. At Station 2 only, egg densities were estimated by the product of ovigerous female density and mean clutch size.

Organisms were identified using Brooks (1957), Edmondson (1959) and Yeatman (1944) as primary taxonomic references.

Cladoceran Population Dynamics

The exponential growth model developed by Edmondson (1960) has been employed by many researchers to describe the dynamic nature of limnetic cladoceran zooplankton populations and to identify influential environmental factors (Hall 1964; Kwik and Carter 1975; Wright 1965). Linear models can seriously underestimate population increases when the sampling interval is longer than the generation time of the species in question whereas exponential models account for this problem (Edmondson 1960).

The following equation is frequently used to describe the growth curve characteristic of species which exhibit periods of exponential growth:

$$N_t = N_0 e^{rt} \quad (1)$$

where N_0 is initial population size (organisms$\cdot l^{-1}$), N_t is population size (organisms$\cdot l^{-1}$) at the end of time interval t (days), and r is the instantaneous rate of population change on a per capita basis (individuals$\cdot$individual$^{-1}\cdot$day^{-1}). When equation (1) is converted to logarithmic form, r is determined as follows:

$$r = \frac{ln N_t - ln N_0}{t} \quad (2)$$

The finite birth rate B (newborn$\cdot$individual$^{-1}\cdot$day^{-1}) was calculated using the formula:

$$B = \frac{E}{N_0 D} \quad (3)$$

where E is egg density (eggs$\cdot l^{-1}$), N_0 is the initial population size, and D is duration of egg development (days).

Cladoceran egg development times used in this study were calculated using the following regressions compiled by Bottrell et al. (1976):

a.) Daphniidae (*Daphnia* spp., *Ceriodaphnia* spp., n=80)

$$ln D = 3.3956 + 0.2193 ln T - 0.3414 (ln T)^2 \quad (4)$$

b.) Other Cladocera (*Bosmina* spp., n=55)

$$\ln D = 2.3279 + 1.2472 \ln T - 0.5647 (\ln T)^2 \qquad (5)$$

where D is egg duration (days) and T is temperature (°C). These regressions were utilized because of their broad data base which encompassed many related species over a wide range of temperatures and also because results were comparable to the findings of more specific studies such as Kwik and Carter (1975).

Considerable controversy exists concerning the proper method of calculating the instantaneous birth rate (b, individuals·individual^{-1}·day^{-1}). Using Wright's (1965) data, Caswell (1972) compared values of b calculated using Leslie's (1948) formula:

$$b = \frac{rB}{e^r - 1} \qquad (6)$$

and that of Edmondson (1960):

$$b = \ln(1 + B) \ . \qquad (7)$$

Edmondson (1974) concluded that the difference between the two methods of calculation was minor and did not alter Wright's conclusions. Edmondson went on to suggest that the method with the stronger theoretical basis be used; consequently equation (6) was employed in this study since it accounts for mortality during the interval t.

Assuming immigration and emmigration rates to be negligible or equal, the rate of population change (r) depends upon the difference between natality (b) and mortality (d):

$$r = b - d \; . \qquad (8)$$

If natality exceeds mortality then r is positive and the population increases. If the mortality rate is greater than natality then r is negative and the population declines. If natality equals mortality the rate of population increase is zero and the population remains at a constant level. Equation (8) can be rearranged:

$$d = b - r \qquad (9)$$

to facilitate calculation of instantaneous death rate (d) based on the previously determined instantaneous population coefficients b and r.

Most workers (George and Edwards 1974; Hall 1964; Kwik and Carter 1975; Wright 1965) calculate finite birth rate B based on total population at time zero (N_0) using equations equivalent to (3). Edmondson's (1960; 1968; 1974; 1977) preferred method of expressing B based on density of adult females in the population can lead to significant error if improperly applied. For example, Geer (1977) expressed B in Edmondson's terms then erroneously applied it to equation (6) to derive the per capita based coefficient b. Excessively positive death rate coefficients resulted when highly inflated values for b were substitued into equation (9).

Copepod Instar Analysis

Since copepods pass through a series of identifiable developmental stages their population dynamics are commonly described by instar analysis. However, identification of copepodite instars is often difficult for inexperienced copepodologists because opaque tissues in preserved specimens hinder observation of key morphological features.

During routine enumeration of zooplankton samples it was noted that the structural details important to instar determination were easily observed on moulted copepod carapaces. Subsequent experimentation by the author with various tissue clearing agents resulted in a simple and rapid method for treating copepods. The method is a modification of the clearing procedure recommended by Pennak (1953) for chitinous insects and other arthropods, and a method used to clear head capsules of larval chironomidae (Mason 1973). It apparently has not been employed in commonly referenced morphological studies (Comita and Tommerdahl 1960; Ewers 1930; Gurney 1933; Humes 1955) nor in published field studies.

A random subsample (approximately 1 ml) was pipetted from the bottom of a sedimented zooplankton sample and transferred to a beaker containing 10-15 mls of 20% potassium hydroxide solution (20 g KOH crystals dissolved in 80 mls distilled water). The zooplankton-KOH mixture was heated over a low flame to a temperature just below the boiling point and maintained at that temperature until the clearing process was completed. Total elapsed time for treatment of a sample ranged from 15-20 minutes. Randomly chosen aliquots of the mixture were transferred to a Sedgewick-Rafter cell and all copepods contained therein were identified to instar and tallied. As many as 300 copepodites of the dominant species in the sample were examined. Calanoid copepodite instars were identified using information provided by Comita (1971) and Comita and Tommerdahl (1960) whereas cyclopoids were identified according to Geer (1977) and Gurney (1935). Specific designations of first copepodite stages of the two major cyclopoid species was based on length-frequency analysis (Appendix Table 20) since they could not be differentiated via morphological features. Whenever possible, 2-10 individuals of each instar of each species were measured as described previously.

Standing Crop

Biomass was calculated for each cladoceran measured using formulae from Botterell et. al. (1976) which appear in Table 3. Standing crop of each species was estimated by the product of average individual biomass and population density. The mean biomass of each copepodite instar for each species was calculated using the average length observed over the course of the study and the formula of Klekowski and Shuskina (1960) as cited in Edmondson and Winberg (1971). A factor of

Table 3. Length-weight relationships for cladoceran species, from Bottrell et. al. (1976). Length (L) is expressed in mm, weight (W) as mg dry weight.

Organism	(n)	Equation
Daphnia spp. (w/eggs, embs, ov.)	(1128)	$\ln W = 1.7769 + 2.7166 \ln L$
Daphnia spp. (w/out eggs, embs, ov.)	(1303)	$\ln W = 1.4681 + 2.8292 \ln L$
Ceriodaphnia quadrangula	(19)	$\ln W = 2.5623 + 3.3380 \ln L$
Bosmina spp.	(77)	$\ln W = 3.0896 + 3.0395 \ln L$

0.15 was used to convert wet weight to dry weight (Patalas, unpublished). Based on Wright's (unpublished) volume estimations, the biomass of a copepod egg was considered to be 0.0077 of the first copepodite instar biomass. Nauplius biomass was arbitrarily considered to be 0.5 of first instar biomass.

Production

Daily production rates were calculated for cladocerans and copepods on each sampling date using the generalized formula:

$$P = N_I \frac{\Delta W_I}{D_I} + N_{II} \frac{\Delta W_{II}}{D_{II}} + \ldots\ldots + N_X \frac{\Delta W_X}{D_X} \qquad (10)$$

where:

P is daily production ($g \cdot m^{-2} \cdot day^{-1}$) of a species.

N_I, N_{II}, ... N_x are the densities of organisms ($\# \cdot m^{-2}$) in each of the developmental classes (I, II, ..., x). Copepod developmental classes are represented by instars, cladoceran classes by length groups.

ΔW_I, ΔW_{II}, ... ΔW_x are the weight gains associated with growth to successive instars or length groups.

D_I, D_{II}, ... D_x represent the amount of time (days) required for an organisms to pass to the next instar or size class.

Daily copepod production was computed for the classes egg to C1; C1 to C2; C2 to C3; C3 to C4; C4 to C5; and C5 to adult. Daily cladoceran production was calculated for the intervals egg to neonate (newly born); neonate to primipara (first maturity); and primipara to adult. Since it is impossible to readily identify specific instars of cladoceran species, developmental stages were delineated by length-frequency analysis. Neonates were defined as the smallest free-swimming individual measured during the study whereas length of the average minimum ovigerous female over the course of the study was used to delineate primiparae. The mean length of all ovigerous females was used to define adults.

Instar duration times for *Cyclops* during the period October 1976 through April 1977 were determined by inspection of field data. From April 1977 until the end of the study, mean instar durations applied were calculated from the results of Geer (1977) and Wright (unpub.). Instar duration times of *Mesocyclops* have been found to consistently range between two and five days in intensive (sampling conducted 1-3 times per week) field studies by Carter (1974) and Comita (1972). Hence, average instar durations computed using Comita's (1972) results were used in estimating *Mesocyclops* production. Since *Diaptomus* was found to be a minor component of the Tongue River Reservoir zooplankton assemblage, mean values for instar duration calculated from Comita (1972) were employed. Copepod instar duration data are presented in Appendix Tables 21 and 22.

The time required by cladoceran species to develop from neonate to first maturity (primipara) was obtained from several sources. Values presented by Pomerantseva (1974) were used for both species of *Daphnia* at all temperatures and for *Ceriodaphnia* at temperatures below 20°C. Hall, Cooper, and Werner's (1970) estimate of 3.5 days was used for *Ceriodaphnia* at temperatures ≥ 20°C. At temperatures ≥ 20°C Patalas's (unpub.) value of 2.3 days was used for *Bosmina*. At lower temperatures (< 20°C) values presented by Pomerantseva (1974) for *Chydorus sphaericus* were employed in *Bosmina* production estimation since both species are small and exhibit high growth rates.

The duration of the adult stage of all cladoceran species were computed according to equation (3) in Hillbricht-Ilkowska and Weglenska (1970) which assumes that upon attainment of maturity, growth in length proceeds at one third the juvenile rate.

Production during an interval between two sampling dates was calculated by multiplying the average of the two estimates by the elapsed time (days) according to equation (25) in Edmondson and Winberg (1971). Hillbricht-Ilkowska and Weglenska (1970) observed that the above method of computing interval production most closely approximated "true" production.

RESULTS

Physical Parameters and Algal Standing Crop

Temperature

Orthograde temperature profiles were observed in the fall of 1976 at Station 2 (Figure 4). Mean water temperature declined rapidly from 16°C to 4°C between early October and early November 1976. During the iced-in period (mid-November to late March) the water column remained nearly homothermic. Wind generated mixing in the shallow exposed reservoir basin and deepwater withdrawal precluded thermal stratification during the summer months. Mean water temperatures at Station 2 during the spring and early summer of 1977 were noticeably higher than those observed by Whalen (1979) for the same period in 1976 (Figure 5).

A comparison of mean water temperatures observed at the three reservoir stations during the period October 1976 to October 1977 (Figure 6) revealed a more variable thermal regime at Station 3 than at either Station 1 or 2. The shallow waters of Station 3 warm more rapidly in the spring, attain higher summer temperatures, and cool more rapidly in the fall than do the waters of the other reservoir stations. Temperature and dissolved oxygen data obtained in the inflowing and outflowing reservoir waters are summarized in Appendix Table 23.

Dissolved Oxygen

Orthograde oxygen profiles were noted during the fall, winter,

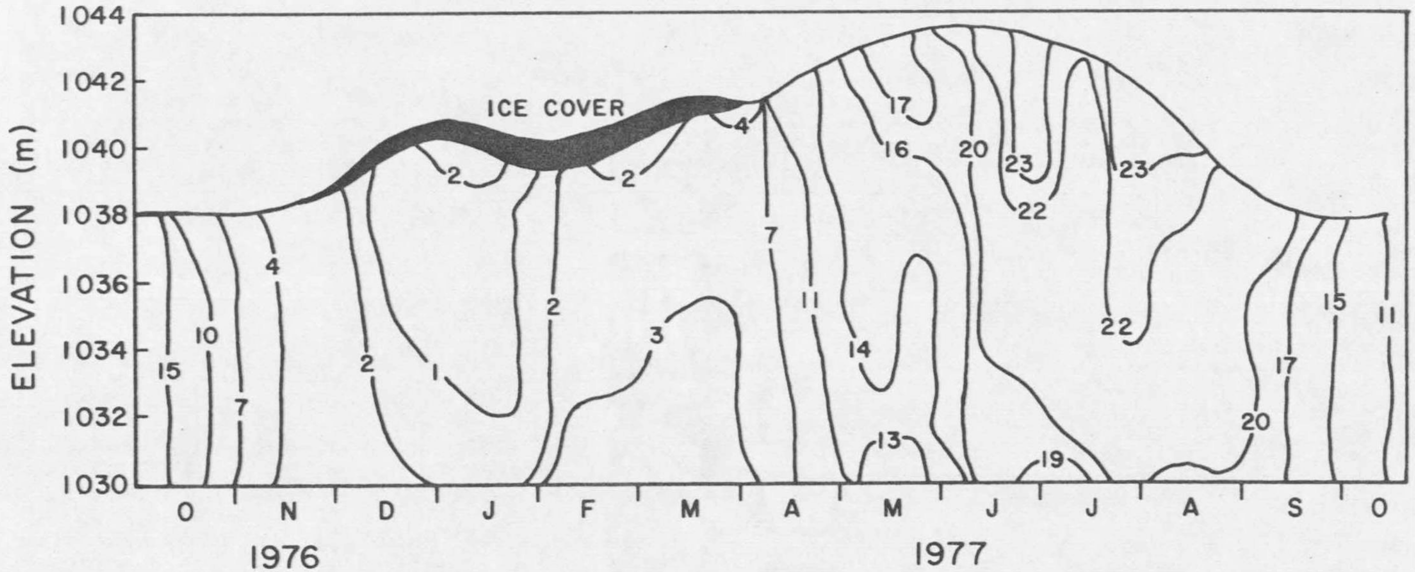

Figure 4. Seasonal isotherms (°C) at Station 2 of the Tongue River Reservoir during the period October 1976 to October 1977.

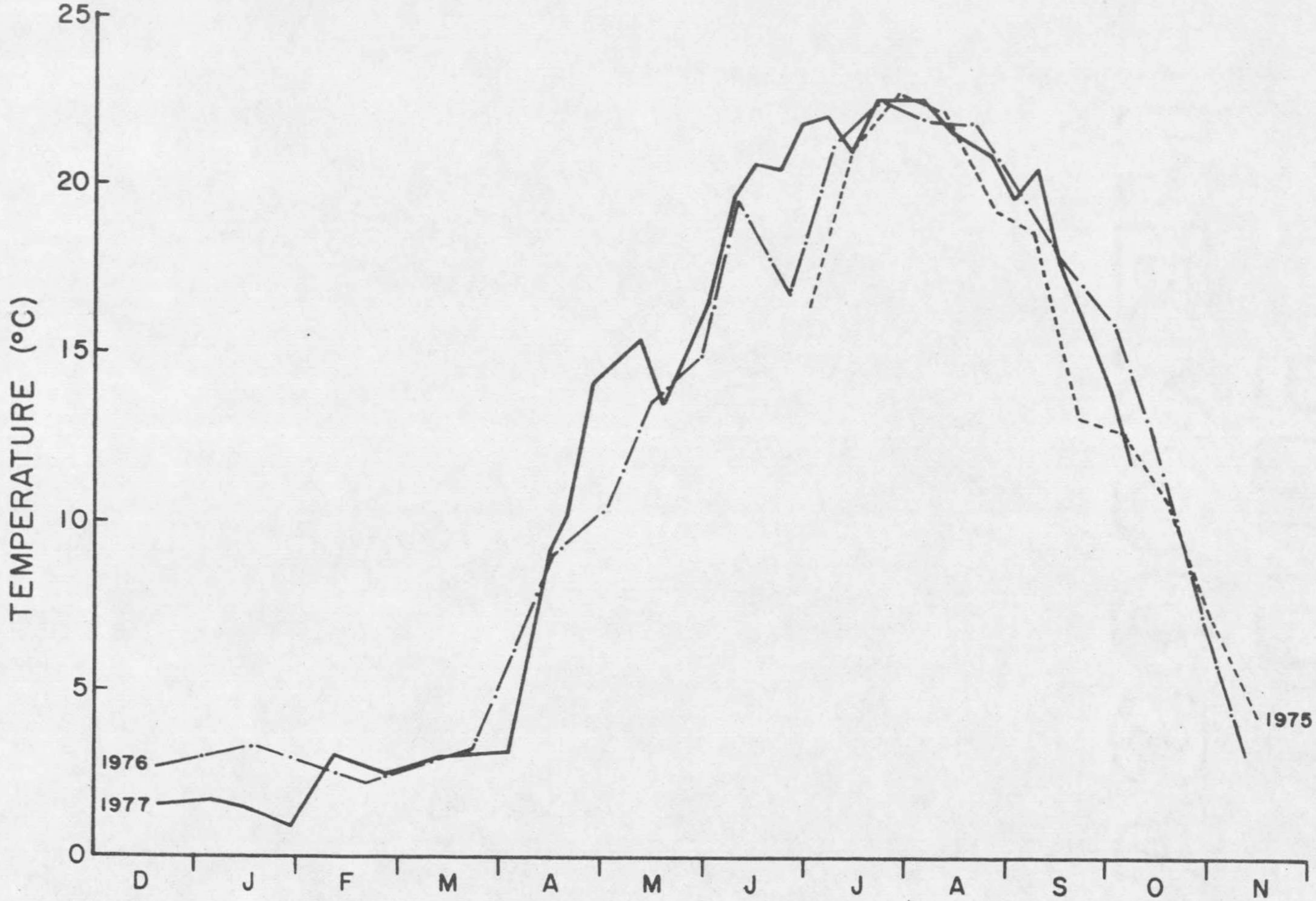

Figure 5. Seasonal trends in mean water temperature (°C) at Station 2 of the Tongue River Reservoir during 1975, 1976, and 1977.

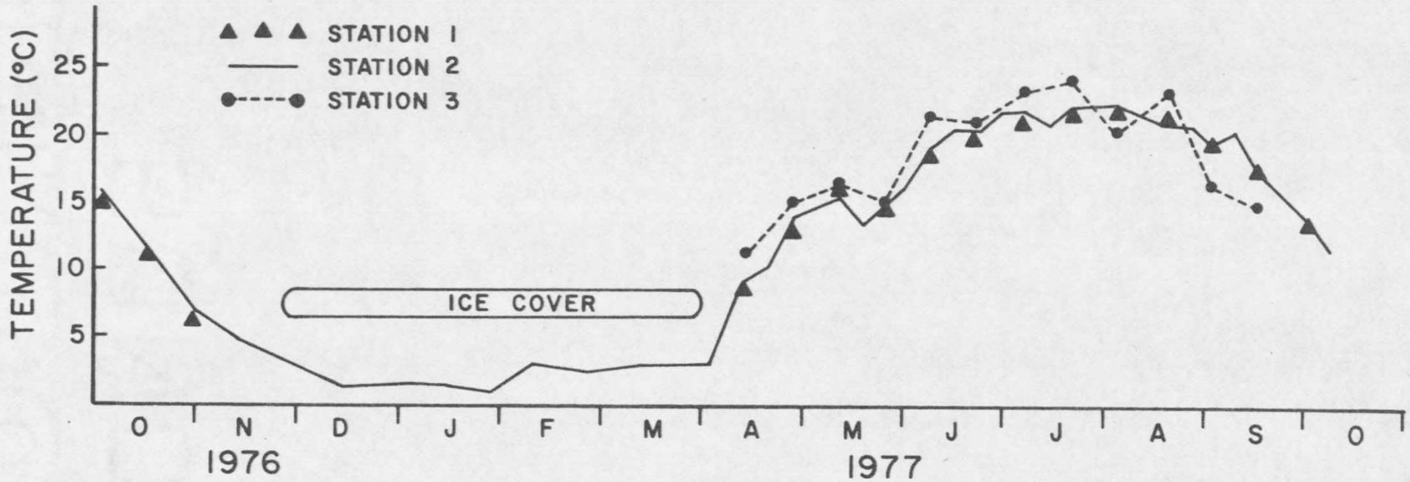

Figure 6. Seasonal trends in mean water temperature (°C) at three stations on the Tongue River Reservoir, October 1976 - October 1977.

and early spring months (Figure 7). The gradual downward trend in winter dissolved oxygen concentrations was reversed in late February when photosynthetic activity (as indicated by chlorophyll *a* concentrations in the water column) began to increase. Winter dissolved oxygen content remained high in the bottom waters presumably due to low rates of primary production in overlying waters, deepwater withdrawal, the influence of inflowing waters, and the absence of decomposing macrophytes whose existence is precluded by highly fluctuating reservoir water levels.

Although reservoir waters were not appreciably stratified in regards to temperature, clinograde dissolved oxygen profiles were observed during the summer months. Dissolved oxygen levels in the bottom waters declined to 1 $mg \cdot \ell^{-1}$ and less for three consecutive summer months when oxygen was being rapidly consumed by microbial decomposition of organic matter synthesized in the overlying trophogenic zone. The well established summer clinograde oxygen distribution was abruptly terminated in late August-early September, presumably as a result of rapidly declining reservoir water level and the increased importance of wind generated mixing of the water column.

Seasonal oxygen saturation isopleths (Figure 8) are useful in describing temporal and vertical variations in dissolved oxygen concentration since oxygen solubility increases with decreasing water temperature. Fall and winter oxygen levels approached or exceeded

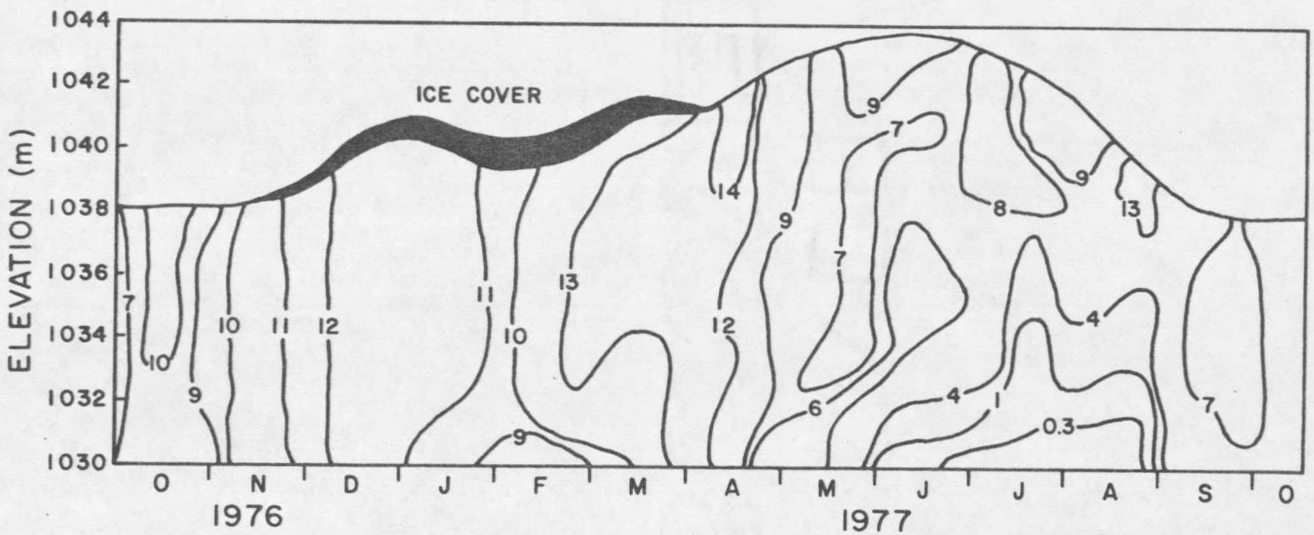

Figure 7. Seasonal dissolved oxygen (mg·ℓ$^{-1}$) isopleths at Station 2 of the Tongue River Reservoir during the period October 1976 - October 1977.

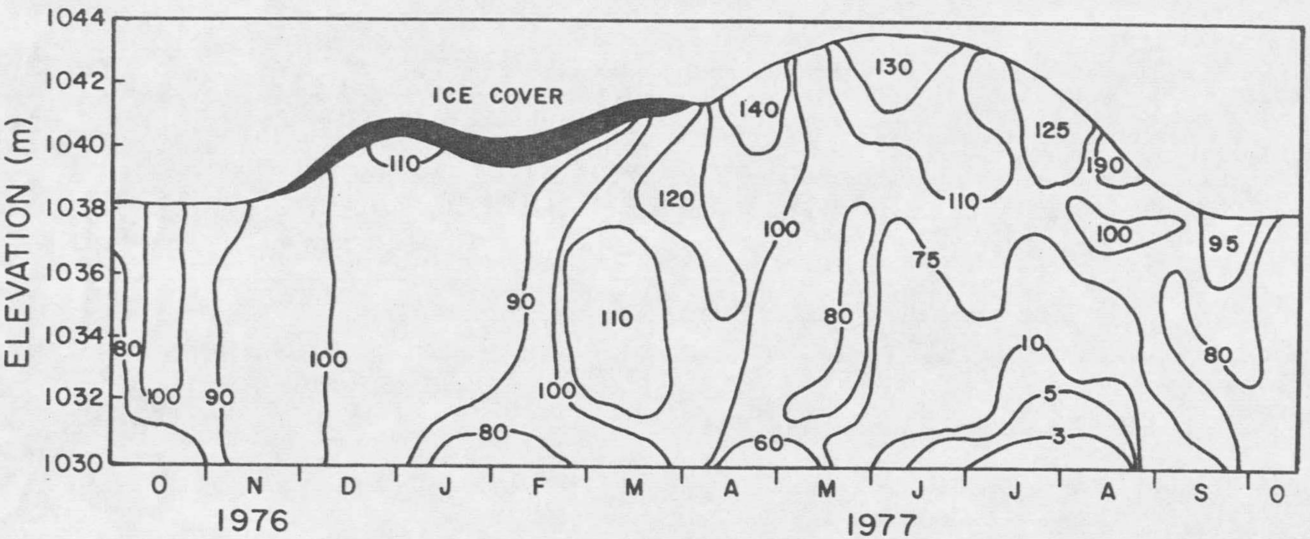

Figure 8. Seasonal percent oxygen saturation isopleths at Station 2 of the Tongue River Reservoir, October 1976 - October 1977.

saturation throughout the water column indicating that the biological processes responsible for oxygen evolution (photosynthesis) and consumption (microbial respiration) were proceeding at balanced rates. Supersaturation of the surface waters with oxygen was frequently noted during the ice free period due to high amounts of photosynthetic activity by phytoplankton in the trophogenic zone. The maximum saturation value encountered was 270%, observed on both 19 August and 9 September 1977. During the summer the bottom waters were typically undersaturated with oxygen, indicating that tropholytic zone oxygen was being consumed faster than it could be regenerated via trophogenic processes.

