Tertiary Production

Fish Relative Abundance, Length Frequency, and Sex Ratio

Estimates of the abundance of trout and brown bullhead in Spada Lake are needed for several purposes, as discussed below for each species.

Brown bullhead

Brown bullhead are presumed to compete with trout for food resources in Spada Lake. An estimate of their abundance (as well as their spatial distribution) is needed to gauge the relative intensity of this competition. If it is determined that their numbers should be reduced to allow increased trout growth, it will be necessary to have a population estimate in order to estimate the costs of a bullhead control, or population reduction program.

Estimating bullhead abundance (and distribution) was beyond the scope of our work planned for 1995-97. Catch statistics from vertical and horizontal gillnet sets are available in WDFW Region 4 databases for future reference, but these methods are probably not most useful for assessing their abundance and distribution. Imamura (1975) soon rejected their use, and utilized frame nets in his work on Lake Washington. These were supplemented with boat electrofishing and hand dipping of young of the year schools as needed. We also believe baited commercial shrimp pots may be an effective means of collection. A feasibility study is needed to determine the most effective means of obtaining a bullhead population estimate in Spada Lake. Such a study would also probably identify the most effective control options and provide the statistics needed for control cost estimation.

Trout

In this section we provide relative trout abundance data which may be used for comparative purposes following future surveys. See Section on Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock for a qualified estimate of the actual trout population size and standing stock.

Methods

General Fish Biological Workup

Rainbow and cutthroat trout field identification was based on scale size, presence of basibranchial teeth, spotting pattern, length of the maxillary, lateral coloration, and presence of a red hyoidal slash on each side of the jaw along the dentary. Hybridization between the two species occurs to a growing extent in the Spada Lake population. Many specimens were examined which had morphometric characteristics associated with both species, which often presents difficulties (Leary *et al.* 1983; 1996). Trout which exhibited characters of both species (most commonly basibranchial teeth in association with a "short" maxillary and/or lateral rainbow hues) were classified as hybrids.

All fish were measured for total length using a measuring board to an accuracy of one millimeter, and weighed on a gram scale to an accuracy of two grams. All trout were given a semi–quantitative internal examination for fat content, gonadal condition, stomach contents, and parasite loads, as described below and in following sections. Results were logged into a database (WDFW file data, Region Four, Mill Creek). Fish samples were sub–sampled for dietary analysis and parasite loads, in which cases the results were quantitative, and those results are presented in Trout Food Habits and Trout Parasitism and Mortality, respectively.

Trout stomachs which were not preserved for laboratory analysis were slit, and the contents noted in order of decreasing volumetric contribution. Stomachs which appeared to be empty were so noted, but it's possible that very small amounts of small organisms, such as zooplankton, may have gone undetected by a gross visual scan.

A gross estimate of the number of *Diphyllobothrium* plerocercoids was made on fish which did not receive meticulous examination for this parasite. Internal organs and pyloric caecae were teased apart and rotated, and encysted plerocercoids counted. This method would tend to underestimate the actual number of plerocercoids as some cysts may carry more than one cestode, or cover one or more. Also, a gross visual scan misses very small plerocercoids migrating to the surface of the stomach lining.

Two adult cestodes were commonly seen in the pyloric caecae, *Proteocephalus salmonidicola*, and *Eubothrium salvelini*. In fish which were not carefully dissected and examined, their abundance was estimated by the number of caecae which were distended with adult worms.

The abundance of these cestode life stages was scored using a system that has been established for Washington inland fisheries since the early 1970s: 0 to 4 parasites = light; 5 to 9 parasites = moderate; $\geq$ 10 parasites = heavy.

Abbreviations that may appear in this report or its appendices are as follows: rainbow trout (rb), westslope cutthroat trout (ct), rainbow X cutthroat hybrids (hyb), and brown bullheads (bb).

Seasons

The sampling period was stratified into three seasons based on reservoir operation, surface water temperature, and likely spawning movements of trout (Winter, or December through March, was not sampled):

1) Spring (April and May); the reservoir is being refilled, and surface temperatures increase from 4° to 5°C to 10° to 12° C;

2) Summer (June through September); reservoir levels may fluctuate, but are at the seasonal maximum, at or near full pool, then gradually drop until the fall rains; temperatures increase to above 20° to 21° C;

3) Fall (October through November); reservoir levels may rise swiftly in mid–late November; temperatures drop to 9° C and below.

Nearshore Zone Fish Abundance

Seasonal and annual fish abundance within the nearshore zone were assessed using floating and sinking horizontal gillnets. Up to seven sinking nets, and one or two floating nets were set per night. No nets were baited or chummed. Great care was taken to avoid draping the gear over stumps or large woody debris.

All sinkers were 60 feet (18.3 m) long and 6 feet (1.8 m) deep, with four equal 15 foot (4.6 m) panels of 1.5, 2.0, 2.5, and 3.0 inch (38, 51, 63.5, and 76 mm) stretched multi–filament mesh. The smallest mesh was always set closest to shore, and the panels increase in size distally. Nets were set perpendicular to shore, with the small mesh fishing as close to the edge as practicable. Sites were chosen which offered the ability to fish as much of the full height of the smallest mesh panel as possible (steep slopes), while at the same time keeping the larger mesh panels in water less than 15 to 20 feet (4.6 to 6.1 m) deep.

Floating nets were 120 feet (36.6 m) long and 6 feet (1.8 m) deep, with six 20 foot (6.1 m) panels. These nets were attached to woody debris or trees in depths and over slopes as with sinkers, and fished perpendicular to the shoreline. The distal end was anchored and buoyed such that the corkline remained level atop the surface. Floaters were of monofilament webbing, with a similar range of mesh sizes as the sinkers, except that two additional 20 foot panels of 3.5 and 4.0 inch (89, 101.5 mm) stretched mesh were located at the distal end of these nets.

Nets were set in mid–afternoon, and retrieved in early to mid–morning. Total counts of all fish species in each net were recorded. All trout were tagged with numbered spaghetti tags, and pooled in a container (on ice in the warmer months) for later biological workup. (All fish were measured for total length.) Separate data sheets were kept on each net set, recording data on water conditions, weather, time of set and retrieval, overnight change in reservoir elevation, water temperature, location, and any other pertinent information ("comments").

All horizontal nets fished the top 6 ft (1.8 m) of the reservoir, and 60 to 120 feet (18.3 to 36.6 m) of its edge.

Offshore Zone Fish Abundance

Vertical gillnets were used to assess the relative abundance and depth distribution of fish species in the offshore, or limnetic zone. An overnight set of six to ten nets was made in a grouping, typically such that the anchored web panels were roughly lined up perpendicular to the shoreline. Usually only one general site on the reservoir was sampled per night. Monofilament nets of a single mesh were wrapped on floating aluminum rollers (Bartoo *et al.* 1973) and deployed from an 18' utility work boat equipped with a gunwale rack. Mushroom anchors were used to hold the panel in position. Panels were 6 ft (1.8 m) wide, and were sufficiently long to fish from the surface to the bottom at all sites (up to 110 ft, or 33.5 m; typically 40 to 70 feet, or 12 to 21 m in 1997). Stretched mesh sizes ranged from 0.75 to 3.0 inches (19.5 to 76.2 mm). Each net was marked in five ft (1.5 m) intervals such that the depth of each fish relative to the bottom could be recorded as it was removed. (These depths were later converted to distance from the surface based on the daily reservoir elevations.)

These nets were also set in mid–afternoon, and retrieved in early to mid–morning. All environmental data were noted, and fish were tagged, stored, and later processed as for the horizontal nets. Most roller groupings were set at locations 100 to 200 feet (30 to 61 m) from shore. None of these nets were baited or chummed.

CPUE Calculations

Catch per unit effort was calculated differently for horizontal gillnets set on the surface, and vertical nets.

Since all horizontal nets fished a nearly–equivalent amount of net surface area per night, and were set in similar habitats (extreme nearshore, at the surface), their CPUE was defined as:

$$\frac{\text{Number of Fish}}{\text{Number of Darkness Hours Fished}}$$

CPUE was calculated separately for each individual net set (Appendix Tables 11 and 12) based on both the actual number of hours fished, and the number of nighttime hours. The latter was estimated from tables of sunset and sunrise times, with no allowance for twilight. A nighttime CPUE was used throughout this report on the assumption that the multi–filament nets were relatively ineffective until after sunset since they could presumably be seen, and avoided by trout.

The monofilament vertical gillnets could presumably catch trout as soon as they were set, since they extended to the bottom, and into regions where ambient light levels would be quite low. Thus, they could catch fish as long as they were deployed. Also, the amount of gear actually fishing varied with the depth of the site, therefore, their CPUE was defined as:

$$\frac{\text{Number of Fish}}{\text{Number of Nets} \times \text{Hours Fished} \times \text{Depth of Water}}$$

Thus, for vertical nets, effort was based on the number of feet of 6–ft wide net fished over time. Hours set were calculated from the actual time of deployment to the time of retrieval, which always included significant numbers of daylight hours. Use of the above formula results in high numerical values for effort, and a resulting CPUE that is a very small decimal fraction. To make the values easier to compare among themselves and to the horizontal net CPUEs, each vertical CPUE value was multiplied by 10^4 to give a number closer to 1.0 (Bartoo 1972).

Length frequencies for trout and brown bullheads were plotted in the standard manner, with trout plots broken out by season and species, as well as for the aggregate season–long sample.

Results and Discussion

A total of 462 trout were taken from Spada Lake in the gillnets in 1997:

Species Collected	Number	Percent
Rainbow	229	49.6
Cutthroat	146	31.6
Hybrids	87	18.8

The proportions of rainbow, cutthroat, and hybrids seen in 1997 compare with samples collected in creel surveys in 1986 and 1992 as follows (percent):

Year	Rainbow	Cutthroat	Hybrids	Total
1986	3828 (33.4)	6259 (54.6)	1372 (12.0)	11,459
1992	163 (33.7)	210 (43.4)	111 (22.9)	484
1997	229 (49.6)	146 (31.6)	87 (18.8)	462

Contingency Chi–square analysis indicated the proportions of individual species varied significantly among the three forms in the three–year comparison, as well as 1986 v. 1992, and 1992 v. 1997 ($\alpha = .05$). Thus, for example, the increase in rainbow from one third to nearly one half of the aggregate population is a significant increase. However, this is probably a sampling artifact since all fish taken in 1997 were from gillnets, and all prior fish were from the sport fishery. If only fish ≥ 12" are sampled (use Figure 53), then the proportions in 1997 are nearly identical (.365, .442, .192).

Horizontal v. Vertical Net CPUE

It was not our objective to test the relative fishing efficiency of the gear types used, but rather to collect suitably large trout sample sizes for age, growth, and mortality analysis. We noticed appreciable differences in the relative catches of the gear used, which is important if future studies are planned which require a heavy statistical dependence on relative catch rates by gear type.

In four of six months in 1997, when both gear types were set concurrently, CPUE for horizontal gillnets was higher than that for vertical nets (Figure 48). In August and September, particularly in August, catch rates for vertical nets exceeded that of the horizontals. These differences, particularly the large one in August, suggest a relative offshore movement of trout at that time.

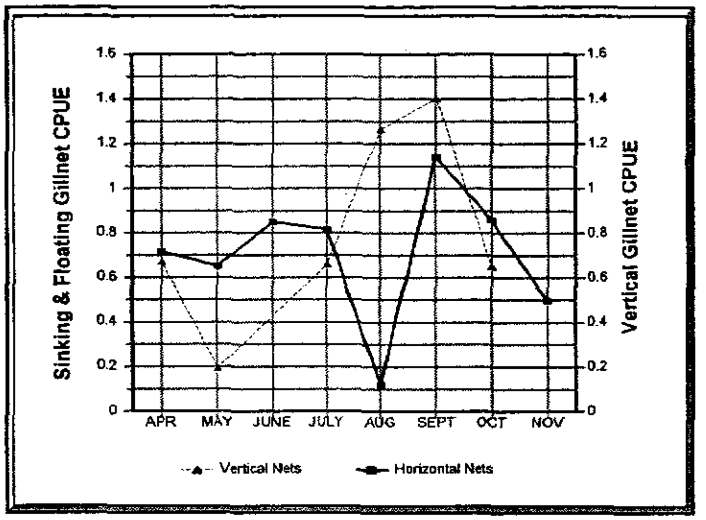


Figure 48. Monthly catch per unit effort of horizontal and vertical gillnets in Spada Lake, 1997.

Whether these differences are statistically meaningful is debatable since the CPUE calculation differs between the gear types. Also, it was obvious to us in working the gear that the vertical nets were much less effective in collecting trout. This was probably due to the minute amount of vertical net fishing the relatively large amount of limnetic habitat. Many fishless vertical nets were retrieved, but "null" horizontal net sets were relatively rare.

The absolute number of trout collected in the vertical nets was always extremely low, and varied appreciably between the mesh sizes fished (Tables 24, 27). We caught no trout in the 3.0 inch (76 mm) mesh, and only seven in the 2.5 inch (63.5 mm) mesh. The low catches in these mesh sizes may be a reflection of the dearth of larger trout (see length frequencies, below). If the objective were to collect 15 to 20 trout of each age group per sample period, the amount of vertical net effort would need to be increased substantially, perhaps four or five times, if not more, particularly in the spring and fall months (Table 27).

Table 24. Monthly trout catches, by stretched mesh size, in vertical gillnets in Spada Lake in 1995-97.

Mesh Size (inches)	APRIL			MAY			JULY			AUGUST			SEPTEMBER			OCTOBER		
	Net-hrs	Catch	Year	Net-hrs	Catch	Year	Net-hrs	Catch	Year	Net-hrs	Catch	Year	Net-hrs	Catch	Year	Net-hrs	Catch	Year
0.75				20.9	1	95	38.7	2	96									
1.00	19.5	0	97	59.8	1	97	55.6	3	96	47.4	6	97	70.2	14	97	38.8	0	96
1.50	19.4	1	97	21.4 58.3	4 1	95 97	55.3	3	96	107.3	8	97	70.9	4	97	39.8	1	96
2.00	41.2	4	97	58.9	2	97	55.3	2	96	106.1	4	97	70.3	3	97	38.5	5	96
2.50	38.8	0	97	20.8 78.9	0 0	95 97	55.2	2	96	107.3	5	97	70.9	0	97	39.3	0	96
3.00				39.8	0	97				52.9	0	97	17.6	0	97	19.4	0	96

Sinking v. Floating Horizontal Net CPUE

The floating gillnets almost always outfished the sinkers, at times substantially so, even when set concurrently (Figure 49). Analysis of variance of net CPUE between sites and gear type was beyond the scope of our study, but it was obvious that catches were much higher in certain locations with the monofilament floating nets. As a result, we focused most of our floater effort at Site NS2, a point located on the north shore near the dam (Figure 11). A point located south of the mouth of Williamson Creek (SWC) was also a "hot spot." These results clearly showed that depending on the explicit research question/s, the type of gear chosen and the sites fished need to be carefully considered, as well as ultimate statistical analysis.

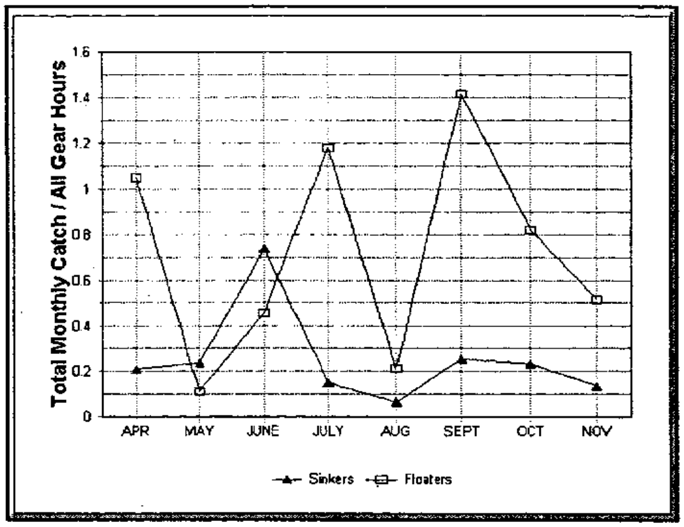


Figure 49. Monthly catch per unit effort of floating versus sinking horizontal gillnets in Spada Lake, 1997.

Relative Catches by Gear Type

Trout

Figure 50 plots the total number of trout collected by all three gear types, by month, in 1997. Total catches by both sinking horizontal and vertical nets were always low, usually ≤ 10 by either gear type, even when two to three outings occurred within a month. Conversely, total catches by the floaters were usually more than 15. Only in August was a larger sample of trout collected by the vertical nets. Although a smaller number of horizontal nets were set in August than in most months (Appendix Table 12), horizontal CPUE was still sharply down (Figure 48), which may represent relatively more fish offshore at that time.

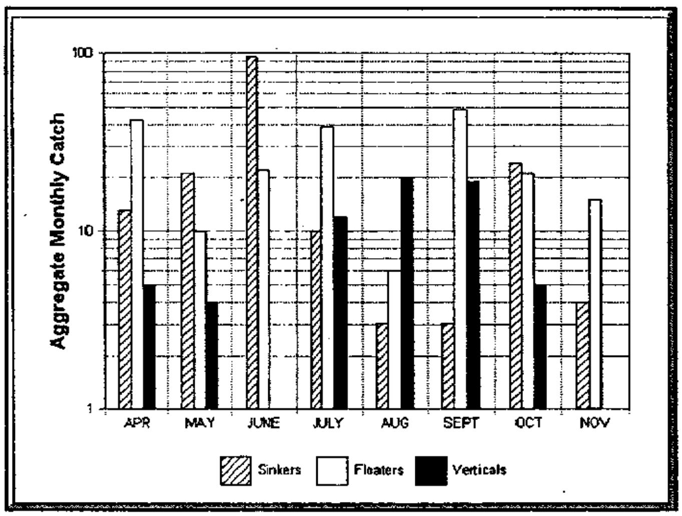


Figure 50. Relative aggregate monthly trout catches by gear type in Spada Lake, 1997.

Stables (1989) found that during the summer months, based on set lines and hydroacoustic data, trout spent daylight hours "almost exclusively offshore", with densities highest at intermediate depths (4 to 16 m). However, from dusk to dawn, he noted an onshore movement into shallow (0 to 4 m) water, while still maintaining a presence in the offshore zone. Trout "were nearly absent from deeper, cooler waters." Based on this, we presumably fished gear in all areas where trout would likely be found, however the amount of gear fished on the bottom, particularly at depths greater than 10 to 15 feet (3 to 4.5 m) was practically nil, and was only represented by the 6–ft wide panels of individual meshes on each vertical net. Other reservoir studies have made good use of sinking horizontal nets of considerable length set offshore on the bottom for tracking year to year abundance trends (Chisholm *et al.* 1989).

Brown Bullhead

We were very surprised at the number of bullheads that were caught in the vertical nets, which were typically set at least 100 ft (30.5 m) offshore, often twice that distance. While bullheads are typically characterized as benthic, edge–oriented species (Emig 1966; Scott and Crossman 1973; Wydoski and Whitney 1979), we repeatedly collected them at depths ranging from the surface to over 20 ft (6 m) in our offshore vertical nets. While this might not be wholly unexpected in the reservoir's shallower, warmer bays and arms, they were also taken in our sets at Site NS4, along the rocky cliffs midway down the north shore (Figure 11). They were most frequently netted in the top 10 ft (3 m) of the water column when taken in offshore nets.

Bullheads were taken in all three gillnet types (Figure 51), but depending on the month (or water temperature), and the local environmental conditions at the site fished, far more were usually taken in the horizontal nets. The highest catch (n=210) occurred in a single floating monofilament net set a few hundred yards west of the mouth of the North Fork Sultan River on July 16. Most of these were probably yearlings, but all ages were represented. The high catches in verticals in July were from a set cluster made on the east side of the inner South Fork arm in 1996.

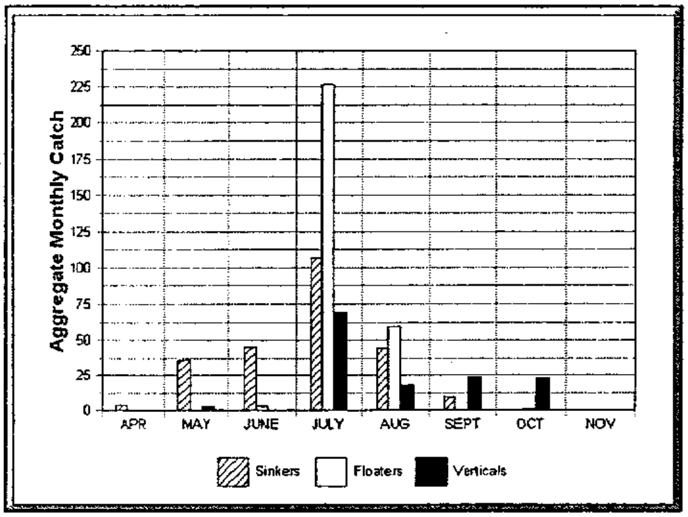


Figure 51. Relative aggregate monthly brown bullhead catches by gear type in Spada Lake, 1997.

Tables 25 through 27 present the monthly aggregate catches of trout and bullheads by gear type, in 1997 unless otherwise indicated.

Table 25. Monthly catch statistics for **floating horizontal gillnets** set from the shore of Spada Lake, 1997. One 150' X 6' monofilament multi-panel gillnet set per site, perpendicular to the shoreline, with 30' panels of 0.75, 1.0, 1.5, 2.0, and 2.5" stretched mesh.

Parameter	April	May	June	July	August	September	October	November
Retrieval Date(s)	11, 25	9, 23	6, 20, 21	2, 17	5, 18	9, 23, 24	10	14
Number of Sites	2	1	4	3	1	1	1	2
Mean Temp (C)	5.8	10.3	13.4	17.0	22.3	19.0	11.8	7.8
Reservoir Elevation(s)	1433 1440	1442 1443	1446 1447	1444 1446	1438 1435	1428 1440	1448	1432
Aggregate Catch of:								
Rainbow	17	10	14	17	3	33	15	2
Cutthroat	19	5	3	17	2	11	2	10
RB x Ct	7	5	5	5	1	5	4	3
Sub Total	43	10	22	39	6	49	21	15
Total Trout CPUE	1.049	0.113	0.455	1.180	0.212	1.416	0.820	0.514
Brown Bullhead	0	0	3	227	59	0	1	0
Total Bullhead CPUE	0.000	0.000	0.062	6.866	2.087	0.000	0.039	0.000

Table 26. Monthly catch statistics for **sinking horizontal gillnets** set from the shore of Spada Lake, 1997. One multi-filament, multi-panel gillnet set per site, perpendicular to the shoreline. Each horizontal net is 60' X 6', with 12' panels of 0.50, 1.0, 1.5, 2.0, and 2.5 inch stretched mesh.

