



Changes in zooplankton species composition in newly filled Bighorn Lake, Montana and Wyoming  
by Abraham Andrew Horpestad

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF  
PHILOSOPHY in Botany  
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Abstract:

The zooplankton community of newly filled Bighorn Lake was studied during 1968 and 1970. Samples were collected from six sampling stations throughout the reservoir on 37 different dates. Birth rates, death rates and rates of population change were calculated for *Daphnia pulex* and *Daphnia galeata mendota*. Assimilation rates for these two species were also calculated.

Genera contributing more than 5% of the total standing crop included two cladocerans, *Daphnia pulex* and *Daphnia galeata mendota*, and two copepods, *Diaptomus ashlandi* and *Cyclops bicuspidatus thomasi*.

*Daphnia pulex* and *Diaptomus ashlandi* became less abundant while *Daphnia galeata mendota*, *Cyclops bicuspidatus thomasi* and rotifers became more abundant over the three year period. Increases in total standing crops of zooplankton and phytoplankton were similar. However, the percentage of the primary productivity assimilated by *Daphnia* species declined. The average length of *Daphnia pulex* was 20% greater than *Daphnia galeata mendota*. These two species were most abundant at different stations, depths and times. There were no significant changes in the mean lengths of the two *Daphnia* species over the three year period.

The observed changes support the hypothesis that declines in sport fish "production" of newly filled reservoirs results from predation by planktivorous fish on large zooplankters.

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by

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A thesis submitted in partial fulfillment  
of the requirements for the degree

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## ABSTRACT

The zooplankton community of newly filled Bighorn Lake was studied during 1968 and 1970. Samples were collected from six sampling stations throughout the reservoir on 37 different dates. Birth rates, death rates and rates of population change were calculated for Daphnia pulex and Daphnia galeata mendota. Assimilation rates for these two species were also calculated.

Genera contributing more than 5% of the total standing crop included two cladocerans, Daphnia pulex and Daphnia galeata mendota, and two copepods, Diaptomus ashlandi and Cyclops bicuspidatus thomasi.

Daphnia pulex and Diaptomus ashlandi became less abundant while Daphnia galeata mendota, Cyclops bicuspidatus thomasi and rotifers became more abundant over the three year period. Increases in total standing crops of zooplankton and phytoplankton were similar. However, the percentage of the primary productivity assimilated by Daphnia species declined. The average length of Daphnia pulex was 20% greater than Daphnia galeata mendota. These two species were most abundant at different stations, depths and times. There were no significant changes in the mean lengths of the two Daphnia species over the three year period.

The observed changes support the hypothesis that declines in sport fish "production" of newly filled reservoirs results from predation by planktivorous fish on large zooplankters.

## INTRODUCTION

In this study, factors which could cause declines in fishing success in newly filled reservoirs and other factors enabling cogenetic species to exist in the same habitat are investigated.

Newly impounded reservoirs usually have a large population of desirable sized sport fishes which soon declines (Bennett, 1971; Carlander, et al., 1963; Neel, 1963). This initial high "productivity" has been attributed to an initially high level of nutrients resulting from decomposition of newly flooded organic matter. However, Bennett established in 1947 (Bennett, 1971) that the high productivity of sport fishes was also related to the numbers and kinds of fish introduced into ponds lacking fish. The mechanisms causing the declines in productivity have not been established.

A comprehensive 3-year limnological investigation of Bighorn Lake which started in 1968, one year after initial filling of the reservoir, afforded an opportunity to determine what could cause a decline in sport fish production. Usable data was not gathered in 1969 due to mechanical failures.

In 1967, the Montana Fish and Game Department started to document the kinds of fish present and their population sizes. The documentation was not done in sufficient detail to be of value to this study. However, Galbraith (1967) demonstrated that rainbow trout, the dominant fish in Bighorn Lake, filter feeds on zooplankton at least until they

are 15 inches long.

Preliminary sampling showed that two similar sized Daphnia species were present in the reservoir. Ecological theory indicates that two such similar species should not continue to coexist unless there are factors which ecologically separate them. This study included a search for such factors.

Soltero (1971) gives physical, chemical and phytological data for this reservoir for the same three year period. My report does not include raw data; complete copies of all raw data are on file with the biology department of Montana State University.

## DESCRIPTION OF THE STUDY AREA

The Bighorn River is impounded by Yellowtail Dam approximately 80.5 kilometers (50 miles) southeast of Billings, Montana. Bighorn Lake, the resulting reservoir, normally extends from the dam at Fort Smith, Montana, latitude  $45^{\circ}18'27''$ , longitude  $107^{\circ}57'26''$ , south into Wyoming for a distance of 98.4 kilometers (61 miles). The water is used for power production, flood control, irrigation and recreation.

The Bureau of Reclamation began construction of Yellowtail Dam in 1961 and completed construction in 1967. Storage began 4 November 1965. The reservoir has a usable capacity of  $169 \times 10^7 \text{ m}^3$  (1,375,000 acre-ft) below elevation 1,114.6 m (3,657 ft). Normal operating capacity is  $144 \times 10^7 \text{ m}^3$  (1,097,000 acre-ft) at elevation 1,109.5 m (3,640 ft) and minimum operating level is  $60 \times 10^7 \text{ m}^3$  (483,400 acre-ft) at elevation 1,081.1 m (3,547 ft). Dead storage amounts to  $234 \times 10^5 \text{ m}^3$  (18,970 acre-ft) below elevation 1,005.8 m (3,296 ft). Other morphometric data for the reservoir are given in Table I.

Water can be discharged from the reservoir through three outlets; (1) the spillway--elevation 1,095.1 m (3,593 ft); (2) the power penstocks--elevation 1,051.6 m (3,450 ft); and (3) the river outlet invert--elevation 1,005.8 m (3,296 ft). All water is normally discharged through the power penstocks.

Six permanent sampling stations were established on the reservoir

Table I. Morphometric data for Bighorn Lake at maximum capacity (elevation 1,115.5 m). Table adapted from Soltero (1971).

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Maximum Length	98.4 km (61 mi)
Maximum Width	3.2 km (2.0 mi)
Mean Width	739 m (2,425 ft)
Maximum Depth	140 m (459 ft)
Mean Depth	24 m (80 ft)

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(Fig. 1). Kilometer 0 (Station 0) was located at the dam site with the remaining stations at approximately 16.1 kilometer (10 mile) intervals up the reservoir for 80.5 kilometers to station 50.

The major tributaries to the reservoir are the Bighorn and Shoshone Rivers (Fig. 1).

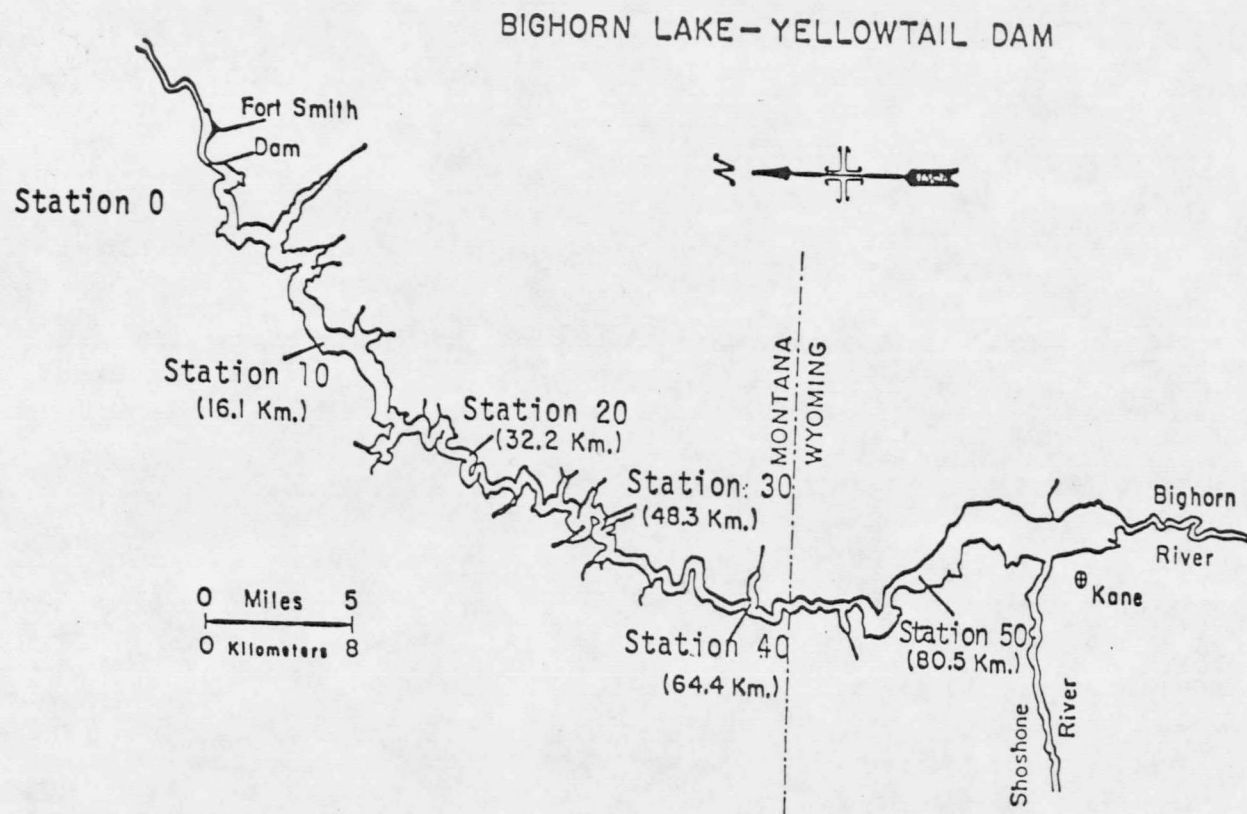


Figure 1. Map of Bighorn Lake (adapted from Soltero, 1971) showing location of the six permanent sampling stations.