Chlorophyll *a*

Trends in chlorophyll *a* amounts observed on an areal basis at Station 2 during the three year period 1975-1977 are illustrated in Figure 9. A statistical comparison between means of data gathered over the period January to early-October showed the 1977 mean of 62.9 mg chlorophyll $a \cdot m^{-2}$ (n=33) to be significantly higher than the 1976 average (n=17) of 31.1 $mg \cdot m^{-2}$ (p=0.03). Although in general the seasonal trends were similar, chlorophyll levels in July and early August of 1977 appeared to be aberrantly high when compared to the same time span during the previous two years. Additionally, the

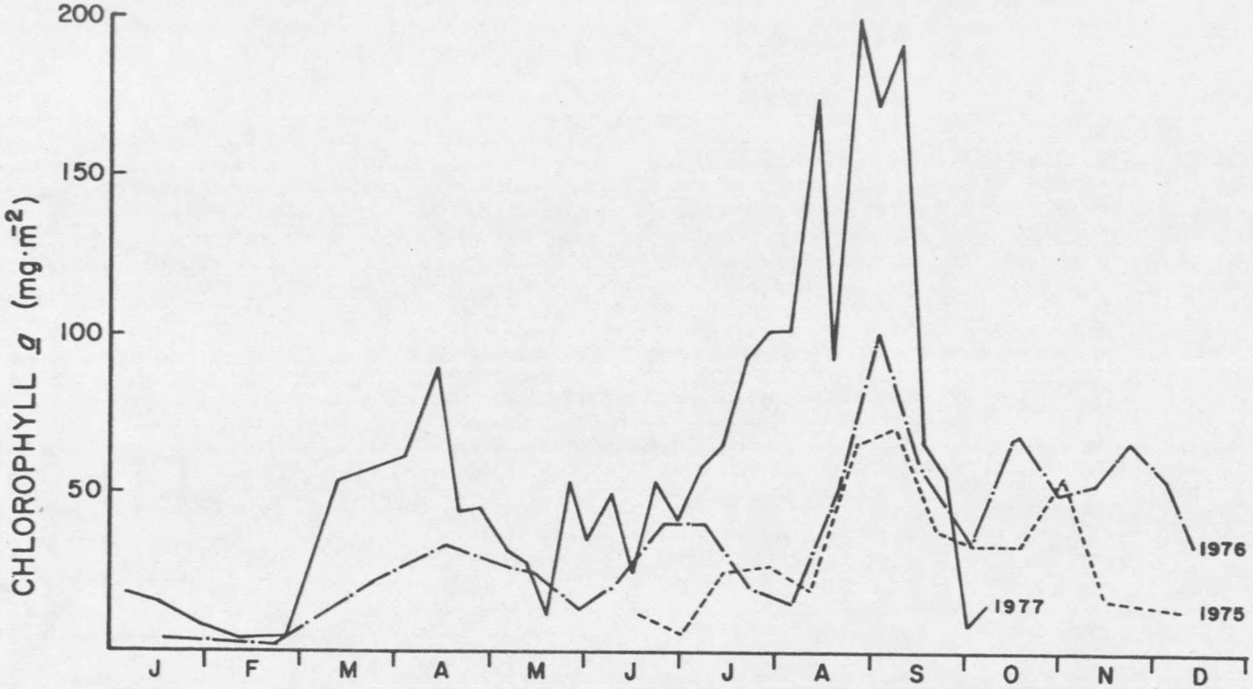

Figure 9. Seasonal trends in areal chlorophyll α concentration ($mg \cdot m^{-2}$) at Station 2 of the Tongue River Reservoir during 1975, 1976, and 1977.

decline of chlorophyll *a* levels was particularly rapid in the fall of 1977 as compared to other years.

A statistical comparison (Randomized Complete Block ANOV) between chlorophyll *a* levels observed at the three reservoir stations on 12 different dates during the 1977 growing season (Figure 10) revealed no significant differences among stations ($p=0.27$). Stations 1 and 2 were most alike, exhibiting similar seasonal trends and comparable average chlorophyll *a* values (63.0 and 75.3 $mg \cdot m^{-2}$ respectively). Station 3 displayed a monacmic seasonal chlorophyll distribution pattern and an average of 49.7 $mg \cdot m^{-2}$ chlorophyll *a* during the period. Whalen (1979) observed markedly greater fluctuations in algal standing crop at Station 3 than at the other two reservoir stations yet he also was unable to attach statistical significance to the inter-station differences.

Limnetic Zooplankton Populations

Taxonomic Analysis

During the course of this study twelve species of crustacean zooplankton were identified in samples collected from the limnetic waters of the Tongue River Reservoir (Table 4).

Two of the seven cladoceran species identified were exceedingly rare. Only one or two individuals each of *Daphnia pulex* and *Schaphloberis kingi* were encountered throughout the course of the study.

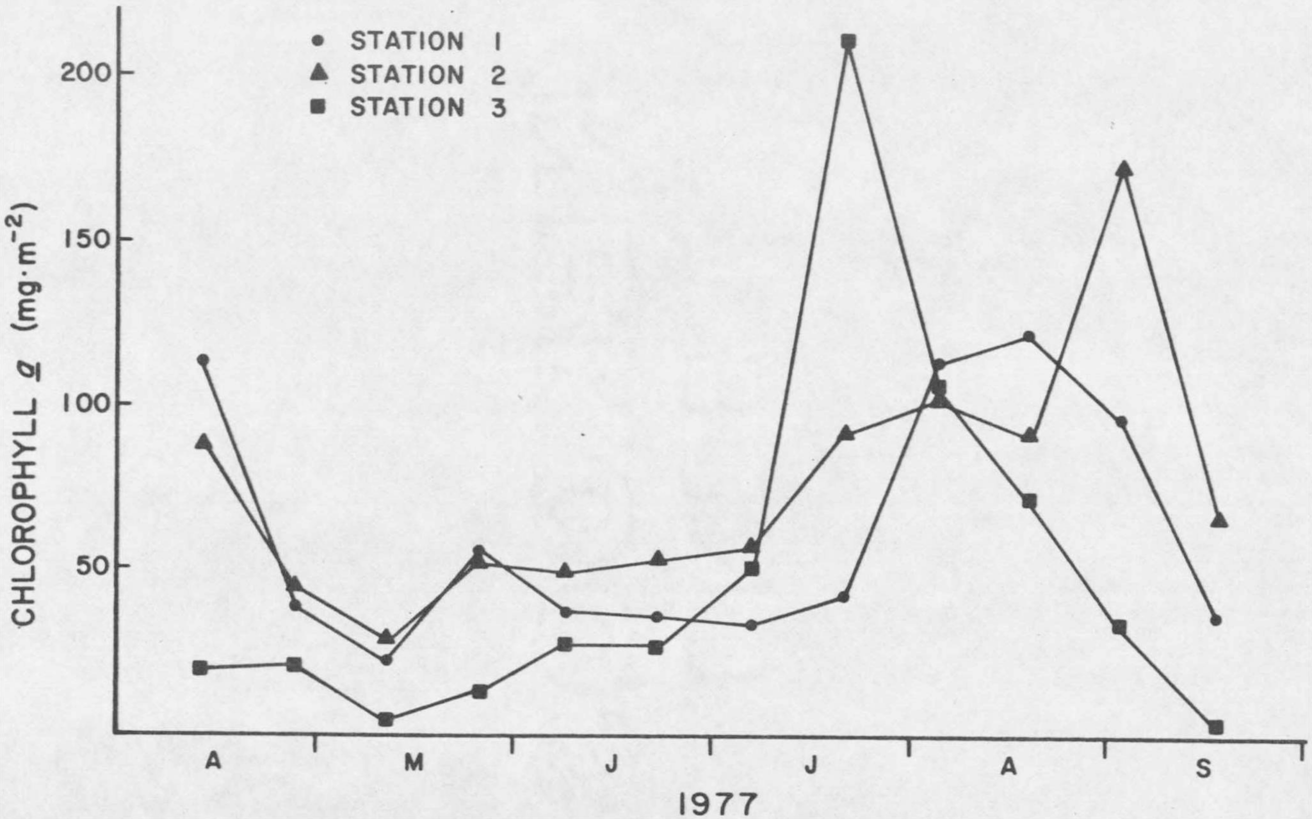

Figure 10. Seasonal trends in areal chlorophyll α concentration ($mg \cdot m^{-2}$) at three stations on the Tongue River Reservoir during the spring and summer of 1977.

Table 4 . Crustacean zooplankton species encountered in the limnetic waters of the Tongue River Reservoir during the period May 1976 to October 1977.

Phylum Arthropoda
    Class Crustacea

        Order Cladocera
            Daphnia pulex Leydig
            Daphnia galeata Sars *mendotae* Birge
            Daphnia parvula Fordyce
            Schapholeberis kingi Sars
            Ceriodaphnia reticulata Jurine
            Bosmina longirostris Muller
            Leydigia quadrangularis Leydig

        Order Copepoda
          Suborder Calanoida
            Diaptomus siciloides Lilljeborg

          Suborder Cyclopoida
            Eucyclops agilis Koch
            Tropocyclops prasinus Fisher
            Cyclops bicuspidatus thomasi Forbes
            Mesocyclops edax Forbes

Leydigia quadrangularis, the sole representative of the cladoceran family Chydoridae, was infrequently collected and was never encountered in densities exceeding 2.0 organisms per liter at Station 2.

The occurrence of *Leydigia* in the limnetic waters of the Tongue River Reservoir is incongruous since it is considered to be a littoral species favoring weedy areas (Brooks 1959). As has been previously mentioned the Tongue River Reservoir is essentially devoid of littoral macrophytic vegetation. *Leydigia* has been infrequently collected in two mainstem Missouri River reservoirs (Garlasco et al. 1978; Selgeby 1974) and also maintained low densities in Big Horn Reservoir, an impoundment of the Bighorn River in southeastern Montana (Horpestad 1974).

Two of the cyclopoid copepod species (*Eucyclops agilis* and *Tropolyclops prasinus*) were also rare and will not be considered in detail. *Eucyclops agilis* was sporadically encountered throughout the course of the study and did not achieve densities in excess of 1.0 per liter at any station. This species has been found in small numbers in three mainstem Missouri River reservoirs (Selgeby 1974; Cowell 1970) and was found to be the most common cyclopoid copepod during June in Lake Sakakawea, a mainstem Missouri River reservoir in North Dakota (Garlasco et al. 1978). *Eucyclops* was rarely encountered in Bighorn Lake in Montana (Horpestad 1977).

Tropocyclops prasinus is a very small cyclopoid copepod which can be easily overlooked in collections containing high numbers of larger copepod species. This species was encountered on ten separate occasions in the Tongue River Reservoir between September and ice-in during both 1976 and 1977. *Tropocyclops* densities up to 9.0 per liter were recorded but the average for the ten occasions was 3.0 copepodites per liter. This species has not been reported in Montana plankton studies but has been found in a lower mainstem Missouri River reservoir (Tash et al. 1966). *Tropocyclops* was seasonally common in Woods Reservoir, Tennessee (Yeatman 1956), and was described as a late summer-early autumn species in two Kansas lakes (Armitage 1961).

A total of eight genera of rotifers representing a minimum of nine species were identified from limnetic zooplankton collections (Table 5). With the exception of *Trichotria* sp., a littoral species encountered infrequently at Station 3, all species are common inhabitants of the limnetic plankton communities of lakes and ponds (Edmondson 1959). Three of the rotifer species (*Polyarthra vulgaris*, *Keratella quadrata*, and *Ascomorpha* spp..) were present in significant numbers and achieved densities in excess of 175 per liter at Station 2. Appendix Table 24 presents seasonal densities of rotifers at Station 2 between October 1976 and October 1977.

Seven genera of dipteran larvae were represented in limnetic zooplankton collections (Table 6). The appearance of organisms of the family Chironomidae in limnetic plankton samples is probably incidental since they typically inhabit lakebed sediments. *Chaoborus*

Table 5. Rotifer species encountered in the limnetic waters of the Tongue River Reservoir during the period May 1976 to October 1977.

Phylum Aschelminthes

Class Rotatoria

Polyarthra vulgaris Carlin

Filinia longiseta Ehrenberg

Keratella cochlearis Gosse

Keratella quadrata Muller

Asplanchna priodonta Gosse

Trichotria sp.

Brachionus calyciflorus

Platyias patulus

Ascomorpha spp.

is a highly predaceous dipteran whose larva typically stage vertical migrations nocturnally from the lakebed to the surface waters where they frequently prey upon zooplankton (Fedorenko 1975). *Chaoborus* appeared during the months of May, June, and July in plankton samples collected on five separate dates at Station 2, on three sampling dates at Station 1, and on one occasion in the reservoir outflow. Maximum numbers encountered were 92.4 $\cdot m^{-2}$ at Station 1 and 44.7 $\cdot m^{-2}$ at

Table 6. Generic list of dipteran larvae appearing in plankton samples collected from the limnetic waters of the Tongue River Reservoir during the period May 1976 to October 1977.

Phylum Arthropoda

Class Insecta

Order Diptera

Family Chironomidae

Subfamily Tanypodinae

Procladius spp.

Subfamily Chironominae

Chironomus spp.

Parachironomus sp.

Paratendipes sp.

Polypedilum sp.

Tanytarsus spp.

Family Chaoboridae

Chaoborus

Station 2 on 6 July 1977. *Chaoborus* was not collected at Station 3. It is possible that more precise estimates of *Chaoborus* abundance could have been obtained if night sampling had been conducted however zooplankton were always collected during the daylight hours.

Ordinal Composition of Crustacean Zooplankton at Station 2

Crustacean zooplankton in the Tongue River Reservoir achieved two major density peaks at Station 2; one in the spring and the other in the late summer and fall months (Figure 11A). The Copepoda were dominant in the early winter and were responsible for the spring pulse of crustacean density (Figure 11B). Cladocerans were most important in the late winter months and during the summer and fall. On an annual basis the Cladocera comprised an average of 58.6% of total crustacean zooplankton density at Station 2, the Copepoda accounted for the remaining 41.4%. Average crustacean zooplankton density for the period was 137.3 per liter.

Species Composition of Crustacean Zooplankton at Station 2

Cladocera. The two cladoceran species *Bosmina longirostris* and *Daphnia galeata mendotae* were perennial constituents of the zooplankton (Figure 12B). *Bosmina* was the most frequently encountered crustacean, averaging 40.4 per liter and comprising an average of 48.1% of cladoceran density (Table 7). This species constituted a major portion of the cladoceran community during the fall and winter months and was found to account for an average of 71.5% of total cladoceran density during the period October 1976 to May 1977. *Daphnia galeata mendotae* was somewhat less important, averaging 12.1 individuals per liter during the entire study, yet the species

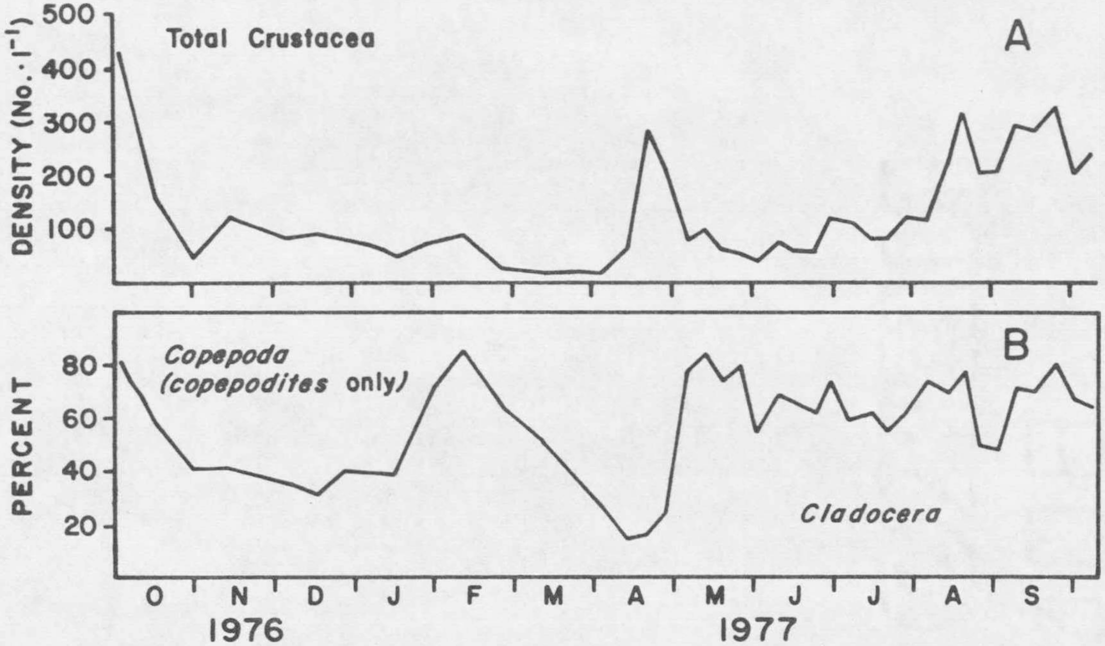

Figure 11. Density (#·ℓ⁻¹; A.) and ordinal composition (percent; B.) of crustacean zooplankton at Station 2 of the Tongue River Reservoir during 1976 and 1977.

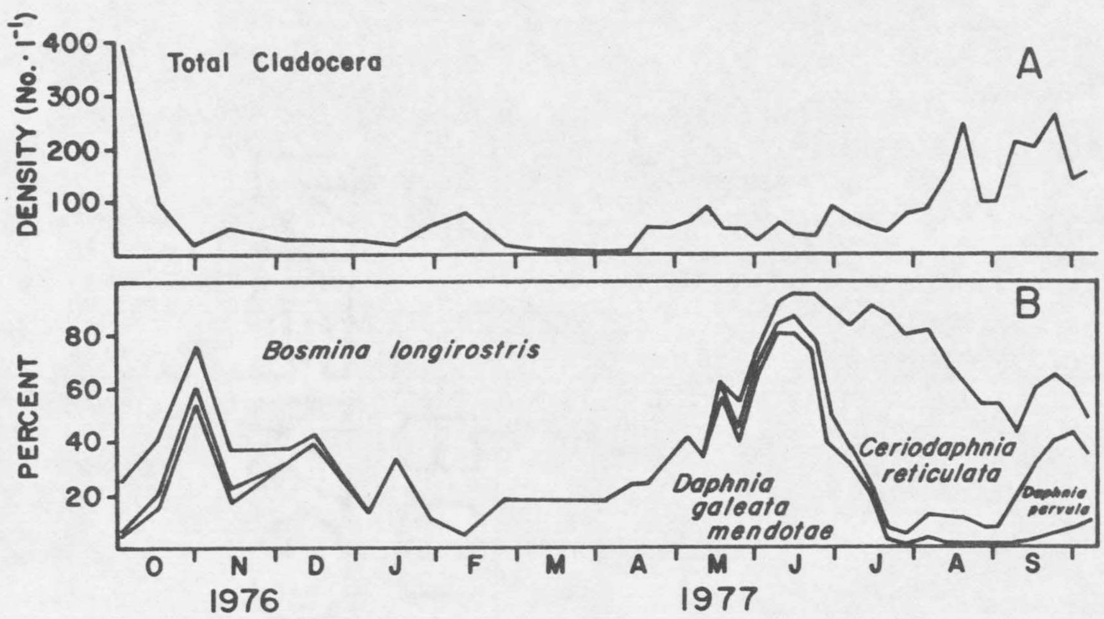

Figure 12. Density (#·ℓ^{-1}; A.) and species composition (percent; B.) of Cladocera at Station 2 of the Tongue River Reservoir during 1976 and 1977.

Table 7. Mean percent composition and average density of the principal cladoceran species at Station 2 of the Tongue River Reservoir for 39 dates during the period 2 October 1976 to 7 October 1977.

Species	Mean percent compositon of cladoceran density	Mean density (#·ℓ$^{-1}$)
Daphnia galeata mendotae	24.9	12.6
Daphnia parvula	6.1	9.1
Ceriodaphnia reticulata	20.8	23.2
Bosmina longirostris	48.1	40.4

comprised an average of nearly 25% of mean annual cladoceran density primarily because of its prevalence during the early summer months.

Ceriodaphnia reticulata and *Daphnia parvula* were virtually absent from limnetic plankton samples collected during the winter months (Figure 12B). The former was an important component of the cladoceran community during the late summer-early fall months and was the second most numerous species on an annual basis, averaging 23.2 per liter and comprising an average of 20.8% of cladoceran density (Table 7). Due to its restricted appearance in the limnetic plankton the latter species was the least frequently encountered of the four principal cladoceran species though it was able to achieve high densities for a short period of time during autumn.

<u>Copepoda</u>. *Cyclops bicuspidatus thomasi* and *Diaptomus siciloides* were both perennial at Station 2 during the study (Figure 13B). *Cyclops* was the most important constituent of the copepod assemblage, averaging 29.2 per liter and comprising an average of 60.2% of total copepod density on an annual basis (Table 8). During the nine month

Table 8. Mean percent composition and average copepodite density of the principal copepod species at Station 2 of the Tongue River Reservoir for 39 dates, 2 October 1976-7 October 1977.

Species	Mean percent composition of copepod density	Mean density ($\# \cdot \ell^{-1}$)
Cyclops bicuspidatus thomasi	60.2	29.2
Mesocyclops edax	26.9	17.4
Diaptomus siciloides	12.9	5.3

period October 1976 to July 1977 *Cyclops* was overwhelmingly predominant, comprising an average of 83.7% of total copepod density. *Diaptomus* was generally a minor component of the copepod community. On an annual basis it constituted an average of 12.9% of total copepod density and displayed a mean density of 5.3 copepodites per liter.

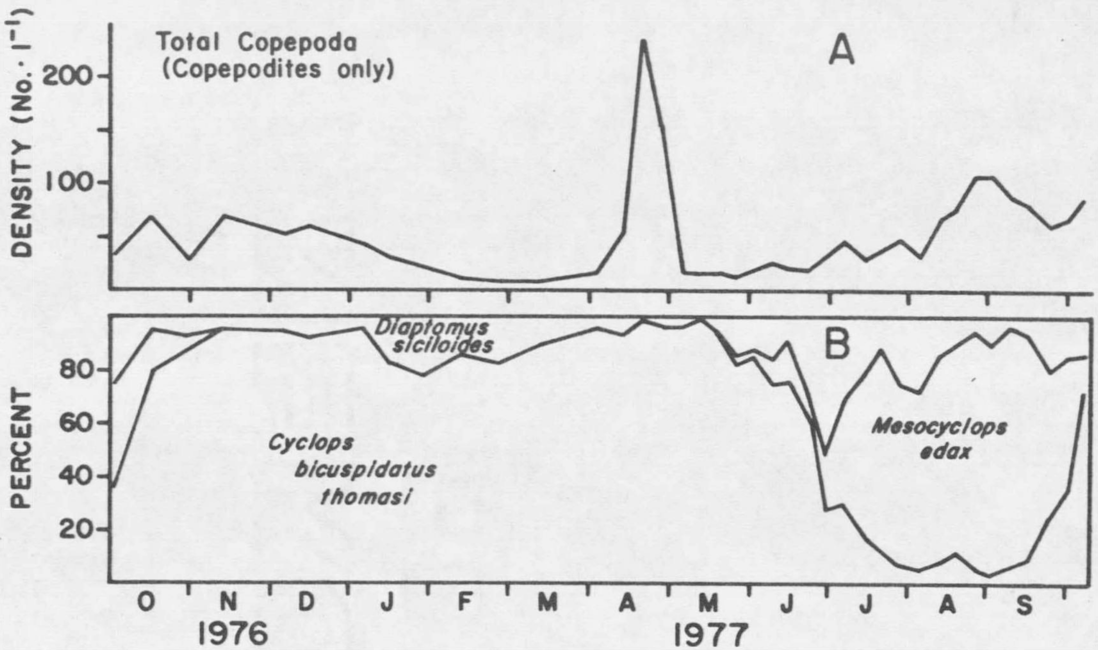

Figure 13. Copepodite density ($\# \cdot \ell^{-1}$; A.) and species composition (percent; B) of the Copepoda at Station 2 of the Tongue River Reservoir during 1976 and 1977.

Mesocyclops edax was an ephemeral species which achieved its maximum importance in late summer (Figure 13B.). Despite the fact of its limited appearance within the limnetic plankton *Mesocyclops* was able to achieve high densities and averaged 17.4 per liter on an annual basis (Table 8).

Peaks in total copepod copepodite density ($236 \cdot \ell^{-1}$ on 20 April 1977, $108 \cdot \ell^{-1}$ on 2 September 1977; Figure 13A.) were much lower than cladoceran abundance maxima ($401 \cdot \ell^{-1}$ on 2 October 1976, $245 \cdot \ell^{-1}$ on 19 August 1977, $260 \cdot \ell^{-1}$ on 24 September 1977; Figure 13A.).

Comparison of Crustacean Zooplankton Populations at Three Reservoir Stations

Population trends of the major cladoceran species at the three reservoir stations during the period 13 April through 2 September 1977 are presented in Figure 14. Data collected in mid-September were not employed in this analysis as the total depth at Station 3 was less than one meter. At this time zooplankton were scarce at Station 3; most species had virtually disappeared. On 1 October 1977 the Station was dry.