Parameter	April	May	June	July	August	September	October	November
Retrieval Date(s)	11, 25	9, 23	6, 20, 21	2, 17	5, 18	23	10	14
Number of Sites	6	6	12	6	4	1	8	2
Mean Temp (C)	5.8	10.3	13.4	17.0	21.8	16.5	11.8	9.4
Reservoir Elevation(s)	1433 1440	1442 1443	1446 1447	1444 1446	1438	1440	1448	1432
Aggregate Catch of:								
Rainbow	6	7	52	5	1	1	9	0
Cutthroat	5	7	25	3	1	1	8	2
RB x Ct	2	7	18	2	1	1	7	2
Sub Total	43	21	95	10	3	3	24	4
Total Trout CPUE	0.209	0.238	0.736	1.151	0.065	0.254	0.234	0.137
Brown Bullhead	4	36	45	107	44	9	0	0
Total Bullhead CPUE	0.064	0.000	0.349	1.618	0.957	0.763	0.000	0.000

Table 27. Monthly catch statistics for **vertical gillnets** set offshore in Spada Lake, 1996-97. One gang (4 to 5 mesh sizes, one size/roller) of monofilament gillnet rollers was set per site. Mesh sizes were 0.75, 1.0, 1.5, 2.0, 2.5, and 3.0 inches stretched. The July and October data are from 1996.

Parameter	April	May	June	July	August	September	October
Retrieval Date(s)	25	9, 23		9, 18, 19	5, 18, 19	23	4
Number of Sites	1	2		3	2	1	1
Mean Temp (C)	6.3	7.8		19.7	22.3	16.5	14.4
Reservoir Elevation(s)	1440	1442 1443		1442 1440	1438 1435	1440	1426
Aggregate Catch of:							
Rainbow	1	3		4	9	1	0
Cutthroat	2	1		5	9	1	4
RB x Ct	2	0		3	2	1	1
Sub Total	5	4		12	20	3	5
Total Trout CPUE	0.666	0.195		0.661	0.973	0.254	0.508
Brown Bullhead	0	3		69	44	18	23
Total Bullhead CPUE*	0.000	0.146		3.795	0.957	0.925	2.339

* Vertical gillnet CPUE calculated differently than for horizontals; see text.

Trout Depth Distribution

Although the number of trout collected in the vertical nets was small, some preliminary insight on their vertical distribution was obtained. Most of the data were collected at Site NS4, and may have very limited application to the broader reservoir environment. We always collected some trout at the surface, but their maximum depth increased as the reservoir warmed, then retracted in the fall (Figure 52). A maximum trout collection depth of 68 ft (20.7 m) occurred on August 18. Although a mean collection depth is plotted in Figure 52, variances among the dates were consistently high, such that either 80 or 95

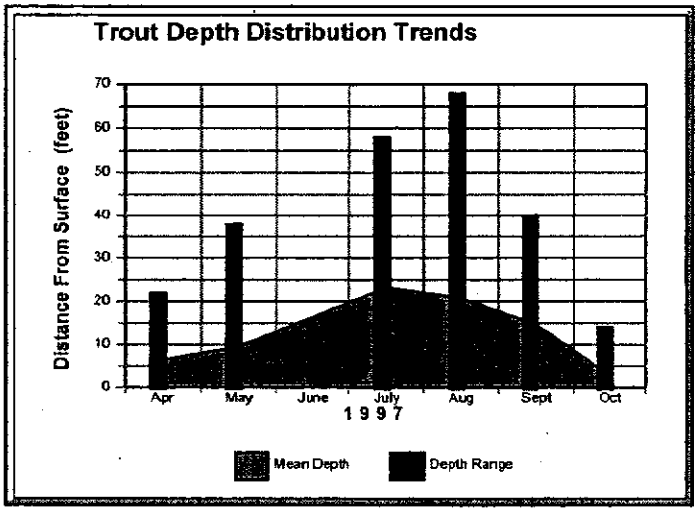


Figure 52. Mean depth and range of vertical distribution of trout caught in vertical gillnets set in Spada Lake, 1997.

percent confidence limits on the mean were nearly equivalent to the observed depth range:

Table 28. Depth range of trout collected in vertical gillnets in Spada Lake, 1997, with 95 and 80 percent confidence intervals on the mean depth (ft).

Month	Number of Trout	Observed Depth Range	Mean Trout Depth	Var.	95% C.I.	80% C.I.
April	5	0 - 22	6.4	9.10	0 - 24	0 - 21
May	9	0 - 38	9.7	13.96	0 - 37	0 - 33
July	12	0 - 58	23.3	17.39	0 - 57	0 - 52
August	26	0 - 68	20.8	17.94	0 - 56	0 - 50
September	21	0 - 40	14.8	13.21	0 - 41	0 - 36
October	6	0 - 14	2.7	5.57	0 - 14	0 - 12

Length Frequencies

The length frequencies of all trout collected from Spada Lake in 1997 are shown in Figure 53. All three graphs show tri–modal histograms to greater or lesser degrees. The aggregate sample is plotted as Figure 54, which shows these modes more clearly. The three modes (13 cm, 20 cm, 26 cm) correlate closely with those of length–at–age (Figure 73), and almost certainly represent Age 1+, Age 2+, and Age 3+ trout. The first two modes in Figure 73 are about 50 mm lower for yearlings, and about 10 mm lower for Age 2 trout, which likely represents the difference between the length at age (Figure 73) versus the trout sampled throughout the summer (Figure 53), which had an opportunity to add growth after the spring time of emergence, or annulus formation.

Although there does not appear to be any appreciable difference in growth between the species (corroborated by scale analysis—Trout Age, Growth, and Condition), the length frequencies suggest that relative survival to Age 3 is higher for cutthroat, and perhaps for hybrids as well. One mechanism which would tend to increase mortality on rainbow would be a preference by rainbow for zooplankton, particularly copepods, which are vectors for cestode plerocercoids that are known sources of mortality (see Trout Parasitism and Mortality). It may be no coincidence that the largest, oldest trout collected in three years of field work was a cutthroat.

Figure 53 further shows that for all three trout forms, fish over 32 cm are rare. We believe this is not an artifact of the sampling gear, since the larger mesh sizes in all nets were consistently empty, or nearly so. Although very few trout less than 10 cm were collected, most do not enter the reservoir from the tributaries until Age 1 or older (Trout Age, Growth, and Condition), thus for all forms, and for all years sampled, the smallest fish taken with regularity by the gillnets were 110 mm in total length.

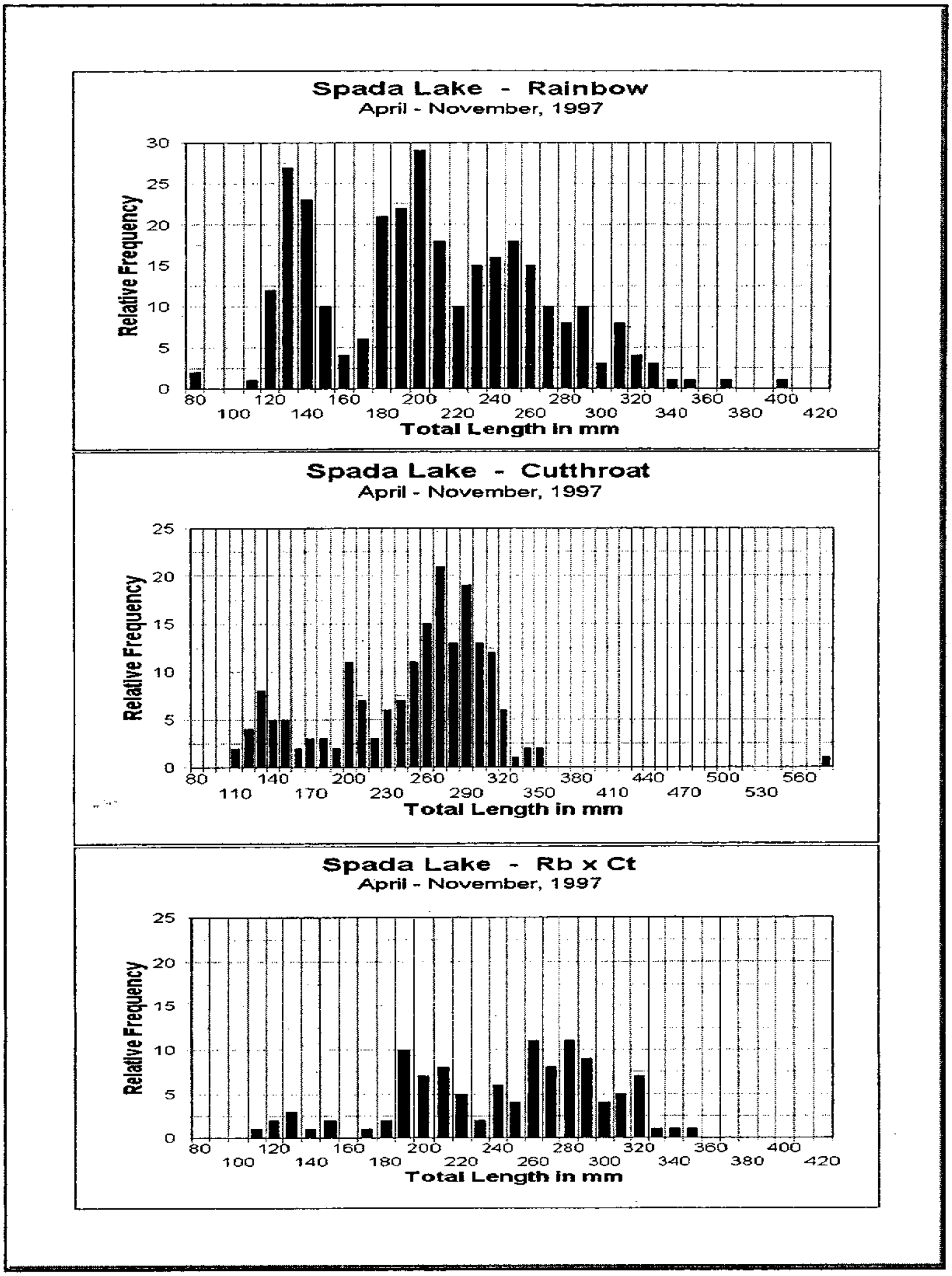


Figure 53. Length frequencies of rainbow, cutthroat, and their hybrids in Spada Lake, Spring through Fall, 1997. One cutthroat at 570 mm is not shown.

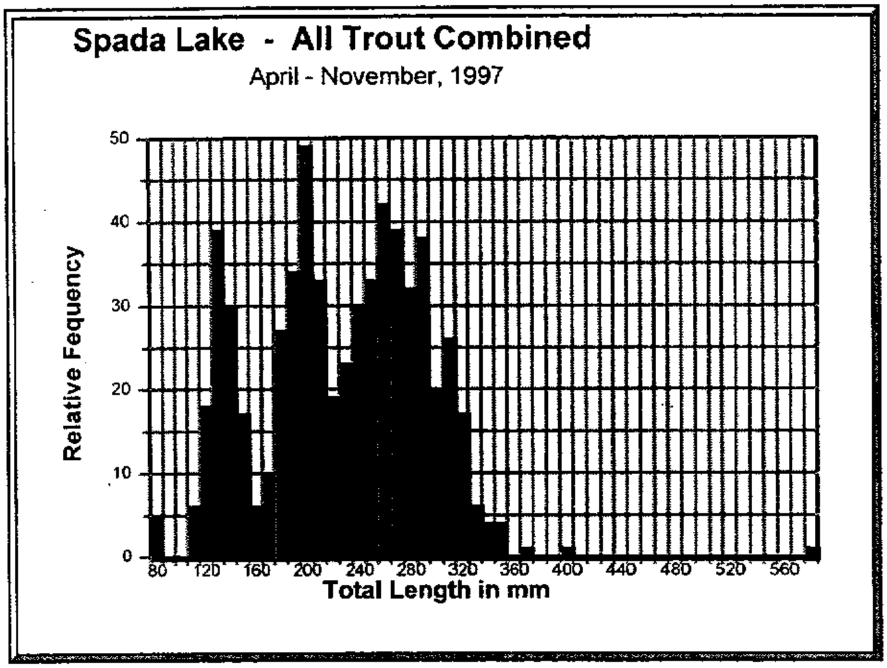


Figure 54. Length frequency of all sampled trout combined from Spada Lake, 1997.

The length frequency of all trout combined is skewed towards the larger fish in the spring and fall collections (Figure 55). Thus, the time of year that sampling occurs is important in Spada Lake. Our empirical observation was that a larger percentage of kelts were seen in the spring collections, as well as maturing fish in the late October and November net sets. Also contributing to this effect is the fact that most of the yearling trout had probably not immigrated from the tributaries prior to June. Their absence in the October-November collections is less–easily explained, but could be caused either by differing behavior and less susceptibility to the gear, or greater mortality going into the fall. We do not believe the lack of smaller fish in the fall is a sampling artifact, since the largest overnight trout collection in three years was made on October 10 (n=99; Appendix Tables 11, 12). Length frequencies from gillnet–caught trout in 1995 and 1996 show nearly identical ranges in the size of fish caught (Figure 56), with very few fish larger than 32 cm.

Brown bullheads were not sampled in as unbiased a manner as trout. We arbitrarily held back portions of , or all of, some daily collections for length measurements. Their distribution appears as Appendix Figure 1.

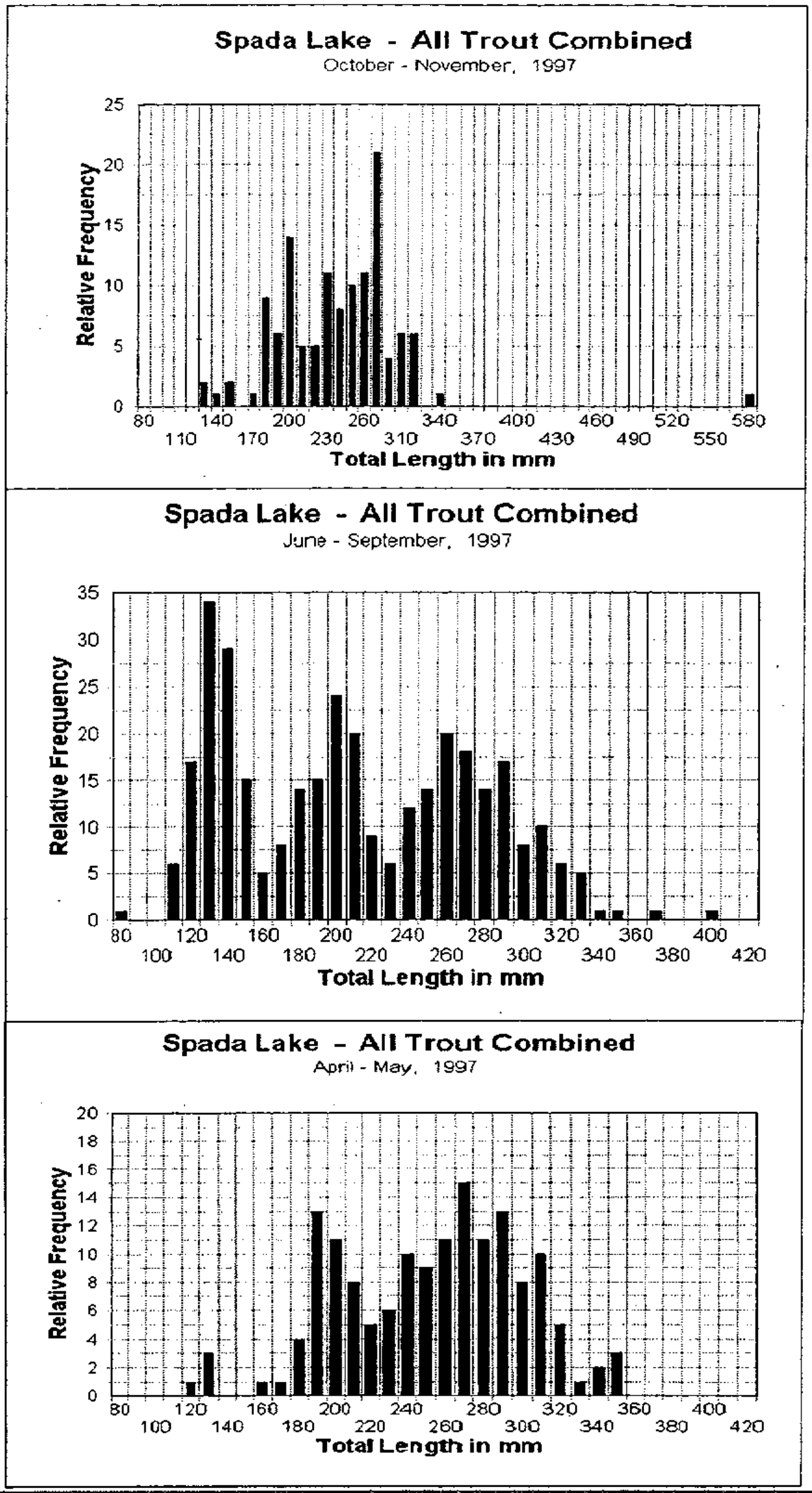


Figure 55. Length frequencies of rainbow, cutthroat, and their hybrids in Spada Lake, by sampling season in 1997. One 570 mm cutthroat was taken in November.

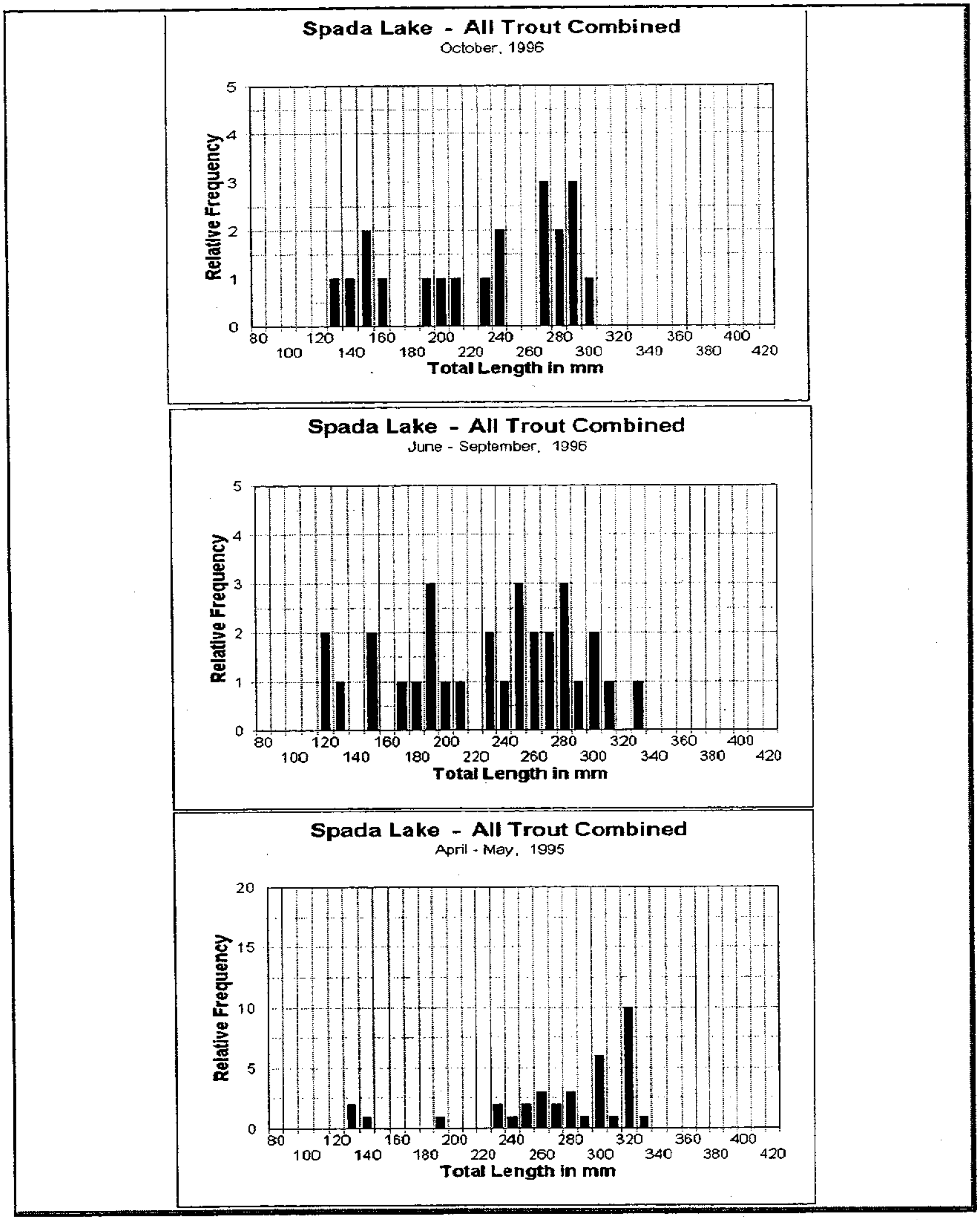


Figure 56. Length frequencies of rainbow, cutthroat, and their hybrids in Spada Lake, by sampling season in 1995-96.

Sex Ratio

Suitably large collections have been made in 1986, 1996, and 1997 to characterize the sex ratio of each species. Tabled values are percentages; sample sizes are in parentheses:

	Rainbow		Cutthroat		Hybrids	
Year	M	F	M	F	M	F
1986	35	65	48	52	40	60
	(252)		(300)		(72)	
1996	47	53	41	59	54	46
	(32)		(22)		(13)	
1997	44	56	52	48	47	53
	(253)		(161)		(100)	

The relatively large disparity from a 50:50 sex ratio in rainbow and hybrid trout collected from the 1986 sport fishery was not explained by Shapiro and Associates and University of Washington (1987). Since the 1986 sample came exclusively from the sport fishery, the possibility of some sort of sampling bias cannot be ruled out, although this seems unlikely. Data presented from 1996 and 1997 are from vertical and horizontal gillnets set inshore and offshore, which we believe are not selective for sex. Mature male trout in Spada Lake exhibit little kype development, or other features which would tend to make them more susceptible to gillnet capture. In any case, departures from an equal ratio usually favored females an average of 2.50 percent (1996 and 1997 data only).

