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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Approved:

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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.

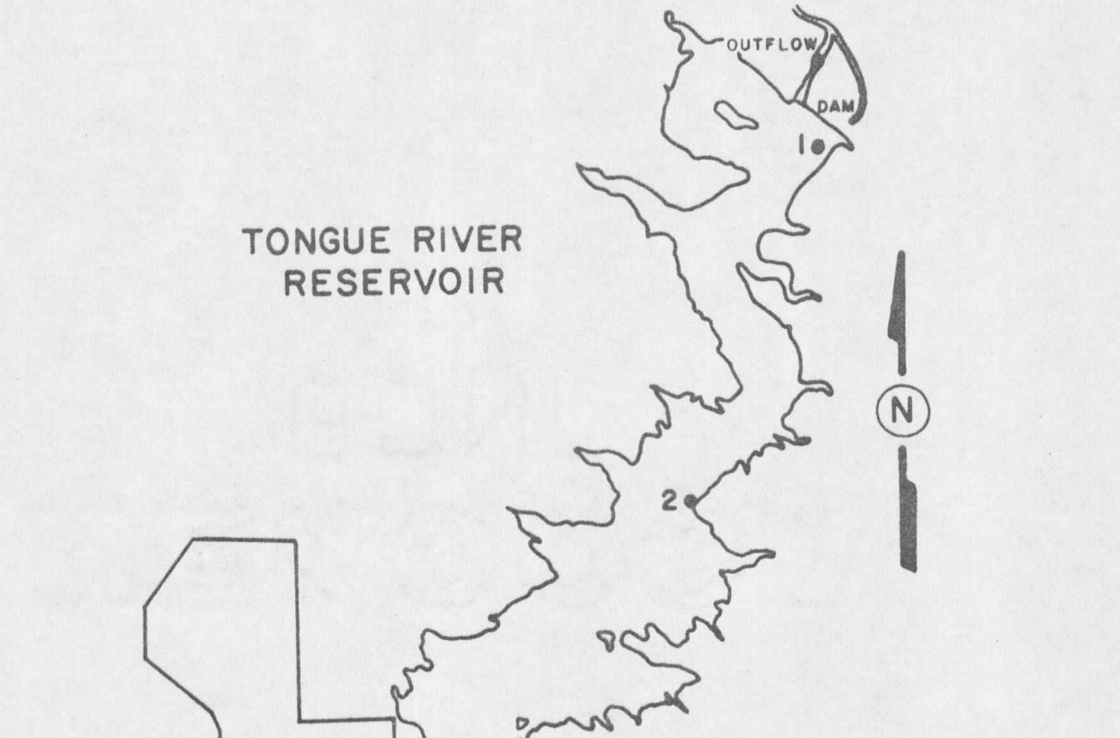

Figure 1. Map of the Tongue River Reservoir detailing the study area.