The *Daphnia* spp. population pulse at Station 3 commenced later, peaked later and declined earlier than corresponding populations at Staions 1 and 2 (Figure 14). Trends were similar at the latter two stations except for a noticeable fact that a mid-August peak in *Daphnia* spp. at Station 2 was not duplicated in Station 1. Inspection

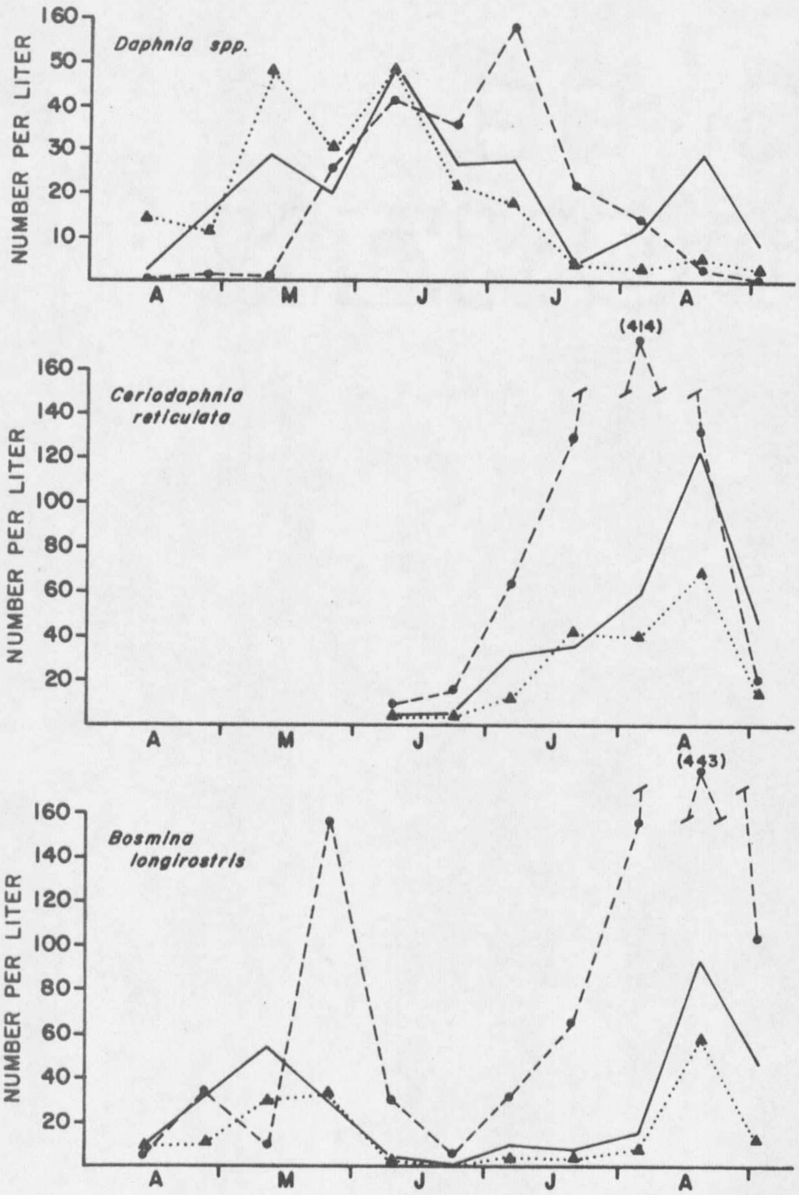

Figure 14. Abundance trends ($\# \cdot \ell^{-1}$) of important cladocerans at Stations 1 (triangles connected by dotted line); 2 (solid line); and 3 (dashed line) of the Tongue River Reservoir during the spring and summer of 1977.

of the raw data reveals that this Station 2 peak was mostly attributable to high numbers of *Daphnia parvula* which achieved a density in excess of 90 per liter in late September (Appendix Table 30). *Daphnia parvula* never achieved similar densities at Station 1. The maximum density observed at this station during the course of the investigation was 12.1 per liter on 1 October 1977 (Appendix Table 25). *Daphnia parvula* dominated the Station 3 population beginning in early July whereas the species was not dominant at Station 2 until one month later (Appendix Table 30).

Abundance trends of both *Ceriodaphnia reticulata* and *Bosmina longirostris* were similar at Stations 1 and 2 (Figure 14). These organisms achieved phenomenally high densities at Station 3 where densities in excess of 400 per liter were noted for both species.

With some exceptions, trends in copepod abundance were similar for most species at Stations 1 and 2 during the spring and summer of 1977 (Figure 15). The dramatic spring *Cyclops* pulse noted at these two stations was apparently never realized at Station 3. The *Mesocyclops* population developed and peaked earlier at Station 3 than at the other two stations. The species also steadily increased during August at Station 2 whereas it did not develop as appreciably at Station 1. *Diaptomus* densities were lowest at Station 3 with Station 1 being intermediate.

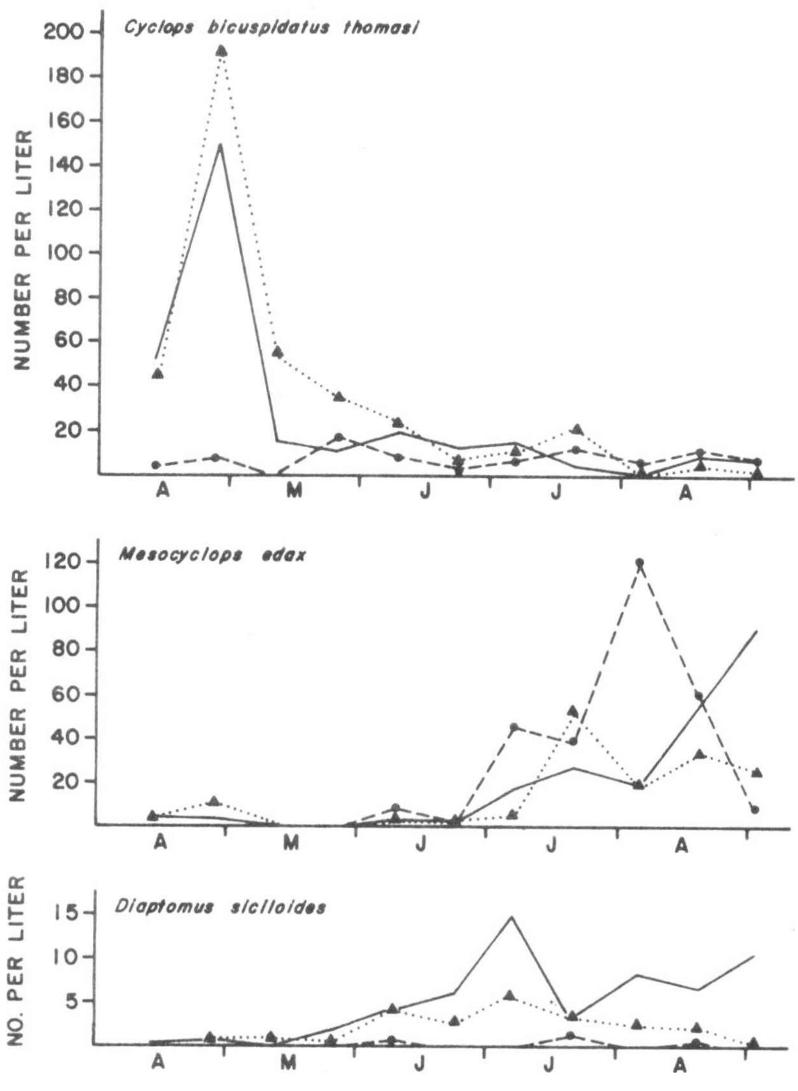

Figure 15. Abundance trends (#·ℓ^{-1}) of the three major copepods at Stations 1 (triangles connected by dotted line); 2 (solid line); and 3 (dashed line) of the Tongue River Reservoir during the spring and summer of 1977.

Expression of plankton density in terms of volume (number per liter) and area (thousands per square meter) provides information which is useful in evaluating inter-station differences. Stations 1 and 2 supported similar numbers of zooplankton expressed either areally or volumetrically (Figure 16). These two stations were also found to be similar during 1976 (Leathe 1977). A relatively small difference in mean *Cyclops* volumetric density between Stations 1 and 2 (Figure 16A) becomes magnified when density is expressed per unit surface area because Station 1 is located in the deep end of the reservoir. When expressed on an areal basis, the striking volumetric preponderance of *Ceriodaphnia* and *Bosmina* at Station 3 is masked and all stations are similar (Figure 16B). Station 3 is the shallowest of the reservoir stations and during much of the summer it represents the euphotic layer of the other stations.

Daphnia spp. have similar mean densities at the three reservoir stations on a volumetric basis (Figure 16A). However, differences between stations on an areal basis are noticeable (Figure 16B).

Seasonal Life Histories and Population Dynamics of Cladoceran Species at Station 2

Bosmina longirostris. This was the smallest of four cladoceran species commonly inhabiting the limnetic zone of the Tongue River Reservoir, females averaged 0.43 mm in length (Table 9). The *Bosmina* population displayed peaks in abundance during mid-winter, spring and

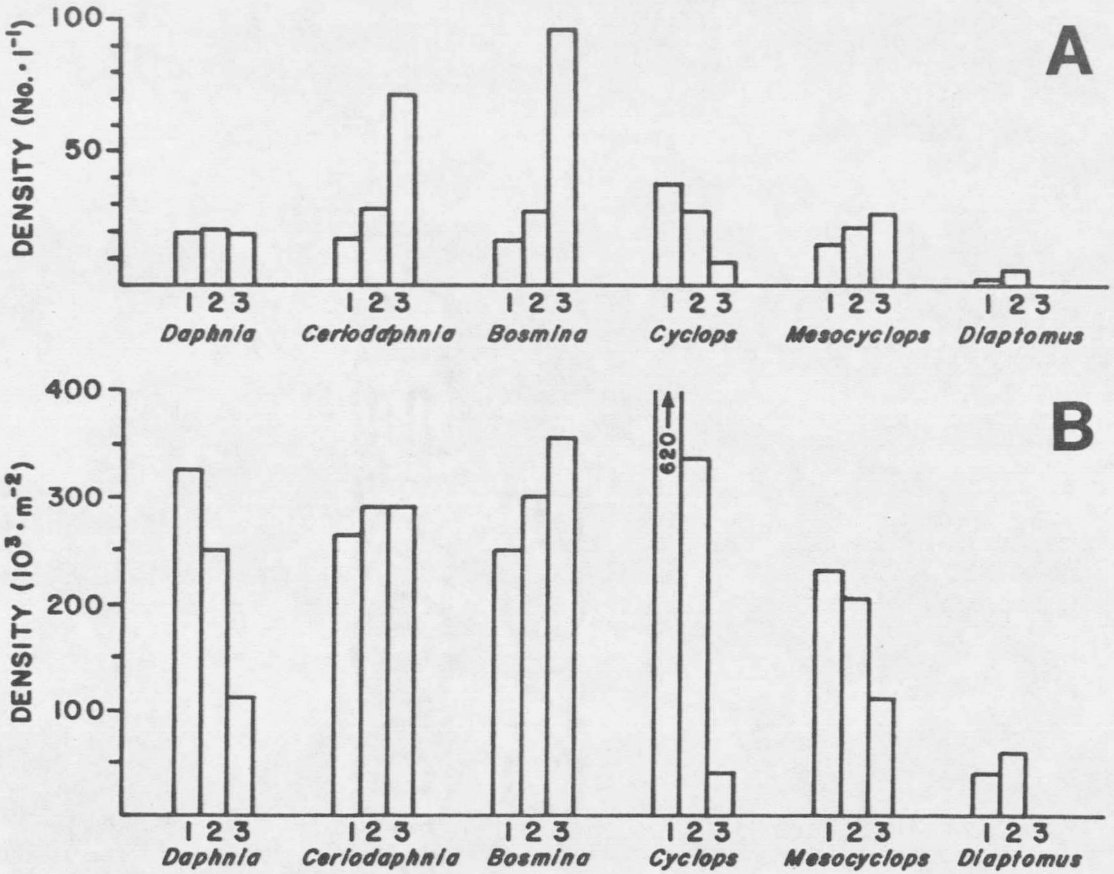

Figure 16. Mean density of the principal zooplankton species at three stations on the Tongue River Reservoir. *A.* Organisms per liter. *B.* Thousands of organisms per square meter. Averages were calculated for 11 dates between 13 April and 2 September 1977.

Table 9 . Length summary (millimeters) of the principal limnetic cladoceran species of the Tongue River Reservoir.

Species	Average female	Maximum female	Minimum female	Average male	Number Measured
Bosmina longirostris	0.43	0.61	0.28	——	453
Ceriodaphnia reticulata	0.61	0.77	0.39	0.58	295
Daphnia parvula	1.06	1.46	0.84	0.69	192
Daphnia galeata mendotae	1.34	1.81	1.01	0.86	270

fall at Station 2 (Figure 17). This was the only cladoceran species which displayed a strong pulse in abundance under rigorous winter conditions.

The early February population was comprised primarily of adults (Figure 17). Although egg densities at this time were quite high (on the order of 20 eggs per liter), instantaneous birth rate (b) and rate of population increase (r) remained low (Figure 17). These low population coefficients are attributable to the fact that egg incubation times were inordinately high (approximately 25 days; Appendix Table 28) due to low ambient water temperature (3°C). It is probable that juvenile survival was low because of low temperatures and an extremely low algal standing crop (Figure 9).

The late summer and early fall months were apparently the most conducive to *Bosmina* population growth. The maximum density achieved by any limnetic crustacean species during the study was attained in early October 1976 when *Bosmina* peaked at 308 per liter, followed by a population crash shortly thereafter (Figure 17). The next highest abundance maximum for the species was 120 per liter observed in early September 1977. In addition, *Bosmina* staged a spring pulse which lasted approximately a month and a half and peaked at 55 per liter in mid-May (Figure 17).

Bosmina egg density trends closely followed the seasonal population abundance pattern (Figure 17). A maximum egg density of 55 per

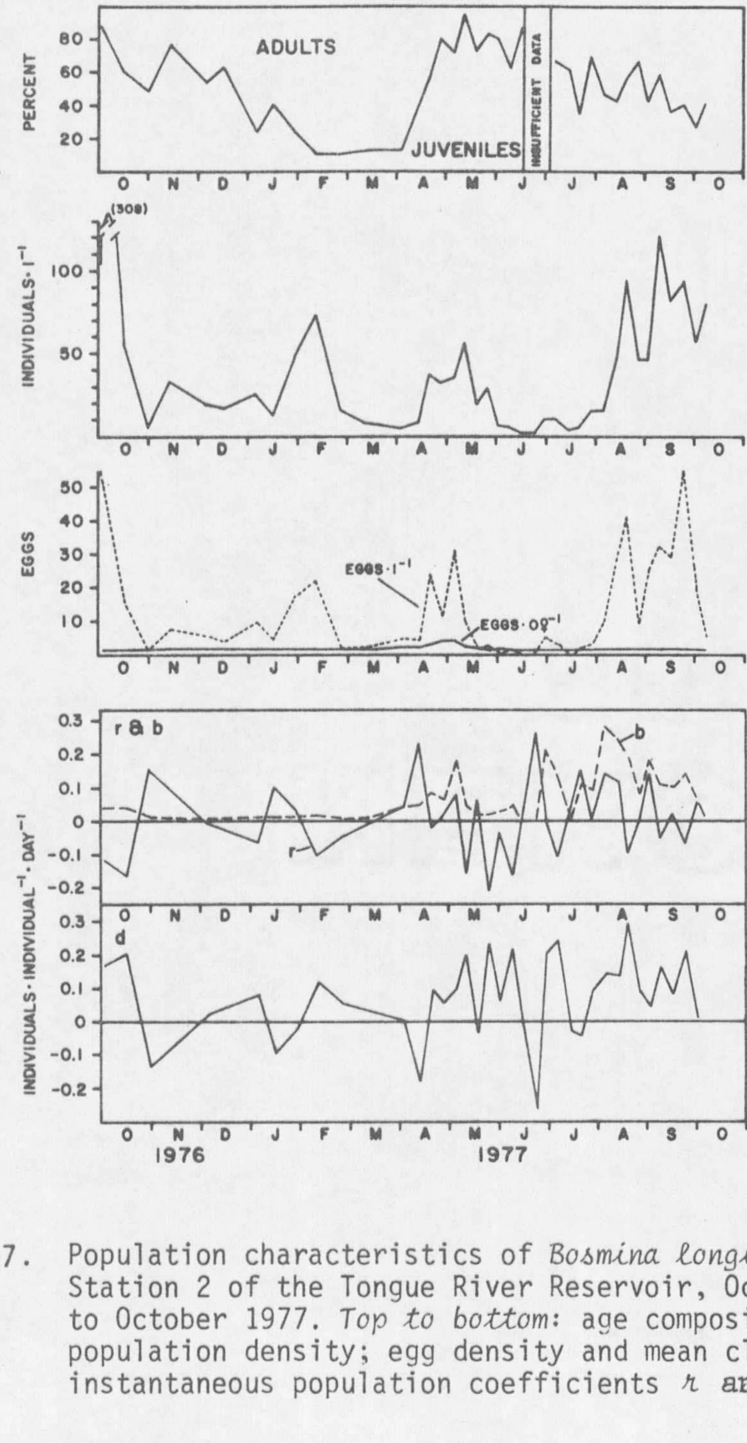

Figure 17. Population characteristics of *Bosmina longirostris* at Station 2 of the Tongue River Reservoir, October 1976 to October 1977. *Top to bottom*: age composition; total population density; egg density and mean clutch size; instantaneous population coefficients r and b, d.

liter was attained on two separate occasions; early October 1976 and late September 1977. *Bosmina* exhibited the least amount of clutch size variation of the four principal cladoceran species. The maximum average clutch size observed for the species was 3.9 eggs per female in early May and the annual average was 1.4 eggs per female. The largest clutch observed was 11 embryos carried by a female on 24 April 1977.

A single male *Bosmina* was identified from a 25 May 1977 sample which agrees with the fact that in general, male bosminids are quite rare (Deevey and Deevey 1971). Epphippial *Bosmina* eggs were never observed. Geer (1977) reported neither male nor ephippial eggs for *B. longirostris* in Georgetown Lake whereas they were both reported for the species in an Ontario beaver pond (Kwik and Carter 1975).

Instantaneous per capita birth rate coefficients for *Bosmina* were low throughout the winter for reasons previously cited (Figure 17). Birth rates were highest in late summer; the maximum value of 0.28 individuals·individual^{-1}·day^{-1} observed on 5 August 1977 initiated the late summer population increase. The species was unique in that negative instantaneous death rates were calculated for six different sampling dates during the year (Figure 17; Appendix Table 28). This enigmatic situation arises when rates of population increase (r) exceed birth rates (b) which suggests that organisms are entering the population from unknown sources. Interestingly, Geer (1977) obtained negative instantaneous mortality coefficients for *Bosmina* on seven dates during a one-year study whereas he seldom if ever computed negative rates for three other cladoceran species. Kwik and Carter (1975) also observed the same phenomenon and ascribed it to either gross sampling error, aggregation of the animals into compact clusters, or to temporary abandonment of the limnoplankton in favor of a benthic existence.

Ceriodaphnia reticulata. This was next smallest of the four principal cladoceran species, an average female was 0.61 mm in length (Table 9). The largest female encountered (0.7 mm) was found to be 27% smaller than an average female of *Daphnia parvula*, the smallest of two *Daphnia* species commonly found in the reservoir.

The most striking feature of the *Ceriodaphnia* population abundance pattern was its virtual absence from the limnetic plankton during the winter months (Figure 18). Observed densities were less than 1.0 per liter for the five month period between December and mid-May (Appendix Table 29). During the months of February and March no specimens were observed in plankton collections. The population was essentially monacmic, attaining a peak density of 124 per liter on 19 August 1977.

The rapid decline of the *Ceriodaphnia* population during the month of October 1976 closely paralleled a rapid decline in mean water temperature from 15.8°C in early October to 5.9°C by the end of the

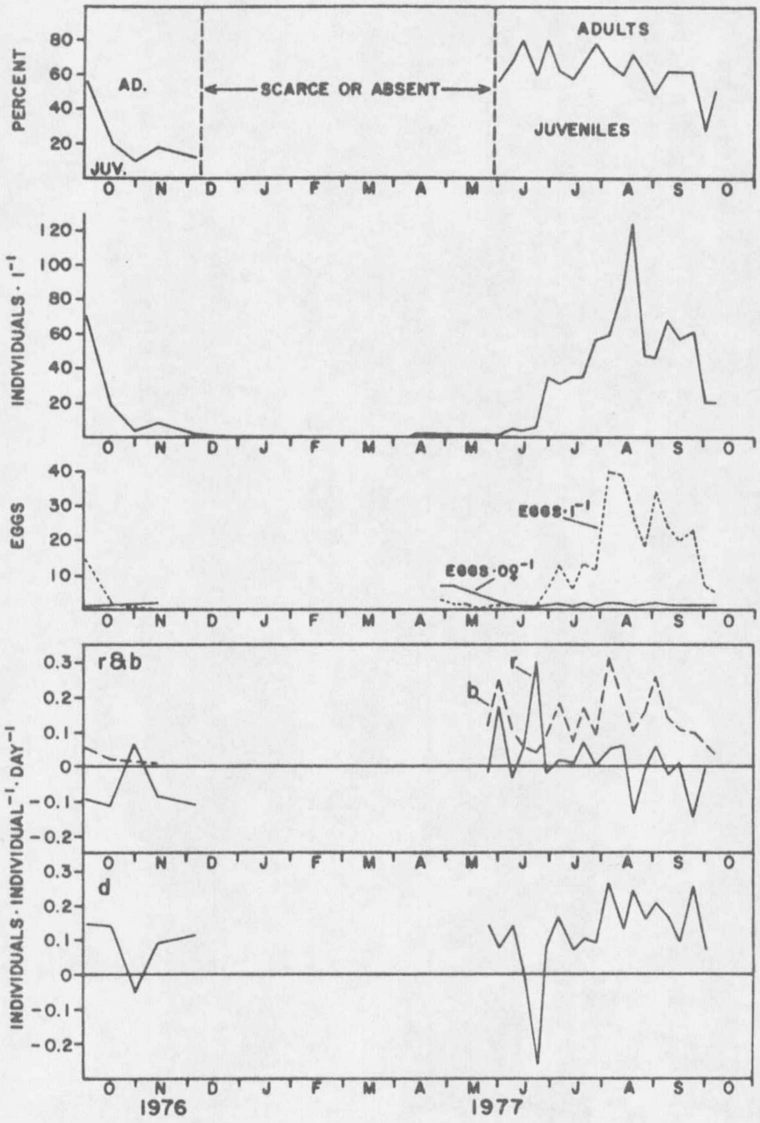

Figure 18. Population characteristics of *Ceriodaphnia reticulata* at Station 2 of the Tongue River Reservoir, October 1976 to October 1977. *Top to bottom:* age composition; total population density; egg density and mean clutch size; instantaneous population coefficients *r* and *b*, *d*.

month (Figure 4). During this timespan adults comprised an increasingly large percentage of the population (Figure 18). Examination of Figure 19B) reveals that the percentage of males and of females carrying ephippial (resting) eggs increased during October. The maximum density of males ($3.1 \cdot l^{-1}$) preceeded that of ephippia ($4.9 \cdot l^{-1}$) by approximately one month (Figure 19A). In mid-November of 1976, females carrying ephippial eggs comprised 32% of the *Ceriodaphnia* population. Ninety-four percent of the mature females present at this time were carrying ephippial eggs.

The age composition of the summer 1977 *Ceriodaphnia* population differed markedly from that observed during the previous fall (Figure 18). During the months of June, July and August juveniles comprised an average of 67% of the population. As the population declined in September and early October the percentage of adults gradually increased (Figure 18) and males and ephippial females appeared once again (Figure 19). It is probable that the peak of ephippial egg production in the fall of 1977 was not documented as sampling was discontinued after 7 October. The presence of ephippia in the water column during April (Figure 19) is probably attributable to spring mixing and consequent bottom agitation and/or increased ephippium bouyancy as a result of hatching. During 1977, female *Ceriodaphnia* carrying ephippia were not noted until September (Figure 19).

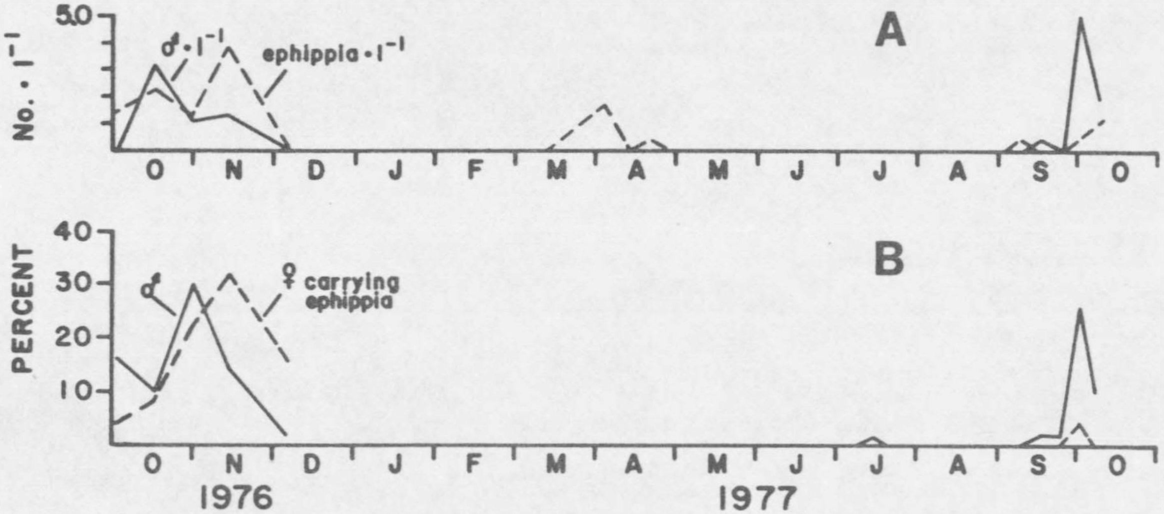

Figure 19. *Ceriodaphnia reticulata* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *A*. Density ($\# \cdot \ell^{-1}$) of males and ephippia. *B*. Percent of population comprised of males and ephippium-bearing females.

Ceriodaphnia egg density closely followed the population density pattern (Figure 18). Maximum egg density ($41 \cdot l^{-1}$) was observed on 5 August which preceeded peak population density by a period of two weeks. Average clutch size for the species was highest (7.0 eggs per female; n=8) in late April-early May but declined rapidly to a value of 1.5 per female by early June and remained at this level thereafter. The largest individual clutch observed was identical to that observed for *Bosmina*; 11 embryos on 27 April.

Since late April-early May chlorophyll *a* levels were steadily declining (Figure 9) it appears as though maximum average clutch size for both *Ceriodaphnia* and *Bosmina* are best related to the rapid warming of reservoir waters to the 14-15°C range by early May (Figure 6). Unfortunately, chlorophyll *a* indicates changes only in agal standing crop. It cannot indicate possible changes in phytoplankton species composition which may favor herbivorous filter feeding cladocerans.