## METHODS

A Clarke-Bumpus plankton sampler with a no. 20 net (0.080 mm aperture size) was used to collect zooplankton samples at each of the permanent stations during daylight hours. Oblique tows from 25 meters depth or the bottom (whichever was less) to the surface were made. Deeper tows were also made on selected dates in 1968 and 1970. Samples were preserved in the field with 95% ethanol. In 1968, collections were made on 24 occasions between May 5th and November 2nd. In 1970, collections were made on 14 occasions between June 10th and September 9th.

Zooplankton were counted using a Sedgwick-Rafter cell and a binocular microscope equipped with a Whipple micrometer. Magnifications ranged from 30X to 90X. Although dilutions were sometimes necessary, at least one 1 ml aliquot was counted. All organisms were counted until approximately 100 of the most abundant cladoceran were counted. The distance from the top of the head to the base of the spine was determined for each Daphnia counted. All of the identifiable cladoceran eggs and embryos in each aliquot were counted. Identification followed Edmondson (1959). Unattached eggs and embryos were assigned to species according to species densities. The entire sample was examined for the presence of large organisms.

Birth rates, death rates and rates of population change were calculated for both Daphnia pulex and Daphnia galeata mendota. If the



populations are sampled at suitable intervals, the average instantaneous rate of population change ( $r$ ) can be calculated from successive pairs of population density values. If the density of the initial population is  $N_0$  and the density after time  $t$  is  $N_t$  then:

$$N_t = N_0 e^{rt}.$$

The finite birth rate ( $B$ ), the number of newborn per individual per day, can be calculated using the methods of Edmondson (1960), if the number of eggs in a population ( $E$ ), the population density ( $N$ ), and the developmental time of the embryonic stage ( $D$ ) are known, as follows:

$$B = \frac{E}{DN_0}.$$

Developmental times under laboratory conditions have been determined by Edmondson (1960) and Hall (1964). Hall's laboratory data were applied to the field data using the temperatures at 12.5 m or the surface. Temperatures used are from Soltero (1971). Developmental times so derived are similar to those Wright (1965) obtained for a comparable field situation.

Instantaneous birth rates ( $b$ ) were estimated using the Leslie method as suggested by Caswell (1972):

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

If estimates of  $b$  and  $r$  have been generated by the equations above then instantaneous death rates ( $d$ ) can be calculated since:

$$r = b - d .$$

These equations assume constant continuous per capita birth rate (b), constant continuous rate of increase (r) and thus a constant continuous death rate (d). They also assume that migration (out or in) does not occur.

Total standing crops (in mg/l) were calculated using the size to weight relationships and the average weights developed by LeSeur (1959) and Hall et al. (1970). For species not listed in these sources, interpolation and size comparisons were used to establish mean dry weights.

Zooplankton population biomass was also computed in areal units ( $\text{g/m}^2$ ).

## RESULTS

### Abundance of Zooplankton

Twenty-six taxa were identified during this investigation; 10 taxa were in the Cladocera, 3 were in the Copepoda, and 13 were in the Rotifera (Tables 2 and 3).

The total standing crop was much higher at station 0 in 1968 than at any other station and it decreased "upstream". In contrast, in 1970 the total standing crop was lowest at station 0 and increased upstream.

The cladoceran, Daphnia galeata mendota was the most abundant and contributed more to the total standing crop than any other taxon. Daphnia pulex was most abundant at station 0 in both years and contributed more to the total standing crop at this station than any other taxon in both years.

The dominant copepods were Diaptomus ashlandi and Cyclops bicuspidatus thomasi. In both 1968 and 1970 Diaptomus ashlandi adults were most abundant at station 0 while nauplii were most abundant at station 40; copepodites were most abundant at stations 0 and 50 in 1968 and 1970, respectively.

Adult Cyclops bicuspidatus thomasi were also most abundant at station 0 in 1968 while nauplii and copepodites were most abundant at station 50; all life stages were most abundant at station 50 in 1970.

Rotifers were generally most abundant at stations 40 and 50 in 1968 and 1970, respectively.

Table 2: Mean number/liter of each taxon at each station in 1968, mean percent contribution to total standing crop (in parenthesis) and mean total standing crop at each station.

taxa	Stations					
	0	10	20	30	40	50
<b>Cladocera</b>						
<u>Daphnia galeata mendota</u> Birge 1881	6.33 (6.2)	12.05 (29.1)	11.81 (42.7)	8.91 (24.6)	16.30 (31.3)	.01 (5.2)
<u>D. pulex</u> Leydig 1860 emend. Richard 1896	18.92 (43.9)	3.70 (17.9)	1.51 (7.6)	1.79 (11.7)	1.10 (4.2)	.02 (10.5)
<u>Diaphanosoma leuchtenbergianum</u> , Fisher 1850		.03 ( $<0.1$ )	.12 (0.3)			
<u>Ceriodaphnia reticulata</u> (Jurine) 1820		1.34 (2.4)	2.72 (4.0)	2.71 (6.1)	4.21 (6.3)	.03 (1.7)
<u>Moina</u> spp. Baird 1850	.04 ( $<0.1$ )	.15 (0.3)	.49 (0.7)	.21 (0.5)	2.01 (3.0)	.01 (0.5)
<u>Bosmina longirostris</u> (O.F. Muller) 1785		2.58 (2.8)	5.37 (3.4)	6.19 (6.1)	2.24 (1.4)	.05 (1.2)
<u>Macrothrix rosea</u> (Jurine) 1820				.01 ( $<0.1$ )	.03 ( $<0.1$ )	.06 (1.6)
<u>Kurzia latissima</u> (Kurz) 1874					.10 ( $<0.1$ )	.03 ( $<0.1$ )
<u>Leydigia quadrangularis</u> (Leydig) 1960	.05 ( $<0.1$ )	.01 ( $<0.1$ )	.002 ( $<0.1$ )	.01 ( $<0.1$ )	.04 ( $<0.1$ )	.05 ( $<0.1$ )

<u>Chydorus sphaericus</u> (O.F. Muller) 1785	.04 (<0.1)	.09 (<0.1)	.13 (0.9)		.02 (<0.1)	
Copepoda						
Calanoida						
<u>Diaptomus ashlandi</u> March 1893						
Adults	15.06 (19.9)	2.84 (20.3)	1.82 (5.3)	1.48 (6.6)	3.32 (9.1)	0.4 (3.5)
Nauplii	4.15 (<0.1)	3.27 (<0.1)	3.81 (<0.1)	6.64 (<0.1)	8.98 (<0.1)	.03 (<0.1)
Copepodites	19.92 (11.9)	8.07 (12.6)	5.64 (7.2)	7.27 (13.4)	8.55 (10.2)	.04 (1.60)
Cyclopoida						
<u>Cyclops bicuspidatus thomasi</u> S.A. Forbes 1883						
Adults	6.81 (8.9)	3.36 (12.1)	4.42 (11.7)	3.07 (12.9)	5.55 (14.5)	0.40 (42.0)
Nauplii	3.87 (<0.1)	3.62 (<0.1)	6.40 (<0.1)	8.17 (<0.1)	13.53 (<0.1)	0.44 (<0.1)
Copepodites	15.81 (7.6)	8.84 (11.6)	14.32 (14.6)	10.57 (16.9)	18.48 (18.4)	0.76 (30.2)
<u>Eucyclops</u> spp. Claus						
					.01 (<0.1)	.01 (<0.1)
Rotifera						
<u>Polyarthra</u> spp. Ehrenberg						
	.72 (<0.1)	1.11 (<0.1)	2.39 (<0.1)	1.29 (<0.1)	4.26 (<0.1)	.05 (<0.1)

