Secondary Production

Zooplankton

Methods

Pelagic crustacean zooplankton were sampled with a Clarke–Bumpus plankton sampler (Clarke and Bumpus 1950) fitted with a No. 10 (153 micron) plankton net. Hauls were made from a utility boat equipped with an outboard motor and a davit, from which the towing line angle could be measured and controlled (Brown and Ball 1940). Hauls were made generally down the long axis of the reservoir, and over the old river channel (areas of greatest depth). As the reservoir was drawn down, we shifted the haul track slightly west in order to minimize the risk of striking the bottom with the sampler (Figure 11).

A Clarke–Bumpus sampler is "especially good in large lakes with small (zooplankton) populations" (Edmondson and Winberg 1971). We rejected the use of vertical hauls of a plankton net (the method used on the reservoir during Stage I in 1979-80) for several reasons. It is well documented that zooplankton is generally not distributed evenly, or at random within a lake, but often is patchy, occurring in very variable densities. Lengthy hauls of a sampler within horizontal strata will strongly tend to smooth, or integrate this patchiness, should it occur. Furthermore, there is usually a strong vertical gradient in abundance related to temperature, light penetration, and phytoplankton abundance. For our purpose of obtaining a measure of generalized zooplankton standing crop that could be used in estimates of potential fish production, we desired average zooplankton densities over a large area and lake volume.

Although vertical hauls of a plankton net can give valid relative comparisons, they cannot guarantee completely quantitative evaluation. This method also has the serious disadvantage of giving a spatially much reduced sampling (Edmondson and Winberg 1971). Further, in order to derive a quantitative measure of the actual density of plankton present, a correction must be made for the well–known fact that plankton nets often do not sample at anywhere near 100 percent efficiency. Rather, net efficiency is more typically on the order of 40 to 60 percent (Hall *et al.* 1970). These efficiencies are representative of more eutrophic systems than Spada Lake, but where commonly found such as in this system, *Holopedium* can reduce net efficiencies similarly. Pederson (1974) placed a current meter in the mouth of the net and determined that it filtered about 47 percent of the volume of the water column through which it was hauled. Although the net attached to a Clarke–Bumpus sampler also is not 100 percent efficient, this is not a problem, since the sampler is designed in such a way that only the water actually passing through it and into the net is measured, and there is no need to make any correction.

We calibrated our C–B sampler in a controlled test flume at the Harris Hydraulics Laboratory at the University of Washington on January 16, 1997. The unit was tested with and without a net attached, and at two velocities. An average value of 4.084 liters/revolution was used in all further calculations of lake water sampled.

We sampled the reservoir every two weeks, beginning on April 10, and ending on October 20, 1997. (A semi–quantitative tow was made on November 14 to verify the absence of *Cyclops*, and the abundance of *Epischura*.)

Oblique (stepwise) hauls were made within 15–ft (4.57 m) strata down the centerline of the reservoir (Figure 12). Tows were of variable duration, generally a minimum of four minutes. Haul lengths were adjusted to prevent excessive clogging of the sample bucket by *Holopedium gibberum*, the most common plankter in Spada Lake. We strove to keep the backwater level above the bucket to a maximum of 1 to 2 cm, and adjusted the haul timing accordingly. Hauls in the surface stratum were generally 4 to 5 minutes; in the depauperate lower strata hauls were made up to 20 minutes.

We generally sampled the top four strata (60 ft), but added deeper layers as the summer progressed, and at least trace levels of organisms were encountered below 60 feet (18 m).

Replicate pelagic hauls were made on several occasions to check on the variability in plankton density between hauls. Replicates were made in the same direction, and for the same length of time.

We sampled the littoral zone of the reservoir on July 3, 1997, by slowly towing a 153 micron plankton net through the top one meter. The net had a mouth diameter of approximately 6" (15 cm). We hauled as close to the shoreline as possible, avoiding stumps and other woody debris. Some submerged grass and aquatic macrophytes were physically brushed with the net mouth. Four shoreline locations were swept (Figure 11): two near the mouth of the North Fork Sultan River, one near the mouth of Williamson Creek, and one in the inner recesses of North Bay 2. The reservoir was at 1443.7' msl on this date (6.3 feet below full pool).

All samples were immediately preserved in a 10 percent formalin solution, and brought up to a 250 ml volume.

Zooplankton Enumeration

In the laboratory, the samples were split until an approximate subsample size of 400 total individuals and 100 individuals of the most abundant species was reached. If the initial split did not achieve both of these criteria, then increasingly larger splits were enumerated until both criteria were met, or until the entire sample was counted (none of the samples in this study fell under this exception). The statistical methodology for this approach is based upon Edmondson and Winberg (1971, p.178), and assumes that the sampling methods (both in the field and during the splitting) follow a Poisson distribution. This assumption is violated for larger species; thus, all individuals of those species found in a sample are always enumerated. Field sampling of such species seriously undercollects them, however, so their measured densities will always be lower than their actual field density despite the correction.

The selected values of 400 and 100 individuals provide a maximum statistical standard error of the mean of five and ten percent, respectively (the formula used is: $s = 1/\sqrt{N}$). While only the confidence limits for total numbers and most abundant species are set by this procedure, the standard error of the mean for each species can be determined from the original tallies, using the previous formula for the Poisson distribution. The standard error for each species observed in a sample has been multiplied in the main data table by the calculated density for each species.

The samples were enumerated using a Wild M–3 microscope at 32X magnification. Species identifications were made at higher levels of magnification as needed. General taxonomic identifications followed Edmondson (1959), Pennak (1989), and Thorp and Covich (1991). Specific group references included Brooks (1957), Brandlova, Brandl, and Fernando (1972), Deevey and Deevey (1971), Patterson (1996), Pontin (1978), and Stemberger (1979). Identifications were to species for all adult and subadult crustaceans, except harpacticoid copepods, and for most rotifers. Immature copepods through copepodite stage IV were identified as far as their developmental stage allowed. In the final density tables, (?) indicates an uncertain species identification.

Evaluation of the availability of the different zooplankton species as food items for particular species of fish ("edible zooplankton") is derived from a lengthy and ongoing literature review starting with Brooks (1969) and continuing with Kerfoot (1980), Zaret (1980), and Carpenter and Kitchell (1993). This evaluation is kept up–to–date by regular reviews of recently published zooplankton predation studies in *Limnology and Oceanography* and the *Proceedings of the International Association of Theoretical and Applied Limnology*. The earlier literature has been summarized in Canale, *et al.* (1975, 1976).

Taxonomic Difficulties

As the primary objective of this part of this study focused on analysis of the plankton food for the trout, extensive identification efforts were not performed on either the rotifers or the incidentally collected epibenthic invertebrates. No significant identification problems occurred with the different copepods, though the diversity of cyclopoids was striking, and initially puzzling. (The diversity was eventually determined to be due to the presence of a number of different upstream habitats that these copepods could wash in from, and the fact that there was no common breeding species from this group present in Spada Lake to block a temporary occupation of this niche. Successful colonization by a species of planktonic cyclopoid requires higher primary productivity than currently found, however.)

Identification questions remain for three cladocerans observed during this investigation: *Ceriodaphnia pulchella*, *Pleuroxus denticulatus*, and *Scapholeberis* sp. All three were based upon single (or only a few) specimen/s, so these questions are ecologically insignificant. The *Ceriodaphnia* were immature, the *Pleuroxus* did not quite match the available keys, and the *Scapholeberis* identification was changed to "species only" after reading a revision of the genus (the original identification, *S. kingi*, is now reserved for an Australian species). The possible species for the *Scapholeberis* from Spada Lake are *S. mucronata*, *S. armata freyi*, and *S. rammneri*. *S. mucronata* has been found in Alaska, *S. armata freyi* in California (Yosemite NP), and *S. rammneri* has been described from lakes in the Canadian Rockies (Dumont and Pensaert 1983). *S. armata freyi* has also just been identified from Castle Lake in the Mt. St. Helens NVM.

Weighted Mean Abundance

Arithmetic ratio expansions were made for all samples (Edmondson and Winberg 1971). Density was recorded as the mean number of organisms/m^3 for each stratum by genus. A weighted mean of abundance throughout the upper 90 feet (27.4 m) of the reservoir for each principal plankton genus was derived by use of the following formula:

$$\frac{\sum_{i=1}^{7} x_i y_i}{\sum_{i=1}^{7} y_i}$$

where x_i = number of zooplankton/m^3 in the ith stratum;

y_i = volume in m^3 of the ith stratum; and

$\sum_{i=1}^{7} y_i$ = the sum of volumes of all strata sampled, in m^3

Results and Discussion

Species Composition

A total of 42 species of crustacean zooplankton, rotifers, and protozoans were found in the zooplankton samples (plus seven miscellaneous organisms). These included 12 cladoceran species, 10 copepods, 16 rotifers, and 4 protozoans. Only the cladocerans and copepods were adequately quantified in these samples as the net mesh was too coarse for accurate sampling of the rotifers and protozoans, and the miscellaneous organisms were all primarily epibenthic forms which were only incidentally collected.

The 12 cladocerans collected are listed in Table 11. The only common planktonic cladocerans (i.e., having a density in excess of $100/m^3$ in any collection) were *D. rosea*, *H. gibberum*, and *B. longirostris*. The remaining nine were either epibenthic forms or "wash–ins" from upbasin lakes. *Diaphanosoma*, *Ceriodaphnia*, and *Chydorus sphaericus* are normally planktonic, so are likely wash–ins; *Macrothrix*, the chydorids other than *C. sphaericus*, *Latona*, and *Scapholeberis* prefer littoral weed habitats.

The ten copepods observed included *Epischura nevadensis*, *Diaptomus kenai* (and apparently its copepodites), a harpacticoid, and seven cyclopoids — *Cyclops vernalis*, *C. bicuspidatus thomasi*, *Microcyclops varians*, *Macrocyclops albidus*, *Mesocyclops edax*, *Eucyclops agilis*, and *Tropocyclops prasinus*. All of the cyclopoids except *Microcyclops varians* appeared to be wash–ins as were the diaptomids (four of these cyclopoids are normally planktonic while two, *M. albidus* and *E. agilis*, are epibenthic). *Epischura nevadensis* (and its copepodites) was the only common planktonic copepod in Spada Lake, although both *M. varians* and the harpacticoid may breed in the lake. Both are epibenthic forms, however.

Table 11. The occurrence of zooplankton species in Spada Lake, Washington, 1979 through 1997. NR = not reported.

Organism	1979-80	1997	Notes
Copepods			
Diaptomus kenai*	NR	X	
Epischura nevadensis	X	X	
Cyclops vernalis*	NR	X	
Cyclops bicuspidatus*	NR	X	
Eucyclops agilis*	NR	X	
Macrocyclops albidus*	NR	X	
Mesocyclops edax*	NR	X	
Microcyclops varians	X	X	
Paracyclops sp.	X		
Tropocyclops prasinus*	NR	X	May have been confused with Microcyclops in 1979-80.
Cladocerans			
Alona costata	NR	X	Epibenthic and/or a "wash–in"; see text
Alonella excisa	NR	X	Epibenthic and/or a "wash–in"; see text
Bosmina longirostris	X	X	
Ceriodaphnia sp.*	NR	X	Epibenthic and/or a "wash–in"; see text. May be C. pulchella
Chydorus sphaericus*	NR	X	Epibenthic and/or a "wash–in"; see text
Daphnia rosea	X	X	
Diaphanosoma brachyurum*	NR	X	Epibenthic and/or a "wash–in"; see text
Holopedium gibberum	X	X	
Latona setifera	NR	X	Epibenthic and/or a "wash–in"; see text
Macrothrix laticornis	NR	X	Epibenthic and/or a "wash–in"; see text
Pleuroxus sp.	NR	X	Epibenthic and/or a "wash–in"; see text. May be P. denticulatus
Scapholeberis sp.	NR	X	Epibenthic and/or a "wash–in"; see text
Rotifers & Protozoans			
Actinophrys sp.	NR	X	Uncertain identification
Arcella sp.	NR	X	
(bdelloid rotifer)	NR	X	
Belonocystis sp.	NR	X	
Brachionus sp.	X	X	
Conochiloides sp.	NR	X	
Conochilus unicornis	NR	X	
Difflugia sp.	NR	X	
Filinia longiseta	NR	X	
Kellicottia bostonensis	NR	X	
Keratella cochlearis	NR	X	
Keratella hiemalis		X	
Keratella quadrata		X	
Keratella sp.	X		
Lepadella sp.	X	X	
Monostyla sp.	NR	X	
Polyarthra major		X	
Polyarthra sp.	X		
Polyarthra vulgaris		X	Uncertain identification
Pompholyx sp.	NR	X	Uncertain identification
Synchaeta sp.	NR	X	
Trichocerca cylindrica	NR	X	

* A likely "wash–in" from high lakes located in the upper watershed.