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

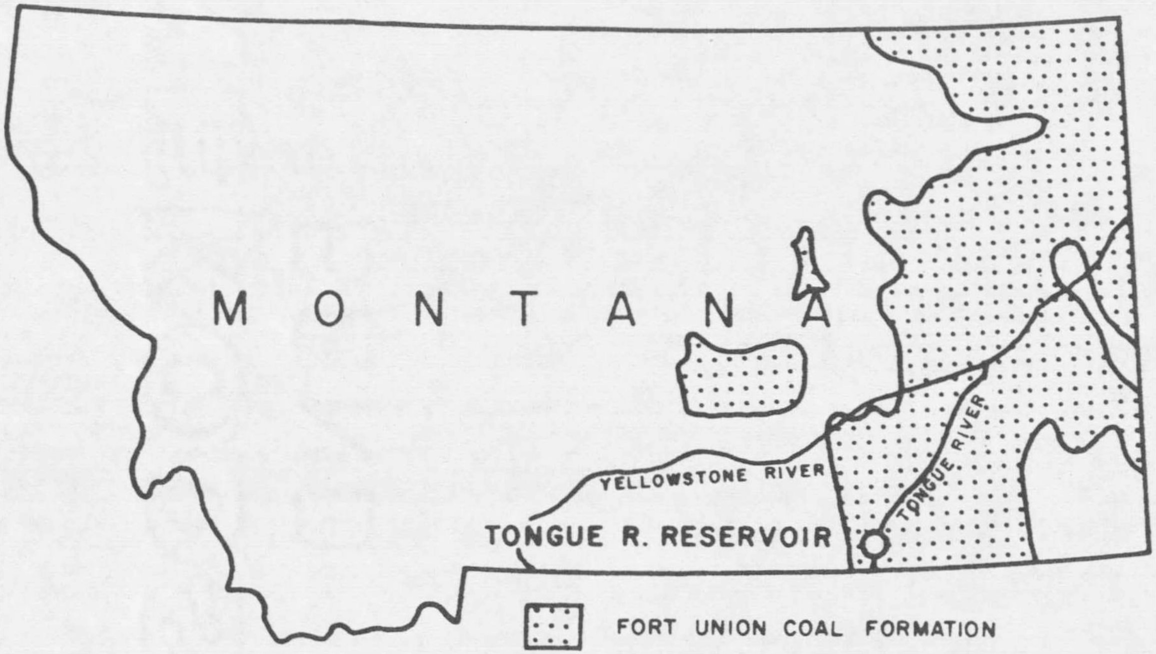

Figure 2. Location map.

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

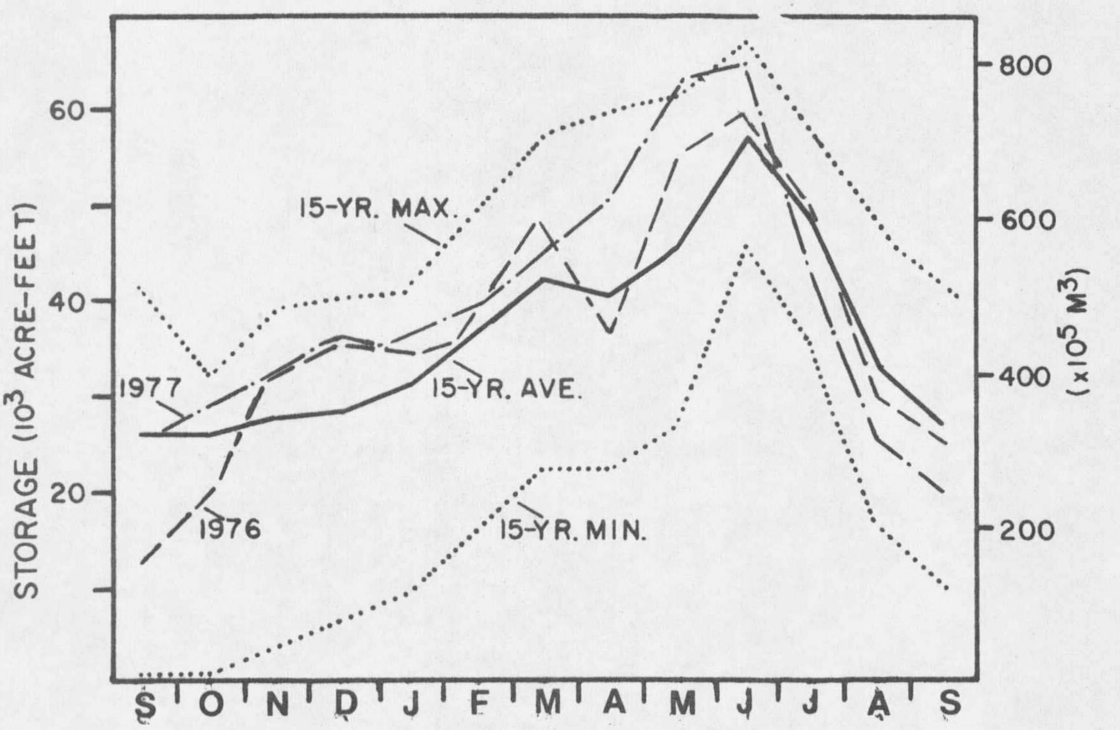

Figure 3. Storage volumes of the Tongue River Reservoir for the 1976 and 1977 water years as compared to the mean and extremes observed over the period 1961-1975.