Instantaneous per capita birth rates (*b*) of *Ceriodaphnia* were uniformly high throughout the summer of 1977 (Figure 18), the maximum (0.310 $\text{individuals} \cdot \text{individual}^{-1} \cdot \text{day}^{-1}$) was noted on 5 August. Instantaneous birth rates declined noticeably each fall. Instantaneous mortality coefficients were also quite high during the summer hence values for *r* were low and the population was kept in check. Negative values for mortality coefficients (*d*) were noted on only two occasions.

Daphnia parvula. This was the second largest of the four principal cladoceran species and was the smaller of the two common *Daphnia* species. Females averaged 1.06 mm in length and attained a maximum length of 1.46 mm (Table 9). This species was similar to *Ceriodaphnia* in that it was absent from plankton samples collected during the winter months (Figure 20). *Daphnia parvula* was not observed for the five month period lasting from 5 December 1976 until 5 May 1977 and displayed densities of less than 1.0 liter during the timespan 5 December 1976 to 9 June 1977 with one slight exception (Appendix Table 30).

On an annual basis *Daphnia parvula* was the least numerous of the principal cladoceran species. Densities remained relatively low throughout the summer of 1977 until a major pulse developed in September and peaked at 92 per liter (Figure 20). Data collected during 1976 (Leathe 1977; Appendix Tables 31 and 32) indicate that *D. parvula* densities were markedly lower than those of 1977, even during October (Figure 20). Males and ephippial females were noted in October and November 1976 samples but their densities were low ($1.0 \cdot l^{-1}$; Appendix Table 30).

Males became numerous on the last two sampling dates of 1977 (Appendix Table 30). On the last sampling date (7 October) males comprised 42% of the population and numbered 16.7 per liter. Ephippial females also appeared at this time although in small numbers ($0.7 \cdot l^{-1}$).

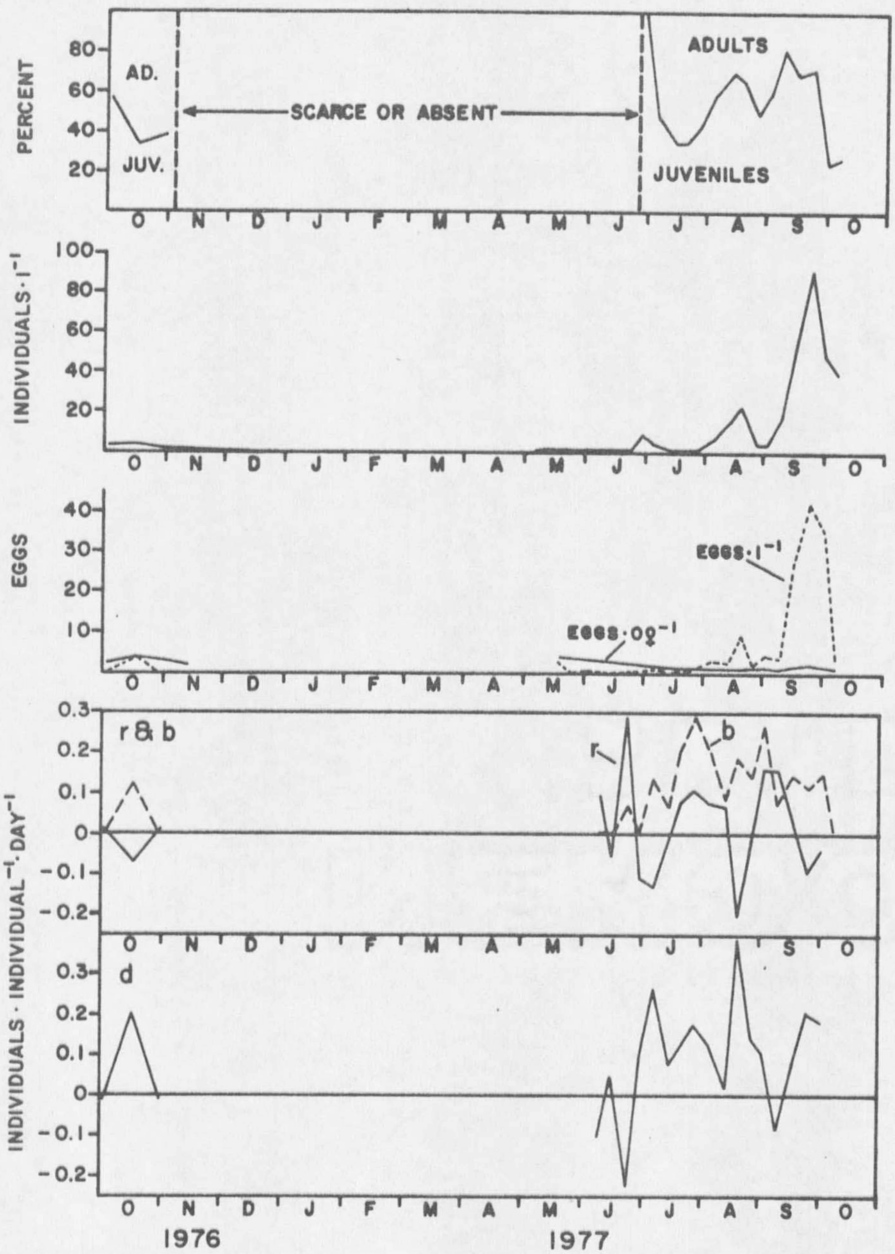

Figure 20. Population characteristics of *Daphnia parvula* at Station 2 of the Tongue River Reservoir, October 1976 to October 1977. *Top to bottom*: age composition; total population density; egg density and mean clutch size; instantaneous population coefficients *r* and *b*, *d*.

It is suspected that ephippial egg production was higher following the termination of sampling. It should be recalled that peak density of *Ceriodaphnia* males preceeded peak ephippium density by one month during the fall of 1976 (Figure 19A).

D. parvula was similar to *Ceriodaphnia* in that the species displayed a uniformly high birth rate (b) throughout its period of abundance (Figure 20). The maximum value for "b" (0.292 individuals·individual^{-1}·day^{-1}) was observed on 27 July 1977 and was not as high as was noted for *Ceriodaphnia*. Death rate coefficients were erratic and one exceptionally high value (0.391 individuals·individual^{-1}·day^{-1}) was noted on 19 August. Negative values for mortality coefficients were calculated on five separate occasions (Figure 20; Appendix Table 30) but on three of these dates total population numbers were less than 2.0 per liter hence the chances for sampling error were great.

Daphnia galeata mendotae. This was the largest of the limnetic cladocerans found in the Tongue River Reservoir. Females averaged 1.34 mm in length and the largest organism encountered was 1.81 mm long (Table 9). This perennial species was not found in densities of less than 1.0 per liter at Station 2 during the study period (Figure 21; Appendix Table 33).

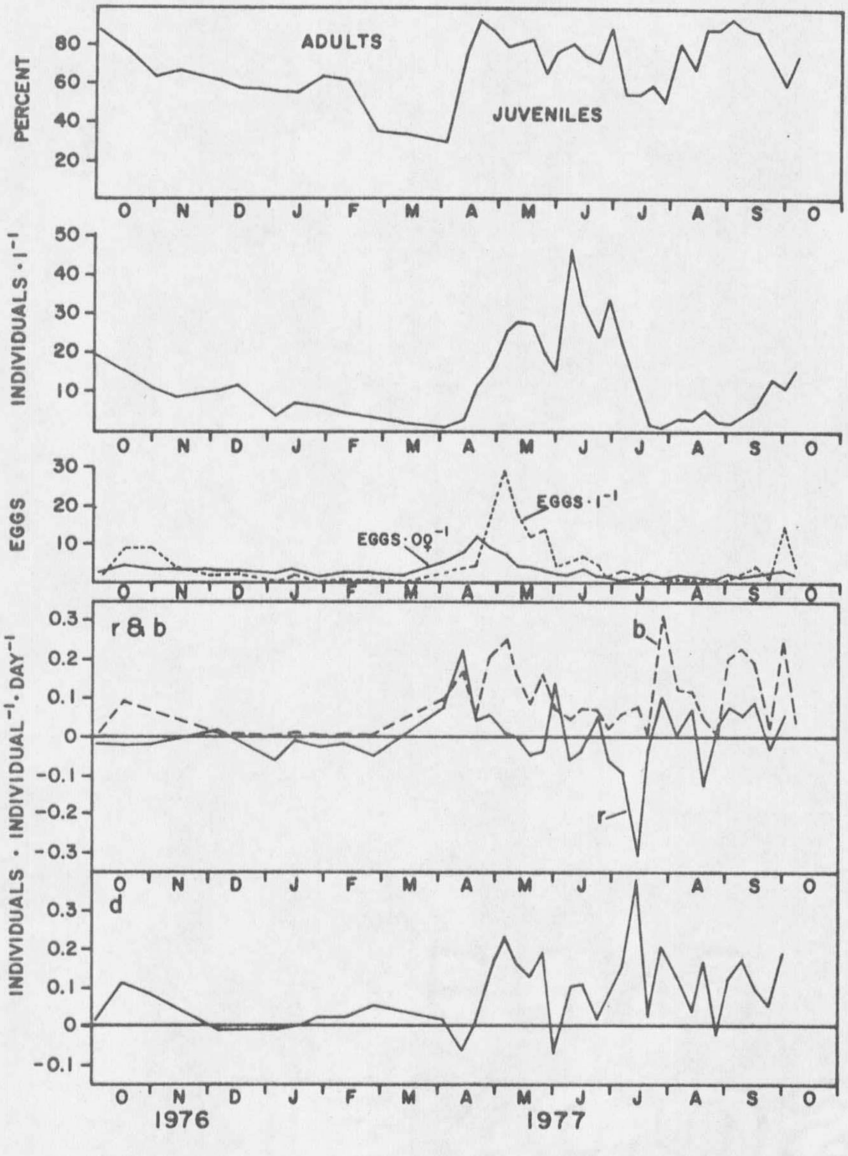

Figure 21. Population characteristics of *Daphnia galeata mendotae* at Station 2 of the Tongue River Reservoir, October 1976 to October 1977. *Top to bottom:* age composition; total population density; egg density and mean clutch size; instantaneous population coefficients *r* and *b*, *d*.

Daphnia g. mendotae displayed a diacmic population abundance pattern, pulses occurred during the early summer months and in the fall (Figure 21). The fall 1976 population declined steadily throughout the winter months to a low of 1.1 per liter on 3 April 1977. This decline in numbers was closely paralleled by an increasing percentage of adults (Figure 21). The maximum density observed during the early summer pulse was 47.0 per liter on 9 June 1977.

The spring-early summer pulse was initiated in March when mean clutch size, egg density, and instantaneous birth rate were all increasing (Figure 21). This population increase appears to be closely related to increasing water temperature (Figure 6) and indirectly associated with changes in algal standing crop (Figure 9). The first peak of the summer population ($28.0 \cdot l^{-1}$ on 11 May 1977) was achieved in spite of a steadily declining algal standing crop. During the period preceeding this peak, clutch size, egg density, and instantaneous birth rate all increased to maxima as algal standing crop declined. The two density peaks in June (Figure 21) were not well related to algal standing crop and resulted from a combination of lowered birth and death rates. Egg density and mean clutch size rapidly declined during this period (Figure 21).

Daphnia g. mendotae displayed the greatest fecundity of the principal cladoceran species. The maximum average clutch size (11.8 eggs per liter on 20 April) and the maximum individual clutch size

(20 eggs carried by females on 20 April and 24 April) were the highest observed for the limnetic Cladocera. Males and ephippial eggs were noted in fall populations of the species, however, density of males never exceeded 1.5 per liter and ephippial densities were less than 1.0 per liter (Appendix Table 33).

Seasonal Life Histories and Population Dynamics of Copepod Species at Station 2

Cyclops bicuspidatus thomasi. This species was the smaller of the two principal cyclopoid copepod species in the Tongue River Reservoir, females averaged 1.24 mm in length (Table 10). Fluctuations in total *Cyclops* copepodite density during the study period were dramatic (Figure 22; top panel). The species exhibited a diacmic seasonal abundance pattern and attained maximum densities in late fall and immediately following iceout in the early spring. The annual maximum copepodite density of 233.3 per liter was noted on 20 April 1977 (Figure 22; Appendix Table 34). If the estimated *Cyclops* nauplius density of 146.8 per liter on this date is added to copepodite density the resulting species density is nearly 380 per liter.

Instar analysis data presented in Figures 22 and 23 reveal that the *Cyclops* population was comprised of two major cohorts. The first cohort apparently originated via increased egg production during September and October and developed slowly during the winter when the reservoir was ice-covered and water temperature (Figure 22; bottom

Table 10. Length summary (millimeters) of the principal limnetic copepod species of the Tongue River Reservoir.

Species	Average female	Maximum female	Minimum female	Average male	Number Measured
Diaptomus siciloides	1.24	1.31	1.10	1.12	208
Cyclops bicuspidatus thomasi	1.25	1.42	1.12	0.98	251
Mesocyclops edax	1.46	1.55	1.42	0.96	118

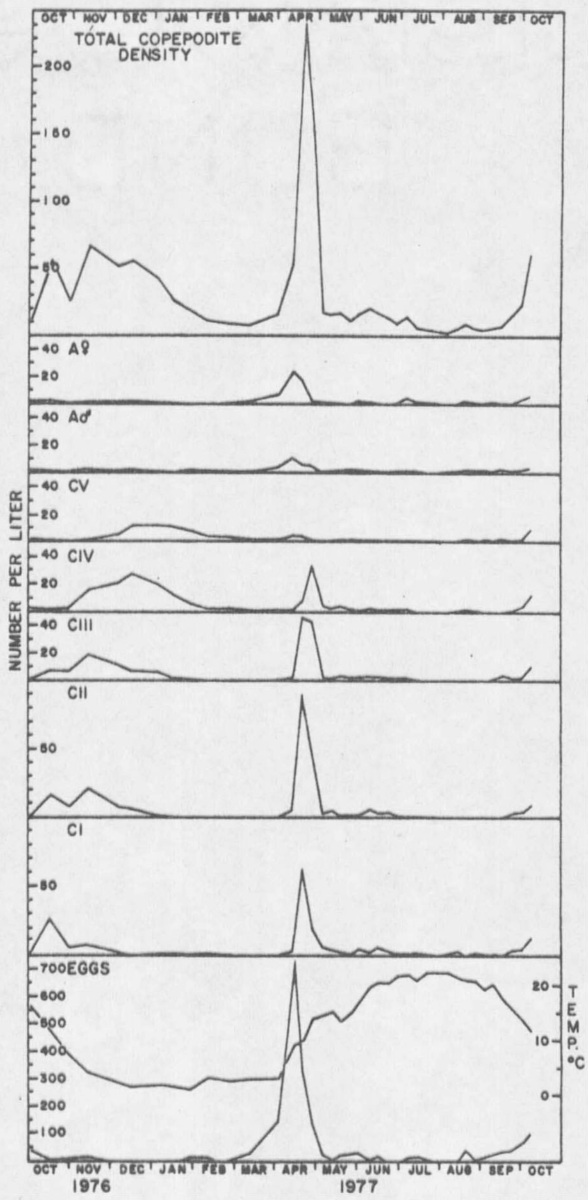

Figure 22. Seasonal abundance of *Cyclops bicuspidatus thomasi* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *Top panel:* Total copepodite density ($\# \cdot \ell^{-1}$). *Middle panels:* Densities ($\# \cdot \ell^{-1}$) of developmental copepodite instars. *Bottom panel:* Egg density ($\# \cdot \ell^{-1}$) and mean water temperature (°C).

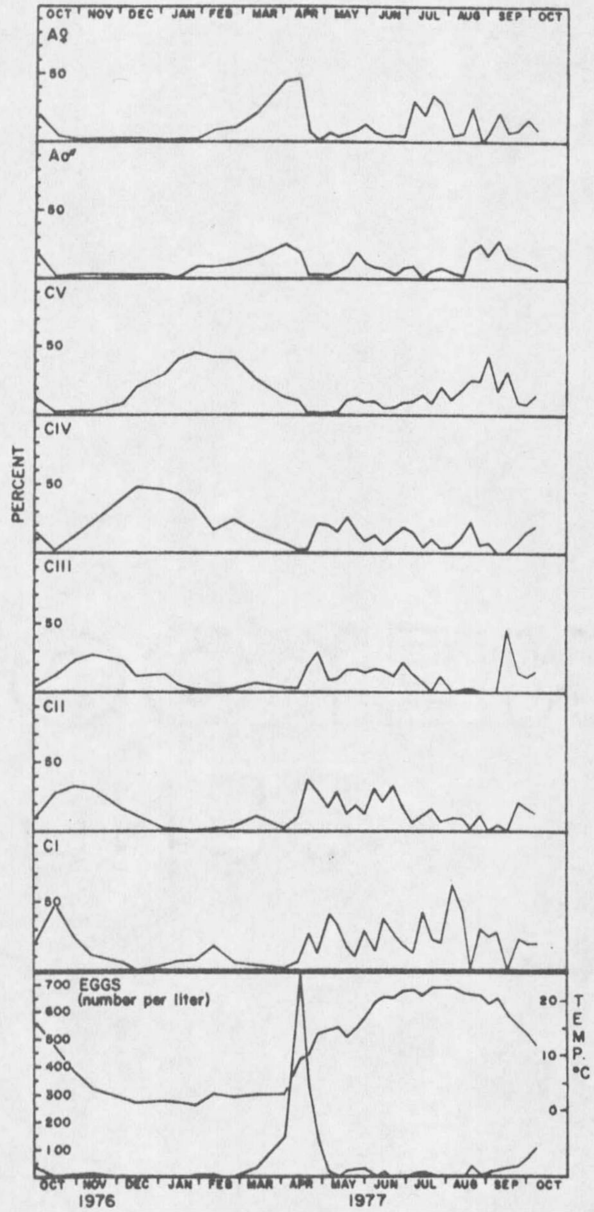

Figure 23. Seasonal abundance of *Cyclops bicuspidatus thomasi* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *Top panels:* Percentage composition of developmental copepodite instars. *Bottom panel:* Egg density ($\#\cdot\ell^{-1}$) and mean water temperature (°C).

panel) and algal standing crop (Figure 9) were low. A maximum density of 66.9 copepodites per liter for this winter cohort was noted on 13 November 1976 when the three youngest instars collectively comprised 69% of the population (Figure 23). Data presented in Figure 23 reveal a gradual uninterrupted cohort development curve commencing with eggs produced during late September and in early October 1976. Cohort development progressed over a period of approximately 196 days until eventual population dominance was achieved by sexually mature CVI copepodites in April 1977. However, when actual limnetic copepodite densities are plotted (Figure 22) the winter cohort development curve appears to be significantly interrupted at the CV instar. The relative scarcity of CV and CVI copepodites in limnetic waters during most of February and March indicates that *Cyclops* copepodites probably shift to a benthic existence during this timespan. It is likely that this hypothesized benthic population consists of diapausing and also slowly developing copepodites since both CV and CVI instars appeared in noticeably increased limnetic numbers on 13 April 1977 although the latter are more numerous by a factor of five (Figure 22). The apparent shift to a benthic lifestyle may be in response to the severely depressed algal standing crop within the limnetic waters (Figure 9) and may represent a change to a detrital food base.

It appears as though a dramatic rise in water temperature from 3.2°C on 3 April to 9.3°C on 13 April (Figure 22; bottom) triggered a phenomenal response in the *Cyclops* population. During this timespan algal stocks increased to a spring maximum (Figure 9). Concommitantly, CVI density increased more than two fold from $11.0 \cdot l^{-1}$ to $25.1 \cdot l^{-1}$ and *Cyclops* egg production increased fivefold from $146.5 \cdot l^{-1}$ to $737.0 \cdot l^{-1}$ (Figure 22) thus giving rise to a fast developing spring cohort. The rapid progression of the spring cohort is best depicted in Figure 22 since percentage changes in population composition are apparently masked by excessive fluctuations in population abundance (Figure 23). Data presented in Figure 22 indicate that the spring cohort required only a span of 14 days (April 13-27) to develop from egg to CIV. This interval is very brief in comparison to the 87 day period required for the winter cohort to achieve the same amount of development (Appendix Table 22).

A most notable feature of the spring cohort data depicted in Figure 22 is the failure of the population to develop beyond the CIV instar. It is doubtful that mortality accounted for the virtual 100% absence of CV copepodites following the peak density of 33.3 per liter observed for CIV organisms on 27 April. Most likely, a large portion of the *Cyclops* population entered diapause and dropped out of the water column to the reservoir bottom. The fate of these organisms is unknown as no noticeable fluctuations in any one particular instar were observed throughout the summer of 1977 and total copepodite density remained low (Figure 22). A gradual increase in egg crop and copepodite density was found to commence in September of 1977 and continued to increase until the last sampling date (7 October). This fall pulse probably initiated the next winter cohort.

Mesocyclops edax. This species was the largest copepod species found in the Tongue River Reservoir, mature females averaged 1.46 mm in length and ranged up to 1.55 mm (Table 10). As is depicted in Figure 24 (top panel) the species was essentially monacmic, attaining a peak copepodite density of 93.2 per liter on 26 August 1977 (Appendix Table 35). *Mesocyclops* was virtually absent from samples collected during the winter (November through March).

Data presented in Figure 25 indicate that the 1976 population entered the winter in the CIV instar. Adults and young instars (CI-CIII) were present in the fall 1976 population (Figure 25) yet their densities were quite low relative to the CIV instar (Figure 24). Little or no egg production was noted in October of either year. It is likely that the population overwintered as diapausing CIV stages since this instar was the first to appear in significant numbers in the early spring; 2.0 per liter were noted on 13 April 1977. Since a small number ($0.6 \cdot l^{-1}$) of adult females also appeared on this date it is possible that either a portion of the population entered diapause as adults in the fall or that a small percentage of the diapausing CIV copepodites developed slowly during the winter months. The

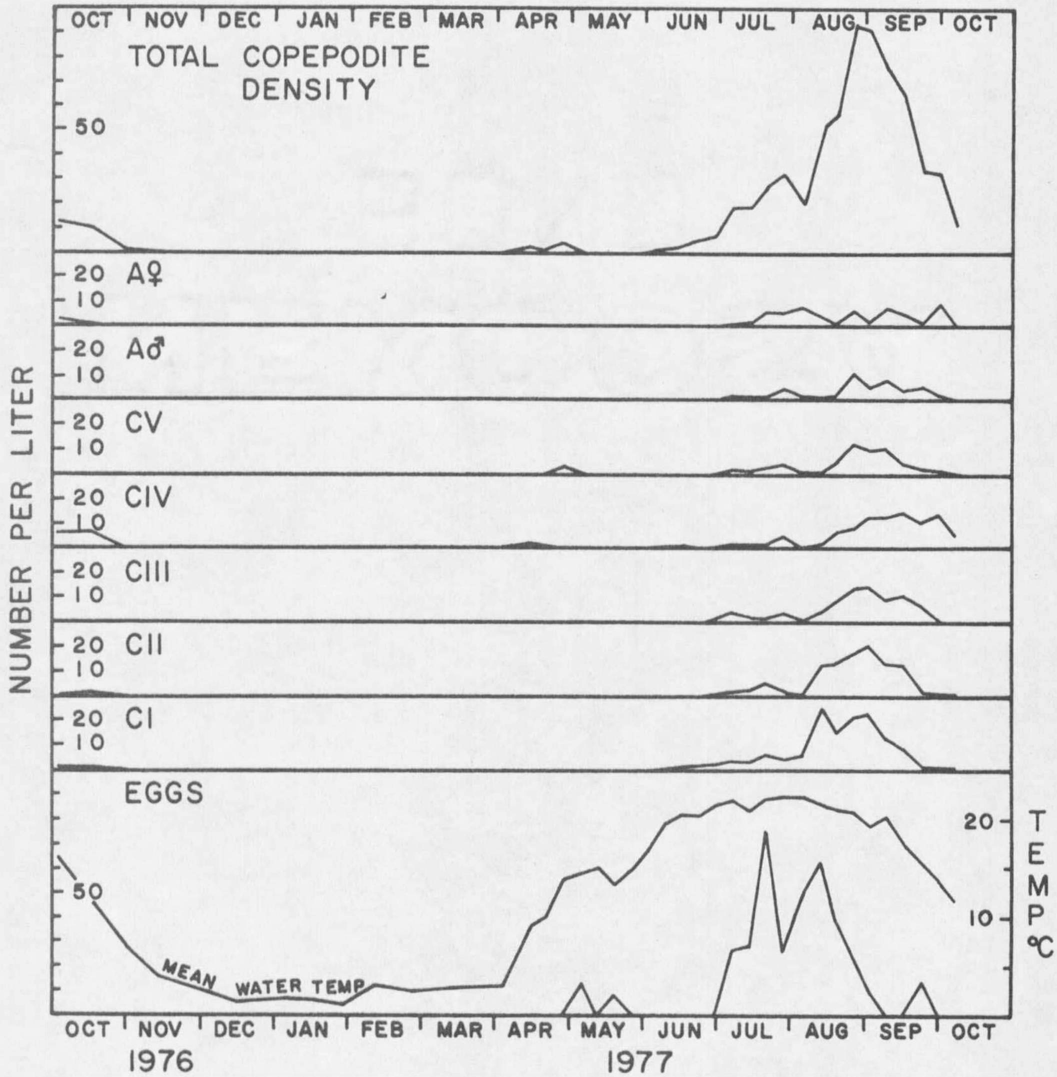

Figure 24. Seasonal abundance of *Mesocyclops edax* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *Top panel*: Total copepodite density ($\# \cdot \ell^{-1}$). *Middle panels*: Density ($\# \cdot \ell^{-1}$) of developmental copepodite instars. *Bottom panel*: Egg density ($\# \cdot \ell^{-1}$) and mean water temperature (°C).