<u>Hexarthra</u> spp. Schmarda	.99 ( $<0.1$ )	.24 ( $<0.1$ )	.04 ( $<0.1$ )	.03 ( $<0.1$ )	.12 ( $<0.1$ )	.36 ( $<0.1$ )
<u>Anuraeopsis</u> spp. Lartenborn		.11 ( $<0.1$ )		.001 ( $<0.1$ )	.36 ( $<0.1$ )	
<u>Ascomorpha</u> spp. Perty	.01 ( $<0.1$ )	.81 ( $<0.1$ )	.05 ( $<0.1$ )	.26 ( $<0.1$ )	.40 ( $<0.1$ )	.05 ( $<0.1$ )
<u>Keratella cochlearis</u> Gosse	.09 ( $<0.1$ )	.35 ( $<0.1$ )	.98 ( $<0.1$ )	1.23 ( $<0.1$ )	1.63 ( $<0.1$ )	.05 ( $<0.1$ )
<u>Keratella quadrata</u> Muller	1.79 ( $<0.1$ )	.79 ( $<0.1$ )	.81 ( $<0.1$ )	.67 ( $<0.1$ )	1.14 ( $<0.1$ )	.02 ( $<0.1$ )
<u>Asplanchna</u> spp. Gosse	8.03 (1.5)	3.42 (1.4)	5.98 (2.1)	1.50 (1.1)	3.14 (1.1)	.05 (0.6)
<u>Brachionus</u> spp. Dallas	.07 ( $<0.1$ )	.30 ( $<0.1$ )	.24 ( $<0.1$ )	.43 ( $<0.1$ )	3.13 ( $<0.1$ )	.19 ( $<0.1$ )
Total Standing Crop						
mg/l dry weight	.544	.204	.267	.179	.284	.007
g/m <sup>2</sup> dry weight	13.60	5.1	6.68	4.48	4.26	.0350

Table 3: Mean number/liter of each taxon at each station in 1970, mean percent contribution to total standing crop (in parenthesis) and mean total standing crop at each station.

taxa	Stations					
	0	10	20	30	40	50
<b>Cladocera</b>						
<u>Daphnia galeata mendota</u> Birge 1881	6.70 (23.3)	12.30 (39.3)	19.78 (59.4)	10.24 (32.9)	22.21 (43.1)	90.48 (48.4)
<u>D. pulex</u> Leydig 1860 emend. Richard 1896	10.40 (32.3)	4.31 (13.3)	1.41 (4.7)	3.45 (9.6)	.10 (0.2)	.03 (<0.1)
<u>Ceriodaphnia reticulata</u> (Jurine) 1820	.97 (1.3)	2.80 (3.5)	2.20 (2.8)	1.73 (8.3)	1.98 (1.6)	2.48 (0.6)
<u>Moina</u> spp. Baird 1850				.06 (<0.1)	.29 (0.2)	1.31 (0.3)
<u>Bosmina longirostris</u> (O.F. Muller) 1785	.49 (0.7)	2.52 (8.0)	1.78 (2.3)	2.81 (3.8)	4.80 (3.9)	34.99 (4.1)
<u>Leydigia quadrangularis</u> (Leydig) 1960	.09 (<0.1)	.02 (<0.1)	.02 (<0.1)	.02 (<0.1)		.01 (<0.1)
<u>Chydorus sphaericus</u> (O.F. Muller) 1785	.10 (<0.1)	.11 (0.1)	.12 (0.1)	.04 (<0.1)	.03 (<0.1)	.04 (<0.1)
<b>Copepoda</b>						
<b>Calanoida</b>						
<u>Diaptomus ashlandi</u> Marsh 1893 (continued)						

Adults	2.08 (5.6)	1.74 (3.8)	1.43 (2.7)	.67 (1.5)	.78 (1.0)	2.1 (0.9)
Nauplii	7.12 (<0.1)	7.34 (<0.1)	9.51 (<0.1)	11.18 (<0.1)	25.43 (<0.1)	7.05 (<0.1)
Copepodites	3.36 (3.1)	2.77 (2.7)	1.11 (1.0)	1.60 (1.5)	1.64 (1.0)	3.98 (0.9)

Cyclopoida

Cyclops bicuspidatus thomasi, S.A. Forbes 1883

Adults	4.72 (20.9)	3.7 (11.2)	5.53 (13.3)	6.54 (18.8)	17.07 (22.5)	44.81 (17.1)
Nauplii	48.82 (<0.1)	59.24 (<0.1)	52.04 (<0.1)	84.56 (<0.1)	238.65 (<0.1)	354.27 (<0.1)
Copepodites	7.84 (11.7)	15.53 (15.9)	21.20 (19.1)	24.16 (25.3)	62.14 (24.2)	162.21 (20.3)

Rotifera

<u>Polyarthra</u> spp. Ehrenberg	42.76 (0.7)	54.02 (0.9)	76.61 (1.1)	85.46 (1.4)	96.15 (0.9)	168.38 (0.5)
<u>Hexarthra</u> spp. Schmarda	1.68 (<0.1)	3.49 (0.1)	14.01 (0.3)	26.98 (0.5)	17.07 (0.2)	58.15 (0.2)
<u>Filinia</u> spp. Bury de St. Vincent	1.49 (<0.1)	.43 (<0.1)	.23 (<0.1)	.10 (<0.1)		.03 (<0.1)
<u>Anuraeopsis</u> spp. Lartenborn	.04 (<0.1)	1.00 (<0.1)	.59 (<0.1)	.18 (<0.1)	.27 (<0.1)	.14 (<0.1)
<u>Ascomorpha</u> spp. Perty	1.03 (<0.1)	1.23 (<0.1)	.54 (<0.1)	6.61 (<0.1)	4.31 (<0.1)	54.12 (<0.1)



<u>Keratella cochlearis</u> Gosse	3.65 (<0.1)	26.16 (<0.1)	29.14 (<0.1)	21.42 (<0.1)	26.85 (<0.1)	3.25 (<0.1)
<u>Keratella quadrata</u> Muller	2.69 (<0.1)	1.30 (<0.1)	1.18 (<0.1)	1.34 (<0.1)	3.17 (<0.1)	1.17 (<0.1)
<u>Asplanchna</u> spp. Gosse	1.67 (1.1)	1.72 (1.1)	2.81 (1.7)	5.19 (3.3)	3.92 (1.5)	5.10 (0.6)
<u>Brachionus</u> spp. Dallas	.06 (<0.1)	2.28 (<0.1)	1.44 (<0.1)	.44 (<0.1)	.45 (<0.1)	.82 (<0.1)
<u>Conochilus unicornus</u> Rousselet	.04 (<0.1)	.09 (<0.1)				
Unidentified (includes <u>Synchaeta</u> spp., <u>Euchlanis</u> spp., <u>Notholca</u> spp., and Unknowns)	.45 (<0.1)	1.79 (<0.1)	.27 (<0.1)	.48 (<0.1)	.64 (<0.1)	1.47 (<0.1)
<b>Total Standing Crop</b>						
mg/l dry weight	.284	.286	.299	.285	.473	1.551
g/m <sup>2</sup> dry weight	7.10	7.15	7.48	7.12	7.10	7.76

For the following reasons, 1968 data from station 50 is not used in the remainder of the report. Several cladocerans which were not present in 1970 were abundant at station 50 in 1968. The abundance of most taxa was very low at station 50 in 1968. The total standing crop was also very low at station 50 in 1968. On 10 of the 23 sampling dates in 1968, station 50 was in the river above the impoundment.

#### Depth Distribution of Zooplankton

At stations 0, 10 and 20, on selected dates, tows were made from two different depths to the surface. The deeper tows were made at the same locations and immediately preceded or followed the shallow tows. The ratios for number/liter calculated from the shallow tow divided by the number/liter calculated from the deep tow are shown in Tables 4, 5 and 6.

If the collecting and counting techniques were comparable between the two tows at a station and the same population was sampled, and if all of the organisms are above the shallow tow, then both tows should have collected the same number of organisms although the deeper tow would have filtered more water. Thus if tows are made from 25 and 100 meters to the surface, the ratio number/liter calculated from the shallow tow divided by number/liter calculated from the deep tow will equal the deeper depth (100 m) divided by the shallower depth (25 m). If some of the organisms are below 25 meters the number/liter ratio will

Table 4: Ratios number/liter shallow tow (25 meters) divided by number/liter deep tow (100 meters) for selected dates at station 0.

Date *	<u>D. pulex</u>		<u>D. galeata mendota</u>		<u>C. reticulata</u>		<u>B. longirostris</u>		<u>D. ashlandi</u>	<u>C. bicuspidatus thomasi</u>		<u>K. quadrata</u>	<u>Asplanchna spp.</u>
	1968	1970	1968	1970	1968	1970	1968	1970	1968	1968	1968	1968	
June (10)		3.05											
(19)		3.33		6.89									
(24)		1.51											
July 2 (3)	0.93	2.05	4.11		2.45	1.00			5.81	0.92	0.39	1.11	
8 (8)		2.68	7.20		2.69	0.95							
15 (16)	2.98	4.71	3.36	3.58	2.37	0.57	2.93	7.76	2.15	2.48	2.14		
23 (23)	4.12	2.59	6.26	2.89	3.33		3.75	3.34	5.01	2.70	3.85		
29 (29)		1.93	7.36		5.05		1.63						
Aug 6 (4)	2.80	3.08	5.42	2.75	3.25	2.29	3.25	3.69	2.57	5.53	9.12		
12 (10)	0.43	3.19	1.50	4.52	9.00	0.32	0.75	0.75	1.21	3.00			
19 (18)	3.14	1.87	0.88	6.76	5.60	4.00	0.48	6.23	3.58	7.00	5.80		
26 (25)	2.17	3.76	4.00	2.45	9.38	3.12	0.60	5.73	2.30	2.67			
Sept 3 (1)	3.49	2.83	9.70	2.17	0.70	0.44	0.16	9.60	3.24	6.40	5.16		
9 (9)	1.48		4.09	6.67	4.21	3.60		5.06	2.56	1.29	2.33		
17	2.17		3.33		0.92		1.11	1.19	1.25		1.98		
Oct 14	1.30		0.25					2.17	0.64				
22	1.81				5.00			1.05	1.27				
Mean	2.23	2.81	3.90	4.60	4.57	2.84	1.46	2.58	3.87	2.15	3.92	3.93	
t **	<u>5.53</u>	<u>4.90</u>	0.13	1.30	0.48	<u>2.37</u>	<u>4.49</u>	1.88	0.15	<u>4.89</u>	0.07	0.06	

\* Number in parenthesis is day of the month in 1970.