Conclusions

Almost exactly one half of all trout collected were classified as rainbow. Somewhat less than one third were cutthroat, and about one fifth were hybrids in the aggregate collection. However, if only fish ≥ 12" are used, then the proportions as rainbow, cutthroat, and hybrids are very similar to that seen in the 1986 and 1992 sport fisheries.

Horizontal gillnet CPUE was higher than that of vertical gillnets in four of six sampling months. In general, vertical gillnets were much less effective in collecting trout from Spada Lake. Floating gillnets substantially outfished sinking nets set from the shoreline.

No trout were caught in 3.0 inch or larger mesh, and only seven in the 2.5 inch mesh.

Brown bullheads were collected in all three gear types, but most were taken in the horizontal nets.

Trout were always taken from near the surface in the vertical nets, but their maximum collection depth increased as the reservoir warmed, then retracted towards the surface again in the fall. The deepest trout sampled was at 68 ft (20.7 m) on August 18. Trout depths in the vertical nets were highly variable. We saw no evidence that older, larger trout preferred deeper water, and were, thus, generally unavailable to the troll fishery.

Length-frequencies of trout collected correlated closely with length–at–age data. Most of the trout sampled with nets were Age 1 to 3, with older trout being relatively scarce. This corroborates the pattern seen in the sport fishery. Trout larger than 32 cm (12.5") were rare. Although samples were smaller in 1995 and 1996, a nearly identical size range was seen, and fish >32 cm were also rare.

The sex ratio in 1996-97 tended to favor females an average of 2.5 percent.

Length-frequency data suggested that a larger percentage of cutthroat survive to Age 3 or older.

Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock

Methods

In developing a management plan for effective regulation of a sport fishery, biologists frequently need to estimate population size, survival, and recruitment. This is particularly true for populations managed on the basis of natural production, rather than put–grow–and–take stocking. Most models of reservoir or lowland lake fisheries require population or mortality estimates of each relevant age group (Taylor 1981; Beamesderfer 1988; Swartzman and Beauchamp 1990). Our specific needs include a determination of the abundance of harvestable trout in Spada Lake, and their annual mortality, in order to establish a meaningful minimum or maximum harvestable size regulation, and to predict potential yield of older age groups.

There is near–unanimity on the use of mark–recapture as the preferred method of gathering population dynamics statistics, particularly with respect to estimation of population size (Murphy 1966; Ricker 1975; Havey *et al.* 1981; Hightower and Gilbert 1984). We fully agree with this need, but were unable to provide a suitably large group of marked trout in time for the 1997 sampling season. Given the assumptions and problems with the methods used (below), we fully support the use of marked trout to acquire more robust information on the population dynamics of the wild trout (Hepworth *et al.* 1991). Mark recovery sampling need not be a major task, since in many cases, the number of sites that need to be sampled can be very small (King *et al.* 1981), and we already know which sites are most productive in providing trout samples (Fish Relative Abundance, Length Frequency, and Sex Ratio).

Lacking a marked population component, population size can be estimated from data on fishing effort and catch rates (Van den Avyle 1993). Leslie or DeLury–type estimates are most commonly employed, however both require relatively constant declines in catch per effort (*C/f*) in their analyses (Everhart *et al.* 1975). These approaches are not applicable in the Spada Lake sport fishery, since no catch and age breakout data are available for the younger fish which must be released (the vast majority in recent years). Further, the latest creel information is from 1995, which precedes the bulk of our field sampling by two years. One of the most important assumptions in a declining *C/f* population estimate, that of minimal or no immigration (or emigration), is certainly violated in Spada, depending on the sampling timing.

A review of the *C/f* statistics from our gillnetting (Figures 57 and 58) showed no such consistent drop, with the possible exception of the September-November samples. Draft calculations of a Leslie and DeLury estimate based on samples from September 8 through November 13 yielded population estimates ranging from 228 to 311 (WDFW file data). In addition to such improbable population estimates, if the sampling period is limited to that time frame, other requisite samples are not satisfied (all ages, all species; suitably large sample sizes for age analysis). It is also possible that declining *C/f* values in October and November may simply reflect declining trout movements due to reservoir cooling. In general, the gillnet *C/f* data show high variability, and no clear downward trend over the summer.

Hydroacoustic population estimation procedures have been used on reservoir populations (City of Seattle Dept. of Lighting 1973), and were tested on Spada Lake (Stables 1989), but often present myriad difficulties (Wyman 1975; R2 Consultants Inc. 1995). Hydroacoustics are most commonly used on pelagic species such as kokanee in reservoir population estimates (e.g., Chisholm *et al.* 1989). However, periods of testing, error analysis, and learning of the unique characteristics of individual reservoirs can lead to methods which are at least fairly precise, if not highly accurate. Acoustic estimates of pelagic and littoral trout are conducted on Ross Lake annually (Looff 1995), and the exact procedures are repeated each year (Jim Johnston, pers.

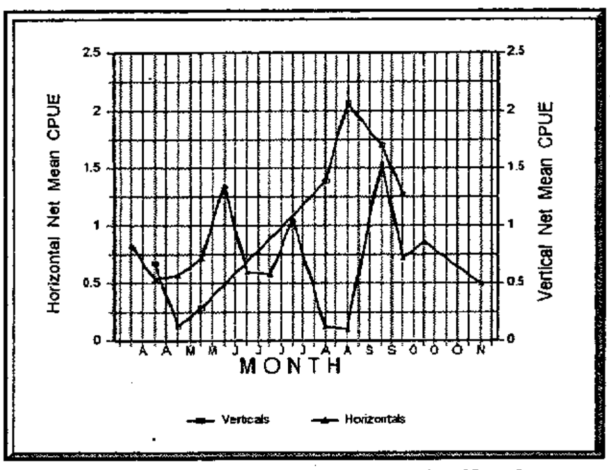


Figure 57. Mean monthly catch per unit effort for horizontal and vertical gillnets, all shore sites combined, Spada Lake, 1997.

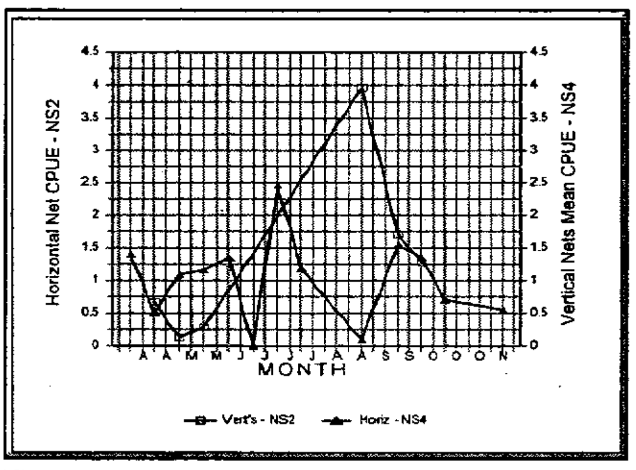


Figure 58. Mean monthly catch per unit effort for horizontal and vertical gillnets, sites NS2 and NS4 only, Spada Lake, 1997.

comm., 1998). This has apparently resulted in a measure which has a high correlation with angler catch rates (below). A period of testing and methods development may be fruitful on Spada Lake (Stables 1989), but this had not been budgeted in time for our work.

Development of hydroacoustic methods, plus one or more population estimates on Spada Lake, would very likely be more costly than a one–time mark-recapture experiment. In addition, a marked fish release could yield far more information than a simple trout abundance estimate, such as relative catch and mortality rates, or parasite immunity of new fish species or stocks.

For the 1997 season, our objective was not to obtain a tight confidence interval on a trout population estimate, but rather to determine relative abundance, and develop baseline data from which more robust estimation procedures may be developed, as needed. To this end, catch rate data are provided by gear type for all trout forms, and brown bullheads, from 1995 through 1997 (Fish Relative Abundance, Length Frequency, and Sex Ratio). However, we examined our catch and effort data, as well as age composition of the trout population, to make several *preliminary, qualified* population estimates. We recognize, and stress, that these estimates are not the product of the most appropriate methods and statistical procedures. They are, however, a useful guideline as to the potential population and standing stock. As such, they provide strong justification for further, more accurate assessment of the abundance of both bullheads and trout in the reservoir.

In order to minimize the possible effect of immigration of Age 1+ and 2+ trout from the tributaries into the lake population, only catch and age data after August 1, 1997, were used. This seemed justified based on length-frequency and age data broken out by seasons, and based on observations while pulling our gear.

Since CPUE varied between horizontal and vertical gillnets (Figure 48), only trout sampled by horizontal nets were used in C/f calculations ($C_t = 190$; $f = 294.27$ nighttime gear–hours). We wished to assure that all ages had equal probability of being sampled (in fact, the only Age 6+ trout seen in three years was taken in this period), therefore, samples from both vertical and horizontal nets were pooled for age analysis (Table 29). Only samples (days) wherein virtually all of the trout were aged were included in Table 29.

Table 29. Age breakout of trout sampled by vertical and horizontal gillnets from Spada Lake in 1997 for estimation of population size.

		AGE						
Date	**Sample n**	**1+**	**2+**	**3+**	**4+**	**5+**	**6+**	**(t)**
8/5	18	5	7	5	1	0	0	
8/18	14	8	3	2	1	0	0	
9/24	42	27	12	4	0	0	0	
11/14	29	7	6	13	2	0	1	
	$\sum N = 104$	47	28	24	4	0	1	(N_t)

Only 422 trout were killed (harvested, or due to hooking mortality) in the 1995 fishing season (Pfeifer 1996a). We firmly believe fishing effort in 1997 was only a fraction of that seen in 1995, perhaps one half or less, based on the number of vehicles and anglers seen during our field work. Therefore, for the purpose of this preliminary estimate, we assumed that fishing mortality (F) was essentially zero.

Results and Discussion

Mortality

Catch curve analysis, and similar analyses of catch data to estimate population dynamics parameters, assumes: immigration is constant (or is zero, i.e., precedes the sampled time frame); *C/f* is a strong correlate of abundance; catchability of age groups is constant through time; age is known without error; the population is in a steady state; and age classes are captured in proportion to their relative abundance.

An estimate of Z, the instantaneous rate of total mortality (Ricker 1975), was estimated from a catch curve regression (Van den Avyle 1993; p. 121) of $\log_e(N_t)$ on age (t), yielding a value of 0.811.

An estimate of M, the instantaneous rate of natural mortality, was estimated using Heincke's formula for S, the rate of survival (equation 2.4 of Ricker, 1975):

$$S = \frac{\sum N - N_o}{\sum N}$$

From this, S = 0.548, and A (annual mortality, or 1-S) = 0.452. Since $A = 1 - e^{-Z}$, and Z = F+M, and we have assumed F=0, then M is derived by solving algebraically for Z: 0.601.

From these, annual mortality (A)=.452, and the instantaneous rate of natural mortality M=.601.

Catchability

A series of years' data on catch and mortality are not available (but are desirable). However, for this estimate, we used a variant of equation 7.13 of Ricker (1975; p. 172) to estimate catchability (q):

$$q = \frac{(Z - M)}{f}$$

and

$$q = \frac{.81051 - .60133}{294.27} = 0.000711$$

Population Estimates

Two approaches were used to derive a rough, preliminary estimate of trout abundance in Spada Lake. The first uses the estimates of mortality and catchability derived from the late summer gillnet catch per unit effort, and the sampled population age breakout based on scale analysis. These parameters are used in the standard catch equation (below) to derive N_o, the population at time t.

$$C_t = N_o(1-e^{-M-qf})\frac{qf}{M+qf}$$

The second approach is based on a strong correlation between hydroacoustically-derived trout population density indices in Ross Lake and concurrent angler catch rates. Drawdown cycles and angler gear use patterns are similar between Spada and Ross, as are many of the trout life history characteristics. A regression model of trout per reservoir surface area and angler *C/f* were used with the 1995 Spada Lake creel survey *C/f* value to estimate trout abundance in Spada. In both cases, the 1997 scale data is used to apportion the estimated trout population into age groups.

Estimate No. 1

With $q = 0.000711$, $f = 294.27$, $C_t = 190$, and $M = 0.60133$, then $qf = 0.209226$, and

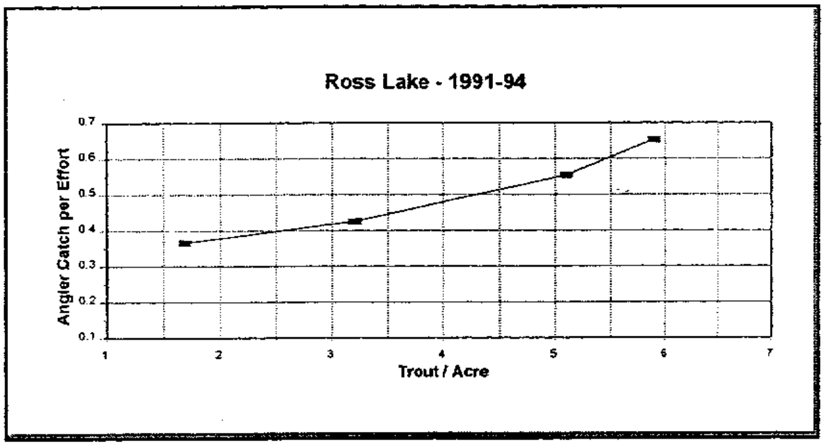
$$190 = N_o(1-e^{-.6013-.2092})\frac{.209}{.6013+.2092} \quad = \quad \mathbf{2{,}269}$$

This estimate seems low, and represents 1.2 trout per surface acre in Spada Lake. The population breakout by age would be:

Age	Percent	Estimated Abundance
1+	.4519	1,025
2+	.2692	611
3+	.2308	524
4+	.0385	87
5+	.0000	0
6+	.0096	22

Estimate No. 2

Trout population estimates have been made using sounding gear in Ross Lake in 1971 and 1972 (Seattle City Light 1973), and between 1991 and 1995 (Looff 1995). While Seattle City Light (1973) felt their acoustic estimates were unreliable, and used mark-recapture data to estimate the population, the current fishery manager feels acoustic methods are still useful so long as the methods are kept constant from year to year (Jim Johnston, pers. comm. 1998). This would tend to minimize the effect of any biases, i.e., hold them constant. This apparently is a valid assumption, for there is a very high correlation between annual creel survey–derived angler catch rates and the acoustically–derived estimate of trout density, transformed into numbers of trout per surface acre:



The equation for the Ross Lake data is Y = 0.0666X + 0.235, with an r value of 0.9802. For an estimate of Spada Lake's population, the 1995 creel survey mean catch rate of 0.597 was used:

$$Y = 0.0666X + .235;$$

$$(C/f - .235) = 0.0666X;$$

$$\frac{C/f - 0.235}{0.06662} = \text{trout / acre};$$

$$\frac{0.597 - 0.235}{0.06662} = 5.434 \text{ trout / acre}$$

For Spada Lake with a full–pool area of 1870 acres, the Ross Lake regression model predicts a trout population of **10,162.**

While this estimate is more reasonable than 2,269, we have difficulty reconciling it with the density of what appear to be trout surfacing on the lake at various times. We feel the estimate may be low.

If 10,162 is an accurate estimate, the population breakout by age would be:

Age	Percent	Estimated Abundance
1+	.4519	4,592
2+	.2692	2,736
3+	.2308	2,345
4+	.0385	391
5+	.0000	0
6+	.0096	98

Immigration

Strictly, recruitment would be a measurement of the number of trout fry produced in the tributaries from a given egg deposition. Mortality would begin soon after emergence. Our primary interest is the number of juvenile trout (Age 1+ and 2+) which enter the reservoir, and contribute to its fishery. This number would presumably be far less than the number of eggs deposited, and probably considerably less than the number of fry produced therefrom.

From scale analysis data, 87.6 percent of the trout spend one year in the tributaries before immigrating in the May-July period; an additional 11.9 percent enter after having spent two years in the tributaries. Since this proportion does not seem to vary appreciably (Tertiary Production — Trout Age, Growth, and Condition), the lake population typically consists almost wholly of four brood years, most of which immigrate after one or two years of tributary rearing (99.5%). A very rough, presumptive estimate of immigration into the lake in 1997 is the product of the fraction of the 85 fish showing little or no lake rearing, i.e., an X.0+ age designation, and the population estimate:

Age Designation	Number	Decimal Fraction
1.0	64	.3459
2.0	20	.1081
3.0	1	.0054
		.4595

For Population Estimate No. 1: .4595 X 2,269 = 1,043 (0.56/acre)
For Population Estimate No. 2: .4595 X 10,162 = 4,669 (2.5 /acre)

These values, recognizing that they are preliminary and highly qualified, suggest that immigration (lake seeding) may be a problem, and warrants further, more definitive assessment.

Standing Stock

Tables 30 and 31 present a theoretical calculation of trout standing stock based on the two population estimates, and the proportion of the population in each age group. The mean total length of each age group (all species combined) was converted to mean weight based on the length:weight relationship calculated for the entire year. Even if the population estimates are off by an order of magnitude, the estimated standing stock of trout is at a very low level. The given population estimates yield standing stock estimates ranging from 0.2 to 1.0 kg/ha (0.2 to 0.9 pounds/acre). To place these values into perspective, Ploskey and Jenkins (1982) found sunfish and bass biomass amounted to 74.9 kg/ha in DeGray Lake, Arkansas. Taylor's (1981) model of fish production in Lake McConaughy, Nebraska estimated walleye (a top predator) biomass at 11.3 kg/ha. With a morphoedaphic index of 0.536 and an estimated total dissolved solids of 13.4 mg/*L*, Spada would be expected to support a biomass ranging from 7.5 kg/ha (Jenkins 1977) to 27 kg/ha (Jenkins 1982), depending on the standing crop model used. We believe the lower value is more applicable. These values certainly beg the question of how much biomass is represented by the brown bullhead population in Spada Lake.

Table 30. Estimation of trout standing stock in Spada Lake in late summer, 1997, based on a population estimate of 2,269.

Age	Mean Length	Weight*	Estimated Cohort Size	Kg	Kg/ha	Lbs	Lbs/ac
1+	73	4.0	1,025	4.1		9.2	
2+	176	51.5	611	31.5		67.0	
3+	249	140.9	524	73.8		154.2	
4+	287	212.7	87	18.5		38.4	
5+	----	----	0	----		----	
6+	571	1,564.0	22	34.4		107.9	
Totals				162.3	0.214	357.9	0.191

* Based on the whole-season length:weight relationship.

Table 31. Estimation of trout standing stock in Spada Lake in late summer, 1997, based on a population estimate of 10,162.

Age	Mean Length	Weight*	Estimated Cohort Size	Kg	Kg/ha	Lbs	Lbs/ac
1+	73	4.0	4,592	18.4		41.0	
2+	176	51.5	2,736	141.0		299.8	
3+	249	140.9	2,345	330.5		690.2	
4+	287	212.7	391	83.2		172.4	
5+	----	----	0	----		----	
6+	571	1,564.0	98	153.3		480.7	
Totals				726.3	0.960	1,601.5	0.856

* Based on the whole-season length:weight relationship.

Total fish standing crop in Lake Keowee, South Carolina, with a total dissolved solids (TDS) content of 20 mg/L, varied closely around its predicted mean of 50 kg/ha six to nine years after initial impoundment (Jenkins 1977). Standing crop dropped from over 100 kg/ha to near 40 kg/ha in four years. Based on its mean conductivity of 20.6 μS, Spada's TDS content is estimated to be 13.4 mg/L (Water Quality — Conductivity, pH, and Other Miscellaneous Water Quality Data), with a standing crop potential that is roughly equivalent to that of Lake Keowee. While a cool, oligotrophic Pacific Northwest reservoir cannot be compared directly with a warmer reservoir located at a more southern latitude, this example serves to illustrate the effect of reservoir aging, and the applicability of the morphoedaphic index in predicting reservoir standing crop. Fish production potential has likely stabilized in Spada, but more precise estimates of the fish standing crop are needed to determine management actions that best utilize its limited potential.

Conclusions

Annual mortality (fishing + natural) for all trout combined was estimated as 45.2 percent in 1997.

Two trout population abundance estimates were made; the more reasonable figure is 10,162, which equates to 5.4 trout/acre. Based on scale analysis, trout Age 4 or older would number roughly 500, or 0.3 fish/acre. Most fish 12" in total length are Age 4 or older, thus such a very low density would explain the lack of harvestable trout in Spada Lake.

Recruitment of Age 1 (or older) fingerlings from the tributaries may be very low, suggesting problems with fry recruitment and/or high mortality in the first year of stream rearing. Fry or fingerling trapping is needed to gain a better understanding of this trout life history stage in Spada Lake.

A marked trout release in the reservoir would be extremely valuable to obtain a more robust trout population estimate, as well as a measure of natural immigration.

Based on the preferred population estimate, and the trout length:weight relationship, trout standing stock in 1997 was a little less than one pound/acre (kg/ha). Based on Spada Lake's water chemistry, standing stock should be more on the order of 40 lbs/ac (or kg/ha). While the trout population estimate may account for much of this discrepancy if it is erroneous, the biomass of brown bullheads may also be substantial, thereby accounting for much of the differential.

Trout Age, Growth, and Condition

Studies of the age, length-weight relationship, and growth rates of fish species provide basic data for the understanding of the population dynamics of these species.

Current growth rates of the trout in Spada Lake were of paramount interest since very few fish over the minimum size (12", 305 mm) were harvested in 1995 (Pfeifer 1996a). We also wished to know if growth rates had declined since the completion of Phase II in 1983. Current information on the relationship between trout length and age at maturity is needed in order to assure an adequate escapement for a fishery based on natural reproduction. Last, the growth potential of the trout is needed to evaluate the practicability of the management goals and objectives set for the reservoir (Background—Relationships to Current Fishery Management Goals and Objectives).

Fish growth is, of course, influenced by many factors (Piper *et al.* 1982; Ploskey 1986). Water temperature and other habitat characteristics, food availability and nutrition, and competition have all been documented to affect fish growth. We have begun to document many of these conditions in Spada Lake in other sections of this report. The effects of reservoir operation on the area or volume of the reservoir may influence fish population densities (Jenkins 1970). However, any effects of reservoir operation on growth are confounded by influences of temperature, competition, food availability, and habitat characteristics.