Although the earlier samples from Spada Lake in 1979 and 1980 (WDG 1982) suggested that cyclopoids and calanoids were common; samples from 1997 indicate that this is no longer true (Table 12). Bradbury *et al.* (1980) identified *Paracyclops* as the most common genus of cyclopoids present, along with unidentified forms. Like all cyclopoid copepods, it requires low mesotrophic conditions at a minimum to maintain its population, and there apparently has been a reduction in primary production in Spada since 1979-80 (i.e., in Stage II). (There is also some question as to the accuracy of the identification of *Paracyclops* as immature *Microcyclops* are easy to confuse with it, and are frequently overlooked by inexperienced taxonomists. *Paracyclops* also typically is an epibenthic littoral form (Edmondson 1959, Pennak 1989), while *Microcyclops* occurs from time to time in the plankton. This difference in their preferred habitat makes the earlier identification even more questionable.)

Support for the apparent reduction in cyclopoid copepods between 1979-80 and 1997 is given by Benson (1982), who noted that in some reservoirs in the Missouri River basin, "long–term trends showed a reduction in cyclopoid abundance following the initial impoundment pulse." They further opined that the cyclopoid abundance curve, which showed a sharp decline over the six to nine years following impoundment, "appeared to be related to the influx of detritus to the system."

Six of the cladocerans and 6 of the copepods in Spada Lake were euplanktonic, but only 4 of these 12 appeared to reproduce. This number was lower than the 15 or 16 predicted by Dodson's (1992) index based upon the lake area (757 ha) and number of other lakes located within 20 km (12.4 miles).

Table 12. Historic zooplankton peak densities in Spada Lake, Washington. "1979" and "1980" data are the highest mean of two stations within each year, and are not directly comparable to 1997 due to differing reporting units. "1979-80" values are estimates for the underlying water column from the vertical net haul, converted from area to volume units using the peak densities between 1979 and 1980. 1997 values are weighted means from the surface 90 feet (27.4m). See text for discussion of adjusted 1979-80 values.

Year/s	Units	1997 Adjust for Net Eficncy (X 2.5)	Holopedium gibberum	Daphnia rosea	Bosmina longirostris	Epischura nevadensis	"Unidntifid" Cyclopoid Copepods	"Unidntifid" Calanoid Copepods
1979	Nos. / m2		25,313 (25 June)	2,000 (22 Aug)	29,125 (25 July)	250 (1 Aug)	125 (25 June)	2,438 (25 June)
1980	Nos. / m2		13,583 (15 July)	3,500 (8 Oct)	22,000 (20 Aug)	0* (- - -)	500 (12 June)	1,000 (12 June)
1979-80	Nos. / m3	No	5,063	700	5,825	50		
1979-80	Nos. / m3	Yes	12,657	1,750	14,563	125		
1997	Nos. / m3		3,700 (5 Aug)	1,685 (18 Aug)	2,835 (18 Aug)	250 (22 May)	7**	0***

* Epischura may have been missed in the vertical hauls due to its low density; 1997 values are also probably conservative due to its greater ability to avoid capture by the small diameter Clarke–Bumpus sampler.

** All cyclopoids collected in 1997 were identified (seven species).

*** All calanoids collected in 1997 were identified. Epischura and Diaptomus were the only calanoids observed. Diaptomus was rare.

Density and Standing Crop

Table 13 provides the weighted mean density of the principal zooplankters in Spada Lake, by month, in 1997. Figure 29 gives a graphical representation of the same data, with these species combined. The four principal plankters built significant numbers in mid–May to an initial peak in the first week of July. This was followed (after a period of heavy rainfall and tributary inflows) with a second maximum in the third week of August. Plankton abundance declined steadily after August 18. A very similar pattern ostensibly occurred in 1980 (Appendix A.3, WDG 1982), but with no reduction in abundance in mid– to late July. This suggests that the late July reduction in 1997 was caused by the unusually heavy inflows at that time.

It is unfortunate that comparisons of the 1997 data with that collected in 1979-80 were exceedingly difficult. The methods used in the two studies are not directly comparable, and the 1979-80 collection methods and sample statistics were poorly documented. With these caveats firmly in mind, Table 12 presents estimates of the density of the principal edible zooplankton in 1979-80 versus 1997. Peak values from "1979-80" are the maxima seen between the two years for each plankter.

Table 13. Weighted mean zooplankton densities (No./m3) calculated from Clarke-Bumpus tows in Spada Lake, Washington, 1997.

Date	Holopedium	Daphnia	Bosmina	Epischura	Cyclopoid Copepods
April 10	91	1	12	0	<1
April 24	44	1	7	0	0
May 8	37	1	4	0	1
May 22	167	2	9	250	2
June 6	731	2	6	244	<1
June 19	1,681	4	15	78	<1
July 3	3,534	26	71	24	<1
July 17	2,183	29	163	0	<1
August 5	75	12	13	<1	<1
August 18	1,797	1,686	2,835	102	7
August 29	775	560	1,283	84	<1
September 9	769	386	412	141	<1
September 23	733	181	41	83	<1
October 9	733	110	21	<1	3
October 20	457	51	9	<1	2
November 14*	22	2	<1	3	<1

* Not weighted means this date; for top one meter of lake only; estimated water volume sampled (horizontal tow length X net mouth area). Near mouth South Fork arm.

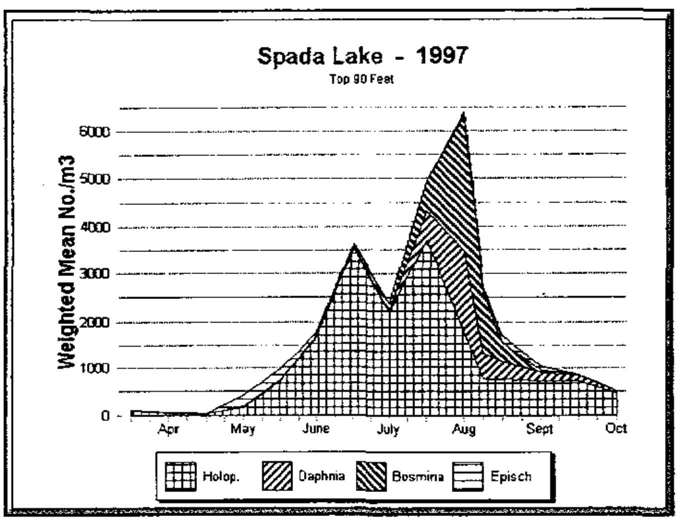


Figure 29. Weighted mean April-October zooplankton abundance in Spada Lake, 1997.

The net used in 1979-80 had an opening of 0.2 m^2, therefore the 1979-80 areal units were converted to volumetric units by dividing by five. (It is assumed that the water column was sampled from top to bottom, and that the column was 36.6 meters deep at full pool. Only

"Station 2" data from 1979-80 are adjusted in this manner, which were collected at the log boom (Station LB in 1997).)

The second adjustment assumes that the 1979-80 data were not adjusted for net efficiency. We assumed a 40 percent efficiency for the 100 micron net used in that study. 1979-80 peak values, in this case, were multiplied by 2.5 to adjust for a 40 percent net efficiency, and the product divided by five to convert from the areal value to a volumetric value.

Extensive studies on Ross Lake reported zooplankton using similar areal units (City of Seattle, Department of Lighting 1973). The 1979-80 Spada Lake investigators were aware of this work, and cited it in their report (WDG 1982). Since the Ross Lake investigators "assumed a 100 percent straining efficiency" (Seattle Dept. Lighting, 1973. p. 123), and made no corrections, it's probable that the Spada Lake data were similarly unadjusted.

Returning to Table 12, and assuming the 1979-80 data were unadjusted for net efficiency (most likely), we found that *Holopedium* is roughly 70 percent less abundant, *Daphnia* densities are roughly unchanged, and *Bosmina* is about 20 percent of its former density in Stage II versus Stage I.

All of the foregoing interpretation of the 1979-80 zooplankton density data is dependent upon unproven assumptions. The limitations of density data collected by vertical hauls are well known, therefore, these comparisons are tentative, at best. The densities reported for the two stations sampled in 1979 and 1980 were extremely variable, both on and between sample dates. The 1997 data should be considered the first reliable density data set, and be used for future reference purposes.

Figures 30 and 31 plot only the species deemed edible for the trout in 1997 (primarily *Daphnia* and *Epischura*). Figure 30 plots only unweighted densities for the lake's top 15 feet, whereas Figure 31 plots densities weighted by each stratum volume, to a depth of 90 feet. Plotting weighted densities, plus smoothing, results in a masking of the late July edible plankton decrease seen in the lake's surface layer (Figure 31).

Figures 32 through 35 illustrate the seasonal pattern of abundance for each species individually. Both *D. rosea* and *B. longirostris* had single population pulses in mid-August, while the *Holopedium* population reached its first peak earlier in July. There were two pulses of Epischura, a maximum in May and a lower, secondary peak in early September. The latter peak of Epischura was composed of two separate groups (Figure 45), reflecting its annual late summer/early fall reproduction pulse.

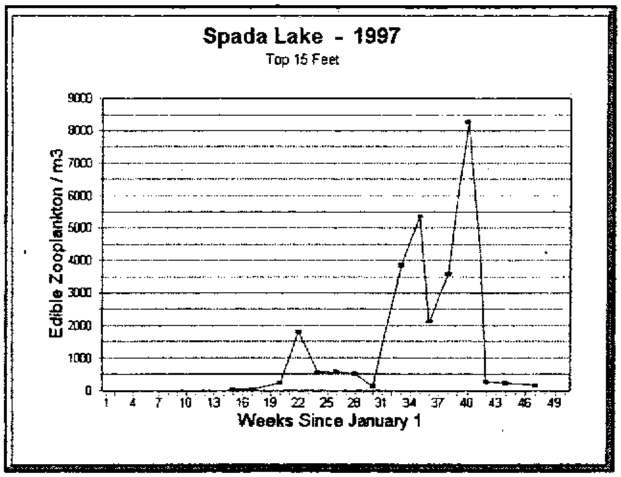


Figure 30. Edible zooplankton abundance in the top 15 feet of Spada Lake, 1997.

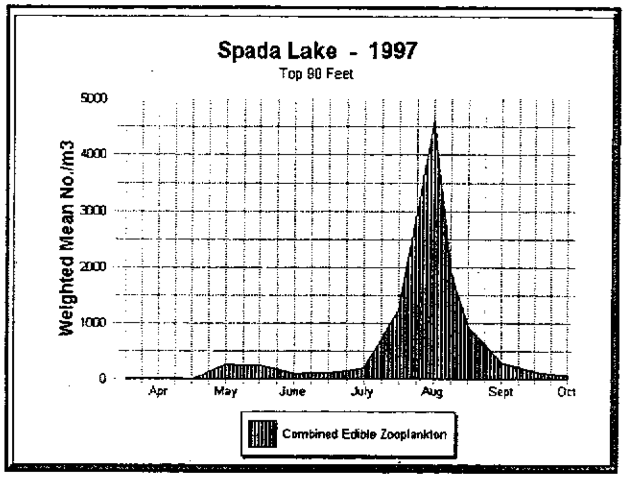


Figure 31. Weighted mean edible zooplankton abundance in Spada Lake, 1997.

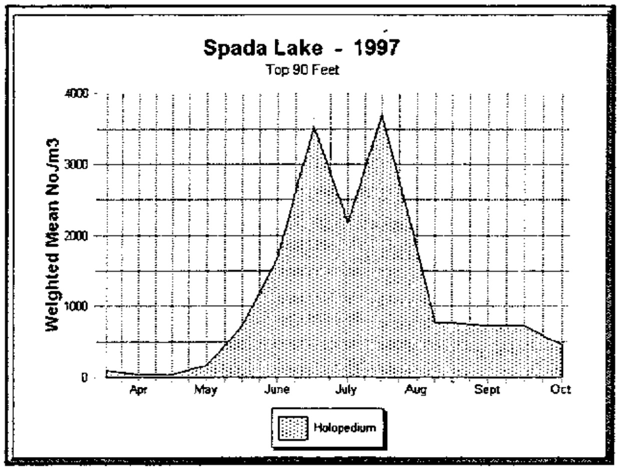


Figure 32. Weighted mean abundance of *Holopedium* in Spada Lake, 1997.

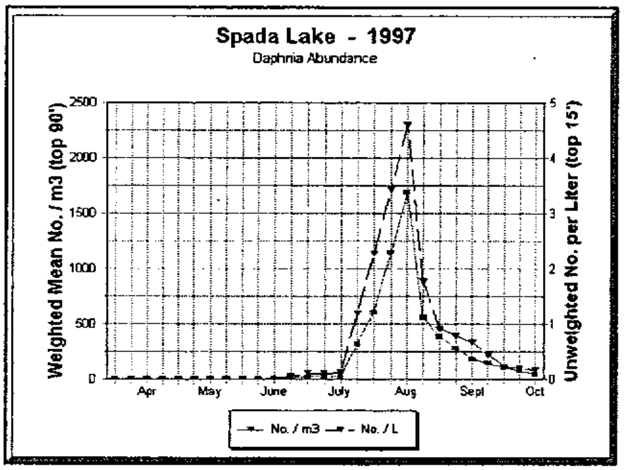


Figure 33. Weighted mean abundance of *Daphnia* in Spada Lake, 1997.

The seasonal plot of the edible zooplankton (Figure 30) showed these three peaks (early Epischura, Daphnia, and late Epischura) as distinctive, non–overlapping events.

In general, the timing of each zooplankton species in 1979-80 was very similar to that seen in 1997 (Appendix A.3, WDG 1982). Gaps and variability in the sampling statistics from those years made plotting their timing of little value.