\*\* Calculated with paired t test. Underlined values deviate from 4 significantly at 2.5% level and indicate that zooplankters were below 25 meters.

Table 5: Ratios number/liter shallow tow (25 meters) divided by number/liter deep tow (50 meters) for selected dates at station 10.

Date*	<u>D.</u>		<u>C.</u>	<u>B. longi-</u>	<u>D.</u>	<u>C. bicus-</u>	<u>K.</u>	<u>Asplanchna</u>
	<u>galeata</u>							
	<u>D. pulex</u>	<u>mendota</u>	1968	1970	1968	1968	1968	1968
July 2 (3)	0.09	0.82				0.61		
8 (8)	1.33	1.76	1.00	0.79	4.51	0.90	0.42	1.81
15 (16)	3.33	3.49	4.36	4.52		1.19	1.46	1.85
29 (29)	3.12	2.19			5.14	2.12	3.96	1.58
Aug 12 (10)	0.77	0.44	1.06		1.21	0.32		0.20
19 (18)	3.02	2.71	4.51	5.34	6.94	5.15	2.43	7.83
26 (25)	1.76	1.53	2.84		2.75	4.69	1.29	1.91
Sept 3 (1)	2.09	2.59	1.27		1.37	3.44	2.00	0.45
9 (9)	1.17	2.59	0.52	1.55	1.75	2.34		1.39
17	1.88		0.84		3.00			
23	0.67		0.81		0.65	5.82		0.85
Oct 8	1.88	0.50	0.92		2.17			0.50
14	1.52	2.75	0.55	2.75	0.92	1.38		
22	1.04		1.51		1.25	1.29		
Mean	1.69	1.94	1.68	2.99	2.63	2.43	1.52	1.83
** t	0.79	0.16	0.77	1.14	1.13	0.80	0.15	0.23

\* Number in parenthesis is day of the month in 1970

\*\* Calculated with paired t test. Underlined values deviate from 2 significantly at 2.5% level and indicate zooplankters are below 25 meters.

Table 6: Ratios number/liter shallow tow (25 meters) divided by number/liter deep tow (50 meters) for selected dates at station 20.

Date	<u>D. galeata</u>		<u>C. reticulata</u>		<u>B. longi-rostris</u>		<u>D. ashlandi</u>	<u>C. bicuspidatus thomasi</u>	<u>K. quadrata</u>	<u>Asplanchna spp.</u>
	<u>1968</u>	<u>1970</u>	<u>1968</u>	<u>1970</u>	<u>1968</u>	<u>1970</u>	1968	1968	1968	1968
July 2 (3)		2.60			1.65			2.21		
15 (16)		2.44	3.71		2.97		1.24	0.44	4.96	0.68
23 (23)		1.60	2.84		1.23		2.11	2.26	1.33	0.80
29 (29)	0.10		2.41		3.08			3.65	2.50	3.21
Aug 12 (10)	2.16	1.21	1.77		3.08		0.23	1.16	3.33	1.93
19 (18)	4.04	2.01	1.43		0.36		2.24	3.17	1.43	2.06
Sept 9 (9)	2.53	2.53	2.48				1.90			
17	3.01	1.65	1.56				3.43	0.43		
Oct 2	1.00	1.00	1.00						1.00	
Mean	2.14	1.88	2.15		2.06		1.85	1.90	2.14	1.73
t**	0.85	0.83	0.48		0.13		0.32	0.20	0.69	0.57

\* Number in parenthesis is day of the month in 1970.

\*\* Calculated with paired t test. Underlined values deviate from 2 significantly at 2.5% level and indicate zooplankters are below 25 meters.

be less than the depth ratio (4 in this case). When no individuals are above 25 meters the number/liter ratio will be zero.

Thus the number/liter ratios in Tables 4, 5 and 6 should be between 0 and 4 for station 0 and between 0 and 2 for stations 10 and 20.

Although there is considerable scatter of individual values about the theoretical maximum, the mean value is very close to the maximum for most of the tested organisms i.e., most of the organisms were in the upper 25 meters. Exceptions were Daphnia pulex in 1968 and 1970, Ceriodaphnia reticulata in 1970, Bosmina longirostris in 1968 and Cyclops bicuspidatus thomasi in 1968, all of which had mean ratios significantly less than the maximums indicating that some individuals of these species were below 25 meters throughout the sampling period. In the case of Daphnia pulex, 30 to 40% of the individuals were below 25 meters. If 60% were above 25 meters, the ratio would be 2.40, i.e., 60% of the individuals diluted in 25 units of water (the depth) divided by 100% (all the individuals) diluted in 100 units of water (the depth) or  $\frac{.60 \text{ divided by } 25}{1.00 \text{ divided by } 100} = 2.40$ . These ratios assume that all of the individuals are above the deepest tow. The deepest tows were in fact taken from the bottom of the reservoir so this assumption should be valid. The scatter of the individual ratios is undoubtedly due to a combination of factors including variation in sampling and counting techniques, and nonuniform distribution of individuals.

Abundance and Percent Contribution to the Standing Crop 1968 vs. 1970

The comparisons in this section are based on data from Tables 2 and 3. The paired t test was used to determine statistical significance. Significant means the observed difference would occur less than 10% of the time due to chance.

Although the mean standing crop over all stations was 52% higher in 1970 than in 1968, the difference was not significant using only five pairs of data. The difference will be shown to be significant later in this report.

Significant changes in cladocerans, copepods and rotifers occurred in three years. The total number of cladocerans did not significantly increase but their contribution to the total standing crop did significantly increase from 1968 to 1970. The total number of copepods did not significantly change. Both the total number and the contribution to the total standing crop of the Rotifera increased from 1968 to 1970.

There were significant increases in both abundance and percent contribution to the total standing crop of the cladocerans, Daphnia galeata mendota, Chydorus sphaericus, the rotifers Polyarthra spp., Hexarthra spp. and the total of all life stages of the copepod Cyclops bicuspidatus thomasi.

There were significant increases in the abundance of both copepod nauplii, i.e., Cyclops bicuspidatus thomasi and Diaptomus ashlandi.

The contribution of these nauplii to the total standing crop was insignificant during both years.

There was no significant change in the abundance or contribution to the total standing crop of the cladocerans, Ceriodaphnia reticulata, Leydigia quadrangularis and Bosmina longirostris or the rotifer, Asplanchna spp.

There was a significant decrease both in the abundance and percent contribution of Diaptomus ashlandi (adults and copepodids) and Daphnia pulex.

The cladocerans, Diaphanosoma lechtenbergianum, Macrothrix rosea and Kurzia latissima, which were present in 1968 were not found in 1970 samples. Conversely the rotifers, Filinia spp., Conochilus unicornus, Syncheata spp., Euchlanis spp. and Notholca spp., which occurred in 1970 were not found in 1968 samples.

#### Comparison of Total Standing Crops and Contributions on a Seasonal Basis 1968 vs. 1970

These comparisons also use the paired t test. This test can give misleading results because the levels of significance are determined in part by the number of observations. In both this section and previously the test was used on means. The number of observations can be changed by suitable grouping of data. Because data in this section (Tables 7 and 8) are in smaller groups (more of them) the differences required to reach significance at the various probabilities is consid-



Table 7: Mean standing crop (mg/l), percent contribution of various taxa and mean number/liter of Daphnids on each date in 1968.