The Spada Lake trout population, zooplankton, and benthic invertebrate communities were sampled during 1997 to evaluate several factors which may be limiting trout production in the reservoir. Zooplankton and benthos studies, trout stomach content analyses, and trout parasite loadings are presented in other sections of this report. Age and growth data from trout scales collected during 1986, 1995, and 1996 are included in this section to provide a more complete historical perspective.

Methods

Age and Growth

General

Trout growth rates and age were evaluated from field measurements of trout total length (mm) and weight (g), and analysis of scales obtained from the sampled fish. Trout were collected by horizontal (nearshore) or vertical (offshore) gillnet approximately every two weeks from April 10 to November 14, 1997.

Trout data and scales from 1986, 1995, and 1996 sampling in Spada Lake and tributaries were also evaluated for this report. Trout sampled in 1986 were collected by recreational fishing in the reservoir and recorded as part of a creel survey (Shapiro and Associates and University of Washington 1987). Trout sampled during 1995 and 1996 were caught in the reservoir using primarily horizontal gillnets; trout sampling in tributaries was done primarily with a Smith–Root Model 12 backpack electrofisher, with a few additional samples collected by hook and line. Trout size, age, and scale data were also obtained from Pentec (1993) for sampling years 1979, 1980, and 1992 (creel survey data) to provide additional background information for age and growth analyses.

Trout collected from Spada Lake and tributaries from 1995 to 1997 were measured for total length (mm) which is the preferred length measure. Length measurements for the 1979 to 1992 sampling periods were fork length (mm). Fork length measurements were multiplied by 1.05 to approximate total lengths equivalent to the measured fork lengths (Carlander 1969).

Weight data from trout sampled from the 1986 and 1992 creel surveys are from whole fish, but could be subject to some slight biases depending on the manner in which fish were stored by anglers prior to being weighed at the Olney Pass check station. All of our 1995 through 1997 fish samples were not allowed to become dessicated prior to weighing.

Appendix Table 19 lists the sample date and other information for all trout considered in age and growth studies. Although not explicitly listed in Appendix Table 19, the sampling location in the reservoir or tributaries are available for each trout collected in 1996 and 1997, but not for other years (WDFW file databases). Total numbers of trout included in Appendix Table 19 for age and growth analyses are as follows:

1979 -	88 trout
1980 -	74 trout
1986 -	70 trout
1992 -	180 trout
1995 -	30 trout
1996 -	65 trout
1997 -	157 trout

Scales from trout sampled in 1986, 1995, 1996, and 1997 (322 total) were collected from the middle region of the side of the body, above the lateral line. Scales were placed in coin envelopes which were labeled for each trout. Dry scales were scraped from each envelope onto a glass microscope slide, and a second glass slide was placed on top of the scales. Cellophane tape wrapped around the slides pressed the scales between the two glass slides.

Scale samples were read by projecting the scale pattern onto a microfiche reader screen. Magnification was approximately 50x. A representative scale was selected after viewing all scales within an individual sample. Trout age was determined by counting annual marks (annuli) on scales. The distance from the scale focus to the outer edge of each annulus, and to the outer edge of the scale, was measured on the screen (see Appendix Table 19). Trout length at a given age was calculated from scale data according to the linear back–calculation procedure in Bagenal and Tesch (1978), with the Fraser–Lee modification (Devries and Frie 1996).

Scale samples were sometimes unreadable or not usable due to scale regeneration, uniform circuli pattern with no apparent annuli, lack of scales or length data from the sample envelope, or other problems. For scale samples that were initially not readable, an additional sample was prepared (if possible) from the envelope and the scale reading process was repeated. Scale samples were deleted if this additional reading attempt was unsuccessful. This resulted in loss of 0 out of 70 samples from 1986, 1 out of 30 samples from 1995, 4 out of 65 samples from 1996, and 1 out of 157 samples from 1997. These losses of data were not considered significant.

Each scale sample was read twice, with the second reading done primarily to verify trout age data for each fish. The second reading was done at least one week after the first reading, and scales were read in a different order than the first reading. Where the two age counts did not match, the scale sample was read a third time and a final determination of age was made (or in one case, the scale was deleted). There was rarely a difference of more than one year in the age determinations for each scale sample. Discrepancies in age assessment between first and second readings occurred in about 5 percent of the samples, mainly due to the following:

- selection of a different individual scale for assessment of age,
- difficulty (at times) distinguishing annuli from other scale irregularities such as "spawning checks" (characterized by irregular circuli pattern or break in circuli pattern suggesting resorption, typically with well--spaced circuli (lake growth) on both sides, commonly indistinct or absent (?), difficult to identify with confidence),
- irregular circuli patterns with unknown causes (possibly changes in trout behavior, lake or tributary residence, or diet), and/or
- indistinct annuli.

Age

Trout ages were recorded as follows. The outer edge of each annulus was assumed to be an "even age" in years such as Age 1, Age 2, etc. For Spada Lake trout, annulus formation was assumed to occur in April or May since a number of scale samples from this time period showed a distinct annulus on the outer edge of the scale, but no new circuli outside the annulus. Trout sampled in April or May, with a distinct annulus on the outer edge, were given an even age in years (e.g., Age 3). More often, there were annuli visible on scales and some circuli outside the last annulus. This was interpreted as growth occurring after annulus formation, and these fish were initially designated Age X+ to denote a fish with complete "X" years of growth, plus additional growth after formation of the last annulus. Trout from Spada Lake characteristically spawn in the early spring, so the age determination would more–or–less correspond to their actual age since being spawned. These age designations are consistent with recommendations of Bagenal and Tesch (1978).

Lake versus Tributary Rearing

Review of scales also resulted in recordings of "stream years" for each scale sample. Identification of these scale characteristics was based on experience and was typically associated with these observations:

Stream years (vs. lake years)—scale circuli closely spaced together, fewer circuli between each annulus compared to trout (from the reservoir) with faster growth, relatively easy to differentiate from growth pattern in reservoir.

Scales collected in 1986, and 1995 through 1997 were examined for the number of years each fish spent rearing in the tributaries. An additional life history designation was made for these scales based on the methods described by Narver and Withler (1971). In our adaptation of this method, the number of tributary years is designated as an arabic numeral as above; the number of complete years of reservoir residence is designated with a second arabic numeral, separated by a decimal point. Any reservoir growth beyond annuli laid down after reservoir entry were designated with a "+." For example, a trout with a 2.2+ designation would have spent two years in tributary rearing, two full years in the reservoir, and show some additional growth in its fifth year of life. While Appendix Table A in Fisheries Consultants and ZP's Taxonomic Services (1997) tabulates "Years in Streams", the WDFW file database converts these data into the X.Y+ format.

Other studies of rainbow or cutthroat in reservoirs found variable periods of tributary residence, similar to our population (May *et al.* 1988; Chisholm *et al.* 1989). These authors placed the trout samples into "migration classes" which reflected the number of years of tributary residence prior to reservoir entry.

Growth

Scale reading data sets from 1979-80 (WDG, n=162) and 1995-97 (WDFW, n=252) were evaluated for the fish total length:scale radius relationship. Previous growth studies on Spada Lake trout suffered from the fact that the fish samples were obtained from the sport fishery. This exerted a severe bias in 1986 and 1992, when a 12" minimum size was in effect. In these years growth to Age 1, Age 2, and in some cases Age 3 could only be inferred by back–calculation. The 1995-97 sample set included fish ranging in Age from 1 to 6.

With respect to general methods, we did not make any adjustment or rigorous search for "Rosa Lee's Phenomenon" since we back–calculated length at age from many more young fish than older ones.

Both a standard linear regression, and a natural log transformation regression were performed on the length:scale radius data. Y–axis intercepts from the ln/ln graphs were used to make the Fraser–Lee modification to the direct back–calculation (Devries and Frie 1996). The correlation coefficient was slightly higher after the natural log transformation, due to slightly non–linear (allometric) growth of trout with age:

Trout Species & Year	Linear regression r^2	Log_e r^2
Cutthroat 1979-1980	0.74	0.75
Rainbow 1979-1980	0.77	0.78
Cutthroat 1995-1997	0.74	0.82
Rainbow 1995-1997	0.76	0.76
Hybrids 1995-1997	0.73	0.80

From the natural log formulae, Y–axis intercepts were selected based on averages of the 1979-80 and 1995-97 data sets, with the exception of rainbow trout. There was an obvious problem with the 1979-80 rainbow growth data, which was very likely due to the influence of hatchery rainbow stocked through 1979. For rainbow, we used the Y–intercept from the 1995-97 regression, only:

Cutthroat trout	Y–axis intercept = 0.66 (average from Figs. 60A and 60B)
Rainbow trout	Y–axis intercept = 0.68 (from Figure 60B)
Hybrid trout	Y–axis intercept = 0.64 (from Figure 60C)

The above intercepts for each species were used for all data sets (1979, 1980. 1986, 1992, 1995, 1996, 1997) to back–calculate length at each age based on the following formula (Fraser (1916) as cited in Bagenal (1978) with natural log transformations):

$$\ln(l_x) = ((\ln(S_x) / \ln(S_c)) \text{ X } (\ln(l_c)\text{-}y)) + y$$

where:

l_x = trout total length at age x
l_c = trout total length at capture
S_x = scale radius at age x
S_c = scale total radius at capture
y = Y–axis intercept ln regressions

Length:weight regressions were calculated on each trout species in each sample year. Regression line slopes (*b*) were thus available on a species–by–species, and year–by–year basis for comparisons.

Since many anglers at Spada Lake "high grade", or keep the largest fish they catch, some degree of size–selective mortality probably has occurred within one or more year–classes. Accordingly, we followed Ricker's (1975) procedure to estimate the true population growth rate (pages 217-219). G was calculated using the functional slope (*b*) from the length-weight equation derived for each age group of rainbow and cutthroat using the following equation:

$$G = b(\log_e l_2 - \log_e l_1)$$

where: l_1 = initial trout length for the last complete year of growth, and
l_2 = final trout length for the last complete year of growth

We grouped all aged samples by brood year within each age class before performing the regression of weight on length. In this way, the derived slope (b) in any given sample year comes from fish which presumably all experienced similar rearing conditions. For example, the b value used to estimate **G** for Age 3 fish in 1980 was derived solely from fish from the 1977 brood year. (No rainbow from any brood year earlier than 1979 were used due to the potential bias of hatchery rearing.)

Instantaneous growth rates were plotted by age stanza for four sample years spaced five or six years apart (1980, 1986, 1992, and 1997). The 1980 and 1986 samples represent fish from Stage I of the Jackson Project. Culmback Dam was raised in 1985, however, the 1986 samples were of fish which had experienced most of their rearing prior to reservoir enlargement (Table 32).

Table 32. Number of trout classified by years in tributaries, from Spada Lake sampling, 1986 to 1997.

Year	Sample Size[1]	1 Year in Streams	2 Years in Streams	3 Years in Streams	Percent of Trout Spending More than 1 Year in Tributaries
1986	69	57	12	0	17%
1995	29	24	5	0	17%
1996	29	26	3	0	10%
1997	150	130	19	1	13%

[1] does not include trout sampled from tributaries, see Appendix Table A referenced page top.

Rainbow and cutthroat annual growth increments were plotted for each age stanza by sampling year to enable comparisons of Stage I and Stage II growth from one year to the next.

Length at Maturity

Although some scales had features which suggested a spawning check, essentially none had reliable characters that would enable estimation (back–calculation) of length at first spawning. This finding was independently verified by the leader of the Washington Department of Fish and Wildlife's Aging Unit (John Sneva, pers. comm. 1998). Mr. Sneva examined mounted scales from a variety of ages from both rainbow and cutthroat, including samples which were from known kelts. The preferred approach is to obtain reference scale samples from known spawners of known age from the spawning grounds, or as fresh kelts. Ideally, it would also be known whether the fish were on their first (or repeat) spawning run. Since two readers examined scales from kelts which had almost certainly recently completed spawning in one of the reservoir's tributaries, it appears that a lack of a spawning check is a characteristic of this population, and may not be available as a tool to estimate length at maturity closely. See Trout Spawning Period and Age at Maturity for an alternate approach.

Condition

A Quattro Pro spreadsheet of tabled values of total length and weight for each trout species were regressed in the standard manner to derive a length-weight relationship per the formula:

$$\log w = \log a + b(\log l)$$

Note: The GM functional regression recommended by Ricker (1975) was not used; raw data are available in a database to make this minor adjustment.

The length-weight relationship for each species was determined from the season–long sample collected in 1997. The 1997 sample has the least bias for size or age, and also includes fish from the widest time frame. Although similar regressions can be made from past years' data, we assumed that the formulae derived from the 1997 sample is applicable to previous years' samples.

Relative condition factors (K_n) were calculated for each trout species on a seasonal basis per:

$$K_n = (W/W')$$

where W is weight of the individual and W' is the length–specific mean weight for this species in the overall Spada Lake population as predicted by that species' length-weight equation. A practical advantage of K_n is that average fish of all lengths have a value of 1.0, regardless of the species or units of measurement (Anderson and Neumann 1996).

Relative weights (W_r) were calculated for each trout species on a seasonal basis by the formula:

$$W_r = (W/W_s) \times 100$$

where W is the weight of an individual and W_s is the length–specific standard weight proposed by Anderson and Neumann (1996), using unpublished data of Hubert, Kruse, and Simpkins of Colorado State University. With appropriate standard weight equations fish of all lengths in "good" condition have a W_r of about 100 (Anderson and Neumann 1996). A major advantage of relative weight over relative condition is its comparability among populations across a broad geographic region, as well as its constancy with increasing fish size (allows for allometric growth).

Proportional stock density was calculated for cutthroat and rainbow using the following formula:

$$PSD = \frac{\text{number of fish} \geq \text{minimum quality length}}{\text{number of fish} \geq \text{minimum stock length}} \times 100$$

where stock and quality total lengths were 20 and 35 cm for cutthroat, and 25 and 40 cm for rainbow, respectively. Although these values seem high for Spada Lake, we used the values reported by Anderson and Neumann (1996) to allow broader and more uniform comparisons among populations studied. Values of PSD range from 0 to 100.

Since "minimum stock length" has been defined variously, we define it as the minimum total length deemed having recreational value to a majority of Spada Lake anglers. In the calculation of PSD, we used the recommended minimum stock length values of Anderson and Neumann (1996) to maintain comparative data. We used a constant minimum stock length value of 250 mm in the calculation of RSD (below).

Relative stock density is the percentage of fish of any designated length–group in a sample:

$$RSD = \frac{\text{number of fish} \geq \text{specified length}}{\text{number of fish} \geq \text{minimum stock length}} \times 100$$

We calculated RSD for cutthroat and rainbow ≥ 10 inches and 12 inches, where 10 inches is assumed to be the minimum acceptable harvestable size for Spada Lake anglers, and 12 inches is the current minimum harvestable size. A "customized" minimum stock length value of 250 mm was used.

Internal Fat

An inspection of internal body fat content was made on every trout sampled from Spada Lake by gillnetting or electrofishing between 1995 and 1997. Fat content was subjectively scored by the senior author using the following scale:

- None: No visible internal fat deposits.
- Trace: Very small, light streaks of fat seen in some areas or on some organs.
- Light: Fat in continuous streaks, but of minimal depth (< 1 mm).
- Moderate: Fat continuous, depths ranging from 1 to 2 mm; organs, stomach, and intestine generally visible.
- Heavy: Fat generally > 2 mm in thickness; organs, stomach, and intestine generally occluded, and only visible by teasing apart fat accumulations.

Given the subjective nature of these ratings, groups were combined for graphing and tabulation purposes (e.g., None, Trace/Light, and Heavy).

Results and Discussion

Data for sampling date and location, species, trout length, age and years residence in tributaries, and scale parameters are listed in Appendix Table A in Fisheries Consultants and ZP's Taxonomic Services (1997). Data from 1979, 1980, and 1992 were obtained from Pentec (1993); data for 1986, 1995, 1996, and 1997 were determined through this study.

Age and Growth

Back–Calculation of Length at Age

Back–calculation of trout length at each age (even age = Age 1, Age 2, etc.) standardizes the growing time for each age group and minimizes length variability due to different sampling times within the same age group. Back–calculation of lengths to even ages ("length at age") also allows the most direct comparison of growth rates for fish from different sampling seasons or years.

Figures 59a through 60c are the transformed, natural log regressions of total length on scale radius for Spada Lake cutthroat, rainbow, and hybrid trout in 1979-80 and 1995-97 (except only 1995-97 for hybrids). (The standard regression plots are presented as Appendix Figures 15 through 19.)

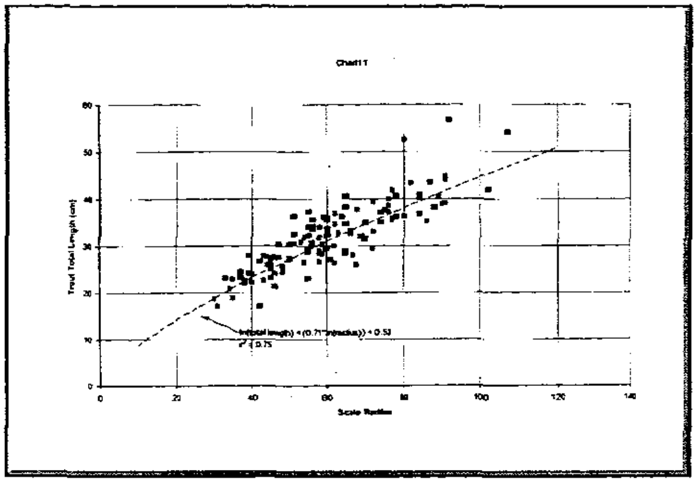


Figure 59a. Cutthroat trout total length as a function of scale radius for trout sampled 1979-1980 from Spada Lake. Line fitted by Least Squares Regression after natural logarithm transformation of data.

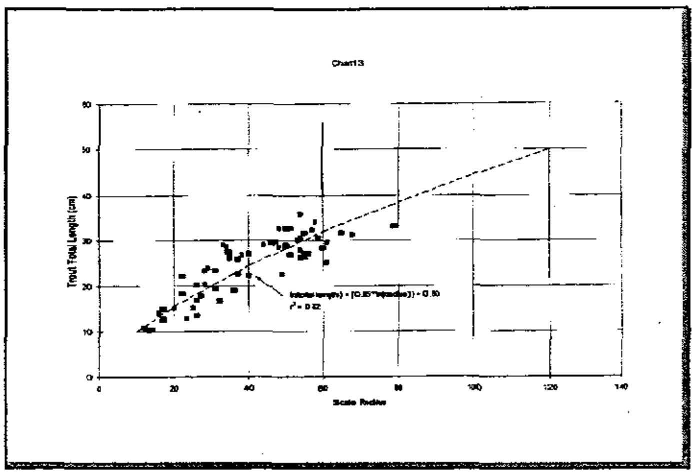


Figure 59b. Cutthroat trout total length as a function of scale radius for trout sampled 1995-1997 from Spada Lake. Line fitted by Least Squares Regression after natural logarithm transformation of data.

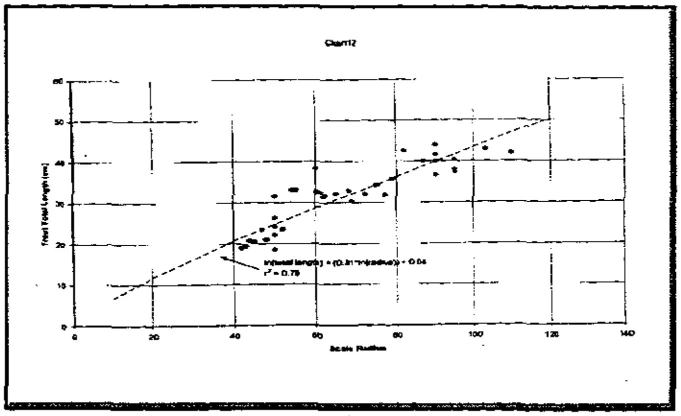


Figure 60a. Rainbow trout total length as a function of scale radius for trout sampled 1979-1980 from Spada Lake. Line fitted by Least Squares Regression after natural logarithm transformation of data.

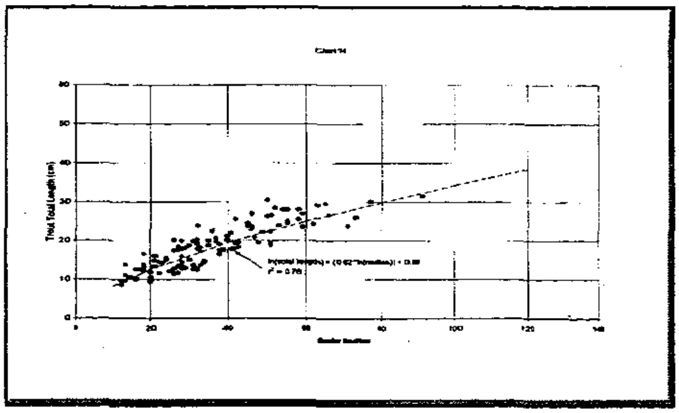


Figure 60b. Rainbow trout total length as a function of scale radius for trout sampled 1995-1997 from Spada Lake. Line fitted by Least Squares Regression after natural logarithm transformation of data.

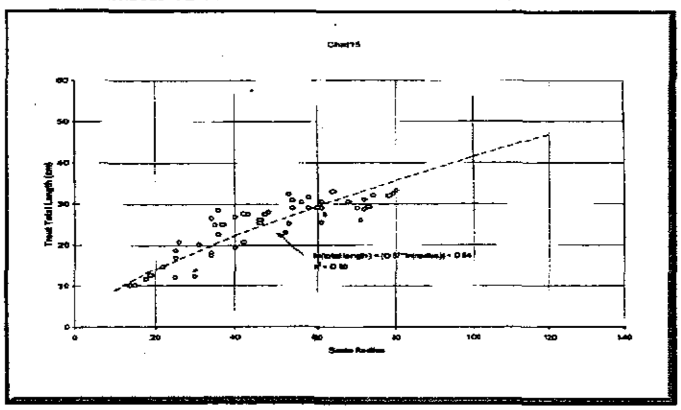


Figure 60c. Hybrid trout total length as a function of scale radius for trout sampled 1995-1997 from Spada Lake. Line fitted by Least Squares Regression after natural logarithm transformation of data.