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:

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

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:

$$r = \frac{lnN_t - lnN_0}{t} \qquad (2)$$

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

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

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)

$$lnD = 3.3956 + 0.2193 lnT - 0.3414(lnT)^2 \qquad (4)$$

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

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

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:

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

and that of Edmondson (1960):

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

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):

$$r = b - d . \tag{8}$$

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:

$$d = b - r \tag{9}$$

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)	$lnW = 1.7769 + 2.7166 lnL$
Daphnia spp. (w/out eggs, embs, ov.)	(1303)	$lnW = 1.4681 + 2.8292 lnL$
Ceriodaphnia quadrangula	(19)	$lnW = 2.5623 + 3.3380 lnL$
Bosmina spp.	(77)	$lnW = 3.0896 + 3.0395 lnL$

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,

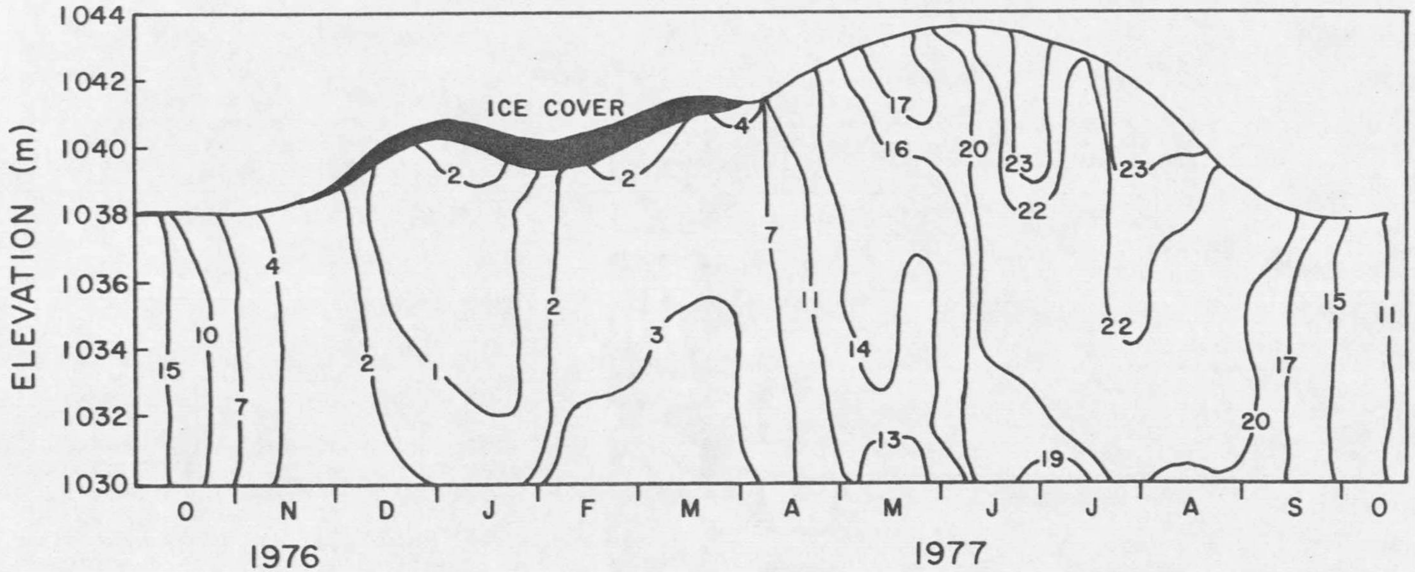

Figure 4. Seasonal isotherms (°C) at Station 2 of the Tongue River Reservoir during the period October 1976 to October 1977.