Date	<u>D. galeata mendota</u>		<u>D. pulex</u>		All Other Cladocera %	<u>D. ashlandi*</u>	<u>C. bicuspidatus thomasi*</u>	<u>Asplanchna spp.**</u>	Total Standing Crop		
	#/l	%	#/l	%					mg/l	g/m <sup>2</sup>	
May 27	6.15	8.1	23.03	41.3	0.3	28.2	22.1	0	0.378	8.34	
June 7	1.45	5.1	14.05	14.6	0.1	54.9	25.3	0	0.479	10.30	
12	23.62	15.8	16.49	43.9	0.9	17.3	22.1	0	0.375	8.27	
20	15.79	43.1	5.73	33.9	2.2	4.2	16.6	0	0.308	6.69	
27	20.61	42.1	9.27	24.6	2.4	12.1	18.9	0.4	0.490	10.55	
July 2	5.41	22.8	5.37	12.1	1.2	31.0	32.4	0.6	0.178	3.75	
8	11.00	23.3	2.32	7.9	3.5	29.5	34.6	1.2	0.118	2.45	
15	31.43	41.4	2.66	7.9	5.0	8.0	32.0	5.6	0.402	7.92	
23	30.60	47.9	2.91	6.6	9.3	5.2	21.2	9.8	0.530	11.11	
29	28.36	38.3	5.99	6.5	10.8	17.9	18.1	3.1	0.556	10.47	
Aug 6	24.67	37.3	1.96	3.7	6.9	20.8	29.2	2.2	0.430	8.01	
12	16.25	29.3	1.96	6.8	6.7	22.7	28.3	6.0	0.316	5.91	
19	6.15	18.0	2.66	14.5	5.5	28.3	23.8	10.0	0.256	5.51	
26	7.53	37.9	3.35	10.1	11.0	27.7	12.6	6.4	0.245	5.52	
Sept 3	13.27	31.4	3.29	11.9	10.0	17.8	27.3	1.4	0.359	5.67	
9	3.30	12.9	3.54	23.0	11.9	29.6	18.0	4.7	0.231	5.16	
17	1.56	9.3	2.28	27.2	6.7	27.6	20.1	9.2	0.109	2.48	
23	5.55	20.3	2.36	12.7	14.0	20.0	31.6	1.4	0.205	4.48	
Oct 2	4.64	18.6	2.38	16.9	10.6	22.3	31.4	0.3	0.155	3.41	
8	5.42	26.2	2.96	15.7	6.6	19.2	31.9	0.1	0.207	4.55	
17	1.34	12.4	1.73	20.3	5.5	26.4	34.9	0.3	0.119	2.55	
22	1.54	23.8	0.80	15.7	8.1	30.0	22.4	0	0.084	1.87	
Nov 2	0.56	7.0	1.53	19.8	2.1	38.4	33.9	0	0.110	2.31	
									Overall Means	0.289	6.11
									Means for Dates		
									Corresponding		
									to 1970 Data	0.342	7.23

\* Nauplii contributions are not significant.

\*\* Contribution of other Rotifera is not significant.

Table 8: Mean standing crop (mg/l), percent contribution of various taxa and mean number/liter of Daphnids on each date in 1970.

Date	<u>D. galeata mendota</u>		<u>D. pulex</u>		All Other Cladocera %	<u>D. ash-landi*</u>	<u>C. bicuspidatus thomasi*</u>	<u>Asplanchna spp.**</u>	<u>Polyarthra spp.**</u>	Total Standing Crop		
	#/l	%	#/l	%						mg/l		
June	10	5.15	23.2	2.94	12.6	4.9	4.9	38.2	11.8	4.5	0.246	3.16
	19	69.49	66.1	8.93	8.0	2.7	1.8	20.9	0.2	0.6	0.841	10.64
	24	50.16	72.2	5.31	7.6	3.2	1.9	14.7	0.1	0.3	0.695	8.60
July	3	27.85	49.7	12.49	24.4	3.9	0.8	14.3	0.3	0.2	0.616	8.36
	8	18.65	50.2	1.91	11.4	3.5	2.5	31.2	0.9	0.3	0.317	4.05
	16	43.27	52.9	1.15	4.2	2.2	1.0	39.2	0.1	0.4	0.696	8.23
	23	32.54	34.5	2.33	3.7	2.5	1.6	56.2	0.2	1.2	0.804	9.12
	29	26.79	38.1	1.52	3.6	2.6	1.6	52.7	0.3	1.1	0.600	6.85
Aug	4	25.76	24.4	2.06	3.2	2.2	3.6	65.6	0.4	0.2	0.907	10.21
	10	20.42	40.8	1.98	7.2	4.5	16.4	29.4	0.9	0.5	0.396	5.30
	18	19.40	31.9	2.26	6.6	5.7	3.0	49.5	2.8	0.5	0.576	6.78
Sept	25	18.36	31.0	1.78	4.3	5.7	4.6	45.9	2.6	1.0	0.680	7.54
	1	6.65	22.7	2.27	19.0	12.0	5.2	31.0	6.8	2.4	0.251	3.43
	9	12.69	24.7	5.82	17.4	15.3	8.1	29.1	2.7	1.7	0.309	4.35
										Overall Means	0.542	6.90

\* Nauplii contributions are not significant.

\*\* Contribution of other Rotifera is not significant.

erably lower.

The mean total standing crop for comparable time periods (14 data pairs) increased from 0.342 mg/l in 1968 to 0.542 mg/l in 1970. This increase is significant at the 0.5% level ( $t = 3.25$ ).

Both the abundance and contribution of Daphnia galeata mendota was significantly (1% level) greater in 1970. The abundance and the contribution of Daphnia pulex was significantly (10% level) less in 1970.

The total contribution of all other cladocerans to the total standing crop was not significantly different from 1968 to 1970.

The decrease in contribution to the total standing crop of the copepod Diaptomus ashlandi from 21.2 percent in 1968 to 4.1 percent in 1970 was significant at the 0.5% level. Similarly the increased contribution of Cyclops bicuspidatus thomasi from 1968 to 1970 was significant at the 0.5% level.

In the rotifera, the contributions of Polyarthra spp. and Hexarthra spp. significantly (0.5% level) increased and the contribution of Asplanchna spp. did not significantly change.

#### Length of Daphnia Species

The mean length of Daphnia pulex was about 20% greater than the mean length of Daphnia galeata mendota in both years (significant at 1%,  $t$  test). Although there were slight increases in length for both species from 1968 to 1970 (Table 9), these increases are not signifi-

Table 9: Mean lengths of *Daphnia* spp. in millimeters by date and station in 1968 and 1970.

Date	<i>D. galeata</i>		<i>D. pulex</i>	
	<i>mendota</i>			
	1968	1970	1968	1970
June 7 (10)	0.62	0.89	0.80	1.10
12 (19)	0.96	0.81	0.72	0.96
20 (24)	0.94	0.91	1.20	1.07
27	1.00		1.25	
July 2 (3)	0.95	0.91	1.20	1.12
8 (8)	1.01	0.98	0.80	1.48
15 (16)	0.85	1.03	1.15	1.75
23 (23)	0.93	1.05	1.18	1.20
29 (29)	0.95	1.09	1.03	1.28
Aug 6 (4)	0.91	1.07	0.96	1.23
12 (10)	0.87	0.98	1.10	1.31
19 (18)	0.95	1.04	1.26	1.38
26 (25)	0.97	1.13	1.40	1.36
Sept 3 (1)	0.99	1.01	1.19	1.21
9 (9)	1.05	0.93	1.30	1.28
17	0.92		1.20	
23	0.95		1.09	
Oct 2	0.90		1.03	
8	1.07		1.26	
14	1.09		1.34	
22	1.20		1.30	
Nov 2	1.23		1.27	
Station				
0	1.09	1.02	1.23	1.32
10	0.92	0.99	1.10	1.32
20	1.03	1.00	1.25	1.08
30	0.85	0.98	1.15	1.20
40	0.90	0.98	1.13	**
50	**	0.97	0.78	**
Mean***	0.96	0.99	1.20	1.25
Standard Deviation	0.20	0.12	0.23	0.27

\* Parenthesis indicates day of month for 1970.

\*\* Too few to average.

\*\*\* Mean of the means at each station for each year.

cant. using grouped data for the t tests. The increases are so small that a t test was not performed using all data.

The mean lengths of both species were shortest during June of both years. The maximum mean lengths for both species occurred during October in 1968 and during August in 1970. Sampling did not continue past September 9th in 1970.

The mean lengths should vary with the rate of population increase ( $r$ ). During periods of rapid increase (high  $r$ 's) relatively large numbers of immature (smaller) individuals should be present. However, there were no significant correlations between the mean lengths and any of the population parameters which were calculated (Tables 11 through 14) for either species in either year.

The minimum, maximum and mean length of all egg carrying females of both species were calculated for both years (Table 10). This data indicates that Daphnia pulex was about 20% longer than Daphnia galeata mendota both at the onset of reproduction and throughout the reproductive period.

The minimum, maximum and mean length values of both species increased from 1968 to 1970, but the increases of the means are much less than one standard deviation and are probably due to random error.

The mean length of egg carrying females of each species was about 40% greater than the mean length of all individuals of that species.

Table 10: Minimum, maximum and mean lengths of all egg carrying females in 1968 and 1970 in millimeters.

	<u>D. galeata</u>		<u>D. pulex</u>	
	<u>mendota</u>			
	1968	1970	1968	1970
Minimum	1.03	1.23	1.26	1.46
Maximum	2.23	2.29	2.86	2.89
Mean	1.61	1.72	1.95	2.09
Standard Deviation	0.27	0.25	0.29	0.30

### Population Parameters of Daphnia Species

Birth rates, death rates and rates of population increase calculated for each station resulted in many undefined and infinite rates. These rates were the outcome of population densities so low that the number of individuals and/or the number of eggs collected in a finite sample was zero. Consequently, the only parameters reported here are for data grouped over all stations (Tables 11, 12, 13 and 14). The comparisons which follow were based on similar dates in 1968 and 1970.