Back–calculation of length at age was done for all trout sampled from Spada Lake for years 1979 to 1997. From these estimates of trout length at each age, annual increments of growth were determined for each trout within each age group for each sampling year. Estimates of trout annual growth for each age class (all same–age groups from multiple years) were then plotted on a frequency chart to look for annual growth data outliers (Figures 61, 62). For instance, the distribution of trout growth during Year 1 of life appeared to follow a normal distribution and there were no obvious data outliers (Figure 61). One cutthroat trout sampled in 1980 was calculated to have 22 cm growth in Year 3, which appeared to be a data outlier (Figure 62). Data for this trout was obtained from Pentec (1993), and there were no apparent keypunch or other errors to explain the datum. Therefore, the datum for this trout remained in the analysis, even though it appeared to have excessively large growth during Year 3. Figures 61 and 62 were used only to identify misreading of scales or other possible data errors; there did not appear to be any.

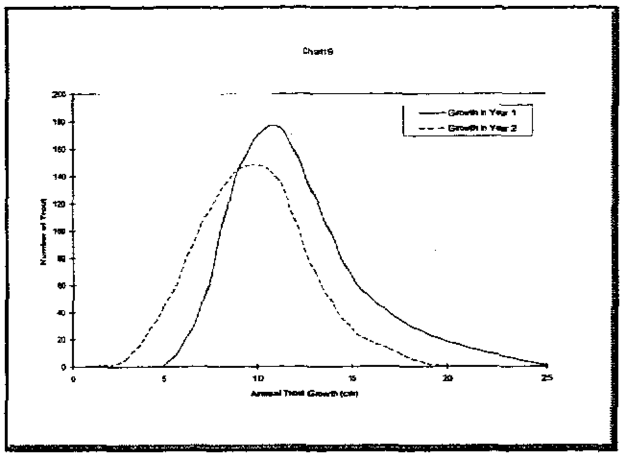


Figure 61. Estimated growth in years 1 and 2 for trout in Spada Lake for all years (1979, 1980, 1986, 1992, 1995, 1996, and 1997) and all species (cutthroat, rainbow, and hybrid) using back–calculated scale data.

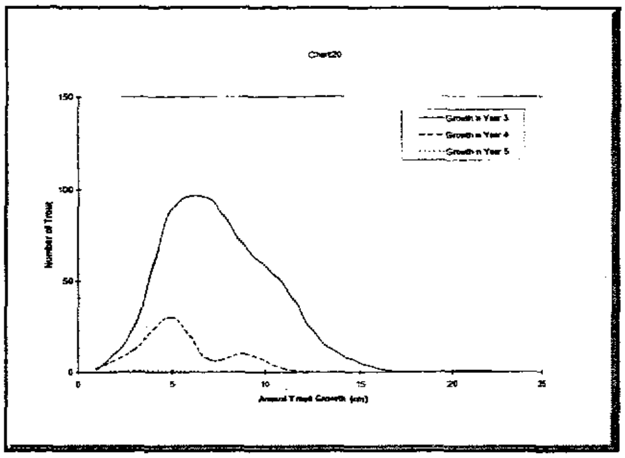


Figure 62. Estimated growth in years 3 to 5 for trout in Spada Lake for all years (1979, 1980, 1986, 1992, 1995, 1996, and 1997) and all species (cutthroat, rainbow, and hybrid) using back–calculated scale data.

Growth Rate Comparisons

The next step in the growth analysis was to see if different trout species (cutthroat, rainbow, hybrid) had different growth rates. For this analysis, it was first necessary to separate trout caught in tributaries during 1996 and 1997 from trout sampled in Spada Lake. In other local studies, trout residing in tributaries to the South Fork Tolt Reservoir and Chester Morse Lake grew slower than trout living in these reservoirs (Fisheries Consultants 1995, R2 Resource Consultants 1996). Similar growth differences by rearing area were seen in the Montana reservoirs. It was considered likely that trout living in Spada Lake tributaries would also have slower growth than their cohorts in the reservoir.

Average back-calculated total lengths for each trout species were plotted versus trout ages for sampling periods 1979-1980, 1986, 1992, and 1997 (Figures 63 to 66). Trout numbers sampled in 1995 and 1996 were considered too low for a representative plot for each species (n = 1 to 13). Also, hybrid trout sampled during 1979-1980 were not plotted due to small sample size (n=4).

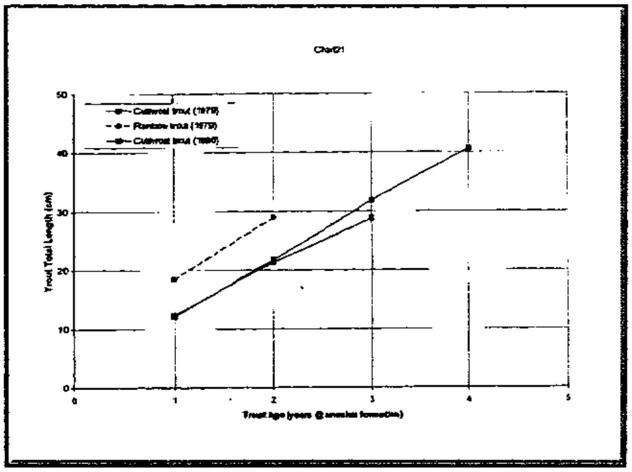


Figure 63. Average lengths of cutthroat and rainbow trout at each age from 1979 and 1980 sampling in Spada Lake.

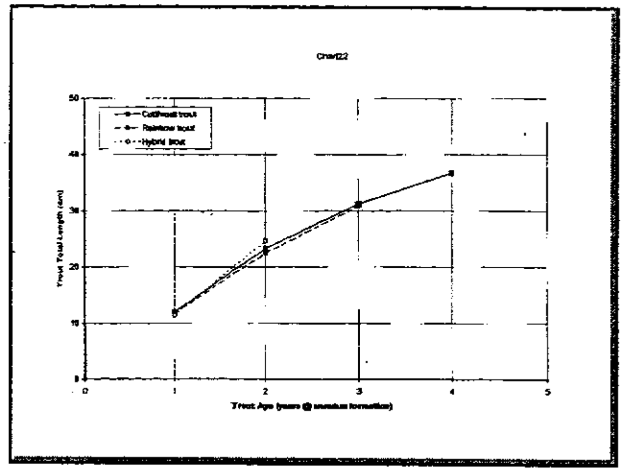


Figure 64. Average lengths of trout at each age from 1986 sampling in Spada Lake.

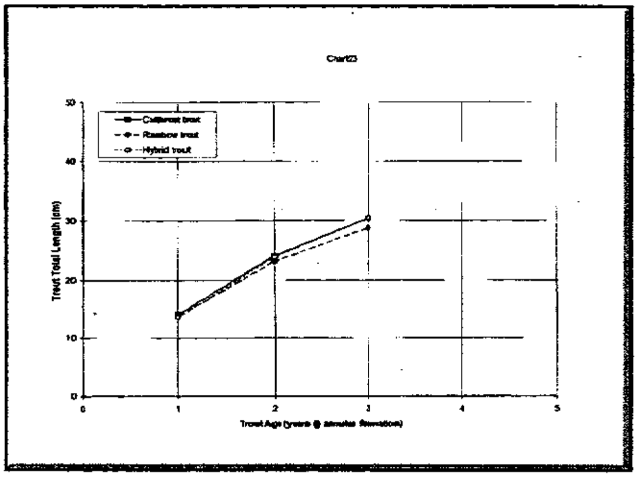


Figure 65. Average lengths of trout at each age from 1992 sampling in Spada Lake.

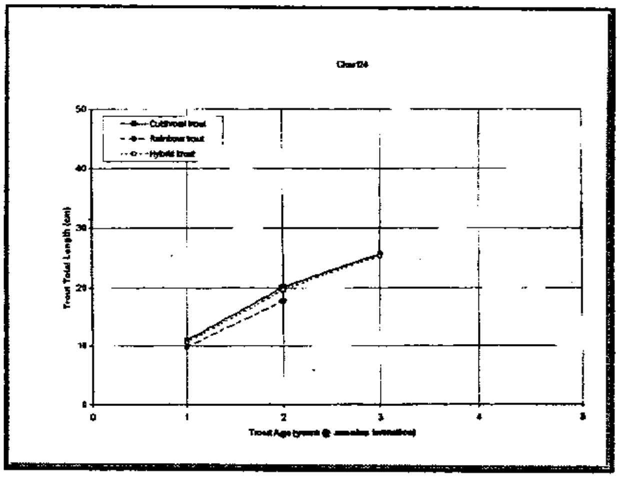


Figure 66. Average lengths of trout at each age from 1997 sampling in Spada Lake.

Average lengths at age for all trout species were very similar for each sample year, except rainbow trout sampled during 1979 were substantially larger at Age 1 and Age 2 than their cutthroat trout counterparts (Figure 63). Hatchery stocking of rainbow trout occurred in Spada Lake through 1979 (Appendix Table 1). It was assumed that the accelerated rainbow trout growth observed in Figure 63 was due to hatchery production. A length:frequency graph for Age 1 trout from the 1979-1980 sample period confirmed that rainbow and hybrid trout in these years had an elevated Year 1 growth compared to cutthroat trout (Figure 67). Rainbow and hybrid trout sampled during 1979 and 1980 were deleted from further analyses of age and growth; this deleted data for 41 trout out of a total sample size (all years) of 664 trout. Deletion of hatchery–produced trout allowed comparisons of growth rates of naturally produced trout in Spada Lake during different years.

Figures 63 through 66 show it was reasonable to combine cutthroat, hybrid, and rainbow trout sampled during a given year for age and growth comparisons between years. This was done to increase sample size and confidence for the between–years comparisons.

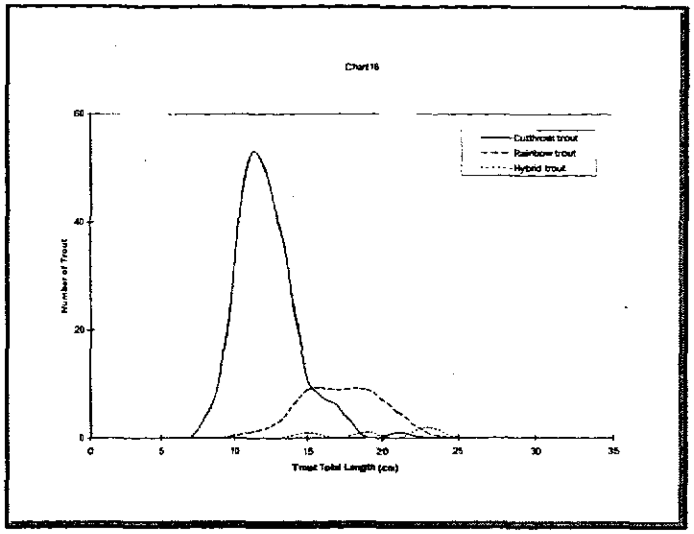


Figure 67. Length frequency distributions for Age 1 back–calculated lengths for trout sampled in Spada Lake during 1979 and 1980 (years with hatchery stocking).

Age at Reservoir Entry

One of the major objectives of the 1997 study was to determine how a trout parasite, *Diphyllobothrium*, affected trout growth and longevity in Spada Lake. One of the factors highly relevant to *Diphyllobothrium* loading is the residence time of trout in the reservoir, compared to residence time in tributaries. Trout living in Spada Lake tributaries would not be exposed to cyclopoid Copepoda which are an intermediate host of this cestode; possibly this would lead to lower rates of infection for trout spending multiple years in streams and rivers (vs. Spada Lake). This possibility made it important to differentiate which years individual trout lived in streams or rivers vs. which years they resided in Spada Lake. (The amount of time trout may spend moving between the reservoir and the tributaries, if any, is unknown. Scale patterns did not suggest significant periods of intermittent tributary residence, and such a life history pattern would not be typical, based on the literature (Gresswell *et al.* 1997). However, tagging studies to ascertain whether this is a significant behavioral trait of wild–origin Spada Lake trout would be very valuable.) In addition, knowledge of age at reservoir entry for each trout was critical to our analysis of the effect of *Diphyllobothrium* infection (Trout Parasitism and Mortality).

The first approach to try to identify the number of years trout lived in streams before migrating to Spada Lake was to develop a "reference collection" of scales from trout collected in tributaries, and compare observed and computed growth rates and scale patterns with trout collected from the reservoir. Streams and rivers tributary to Spada Lake were sampled by electrofishing during 1996 and 1997, and 34 scale samples from these fish were evaluated (see Appendix Table 18 for sample locations, dates, etc.).

Average lengths at age for trout sampled in tributaries and Spada Lake showed that trout growth rates for these two data sets were essentially equal (Figure 68). However, the sample size for "tributary trout" was very small for all ages except Age 1 (probably due to a combination of "washdown" during flooding, or purposeful emigration prior to Age 2). It is believed that the two Age 2/2+, one Age 3+, and one Age 4+ trout sampled in tributaries had recently migrated upstream from Spada Lake, rather than being year–round tributary residents. Two of these trout were sampled in early June 1997, possibly during spawning migrations, and the other two trout were sampled in July 1996 or September 1996 (one of which was collected by hook and line in the North Fork Sultan River).

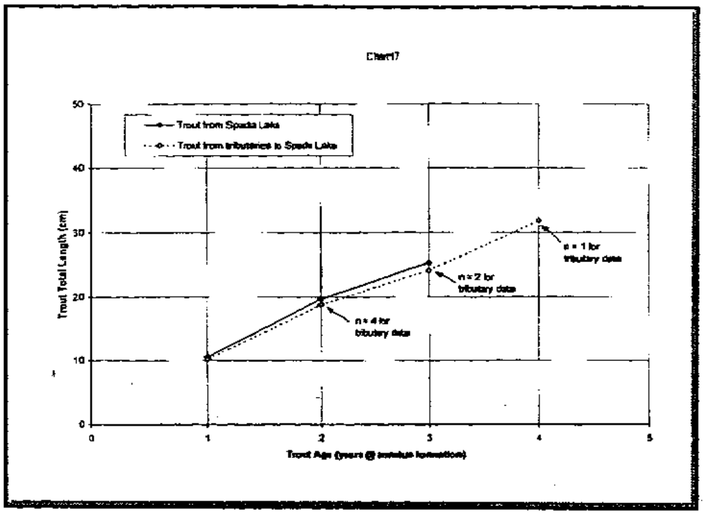


Figure 68. Average lengths of trout sampled from Spada Lake and tributaries to Spada Lake during 1996 and 1997.

Trout growth rates in South Fork Tolt Reservoir and Chester Morse Lake were faster than growth rates in tributaries to these reservoirs (Fisheries Consultants 1995 and R2 Resource Consultants 1996), and the differences were apparent on plots of average length at age (Figure 69). Lower growth rates in tributaries observed in these systems were found using substantially larger sample sizes for trout in tributaries, compared to the Spada Lake data set. Based on these data, Figure 69 comparing trout growth in tributaries with trout growth in Spada Lake was assumed to be misleading due to low sample size.

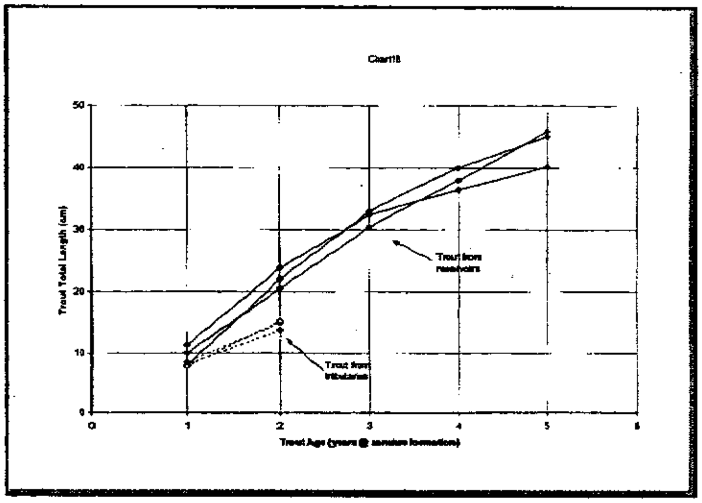


Figure 69. Average lengths of cutthroat trout sampled from South Fork Tolt Reservoir and tributaries (Fisheries Consultants 1995) and rainbow trout and bull trout sampled from Chester Morse Lake (reservoir) and tributaries (R2 Resource Consultants 1996).

Visual examination of scales provided the best measure of how many years each trout resided in streams or rivers, as outlined in Trout Age, Growth, and Condition — Methods. Observations recorded on data sheets were substantiated by calculations of annual growth for each trout. Trout recorded as "2 years in streams" always had low growth during Year 2 of life, compared to trout recorded as residing in the reservoir. These correlations are described in detail later in this section. "Years in streams" recorded on data sheets (Appendix Table A in Fisheries Consultants *et al.* (1997)) were interpreted as follows:

Years in streams (or rivers) = 1 = trout which appeared to live in tributaries part or all of one year before migrating to Spada Lake.

Years in streams = 2 = trout which appeared to live in tributaries their entire first year, plus part or all of their second year before migrating to Spada Lake.

Years in streams = 3 = (only 1 trout) similar interpretation as above.

Frequency distributions for trout total length (all species combined) were plotted for trout collected in 1986, 1995, 1996, and 1997 to see if back–calculated lengths at each age would help identify trout which probably spent more than one year in tributaries (Figures 70 to 73). For trout collected in 1986, there was a moderate bimodal length frequency for Age 2 trout (Figure 70). In previous studies on other local, similar systems (South Fork Tolt Reservoir and Chester Morse Lake), a bimodal length frequency at Age 2 was attributed to trout growth differences between tributary and reservoir environments. There was a weak bimodal distribution for Age 2 trout collected during 1995, and trout sampled in 1996 and 1997 appeared to have a single Age 2 mode for length frequency (Figures 71 to 73).

The percentage of trout sampled from Spada Lake that resided more than one year in tributaries ranged from 10 to 17 percent for years 1986 to 1997 (Table 32). Only one trout sampled from Spada Lake in 1997 was recorded as spending 3 years in tributaries prior to capture in the reservoir.

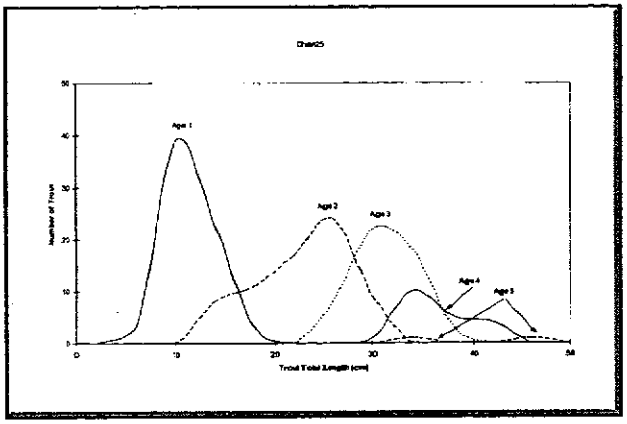


Figure 70. Frequency distribution for back–calculated trout lengths at even ages (Age 1, Age 2, etc.) for cutthroat, rainbow, and hybrid trout sampled in Spada Lake during 1986.

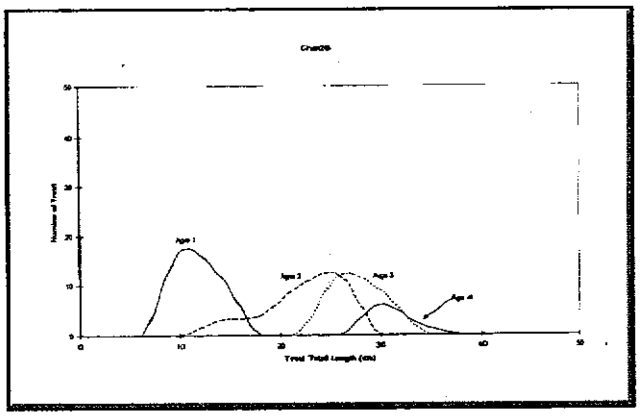


Figure 71. Frequency distribution for back–calculated trout lengths at even ages for cutthroat, rainbow, and hybrid trout sampled in Spada Lake during 1995.

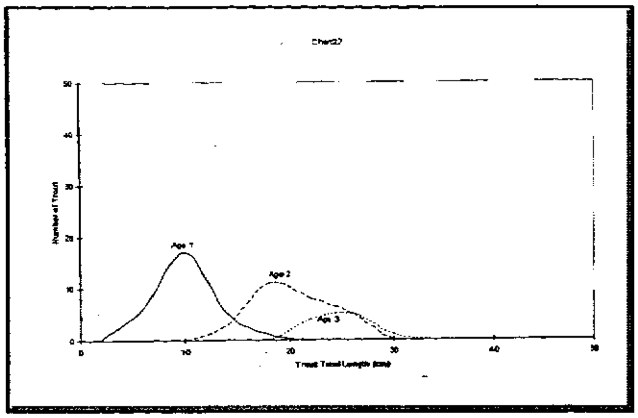


Figure 72. Frequency distribution for back–calculated trout lengths at even ages for cutthroat, rainbow, and hybrid trout sampled from Spada Lake during 1996.

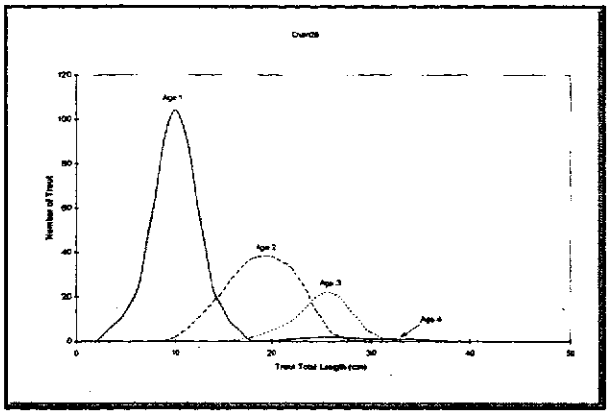


Figure 73. Frequency distribution for back–calculated trout lengths at even ages for cutthroat, rainbow, and hybrid trout sampled from Spada Lake during 1997.