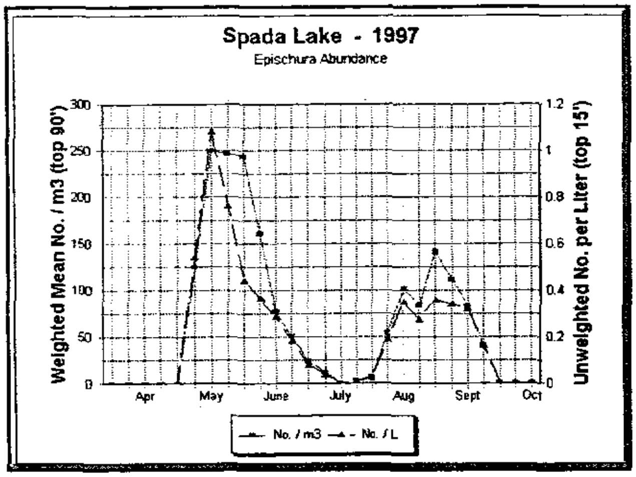


Figure 34. Weighted and unweighted abundance of *Epischura* in Lake Spada, 1997.

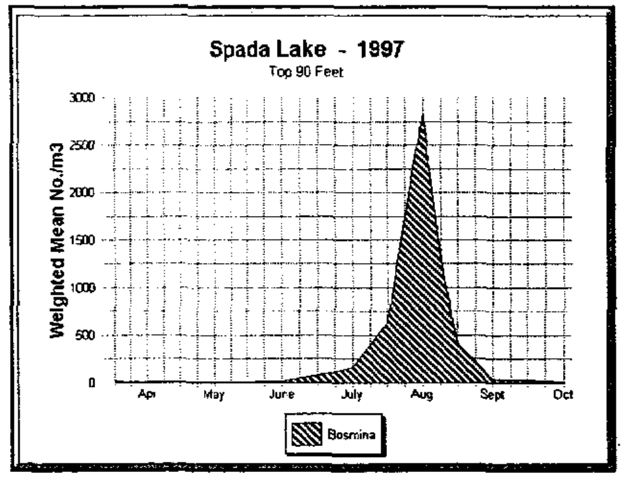


Figure 35. Weighted mean abundance of *Bosmina* in Spada Lake, 1997.

The seasonal plot of the total density of all crustacean zooplankton in the lake's top fifteen feet (Figure 36) provides an indirect estimate of primary production in Spada Lake. It revealed three pulses during the sampling season, all of which attained similar totals in the 12,500 to 16,000 individuals per cubic meter range. As seen in Table 14, this maximum is similar to, or even higher than that seen in other area lakes and reservoirs having similarly low potential production. However, Spada has a disproportionate percentage of *Holopedium* in its zooplankton community (Figure 37). Owing to differences in species timing, *Holopedium* constitutes only a small percentage of the peak plankton community in Lake Chester Morse, Ross Lake (reservoir), and South Fork Tolt Reservoir, but *Holopedium* was still about 30 percent of the crustacean plankton in Spada on August 18, 1997. For much of the rest of the year it constituted 75 to 95 percent of the plankton (Figure 37).

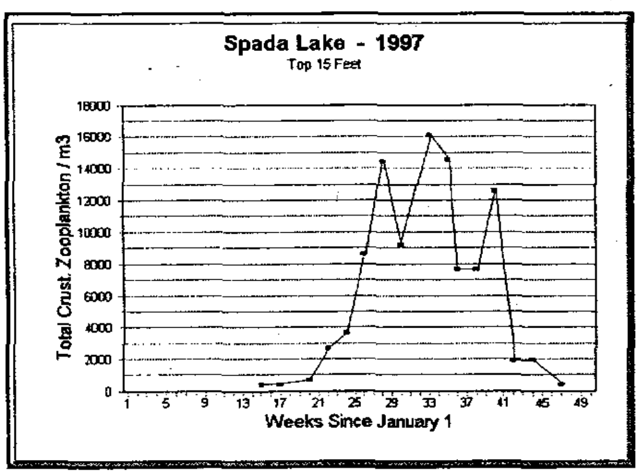


Figure 36. Total crustacean zooplankton in the top 15 feet of Spada Lake, 1997.

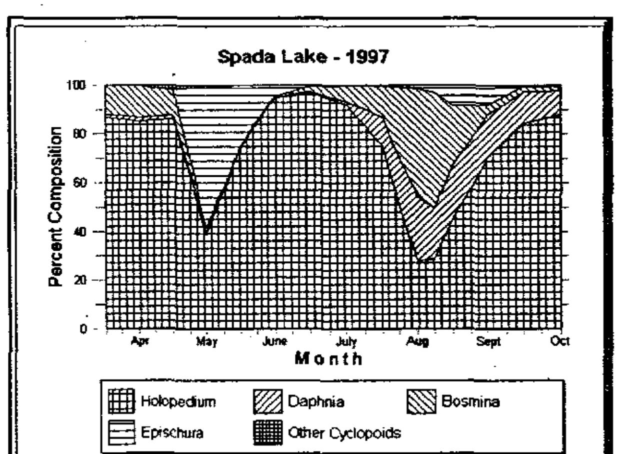


Figure 37. Monthly species percent composition of the zooplankton of Spada Lake, 1997.

Table 14. Zooplankton densities in Spada Lake in comparison to other lakes and reservoirs of the Pacific Northwest. All waters are in western Washington except Lake Pend Oreille (ID) and Hungry Horse Reservoir (MT).

	Maximal Number per Cubic Meter (Unweighted)				Maximal Number per Cubic Meter (Weighted)				Maximum Total Crustacean Zooplankton	Morphoedaphic Index*
Lake or Reservoir	**Holopedium**	**Daphnia**	**Bosmina**	**Espischura**	**Holopedium**	**Daphnia**	**Bosmina**	**Espischura**		
Spada Res. (1997)**	12,900	4,600	9,400	1,085	3,535	1,685	2,835	250	14,535	0.54
Ross Res. (1973)	58	817	1,896	0	-----	-----	-----	-----	2,589	0.82
Chester Morse L. (1973)	2,900	1,400	3,100	100	-----	-----	-----	-----	3,000	1.48
Findley Lake (1973)***	0	2,800	0	0	-----	-----	-----	-----	7,190	1.63
Mayfield Res. (1997)	-----	-----	-----	-----	-----	-----	-----	-----	10,200	1.65
Hungry Horse Res. (1987)	0	2,200	2,600	0	-----	-----	-----	-----	13,300	1.97
Riffe Reservoir (1997)	-----	-----	-----	-----	-----	-----	-----	-----	20,000	0.68
Pend Oreille Lake	0	5,000	7,000	210	-----	-----	-----	-----	23,000	0.65
So. Fork Tolt Res. (1992)	4,910	4,440	5,390	0	-----	-----	-----	-----	24,900	0.78
Sammamish Lake (1973)	0	800	1,600	ND	-----	-----	-----	-----	45,940	3.42
Stevens Lake (1975-76)**	0	26,810	15,890	1,200	0	12,700	7,900	400	47,200	5.30
Washington Lake (1992)**	0	40,230	1,800	1,850	-----	-----	-----	-----	86,350	1.81

* See Transactions of the American Fisheries Society Vol. 111, Number 2 (March 1982).

** Collected with a Clarke–Bumpus sampler; all other lakes were sampled with vertical net hauls.

*** A fishless subalpine lake.

Note: Lakes or reservoirs sampled with vertical net hauls may have missed *Epischura*.

Descriptive Population Dynamics

After a slow start in April and early May, primary productivity apparently began to improve, and the zooplankton followed in June. The first zooplankton pulse in early July was dominated by *Holopedium* with a small quantity of Epischura (Figure 29). The primary productivity supporting this pulse was apparently sharply reduced by the unusually heavy precipitation and reservoir filling that occurred about this time. May, June, and July inflows were far above average in 1997 (Figures 5 and 7, Description of Study area—Annual Drawdown and Summer Rearing Areas), representing 59.6, 47.0, and 36.1 percent of the reservoir volume in those months, respectively. Populations of both phytoplankton and zooplankton rebuilt throughout July and early August with the highest densities of crustacean zooplankton for the year (16,087 individuals per cubic meter) occurring in the August 5 surface collection. About 63 percent of this peak was *Holopedium*. *Daphnia* and *Bosmina* reached their seasonal peaks about 13 days later, at which time the total crustacean zooplankton density was about the same at 14,500 per cubic meter.

There was a decline in total densities after the mid–August pulse, but the fall reproduction of *Epischura* again raised zooplankton numbers in late September. Although the *Holopedium* population declined continuously from August 5 (Figure 32), it was still the second most common crustacean in the September pulse.

The late August reduction observed between the latter two pulses is a common phenomenon in many temperate lakes. It is known as the "clear water phase", and occurs when the zooplankton heavily graze the phytoplankton during low epilimnetic nutrient conditions. There is usually insufficient vertical mixing at this time to regenerate enough nutrients for the phytoplankton to outgrow this grazing pressure.

After the late September *Epischura* pulse the zooplankton rapidly decreased in abundance, and returned to mid–May densities by October 9. The final decline was due to the seasonal cessation of primary production caused by the higher rates of mixing and shorter duration of insolation characteristic of fall. The growing season, hence available food for the zooplankton, was effectively over by mid–October, although the zooplankton did not decline below 10 percent of their seasonal peak until sometime between October 20 and November 14.

Indicators of Trophic Status

The average number of edible zooplankters declined rapidly below the top stratum in Spada Lake. The mean densities from May through October were 512, 61, and 18 animals per cubic meter for the second through fourth strata, respectively, producing a mean density in the top 18.3 meters of 661 animals per cubic meter. When just the values from the top four strata in August and September were averaged, a technique which gave the most comparable data with average water column densities from other lakes, the mean density was 1,440 edible zooplankters per cubic meter. In addition, the mean percent composition of edible forms in the top stratum between mid–July and mid–October was 31 percent of the total number of crustacean zooplankton collected. These values are representative of a zooplankton assemblage from an oligotrophic lake.

This analysis combines absolute densities with percentage composition, and makes note of indicator species. Values of over 3000 edible zooplankters per cubic meter, which comprise better than 25 percent of the total crustacean zooplankton, are considered to indicate a healthy mesotrophic lake, based on an average of August-September densities observed in Pacific Northwest lakes. Densities less than 1000 per cubic meter and/or edibles comprising less than 10 percent of the total plankton in this time frame represent ultraoligotrophic and/or severely stressed assemblages. Locally, the presence of high numbers of *Diaptomus kenai* and *Daphnia rosea* are considered to be positive indicators, while the presence of the gelatinous *Holopedium gibberum* is regarded as suggesting a relatively high level of predation (Zaret 1980; Tessier 1986). *Holopedium* is a poor competitor with daphnids, so where it is more numerous, this suggests that the edible daphnid population is being suppressed by planktivory (Allan 1973).

While the level of edible zooplankton of Spada Lake simply indicates that it is an oligotrophic system, the absence of *D. kenai* and the quantity of *Holopedium* relative to *Daphnia rosea* suggest that the assemblage is also being somewhat stressed by planktivory. That is, the edible zooplankters of Spada Lake appear to have been moderately overgrazed by fish.

Vertical Distribution

With two exceptions all of the common forms were most abundant in the top 0 to 15 feet (4.6 m) stratum. The two exceptions were the cyclopoids and *Bosmina longirostris*. The most common cyclopoid observed in Spada, *Microcyclops varians*, is an epibenthic form, so the vertical distribution of these copepods will reflect its mid–depth to bottom pattern. *Microcyclops* was always scarce in our pelagic samples, and is not plotted.

Holopedium was predominantly in the top stratum most of the year (Figure 38). It made three "significant" incursions into deeper waters, wherein more than 20 percent of the organisms were found in the second (or third) stratum. These events in early May, August-September, and October, corresponded to periods of high clarity and warming, a deeper euphotic zone, or fall mixing, respectively.

At least 43 percent of the *Daphnia* population was located in the top stratum; for much of the year between 80 and 100 percent were in that layer (Figure 39). A considerable fraction occupied the 15 to 30 foot (4.5 to 9.2 m) stratum, particularly in the August-September period of increased clarity, and greater euphotic zone depth. In the summer and early fall months, we found a small percentage in the 45 to 60 foot (13.7 to 18.3 m) stratum, but almost none below that depth.

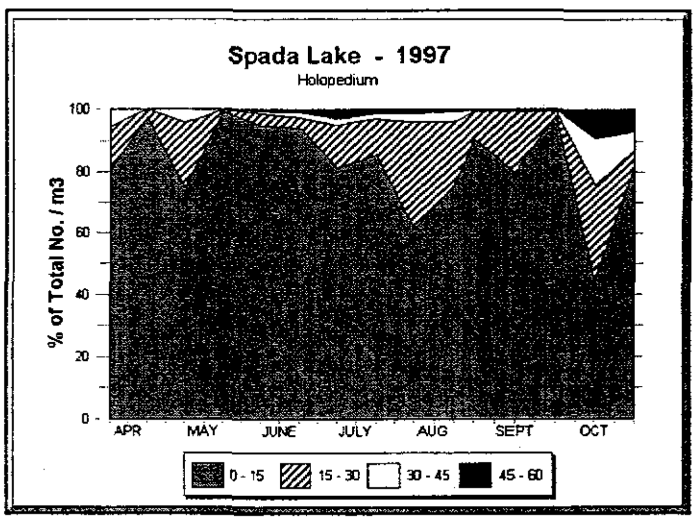


Figure 38. Monthly relative percentage of *Holopedium* in the water column of Spada Lake, 1997, by 15 foot strata.