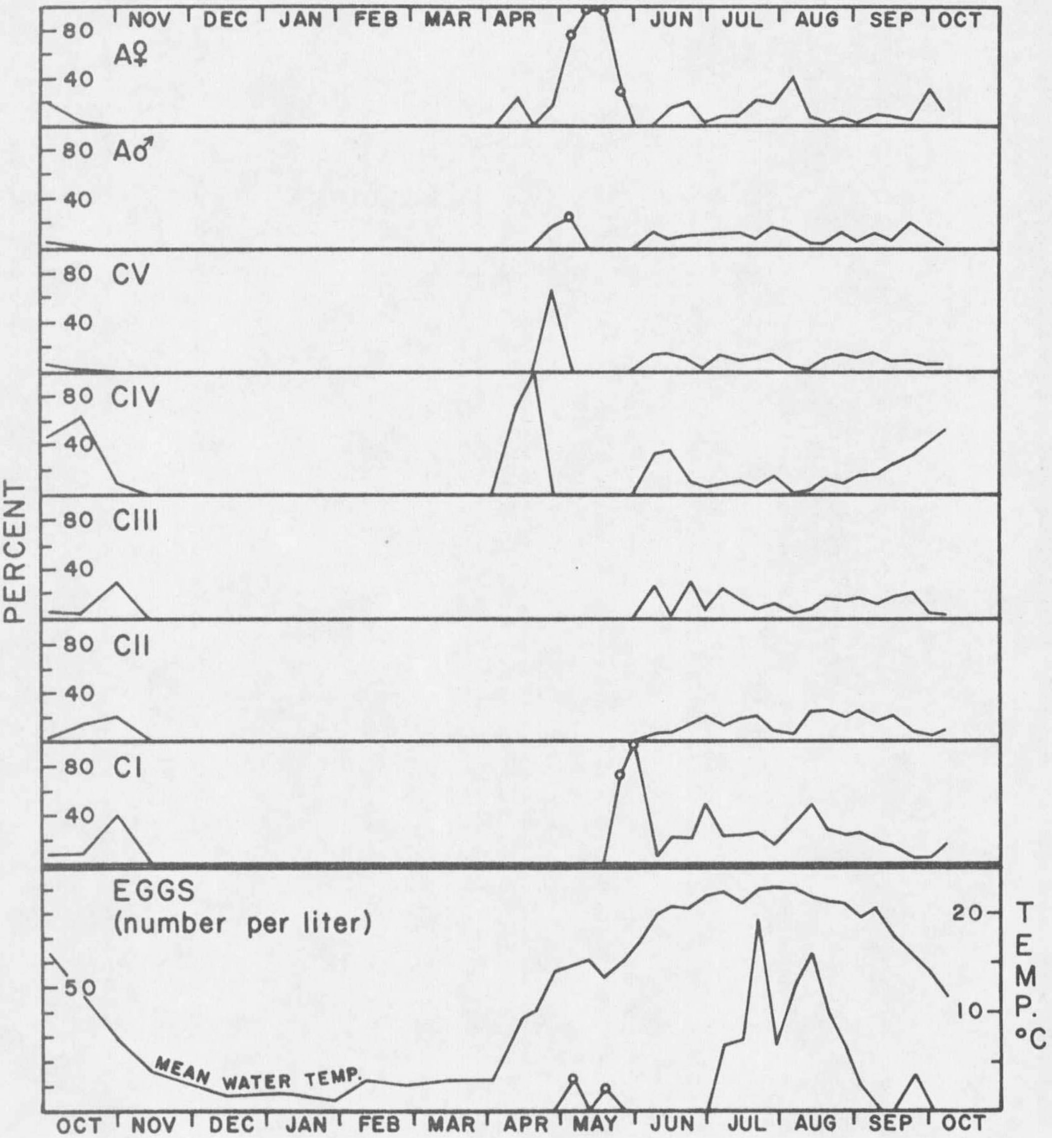

Figure 25. Seasonal abundance of *Mesocyclops edax* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *Top panels*: Percentage composition of developmental copepodite instars. *Bottom panel*: Egg density ($\# \cdot \ell^{-1}$) and mean water temperature (°C). Open circles identify dates when total copepodite density was $<1.0 \cdot \ell^{-1}$.

latter possibility is granted less credence than the former since CIV organisms were observed to appear in the limnetic population two weeks earlier than any CV's were found (Appendix Table 35).

Although actual densities were very low (Figure 24), a clear progression from CIV to adult (CVI) stages during April and May 1977 is illustrated in Figure 25. The very small adult population of less than 1.0 female per liter during late April and early May is responsible for a small amount of egg production during May. This small beginning was apparently sufficient to commence population growth, as total copepodite density continually increased during the ensuing summer months (Figure 24). The population density pulse during August and September resulted from two major peaks in egg production, 76.9 eggs$\cdot l^{-1}$ on 20 July and 64.1 eggs$\cdot l^{-1}$ on 13 August. This diverticulation of summer egg production presumably resulted in the development of two ill-defined summer cohorts (Figures 24 and 25) with the latter achieving greater densities (Figure 24). Examination of successive peaks in instar abundance led the author to believe that in most cases the development time between instars was shorter than the sampling interval of seven days. Hence, literature values for instar durations (Appendix Table 21) were employed in the calculation of *Mesocyclops* production.

The population became increasingly comprised of CIV organisms during September and October 1977 as mean water temperature declined

(Figure 25). On the last sampling date, CIV copepodites comprised 51.4% of the population and were apparently still increasing in importance. CI and CII instars which originated from a minor egg crop on 24 September 1977 exhibited small percentage increases on the last sampling date (Figure 25) although actual numbers were quite low (Figure 24). These results correspond closely with those of the previous fall and tend to support the hypothesis that the population overwinters primarily as fourth instar copepodites.

Diaptomus siciloides. This calanoid copepod species was found to be nearly equivalent to an average to *Cyclops* in length (Table 10). As was typical of all limnetic crustaceans, sexual dimorphism was marked with females being larger than males.

Diaptomus was a perennial species which seldom achieved densities comparable in magnitude to the other principal copepod species. Peak copepodite density for the species was 16.0 per liter observed on 29 June 1977 (Figure 26). Densities were below 10.0 per liter on 32 of 39 sampling dates although with only one exception (11 May 1977) copepodites of the species were present in detectable numbers (Appendix Table 36).

One striking feature of the *Diaptomus* population was the predominance of adults during the winter months (Figure 26). During the six month period November 1976 through April 1977, adults comprised an

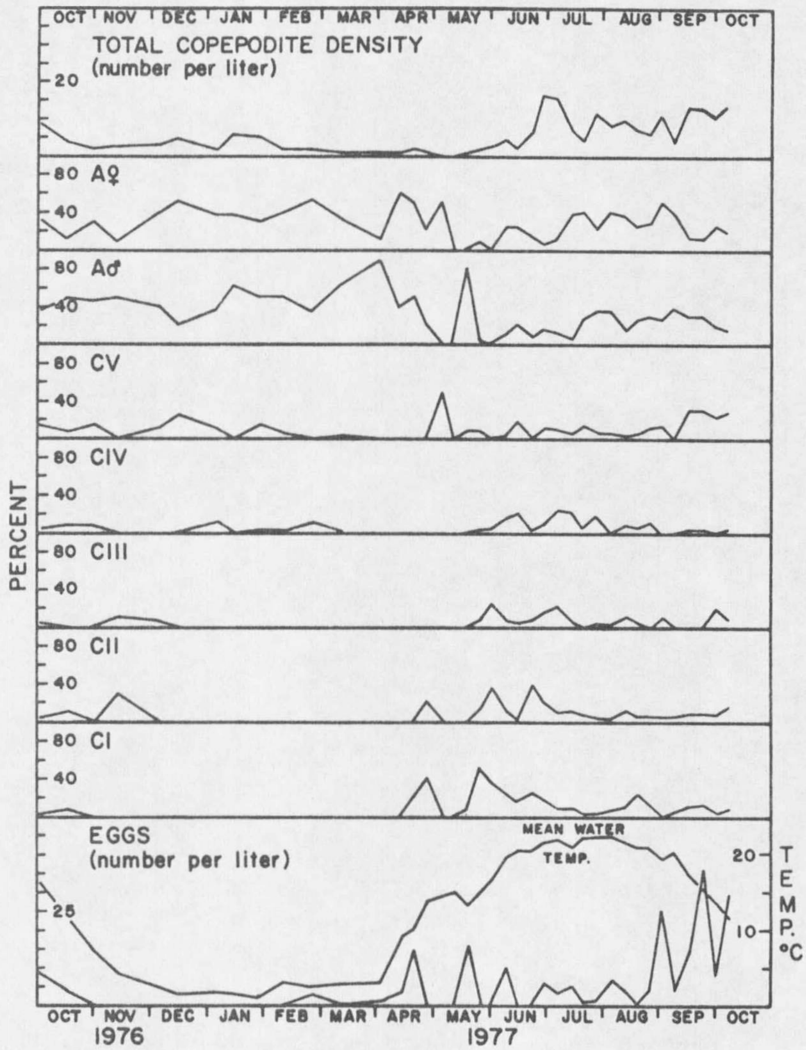

Figure 26. Seasonal abundance of *Diaptomus siciloides* at Station 2 of the Tongue River Reservoir during 1976 and 1977. *Top panel:* Total copepodite density ($\# \cdot \ell^{-1}$). *Middle panels:* Percentage composition of developmental copepodite instars. *Bottom panel:* Egg density ($\# \cdot \ell^{-1}$) and mean water temperature (°C).

average of 82.9% of the population and constituted 100% of the population on four of the 14 dates sampled. The three youngest instars were absent from the population for four to five months during the winter. The absence of younger instars in the winter population is consistent with the finding that egg production was virtually nil during the same timespan.

Production of Limnetic Crustacean Zooplankton at Station 2

Cladoceran and copepod species respectively comprised 53 and 47 percent of the estimated total annual production of 182.9 $g \cdot m^{-2}$ dry weight at Station 2 during the period 2 October 1976 to 7 October 1977 (Table 11). Data presented in Figure 27 reveal that during most of the study period cladoceran production exceeded that of copepods and that little production by either group occurred during the five month period extending between November and March. Due to the development of a previously described phenomenal spring cohort, *Cyclops* production during the month of April 1977 amounted to 38.2 $g \cdot m^{-2}$. This represents 81% of the total annual *Cyclops* production and 44.5% of the combined annual production of all copepod species. Based on the strength of this cohort, *Cyclops* ranked first in production followed by *Daphnia g. mendotae* and *Mesocyclops* (Table 11).

Production estimates are useful in describing the structure of plankton communities because their calculation incorporates estimates

Table 11. Total annual production ($g \cdot m^{-2}$ dry weight) of the principal crustacean zooplankton species at Station 2 of the Tongue River Reservoir during the period 2 Oct 1976 - 7 Oct 1977.

Cladocera Species	Production	Copepoda Species	Production
Daphnia g. mendotae	39.5	*Cyclops b. thomasi*	47.4
Daphnia parvula	10.7	*Mesocyclops edax*	32.2
Ceriodaphnia reticulata	23.7	*Diaptomus siciloides*	6.1
Bosmina longirostris	23.4		
All Cladocera	97.2	All Copepoda	85.7

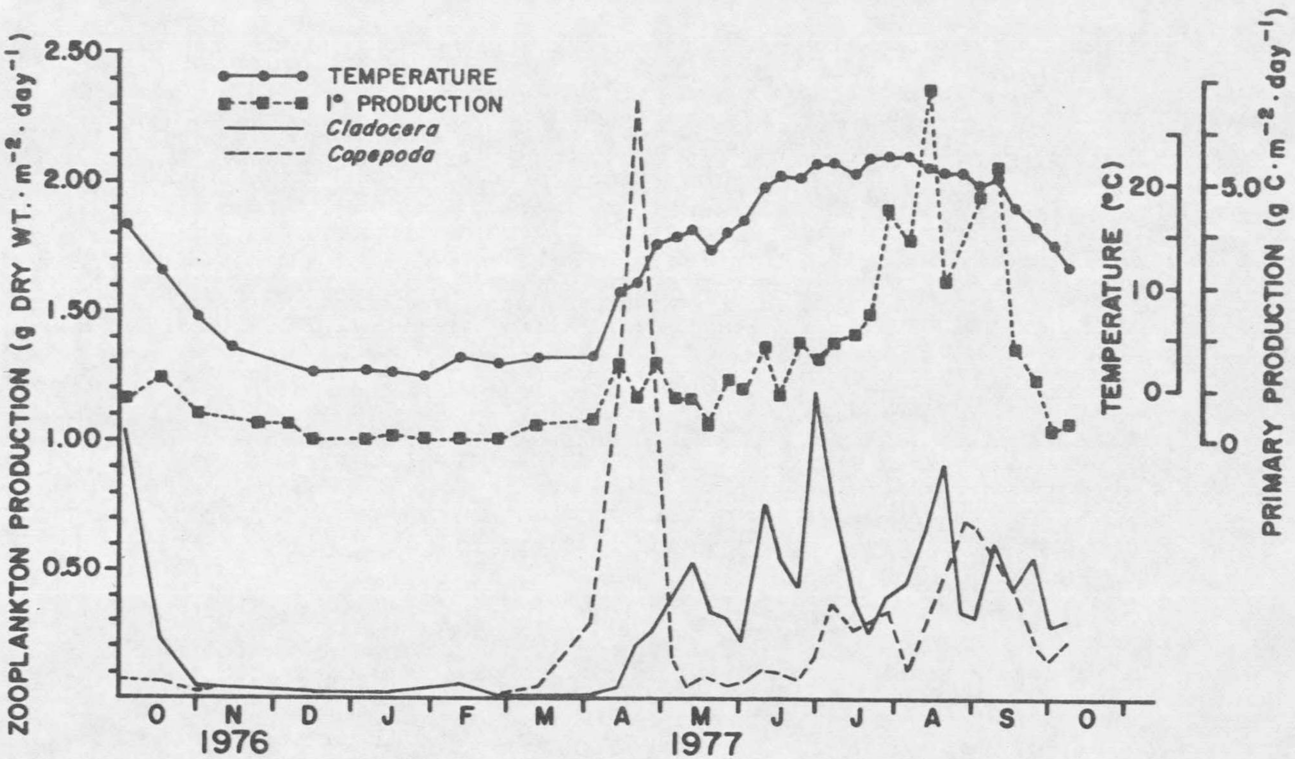

Figure 27. Seasonal trends in production of Cladocera and Copepoda (g dry wt·m^{-2}·day^{-1}) and in primary production (gC·m^{-2}·day^{-1}) and temperature (°C) at Station 2 of the Tongue River Reservoir, 2 Oct 1976 - 7 Oct 1977.

of species density, biomass, and growth rate. Data presented in Table 12 illustrate the relationship between various descriptors of species importance within the limnetic crustacean zooplankton community.

If one were to weigh the importance of a species within this community based solely on density, *Bosmina* would be ranked first since this species achieved an average annual density of 40.4 per liter (Table 12). The second and third most numerous organisms were *Cyclops* and *Ceriodaphnia* with average annual densities of 29.2 and 23.2 per liter. The cladocerans were more numerous than copepods on an annual basis, accounting for an average density of 85.3 per liter as opposed to 51.9 per liter for copepods (Table 12).

The above situation is nearly reversed if one rates species importance based solely on average annual biomass. Copepods account for nearly double the average standing crop (3.25 $g \cdot m^{-2}$ dry weight) than that noted for cladoceran species (1.71 $g \cdot m^{-2}$; Table 12). Using the biomass criterion the copepods *Cyclops* and *Mesocyclops* are ranked first and second, followed by the largest cladoceran, *Daphnia g. mendotae*. The small cladocerans *Bosmina* and *Ceriodaphnia* rank fifth and sixth respectively.

Rankings based on production estimates tend to strike the median between rankings based on density and those based on biomass. Production based rankings agree with biomass and density ratings on two

Table 12. Relative contribution of the principal crustacean zooplankton to average annual density, biomass, and production at Station 2 of the Tongue River Reservoir, 2 October 1976 - 7 October 1977.

Species		(D) Density $(\#\cdot \ell^{-1})$	(B) Biomass $(g\cdot m^{-2})$	(P) Production $(g\ m^{-2}\cdot day)$		P/B $(\cdot day^{-1})$	Turnover (B/P ; days)	Rank D	Rank B	Rank P
Cyclops		29.2	1.56	0.128		0.08	12.1	2	1	1
Mesocyclops		17.4	1.16	0.087		0.07	13.4	4	2	3
Diaptomus		5.3	0.53	0.016		0.0	31.3	7	4	7
All Copepoda	Σ	51.9	3.25	0.231	$\overline{X}$	0.07	14.1			
Daphnia g. mendotae		12.6	0.74	0.106		0.14	6.9	5	3	2
Daphnia parvula		9.1	0.26	0.029		0.11	9.1	6	7	6
Ceriodaphnia		23.2	0.32	0.064		0.20	4.9	3	6	4
Bosmina		40.4	0.39	0.063		0.16	6.3	1	5	5
All Cladocera	Σ	85.3	1.71	0.262	$\overline{X}$	0.15	6.5			

occasions each whereas biomass and density rankings never occur (Table 12).

Tongue River Reservoir copepods were relatively slow growing and displayed an average turnover time of 14.1 days versus 6.5 days for the Cladocera (Table 12). Geer (1977) observed an average annual turnover time of 20 days for *Cyclops bicuspidatus thomasi* as opposed to an average of 2.0 days for the four principal cladocerans. Wright (unpub.) calculated an average turnover time of 65 days for *Cyclops bicuspidatus thomasi* versus times of 6.7 and 10.0 days for two *Daphnia* species (Wright 1965). Examination of the results of several production studies tabulated by Wetzel (1975) reveals that in a given body of water cladoceran turnover times are shorter than those of copepods.

The relationships between primary production, mean water temperature, and the production of the limnetic Cladocera and Copepoda are depicted in Figure 27. Primary production was estimated using Equation (2) from Whalen (1979) which employs measures of algal standing crop (chlorophyll *a*), mean euphotic zone temperature, and extinction coefficient.

Cladoceran production and biomass correlated more strongly with mean water temperature than with algal standing crop or primary production (Table 13). Significant correlations were observed between cladoceran production and algal production and also between copepod biomass and algal standing crop and production.

Table 13. Simple correlation coefficients describing the relationship between standing crop and production of crustacean zooplankton and mean water temperature, algal standing crop, and primary production for 39 dates at Station 2 of the Tongue River Reservoir. Asterisks indicate significance at .05 level.

	Water temp.	Chlorophyll α	Primary production
Production			
Cladocera	.76 *	.23	.41 *
Copepoda	.16	.28	.25
Biomass			
Cladocera	.54 *	-.04	.11
Copepoda	.28	.43 *	.44 *

However, the associated coefficients of variation were less than 0.20; variations in algal standing stocks and production explained less than 20 percent of the variation in zooplankton production or biomass. George and Edwards (1974) were unable to obtain a significant positive correlation between *Daphnia* population size and chlorophyll *a* but did obtain a significant negative correlation ($p<.01$, $r>.40$) between *Daphnia* population size and the amount of food available per individual. They suggested the incorporation of a lag factor in the regressions. The introduction of one and two-week lags into the Tongue data did not significantly alter the results, nor did the use of multiple regression analysis.

Flushing Loss of Crustacean Zooplankton from the Reservoir

Seasonal density trends of the principal Cladocera at Station 1 and in the reservoir outflow during the spring and summer of 1977 are presented in Figure 28. Outflow density trends of *Ceriodaphnia reticulata* and *Bosmina longirostris* closely approximated patterns observed at Station 1. The percentage difference between station means for these two species were 20.4 and 23.3 percent respectively (Table 14). Although the percent difference between average *Daphnia* spp. density at the two stations was large (77%, Table 14), peaks in outflow density did correspond with Station 1 peaks (Figure 28).

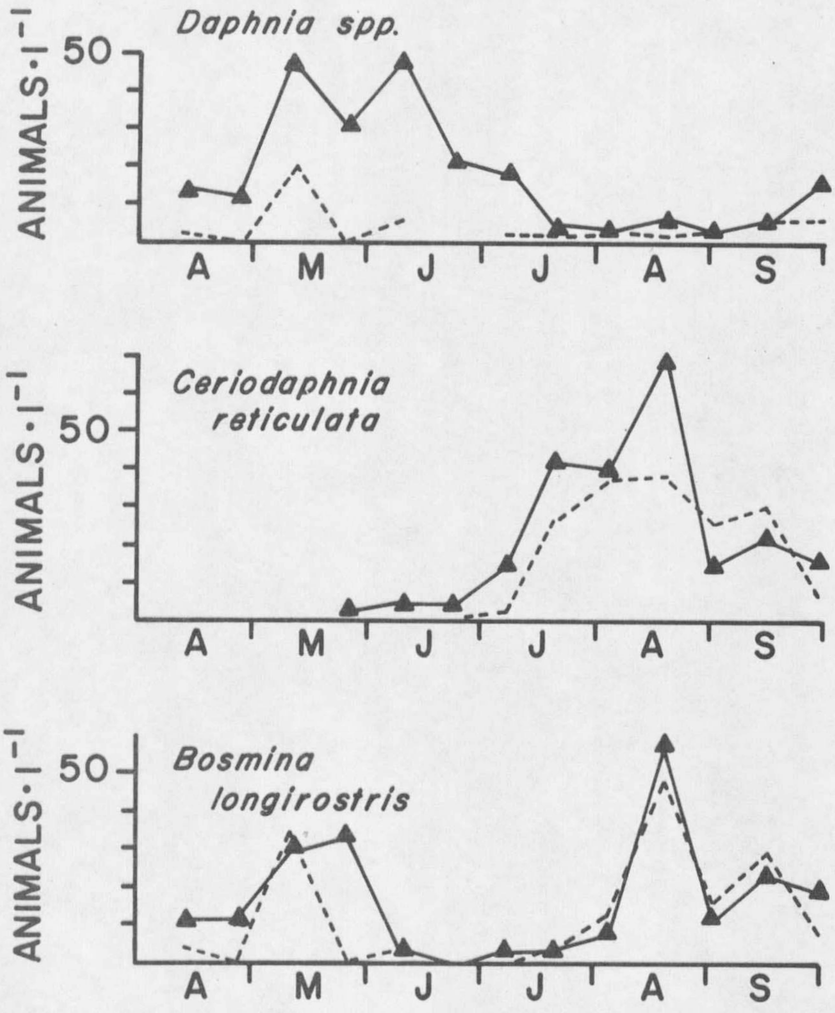

Figure 28. Seasonal density trends (number per liter) of the principal Cladocera at Station 1 (triangles connected by solid line) and in the outflowing waters (dotted line) of the Tongue River Reservoir during the spring and summer of 1977.

Table 14. Mean density (number per liter) and percent difference of principal crustacean zooplankton at Station 1 and in the outflowing waters of the Tongue River Reservoir for 13 dates between 13 April and 1 October 1977.

	Station 1	Outflow	% difference
Daphnia spp.	17.8	4.1	77.0
Ceriodaphnia reticulata	17.6	14.0	20.4
Bosmina longirostris	16.7	12.8	23.3
All Cladocera	54.2	30.9	43.0
Cyclops b. thomasi	36.5	18.9	48.2
Mesocyclops edax	16.2	7.7	52.5
Diaptomus siciloides	2.5	0.9	64.0
All Copepoda	58.7	27.4	53.3

Seasonal trends in outflow copepod densities closely paralleled density changes at Station 1 (Figure 29). As was found for Cladocera, the average copepod density in outflowing waters was less than that of Station 1 (Table 14). The difference between copepod density at the two stations was larger (53.3%) than that observed for Cladocera (43.0%; Table 14).

Cowell (1967) found that periodic sampling of the discharge from a re-regulating reservoir accurately represented the zooplankton community within the reservoir. He noted however that during much of the year the retention time of the reservoir was only eight to ten days. Brook and Woodward (1956) concluded that retention time must exceed 18 days in order to achieve zooplankton community development and Johnson (1964) observed zooplankton standing crop to decline at an accelerated pace if mean flushing time was less than 15 days. Hence, Cowell (1967) was essentially sampling the discharge of the larger upstream reservoir.

Mean monthly retention time in the Tongue River Reservoir was lowest in June of both 1976 and 1977 (Appendix Table 19). The mean time of 22 days in June 1976 and 19 days in June of 1977 are close to the critical values cited above. Data presented in Figures 11, 12, 14, and 15 reveal that the predominant plankter during June at Stations 1 and 2 was *Daphnia*. Consequently, one would expect this organism to be most impacted by short reservoir retention time. However,

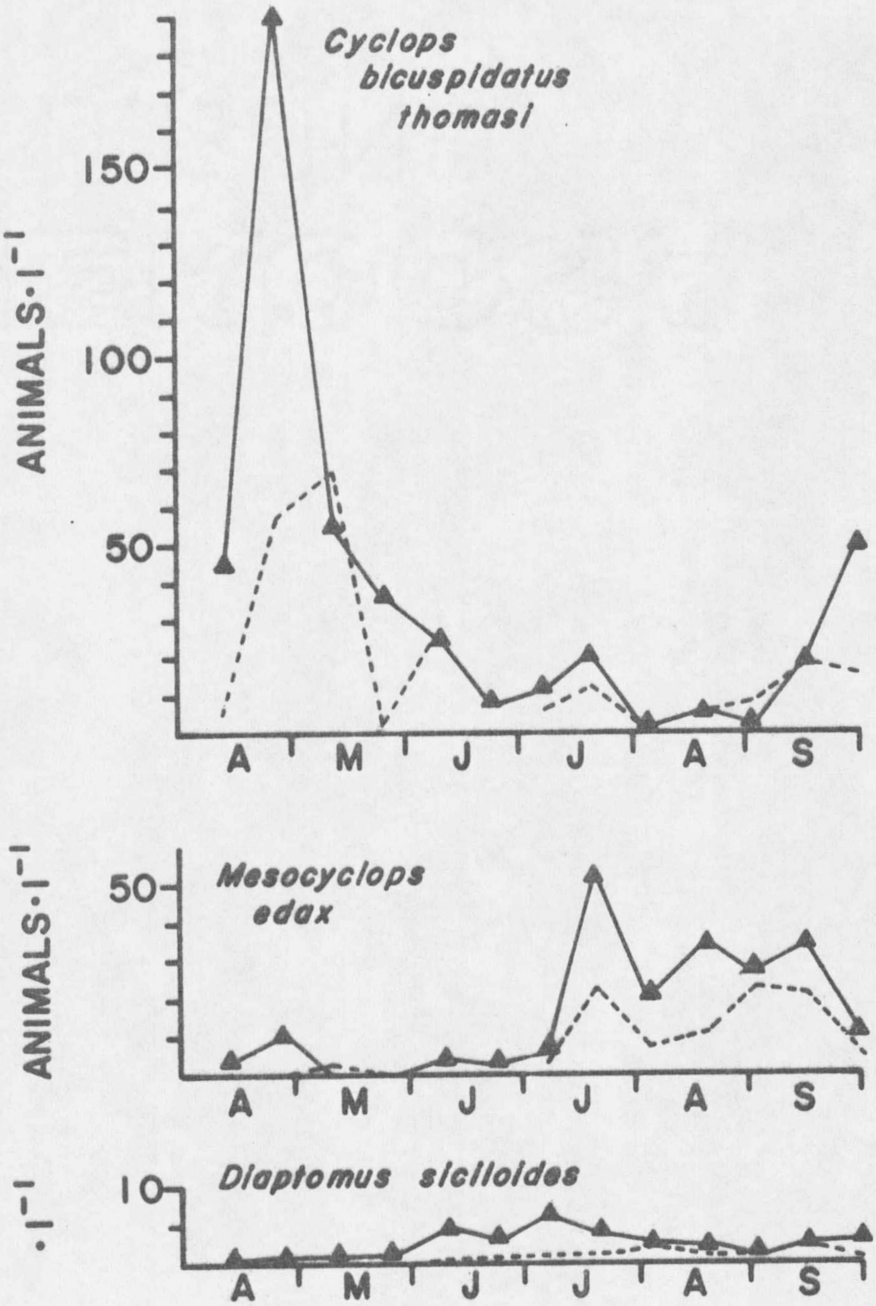

Figure 29. Seasonal density trends (number per liter) of the principal Copepoda at Station 1 (triangles connected by solid line) and in the outflowing waters (dotted line) of the Tongue River Reservoir during the spring and summer of 1977.

outflow *Daphnia* concentration was substantially lower than corresponding density at Station 1 (Figure 28; Table 14).