Annual Growth Increments

Annual growth increments for trout during their second year of life were examined for trout sampled in 1986 from Spada Lake. As expected (from Figure 70), Year 2 growth was bimodal for trout sampled in 1986 (Figure 74). Data from scale reading were reviewed for all trout that had Year 2 growth less than 10 cm, to see how many of these trout were recorded as "2 years in streams". All 11 trout recorded on data sheets as "2 years in streams" had Year 2 growth less than 10 cm. Trout growth differences between tributary and reservoir environments, as reflected in scale appearance and scale reading data, effectively identified which trout spent more than one year in tributaries. These differences largely explained the Year 2 bimodal distribution for trout sampled in Spada Lake during 1986 (Figure 75). One trout with only about 4 cm growth during Year 2 was classified as a "reservoir trout" (Figure 75). Scales from this trout were reviewed and it was classified as an anomaly (reservoir trout) rather than a trout residing in tributaries more than one year.

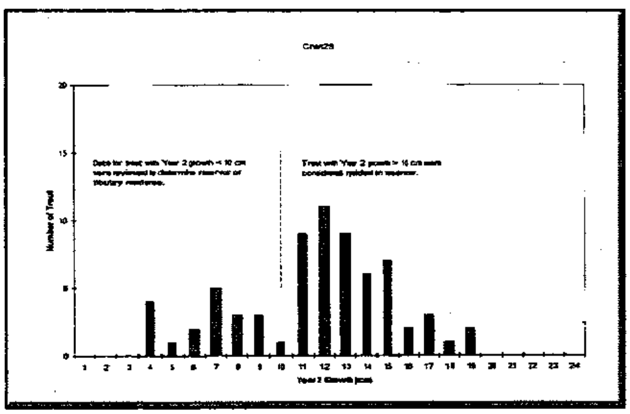


Figure 74. Annual increment of growth during second year of life for trout sampled from Spada Lake during 1986.

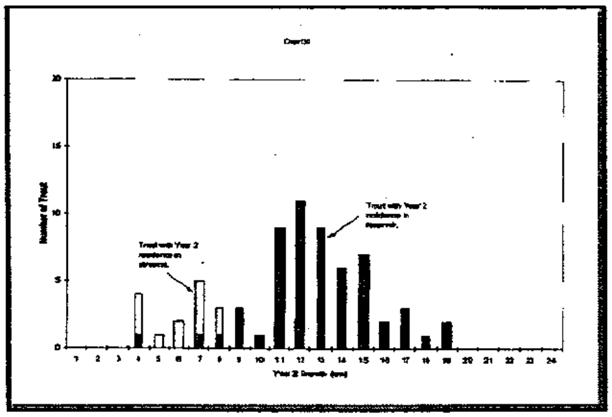


Figure 75. Annual increment of growth during second year of life for trout sampled from Spada Lake during 1986, with breakdown of stream residence time.

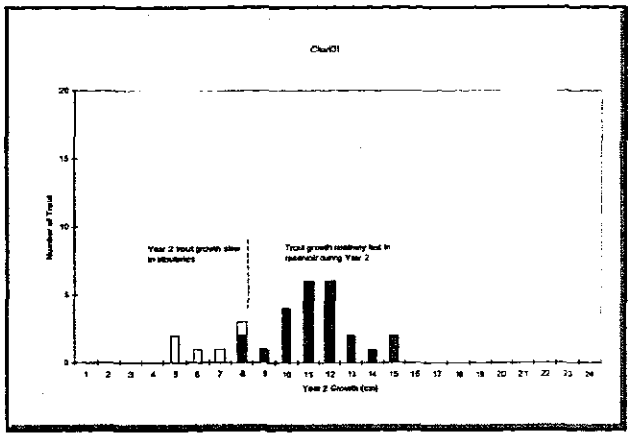


Figure 76. Annual increment of growth during second year of life for trout sampled from Spada Lake during 1995, with breakdown of stream residence time.

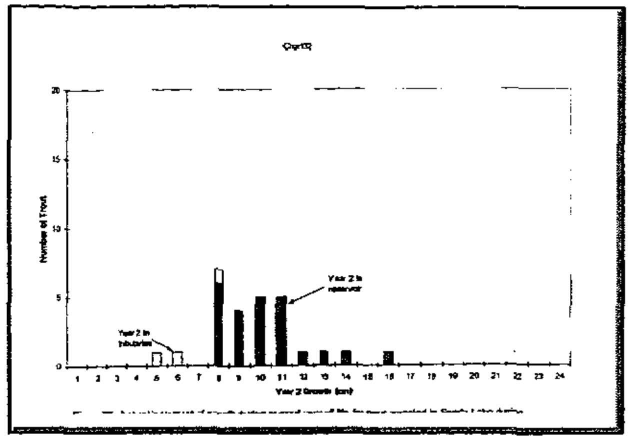


Figure 77. Annual increment of growth during second year of life for trout sampled in Spada Lake during 1996, with breakdown of stream residence time.

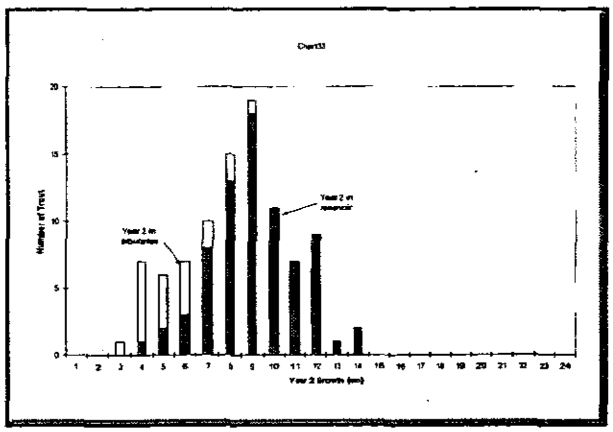


Figure 78. Annual growth increment during the second year of life for trout sampled from Spada Lake during 1997, with breakdown of stream residence time.

Histograms showing annual increments of growth for Year 2 were also plotted for 1995, 1996, and 1997 (Figures 76 to 78). As done for 1986, scale data were reviewed for all trout with Year 2 growth less than 10 cm to see if there was any correlation with trout listed as "2 years in streams" on scale reading data sheets. For all years, trout with Year 2 growth less than 10 cm included all trout subjectively labeled as "2 years in streams" on data sheets ("3 years" in one case). This differentiation is shown on Figures 76 through 78.

We call attention to the fact that a substantial fraction of the Age 2 growth increment histogram for 1997 fell below 9 cm (Figure 78), much more than seen in 1995 or 1996 (Figures 76 and 77). The specific cause/s can only be speculated upon, but may reflect deteriorating reservoir rearing conditions for trout.

Inter–Annual Growth Comparisons

A major advantage of back–calculation of length at even ages is that data from several years can be directly compared without variability induced by different seasonal sampling times. Additionally, growth data from several similar systems can be directly compared as long as the definition of "even age" remains consistent.

Figure 79 shows average length at age for trout from Spada Lake from 1979 to 1997. Data from 1979-1980 are for cutthroat trout only, and other years include cutthroat, rainbow, and hybrid trout. Trout sampled in tributaries during 1996 and 1997 are not included in Figure 79. Average trout length in Spada Lake at Age 1 and Age 2 appeared to be relatively constant from 1979 through 1997. However, the average length of trout at Age 3 and Age 4 was noticeably less for trout sampled 1995 to 1997, compared to average lengths estimated from previous years' sampling (Figure 79).

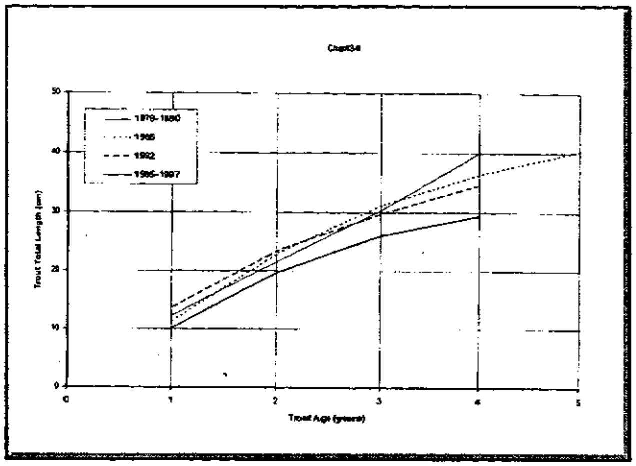


Figure 79. Average total length for cutthroat, rainbow, and hybrid trout sampled 1979 to 1997 from Spada Lake as determined by back–calculation of scale data to even age.

The low growth observed for Age 3 (n=67) and Age 4 (n=13) trout sampled 1995 to 1997 spanned all growing seasons between 1993 and 1996. Data for these years was examined to see if growth rates were noticeably different between separate years. Average growth rates were slightly higher for trout sampled during 1995 and 1996, compared to trout sampled 1997, but the difference was not substantial. Data from trout sampled 1995 to 1997 remained pooled to increase confidence in comparisons with other years.

A series of one–tailed t–tests (Ott 1977) were done to compare average Age 3 and Age 4 trout lengths from 1995-97 sampling of Spada Lake with other years' data (1979-80, 1986, 1992). The average Age 3 and Age 4 lengths for 1995-97 (Figure 79) were significantly lower ($P<0.001$) for all tests.

One potential bias in the pooled length at age data presented so far is that this usually includes fish from more than one brood year for any given age. Although the data plotted in Figure 79 are valid and accurate values, they represent the "whole population" length at age, and may be somewhat less meaningful than brood year length at age. For the purpose of making minimally–biased comparisons of growth between Stage I and Stage II, we wished to use data from brood years that had experienced similar rearing conditions. Therefore, the entire age and growth data set was organized on the basis of brood years for each trout species, and growth

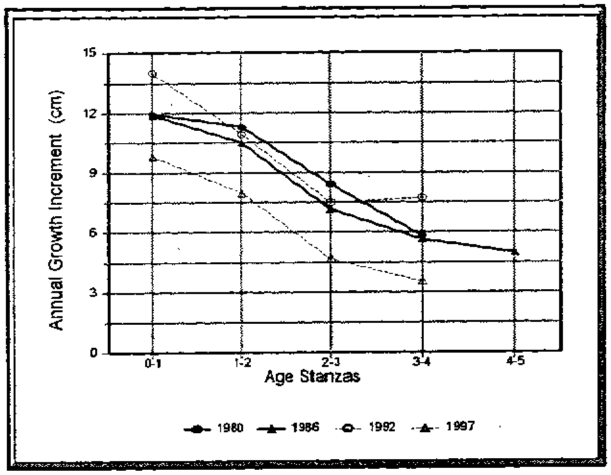


Figure 80. Annual growth increment for Spada Lake cutthroat collected in 1980, 1986, 1992, and 1997.

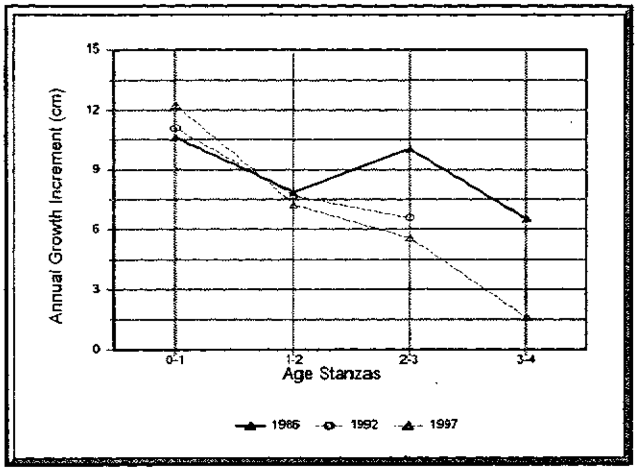


Figure 81. Annual growth increment for Spada Lake rainbow collected in 1986, 1992, and 1997.

increments were back–calculated on the basis of regression slopes determined for each brood year. These data appear as Figures 80 and 81.

Cutthroat exhibited little change in annual growth increments between 1980 and 1992, but dropped appreciably in all age stanzas when sampled in 1997 (Figure 80). For this species, growth in Stage II has diminished from that seen in Stage I (1980), but this reduction did not appear until quite recently. It's possible that the reduction seen in 1997 may be due to normal variation, since in 1992 two of four stanzas showed greater growth than in 1980 (Age 0 to 1 and Age 3 to 4). The following table places the current growth of Spada cutthroat into regional perspective:

	Growth Increments by Age Stanza				
Reservoir	0-1	1-2	2-3	3-4	4-5
Spada	98	80	47	36	
Libby	196	74	23		
Hungry Horse	57	47	136	67	41

Since unbiased growth data are not available for rainbow in Stage I due to hatchery fingerling releases, we cannot determine with certainty whether there has been a reduction in incremental growth similar to that seen in the cutthroat. Growth to Age 3 and Age 4 was heightened in 1986, shortly after reservoir enlargement (Figure 81), but the cause is a matter of speculation. Rainbow growth in 1992 and 1997 mirrored that of cutthroat. Since our earlier mixed–brood analysis showed little or no difference between rainbow and cutthroat within years (Figures 63 through 66), it seems likely that rainbow have also experienced reduced growth in Stage II. Rainbow growth was not consistently higher or lower than that of cutthroat in 1997. The following table puts the Spada Lake values in perspective:

Growth Increments by Age Stanza

Reservoir	0-1	1-2	2-3	3-4	4-5
Spada	123	72	56	16	
Ross	55	160	105	44	14
Libby	195	61	45	2	

Comparison of Figures 80 and 81 shows that for most of the years sampled, cutthroat exhibited greater inter–annual growth than rainbow. This is especially notable for the second stanza, which for most of the trout in Spada is their first year of reservoir residence. The cutthroat growth increment between Age 1 and 2 exceeded that of rainbow by over 4 cm (except in 1997). Instantaneous growth rates (**G**) are the least–biased measure since they are calculated on the actual observed length:weight relationship and growth increment of each brood year. With this method, no appreciable change in growth rates were seen for either cutthroat or rainbow in Stage II versus Stage I, with the single exception of 1997 rainbow growth between Ages 3 and 4 (Table 33; Figure 83). These results are consistent with that of our earlier method (Figures 63 and 66).

In summary, rainbow and cutthroat growth rates did not seem to drop appreciably or consistently in Stage II versus Stage I, but actual incremental growth values are very low compared with other area reservoirs. Incremental annual growth of cutthroat may have dropped below the previous trend line in 1997; further sampling is needed to determine whether this is normal variation.

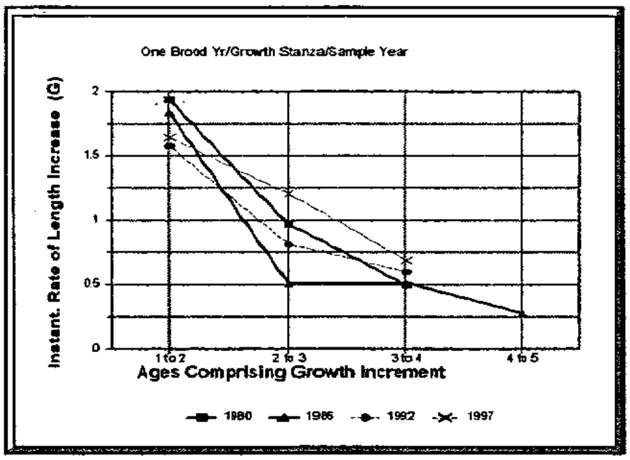


Figure 82. Instantaneous rate of length increase (*G*) between years for Spada Lake cutthroat sampled in 1980, 1986, 1992, and 1997.

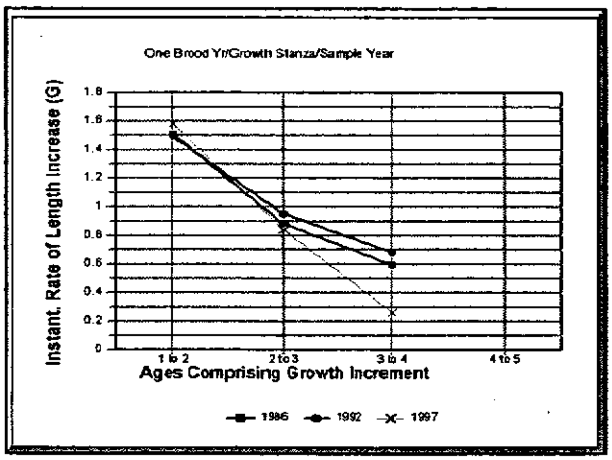


Figure 83. Instantaneous rate of length increase (*G*) between years for Spada Lake rainbow sampled in 1986, 1992, and 1997.

Table 33. Comparison of mean instantaneous growth rates of trout in Spada Lake in Stages I and II, 1979 through 1997.

		Cutthroat				Rainbow		
	Brood Year	**Age 1-2**	**Age 2-3**	**Age 3-4**	**Age 4-5**	**Age 1-2**	**Age 2-3**	**Age 3-4**
	1975			0.644				
	1976		0.889	0.496				
	1977	1.641	0.971					
	1978	1.940						
STAGE I								
	1981				0.280			
	1982			0.516				0.680
	1983		0.508				0.881	
	1984	1.837				1.510		
	1988			0.600				0.680
	1989		0.815				0.950	
	1990	1.579				1.493		
STAGE II								
	1992		0.369					
	1993		1.088	0.689				0.264
	1994	1.612	1.208				0.841	
	1995	1.645				1.582		

Growth in Other Lakes/Reservoirs

Average total length data for Spada Lake trout sampled 1995 to 1997 were lower than growth curves from other similar systems, particularly for Age 3 and Age 4 trout (Figure 84). Rainbow, cutthroat, and their hybrids are plotted as a single line for Spada Lake since their annual growth increments were nearly identical (see above). Rainbow and cutthroat growth rates in all other systems except one were substantially greater than in Spada, particularly for fish Age 3 or older. (Also, Age 4 and older trout are nearly completely absent in Spada lake.) The single exception noted in local literature are cutthroat in Hungry Horse Reservoir, MT, a system referred to as ultraoligotrophic by May *et al.* (1989).

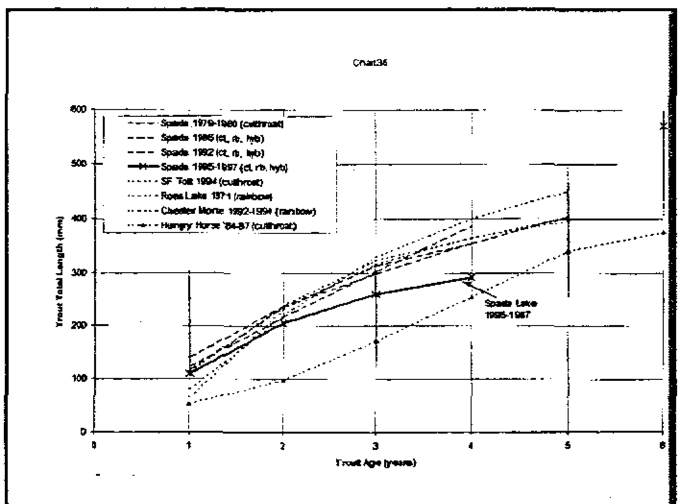


Figure 84. Average total length at age for trout from Spada Lake, 1979 through 1997, in comparison with other area reservoirs. Only one Spada Lake data point (Ct) plotted for Age 6 in 1997. Libby Reservoir (MT) rainbow growth ('84-87) nearly identical to that seen in Ross Lake in 1971.

Statistical comparison of differences in length at each age for trout from graphed local waters, or from Montana reservoirs (Table 34) were not done. However, the growth lag seen in Spada Lake "rainbow" is noteworthy in that it is appreciably less than that seen in other lakes with similarly low fish species diversity (Ross: rainbow and bull trout; SF Tolt: cutthroat only; Chester Morse: rainbow and bull trout). This shortfall is particularly significant with respect to cutthroat in the South Fork Tolt reservoir, and rainbow in Ross Lake, which have low morphoedaphic indices (0.78 and 0.82, respectively), very similar to Spada's index of 0.54. That is, although all three Washington reservoirs have physical and chemical characteristics which severely limit their potential production, annual growth increments of Spada Lake trout are nevertheless currently substantially lower than the other two systems.

Table 34. Length at age for trout sampled from Spada Lake and other Pacific Northwest regulated lakes and reservoirs.

Reservoir	Sample Years	Trout Species	Average Length at Age (mm)					
			Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Spada Lake (Washington)	1979-80	Cutthroat	123	216	303	387		
	1986	Ct, Rb, Hyb	117	235	314	354	404	
	1992	Ct, Rb, Hyb	140	237	299	355		571
	1995-97	Ct, Rb, Hyb	110	205	260	292		
SF Tolt Reservoir (Washington)	1976	/1 Cutthroat		190	273	399	362	
	1994	/2 Cutthroat	113	238	324	364	402	
Chester Morse Lake (Washington)	1992-94	/3 Rainbow	80	220	330	400	450	
Ross Lake (Washington)	1971	/4 Rainbow	65	231	317	365	396	
Libby Reservoir (Montana)	1984-87	/5 Rainbow	104	234	326	375		
Hungry Horse Res. (Montana)	1984-87	/6 Cutthroat	53	98	171	254	341	376

/1 Estimated from graphs in Congleton et al. (1977).
/2 Fisheries Consultants (1995).
/3 R2 Resource Consultants, Inc. (1996).
/4 Seattle Dept. of Lighting (1973).
/5 Chisholm et al. (1989).
/6 May et al. (1988).

Since all three reservoirs have aged at least ten years, the only obvious difference between them is the potentially large brown bullhead population in Spada Lake, which likely competes for relatively scarce food resources. *Daphnia*, the putative preferred food of rainbow, is no less abundant in Spada Lake than in these other reservoirs, or is at least seasonally more abundant (Table 14). Unfortunately, cladocerans are a relatively unimportant food item in Spada (usually <5 percent of stomach volume, and have only a brief period of abundance—roughly 11 weeks (Secondary Production—Abundance, Size, and Value as Fish Food and Trout Food Habits). In Ross Lake, however, daphnids are available and preyed upon by rainbow for a considerably longer period, essentially all summer (Johnston 1989). Other large plankters also are important in Ross Lake, such as *Leptodora, Epischura*, and *Diaptomus* (Seattle Dept. of Lighting 1973). Although chironomids may be more abundant in Spada than in Ross (Table 21), they are relatively low in nutritive value. Nevertheless, it is not surprising that they are the principal food item for trout in Spada Lake (Trout Food Habits).