In the first half of the growing season (April-July), the Spada Lake *Bosmina* population tended to be most abundant in the top stratum, but showed a distinctly greater depth distribution beginning in August (Figure 40). *Bosmina* populations in deep lakes have frequently been found to possess subsurface maxima instead of being concentrated in the epilimnion. This vertical distribution pattern may be due to one or more causes. The most likely factor is competition from larger cladocerans (or in some lakes, diaptomids). Less likely, though frequently occurring causes are predation from adult *Epischura*, adult *Leptodora*, or larval *Chaoborus* and/or avoidance of high light intensities (the latter factor has been found in several high Cascades lakes in Oregon).

Epischura appeared in our samples for three periods. It was almost entirely in the top two strata, with the bulk of the animals being in the top fifteen feet roughly half of the time (Figure 41). Only very small percentages were seen below 30 feet (9 m).

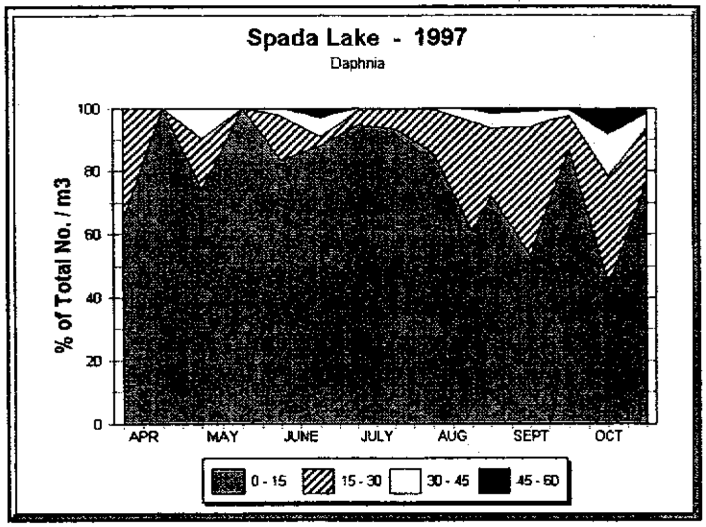


Figure 39. Monthly relative percentage of *Daphnia* in the water column of Spada Lake, 1997, by 15 foot strata.

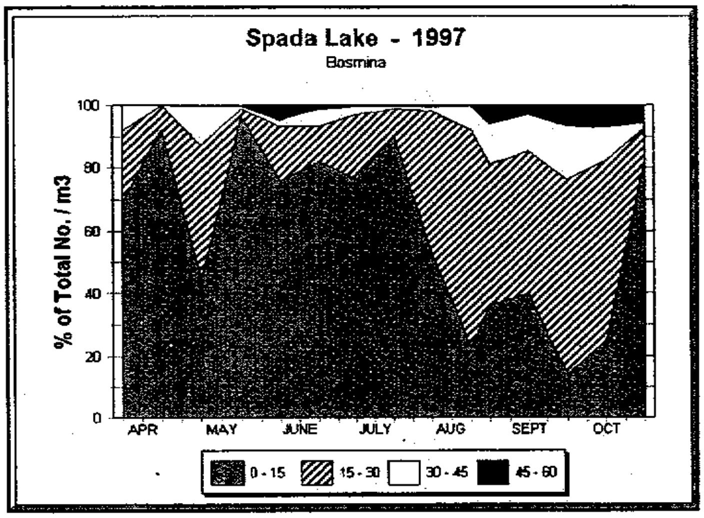


Figure 40. Relative percentage of *Bosmina* in the water column of Spada Lake, 1997, by 15 foot strata.

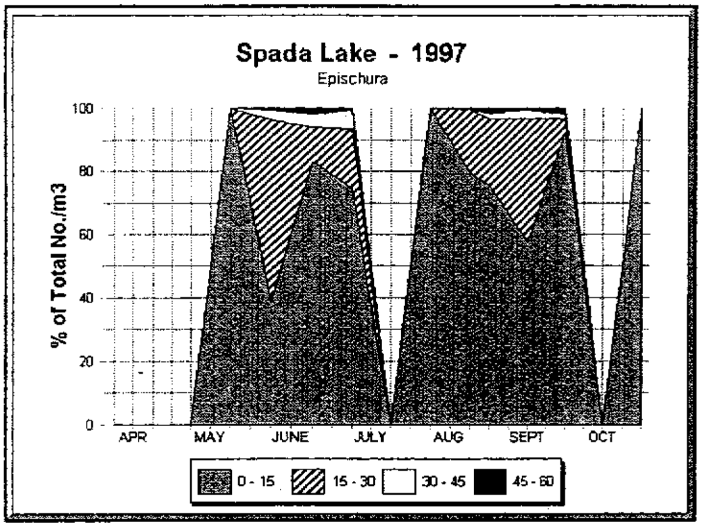


Figure 41. Monthly relative percentage of *Epischura* in the water column of Spada Lake, 1997, by 15 foot strata.

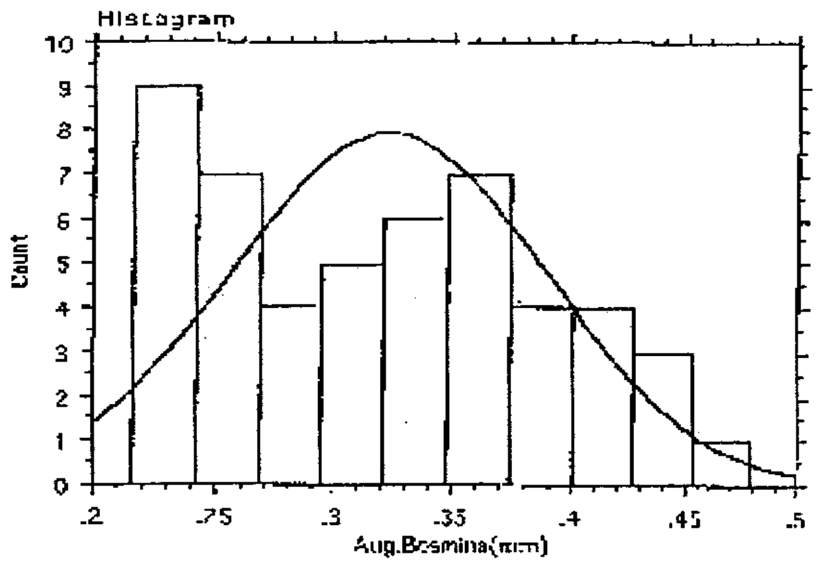
Abundance, Size, and Value as Fish Food

Of the 22 species of zooplankton occurring in Spada Lake, only three are sufficiently large or abundant enough to be considered potential food for rainbow, cutthroat, or their hybrids. *Holopedium's* gelatinous coating and low caloric content make it undesirable to trout. While *Diaphanosoma* often contributes significantly to salmonid diets, including planktivores such as Lake Washington sockeye (Eggers 1978), it occurs at only trace levels in Spada Lake. Similarly, cyclopoid copepods such as *Cyclops*, or calanoid copepods such as the smaller species of *Diaptomus* are typically only food for very small, young trout, and are usually replaced by larger cladocerans early in the fish's life. Despite the potential entry of these copepods into the trout diet, their scarcity in Spada make their contribution moot. The only species found in sufficient abundance or of sufficient size in 1997 were *Daphnia rosea, Bosmina longirostris,* and *Epischura nevadensis.*

Effect of Size

Bosmina

Trout which enter a reservoir or lake after one to three years of tributary residence are relatively large, and *Bosmina* is too small to offer sufficient caloric reward to offset the energy required by trout to utilize it. It is too small (0.23 to 0.58 mm) to be strained by the gill rakers of larger rainbow or cutthroat (Galbraith 1967), and is usually completely absent from their diet, or nearly so, in lakes and reservoirs, despite its being numerically one of the most important plankton species (Seattle Department of Lighting 1973; May *et al.* 1988; Chisholm *et al.* 1989; Johnston



Descriptive Statistics

	Aug.Bosmina(mm)
Mean	.323
Std. Dev.	.066
Std. Error	9.387E-3
Count	50
Minimum	.216
Maximum	.480
# Missing	0
Geom. Mean	.316
Skewness	.240
Kurtosis	-.857
Median	.324

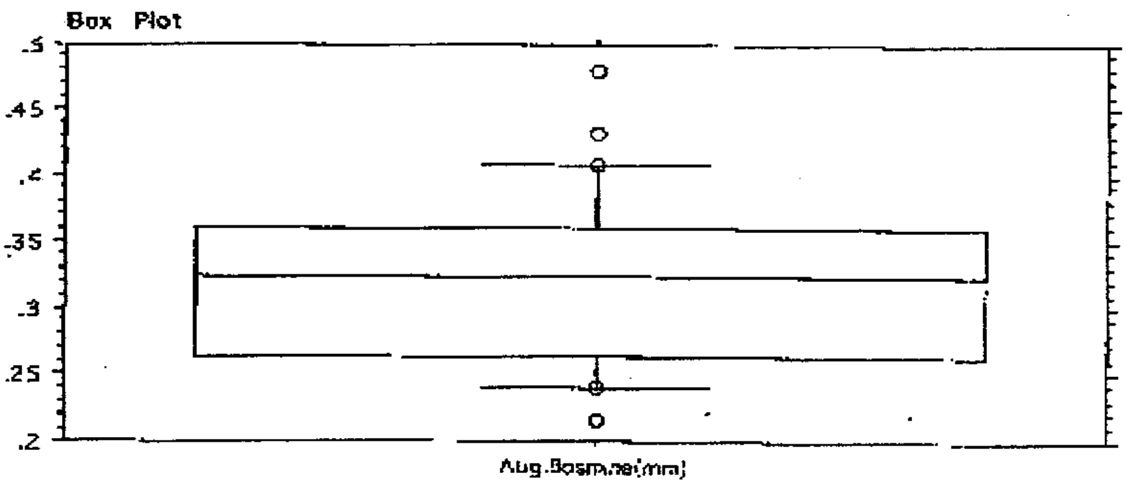


Figure 42. Body length statistics for *Bosmina* from Spada Lake in August 1997.

1989). Bosmina lengths in Spada Lake are among the lowest seen in the literature (Figure 42; Table 15), and are indicative of a very oligotrophic system. Bosmina was not seen in the trout diet (Tertiary Production — Trout Age, Growth, and Condition), and is not considered a trout food item in Spada Lake. (However, it is probably utilized by brown bullhead young of the year, or juveniles.)

Daphnia

Fish visually select each plankter (Brooks 1968), choosing only those individuals above a certain size (Hrbacek *et al.* 1961; Brooks and Dodson 1965; Galbraith 1967; Zaret 1972). A variety of dietary studies on rainbow in North American lakes and reservoirs consistently show that they actively select for zooplankton prey species above a minimum size, typically 1.15 mm for the larger cladocerans such as *Daphnia* or *Leptodora* (Galbraith 1967; Taylor and Gerking 1980; Beauchamp 1987; Schneidervin and Hubert 1987; Johnston 1989; Tabor *et al.* 1996). Trout actively search for prey and are energy maximizers (Griffith 1975). They do not capture food items as they are encountered but are selective, taking only those animals which are superior in terms of energy (Emlen 1966; 1968) or nutrients (Pulliam 1975).

These ecological and dietary studies are completely consistent with what we observed in Spada Lake (Tertiary Production—Trout Age, Growth, and Condition). For example, *Daphnia* did not appear in trout stomachs until the July 17 samples, which were coincident with the onset of accelerated *Daphnia* reproduction (Figure 33). Larger, ovigerous females would be increasing in number at that time, and it is believed that these maturing *Daphnia* are selected for on the basis of greater visibility, or greater nutritive value (Richman 1958; Mellors 1975; Taylor and Gerking 1980).

While rainbow, cutthroat, and their hybrids are present in Spada (Shapiro and Associates and University of Washington 1987; Leary *et al.* 1996), diet studies on cutthroat and "cuttbows" from other systems (May *et al.* 1988; Beauchamp *et al.* 1992) show similar discrimination against small plankton forms similar to that of rainbows. We expect that the dietary observations made in 1997 are typical, and that trout in Spada Lake will continue to select for the larger plankton (*Daphnia, Epischura* > 1.15 mm) while ignoring *Bosmina.*

Table 15. Seasonal mean or annual range in total lengths (mm) of Spada Lake zooplankton, with similar data from other lakes or reservoirs.