The mean birth and death rates (b and d) of Daphnia pulex were lower than the mean rates of Daphnia galeata mendota in 1968 and 1970 but the differences were significant only in 1970 (10% level, t test). The mean birth rate of both species increased from 1968 to 1970, but the increase was significant for Daphnia galeata mendota (10% level) only. The mean death rate of Daphnia galeata mendota insignificantly increased from 1968 to 1970 while the mean death rate of Daphnia pulex significantly decreased. This decrease probably reflects an actual decrease but may be the result of sampling and/or counting errors caused by the very low population densities of Daphnia pulex in 1970.

### Correlations of Zooplankton Parameters and Phytoplankton Parameters by Stations

Soltero (1971) gathered extensive physical, chemical and phyto-logical data at the same stations and on the same dates as the zoo-

Table 11: Population data for D. pulex, 1968 mean of all stations except 50.

Date	Number per liter (N)	Eggs per liter (E)	Egg duration in days (D)	Finite birth rate (B)	Instantaneous birth rate (b)	Population change rate (r)	Mortality rate (d)
May 27	39.03	9.77	9	.03			
June 7	17.46	1.03	5	.01	.01	-.07	+.08
12	41.19	9.27	4	.06	.06	+.17	-.11
20	5.73	2.58	3	.15	.17	-.25	+.42
27	9.27	.18	3	.01	.01	+.07	-.06
July 2	5.37	.08	3	.01	.01	-.09	+.10
8	2.32	.24	3	.03	.03	-.14	+.17
15	2.66	.14	2	.03	.03	+.02	+.01
23	2.91	.36	2	.06	.06	+.01	+.05
29	5.99	1.35	2	.11	.10	+.12	-.02
Aug. 6	1.96	.55	2	.14	.15	-.14	+.29
12	1.96	.04	2	.01			
19	2.66	.34	2	.06	.06	+.04	+.02
26	3.35	1.25	2	.19	.19	+.03	+.21
Sept. 3	3.29	.46	3	.05	.05	-.01	+.05
9	3.54	.29	3	.03	.03	+.01	+.02
17	2.28	.18	3	.03	.03	-.06	+.09
23	2.36	.11	3	.02	.02	+.01	+.01
Oct. 2	2.38	.51	3	.07	.07	+.001	+.07
8	2.96	.78	4	.07	.07	+.04	+.03
14	1.73	.72	4	.10	.11	-.09	+.20
22	.80	.09	4	.03	.03	-.09	+.12
Nov. 2	1.53	1.92	5	.25	.24	+.07	+.17



Table 12: Population data for D. galeata mendota, 1968 mean of all stations except 50.

Date	Number per liter (N)	Eggs per liter (E)	Egg duration in days (D)	Finite birth rate (B)	Instantaneous birth rate (b)	Population change rate (r)	Mortality rate (d)
May 27	6.15	1.56	9	.03			
June 7	1.45	.63	5	.09	.10	-.14	+.24
12	23.62	6.97	4	.07	.07	+.07	0
20	15.79	4.56	3	.10	.10	-.05	+.15
27	20.61	4.06	3	.07	.06	+.04	+.02
July 2	5.41	.48	3	.03	.03	-.22	+.25
8	11.00	5.02	3	.15	.14	+.12	+.02
15	31.43	15.25	2	.24	.22	+.15	+.07
23	30.60	4.06	2	.07	.07	-.003	+.07
29	28.36	5.45	2	.10	.10	-.01	+.11
Aug. 6	24.67	12.12	2	.25	.25	-.02	+.27
12	16.25	2.33	2	.07	.07	-.07	+.14
19	6.15	.65	2	.05	.05	-.14	+.19
26	7.53	.88	2	.06	.06	+.03	+.03
Sept. 3	13.27	4.11	3	.10	.10	+.07	+.03
9	3.30	.41	3	.04	.04	-.20	+.24
17	1.56	.48	3	.10	.11	-.09	+.20
23	5.55	1.23	3	.07	.07	+.21	-.14
Oct. 2	4.64	2.45	3	.15	.15	-.03	+.18
8	5.42	1.46	4	.07	.07	+.03	+.04
14	1.34	.05	4	.01	.01	-.20	+.21
22	1.54	.28	4	.05	.05	+.02	+.03
Nov. 2	.56	.56	5	.20	.22	-.15	+.37

Table 13: Population data for D. pulex, 1970 mean of all stations.

Date	Number per liter (N)	Eggs per liter (E)	Egg duration in days (D)	Finite birth rate (B)	Instantaneous birth rate (b)	Population change rate (r)	Mortality rate (d)
June 10	2.94	0	4	0			
19	8.93	.60	4	.02	.02	+.12	-.14
24	5.31	1.13	3	.07	.07	-.10	+.17
July 3	12.49	.13	2	.01	.01	+.10	-.09
8	1.91	.55	2	.14	.17	-.38	+.55
16	1.15	0	2	0	0	-.06	+.06
23	2.33	.10	2	.02	.02	+.10	-.08
29	1.52	.45	2	.15	.16	-.07	+.23
Aug. 4	2.06	.09	2	.02	.02	+.05	-.03
10	1.98	1.64	2	.41	.41	-.01	+.42
18	2.26	.21	2	.05	.05	+.02	+.03
25	1.78	.52	2	.15	.15	-.03	+.18
Sept. 1	2.27	.22	2	.05	.05	+.04	+.01
9	2.82	.55	2	.10	.10	+.03	+.07

Table 14: Population data for D. galeata mendota, 1970 mean of all stations.

Date		Number per liter (N)	Eggs per liter (E)	Egg duration in days (D)	Finite birth rate (B)	Instantaneous birth rate (b)	Population change rate (r)	Mortality rate (d)
June	10	5.65	2.16	4				
	19	69.49	8.44	4	.03	.01	+.28	-.27
	24	50.16	13.61	3	.09	.09	-.05	+.04
July	3	27.85	5.44	2	.09	.10	-.08	+.18
	8	18.65	1.35	2	.03	.04	-.06	+.10
	16	43.27	34.10	2	.39	.37	+.12	+.25
	23	32.54	12.94	2	.20	.20	-.04	+.24
	29	26.79	15.83	2	.29	.30	-.03	+.33
Aug.	4	25.76	12.24	2	.23	.24	-.01	+.25
	10	20.42	10.65	2	.26	.27	-.03	+.30
	18	19.40	11.33	2	.29	.29	-.01	+.30
	25	18.36	10.77	2	.29	.29	-.01	+.30
Sept.	1	6.65	0.73	2	.05	.06	-.15	+.21
	9	12.69	0.40	2	.01	.02	+.09	-.07

plankton collections made for this study. Selected zooplankton parameters were examined for correlations with the phytological data. Those parameters for which the correlation coefficient was significant at the 5% level (or higher) are given in this and the following sections.

In 1968 the total standing crop of zooplankton was negatively correlated ( $r=-.89$ ) with the total standing crop of phytoplankton and Myxophyceae ( $r=-.85$ ).

The abundance of Daphnia pulex was negatively correlated with total standing crop of phytoplankton ( $r=-.88$ ) and Myxophyceae ( $r=-.95$ ).

The abundance of Daphnia galeata mendota was positively correlated with microplankton ( $r=.96$ ).

The abundance of Diaptomus ashlandi adults was negatively correlated with total phytoplankton ( $r=-.86$ ) and Myxophyceae ( $r=-.92$ ). The abundance of copepodites was also negatively correlated with total phytoplankton ( $r=-.81$ ) and with Myxophyceae ( $r=-.89$ ). However, the abundance of Diaptomus ashlandi nauplii was positively correlated with chlorophyll a ( $r=.82$ ).

The abundance of Cyclops bicuspidatus thomasi nauplii was positively correlated with microplankton ( $r=.86$ ) and chlorophyll a ( $r=.88$ ).

Polyarthra spp. abundance was positively correlated with microplankton ( $r=.93$ ).

Keratella cochlearis abundance was positively correlated with to-

tal phytoplankton ( $r=.87$ ), Myxophyceae ( $r=.90$ ), microplankton ( $r=.85$ ), and chlorophyll a ( $r=.98$ ).

Asplanchna spp. abundance was negatively correlated with total phytoplankton ( $r=-.86$ ) and Myxophyceae ( $r=-.83$ ).

In 1970 the total standing crop of zooplankton was positively correlated with Cryptophyceae ( $r=.76$ ) and with microplankton ( $r=.99$ ).

Daphnia pulex abundance was positively correlated with Myxophyceae ( $r=.93$ ) and negatively correlated with Cryptophyceae ( $r=-.85$ ) and chlorophyll a ( $r=-.92$ ).

Daphnia galeata mendota abundance was positively correlated with Cryptophyceae ( $r=.81$ ) and with microplankton ( $r=.98$ ).

None of the life stages of Diaptomus ashlandi were correlated with any of the phytological parameters in 1970.

The abundance of Cyclops bicuspidatus thomasi adults was positively correlated with Cryptophyceae ( $r=.81$ ) and microplankton ( $r=.98$ ). Copepodite abundance was positively correlated with Cryptophyceae ( $r=.85$ ) while nauplii abundance was positively correlated with Cryptophyceae ( $r=.82$ ), microplankton ( $r=.89$ ) and chlorophyll a ( $r=.99$ ).