Condition

Length-Weight Relationship

Standard length-weight equations for rainbow, cutthroat, and hybrid trout in Spada Lake (whole–season collections in 1997; all brood years and ages combined) are tabled below, along with sample sizes and summary statistics. The data are plotted in logarithmic and standard form in Figures 85 through 90. All three trout forms exhibited allometric growth with *b* values (slopes) less than 3.0.

Species	Equation	Sample *n*	*df*	r^2
Rainbow	log(w) = -4.831 + 2.901 log(TL)	299	297	0.8373
Cutthroat	log(w) = -4.805 + 2.900 log(TL)	184	182	0.9888
Hybrids	log(w) = -4.773 + 2.900 log(TL)	112	110	0.9884

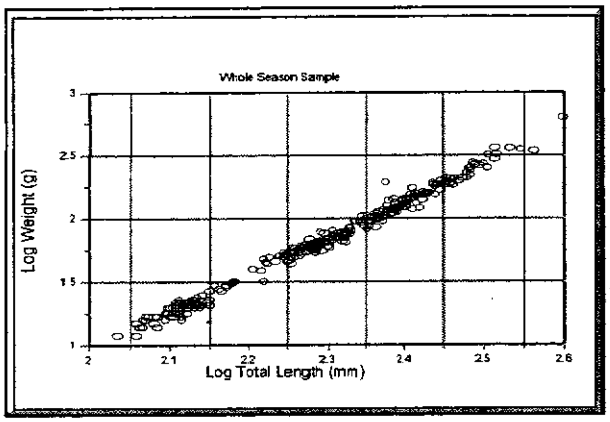


Figure 85. Logarithmic length-weight relationship of Spada Lake rainbow in 1997.

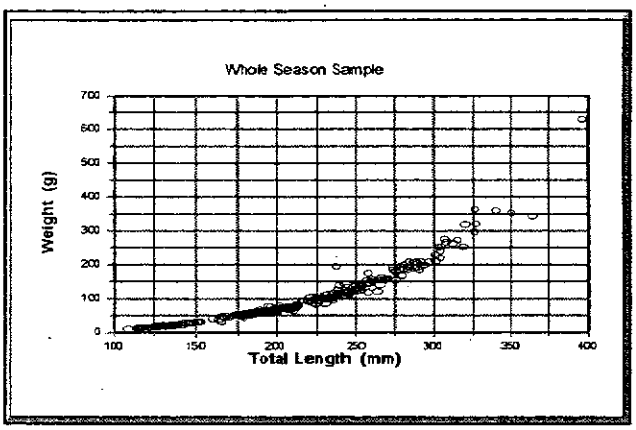


Figure 86. Length-weight relationship of Spada Lake rainbow in 1997.

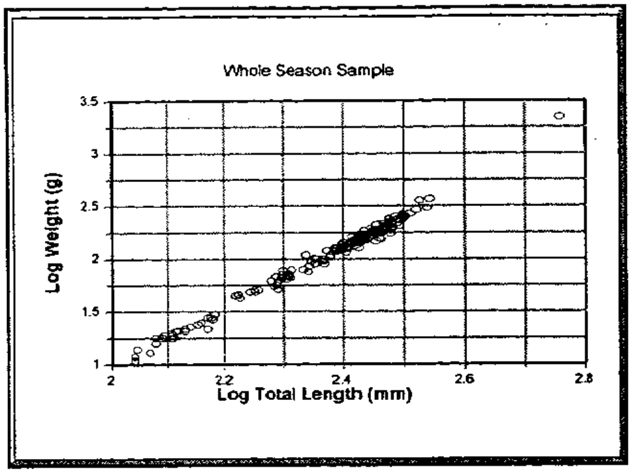


Figure 87. Logarithmic length-weight relationship of Spada Lake cutthroat in 1997.

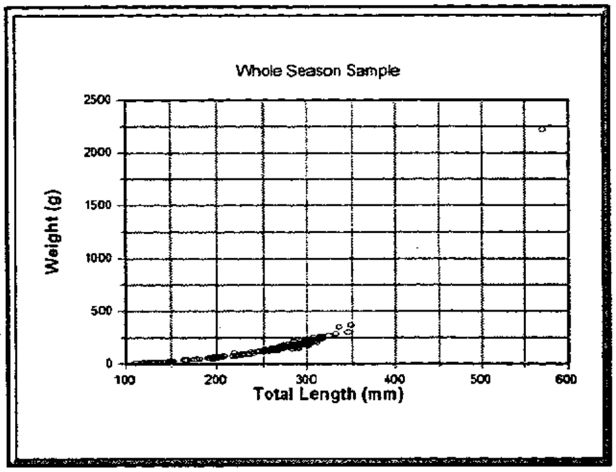


Figure 88. Length-weight relationship of Spada Lake cutthroat in 1997.

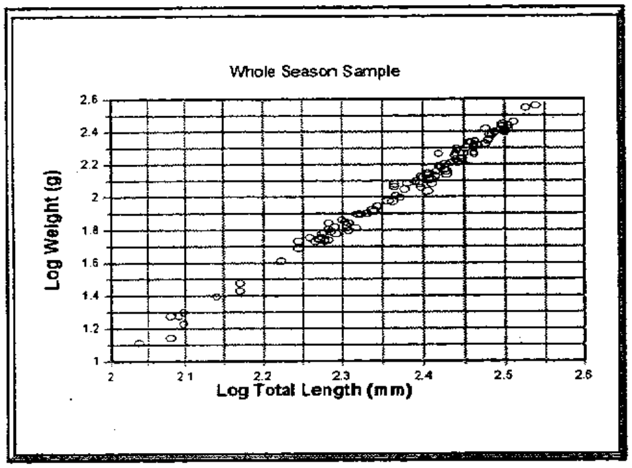


Figure 89. Logarithmic length-weight relationship of Spada Lake hybrid trout in 1997.

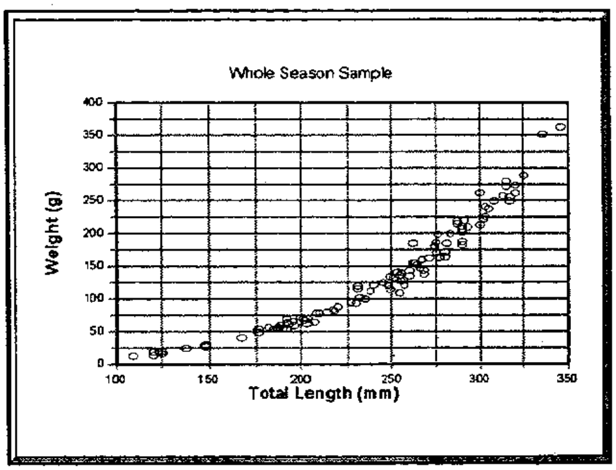


Figure 90. Length-weight relationship of Spada Lake hybrid trout in 1997.

Relative Weight and Condition

Relative weights of both rainbow and cutthroat are almost universally below the median, or "good" value of 100 that would be expected *if the Spada Lake stocks had a length-weight relationship well–represented by the standard equation of Anderson and Neumann* (1996) (Table 35). Only five instances of values >100 occurred, and all involved very low sample sizes (e.g., Age 4 rainbow in the summer of 1986; n=1). An unexpected finding was that cutthroat relative weights were consistently higher than that of rainbow in all age–by–age comparisons within seasons and years (Table 35). Example: W_r = 75.89 for Age 1 rainbow in Spring 1996, v. 96.74 for Age 1 cutthroat at that same time.

Table 35. Seasonal relative weights of rainbow and cutthroat in Spada Lake, Washington, 1985 through 1997. Shaded data show consistently higher relative weights for cutthroat, by age and season, within years. Cutthroat also show greater longevity.

Season	1985	1986	1992	1996	1997
AGE 1		**RAINBOW**			
SPR					
SUM				75.89	76.32
FALL				75.89	77.03
ALL					76.18
AGE 2					
SPR					67.79
SUM	77.01	95.48		67.57	75.2
FALL	77.01	95.48		67.33	75.26
ALL					73.28
AGE 3					
SPR		88.23	63.92		68.28
SUM	81.87	87.91		65.63	69.5
FALL					73.28
ALL	81.87	88.04	64.19	65.63	68.87
AGE 4					
SPR		92.84	64.21		70.43
SUM	73.32	104	n=1		73.33
FALL					71
ALL	73.32	95.55	67.62		71.38
AGE 5					
SPR					
SUM					
FALL					
ALL					
AGE 6					
SPR					
SUM					
FALL					
ALL	76	(n=1)			

Season	1985	1986	1992	1996	1997
AGE 1		**CUTTHROAT**			
SPR					
SUM	103.82	n=4		96.74	89.62
FALL	103.82			96.74	80.52
ALL					87.9
AGE 2					
SPR					
SUM	98.4	97.07		73.3	81.53
FALL					78.9
ALL	98.4	97.07		71.54	81.1
AGE 3					
SPR		117.65	73.95		75.24
SUM	90.64	92.18		78.34	77.73
FALL					77.16
ALL	90.64	103.76	74.14	78.34	76.18
AGE 4					
SPR		95.56	68.26		70.71
SUM	80.7	98.28			
FALL					90
ALL	80.7	96.4	68.29		73.68
AGE 5					
SPR		82.74	62.23		
SUM	121				
FALL					
ALL	(n=1)121	82.74	62.23		
AGE 6					
SPR					
SUM					
FALL					108
ALL				(n=1)	108

Although relative weight values were low, with no age group exhibiting average values above 90 in 1997, nonetheless most age groups exhibited slight increases between Spring and Fall (Figures 91 and 92). All rainbow under Age 4 showed an increase through the Summer (Figure 91), however, most cutthroat either showed little improvement, or actually lost condition (Figure 92). (1997 is the only year from which adequate Fall trout samples are available.)

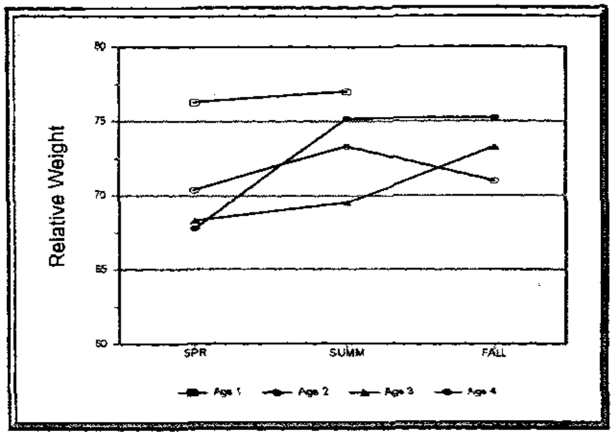


Figure 91. Seasonal relative weight of Spada Lake rainbow in 1997.

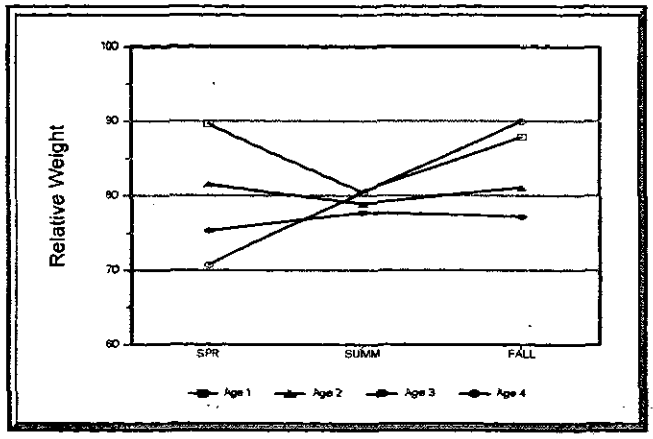


Figure 92. Seasonal relative weight of Spada Lake cutthroat in 1997.

Figures 93 and 94 illustrate the change in summer-fall relative weights between 1985-86 and 1996-97 for trout of equivalent age in Spada Lake. With the exception of one low relative weight of Age 2 rainbow in 1985 (which may be a small sample artifact), all 1996-97 values represent sharp declines in condition after 11 to 12 years of reservoir aging.

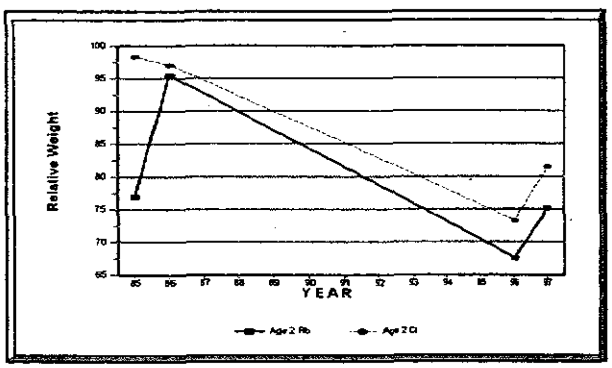


Figure 93. June through September relative weight of Spada Lake Age 2 rainbow and cutthroat in 1985-86 and 1996-97.

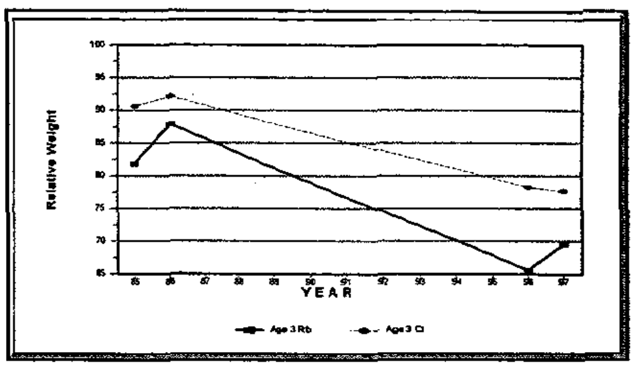


Figure 94. June through September relative weight of Spada Lake Age 3 rainbow and cutthroat in 1985-86 and 1996-97.

Table 36 provides additional historical perspective. Regardless of which index of condition one prefers, all 1997 values represent appreciable reductions from 1986 in age–by–age comparisons within seasons, as well as all ages combined in the summer samples.

Relative weight is probably the most appropriate index of condition as it is based on a length-weight relationship from a large aggregate of populations, many of which exhibit much better condition than trout in Spada Lake. It is remarkable that even as early as 1986, most trout in the

Table 36. Comparative values of relative condition (Kn) and relative weight (Wr) for trout from Spada Lake, 1986 and 1987.

			Rainbow		Cutthroat	
Year	**Season**	**Age**	**Kn**	**Wr**	**Kn**	**Wr**
		3	1.26	88.2	1.25	117.65
1986	Spring	4	1.35	92.8	1.17	95.6
		5	----	----	1.03	82.7
		2	1.34	95.5	1.15	97.1
1986	Summer	3	1.26	87.9	1.10	92.2
		4	1.50	104.0	1.20	98.3
		Mean of all ages:	1.37	95.8	1.15	95.9
		2	0.93	67.8	----	----
1997	Spring	3	0.96	68.3	0.88	75.2
		4	1.01	70.4	0.84	70.7
		1	----	76.3	----	89.6
1997	Summer	2	1.04	75.2	0.92	81.5
		3	0.99	69.5	0.91	77.7
		4	1.05	73.3	----	----
		Mean of all ages:	1.03	73.6	0.92	82.9
		1	----	77.0	----	80.5
1997	Fall	2	----	75.3	----	78.9
		3	----	73.3	----	77.2
		4	----	71.0	----	90.0

reservoir did not even meet the average relative weight value of 100. Relative weights as low as 68, seen in the spring of 1997 for Age 3 rainbow, are strikingly low.

Using relative condition (K_n), cutthroat appear to be faring a bit more poorly than rainbow in 1997 versus 1986 (Table 36). In 1997, at least some rainbow cohorts exhibited relative condition ≥ 1.0, whereas no cutthroat did. Using relative weight (W_r), just the reverse is true. Relative weights for cutthroat were higher than for rainbow in 1997, but the difference is probably not statistically significant. This difference is no doubt due to the use of standard equations developed from populations sampled across North America, rather than being limited to Spada Lake or regional waters.

Internal Fat

The subjective rating of internal fat mirrored the quantitative assessments of condition. Each trout species showed a reduction, over the summer, in the percentage that had no internal fat (Figure 95). Yet, 20 percent of all rainbow entered the winter with no internal fat reserves. When all species and ages are pooled, the trend over the summer is the same (Figure 96), with a

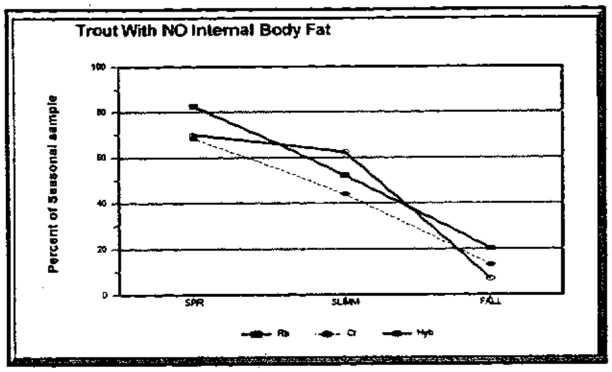


Figure 95. Percent of seasonal trout sample from Spada Lake in 1997 having no internal body fat.

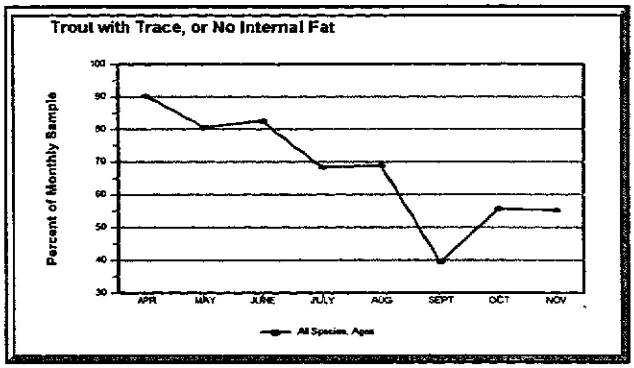


Figure 96. Percent of monthly trout sample from Spada Lake in 1997 having trace or no internal body fat.

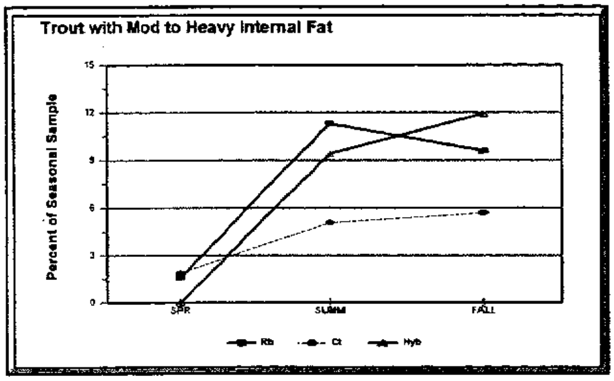


Figure 97. Percent of seasonal trout sample from Spada Lake in 1997 having moderate to heavy internal body fat.

startling 55 percent of the October and November fish entering the winter with little or no fat reserves. The increase in fish with some fat in September probably reflects the "optimum" feeding conditions at that time, but the benefits were apparently short–lived. Some trout were able to build internal fat deposits, but no species had more than 12 percent with moderate deposits (Figure 97). Rainbow and hybrid trout seemed to be slightly better able than cutthroat to garner some fat, but the difference is only a few percentage points of the entire population of each species. Figure 97 plots data from the combined moderate and heavy fat groups. In reality, none of the hybrids exhibited what were deemed heavy fat levels, and never more than 1.9 percent of the rainbow or cutthroat had similar fat levels.

The following table summarizes the sample sizes and grouping of assessed fat levels. It is remarkable that of the season–long sample, over 93 percent of the trout had only light fat, or less:

Fat Content	Sample Size	Percent
None	236	44.3
Trace	129	24.2
Light	131	24.6
Moderate	33	6.2
Heavy	4	0.7
	533	100.0

Proportional and Relative Stock Density

PSD in Spada Lake in 1997 was zero (0) for rainbow, and one (1) for cutthroat. These pathetically low values are partly caused by the somewhat high standard values set for the "quality' length (40 cm for rainbow, 35 cm for cutthroat). We only collected one fish that could meet these standards (below). Given Spada's low potential productivity, Relative Stock Density may be a more meaningful index of the population size structure.

Species	Threshold Length	Number Sampled	PSD	RSD
Rainbow	400	0	0	
Rainbow	254	60		24
Rainbow	305	13		5
Cutthroat	350	1	1	
Cutthroat	254	101		40
Cutthroat	305	17		7

RSD for rainbow indicates that about 1 in 20 are above 12 inches, and are harvestable. About one quarter of all rainbow are 10 inches or larger, and are likely to be acceptable to anglers. These proportions are slightly higher for cutthroat.

Conclusions

Annual incremental growth of trout Age 3 or older was significantly lower in 1997 than even five years earlier. It is clear that trout rearing conditions in Spada Lake in Stage II are distinctly adverse. Further field research is needed to clearly identify the cause/s; comparative abundance and diet studies with the brown bullheads is a first priority.

Relative weights of both rainbow and cutthroat were almost universally below the median, or "good" W_r value of 100. Cutthroat relative weights tended to be higher than those of rainbow in age–by–age comparisons within seasons and years. Most rainbow age groups showed slight increases in relative weight between spring and fall, but cutthroat did not.

The 1997 trout samples showed sharp declines from 1986 in both relative weight (W_r) and relative condition (K_n) after 11 to 12 years of reservoir aging. Based strictly on relative condition, cutthroat appear to be faring less well than rainbow.

Both trout species showed a reduction over the summer in the percentage of fish that had no internal fat. However, 55 percent of all trout in late October or early November had little or no internal fat.

Trout Food Habits

The primary objectives of our trout dietary survey in 1997 was to look for gross changes in diet between 1997 and earlier studies (1979-80 and 1986), and to relate diet to trout species and indices of their condition. The basic questions to be answered were whether dietary preferences had changed, and whether most fish were obtaining adequate amounts of food to maintain good condition. One measure of the adequacy of food resources is the percentage of empty stomachs observed throughout the growth season. Bioenergetics modeling or calculations, and comprehensive calculations of selection indices were beyond the scope of this survey. As is often the case, we learned much more about the food and feeding conditions than had been previously reported, and make recommendations for the design of more detailed dietary studies at the end of this section.

Methods

Trout stomachs for dietary analysis were obtained from the semi–weekly gillnet sampling of Spada Lake from May 9 to October 10, 1997. Trout caught in gillnets were subsampled and whole stomachs were removed and placed in small bottles containing 10 percent formaldehyde (formalin). A total of 160 trout stomachs were sampled for this report (Fisheries Consultants and ZP's Taxonomic Services 1997).