		Daphnia spp.		Bosmina spp.		Epischura		
Water	**Year**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Reference and notes**
Spada Lake, WA	1997	1.22	0.7 - 1.7	0.32	0.23 - 0.47	1.32	0.55 - 1.88	
Crystal Lake, CT	1942	1.30				1.67		Brooks 1969. Obligate planktivore not established.
Crystal Lake, CT	1964			0.30				Brooks 1969. Obligate planktivore established.
Sporley, Stager Ls, MI	1960	1.30	0.4 - 2.9					Galbraith 1967.
Flaming Gorge, UT	1984	0.99	0.6 - 2.3					Schneidervin and Hubert 1987.
25 No. Swedish lakes	1967-70		1.25 - 3.2		0.26 - 1.0			Nilsson and Pejler 1973.
Baker Lake, WA	1997	1.31	1.0 - 1.8	0.41	0.27 - 0.58	1.80	? - 2.0	Arni Litt, Univ. of WA Dept. Zoology, pers. comm.
Washington L., WA	1997	2.50	1.3 - 3.0	0.42	0.29 - 0.56	2.18	1.8 - 2.3	Arni Litt, UW, pers. comm. The mean is for May.
	1975	1.72		0.41		2.29		Eggers 1982. The means are for August.
Gatun Lake, Panama	1969			0.28				Zaret and Kerfoot 1975.

About 52 percent of the *Daphnia* population is ≥ 1.15 mm (Figure 43), therefore, not all of the *Daphnia* densities reported in Secondary Production — Species Composition are truly available as food. In Spada Lake it makes an appreciable contribution to the trout diet only between mid–July and mid–September (Tertiary Production — Trout Food Habits). Ovigerous females, or individuals ≥ 1.15mm are available at least 0.3 organisms per liter in the lake's top layer in that time frame (Figure 33). Although a peak count of 4600 individuals per cubic meter is among the higher levels seen among area lakes and reservoirs of roughly equivalent productivity (Table 14), *Daphnia* are only available to, and utilized by trout in Spada for about 11 weeks, or 31 percent of the trout active growing/feeding season (April-November). And, only about one half of that peak density is composed of suitably large individuals taken as food.

Epischura

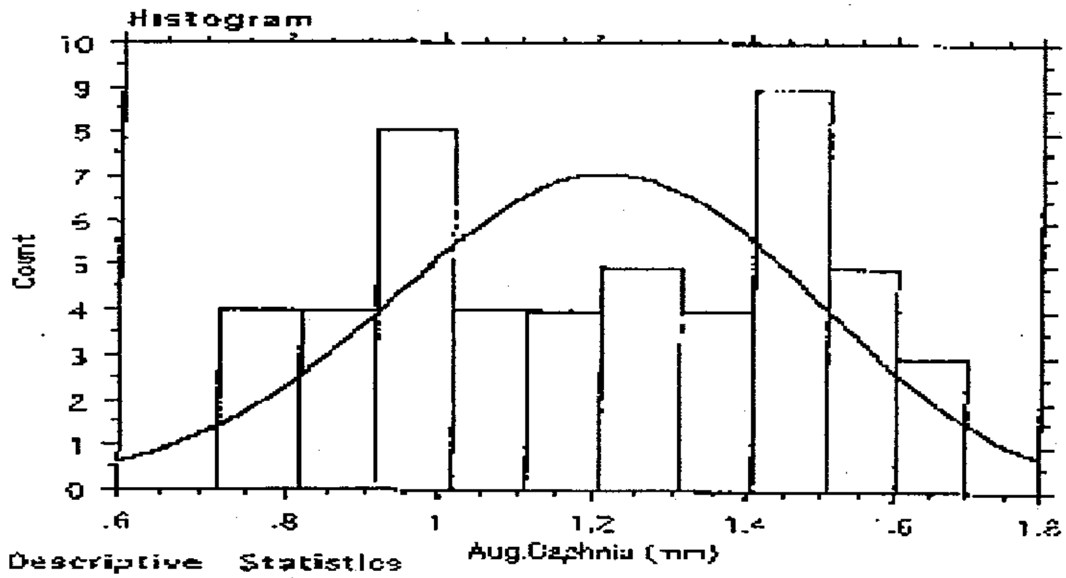
If *Epischura* is present, it usually contributes little, if at all to rainbow or cutthroat diets (May *et al.* 1988; Chisholm *et al.* 1989). This is probably due to the fact that it is usually only present in low numbers in the plankton, often much less than 300 per cubic meter. Since it is a relatively large copepod, it is usually eaten at least part of the time, when it is present. However, in no study that we reviewed did it contribute more than a few percentage points to trout diets.

Epischura is a relatively large calanoid copepod, and occurs in Spada Lake at a size suitable to attract the attention of trout (Figures 44 and 45). It was abundant in at least two of the stomachs sampled, but was not a regular food item (Tertiary Production — Trout Food Habits). This is consistent with other trout diet studies. *Epischura* exhibited two seasonal maxima, but its absolute abundance was still very low, less than 1.2 animals per liter in the lake's top 15 feet (Figure 34).

Combined Edible Species Overview

Since zooplankton as a food prey item is a function of both size and numerical abundance (and perhaps also nutritive value), we found that plankton of a suitable size was only sufficiently abundant in Spada Lake to serve as trout food during the mid–July to mid–September period (Tertiary Production—Trout Food Habits). This incorporated the mid–July to mid–September *Daphnia* pulse, and the early August to mid–September *Epischura* pulse, but did not include the mid–May to mid–June *Epischura* pulse (Figure 46).

Although between 25 and 35 percent of the total zooplankton was edible in May and June (Figure 47), overall plankton abundance was very low, and we saw no evidence that either *Daphnia* or *Epischura* were eaten at that time. In late summer, when *Holopedium* numbers subsided, the plankton percentage that was edible attained maxima of 55 to 65 percent.



Descriptive Statistics

	Aug-Daphnia (mm)
Mean	1.215
Std. Dev.	.277
Std. Error	.039
Count	50
Minimum	.720
Maximum	1.704
# Missing	0
Geom. Mean	1.183
Skewness	-2.857E-3
Kurtasis	-1.273
Median	1.236

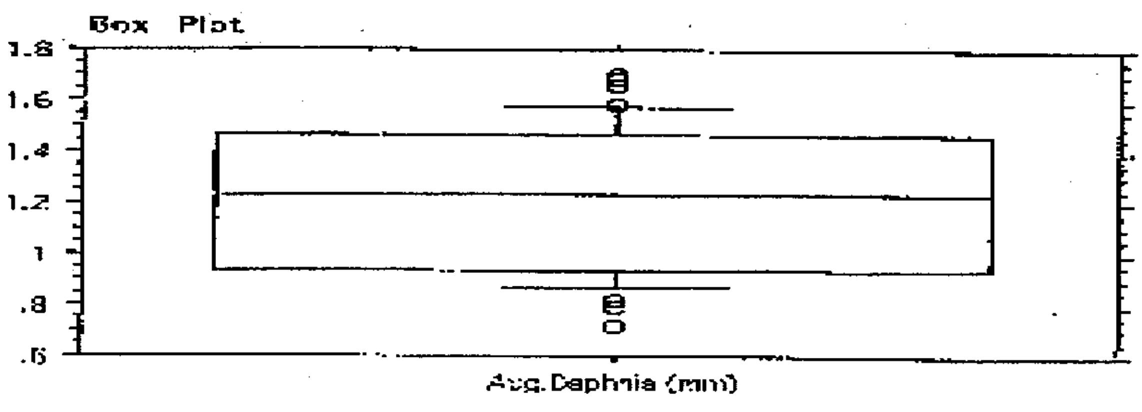
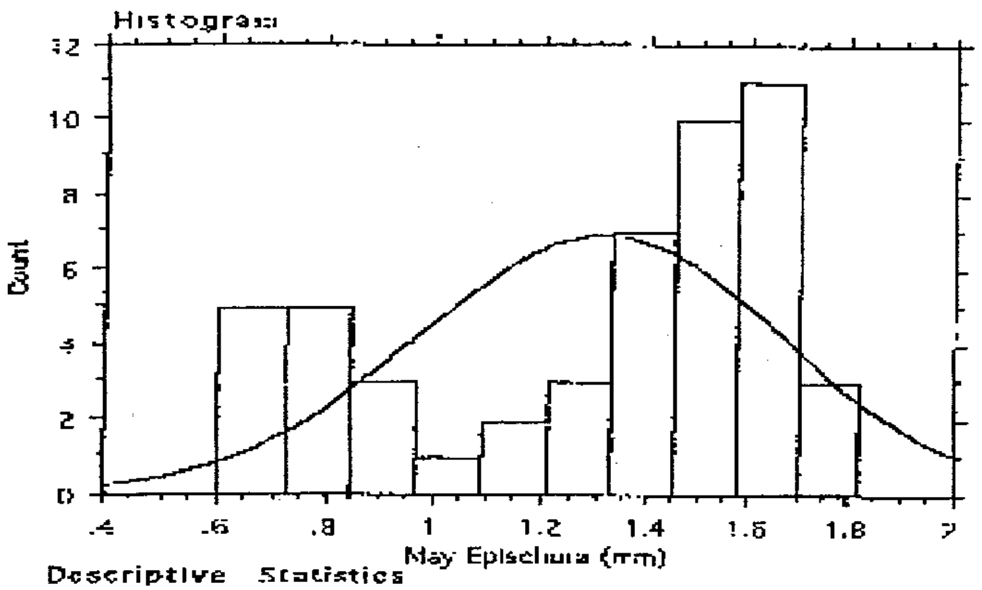


Figure 43. Body length statistics for *Daphnia* from Spada Lake in August 1997.



Descriptive Statistics

	May Epischura (mm)
Mean	1.319
Std. Dev.	.352
Std. Error	.050
Count	50
Minimum	.600
Maximum	1.824
# Missing	0
Geom. Mean	1.263
Skewness	-.678
Kurtosis	-.976
Median	1.443

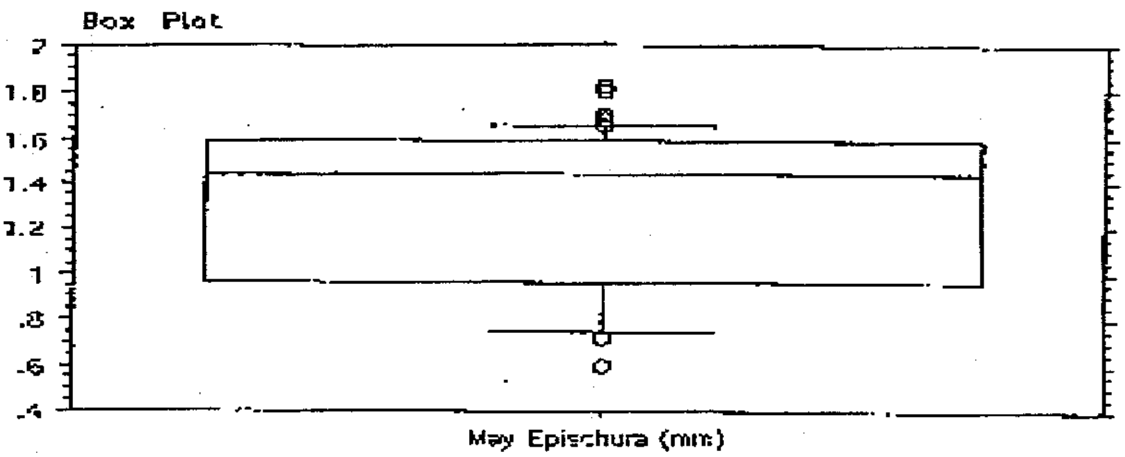
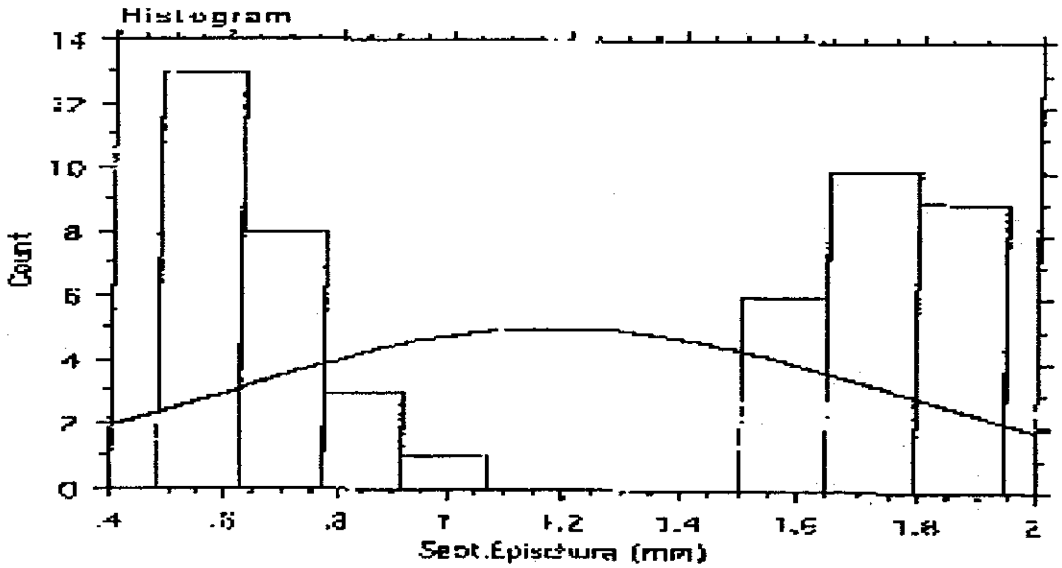


Figure 44. Body length statistics for *Epischura* from Spada Lake in May 1997.