Polyarthra spp. abundance was negatively correlated with Myxophyceae ( $r=-.77$ ), and positively correlated with Cryptophyceae ( $r=.90$ ), microplankton ( $r=.92$ ) and chlorophyll a ( $r=.78$ ).

Asplanchna spp. abundance was positively correlated with chloro-

phyll a ( $r=.86$ ).

Ascomorpha spp. abundance was positively correlated with microplankton ( $r=.99$ ).

Correlations of Phytoplankton Parameters and Selected Zooplankton Parameters by Dates

In 1968 the total standing crop of zooplankton was significantly (5% level) positively correlated with the abundance of Chlorophyceae ( $r=.63$ ), Cryptophyceae ( $r=.41$ ), microplankton ( $r=.50$ ) and chlorophyll a ( $r=.43$ ).

The abundance of Daphnia pulex was not correlated with any of the phytological data while Daphnia galeata mendota abundance was positively correlated with total phytoplankton ( $r=.77$ ), Chlorophyceae ( $r=.40$ ), Cryptophyceae ( $r=.62$ ) and microplankton ( $r=.50$ ). None of the rates (b, r or d) calculated for either species were correlated with any of the phytological parameters.

In 1970, the total standing crop of zooplankton ( $r=.53$ ) and the abundance of Daphnia galeata mendota ( $r=.78$ ) were positively correlated with chlorophyll a.

The abundance of Daphnia pulex was negatively correlated with the total phytoplankton ( $r=-.61$ ).

The birth rate (b) of Daphnia galeata mendota was positively correlated with total phytoplankton ( $r=.60$ ) and microplankton ( $r=.54$ ).

The rate of increase ( $r$ ) of Daphnia galeata mendota was positively correlated ( $r=.58$ ) with chlorophyll a, and the death rate ( $d$ ) was positively correlated ( $r=.58$ ) with total phytoplankton.

The birth rate of Daphnia pulex was positively correlated ( $r=.60$ ) with microplankton.

### predation

Predation could affect the abundance of zooplankton. However, Leptodora kindtii and Chaoborus spp., the commonest invertebrate predators of zooplankton, were not present in Bighorn Lake.

Rainbow trout, a filter feeding planktivore, was present in the reservoir. The Montana Fish and Game Department planted more than 2 million 0-6 inch rainbow trout in Bighorn Lake between 1967 and 1970 (Montana Fish and Game Department records, 1975).

Many samples contained Cyclops bicuspidatus thomasi adults attached to and presumably eating Diaptomus ashlandi adults and copepodites.

## DISCUSSION

### Ecological Separation of Daphnia Species

Most of the planktonic crustaceans and some of the planktonic rotifers undergo substantial diurnal vertical migration. Some populations of these organisms may occur in fairly discreet "bands" less than 10 meters thick which contain more than 90% of the population (Hutchinson, 1967). Thus, even if the population densities of different taxa are the same (as determined by oblique tows from one depth), the taxa can be partitioning the spatial resources in the sense of MacArthur (1958), Brown (1973), and others. There is direct evidence of spatial separation between Daphnia pulex and Daphnia galeata mendota in the study. On an average basis throughout the sampling periods, 30 to 40% of the Daphnia pulex population was below 25 meters while essentially all of the Daphnia galeata mendota population was above 25 meters. The results of this study do not permit an estimation of the degree of spatial separation between the remaining 60 to 70% of the Daphnia pulex population and the Daphnia galeata mendota population.

Huxley (1942) proposed and Lack (1944) documented that size differences between cogenetic species could cause ecological isolation. Hutchinson (1959) tentatively estimated that the size difference necessary for such isolation would require a ratio of trophic structure size of the larger to the smaller of about 1.28. In both 1968 and 1970, the



ratio of mean body lengths of the larger Daphnia pulex to the smaller Daphnia galeata mendota was about 1.25. This partitioning of resources due to size difference presumably results from 1) larger animals being capable of eating larger food items (Burns, 1968; Dodson, 1974; Brooks and Dodson, 1965; and numerous others) and 2) larger animals having greater gathering efficiencies for smaller food items than smaller animals (Brooks and Dodson, 1965; Burns, 1969). In order for the size difference to be completely effective it would be necessary that the smallest life stage of the larger species always be larger than any life stage of the smaller species if both species eat the same food at all life stages (Hutchinson, 1959). The life stages of Daphnia pulex and Daphnia galeata mendota overlap in size and, unfortunately, the foods eaten at different stages are not known.

Daphnia species may have different temperature optima. Burns (1969) has demonstrated (in vitro) that for animals of the same weight, Daphnia pulex filtered food particles from the environment considerably faster than Daphnia galeata mendota at 15°C. At 20 and 25°C Daphnia galeata mendota filtered faster than Daphnia pulex. These laboratory results are in accord with the actual temporal distribution of these species in the study. Daphnia pulex was most abundant and its birth rate (b) was highest in May and June when water temperatures were less than 20°C (Soltero, 1971). There was a peak in Daphnia pulex abundance

in July of 1970 and several peaks in the birth rate during the warmer periods of both 1968 and 1970 which cannot be explained on this basis. During these midseason peaks of Daphnia pulex birth rates, the population density was very low and there were corresponding peaks in mortality (d) which prevented appreciable changes in density. These high mortality and birth rate estimates may be inaccurate as the population densities were so low that sampling errors could have caused the large changes observed in the population estimates. Furthermore, even if changes in density were real, the calculation of birth rates may not be accurate for populations which are changing greatly in numbers (Hutchinson, 1967).

The Daphnia species tended to occupy geographically different sites. The majority of the Daphnia pulex population occurred at station 0 while Daphnia galeata mendota was most common further "upstream". There were no correlations of any parameters of Daphnia pulex with any phytological parameters on a station basis in 1968, but in 1970 Daphnia pulex abundance was positively correlated with Myxophyceae abundance and negatively correlated with Cryptophyceae abundance and chlorophyll a concentration on a station basis. It is possible that Daphnia pulex is better able to utilize very small particles (or lower densities) of algae for food than Daphnia galeata mendota which would be substantiated by the negative correlations with the chlorophyll concentration.

This is supported by the greater filtering rate at lower temperatures of Daphnia pulex and its abundance at greater depths where the temperatures are lower and the amount of food (and chlorophyll) were probably less. Other possible explanations for the abundance of Daphnia pulex near the dam are the greater depth (over 100 meters) and the demonstrated greater depth distribution of Daphnia pulex which may enable it to out compete Daphnia galeata mendota in deeper areas.

The longer turnover times (1/b) of Daphnia pulex (11 days versus 5.9 to 10 days for Daphnia galeata mendota) may also contribute to their geographical separation. Longer turnover times would make Daphnia pulex less able to maintain its position against the flow-through effect in the reservoir. Soltero (1971) established mean flushing times of 108 and 184 days in 1968 and 1970 respectively. These flushing rates imply that plankters could have passively moved up to 0.6 miles a day in 1968 and 0.2 miles a day in 1970. Because of the complexity of the currents in the reservoir (Soltero, 1971) it was not possible to substantiate this possibility. However, the occurrence of negative death rates at individual stations, as mentioned earlier, supports this possibility.

Still another factor which may enable the two Daphnia species to coexist is nonselective predation. There was a significant decrease in the abundance of Daphnia pulex from 1968 to 1970, although there was no change in its birth rate and a significant decrease in its death rate.

These results imply that at the low population densities of Daphnia pulex in 1970 (generally less than 3 individuals/liter) it was not worthwhile for predators to selectively pursue Daphnia pulex.

#### Relationships Between Zooplankton and Phytoplankton in 1968

Positive correlations between total standing crops of zooplankton and phytoplankton on a station basis did not exist when data from all dates were compared. The correlation on a station basis may reflect only a similar location of abundances, especially since there was also a positive correlation between total standing crops of zooplankton and Myxophyceae. The Myxophyceae are not considered suitable food for most zooplankton (Hutchinson, 1967; Burns, 1968; Arnold, 1971).

Most other correlations between zooplankton abundances and phyto-logical parameters on a station basis probably also reflect location rather than causitive relationships. However, the positive relationship of Diaptomus ashlandi abundance with total phytoplankton, Cyclops bicuspidatus thomasi with microplankton and chlorophyll a, and Polyarthra spp. with microplankton are interesting and may reflect nutritional relationships.

When data from all stations are grouped on the basis of date, the total standing crops of zooplankton and Daphnia galeata mendota abundances were positively correlated with chlorophyll a, Chlorophyceae, Cryptophyceae and microplankton. In addition, Daphnia galeata mendota

abundance was positively correlated with total phytoplankton standing crop. These results indicate that the abundance of this zooplankton community as a whole, and Daphnia galeata mendota in particular, was related to the abundance of the phytoplankton. Although detritus and bacteria are probably important energy sources at times, the phytoplankton normally constitute the primary food source of zooplankton (Saunders, 1969).