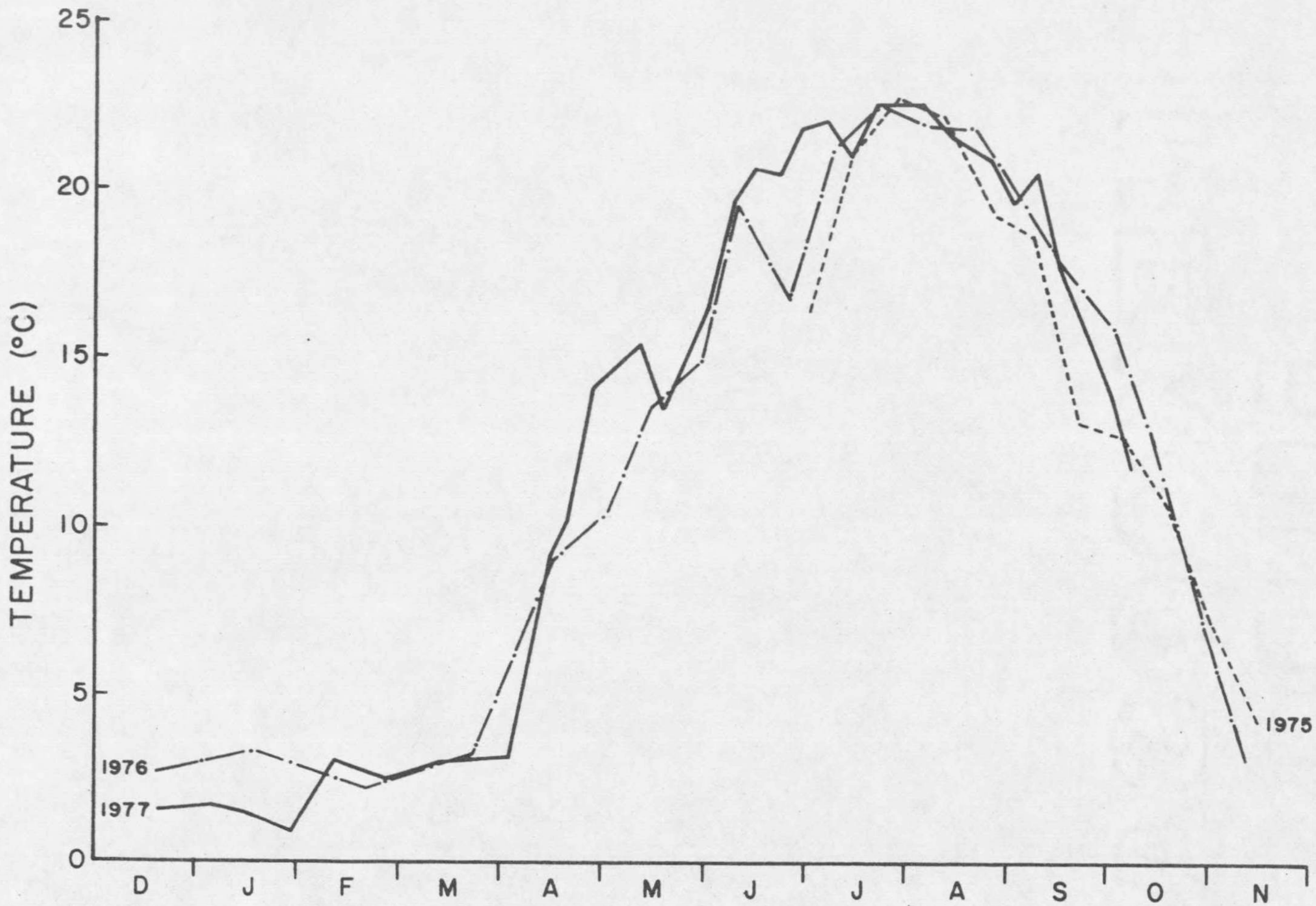

Figure 5. Seasonal trends in mean water temperature (°C) at Station 2 of the Tongue River Reservoir during 1975, 1976, and 1977.