Descriptive Statistics

	Sept.Episcrura (mm)
Mean	1.1319
Std. Dev.	.580
Std. Error	.082
Count	50
Minimum	.480
Maximum	1.944
# Missing	0
Geom. Mean	1.036
Skewness	-.028
Kurtosis	-1.834
Median	1.284

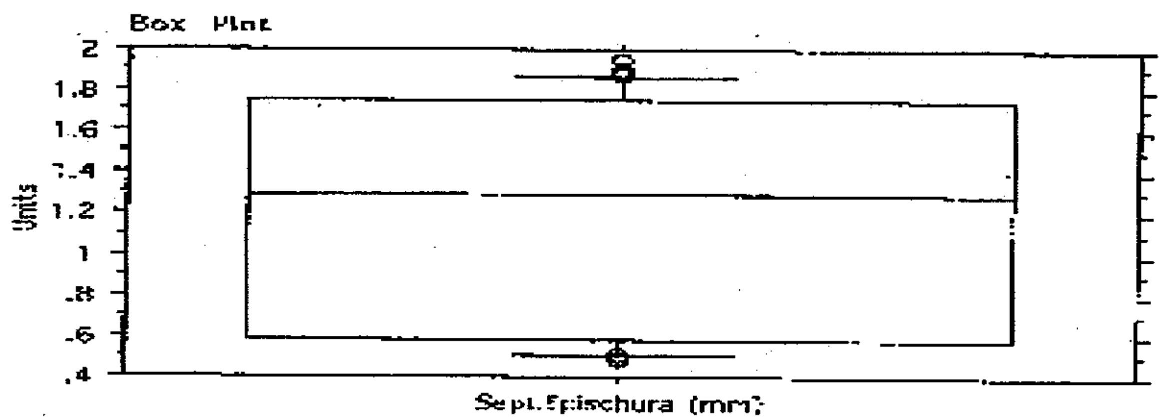


Figure 45. Body length statistics for *Epischura* from Spada Lake in September 1997.

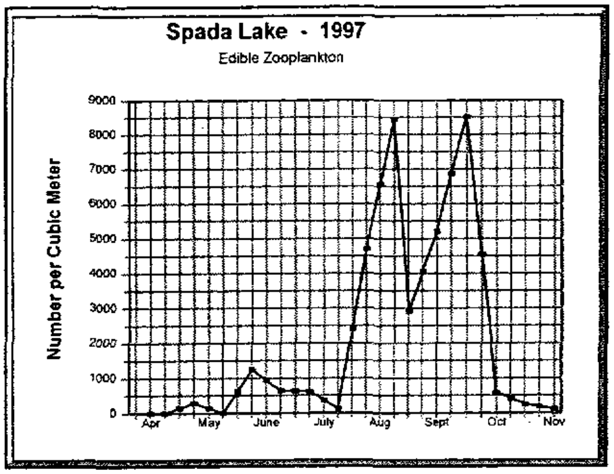


Figure 46. Monthly abundance (nos/m^3) of edible zooplankton in Spada Lake, 1997.

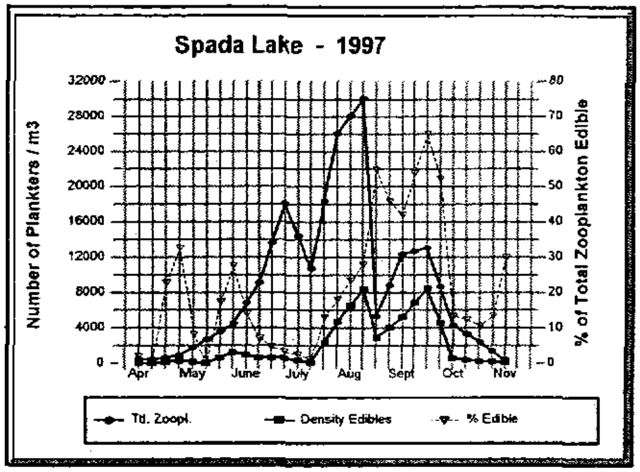


Figure 47. Monthly abundance (nos/m^3) of total and edible zooplankton in Spada Lake, 1997.

Several studies (e.g., Allan 1973; Tessier 1986; Carpenter and Kitchell 1993) have demonstrated a clear preference by trout for larger (>1.15 mm) species of *Daphnia* over *Holopedium gibberum* as the gelatinous covering of the latter organism appears to make it distasteful to fish (McNaught 1978). However, juveniles and recently molted individuals of *Holopedium* are eaten by planktivores (Tessier 1986). Moreover, stomach samples taken late in the 1997 season revealed that *Holopedium* were consumed by trout in Spada Lake, though they were less abundant than their relative population density at that time, and the proportion of *Daphnia* in these stomachs was higher than their relative numbers in the plankton. Indirect evidence of the greater nutritive benefit of zooplankton for trout in Spada Lake is seen in Figure 97 (Tertiary Production—Trout Age, Growth, and Condition). September samples showed a definite increase in the percentage of trout that had "light" or greater amounts of internal body fat. In our diet study, the only trout stomachs that were distended, or judged to be >100 percent "full", occurred between early August and early October (Figure 102, Tertiary Production—Trout Food Habits), coincident with the late summer/fall *Daphnia* pulse (Figures 33 and 46). While other invertebrates were probably experiencing seasonal maxima, and contributed to the somewhat higher number of full stomachs, the percentage of trout stomachs containing zooplankton reached its seasonal peak at this time:

Month	Sample Size	Stomachs with Zooplankton	Percent
May	19	0	0.0
June	22	0	0.0
July	26	2	7.7
Aug	28	11	39.3
Sept	35	21	60.0
Oct	30	9	30.0

Daphnia was clearly the most important rainbow and cutthroat dietary species in the zooplankton community, which has been demonstrated repeatedly in similar studies on Pacific Northwest waters. Galbraith (1967) stressed that "the usual measurements of abundance of *Daphnia*, i.e., numerical counts or total volume, can be quite meaningless as far as indicating their availability to plankton–eating fish. Thus, the abundance of *Daphnia* of the proper size, rather than just the total numbers or volume, should be the subject of study in any investigation concerning the successful management of rainbow trout and other plankton feeding fishes in lakes." Further supporting this assessment, it has been determined from zooplankton analyses of a number of Oregon lakes that the small (maximum adult size <1.0 mm) daphnid, *Daphnia ambigua*, is essentially free from rainbow predation (Vogel unpublished data). Tabor *et al.* (1996) made a similar argument. Additional analysis of our data, and bioenergetic modeling such as suggested by Tabor *et al.* (1996), are needed to refine our understanding of the true relative value of the edible plankton in Spada Lake.

Our primary conclusion obtained from this analysis of the zooplankton assemblage of Spada Lake is that the fish population is probably too numerous for the level of planktonic secondary productivity (see also Tertiary Production — Fish Relative Abundance, Length Frequency, and Sex Ratio; and Trout Age, Growth, and Condition). This conclusion is reached, first, from the calculations and observations in this section; second, from the relatively poor growth and condition of the trout (Tertiary Production — Trout Age, Growth, and Condition); and third, indirectly from Dodson's (1992) index. This index predicts 15 or 16 pelagic crustacean zooplankton species based on the reservoir's area, and the existence of 45 lakes of varying size and elevation within 20 km (12.4 miles) of Spada Lake. When the number of breeding zooplankton species is lower than predicted, then either the assemblage has undergone extinctions caused by high levels of planktivory, or the primary productivity of the lake is quite low. Either, or both mechanisms could be the cause for the low species richness in Spada Lake.

With respect to the plankton food supply, we believe the trout are stressed, will remain so without significant management correctives, and may continue to overgraze the zooplankton assemblage (particularly *Daphnia*) due to a general lack of food for fish (see also Secondary Production — Benthos). Second, although the low zooplankton numbers contribute to the reduction in availability of food for the trout, these levels are not the ultimate cause for the food shortage. The low quantity of zooplankton in Spada Lake is due to the low phytoplankton production rates. Whether the trout gain the bulk of their energy needs from planktonic or from epibenthic secondary production, both of these routes are dependent upon primary production within the lake and its watershed. Thus, the lack of food for the trout is mainly due to low primary production, aggravated by the presence of numerous brown bullheads competing with the trout for relatively scarce epibenthic invertebrates.

Primary production in Spada Lake is apparently at an oligotrophic level, and will remain there because the reservoir is deep, and the amount of nutrients initially added by flooding the soils has probably been exhausted due to first, ongoing sedimentation into the deeper parts of the reservoir (Ploskey 1983; Kimmel and Groeger 1986), and second, their removal from the ecosystem through the past fisheries. Trout growth will probably vary from year to year based upon the variability in primary productivity in the reservoir and its watershed. However, based on constant, but extremely low conductivity levels (Water Quality — Conductivity, pH, and Other Miscellaneous Water Quality Data) and a relatively constant reservoir management regime (Description of the Study Area — Reservoir Morphology and Operation), we expect secondary production to be on the low end of the scale, and fishery yields to be on the order of, at most, one pound per acre (1.1 kg/ha) per year.

Conclusions

A total of 42 species of crustacean zooplankton, rotifers, and protozoans were identified in the 1997 samples. Of 12 cladocerans identified, only *Daphnia rosea* was seasonally important in the trout diet. *Epischura* was the only copepod eaten, and then only occasionally. *Holopedium gibberum*, a cladoceran, was the numerically most important plankter, but did not contribute to the trout diet in a meaningful way. *Holopedium* constituted 75 to 95 percent of the plankton for much of the year.

Cyclopoid copepods were far less abundant than in Stage I. This is probably due to reservoir aging.

Daphnia and *Epischura* were the only important edible species. *Epischura* had two peaks of abundance: one in May and early June, and one in August-September. *Daphnia* was far more important, and had one peak in August and early September. Zooplankton (principally *Daphnia*) occurred in up to 60 percent of trout stomachs during the August-September pulse.

Although it was very difficult to compare data from Stage I to Stage II due to differing methods, we determined that *Holopedium* is roughly 70 percent less abundant, *Daphnia* is roughly unchanged, and *Bosmina* is about 20 percent of its Stage I density. We could not make any inferences regarding *Epischura*, but it is not important from a dietary standpoint (but may be as a parasite vector).

The total density of all crustacean zooplankton in the reservoir's top fifteen feet was used as an indirect estimate of primary production. Three pulses in the sampling season were all in the 12,500 to 16,000 individuals per cubic meter range. This maximum is similar to, or even higher than, that seen in other area lakes and reservoirs having similarly low potential production. (A regression of peak crustacean zooplankton abundance and the morphoedaphic index for these lakes was marginally significant, but predicted a level in Spada Lake that was 7.1 percent above that actually observed.)

The growing season extended from early May through mid–October, but zooplankton did not drop below 10 percent of their seasonal peak until early November.

The mean density of edible zooplankton was 1440 organisms per cubic meter. The mean percent of edible forms between mid–July and mid–October was 31 percent of the total number of crustacean zooplankton collected. These values are representative of an oligotrophic system.

The overwhelming abundance of *Holopedium* relative to *Daphnia*, plus the near–absence of *Diaptomus*, may be a reflection of excessive planktivory since *Holopedium* is a poor competitor with daphnids.

Daphnia was clearly the most important rainbow and cutthroat dietary species. However, due to its relatively small size in Spada Lake, only about one half of the *Daphnia* in Spada are suitable as trout food.

The fish population (brown bullheads plus trout) is probably too numerous for the level of planktonic secondary productivity. Overgrazing may continue due to a general lack of food. Low phytoplankton (primary) production is the ultimate cause of food shortages.

Spada Lake in Stage II is oligotrophic, and is expected to remain at that level. The amount of nutrients added by flooding of soils in 1985 has probably been exhausted due to ongoing sedimentation into the deeper parts of the reservoir, and earlier removal in intensive fisheries in the mid– to late 1980s.

Benthos

Sampling the lake's benthic invertebrates was not originally part of the research planned for 1997. However, we took the opportunity to collect a very limited number of samples, and made what comparisons we could with benthos data collected in 1979 and 1980 (Stage I). We recognized that a much larger sampling program is necessary to adequately estimate benthos standing crop, or other measures of its secondary productivity. Our objective was to look for any obvious changes in invertebrate diversity or abundance and identify potential further, more detailed sampling needs. Because the number of samples was purposefully kept small, we did not follow a formal sampling design with statistical bounds in mind.

Methods

In 1979-80, 0.0232 m^2 Ponar grabs were made at two stations (WDG 1982), but unfortunately, the specific sites, the dates, the reservoir elevations on the sample dates, and the depths sampled were not reported. Only generalized sample locations and the month sampled were reported. Two grabs were made at each station in 1979, and single grabs in 1980. The samples were preserved in 70 percent ethanol. Other details on processing are given in Bradbury *et al.* (1980). Results were reported as organisms/m^2.

In 1997, we used an Ekman bottom grab with a nominal square opening of 0.0232 m^2. However, the jaws did not fully open, and the actual sampled area was 0.0194 m^2. At some sites several grabs were made in order to retrieve a sample which did not include stones or woody debris which prevented the jaws from closing tightly. Dates and sites were selected to replicate the 1979-80 locations and dates as best we could, given the limitations of the 1982 report. In addition, depths were chosen in 1997 to assure that bottom elevations were sampled that are exposed at varying frequencies, as well as having been covered by water since Stage I (early 1985).