It is believed that *Daphnia* as well as the other crustacean zooplankton species are under represented in the outflow because discharge waters are withdrawn from the bottom of the reservoir. On 30 May and 11 June 1976, daytime *D. g. mendotae* densities within the euphotic zone were twice as high as total water column concentrations. As a result, fewer *Daphnia* than expected were flushed from the reservoir.

DISCUSSION

The composition of the Tongue River Reservoir limnetic crustacean zooplankton community conforms rather well with the findings of other researchers. Pennak (1957) found that on a given sampling date in a "typical" lake one would expect to find that 80% of the copepods present would belong to a single species. The average was 79.4% for 39 dates at Station 2 of the Tongue River Reservoir.

Momentarily, a typical lake is expected to have 78% of total cladoceran density comprised of one species (Pennak 1957). Patalas (1964) observed altitudinal variation in this percentage and found that non-alkaline plains lakes displayed a lower percentage (63.5%) than did montane and alpine lakes (>80%). Momentarily at Station 2 of the Tongue River Reservoir, 64% of the cladocerans present were of a single dominant species.

Momentarily, limnetic communities typically are comprised of one or two copepod species and one to three cladoceran species (Pennak 1957). However, the average number of species present appears to be inversely correlated with lake elevation (Patalas 1964). An average of 3.8 cladoceran and 3.0 copepod species for a total of 6.8 crustacean species was calculated for 39 dates at Station 2 of the Tongue River Reservoir. In non-alkaline plains lakes in Colorado, Patalas (1964) encountered an average of 6.5 crustacean species on a given date as opposed to 2.6 species in alpine lakes.

The species assemblage of the Tongue River Reservoir limnetic community was virtually identical to that reported by Patalas (1964) for non-alkaline plains lakes in Colorado. Three of the principal Tongue species (*Daphnia parvula, Diaptomus siciloides* and *Mesocyclops edax*) were characteristically found in such lakes in Colorado. Evidently the lower elevation of the Tongue (1043 m) than the Colorado plains lakes (1480-1700) is compensated by its more northerly location.

A substantial amount of information concerning the zooplankton communities of five lakes and reservoirs at various elevations in the upper Missouri River basin as well as one (Georgetown Lake) west of the Continental Divide in Montana has been published (Table 15). Some interesting trends in the species composition of the limnetic crustacean zooplankton communities of upper Missouri lakes and reservoirs are apparent.

The crustacean plankton community of Yellowstone Lake was dominated by two *Diaptomus* species, one of which (*Diaptomus shoshone*) was characteristic of Colorado alpine lakes (Patalas 1964). *Daphnia schodleri* was present in very small numbers in Yellowstone. This situation is reversed in the three other reservoirs in the uppermost Missouri River drainage. In Hebgen Lake, *Daphnia schodleri* and *Daphnia g. mendotae* were the dominant plankters, outnumbering *Diaptomus nudus* and *Diaptomus letopus* by a factor of three. These two Hebgen Lake diaptomids were typically found in montane lakes of Colorado (Patalas

Table 15. Synopsis of several lake and reservoir investigations conducted in and around the upper Missouri River basin.

Lake/Reservoir	Elevation (m)	Mean primary production ($gC \cdot m^{-2} \cdot day^{-1}$)	Study period	Author
Yellowstone L.	2358	0.14	Jun-Oct	Knight (1975)
Hebgen R.	1991	0.26	Jun-Sept	Martin (1967)
Georgetown L.	1958	0.52	Jan-Nov	Geer (1977)
Clark Canyon R.	1689	?	Jan-Dec	Berg (1974)
Canyon Ferry R.	1157	0.50	May-Sept	Martin (1975)
				Wright (1965)
				Wright (1958)
				Wright (unpub)
Bighorn R.	1110	1.00	May-Oct	Horpestad (1977)
Tongue River R.	1043	1.28	Oct-Oct	This study

1964). In Clark Canyon Reservoir, average *Daphnia schodleri* density was an order of magnitude higher than *Diaptomus* spp. In Canyon Ferry Reservoir, *Daphnia schodleri* and *Daphnia g. mendotae* also significantly outnumbered *Diaptomus letopus*.

Data presented in Table 15 indicate that there is a primary production gradient in addition to an elevational gradient as one proceeds from the oligotrophic Yellowstone Lake to the slightly eutrophic (Rada 1974) Canyon Ferry Reservoir. Among this gradient *Diaptomus* is replaced by *Daphnia* as the dominant herbivore. McNaught (1975) suggested that *Diaptomus* is competitively superior in oligotrophic situations because it is a nannoplankton specialist which exhibits a significantly higher ingestion efficiency than *Daphnia* at low food particle concentrations. He called *Daphnia* a "generalist" which can ingest nannoplankton and netplankton with equal efficiency whereas *Diaptomus* was three times more efficient on nannoplankton than netplankton. The ecological consequence of such adaption, however, is a lowered *Diaptomus* reproductive potential (McNaught 1975) and consequent higher turnover time (Table 12).

Concommitant to the decline in the relative importance of *Diaptomus* there appears to be a compensatory increase in the proportion of *Cyclops b. thomasi* in the crustacean communities of these lakes. *C. b. thomasi* represented less than one percent of the copepods in Yellowstone Lake. In Hebgen it was substantially outnumbered by *Diaptomus* but was found to sustain limited numbers at every station throughout the season. In Clark Canyon, *C. b. thomasi* outnumbered *Diaptomus* but was still subordinate to *Daphnia.* In Canyon Ferry however, *C. b. thomasi* was the most abundant plankter, outnumbering *Daphnia* and *Diaptomus* (Martin 1975). It is unclear why *C. b. thomasi* was sparsely represented in Yellowstone and Hebgen Lakes; in Colorado this species maintained sizeable populations in alpine and deep montane lakes (Patalas 1964). In Montana it appears as though *C. b. thomasi* abundance is inversely related to lake elevation and productivity.

Georgetown Lake has not been included in the above discussion because it is not similar to the uppermost Missouri basin lakes. Georgetown is considered to be eutrophic because of periodic algal blooms, dense stands of aquatic macrophytes and occasional winter fish kills as a result of oxygen depletion (Geer 1977). This lake was found to support moderate phytoplankton production, but it was felt that macrophyte production was the major factor in regulating lake metabolism (Knight et al. 1976).

Of those listed in Table 15, the more productive reservoirs (Tongue River, Georgetown, and Canyon Ferry) support sizeable populations of *C. b. thomasi.* Armitage (1961) concisely reviewed a large amount of literature concerning the seasonal abundance patterns of this species in various lakes and concluded that is is a cold water species. He observed that the seasonal distribution of *C. b. thomasi* shifts towards winter and early spring in lakes having summer temperatures above 15°C and the species tends to be perennial in lakes having water temperatures not in excess of 18°C. In the Tongue River Reservoir, the *C. b. thomasi* population peaked dramatically in April (Figure 22) when mean monthly water temperature was 9.2°C then declined to low summer population levels in May when mean monthly water temperature was 14.7°C. The population did not increase substantially during the summer until 24 September 1977 when mean water temperature (15.6°C) was the lowest since 25 May. Mean water temperature during July and August averaged 21.8°C and means ranged between 20.9 and 22.5°C.

It is difficult to accurately compare the life cycle of *C. b. thomasi* in the Tongue River Reservoir with other published studies since winter sampling was seldom conducted by other researchers. In spite of some data gaps, it appears as though the wide variation in the life cycle of this species is closely related to the critical temperatures presented by Armitage (1961).

The life cycle of *C. b. thomasi* as determined in four different studies (Carter 1974; McQueen 1969; Armitage and Tash 1967; Andrews 1953) is sufficiently similar hence they will be lumped together. In these lakes and ponds the cycle is quite simple. Overwintering CIV copepodites mature in early spring and produce an egg crop which initiates a spring cohort. This spring cohort takes approximately

2 1/2-4 weeks to develop to the CIV instar at which time they initiate diapause and drop to the bottom. These organisms stay on the bottom in either an encysted (McQueen 1969) or free swimming form (Watson and Smallman 1971) throughout the summer and fall. The date at which diapause is broken seems to be quite variable. Armitage and Tash (1967) found that diapause was terminated over the prolonged interval October through January, Andrews (1953) believed that it occurred after December. Carter (1974) and McQueen (1969) believed that diapause was broken during or shortly after spring iceout. Once diapause is broken these CIV organisms mature at a pace consonant with ambient water temperature and produce eggs which initiate the spring cohort and thus complete the cycle.

Summer water temperatures in three of the above lakes and ponds are quite high. Carter (1974) reported surface temperatures in the shallow beaver pond to range between 20 and 30°C during much of the summer. Andrews (1953) observed a mean water temperature of 24°C in western Lake Erie and mean water temperature was 18°C in May in the Kansas study (Armitage and Tash, 1967). Marion Lake is cooler than the other lakes (Hall and Hyatt, 1974) and the life cycle events of *C. b. thomasi* outlined above begin in early summer and progress through August (McQueen 1969). The life cycle of this species in Marion Lake is abruptly terminated in late summer when high rainfall and a high flushing rate disrupts the limnetic community (McQueen 1969).

The spring portion of the *C. b. thomasi* life cycle in the Tongue River Reservoir is similar to that described above although the time frame is compressed. A tremendous egg crop was noted on 13 April and it took a remarkably short time (14 days) for these eggs to develop to the CIV instar. McQueen (1969) observed that it took 38-45 days for Marion Lake *Cyclops* to achieve this development; Wright (unpub.) found that it took 38-47 days. Most of these CIV organisms in the Tongue entered diapause and descended from the limnetic zone. However, a small number apparently did not and these organisms were able to maintain a small population sustained by low egg production throughout the summer. Population density of these surviving organisms increased in September and a sizeable fall egg crop was produced which initiated a slow developing winter cohort. This cohort was temporarily arrested in the CV instar during February and March after which these organisms matured and produced a massive spring egg crop upon iceout. The fate of these organisms which entered CIV diapause the previous spring is unknown.

Canyon Ferry Reservoir is much cooler than the Tongue River Reservoir, maximum average water temperature seldom exceeds 18°C (Rada 1974). Wright (unpub.) documented three *C. b thomasi* cohorts which developed from peak egg crops in April, June and July. As was found in the Tongue, a large number of CIV organisms of the first cohort in Canyon Ferry entered diapause but it may well represent a smaller percentage of the CIV's present. The June egg crop was larger than the April crop but instar survival was much lower in the second spring cohort. Wright's sampling terminated in August, hence it is difficult to predict winter dynamics, although it is logical to assume that they would resemble those of the Tongue.

Georgetown Lake is cooler yet than Canyon Ferry, maximum surface water temperature seldom exceeds 20°C (Knight et al. 1976) whereas it commonly exceeds 20°C during late summer in Canyon Ferry (Rada 1974). Mean water temperature in Georgetown never exceeded 18°C (Geer 1977). Significant amounts of egg production by *C. b. thomasi* did not occur until June and Geer (1977) identified ten cohorts arising between February and October. It is interesting to note that Geer's data does not show the prominent CIV diapause characteristic of most *C. b. thomasi* populations. The species is clearly perennial in Georgetown Lake and it is noteworthy that the temperature regime agrees extremely well with Armitage's (1961) generalization.

The Tongue River Reservoir is the only body of water presented in Table 15 which supports a population of *Mesocyclops edax*. In fact, this species was not even reported in the above mentioned lakes and reservoirs. *M. edax* is typically a "summer species" of cyclopoid copepod which rises to prominence in limnetic communities of lakes and ponds after populations of *C. b. thomasi* decline to low summer levels (Carter 1974; Comita 1972; Armitage 1961; Tash et al. 1966). In lakes where *M. edax* is common the species typically disappears in mid-autumn. Interestingly, of the lakes and reservoirs in Table 15, the Tongue is the only one that does not support populations of cold water fish species. A plant of more than two million rainbow trout during 1958-60 essentially failed (U.S. Geol. Surv. and Mont. Dept. State Lands 1977).

The life cycle of *M. edax* in the Tongue River Reservoir is remarkably similar to patterns identified in two other bodies of water. In the Tongue as well as in an Ontario beaver pond (Carter 1974) and in a shallow Minnesota lake (Comita 1971), *M. edax* was found to overwinter as diapausing CIV copepodites. Small numbers of CIV copepodites terminate diapause in the spring and mature to adults which produce the eggs that initiate the development of a typically small early summer cohort. Thereafter, two cohorts successively develop, the second of which terminates via the initiation of CIV diapause in late September or during October.

Diaptomus siciloides, the only calanoid copepod species present in the Tongue River Reservoir was found in none of the studies cited in Table 15. It is apparently a plains species restricted to warmer, more productive environments. As mentioned previously it was specific to plains lakes in Colorado (Patalas 1964) and was typically found to be perennial in large shallow Kansas lakes (Armitage 1961). Comita (1972) noted five generations of *D. siciloides* during the growing season of a small shallow Minnesota lake. Interestingly, he concluded that the population overwintered as resting eggs whereas the Tongue River Reservoir population overwintered primarily as later instar copepodites.

Associations between *D. siciloides* and cyclopoid species (particularly *M. edax*) are typical in lowland lakes (Patalas 1964; Comita 1972; Armitage 1961) in spite of the fact that later instars of cyclopoids have repeatedly been identified as significant predators on the nauplii and youngest copepodite instars of diaptomids (McQueen 1969; Confer 1971; Anderson 1970). However, the applicability of laboratory-determined predation rates to naturally occurring populations has been questioned (Carter 1974; Comita 1972).

The relatively low population density of *D. siciloides* in the Tongue River Reservoir is probably attributable to a combination of competitive factors described by McNaught (1975) and the predatory influence of cyclopoid copepods outlined above. This line of reasoning applies particularly well in the attempt to explain the progressive decline in the relative importance of *Diaptomus* spp. in the copepod communities of Yellowstone, Hebgen, Clark Canyon, and Canyon Ferry lakes. *C. b thomasi* becomes a progressively more important component as lake elevation declines, it first achieves dominance in

Clark Canyon Reservoir and becomes overwhelmingly predominant in Canyon Ferry Reservoir. It is interesting to note that maximum summer density (Figure 26) and percent composition (Figure 13) of *D. siciloides* in the Tongue occurred in late June-early July, precisely when community dominance was shifting from *C. b. thomasi* to *M. edax* (Figure 13).

The species assemblage of the Tongue River Reservoir cladoceran community is more typical of lower Missouri River reservoirs (Selgeby 1974; Garlasco et al. 1978; Tash et al. 1966) and small productive lakes and ponds (Lynch 1979; Cummins et al. 1969; Armitage 1961) than it is of the lakes and reservoirs of the uppermost Missouri River basin listed in Table 15.

Daphnia galeata mendotae is a widely distributed cladoceran species which exhibits considerable variation in its abundance patterns in various lakes. In Hebgen Lake it was a late summer species whereas in Canyon Ferry it could be found commonly in almost any summer month although it was most numerous in early summer. In Bull Shoals Reservoir the species was monacmic or diacmic in different years (Applegate and Mullan 1969). The Tongue River Reservoir population was found to be diacmic, reaching peak numbers in May and June followed by a mid-summer decline then increasing again in October. This pattern closely parallels that reported for the same species in a Michigan lake by Hall (1964).

Daphnia parvula is a plains species in Colorado (Patalas 1964) that has not been reported in the upper Missouri lakes and reservoirs listed in Table 15. In the Tongue River Reservoir it appeared in mid-summer and peaked dramatically in the early fall whereas in a shallow Minnesota lake the species peaked in June and maintained significant densities throughout the summer and fall (Comita 1972).

Ceriodaphnia and *Bosmina* populations tend to achieve high densities in productive low-elevation lakes. Neither species was listed in the Hebgen and Yellowstone Lake studies in the upper Missouri basin. *Bosmina* was rarely found in Clark Canyon Reservoir and was infrequently encountered in Canyon Ferry Reservoir, whereas *Ceriodaphnia* was found in neither. Both genera were common in Bighorn Lake and abundant in the Tongue River Reservoir. In Colorado lakes, Patalas (1964) observed two *Ceriodaphnia* species at "unimportant" population levels in montane lakes and found them as dominants in plains lakes. He listed *Bosmina* as a dominant species in montane and plains lakes. The Montana information on these two species suggests that they are primarily plains species although they can achieve high densities in highly productive montane lakes such as Georgetown Lake.

Most studies of the population dynamics of *Ceriodaphnia* spp. has shown this cladoceran to inhabit limnetic communities exclusively in the midsummer and early fall months (Geer 1977; Kwik and Carter 1975; Hall et al. 1970). Typically, populations begin to develop in June when ephippial eggs from the previous autumn begin to hatch. Population development is rapid and density usually peaks in July or August at levels of between 80 and >200 animals per liter. From this point populations decline progressively and females produce resistant ephippial eggs in September and October. Kwik and Carter (1975) concluded that ephippial eggs produced by *C. quadrangula* were pseudosexual since males of the species were never observed. Males were common at the time of ephippial egg production in the Tongue population of *C. reticulata*. Geer (1977) provided no information on the occurrence of *C. reticulata* males in Georgetown Lake.

Bosmina longirostris has been termed a "versatile" animal due to its ability to inhabit many types of habitats in freshwater environments (Kwik and Carter 1975). In the Tongue it was indeed versatile, it was the only cladoceran species which staged a winter population pulse and was also an important species in the spring and fall. The winter pulse may be due in part to the finding that *Bosmina* embryos are more tolerant of low water temperatures than other cladoceran species (Kwik and Carter 1975). This species has been found year around in Kansas lakes (Armitage 1961) although in Georgetown Lake, Montana the species was seldom seen before June and reached maximum density in midsummer before declining to low numbers during the fall (Geer 1977). Fluctuations in the Tongue River Reservoir population during the growing season are similar to those observed in a Minnesota pond by Comita (1972).

Cladoceran production in the Tongue River Reservoir averaged 0.26 $g \cdot m^{-2} \cdot day^{-1}$ dry weight during the one-year period October 1976-October 1977. This is equivalent to 0.11 $gC \cdot m^{-2} \cdot day^{-1}$ if a factor of 0.44 is employed to convert dry weight to weight of carbon (Wright 1965). Average primary production during this timespan was 1.28 $gC \cdot m^{-2} \cdot day^{-1}$, hence cladoceran production represented 8.6% of primary production. Production of the principal cladocerans (*Daphnia g. mendotae* and *Daphnia schodleri*) in Canyon Ferry Reservoir averaged 0.15 $gC \cdot m^{-2} \cdot day^{-1}$ and accounted for 13.5% of gross primary production (Wright 1965). In Hebgen Lake, production of the same two *Daphnia* species averaged 0.11 $gC \cdot m^{-2} \cdot day^{-1}$ which represented 42% of primary production (Martin 1967). Production of Georgetown Lake cladocerans averaged 0.23 $gC \cdot m^{-2} \cdot day^{-1}$, accounting for approximately 44% of primary production (Geer 1977).

Overall crustacean zooplankton production in the Tongue River Reservoir (0.49 $g \cdot m^{-2} \cdot day^{-1}$ or 0.22 $gC \cdot m^{-2}$) represented 17% of primary production. In Canyon Ferry, *Daphnia* spp. and *Cyclops b. thomasi* production averaged 0.19 $gC \cdot m^{-2} \cdot day^{-1}$ which was also 17% of primary production (Wright 1965; Wright unpub.). Georgetown Lake crustacean zooplankton production averaged 0.25 $gC \cdot m^{-2} \cdot day^{-1}$, representing approximately 52% of primary production (Geer 1977).

The reasons behind the unusually high ecological efficiences of Georgetown and Hebgen herbivore communities are unclear. Martin's (1967) methods were identical to those of Wright (1965); those employed by Geer (1977) were similar to those used in this study. It is entirely possible that a significant amount of macrophyte production was unmeasured in Georgetown Lake, however, it is unlikely that the same is true for the Hebgen Lake study.

Average daily crustacean zooplankton production over a one-year period in the Tongue River Reservoir (0.49 $g \cdot m^{-2} \cdot day^{-1}$) is similar to that of Georgetown Lake (0.57 $g \cdot m^{-2} \cdot day^{-1}$) which was considered to be mildly eutrophic based on comparison with other zooplankton production studies (Geer 1977). Tongue River Reservoir custacean zooplankton production totaled 4.33 $g \cdot m^{-3}$ for the period May through October. This level is similar to that of several mesotrophic and eutrophic reservoirs tabulated in Wetzel (1975).

In view of the fact that zooplankton production methodology is in a state of continual refinement (Bottrell et al. 1976), the trophic status of lakes and reservoirs is best evaluated using more commonly accepted techniques which address nutrient loading rates, primary production, and phytoplankton species composition. Whalen (1979) thoroughly evaluated these parameters and concluded that the Tongue River Reservoir is mildly eutrophic. Apparently the high flushing rate moderates the hypereutrophic tendency of this reservoir.

The classic study of Brooks and Dodson (1965) concerning the impacts of fish predation on the species composition and size structure of limnetic crustacean zooplankton communities prompted vigorous research into the structure of fresh-water zooplankton communities. They proposed the now famous size-efficiency hypothesis which simply states that large zooplankters are more efficient at utilizing fine particulate foods than are small plankters. Hence, size-selective predation on larger forms by fish allows smaller zooplankton to coexist within or even dominate limnetic communities. Recent review (Hall et al. 1976) has supported the basic tenets of the size-efficiency hypothesis with the exception that predation by planktonic invertebrates (such as *Leptodora*, *Chaoborus*, and certain copepods) can benefit large bodied plankters by selectively eliminating smaller bodied organisms. Therefore, the competitive edge attributed to large plankters via their supposed superior efficiency in utilizing the algal food base is also a function of size-selective predation by invertebrates.

Research continues to focus on predation as the dominant factor in shaping the structure of limnetic zooplankton communities (O'Brien 1979; Lynch 1977). This is probably due in part to the fact that predation is a relatively simple pathway to quantify. It has been historically difficult to measure competition (Lynch 1977) especially between planktonic organisms whose natural populations typically undergo frequent violent oscillations.

Three potential invertebrate predators have been identified in the Tongue River Reservoir limnetic ommunity. The later instars of *Cyclops b. thomasi* and especially *Mesocyclops edax* were numerous during the summer months, however, the impact of the latter species on the small cladoceran *Ceriodaphnia* is questionable. Peaks in the Tongue River Reservoir *Ceriodaphnia* population coincided closely with maximum *Mesoclops* copepodite density. Confer (1971) found *Mesocyclops* to prey much more heavily on *Diaptomus* copepodites than on cladocerans. The actual population levels of *Chaoborus* in the Tongue River Reservoir are unknown but it is certain that this organism can exert substantial impact on cladoceran populations. Lynch (1979) observed that *Ceriodpahnia* was replaced by the larger *Daphnia pulex* when *Chaoborus* predation was intense.

White crappie are numerous in the Tongue River Reservoir. In 1975, this species dominated trap and gill net catches and a population of 76.8 fish per acre was estimated (U. S. Geol. Surv. and Mont. Dept. State Lands 1977). O'Brien (1979) identified this species to be the dominant planktivore in an eastern Kansas reservoir. In the Tongue River Reservoir this species was collected in gill nets suspended vertically at the mid-reservoir station in late May and in late July. Analysis of the stomach contents of five of these fish revealed that they had been feeding exclusively on zooplankton. These fish exhibited strong size-selective predation on *Daphnia* larger than 0.75 mm in length. *Daphnia* of this size and larger comprised 74% of the total organisms ingested but less than 3% of the organisms present in the limnetic waters at Station 2.

Size-selective predation by white crappie could substantially impact Tongue populations of *Daphnia g. mendotae* since females of this species did not mature until attaining a minimum length of 1.01 mm. *Daphnia parvula* could be at a selective advantage since females could mature at a length of 0.84 mm. Threlkeld (1979) attributed midsummer *Daphnia* declines to bluegill sunfish predation and noted that a large bodied spring blooming *Daphnia* species was replaced during the summer by a smaller species of the same genus. The same pattern of seasonal abundance and body size was true of Tongue River Reservoir populations of *D. g. mendotae* and *D. parvula*. Yellow perch, noted for their predatory impacts on *Daphnia* populations (Galbraith 1967) were also captured in July gill net sets at Station 2.

The structure of limnetic zooplankton communities is exceedingly complex. Factors such as water temperature and vertebrate and invertebrate predation have demonstrable effects on the population dynamics and life cycles of crustacean zooplankton populations. The influences of factors such as algal species composition and standing crop, and competition between limnetic crustaceans are subtle. Porter (1977) concluded that the impacts of grazers on algal populations can be significant but this influence varies temporally. Gross measures of algal standing crop are seldom strongly correlated with limnetic zooplankton population levels because algal populations are frequently dominated by species which are unpalatable to limnetic herbivores (Porter 1977; Lynch 1977). It has also been found that the competitive abilities of limnetic cladoceran species can shift over very short time periods (i.e. four weeks) and that one or more cladoceran species can alter algal species composition significantly enough to favor other cladoceran species (Lynch 1979).