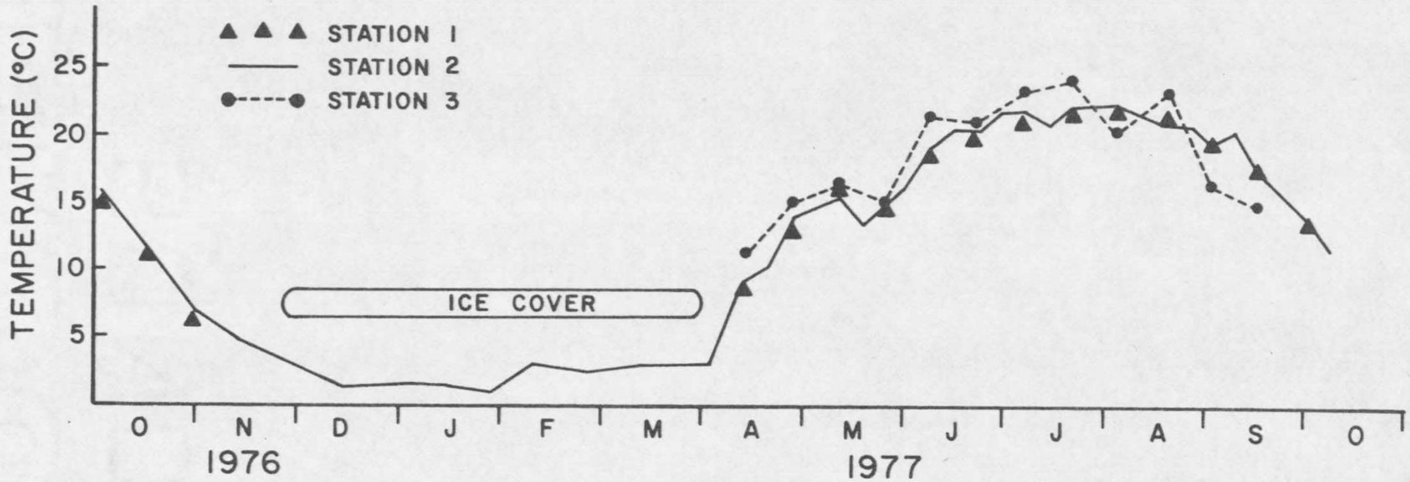

Figure 6. Seasonal trends in mean water temperature (°C) at three stations on the Tongue River Reservoir, October 1976 - October 1977.

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

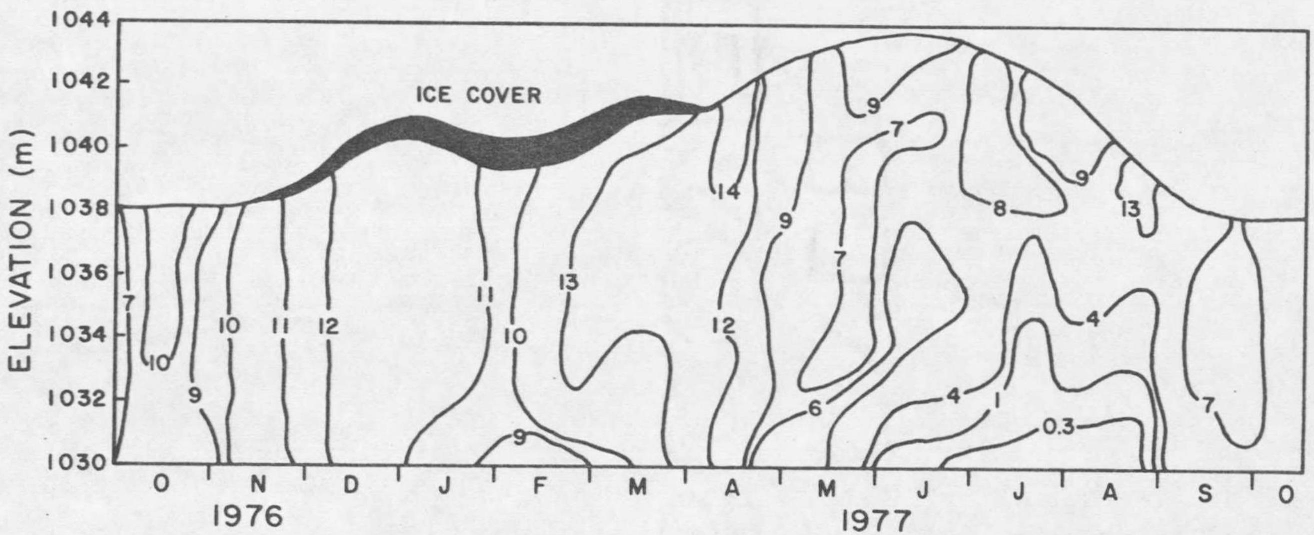

Figure 7. Seasonal dissolved oxygen (mg·ℓ⁻¹) isopleths at Station 2 of the Tongue River Reservoir during the period October 1976 - October 1977.