The lack of correlations between the birth rates (b), and rates of increase (r), and the phytoplankton parameters is not surprising as changes in these rates could lag behind the changes in the phytoplankton parameters. In addition, there are indications that zooplankton distributions may have been affected by currents. This would have confused relationships between zooplankton and phytoplankton parameters.

It is worth noting that there were no correlations in 1968 between Daphnia pulex abundances (or other population parameters) and any phytoplankton parameter.

#### Relationships Between Zooplankton and Phytoplankton in 1970

The positive correlations between the total standing crop of zooplankton and chlorophyll a concentrations (on a date basis) indicate that in both 1968 and 1970, greater amounts of zooplankton occurred at higher levels of phytoplankton. On a date basis, microplankton appeared to be a major factor in this relationship as its abundance was cor-

related with the total standing crop of zooplankton, the abundances of Daphnia galeata mendota and Cyclops bicuspidatus thomasi and several of the rotifers.

In contrast, Daphnia pulex abundance was negatively correlated with both chlorophyll a (on a station basis) and total phytoplankton (on a date basis) indicating the abundance of this species was probably related to factors other than food supply. Temperature was one such factor as Daphnia pulex was most abundant and algae were least abundant early in the season. Temperature is discussed in the first section of the Discussion. Predation is another possible reason for the lack of relationship with food supply. This possibility is supported by the positive correlation (on a date basis) between the birth rate (b) of Daphnia pulex and microplankton abundance. Although the birth rate increased with increasing supply of a suitable food (microplankton), the Daphnia pulex population did not increase in response.

Daphnia galeata mendota abundance on a station basis and birth rate (b), rate of increase (r) and death rate (d) on a date basis were all positively correlated with microplankton abundance or some other phytological parameter. This indicates that food supply was an important factor affecting the size of the Daphnia galeata mendota population. This assumption is supported by the increase in relative contribution of Daphnia galeata mendota to the total standing crop of zoo-

plankton from 1968 to 1970. The increasing death rate (d) of Daphnia galeata mendota with increasing abundance of total phytoplankton is interesting, but can be explained in two ways. The first is that the total phytoplankton abundance is greatly affected by the abundance of Myxophyceae which are not important food items. The second is the possibility of increased predation during periods of high abundances of total phytoplankton.

#### Changes From 1968 to 1970

The mean total standing crop of zooplankton increased from 0.35 mg/l in 1968 to 0.57 mg/l (dry weight) in 1970. There was comparable increase in total phytoplankton standing crop (Soltero, 1971). The mean standing crop of zooplankton was highest at station 0 (near the dam) in 1968 and highest at station 50 in 1970. The total standing crop of algae was highest at station 3 in 1968 and station 2 in 1970 (Soltero, 1971). This difference in the locations of maxima in 1968 may be due to the comparatively rapid mean flushing rate (108 days) in 1968. The turnover times for most of the zooplankton are higher than for most of the phytoplankton (Fenchel, 1974) and thus, the zooplankton may have accumulated at the dam.

Most zooplankton taxa were more abundant in 1970 than in 1968, but only Daphnia galeata mendota, Cyclops bicuspidatus thomasi and some of the rotifers increased significantly. Conversely, Daphnia pulex and

Diaptomus ashlandi were significantly less abundant in 1970.

Several species of cladocerans which are common in the littoral area of lakes and ponds were present in 1968 but not in 1970. These species were Diaphanosoma leuchtenbergianum, Moina rectirostris and Kurzia latissima. These species are probably fugitive species in the sense of Hutchinson (1951).

Although Daphnia pulex was less abundant in 1970 than in 1968 it probably is not a fugitive species due to the ecological separating factors discussed in another section of this report.

#### Production of Daphnia Species

If the carbon content of zooplankton is assumed to be 40% (Sverdrup, Johnson and Fleming, 1942) then the average biomass for comparable time periods was 0.076 and 0.058 g C/m<sup>2</sup> for Daphnia pulex and 0.23 and 0.47 g C/m<sup>2</sup> for Daphnia galeata mendota for 1968 and 1970 respectively.

The average birth rates of Daphnia pulex were 0.07 and 0.09, and those of Daphnia galeata mendota were 0.10 and 0.17 in 1968 and 1970. These birth rates correspond to average turnover rates of 14.3 and 11.1 days for Daphnia pulex and of 10.0 and 5.9 days for Daphnia galeata mendota in 1968 and 1970 respectively. These values imply an average production rate of 0.033 and 0.26 g C/m<sup>2</sup>/day for Daphnia pulex in 1968 and 1970. Production rates of Daphnia galeata mendota were 0.099 and



0.21 g C/m<sup>2</sup>/day.

Soltero (1971) estimated the primary production of this reservoir at 0.51 and 1.42 g C/m<sup>2</sup>/day in 1968 and 1970. The production of Daphnia pulex consumed 6.5% and 5.1% of the gross primary production in 1968 and 1970. Production of Daphnia galeata mendota consumed 19% and 14% of the gross primary production in 1968 and 1970, respectively.

The average respiratory rate of Daphnia for temperatures and sizes encountered in this study would be 0.26 g C/g C/day (LeSeur, 1959). In the case of Daphnia pulex, respiration would account for 0.02 g C/m<sup>2</sup>/day in both years. Respiration of Daphnia galeata mendota would account for 0.06 and 0.12 g C/m<sup>2</sup>/day in 1968 and 1970, respectively.

Considering Daphnia assimilation to be the sum of net production plus respiration, assimilation of Daphnia pulex (0.035 and 0.028 g C/m<sup>2</sup>/day) was 6.9 and 5.5% of gross primary production in 1968 and 1970. Corresponding values for Daphnia galeata mendota were 31% and 25%.

The decrease in the assimilation of Daphnia pulex from 1968 through 1970 was much less than the decrease in the abundance (from 11 to 3.6/l). This implies that assimilation per individual increased at low population densities. This has not been recorded in the literature and very likely results from sampling or analytical errors.

Copepod production was not estimated. The contribution of the group to the total standing crop of zooplankton did not significantly

change from 1968 to 1970. However, Cyclops bicuspidatus thomasi accounted for a much larger portion of the standing crop in 1970 than in 1968. Despite the change in species it is reasonable to assume that production of the group did not decline and that it probably increased as the abundance of nauplii, especially of Diaptomus ashlandi significantly increased.

Rotifera production was not estimated either, but because this group was significantly more abundant in 1970, it is reasonable to assume that production increased from 1968 to 1970.

#### Predation

Kerfoot (1975) and Dodson (1974) have emphasized the importance of invertebrate predation on the size composition of the zooplankton community. Such predation is usually restricted to smaller zooplankton. Predation by Cyclops bicuspidatus thomasi on Diaptomus ashlandi would explain the concurrent decline in Diaptomus ashlandi abundance and increase in Cyclops bicuspidatus thomasi abundance. This hypothesis is substantiated by the significant increase in abundance of Diaptomus ashlandi nauplii and concurrent decrease in abundance of Diaptomus ashlandi adults and copepodites in 1968 and 1970.

Several investigators have documented shifts in dominance by larger to smaller zooplankters caused by size selective predation by planktivorous fish (Brooks and Dodson, 1965; Galbraith, 1967). Gal-

braith (1967) showed that the introduction of rainbow trout into a lake which lacked fish planktivores caused the replacement of Daphnia pulex by smaller daphnids within four years. This shift in species decreased the mean length of daphnids from 1.4 mm to 0.8 mm. The decrease in abundance of Daphnia pulex from 1968 to 1970 is in accord with size selective predation as this species was 20% longer than Daphnia galeata mendota. However, the combined contribution of these two species to the zooplankton standing crop did not significantly change from 1968 to 1970. Furthermore, there was no significant change in the mean length of either species.

Hall (et.al., 1970) presented evidence that planktivorous fish production is not related to total zooplankton production, but is related to the production of larger zooplankters. The decrease in percentage of the total gross primary productivity assimilated by Daphnia galeata mendota and Daphnia pulex in 1970 indicates that less of the primary productivity was available for fish consumption as large zooplankters.

The rainbow trout planted by the Montana Fish and Game Department together with increases in riverine fish populations trapped in the reservoir would have increased size selective predation during this study. This increase in size selective predation is probably the reason for the decline in assimilation by large zooplankters and the de-

crease in abundance of the larger Daphnia pulex.

## CONCLUSIONS

Daphnia pulex and Daphnia galeata mendota were not competing directly in this reservoir. They were most abundant at different times and at different depths and horizontal locations. In addition, significant size differences would have enabled them to partition food resources even if both species were present at the same location at the same time.

Selective predation by fish on larger zooplankters can decrease the populations and production of larger zooplankters. The abundance and the contribution of Daphnia species to the total standing crop did not significantly change from 1968 to 1970. However, the decreased abundance of the larger Daphnia pulex and the decreased percentage of the gross primary productivity assimilated by Daphnia species probably resulted from increased size selective predation by fish. Predation by the smaller Cyclops bicuspidatus thomasi on the larger Diaptomus ashlandi also increased from 1968 to 1970. A continuation and intensification of such predation would result in lower abundances of large zooplankters and could result in a decline in fish production.

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