The impact of man's activities on the dynamics of limnetic crustacean zooplankton communities is complicated by the above factors plus the fact that most species are eurytopic in regards to chemical and physical characteristics of lacustrine environments. This is best illustrated by the finding that the species composition and population dynamics of the Tongue River Reservoir crustacean zooplankton community are remarkably similar to that of Ontario beaver ponds (Carter 1974; Kwik and Carter 1975). The average pH (4.7-5.1) and standard conductance ($28 \cdot \mu mho \cdot cm^{-1}$) of these ponds are markedly lower than corresponding values in the Tongue (pH=8.5, specific conductance=645 $\mu mho \cdot cm^{-1}$; Whalen 1979; Appendix Table 17).

The author strongly suspects that changes in populations of planktivorous fishes in the Tongue River Reservoir would have a more dramatic impact on the crustacean zooplankton community than direct alteration of reservoir water quality via surface coal mining on adjacent lands. Planktivorous fish populations can be directly modified by fisheries management techniques (introductions of new species or enhancement or removal of existing species), and indirectly altered by land use practices and manipulation of reservoir water level. Long-term changes in the crustacean zooplankton communities in the Great Lakes are usually attributed to changes in populations of planktivorous fishes, particularly the alewife (McNaught 1975). Based on the examination of fossilized plant pollen and microcrustacean remnants in the sediments of Frains Lake, Michigan, Kerfoot (1974) concluded that deforestation and agricultural development of the drainage basin 140 years ago accelerated the development of the littoral zone of the lake. This presumably enhanced populations of planktivorous warm water fishes which in turn selectively removed large *Daphnia* species and caused a shift in community dominance to the smaller *Bosmina* and *Ceriodaphnia*.

In view of the fact that present and future mining activities are not expected to noticeably alter reservoir water quality (Whalen 1979), it can safely be said that effects on the zooplankton community will also be minimal. Mercury contamination from upstream sources has been documented in reservoir sediments and in reservoir fish tissues (Phillips 1979) and a study concerning trophic interrelationships in regards to biological magnification of this element will soon be underway (Phillips, personal communication). Present reservoir mercury levels do not appear to be injurious to fish or zooplankton populations; future effects are uncertain.

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APPENDIX

Table 16 . Useable capacity of selected Montana reservoirs

	USEABLE CAPACITY	
	Acre-Feet ($x10^3$)	M^3 ($x10^6$)
Fort Peck	18,910	23,320
Canyon Ferry	2,040	2,520
Bighorn	1,360	1,670
Hebgen Lake	378	470
Gibson	99	122
Lima	84	104
Holter	82	101
Tongue	68	84
Nelson	67	82
Hauser	51	63
Ennis Lake	41	51
Ruby	39	48
Georgetown Lake	31	38
Martinsdale	23	28
Mystic Lake	21	26
Nilan	10	12

Table 17. Ranges and averages of some chemical and physical parameters of the Tongue River Reservoir from November 1975 through November 1976. (From Whalen 1979).

Parameter	Station 1	Station 2	Station 3
Ca^{++} ($me \cdot L^{-1}$)	1.26-3.80 2.86	1.30-4.31 2.79	1.09-3.63 2.81
Mg^{++} ($me \cdot L^{-1}$)	0.96-4.29 2.99	0.84-4.59 2.91	0.79-3.81 2.99
Na^{+} ($me \cdot L^{-1}$)	0.34-1.92 1.25	0.29-22.7 1.23	0.28-2.02 1.26
K^{+} ($me \cdot L^{-1}$)	0.04-0.16 0.10	0.04-0.16 0.10	0.03-0.13 0.10
Total alkalinity ($me \cdot L^{-1}$)	1.92-4.70 3.70	1.68-5.62 3.59	1.56-4.71 3.69
$SO_4^{=}$ ($me \cdot L^{-1}$)	0.81-5.18 3.44	0.66-6.24 3.35	0.54-5.27 3.37
Cl^{-} ($me \cdot L^{-1}$)	0.03-0.12 0.08	0.03-0.13 0.08	0.03-0.12 0.08
SiO_2 ($mg \cdot L^{-1}$)	1.4-11.8 5.6	1.1-10.0 5.7	2.5-13.0 6.8
NH_3-N ($\mu g \cdot L^{-1}$)	0-236 24	0-142 18	0-220 21
NO_3-N ($\mu g \cdot L^{-1}$)	0-204 27	0-187 26	0-47 27
NO_2-N ($\mu g \cdot L^{-1}$)	0-20 3	0-10 3	0-10 3
PO_4-P ($\mu g \cdot L^{-1}$)	0-100 10	0-77 8	0-27 12
Total-P ($\mu g \cdot L^{-1}$)	16-144 40	10-109 41	37-260 71
Spec. cond. ($\mu mhos \cdot cm^{-1}$@25°C)	246-929 660	221-1032 645	197-948 654
pH	7.5-8.9 8.4	7.5-9.0 8.5	7.9-9.0 8.4
Turbidity (JTU)	1.9-24 7.3	1.3-32 8.6	5.5-62 20.3
Temperature (°C)	1.2-23.5 10.6	1.2-23.8 10.9	1.2-23.9 11.4
Dissolved Oxygen ($mg \cdot L^{-1}$)	0.2-13.4 8.5	0.8-19.6 9.3	2.5-17.6 10.1

Table 18. Historical comparison of hydrological data for the Tongue River Reservoir.

	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	AVERAGE
RESERVOIR STORAGE ($m^3 \cdot 10^5$)													
1961-1975													
min.	(12.0)	(50.2)	(88.4)	(121.3)	(203.8)	(279.0)	(279.0)	(331.7)	(567.2)	(439.8)	(203.0)	(126.3)	
max.	(402.1)	(481.4)	(498.6)	(506.5)	(598.6)	(706.6)	(733.4)	(756.2)	(834.5)	(721.3)	(591.6)	(515.3)	
$\bar{x}$	324.2	334.6	349.7	370.1	416.6	484.8	511.6	532.3	635.0	651.3	502.0	371.1	456.9
(AC-FT)	(26,285)	(27,135)	(28,365)	(30,015)	(33,790)	(39,315)	(41,495)	(43,175)	(51,500)	(52,825)	(40,715)	(30,095)	(37,059)
1976	201.3	330.2	426.8	431.7	441.6	529.4	528.2	568.0	711.0	677.9	499.7	348.1	474.5
1977	339.2	384.0	424.3	437.9	459.8	522.4	594.2	704.3	789.1	668.2	426.2	282.3	502.7
OUTFLOW ($m^3 \cdot sec^{-1}$)													
1961-1975													
min.	(2.2)	(1.7)	(2.5)	(2.3)	(1.6)	(0.7)	(3.3)	(5.5)	(11.0)	(8.7)	(6.8)	(3.9)	
max.	(14.4)	(9.8)	(8.3)	(6.7)	(8.2)	(19.1)	(27.1)	(53.6)	(92.3)	(59.0)	(21.7)	(19.5)	
$\bar{x}$	7.4	6.1	5.1	4.8	6.0	8.3	12.8	32.0	54.9	18.9	11.8	9.7	14.3
(CFS)	(264)	(214)	(181)	(168)	(212)	(292)	(452)	(1130)	(1940)	(666)	(416)	(341)	(523)
1976	4.3	1.2	7.2	6.9	6.7	7.3	10.5	20.4	38.0	14.2	13.0	9.5	11.7
1977	6.3	5.2	4.3	4.8	4.6	4.8	16.8	44.0	25.2	14.1	10.8	6.7	12.4
INFLOW ($m^3 \cdot sec^{-1}$)													
1961-1975													
min.	(3.3)	(4.2)	(4.1)	(3.1)	(4.4)	(3.7)	(3.5)	(14.2)	(9.7)	(2.5)	(0.5)	(2.1)	
max.	(11.4)	(9.2)	(7.1)	(9.3)	(19.0)	(24.2)	(163.3)	(55.6)	(89.6)	(23.1)	(13.5)	(17.4)	
$\bar{x}$	7.5	6.8	5.5	5.6	7.8	9.9	22.0	33.7	55.5	13.6	4.7	7.0	14.0
(CFS)	(265)	(241)	(194)	(198)	(274)	(350)	(776)	(1189)	(1960)	(479)	(166)	(246)	(496)
1976	10.3	7.2	7.7	8.2	10.7	10.0	8.6	29.5	42.5	12.9	7.0	5.8	13.1
1977	7.9	6.5	6.2	5.2	6.8	6.9	19.1	47.1	27.0	5.5	4.7	5.1	12.4

Table 19 . Summary of hydrological data for the Tongue River Reservoir for the water years 1976 and 1977.

Year	Month	$\bar{x}$ monthly inflow ($m^3 \cdot sec^{-1}$)	$\bar{x}$ monthly outflow ($m^3 \cdot sec^{-1}$)	$\bar{x}$ monthly outflow ($10^5\ m^3 \cdot day^{-1}$)	$\bar{x}$ monthly storage ($10^5\ m^3$)	Retention time (days)
1976	OCT	7.4	4.3	3.7	201.3	54
	NOV	7.2	1.2	1.1	330.2	300
	DEC	7.7	7.2	6.2	426.8	69
	JAN	8.2	6.9	6.0	431.7	72
	FEB	10.7	6.7	5.8	441.6	76
	MAR	10.0	7.3	6.3	529.4	84
	APR	8.6	10.5	9.1	528.2	58
	MAY	29.5	20.4	17.6	568.0	32
	JUN	42.5	38.0	32.8	711.0	22
	JUL	12.9	14.2	12.3	677.9	55
	AUG	7.0	13.0	11.2	499.7	45
	SEP	5.8	8.5	8.2	398.1	42
	$\bar{x}$	13.1	11.6	10.0	474.5	76
		(463 CFS)	(410 CFS)	(811 AC-FT)	(38,467)	
1977	OCT	7.9	6.3	5.4	339.2	63
	NOV	6.5	5.2	4.5	384.0	85
	DEC	6.2	4.3	3.7	424.3	115
	JAN	5.2	4.8	4.1	437.9	107
	FEB	6.8	4.6	4.0	459.8	115
	MAR	6.9	4.8	4.1	522.4	127
	APR	19.1	16.8	14.5	594.2	41
	MAY	47.1	44.0	38.0	704.3	19
	JUN	27.0	25.2	22.0	789.1	36
	JUL	5.5	14.1	12.2	668.2	55
	AUG	4.7	10.8	9.3	426.2	46
	SEP	5.1	6.7	5.8	282.3	49
	$\bar{x}$	12.3	12.3	10.6	502.7	72
		(434 CFS)	(434 CFS)	(859 AC-FT)	(40,751)	

Table 20. Length-frequency diagram for C1 *Cyclops* and *Mesocyclops* in the Tongue River Reservoir.

	LENGTH (mm)																	DENSITY (animals·l^{-1})	
DATE	0.35	0.36	0.37	0.39	0.40	0.41	0.43	0.44	0.46	0.47	0.48	0.50	0.51	0.52	0.54	0.55	0.57	Σ	*Cyclops*	*Mesocyclops*
-1976-																				
2 Oct		1		3	2							1	1	1				9	12	13
16 Oct		1		1	2	4	3	10	6	2							1	30	55	10
31 Oct				1	1	1	2	5	2						1			13	25	1
13 Nov					1	3	6	1	1									12	67	0
5 Dec			3	2														5	51	0
15 Dec						1	1											2	57	0
-1977-																				
5 Jan				1			1	1	1									4	42	0
15 Jan		1					4	1	1		1							8	26	0
28 Jan						1		2	1		1							5	18	0
11 Feb						1	3	2	4									10	11	0
26 Feb						3	1	1		2								7	9	0
12 Mar								2	1		2			1				6	8	0
3 Apr														1	2	1		4	16	0
13 Apr								1	1	1		1						4	52	3
20 Apr										1	1	1	5	2				10	233	1
27 Apr								2		3	2	3						10	150	4
5 May					1	2	4		1	1	1							10	18	0
11 May							2	1	2	3	1	1						10	16	0
18 May					1	1	1	1	3	1	2							10	17	0
25 May			1	1	1	2	3					1	1					10	11	0
1 Jun					1	1	2	3	2					1				10	16	0
9 Jun			1	1	3	3	1	1										10	20	2
15 Jun		1		2	3	2		1			1							10	17	3
23 Jun		2	4	5	3	3				1	1							19	13	2
29 Jun	2	1			4			1	3	2	2	1	2					18	9	7
6 Jul			2		1	2	1		2	6	3	3						20	15	18
14 Jul		1	1	2	1	1	1		3	5	3	1	1					20	6	19
20 Jul			1		1		1	1	1	2	8	3	2					20	5	28
27 Jul				1	1		1		2	12	3	2			1			23	4	32
5 Aug				2			1				3	7	6		1			20	2	21
13 Aug						3		3	2	5	4	12	7	4				40	6	52
19 Aug									1	1	4	10	6	3				25	9	57
26 Aug						1	1		1	5	1	6	6	3	1			25	6	93
2 Sep							1				1	4	5	5	4			20	5	92
9 Sep								2	1		2	2	4	8	4	3		26	6	76
16 Sep													1	6	4	2		13	8	65
24 Sep				1		2	1	3	2	1	1			1	3	2	2	23	16	34
1 Oct			1		1	2	1	4	3					1	1		2	16	24	33
7 Oct				1	4	8	8	4				1		1	1			28	61	12

CYCLOPS

MESOCYCLOPS

Table 21. Development time (days) for specific life stages of *Mesocyclops edax* and *Diaptomus siciloides*. Data from Carter (1974) and Comita (1972).

	EGG-C1	C1-C2	C2-C3	C3-C4	C4-C5	C5-AD.	TOTAL EGG-AD.
Mesocyclops edax							
Carter (1974)							
$\bar{x}$	—	2.8	2.3	4.1	3.7	—	
(range)		(1.4-3.8)	(1.0-3.8)	(2.6-6.1)	(2.5-4.6)		
Comita (1972)							
$\bar{x}$	16.5	3.5	2.7	2.8	3.1	1.9	30.5
(range)	(12.6-18.6)	(2.8-3.8)	(2.6-2.7)	(2.7-2.9)	(2.6-3.3)	(1.7-2.0)	
Diaptomus siciloides							
Comita (1972)							
$\bar{x}$	13.6	3.0	2.2	2.6	3.2	4.7	29.3
(range)	(9.0-33.0)	(1.7-4.9)	(1.4-2.9)	(1.5-4.3)	(1.8-5.3)	(2.7-7.7)	

Table 22. Development time (days) for specific life stages of *Cyclops bicuspidatus thomasi* in the Tongue River Reservoir, Georgetown Lake (Geer 1977) and Canyon Ferry Reservoir (Wright 1967).

	Temperature range (°C)	EGG-C1	C1-C2	C2-C3	C3-C4	C4-C5	C5-AD.	TOTAL (Days)
This study								
Winter Cohort (Oct 1976-Feb 1977)	(1.0-11.6)	15.0	15.0	14.0	43.0	34.0	75.0	EGG-AD. 196.0
Spring Cohort (Mar 1977-11 May 1977)	(3.0-15.4)	7.0	1.5	1.5	4.0	Diapause		EGG-C4 14.0
Geer (1977)								
Generation 6	(13.5-18.0)	16.0	7.0	7.0	14.0	14.0	21.0	79.0
Generation 7	(13.4-18.0)	14.0	7.0	7.0	12.0	16.0	15.0	71.0
Wright (1967)								
Generation I	?	28.0	6.0	7.0	6.0	7.0	11.0	65.0
Generation II	?	28.0	4.0	3.0	3.0	7.0	7.0	52.0
Average of Geer (1977) and Wright (1967)		21.5	6.0	6.0	8.8	11.0	13.5	66.8

Table 23. Temperature (°C) and dissolved oxygen ($mg \cdot l^{-1}$) content of the inflowing and outflowing waters of the Tongue River Reservoir during 1977.

DATE	INFLOW TEMP	INFLOW D.O.	OUTFLOW TEMP	OUTFLOW D.O.
3 Apr	6.0	13.5	-	-
13 Apr	13.7	9.7	10.0	12.0
20 Apr	11.6	10.4	11.0	11.2
27 Apr	14.3	9.5	11.2	10.9
5 May	10.5	10.2	14.2	9.7
11 May	-	-	16.8	8.8
18 May	11.0	10.1	12.7	9.8
25 May	14.4	8.4	13.1	8.7
1 Jun	20.3	9.1	15.0	9.6
10 Jun	20.2	8.0	17.8	8.6
15 Jun	18.2	8.1	19.9	7.9
22 Jun	23.5	8.3	no discharge	
29 Jun	23.3	9.3	18.8	7.9
6 Jul	22.2	6.9	20.2	9.2
13 Jul	25.7	9.3	21.1	8.8
20 Jul	21.7	5.5	21.7	8.1
27 Jul	-	-	22.4	8.2
4 Aug	-	-	21.7	6.6
13 Aug	20.3	8.2	20.7	6.0
19 Aug	25.0	11.4	22.4	8.4
26 Aug	17.5	8.2	20.5	6.7
2 Sep	23.0	12.0	20.2	6.8
9 Sep	20.2	7.7	17.8	9.1
16 Sep	17.2	8.5	16.0	10.4
24 Sep	10.3	9.0	16.3	8.1
1 Oct	-	-	13.2	9.0

Table 24. Density ($\# \cdot \ell^{-1}$) of rotifer species at Station 2 of the Tongue River Reservoir, 1976 - 1977.

DATE		*Polyarthra*	*Filinia*	*K. cochlearis*	*K. quadrata*	*Asplanchna*	*Brachionus*	*Platyias*	*Ascomorpha*	
1976	2 Oct	14.0		0.7	0.7	0.7			1.4	
	16 Oct	31.5		2.3	2.3	1.2			1.8	
	31 Oct	4.2		0.3	1.4	1.1			14.9	
	13 Nov	1.6		0.3	8.1	2.4			91.7	
	5 Dec	0.2			3.4	1.0			72.8	
	15 Dec			0.7	5.1	1.3			29.3	
1977	5 Jan				4.0	0.7			9.5	
	15 Jan				8.2	1.1			3.6	
	28 Jan	0.2		0.2	12.5	0.2			1.9	
	11 Feb				6.7	0.2			1.3	
	26 Feb	0.3			3.0	0.2			2.7	
	12 Mar	0.1			4.6	0.1			0.8	
	3 Apr	1.9			9.4				20.5	
	13 Apr	7.1			34.4	0.5			105.4	
	20 Apr	7.7		0.7	96.0	1.5	7.0		186.2	
	27 Apr	9.4	0.7	2.2	176.7	4.0	14.5		113.7	
	5 May	3.0		0.6	6.7	5.8	1.8		3.0	
	11 May	1.8			2.0	4.0			13.4	
	18 May	0.8		0.2	0.5	2.2			9.4	
	25 May	2.4			0.2	4.2			31.5	
	1 Jun	4.7		2.4	0.3	3.3	0.2		22.2	
	9 Jun	34.7		0.6	0.2	1.9			13.1	
	15 Jun	92.2	0.3		0.5				0.3	
	23 Jun	185.4		0.7	0.5	0.2			1.7	
	29 Jun	29.1	0.2		3.6	8.0		1.8	3.6	
	6 Jul	24.8	1.1	0.8	4.7	14.1		4.1	11.6	
	14 Jul	38.1			2.3	8.2		1.9	3.5	
	20 Jul	27.8			0.7	5.3		0.2		
	27 Jul	14.6		0.3	3.0	13.2		1.7	1.7	
	5 Aug	6.5			1.1	1.6			1.1	
	13 Aug	15.3			0.9	9.9		1.2	3.3	
	19 Aug	24.9		0.4	1.8	8.1		0.4		
	26 Aug	16.1			1.2	2.1		0.6		
	2 Sep	30.9			1.1	3.0		0.4		
	9 Sep	16.1			0.7	1.8				
	16 Sep	31.1		0.4	0.9	6.6				
	24 Sep	66.7			0.5	7.4				
	1 Oct	67.7			0.5	10.2				
	7 Oct	40.3			1.1	3.3				
$\bar{x}$ (39 dates)		21.9	<1	<1	10.6	3.6	<1	<1	19.9	Σ=57.6

Table 25. Density (number per liter) of the principal Cladocera at Stations I, III and outfow of the Tongue River Reservoir, 1977.

	Daphnia g. mendotae			*Daphnia Parvula*			*Ceriodaphnia*			*Bosmina*		
Date	Out	I	III	Out	I	III	Out	I	III	Out	I	III
13 April	1.4	14.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	3.8	11.9	5.8
27 April	0.0	11.7	1.4	0.0	0.0	0.0	0.0	0.4	0.2	0.3	12.1	32.6
11 May	19.7	47.8	1.2	0.0	0.0	0.0	0.7	0.8	0.0	34.4	29.2	10.1
25 May	0.5	30.6	22.1	0.0	0.0	3.6	0.1	1.6	1.5	0.5	33.7	158.7
9 June	5.9	48.1	25.7	0.0	0.3	15.8	0.9	3.7	8.6	1.4	3.3	30.3
23 June	dry	20.5	31.2	dry	1.2	4.6	dry	3.9	15.7	dry	0.0	5.6
7 July	0.6	16.4	23.0	0.8	1.5	35.8	2.6	13.3	63.5	0.2	3.1	31.8
20 July	0.2	3.4	2.1	1.2	1.0	20.2	25.8	42.1	129.8	1.7	3.4	65.6
4 August	0.3	0.8	0.0	1.7	2.2	14.0	37.2	40.3	414.2	12.2	7.6	156.2
19 August	0.4	1.7	0.0	1.1	3.9	2.8	38.5	69.1	132.2	47.5	58.4	442.7
2 Sept	0.0	0.3	0.2	3.1	2.8	0.2	25.6	15.2	16.3	14.7	12.3	103.4
16 Sept	5.1	1.7	——	1.8	4.6	——	29.8	21.9	——	29.0	23.9	——
1 Oct	3.9	4.2	——	2.1	12.1	——	6.6	15.8	——	8.0	18.8	——

Table 26. Density (copepodites per liter) of the principal Copepoda at Station I,III and outflow of the Tongue River Reservoir, 1977.

	Cyclops b. thomasi			*Mesocyclops edax*			*Diaptomus siciloides*		
Date	Out	I	III	Out	I	III	Out	I	III
13 April	6.2	45.0	3.7	0.0	4.3	0.3	0.8	0.4	0.0
27 April	56.6	191.5	8.2	0.0	10.5	0.0	0.0	0.8	0.2
11 May	68.7	56.2	0.2	2.5	0.5	0.0	0.4	1.1	0.0
25 May	1.4	36.7	18.1	0.0	0.0	0.0	0.0	1.6	0.2
9 June	26.3	24.7	8.8	0.0	4.1	5.5	0.5	4.4	4.5
23 June	dry	7.7	3.6	dry	3.2	3.6	dry	3.2	13.8
7 July	5.7	11.8	10.1	1.4	5.9	46.6	1.0	6.3	12.2
20 July	12.2	21.2	13.3	21.8	54.4	39.8	1.2	3.7	30.7
4 August	1.4	2.4	5.5	7.1	20.6	122.6	2.0	2.8	29.3
19 August	4.5	6.1	9.7	10.8	35.3	61.2	0.7	2.5	7.7
2 Sept	7.8	3.3	7.0	23.3	27.0	9.3	0.4	0.9	0.6
16 Sept	19.4	17.6	—	20.6	33.9	—	2.4	2.5	—
1 Oct	16.4	49.9	—	4.5	11.3	—	0.9	2.7	—

Table 27. Definition of population statistic abbreviations.

N	is the population density (animals per liter).
N_{af}	is the density of adult females (animals per liter).
N_{am}	is the density of adult males (animals per liter).
E_{af}	is mean clutch size (eggs per adult female).
E	is egg density (eggs per liter).
E_p	is ephippial density (ephippia per liter).
D_e	is the duration of egg development (time required for an egg to hatch, days).
B	is the finite birth rate (individuals per individual per day).
b	is the instantaneous birth rate (individuals per individual per day).
d	is the instantaneous death rate (individuals per individual per day).
r	is the instantaneous rate of population increase (individuals per individual per day).

Table 28. Population data for *Bosmina longirostris* at Station 2 of the Tongue River Reservoir, 1976 and 1977.*

Date	N	N_{af}	E_{af}	E	D_e	*B*	*b*	*d*	*r*
1976									
2 Oct	307.3	49.0	1.1	53.9	4.3	.040	.042	.164	-.122
16 Oct	55.8	15.2	1.0	15.2	7.3	.037	.040	.204	-.164
31 Oct	4.8	1.1	1.0	1.1	13.9	.017	.016	-.133	.149
13 Nov	33.3	5.8	1.3	7.5	20.9	.011	.011	——	——
5 Dec	18.9	4.6	1.1	5.1	24.3	.011	.011	.021	-.010
15 Dec	17.1	3.1	1.1	3.4	29.5	.007	.007	——	——
1977									
5 Jan	25.5	9.5	1.0	9.5	28.0	.013	.013	.080	-.067
15 Jan	13.0	4.1	1.0	4.1	30.0	.011	.010	-.090	.100
28 Jan	47.5	17.3	1.0	17.3	35.0	.010	.010	-.021	.031
11 Feb	73.3	22.3	1.0	22.3	24.3	.013	.014	.118	-.104
26 Feb	15.5	1.7	1.0	1.7	25.8	.004	.004	.052	-.048
12 Mar	7.9	1.9	1.1	2.1	24.3	.011	.011	——	——
3 Apr	5.1	2.4	1.9	4.6	23.0	.039	.038	-.002	.040
13 Apr	7.6	2.2	1.9	4.2	10.0	.055	.049	-.178	.227
20 Apr	37.2	8.1	2.9	23.5	8.7	.072	.073	.095	-.022
27 Apr	31.9	2.9	3.9	11.3	5.3	.066	.066	.054	.012
5 May	35.0	8.2	3.8	31.2	4.9	.182	.175	.101	.074
11 May	54.7	4.8	2.2	10.6	4.6	.043	.046	.200	-.154
18 May	18.6	1.6	1.4	2.2	5.8	.021	.020	-.041	.061
25 May	28.5	2.0	1.1	2.2	4.7	.016	.018	.229	-.211
1 Jun	6.5	0.5	1.3	0.7	4.0	.027	.027	.062	-.035
9 Jun	4.9	0.6	1.0	0.6	2.8	.043	.047	.214	-.167
15 Jun	1.8	0	1.0	0		0	0	-.019	.019
23 Jun	2.1	0		0		0	0	-.260	.260
29 Jun	10.0	3.1	1.5	4.7	2.2	.210	.209	.202	.007

Table 28. *Bosmina longirostris.* Continued

Date	N	N_{af}	E_{af}	E	D_e	*B*	*b*	*d*	*r*
6 Jul	10.5	2.2	1.3	2.9	2.2	.126	.133	.242	-.109
14 Jul	4.4	0	1.2	0		0	0	-.031	.031
20 Jul	5.3	1.2	1.1	1.3	2.1	.115	.107	-.044	.151
27 Jul	15.2	2.8	1.0	2.8	2.1	.088	.088	.089	-.001
5 Aug	15.1	7.3	1.3	9.5	2.1	.301	.280	.138	.142
13 Aug	47.1	21.9	1.3	28.5	2.3	.264	.249	.136	.113
19 Aug	92.8	27.0	1.5	40.5	2.4	.183	.192	.293	-.101
26 Aug	45.9	7.6	1.2	9.1	2.5	.081	.081	.080	.001
2 Sep	46.1	15.6	1.6	25.0	2.8	.192	.179	.043	.136
9 Sep	119.6	25.1	1.3	32.6	2.6	.106	.109	.163	-.054
16 Sep	81.9	26.3	1.1	28.9	3.6	.099	.098	.082	.016
24 Sep	93.4	39.1	1.4	54.7	4.5	.132	.137	.209	-.072
1 Oct	56.6	13.5	1.4	18.9	5.5	.061	.059	.004	.055
7 Oct	78.8	4.4	1.1	4.8	7.1	.009	.009	——	——

*Population statistic abbreviations defined in Appendix Table 27.