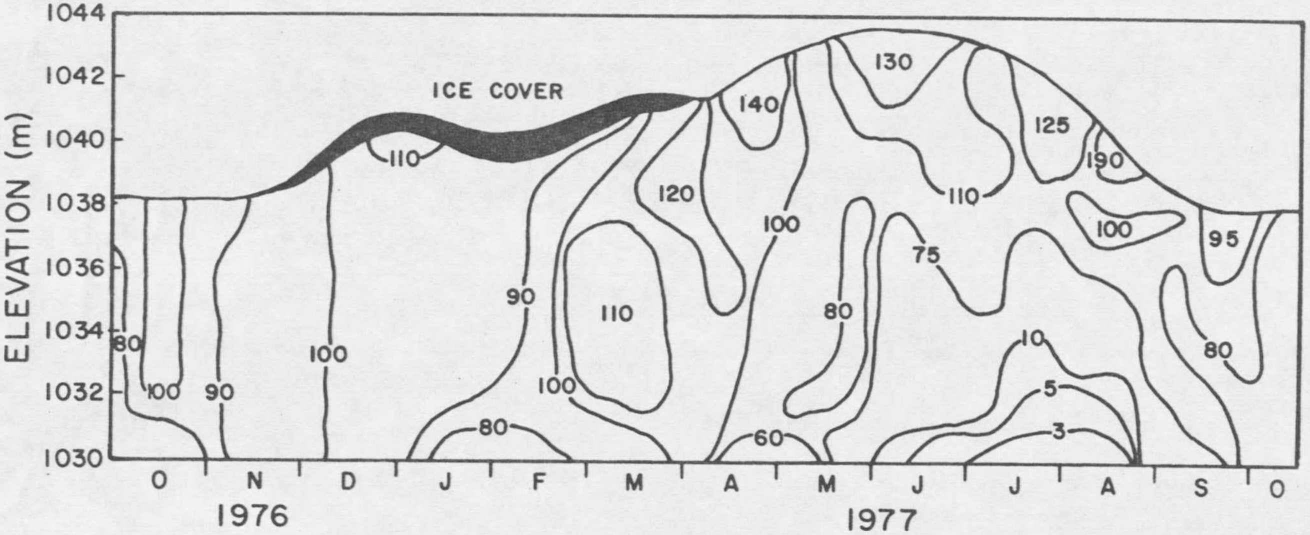

Figure 8. Seasonal percent oxygen saturation isopleths at Station 2 of the Tongue River Reservoir, October 1976 - October 1977.