We had not studied historic reservoir operational (elevational) data prior to collecting bottom samples in 1997. Our intent was to sample the bottom which had experienced a continuum of exposure duration. Following the field season, we determined annual exposure durations for each elevation sampled. From this, we grouped the samples into two elevational strata. The first stratum included elevations above that permanently wetted ($\geq$ 1414 ft msl) and the second included elevations below 1414 ft. A total of 13 discrete sites were sampled between these strata, with 5 in the periodically exposed zone, and 8 in the continually wetted area. Samples were not collected in substrates exposed by drawdown at the time we sampled.

Reservoir elevation at the time of each sampling was obtained from the Jackson Project powerhouse personnel. Sample sites are shown as E_x in Figure 11, where x is an arbitrary sequence number. Five disparate locations were sampled around the reservoir. A longitudinal depth series of four samples were taken in North Bay 2 on August 5 (see Table 17 for depths and bottom elevations). Single samples were taken in North Bay 1, at shoreline site SS1, and in South Bay 1. Two sites were sampled off the point which forms the eastern mouth of the South Fork arm (Figure 11).

Samples were initially reduced in the field by wet-sieving through a Tyler sieve series, with the smallest mesh opening being 0.420 mm (Twenhofel and Tyler 1941; Welch 1948). The residue was transferred to glass sample bottles and preserved with 10 percent formalin. All site samples had high fractions of coarse organic or fine woody debris, which necessitated distributing the sample into several bottles in some cases.

Greg Hood of the University of Washington Fisheries Research Institute processed the preserved samples. Organisms were identified to the Order or Class level, except the Family level for Diptera. Total organism counts were provided from each sample by Mr. Hood. We later converted the counts to number of organisms per square meter of reservoir bed by elevational strata and geographic site.

Results and Discussion

Table 16 relates the depths (bottom elevations) we sampled and historic drawdowns of Spada Lake. The mean drawdown elevation for the previous 13 years (July to July) was 1,417.2 feet (msl). (The drawdown to 1,396 feet in 1992-93 was exceptional, and is not likely to recur, and is not included in the mean.) The mean for the most recent four years was 1,414.5 feet. The maximum drawdown immediately preceding our field sampling was 1,414.0, very close to the mean value. Five of our samples were at elevations that are exposed for varying periods, but at least annually. Eight samples were at elevations that are essentially perennially wetted. By coincidence, one sample occurred at elevation 1,414, which was very briefly exposed (if at all) in November 1996. Otherwise, this elevation had not been exposed for about 3.5 years.

The raw count data from the bottom samples appear in Table 17. Samples collected below elevation 1,414 are shaded. Immediately noteworthy are the very high densities of nematodes, and complete lack of clams (*Pisidium*) in the reservoir regulation zone. Additional detailed remarks about the various taxons occur below. These data suffer from the fact that all samples collected in the regulated zone were collected from just one general area, North Bay 2, about midway down the reservoir's north shore (Figure 11). It is interesting to note that the replicated sample at elevation 1,436 showed relatively low variance for the chironomids and oligochaetes.

Changes Since Stage I

As with zooplankton, it was exceedingly difficult to make comparisons with the "data" from 1979-80 since much of the pertinent information was not reported (WDG 1982). Our purpose was to extract what relatively obvious differences there may be, and identify areas of additional survey, or alternate sampling methods.

Table 16. The relationship between Spada Lake benthic samples in 1997 and frequency of exposure due to drawdown. Values are the number of discrete periods of exposure at least three days long. Exposure periods are given for the events where exposure dropped below elevation 1414. Time blocks are 1 July to 30 June. Values in parentheses are the annual maximum drawdown elevation in feet msl.

1997 Sampling Season		WATER YEAR												
Elevation (ft msl)	Number of Bottom Samples	1996-97 (1414)	1995-96 (1421)	1994-95 (1414)	1993-94 (1409)	1992-93 (1396)	1991-92 (1404)	1990-91 (1419)	1989-90 (1419)	1988-89 (1422)	1987-88 (1409)	1986-87 (1426)	1985-86 (1424)	1984-85 (1425)
1436	2	2	3	4	1	1	2	5	3	3	1	3	4	2
1431	1	6	2+	2	1	1	3	4	3	3	2	3	2	3
1426	1	2	1	3	3	1	2	2	3	1	2	0	1	1
1421	1	2	0	2	3	3	2	0	1	0	1	0	0	0
1414	1	0	0	0	1 (6.5 wks)	1 (7 wks)	1 (5 wks)	0	0	0	1 (3 wks)	0	0	0
1406	1	0	0	0	0	1 (3 wks)	1 (1 week)	0	0	0	0	0	0	0
< 1395	6	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 17. Dates, Spada Lake elevations, depths sampled, bottom elevations sampled, and sample codes for benthic invertebrate samples, 1997. A replicate sample was collected at Site E-1. Samples from below a four–year mean minimum drawdown of 1414 (ft msl) are shaded. Taxon values are in numbers/m2.

Date (1997)	Reservoir Elevation (feet msl)	Sample Depth (feet)	Bottom Elevation (feet msl)	Site Sample Code	Location	Chironomid larvae	Chironomid pupae	Ceratopogonid larvae	Oligochaetes	Hirudinea	Pisidium	Nematodes	Hydracarina
5 August	1438.1	2.0	1436.1	E-1A	N Bay 2	5,361	412	0	6,186	0	0	15,670	0
5 August	1438.1	2.0	1436.1	E-1B	N Bay 2	5,155	0	0	5,979	0	0	29,485	0
5 August	1438.1	7.0	1431.1	E-2	N Bay 2	4,742	0	0	3,918	0	0	18,351	0
5 August	1438.1	12.0	1426.1	E-3	N Bay 2	2,062	0	206	9,485	206	0	14,639	206
5 August	1438.1	16.5	1421.6*	E-4	N Bay 2	258	0	0	773	0	0	0	0
10 Oct	1447.6	53.0	1394.6	E-10	N Bay 2	3,299	0	206	1,649	0	412	412	206
10 Oct	1447.6	58.0	1389.6	E-5	N Bay 1	1,031	0	0	2,474	0	206	0	0
10 Oct	1447.6	57.0	1390.6	E-6	SS1	825	103	0	722	0	1,031	0	0
9 Oct	1448.5	55.0	1393.5	E-8	mouth SF	309	0	0	825	0	309	0	0
9 Oct	1448.5	58.0	1390.5	E-9A	mouth SF	1,649	0	0	412	0	619	412	0
9 Oct	1448.5	42.0	1406.5	E-9B	mouth SF	52	0	0	412	0	412	0	0
9 Oct	1448.5	35.0	1413.5	E-9C	mouth SF	206	0	0	309	0	309	0	0
10 Oct	1447.6	55.0	1392.6	E-7	S Bay 1	361	0	0	619	0	1,082	0	0

* Exposed about four weeks in December 1996, otherwise previous exposure was 24 days in October 1994.

Density

Table 18 presents 1979-80 and 1997 data for a transect run down the center of North Bay 2 (Figure 11). Our best judgment is that "Station 2" in the 1979-80 surveys was off the current mouth of this bay. Since we had no way of knowing exactly where samples were collected in 1979-80 relative to the drawdown limit(s), we chose this site to try to have at least a geographic basis of comparison.

Table 18. Benthic invertebrate densities (no./m2) near Site 2 (WDG 1982) or in N Bay 2 of Spada Lake, 1979-80 and 1997. Nematodes may not have been accounted for in 1979-80. The "shallow" stratum is exposed periodically.

Year	Month	Stratum	n	Chironomid larvae	Oligochaetes	Pisidium	Leeches	Nematodes
1979	August	shallow	2	3230	600	0	0	0
	October	shallow	2	610	0	0	0	0
1980	August	shallow	1	340	21	0	0	0
	October	shallow	1	340	0	0	0	0
1997	August	shallow	5	3515	5270	0	40*	15630
	October	deep	1	205	310	310	0	0

* Mean of five grabs.

August densities of chironomids in the regulated zone were nearly identical between 1979 and 1997, but the single grab in 1980 came up with far fewer midges. No statistical bounds can be put on these comparisons. Oligochaetes (segmented burrowing worms) may have been far more abundant in 1997 than in the previous survey. We found a complete lack of freshwater clams (*Pisidium*) in the regulated zone, which is to be expected. This was consistent with the 1979-80 collections. One of our five samples in 1997 had a few leeches; none were noted in 1979-80.

Finally, we provide data on nematode abundance; it's possible that the earlier investigators made no attempt to account for these organisms. The single "deep" sample below elevation 1,414 in 1997 is provided for reference; there were no "deep" samples collected at this site in 1979-80 since it was (presumably) at an elevation subject to drawdown during Stage I.

Table 19 focuses a Stage I: Stage II comparison on the midges and worms since these are typically the most important benthic invertebrates in salmonid diets in regulated reservoirs. The data in this table are arranged to compare samples from sites which are subject to periodic exposure, and those that are not. The reader is admonished to note that we could not verify the location and depths of the sample data from 1979-80, and this table's data arrangements assume Stations 2, 5, and 7 were at sites and elevations that are periodically exposed (inferred from the context of WDG (1982)).

Table 19. Comparisons of chironomid and oligochaete densities (no/m2) in Spada Lake, 1979-80 and 1997. Density ranges are given unless only one sample was taken. Mean values are in parentheses. Sample sites are classed as periodically exposed, or continually wetted. This determination was difficult for the 1979-80 data (see text).

		Periodically Exposed			Continually Wetted	
	Month	**1979**	**1980***	**1997**	**1979**	**1997**
CHIRONOMIDS	April	------	1385 - 4045 (2715)	------	------	------
	June	2520	75 - 1460 (765)	------	265 - 5210 (2080)	------
	August	3230	340 - 1965 (1150)	58 - 5360 (3515)	850 - 1110 (960)	------
	October	610	340 - 810 (575)	205	720 - 4050 (2285)	52 - 3300 (967)
OLIGOCHAETES	April	------	15 - 55 (35)	------	------	------
	June	175	0 - 124 (60)	------	0 - 430 (180)	------
	August	600	20 - 440 (230)	773 - 9485 (5270)	24 - 265 (115)	------
	October	0	0 - 70 (35)	------	345 - 780 (540)	310 - 2475 (928)

* Assumed Sites 2, 5, 7 periodically exposed..

Although our collections in 1997 can only be considered a rough reconnaissance, it appears that chironomid densities in the regulated zone are roughly equivalent to Stage I levels, based on August samples only (1150 v. 3515 orgs/m^2). Their abundance in the continually wetted zone may be reduced in 1997, but the number of samples is too low, and there is great uncertainty as to the actual depth sampled in 1979.

Oligochaete densities in the regulated zone appear to be higher in Stage II; both the range and mean values in 1997 were substantially higher than in 1979-80 (230 v. 5270 orgs/m^2). There may also have been an increase in worms in the deep zone, but the difference here did not appear to be as great (540 v. 928).

Species Diversity

Given the small sample sizes in all years, and the problems with locations and depths, a more meaningful comparison may be the species diversity seen in Stage I versus Stage II (Table 20).

Table 20. Occurrence of benthic invertebrates in benthic samples and trout diets from Spada Lake, 1979-80, 1986, and 1997. Nematodes may not have been accounted for in 1979-80.

Year/s	Source	Midges	Oligochaetes	Leeches	Clams	Snails	Nematodes
1979-80	Benthic grabs	X	X				
	Trout diet	X		X	X	X	
1986	Trout diet	X		X			
1997	Benthic grabs	X	X	X	X		X
	Trout diet	X			X	X	

Midges were seen in both bottom samples and trout stomachs in all years. Oligochaetes have been present in both Stage I and II, but have not appeared in trout stomachs.

While leeches have been present in both Stage I and II, they were not collected by bottom sampling in 1979-80 (a total of 32 separate samples). They were found in low numbers in the regulated zone in 1997 (Table 17). More information on the depth distribution and abundance of these animals is needed, since their occurrence in the trout diet took a sharp drop in 1997 when compared with 1979 (Tertiary Production — Trout Food Habits). The increase in leech density suggested by the 1997 bottom sample(s) is probably an artifact of small sample sizes in both surveys, and is counter to what was well–documented in the trout diet (Tertiary Production— Trout Food Habits).

Freshwater clams and snails had not been sampled from the benthos in 1979-80, however the earlier authors had seen them in the diet (WDG 1982). (Snails have not been sampled appropriately in any year, and are under–represented in the invertebrate data.) These molluscs have been a small component of the trout diet in all years, and were only found in cutthroat in 1979-80. We can make no inferences about changes (if any) in mollusc abundance between Stages I and II due to sampling deficiencies.

No gammarids have been noted in the benthos or in the trout diet. This is not surprising, since these invertebrates are among the first species to be eliminated from the regulated zone of most reservoirs (Hunt and Jones 1972). The 1979 and 1997 benthic invertebrate and trout diet studies conducted on Spada Lake have occurred after significant periods of water level fluctuation following completion of each Stage (1965 through 1978, and 1985 through 1996). However, the diet study associated with the 1986 sport catch made no mention of them either. One might speculate that the recent flooding of new soils could have allowed some development of a scud population, if they were present in low numbers, or somehow introduced, but none were seen in 239 stomachs sampled in 1986.