Table 29. Population data for *Ceriodaphnia reticulata* at Station 2 of the Tongue River Reservoir, 1976 and 1977.*

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	B	b	d	r
1976											
2 Oct	71.4	12.6	0	1.1	13.9	1.4	4.1	.048	.050	.145	-.095
16 Oct	19.0	2.0	3.2	1.3	2.6	2.3	6.6	.021	.022	.137	-.115
31 Oct	3.4	0.3	1.1	1.6	0.5	1.4	12.8	.012	.012	-.053	.065
13 Nov	7.9	0	1.3	2.0	0	3.9		0	0	.086	-.086
5 Dec	1.2		0			0.2				.110	-.110
15 Dec	0.4					0					
1977											
5 Jan	0.2										
15 Jan											
28 Jan	0										
11 Feb											
26 Feb											
12 Mar						0					
3 Apr						1.7					
13 Apr	0					0					
20 Apr	0.7	0			0	0.4		0	0	.080	-.080
27 Apr	0.4	0.4		7.0	2.8	0	4.9	1.434	1.338	1.201	.137
5 May	1.2	0.3		7.0	2.1		4.5	.387	.416	.562	-.146
11 May	0.5	0.3		5.0	1.5		4.2	.709	.700	.674	.026
18 May	0.6	0			0			0	0	-.121	.121
25 May	1.4	0.2		3.3	0.7		4.4	.114	.115	.137	-.022
1 Jun	1.2	0.5		2.4	1.2		3.7	.268	.246	.075	.171
9 Jun	4.7	0.9		1.4	1.3		2.8	.099	.101	.136	-.035
15 Jun	3.8	0.5		1.2	0.6	0	2.6	.062	.060	.009	.051
23 Jun	5.7	0.5		1.3	0.7	0.2	2.6	.048	.041	-.260	.301
29 Jun	34.6	3.1	0	1.7	5.3	0	2.3	.067	.068	.084	-.016

Table 29. *Ceriodaphnia reticulata.* Continued

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	*B*	*b*	*d*	*r*
6 Jul	30.9	8.3	0	1.5	12.5	0	2.3	.180	.179	.165	.014
14 Jul	34.6	5.4	0.2	1.1	5.9	0	2.5	.069	.069	.067	.002
20 Jul	35.0	7.4	0	1.8	13.3	0.2	2.2	.174	.168	.099	.069
27 Jul	56.6	8.8	│	1.3	11.4	0.3	2.2	.093	.093	.089	.004
5 Aug	58.9	21.3	│	1.9	40.5	0	2.2	.318	.310	.262	.048
13 Aug	86.4	27.9	│	1.4	39.1	0	2.3	.194	.188	.128	.060
19 Aug	123.6	22.8	│	1.2	27.4	0	2.4	.092	.099	.238	-.139
26 Aug	46.8	13.1	│	1.4	18.3	0	2.5	.158	.158	.159	-.001
2 Sep	46.5	17.9	│	1.9	34.0	0	2.8	.262	.255	.201	.054
9 Sep	67.7	15.0	0	1.6	24.0	0.4	2.6	.138	.140	.165	-.025
16 Sep	56.9	11.8	0.4	1.7	20.1	0	3.4	.104	.104	.095	.009
24 Sep	61.2	14.3	0	1.6	22.9	0	4.1	.090	.097	.248	-.151
1 Oct	21.3	4.2	5.1	1.7	7.1	0.5	5.0	.067	.067	.069	-.002
7 Oct	21.1	3.7	1.9	1.3	4.8	1.1	6.4	.035	.035	——	——

*Population statistic abbreviations defined in Appendix Table 27.

Table 30. Population data for *Daphnia parvula* at Station 2 of the Tongue River Reservoir, 1976 and 1977.*

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	*B*	*b*	*d*	*r*
1976											
2 Oct	3.5	0	0.7	1.9	0	0		0	0	-.013	.013
16 Oct	4.2	0.9	1.2	3.7	3.3	0	6.6	.120	.124	.197	-.073
31 Oct	1.4	0	0.3	3.0	0	0		0	0	-.010	.010
13 Nov	1.6	0.3	0	2.0	0.6	0.3	21.0	.018	.018	—	—
5 Dec	0	0	0		0	0		0	0		
15 Dec	0	0	0		0	0		0	0		
1977											
5 Jan	0	0	0		0	0		0	0		
15 Jan											
28 Jan											
11 Feb											
26 Feb											
12 Mar											
3 Apr											
13 Apr											
20 Apr											
27 Apr											
5 May	0	0	0		0			0	0		
11 May	0.8	0.3	0.3	4.7	1.4		4.2	.414	.390	.274	.116
18 May	1.8	0.5	0	4.7	2.4		5.2	.255	.283	.498	-.215
25 May	0.4	0			0			0	0	0	0
1 Jun	0.4	0.2		3.5	0.7		3.7	.469	.433	.276	.157
9 Jun	1.4	0			0			0	0	-.103	.103
15 Jun	2.6	0			0			0	0	.046	-.046
23 Jun	1.8	0.2		2.0	0.4		2.6	.086	.074	-.217	.291
29 Jun	10.3	0	0		0	0		0	0	.100	-.100

Table 30. *Daphnia parvula*. Continued

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	*B*	*b*	*d*	*r*
6 Jul	5.1	0.8	0	1.9	1.5	0	2.3	.131	.139	.269	-.130
14 Jul	1.8	0.2		1.7	0.3		2.5	.068	.071	.081	-.010
20 Jul	1.7	0.5		1.5	0.8		2.2	.215	.206	.125	.081
27 Jul	3.0	1.4		1.4	2.0		2.2	.309	.292	.183	.109
5 Aug	8.0	2.2	0	1.7	3.7		2.2	.214	.205	.124	.081
13 Aug	15.3	2.1	0.3	1.5	3.2		2.3	.090	.087	.018	.069
19 Aug	23.1	5.6	0	1.7	9.5		2.4	.171	.189	.391	-.202
26 Aug	5.6	1.2		1.7	2.0		2.5	.144	.144	.144	0
2 Sep	5.6	2.2		2.1	4.6		2.8	.294	.271	.107	.164
9 Sep	17.7	2.3		1.8	4.1		2.6	.090	.083	-.081	.164
16 Sep	55.6	14.9	0	1.9	28.3		3.4	.149	.144	.082	.062
24 Sep	91.5	16.6	0.5	2.6	43.2		4.1	.114	.119	.208	-.098
1 Oct	49.0	18.1	2.3	2.0	36.2	0	5.0	.148	.151	.186	-.035
7 Oct	39.8	2.2	16.7	1.6	3.5	0.7	6.4	.014	.014	——	——

*Population statistic abbreviations defined in Appendix Table 27.

Table 31. Density (animals per liter) of the principal crustacean zooplankton at Station 1 of the Tongue River Reservoir during 1976. Samples collected using Wisconsin net.

Date	*Daphnia g. mendotae*	*Daphnia parvula*	*Ceriodaphnia*	*Bosmina*	*Leydigia*	*Cyclops*	*Mesocyclops*	*Diaptomus*
15 May	13.1	0.3	0.1	1.7	——	38.0	1.5	0.1
30 May	65.0	0.3	1.2	55.3	——	55.4	0.4	0.4
11 Jun	53.9	——	0.5	12.0	0.1	30.8	0.4	1.3
26 Jun	24.4	0.7	0.5	2.0	0.4	20.0	1.6	2.5
9 Jul	10.9	0.1	1.1	6.1	0.1	10.1	1.3	5.5
23 Jul	17.9	0.3	7.7	17.2	0.2	7.9	6.8	4.3
7 Aug	6.9	0.1	12.0	12.0	0.3	2.3	34.4	1.3
21 Aug	25.6	1.0	80.0	37.6	——	2.5	23.5	4.3
3 Sep	7.1	1.9	74.7	40.0	0.2	2.9	15.3	2.0
16 Sep	4.9	0.9	45.0	74.2	——	9.8	11.7	3.8

Table 32. Density (animals per liter) of the principal crustacean zooplankton at Station 2 of the Tongue River Reservoir during 1976. Samples collected using Wisconsin net.

Date	*Daphnia g. mendotae*	*Daphnia parvula*	*Ceriodaphnia*	*Bosmina*	*Leydigia*	*Cyclops*	*Mesocyclops*	*Diaptomus*
15 May	15.1	0.1	0.3	5.8	0.1	53.0	0.1	0.5
30 May	38.3	0.1	0.3	7.1	0.1	11.9	0.1	0.2
11 Jun	47.7	0.1	0.6	4.8	0.1	9.2	0.2	2.9
26 Jun	71.5	1.2	1.2	19.5	1.1	38.4	4.4	12.2
9 Jul	33.3	0.1	2.7	5.1	0.3	10.5	3.7	8.4
23 Jul	40.3	0.2	12.9	64.6	0.3	11.3	19.3	10.3
7 Aug	15.7	0.8	24.2	28.1	0.3	1.4	34.2	2.7
21 Aug	16.0	0.9	73.5	12.6	0.3	2.2	18.1	9.6
3 Sep	8.3	0.9	69.4	15.5	—	2.9	20.0	10.3
16 Sep	14.8	0.8	69.6	194.5	—	11.0	26.0	7.8

Table 33. Population data for *Daphnia g. mendotae* at Station 2 of the Tongue River Reservoir, 1976 and 1977.*

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	*B*	*b*	*d*	*r*
1976											
2 Oct	18.9	0	0	2.7	0	0.7	4.1	0	0	.017	-.017
16 Oct	15.0	2.0	1.5	4.4	8.8	0.3	6.6	.089	.080	.109	-.019
31 Oct	11.3	2.8	0.3	3.3	9.2	0.3	12.8	.064	.065	.086	-.021
13 Nov	8.6	1.3	0.3	3.4	4.4	0	21.0	.024	—	—	—
5 Dec	9.9	0.7	0	2.9	2.0	0.2	25.1	.008	.008	-.008	.016
15 Dec	11.6	0.7	0.2	2.9	2.0	0	30.9	.006	—	—	—
1977											
5 Jan	3.8	0	0.4	2.5	0	0	30.4	0	0	-.060	.060
15 Jan	6.9	0.5	0.3	3.5	1.8		30.8	.008	.008	-.001	-.009
28 Jan	6.1	0	0	1.6	0		31.0	0	0	.025	-.025
11 Feb	4.3	0.2		2.6	0.5		25.1	.005	.005	.023	-.018
26 Feb	3.3	0.2		2.6	0.5		27.4	.006	.006	.053	-.047
12 Mar	1.7	0.1		2.0	0.2	0	25.1	.005	—	—	—
3 Apr	1.1	0.5		5.4	2.7	0.1	24.3	.101	.097	.019	.078
13 Apr	2.4	0.5		8.0	4.0	0	8.9	.187	.166	-.060	.226
20 Apr	11.7	0.4		11.8	4.7		7.8	.052	.051	.007	.044
27 Apr	15.9	1.8		9.2	16.6		4.9	.214	.208	.149	.059
5 May	25.5	4.0		7.3	29.2		4.5	.253	.251	.235	.016
11 May	28.0	4.0		4.7	18.8		4.2	.159	.159	.162	-.003
18 May	27.5	2.9		4.1	11.9		5.2	.083	.085	.132	-.047
25 May	19.8	3.8		3.6	13.7		4.4	.158	.161	.197	-.037
1 Jun	15.3	1.8		2.4	4.3		3.7	.075	.070	-.070	.140
9 Jun	47.0	2.4		2.4	5.8		2.8	.044	.045	.103	-.058
15 Jun	33.2	1.8		3.5	6.3		2.6	.074	.075	.112	-.037
23 Jun	24.6	2.1		2.2	4.6		2.6	.073	.071	.018	.053
29 Jun	33.9	1.1	0	1.5	1.7	0	2.3	.022	.023	.083	-.060

Table 33. *Daphnia g. mendotae*. Continued

Date	N	N_{af}	N_{am}	E_{af}	E	E_p	D_e	*B*	*b*	*d*	*r*
6 Jul	22.2	2.5	0	1.2	3.0	0	2.3	.060	.063	.155	-.092
14 Jul	10.6	1.4		1.3	1.8		2.5	.069	.080	.385	-.305
20 Jul	1.7	0		2.5	0		2.2	0	0	.028	-.028
27 Jul	1.4	0.8		1.3	1.0		2.2	.331	.314	.209	.105
5 Aug	3.6	0.5		2.0	1.0		2.2	.129	.129	.129	0
13 Aug	3.6	0.6		1.6	1.0		2.3	.119	.115	.041	.079
19 Aug	5.6	0.4		1.5	0.6		2.4	.044	.047	.174	-.127
26 Aug	2.3	0		1.3	0		2.5	0	0	-.018	.018
2 Sep	2.6	0.7		2.2	1.5		2.8	.207	.199	.121	.078
9 Sep	4.5	1.4		1.9	2.7		2.6	.233	.227	.172	.055
16 Sep	6.6	1.8	0	2.5	4.5		3.4	.200	.191	.099	.092
24 Sep	13.8	0.5	1.4	3.0	1.5		4.1	.026	.026	.053	-.027
1 Oct	11.4	4.2	0.5	3.5	14.7		5.0	.258	.251	.193	.058
7 Oct	16.1	1.5	0	2.5	3.8	0	6.4	.037	.037	——	——

*Population statistic abbreviations defined in Appendix Table 27.

Table 34. Density (number per liter) of the developmental stages of *Cyclops b. thomasi* at Station 2 of the Tongue River Reservoir, 1976-1977.

Date	Eggs	Nauplii	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
1976										
2 Oct	34.9	18.0	2.6	1.2	0.6	1.7	1.5	2.0	2.3	11.9
16 Oct	0	59.4	26.4	15.5	7.1	1.3	1.1	0.8	2.5	54.6
31 Oct	0	11.8	6.1	8.4	5.9	3.2	0.6	0.9	0.4	25.4
13 Nov	11.6	39.7	8.0	20.1	18.1	14.9	1.6	2.4	1.6	66.9
5 Dec	0	9.6	2.9	8.1	11.4	20.5	4.8	1.4	1.4	50.6
15 Dec	0	8.7	0	6.8	6.8	27.3	12.3	2.1	2.1	57.3
1977										
5 Jan	0	12.4	1.6	1.4	5.7	19.3	12.2	1.1	0.8	42.2
15 Jan	0	3.6	1.8	0.2	1.6	11.5	10.6	0	0.6	26.4
28 Jan	8.0	2.0	1.3	0	0.4	6.2	8.4	1.7	0.4	18.4
11 Feb	8.0	2.3	1.9	0.3	0.1	1.8	4.5	0.9	1.0	10.6
26 Feb	0	0.8	0.5	0.4	0.2	2.1	3.6	0.9	0.9	8.7
12 Mar	29.0	3.0	0.4	0.9	0.6	1.3	2.2	1.2	1.8	8.4
3 Apr	146.5	17.6	0.3	0.4	0.6	1.2	2.0	3.9	7.1	15.7
13 Apr	737.0	56.7	3.7	5.7	2.0	1.4	5.1	9.9	24.2	51.9
20 Apr	334.9	146.6	62.8	89.4	46.0	8.4	3.7	6.1	17.0	233.3
27 Apr	139.5	61.3	20.0	45.4	43.4	33.3	1.4	4.7	2.0	150.2
5 May	22.4	28.6	7.0	3.1	1.6	3.7	0.4	0.4	1.3	17.6
11 May	0	25.4	5.4	4.7	1.7	2.5	0.4	0.8	0.7	16.0
18 May	21.0	14.9	3.0	2.2	2.8	4.4	1.9	1.5	1.0	16.7
25 May	26.0	21.5	1.0	2.0	1.8	1.6	1.4	2.0	0.9	10.7
1 Jun	30.0	30.4	4.8	2.2	2.5	1.5	1.5	1.8	2.2	16.4
9 Jun	0	37.9	2.8	6.0	3.3	2.5	1.9	1.6	1.3	19.5
15 Jun	13.5	18.1	6.3	3.6	2.9	1.1	0.9	1.1	0.7	16.6
23 Jun	0	11.9	3.5	4.3	1.6	1.8	0.8	0.4	0.6	13.0
29 Jun	0	12.4	1.7	1.7	2.0	1.7	0.8	0.7	0.4	8.9

Table 34. *Cyclops b. thomasi.* Continued

Date	Eggs	Nauplii	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
6 Jul	9.1	63.8	1.9	1.0	2.0	2.4	1.3	1.3	4.6	14.5
14 Jul	15.5	22.0	2.4	0.7	0.4	0.3	0.8	0	1.1	5.7
20 Jul	6.3	33.0	1.1	0.8	0	0.6	0.4	0.3	1.7	4.9
27 Jul	0	20.6	0.7	0.3	0.4	0.1	0.7	0.3	1.0	3.6
5 Aug	0	1.5	1.2	0.2	0	0.1	0.2	0.1	0.1	1.9
13 Aug	0	6.5	2.8	0.6	0.2	0.8	1.2	0.2	0.4	6.2
19 Aug	37.4	76.5	0	0.3	0.3	2.0	2.3	1.7	2.3	8.9
26 Aug	0	0	1.9	0.8	0	0.4	1.6	1.6	0	6.2
2 Sep	14.6	5.4	1.2	0	0	0.4	2.0	0.8	0.4	4.8
9 Sep	26.6	7.3	1.6	0.3	0	0	1.0	1.6	1.3	5.7
16 Sep	35.4	5.9	0	0	3.8	0	2.6	1.3	0.6	8.3
24 Sep	39.2	28.7	3.8	3.3	2.4	1.4	1.4	1.9	1.4	15.6
1 Oct	68.2	28.5	4.7	4.1	2.8	4.1	1.9	2.5	4.1	24.1
7 Oct	101.2	54.8	12.2	8.6	9.6	12.2	8.9	4.0	5.6	60.9

Table 35. Density (number per liter) of the developmental stages of *Mesocyclops edax* at Station 2 of the Tongue River Reservoir, 1976-1977.

Date	Eggs	Nauplii	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
1976										
2 Oct	0	20.4	1.2	0.3	0.9	6.4	0.9	0.9	2.6	13.0
16 Oct	0	14.3	0.9	1.5	0.6	6.6	0.2	0.0	0.6	10.4
31 Oct	0	0	0.6	0.3	0.4	0.1	0	0	0	1.4
All stages absent from samples collected 13 Nov 1976 - 3 April 1977										
13 Apr	0	1.4	0	0	0	2.0	0	0	0.6	2.6
20 Apr	0	0	0	0	0	1.1	0	0	0	1.1
27 Apr	0	21.5	0	0	0	0	2.7	0.7	0.7	4.0
5 May	12.9	4.4	0	0	0	0	0	0.1	0.2	0.3
11 May	0	3.6	0	0	0	0	0	0	0.1	0.1
18 May	8.6	3.0	0	0	0	0	0	0	0.2	0.2
25 May	0	2.4	0.3	0	0	0	0	0	0.1	0.4
1 Jun	0	0	0.3	0	0	0	0	0	0	0.3
9 Jun	0	0	0.2	0.2	0.6	0.8	0.3	0.3	0	2.4
15 Jun	0	12.9	0.7	0.2	0	1.1	0.5	0.2	0.5	3.2
23 Jun	0	7.9	0.4	0	0.6	0.2	0.2	0.2	0.4	2.0
29 Jun	0	6.2	3.2	1.4	0.6	0.4	0.2	0.7	0.2	6.7
6 Jul	26.1	20.8	4.1	2.4	4.2	1.5	2.4	2.0	1.5	18.1
14 Jul	28.1	36.0	4.3	3.5	2.7	2.1	2.1	2.4	1.8	18.8
20 Jul	76.9	110.7	6.6	5.7	2.4	1.8	2.9	2.3	5.7	27.5
27 Jul	25.9	123.4	4.8	2.8	3.8	4.7	4.6	5.4	6.0	32.3
5 Aug	50.4	124.4	6.7	1.2	0.9	0.2	0.9	2.4	8.3	20.5
13 Aug	64.1	72.0	25.2	13.0	4.6	1.8	1.2	2.2	4.4	52.4
19 Aug	40.3	76.5	16.0	14.3	8.9	6.9	6.0	2.6	2.3	56.9
26 Aug	25.6	122.4	22.3	18.0	13.7	8.2	12.5	11.4	7.1	93.2
2 Sep	11.2	33.7	23.6	21.6	15.4	13.0	10.2	5.7	2.5	91.9

Table 35. *Mesocyclops edax*. Continued

Date	Eggs	Nauplii	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
9 Sep	0	44.9	13.1	12.8	9.6	13.1	10.6	9.0	8.0	76.4
16 Sep	0	56.5	9.5	13.3	11.4	15.2	5.1	4.5	5.7	64.8
24 Sep	14.5	38.9	1.9	2.4	7.1	10.4	3.3	6.6	1.9	33.6
1 Oct	0	67.5	1.6	1.2	1.2	13.8	1.9	3.1	9.7	32.7
7 Oct	0	15.6	1.6	1.0	0.3	5.9	0.7	0.3	1.6	11.5

Table 36. Density (number per liter) of the developmental stages of *Diaptomus siciloides* at Station 2 of the Tongue River Reservoir, 1976-1977.

Date	Eggs	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
1976									
2 Oct	8.6	0.3	0.4	0.4	0.3	1.2	3.1	2.7	8.4
16 Oct	3.9	0.3	0.4	0	0.3	0.3	1.8	0.4	3.5
31 Oct	0	0	0	0	0.2	0.3	0.9	0.6	2.0
13 Nov	0	0	0.8	0.3	0	0	1.3	0.3	2.6
5 Dec	0	0	0	0.2	0	0.4	1.2	1.2	2.9
15 Dec	0	0	0	0	0	1.2	0.9	2.3	4.4
1977									
5 Jan	0	0	0	0	0.2	0.2	0.8	0.8	1.8
15 Jan	0	0	0	0	0	0	3.4	2.0	5.4
28 Jan	0	0	0	0	0.2	0.7	2.5	1.5	4.9
11 Feb	0	0	0	0	0.1	0.1	0.9	0.7	1.7
26 Feb	2.8	0	0	0	0.2	0	0.6	1.0	1.8
12 Mar	0	0	0	0	0	0	0.6	0.3	0.9
3 Apr	1.3	0	0	0	0	0	0.6	0.1	0.7
13 Apr	3.5	0	0	0	0	0	0.2	0.3	0.5
20 Apr	14.6	0	0	0	0	0	0.8	0.8	1.6
27 Apr	0	0.3	0.1	0	0	0	0.1	0.1	0.7
5 May	0	0	0	0	0	0.2	0	0.2	0.4
11 May	0	0	0	0	0	0	0	0	0
18 May	15.8	0.1	0	0	0	0.1	0.5	0	0.7
25 May	0	0.9	0.2	0.2	0.1	0.2	0.1	0.2	1.8
1 Jun	0	0.8	0.8	0.5	0.1	0	0	0	2.2
9 Jun	9.9	1.0	0.5	0.3	0.7	0.2	0.5	1.0	4.1
15 Jun	0	0.2	0.1	0.1	0.4	0.4	0.4	0.5	2.0
23 Jun	0	1.6	2.4	0.5	0.3	0	0.5	0.9	6.2
29 Jun	5.5	2.9	3.2	2.5	1.7	1.9	2.6	1.1	16.0

Table 36. *Diaptomus siciloides.* Continued

Date	Eggs	CI	CII	CIII	CIV	CV	AM	AF	Tot. copepodites
6 Jul	3.4	1.5	1.7	3.2	3.6	1.5	1.7	1.7	14.9
14 Jul	5.1	0.6	0.8	0.4	1.4	0.4	0.4	2.5	6.6
20 Jul	1.1	0.1	0.4	0	0.2	0.6	1.2	1.6	4.1
27 Jul	1.4	0.4	0.5	0.5	2.0	0.9	4.2	2.7	11.3
5 Aug	6.6	0.7	0.4	0.2	0.1	0.6	3.0	3.4	8.4
13 Aug	3.5	1.1	1.2	1.1	0.8	0.4	1.5	3.3	9.3
19 Aug	0	1.6	0.4	0.4	0.4	0.4	1.9	1.9	7.0
26 Aug	4.7	0.7	0.3	0	0.7	0.7	1.7	1.7	5.8
2 Sep	25.2	0	0.5	0	0	1.5	3.1	5.6	10.8
9 Sep	3.7	0.2	0.2	0.4	0	0	1.4	1.4	3.6
16 Sep	13.3	1.7	1.1	0	0.6	4.0	4.0	1.7	13.1
24 Sep	36.4	1.6	1.1	0	0.5	3.8	3.8	1.6	12.4
1 Oct	7.9	0.4	0.7	1.9	0	2.2	1.9	2.6	9.7
7 Oct	24.0	1.0	2.0	1.0	0.7	3.3	2.0	2.3	12.2