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

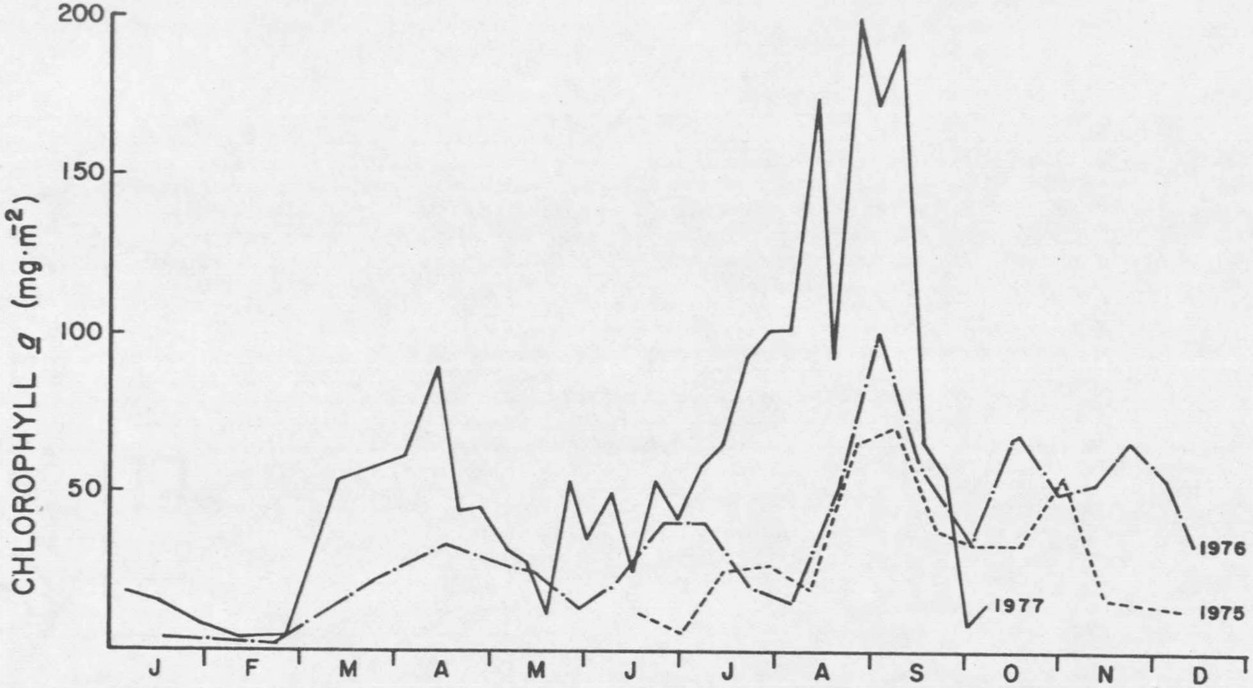

Figure 9. Seasonal trends in areal chlorophyll α concentration ($mg \cdot m^{-2}$) at Station 2 of the Tongue River Reservoir during 1975, 1976, and 1977.

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.