In summary, there has been no apparent loss or gain in the number of major taxons in the benthic invertebrate community in Stage II. However, benthic sampling to date has been completely inadequate to fully assess changes in numerical abundance or distribution since Stage I. Based on trout dietary information (Tertiary Production—Trout Food Habits), we believe leech abundance or distribution has changed such that they are significantly less available to the trout. Sketchy data on the chironomids suggests they have not been affected greatly by dam–raising, but oligochaetes may have been enhanced. Further sampling is mandatory to at least understand current conditions; it is probably impossible to gauge or assess benthos changes since Stage I due to inadequate sampling and reporting at that time.

Comparisons to Other Reservoirs

We organized the 1997 data in ways that can be compared to that reported by others (Tables 21 through 23). Two general schemes emerged from the literature: dividing the reservoir basin into two or more zones that reflect the frequency of exposure (Table 21), or relating invertebrate densities from a range of elevations to the most recent, or an average drawdown maximum (Tables 22, 23).

Table 21. Late–summer mean densities (no./m2) of benthic invertebrates from Spada Lake, Washington, and other waters of similar latitude. The "shallow" stratum is exposed frequently; the "deep" stratum is continually wetted.

Water	Time Frame	Depth Stratum	Chironomids	Oligochaetes	Pisidium	Authority
Spada Lake (reservoir), WA	August-October	shallow	3515	5270	0	This study
(1997)	August-October	deep	965	930	550	
Hungry Horse Reservoir, MT	August-October	shallow	292	57	----	May et al. (1988)
(1987)	August-October	deep	343	42	----	
Libby Reservoir, MT	July-September	shallow	140	7	----	Chisholm et al. (1989)
(1987)	July-September	deep	280	360	----	
Ross Lake (reservoir), WA	August	shallow	130	635	0	Seattle City Light (1973)
(1972)	August	deep	335	320	0	
Lake Francis Case (reservoir), SD (1968 through 1973)	September	shallow	2540	200	0	Benson and Hudson (1975)
Barrier Reservoir, Alberta	"annual"	shallow	1180	120	.200	
(1960-62)	"annual"	deep	4180	415	2200	Fillion (1967)

Table 22. Mean numbers of benthic invertebrates (/m2) from the N Bay 2 transect of Spada Lake, August 5, 1997 (pool elevation 1438' msl). Sample locations are designated by depth of water at full pool elevation (1,450') and by feet above (+) and below (-) the 1996 maximum drawdown elevation of 1414 ft msl (represented by vertical line in table.

Depth on Date (ft):	2.0	7.0	12.0	16.5	53.0
Depth of station at maximum pool (1450' msl)	14.0	19.0	24.0	28.5	65.0
Feet above (+) and below (-) max. drawdown	+ 22.0	+ 17.0	+ 12.0	+ 7.5	- 29.0
Chironomids	5260	4740	2060	258	3300
Oligochaetes	6080	3920	9485	773	1650
Leeches	0	0	206	0	0
Clams	0	0	0	0	412
Nematodes	22,580	18,350	14,640	0	412
Total Edibles	5260	4740	2270	258	3710

Table 23. A comparison of the vertical distribution of mean numbers of chironomids (per m2) from benthic studies in Spada, Ross, Barrier, and Blasjon Reservoirs, and Lake Ankarvattnet. The stepped horizontal line represents the approximate drawdown level affecting each study's sample series.

Feet*	**Meters**	**Spada Lake**	**Ross Lake/1**	**Barrier Reservoir/2**	**Blasjon Reservoir/3**	**Lake Ankarvattnet/3**	
		1997	1971	1960	1959	1959	0 drawdown
0.0 - 16.4	0 - 5	5260	931	1105	205	2610	level
16.4 - 32.8	5 - 10	2355	532	675	872	1740	
32.8 - 49.2	10 - 15	129		2940 10m	491	1335	
49.2 - 65.6	15 - 20	1245 11m	304	1435	392	1000	
65.6 - 80.0	20 -25		1180	1405	334	584	
80.0 - 98.4	25 - 30		2525 22m	2215	334	584	
98.4 - 114.8	30 - 35		817	1915	359	457	
114.8 - 131.2	35 - 40			1190			
Maximum drawdown during previous winter		36 ft	71 ft	33 ft	20 ft	unregulated	
Sampling date		August	Sept	----	----	----	
Location		Northwest Washington		SW Alberta	northern Sweden		

* From full pool level.

/1 Seattle Department of Lighting
/2 Fillion (1967)
/3 Grimås (1961)

Exposed/Unexposed Zone Method

Based on our very limited data from 1997, both midges and segmented benthic worms seemed to be at above–average densities in the regulated zone. We caution that this must be confirmed through more extensive sampling. This seemed to be particularly true for the oligochaetes. Clams were relatively abundant below the drawdown zone in Spada, but far below densities seen in at least one other reservoir.

Proximity to Maximum Drawdown Method

(Tables 22 and 23 provide the most information on densities relative to drawdown depths; future sampling should be based on this general scheme. Additional treatment considerations would include the number of shoreline habitats to be sampled, and the number of replicates taken at each station. Future sampling should focus on the stream mouths, where higher rates of allochthonous detritus sedimentation would be expected, and which would support greater density or diversity of organisms. The balance of the reservoir shoreline could probably be partitioned into a very limited number of representative habitats.)

A series of samples were taken down the midline of North Bay 2 on August 5, 1997 (Table 22). The sample depths ranged from 2.0 feet near the extreme inner end of this bay, to 53 feet near its outer mouth. The sample elevations ranged from 7.5 to 22 feet above the maximum drawdown the previous winter, and one 29 feet below that same point. Healthy numbers of midges and worms were seen both above and below the drawdown point. Clams were only found below the drawdown level. Nematodes were vastly more abundant at the upper range of the regulated zone.

It is important to note that the samples from this bay may not be representative of much of the more exposed shoreline areas of the reservoir. It is a curved, narrow bay, well–protected from the prevailing winds and wave action. Therefore, it may have accumulated a richer than average deposit of soft sediments and resultant fauna. We also were struck by the extremely small size of the organisms, as was Greg Hood, who processed the samples. Future sampling must include biomass estimates to put these densities into better perspective. Failure to see oligochaetes in the trout diet may be due to a combination of their being too small to be noticeable by the fish, or offering too little nutrition to stimulate the requisite searching behaviors. Finally, if any are eaten, they would be subject to rapid digestive degeneration, and would be difficult to sample in the diet unless special sampling precautions were taken.

The Spada Lake chironomid density data presented in Table 23 combines all samples from around the reservoir, separated only by depth stratum. Although the number of stations and samples from Spada is too small to make reliable inferences, this data presentation method suggests that Spada may have a healthy level of midges relative to other reservoirs. Most reservoirs show heightened insect densities just below the zone of maximum drawdown (Grimås 1961; Fillion 1967; Seattle Dept. Of Lighting 1973; Chisholm *et al.* 1989). The higher densities in the highest elevations in our samples may have been an artifact of the protected bay that they came from. While the data are accurate, they may not be representative of much of the reservoir's shoreline.

Trout Dietary Considerations

Fluctuations in water level influence benthic invertebrate populations by eliminating macrophytes in much of the regulated zone (Quennerstedt 1958), altering substrates by erosion in this zone (Grimås 1961), and by exposing substrates to air or ice cover (Paterson and Fernando 1969). Successful establishment of benthic fauna in the regulated zone depends upon management of minimum pool levels, duration and season of drawdown, the ability of benthic fauna to adapt to water fluctuations by following receding water levels, their survival in areas exposed to air or ice cover, and their recolonization of inundated areas after refilling (Kaster and Jacobi 1978). The most common benthic species remaining under a fluctuating water levels regime is chironomid midges and oligochaete worms. Larger forms such as leeches are typically greatly reduced, or eliminated. Mobile forms such as *Gammarus* spp., Hydracarina, larger insect forms such as Coleoptera and Corixidae etc., and gastropods are often greatly reduced or lost due to physical deficiencies in the littoral environment (Grimås 1961; Hunt and Jones 1972). Filter–feeders such as freshwater clams are often relegated to the bottom zone below the level of maximum drawdown (Fillion 1967). These are precisely the conditions our initial reconnaissance survey revealed in Spada Lake in 1997.

It is important to note, however, that certain species are better able to accommodate to water level fluctuations than others (Paterson and Fernando 1969). Future benthic surveys in Spada should include derivation of a species list (e.g., Table 11) from which any long–term changes in species composition can be determined. This is relevant in that the small size of the oligochaetes may be due more to the species present (genetic effects) than their growth potential in the substrate (environmental effects).

Future surveys must include derivation of biomass, in addition to numerical density. Although our preliminary survey suggests relatively strong numbers of midges and worms, their actual accumulation of organic mass (production) may be low, with little actually being utilized by the fish community.

This is particularly important if, in fact, little or no oligochaetes are being utilized, and if much of the midge production is being lost to emerging adults. Studies by Nilsson (1955, 1961) showed that chironomids were available as fish food mainly in the form of pupae and imagoes, with predation probably taking place in connection with insect emergence and egg deposition. Due to changes in the species composition of the dipteran community, and resultant changes in emergence timing and intensity (briefer, more intense), an actual increase in bound energy is lost from the lake's food chain. The long–term effect of level fluctuation is often an increasing relative abundance of oligochaetes, nematodes, and pisidians (strongly suggested by our limited data as having occurred in Spada in Stage II). An increased relative abundance of midges can be counteracted by their actual reduced availability as food, depending on the nature and effect of the level fluctuation regime. The net effect can be a changed balance within species, especially within the chironomids, and an arctification of the bottom environment and a sharpening of the oligotrophic character of the reservoir (Grimås 1961).

The relevance of this gloomy scenario is underscored by the fact that terrestrial insects and washed–in annelids comprised between 47 and 89 percent of the trout diet, *by volume*, for most of the trout growing season in 1979-80 (WDG 1982). Non–lake food groups continue to be the major portion of the trout diet (Tertiary Production—Trout Food Habits); in fact, the contribution by midges has actually decreased since 1986 (Figure 98).

Summary Remarks

Fluctuating water levels almost always result in greatly diminished benthic invertebrate species diversity (Hynes 1961; Baxter 1977). Placement of a dam on Llyn Tegid in North Wales increased annual fluctuations from two to about five meters. Although total density of bottom organisms increased along the shores, many littoral species (e.g., sponges, flatworms, snails, stoneflies, caddisflies, and amphipods) that were very important fish dietary items were reduced in number or completely eliminated. A 42 percent increase in total density after fluctuations increased resulted almost exclusively from increases in chironomids and oligochaetes (Hynes 1961; Hunt and Jones 1972). The remaining fauna, even if relatively abundant, may be inefficient in the transfer of accumulated energy to the fish community due to narrow insect emergence timing (Grimås 1961). A more thorough survey of current benthos standing crop and dietary use by trout in Spada Lake may reveal that actual secondary production by invertebrates, and its transfer to trout, is low and inefficient.

A rough gauge of the relative magnitude or impact of drawdowns in Spada is the percent change in reservoir area between full pool (1,450) and the average drawdown level (1,414). About 410 acres of bottom are exposed at 1,414 ft, which represents a 21.9 percent reduction in surface area. Another index to the effect of drawdown on the upper shore (there is no true littoral zone in the regulated area of a reservoir (Baxter 1977)) is the change in the product of mean depth and surface area, $\pm zA$ (Ploskey 1983). Spada Lake experiences a 39 percent reduction in this index between elevations 1,450 and 1,414. The near–doubling of the percent reduction between these indices is due to the effect of the shape of the basin. Although we do not possess a model to translate these indices to expected reductions in secondary or tertiary production, they are a useful basis of comparison between other lakes and reservoirs. Ploskey (1983) referred to reduced surface areas of 20 to 30 percent and resultant "large" negative zA values as "reflecting significant losses of productive littoral area."

Conclusions

It was very difficult to make comparisons with 1979 (Stage I) benthos data due to poor documentation of sample sites in 1979-80. Sample sizes in both 1979-80 and 1997 were too small to make reliable comparisons. The data collected in 1997 should be used to design a more complete survey of benthic invertebrates.

Chironomid densities in the drawdown zone appeared to be roughly equivalent to Stage I levels.

Oligochaete densities in 1997 appeared to be higher in Stage II, but do not appear in trout stomachs.

Both midges and segmented worms may be at above–average densities in Spada Lake when compared with other area reservoirs, but the sampling data are too sparse to be sure.

Leeches and clams, while still present in the reservoir, are minimally present in the trout diet. Clams are not found in the regulated zone. Sampling deficiencies in both Stage I and II prevent conclusions about relative abundance between 1979-80 and 1997.

There was no apparent loss or gain of species between Stages I and II. However, sampling to date has been inadequate to fully assess changes in numerical abundance or distribution.

Future benthos surveys must include compilation of a complete species list, and derivation of biomass estimates. Surface insect drift should also be quantified, as it is a significant portion of the trout diet.