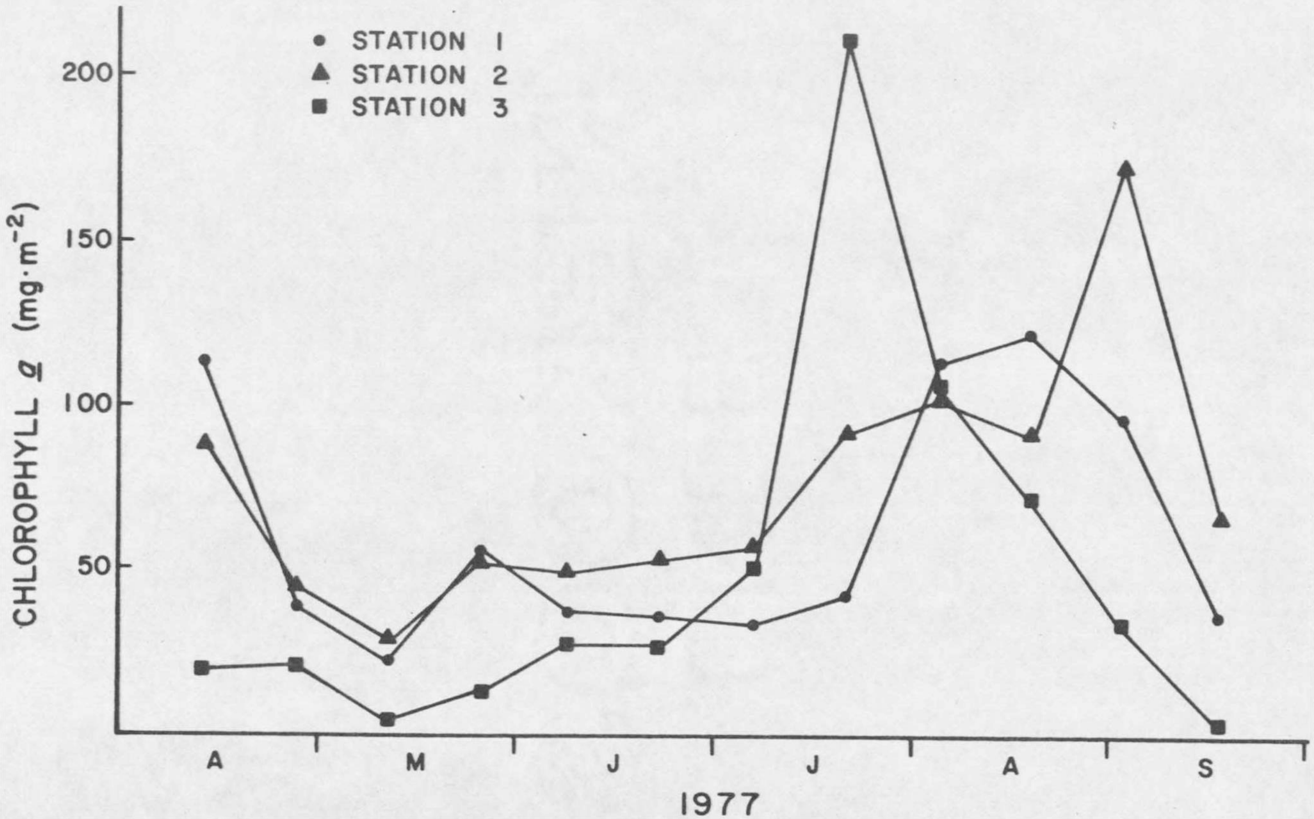

Figure 10. Seasonal trends in areal chlorophyll α concentration ($mg \cdot m^{-2}$) at three stations on the Tongue River Reservoir during the spring and summer of 1977.

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

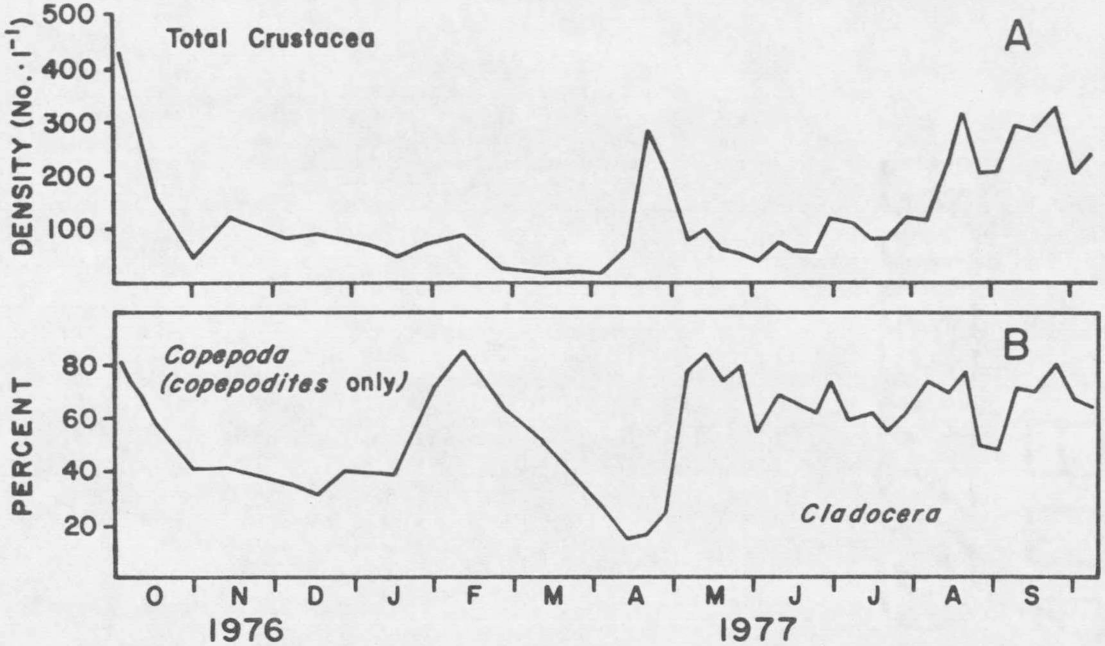

Figure 11. Density ($\#\cdot\ell^{-1}$; A.) and ordinal composition (percent; B.) of crustacean zooplankton at Station 2 of the Tongue River Reservoir during 1976 and 1977.