Stomach contents for each trout were emptied into a Petri dish with a small amount of water, and spread out for viewing under a variable magnification dissecting scope. A subjective judgment was made for each stomach on how full the stomach was, with a "full stomach" recorded as 1.0 on the data forms and an empty stomach recorded as zero. The volume of stomach filled with food items was estimated to the nearest 10 percent (0.1) and recorded. An initial scan of contents was made under low power (4x) to separate easily identified food items by Order (Coleoptera, Diptera, etc.). Identification of food items was done using standard references including Edmondson (1959), Pennak (1989), Thorp and Covich (1991), and Usinger (1974).

A portion of most stomachs was composed of partly digested food items in small fragments that were difficult to identify and impractical to separate individually. This mass was typically less than 20 percent of the total stomach content volume. This mass was spread out in the Petri dish and slowly scanned under high power (25x) to get a general idea of what most fragments were (e.g., Diptera limbs separated from digested bodies). The scan resulted in a subjective assessment of what proportion of the mass should be allocated to each of the previously separated piles (Orders) of food items. The mass was then divided into reasonable fractions (by Order) and included in piles of whole organisms.

The volumes of food items in each Order (pile in the Petri dish) were then measured by displacement of water in small graduated test tubes. The accuracy of this volumetric measurement was 0.05 ml. If a single food item (Order) was present in the stomach but the volume was less than 0.05 ml, volume was listed as 0.05 ml (lowest limit of measurement). In subsequent analyses of stomach contents, this would result in a slight over–estimation of the volume of food items found in low amounts in each stomach.

During the high power scan of stomach contents mass, zooplankton were observed (if present) and identified to Order (Cladocera or Copepoda). For most stomachs where zooplankton were observed, the volume of zooplankton was very small, not measurable, and substantially less than the 0.05 ml assumed for small amounts of other food groups. Tiny volumes of zooplankton were given an assumed volume of 0.005 ml so that they would be volumetrically represented in quantitative analyses of stomach contents, but at less than 1 percent of total stomach volume. Therefore, zooplankton volumes listed in Fisheries Consultants and ZP's Taxonomic Services (1997) as less than 1 percent of total stomach volume are assumed values.

Some trout fed exclusively or heavily on zooplankton and a large mass inside the stomach was readily identifiable as zooplankton organisms. In these cases, the zooplankton mass was spread out in the Petri dish, identified to Order, and then measured volumetrically as described above for other types of food items. Where zooplankton accounted for more than 5 percent of stomach contents volume, zooplankton volume measurements were considered accurate within 0.05 ml (Fisheries Consultants and ZP's Taxonomic Services 1997).

Results and Discussion

The presence/absence and volume of food items found in each stomach were identified and measured for food groups listed in Table 37 (see also Fisheries Consultants and ZP's Taxonomic Services [1997]).

Table 37. Food groups by Order, common name, and prevalent life stages observed in trout stomachs from Spada Lake in the 1997 sampling season.

Order (or food group)	**Common Name**	**Prevalent Life Stage**
Ephemeroptera	Mayflies	Nymph
Odonata	Dragonflies, damselflies	Nymph
Plecoptera	Stoneflies	Nymph
Hemiptera	Boatmen, striders. etc.	Adult
Trichoptera	Caddisflies	Larva
Coleoptera	Water beetles	Adult
Diptera	Midges, flies	Pupa
Cladocera	*Daphnia*, water fleas	Adult
Copepoda	(*Epischura nevadensis*)	Adult
Other Aquatic Org's	Snails, clams	Adult
Terrestrials	Insects, spiders, worms	Adult

Trout stomachs analyzed in 1997 were from trout slightly smaller than trout sampled in 1986. This was because the 1986 sample came from trout caught and kept in the recreational fishery (creel survey), whereas the 1997 sample was collected using variable mesh gillnets which also sampled small trout (Table 38). Minor differences in average length of trout between the 1986 and 1997 samples probably did not affect overall results of the stomach contents analysis. As shown below, Age 1, Age 2, and Age 3 trout sampled in 1997 from Spada Lake appeared to have diets which did not substantially differ with age (or length).

Table 38. Mean lengths of trout sampled in 1986 and 1997 for analysis of stomach contents (whole sampling seasons).

	Average Total Length (cm)		
Year	**Cutthroat**	**Rainbow**	**Hybrid**
1986	28.5	23.6	25.7
1997	22.7	18.8	23.0

Shapiro and Associates and University of Washington (1987) reported stomach contents data for two sampling periods: Spring (April 20 to May 31) and Summer (June 1 to September 1). This seasonal breakdown was not practical for the 1997 study because of low sample numbers of each trout species during the "Spring" period (n = 4 cutthroat, 4 hybrid, and 11 rainbow trout). Data for the 1997 study were pooled into one sampling period stretching from May 9 through October 10, 1997.

Major Dietary Changes

Trout stomach contents from the 1997 sample period were compared with stomach contents evaluated by Wash. Dept. of Game (1982) for trout sampled in 1979-80, and by Shapiro and

Associates and University of Washington (1987) for trout sampled in 1986. The overall comparison of stomach contents concluded the following (Table 39):

- Mayflies (nymphs) were commonly found in trout stomachs sampled in 1979-80 and 86, but were almost absent in stomachs sampled in 1997.
- Stoneflies, aquatic beetles, and terrestrial organisms (mostly winged insects and spiders) were found in a higher percentage of stomachs sampled in 1997 compared to 1986, but were at nearly equivalent levels seen in 1979-80.
- The percentage of trout stomachs containing caddisflies, zooplankton, and other food items (snails, clams, etc.) were about the same when comparing 1986 and 1997 samples. Comparisons with 1979-80 data were not possible due to differing reporting methods.
- Leeches were commonly taken in 1979-80, particularly by cutthroat, but this group was no longer seen in the diet by 1986.

Comparisons of 1979-80, 1986, and 1997 trout stomach contents (Table 39) are shown in Figures 98, 99, and 100 for rainbow, cutthroat, and hybrid trout, respectively. Diptera (principally chironomids) were the most common food item in all sampling years, with the possible exception of rainbow in 1979-80.

Several groups exhibited sharp reductions in occurrence. The graphs show a substantial reduction in mayfly abundance in trout stomachs from 1979-80 and 1986 to 1997 (none were found in cutthroat stomachs in 1997). Similarly, leeches were important in 1979-80, but were not seen in either trout species in 1986 or later. Both of these changes are probably explained by reservoir aging (below).

Midges and zooplankton were the only food groups which showed important increases in 1997 over 1979-80.

In 1979-80 zooplankton was relegated to an "Other" category as it was infrequently seen in the diet, but it occurred with sufficient frequency to be graphed separately in 1986. Zooplankton was eaten at the same frequency (hybrid trout) or more frequently (Rb and Ct) in 1997, particularly by rainbow. Over 30 percent of non–empty rainbow stomachs now contain some amount of zooplankton, which was almost entirely cladocerans.

The increased incidence of chironomids by 1986 is very likely a reflection of reservoir aging, which tends to favor these species, while at the same time reducing invertebrate diversity (below).

Table 39. Frequency of occurrence of major food groups in rainbow, cutthroat, and hybrid trout sampled from Spada Lake during 1979-80 (WDG 1982) 1986 (Shapiro and UW 1987), and 1997. Hybrids were not recognized in 1979-80.

		Number of Stomachs		Percentage of Non–Empty Stomachs Containing Each Food Group								
Species	Year	With Food	Empty	Midges Diptera	Mayflies Ephemeroptera	Caddisflies Trichoptera	Stoneflies Plecoptera	Beetles Coleoptera	Zooplankton	Leeches Hirudinea	Terrestrial	Other*
	1979-80	63	0	54	40	45	29	0 - ?	0 - ?	14	60	-----
Rainbow	1986	93	0	87	47	33	11	41	23	0	18	48
	1997	84	1	76	2	24	27	56	33	0	64	37
	1979-80	63	0	63	56	28	30	0 - ?	0 - ?	38	40	-----
Cutthroat	1986	87	1	97	28	31	6	31	21	0	25	48
	1997	42	1	90	0	24	17	48	24	0	64	45
Hybrids	1986	57	1	96	39	21	7	32	14	0	23	58
	1997	28	1	79	4	29	25	50	14	0	64	46

* In 1979-80, "other aquatics" included clams, alderfly larvae, snails, and water boatmen. Their frequency of occurrence was not noted, but "Other Aquatics" constituted 17 percent of total stomach volume.

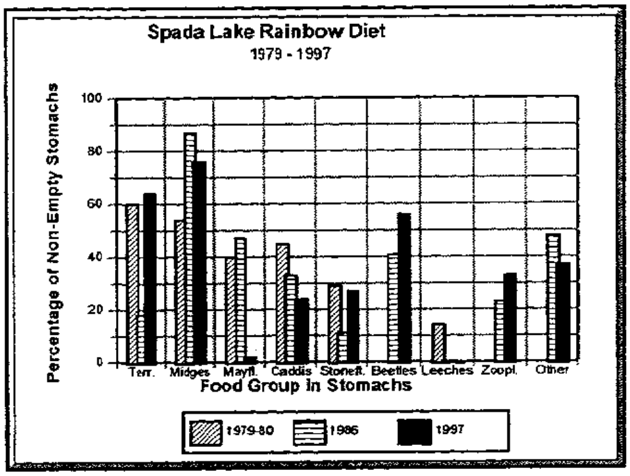


Figure 98. Percent occurrence of food groups in Spada Lake rainbow stomachs, 1979-80, 1986, and 1997.

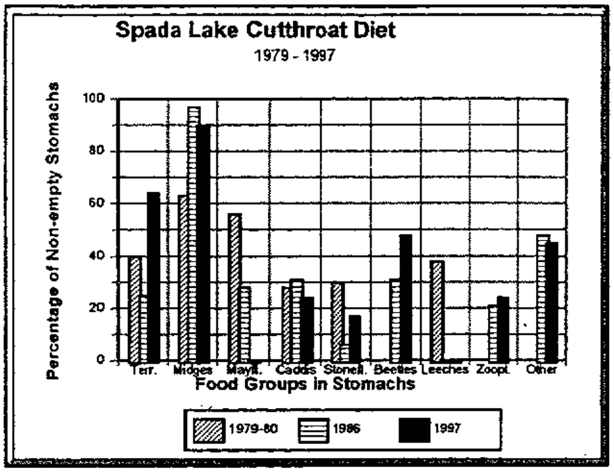


Figure 99. Percent occurrence of food groups in Spada Lake cutthroat stomachs, 1979-80, 1986, and 1997.

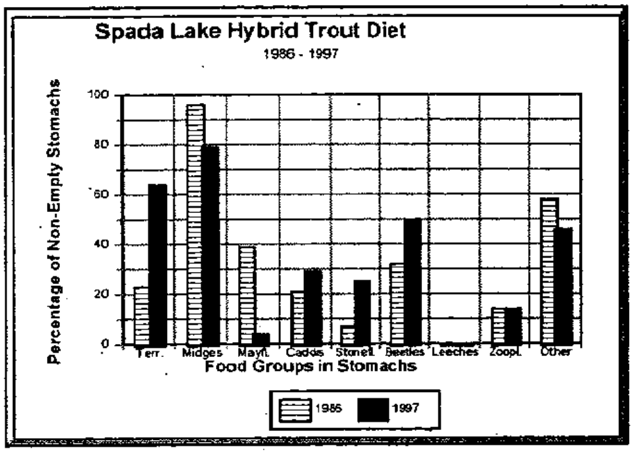


Figure 100. Percent occurrence of food groups in Spada Lake hybrid trout stomachs, 1986 and 1997.

Diet Analysis by Trout Species, Age, and Food Group

Several analyses of trout stomach volumes were done to get a better understanding of trout feeding during the 1997 sampling period on Spada Lake, and to review possible differences between trout age groups.

Stomach Fullness

First, an evaluation was done to estimate the proportion of each trout's stomach that contained food during the 1997 sampling season. Stomach examinations included a subjective estimate of the proportion of each trout's stomach that contained food (Fisheries Consultants and ZP's Taxonomic Services 1997). The volume of food measured in each stomach considered to be full was plotted versus trout total length (Figure 101). Least squares regression of these data was done to plot a line approximating the relationship between trout length and "full stomach volume" (Figure 101). "Full stomach volume" calculated for each trout using this regression equation was then compared to measured stomach volume for each trout to estimate the percentage volume of each trout stomach containing food items.

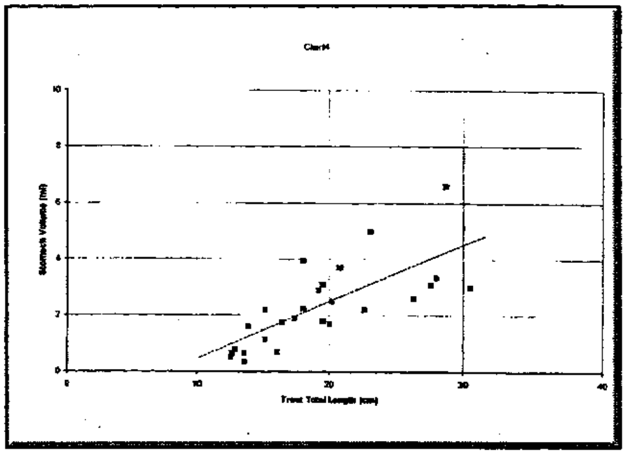


Figure 101. Trout length versus volume of stomach contents for trout considered to have a "full stomach." Line from Least Squares Regression.

The percentages of "full stomach" containing food items for each trout are plotted in Figure 102 to show the overall seasonal trend in trout feeding during the 1997 sampling period. During the entire sampling period, some trout stomachs were full or near full, while other trout stomachs were empty or near empty. (As seen in Table 40, only a very small percentage of stomachs were completely empty, and this held for all species and seasons.) Overall, it appeared that trout stomachs averaged about half full during the entire season, with a slight dip in stomach content volume during June and July 1997. The apparent reduction in trout feeding rates during June and July may have been due to capture of spawning or post–spawning trout, several unseasonably cold and wet weather events which may have affected trout feeding, other causes, or sampling variability. It was expected that trout stomachs would be fuller near the end of the sampling season when prey items would presumably be larger and more abundant, and warmer water temperatures would promote feeding. This was not the case (Figure 102).

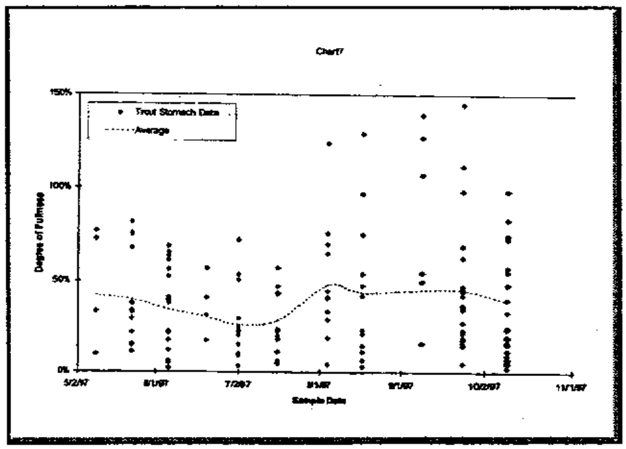


Figure 102. Trout stomach contents as a percentage of "full stomach" during 1997 sampling period on Spada Lake. Average line smoothed by eye for sampling dates with n<10 stomachs.

Two points are noteworthy from Figure 102. First, almost no trout were found with completely empty stomachs. Second, since a relatively large percentage of all trout had stomachs at least half full, why was trout relative weight (condition) so poor (Tertiary Production—Trout Age, Growth, and Condition: Results and Discussion)? The answer probably lies in the caloric value of the major dietary items.

Table 40. Frequency of empty trout stomachs in Spada Lake, 1986 and 1997. Spring = April-May; Summer = June-August; Fall = September-November.

		1986 Number of Stomachs		1997 Number of Stomachs	
Species	**Season**	**With Food**	**Empty**	**With Food**	**Empty**
	Spring	31	0	11	0
Rainbow	Summer	62	0	34	2
	Fall	----	----	40	1
	Spring	30	0	4	0
Cutthroat	Summer	57	1	24	1
	Fall	----	----	14	0
	Spring	19	0	4	0
Hybrids	Summer	38	1	15	0
	Fall	----	----	9	1
All		237	2 (0.8%)	155	5 (3.2%)

The Trout Age, Growth, and Condition section of this report concluded that trout sampled in Spada Lake during 1997 had back–calculated lengths at Age 1 and Age 2 that were comparable to previous (e.g., 1986) studies of trout growth in the reservoir. However, trout sampled during 1997 were considerably smaller at Age 3 and Age 4 than equal–aged trout sampled in 1986 (Figure 79). Trout stomach samples were matched with trout age data to see if there were any age–related differences in stomach volume filled by food items, for the 1997 sampling period.

The percentage of stomach volume containing food items was separately plotted for each age group sampled in Spada Lake during 1997 (Figures 103 to 105). Trout aged 1 to 4 years did not seem to have substantially different volumes of food items in their stomachs, compared to stomach size, and there were no strong relationships between sampling time and stomach content volume for any age group. This analysis did not help explain why trout sampled from Spada Lake during 1997 appeared to grow relatively slow during their third and fourth years of life.

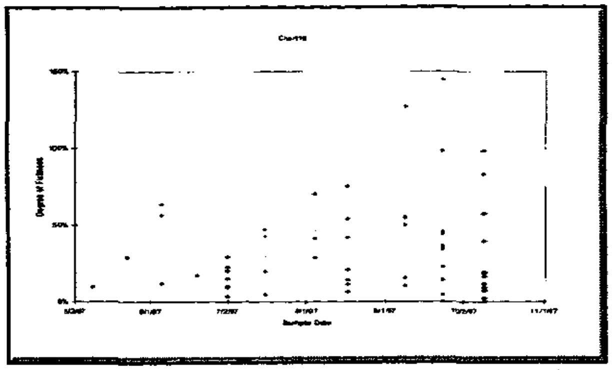


Figure 103. Age 1/1+ trout stomach content volume as a percentage of "full stomach" during 1997 sampling period on Spada Lake.

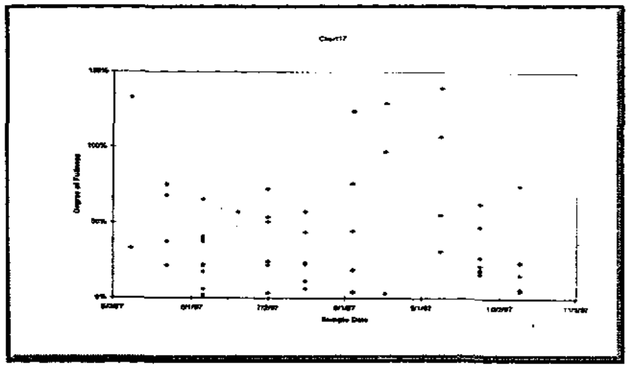


Figure 104. Age 2/2+ trout stomach content volume as a percentage of "full stomach" during 1997 sampling period on Spada Lake.

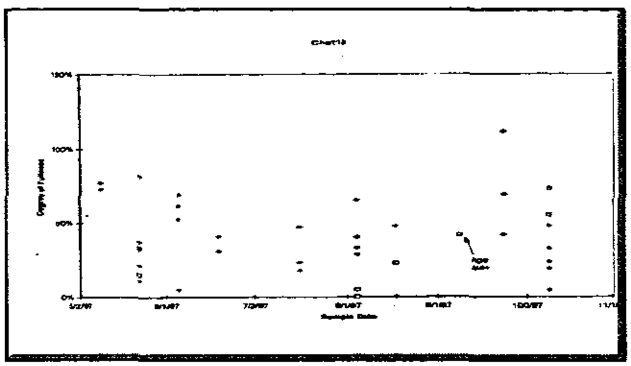


Figure 105. Age 3/3+ and 4/4+ trout stomach content volume as a percentage of "full stomach" during 1997 sampling period on Spada Lake.

Diet v. Age and Species

Volumetric data from 1997 sampling of stomach contents were reviewed to see if there were any major diet differences between trout species and/or trends in trout diet with age. The most abundant food groups (by volume) for cutthroat and rainbow trout were Diptera (midges) and terrestrial organisms. These two food groups totaled about half of the measured stomach contents for all age groups of these two species (Figures 106 and 107). Major differences between cutthroat and rainbow trout diets were not apparent by comparison of Figures 106 and 107; therefore, data were pooled for all trout species (cutthroat, rainbow, hybrid) to further review possible diet shifts with trout age.

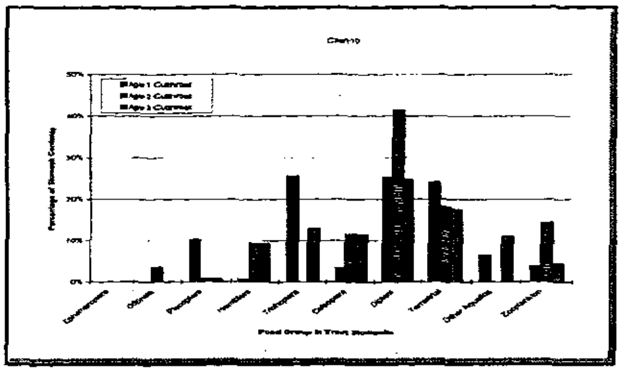


Figure 106. Average percentage (by volume) of each food group found in stomachs of cutthroat trout *sampled from* Spada Lake *during 1997.*

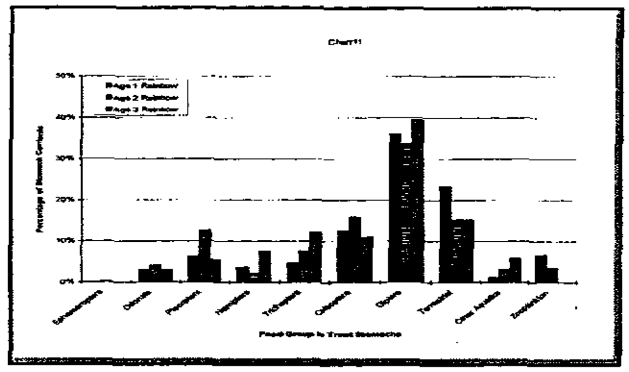


Figure 107. Average percentage (by volume) of each food group found in stomachs of rainbow trout sampled from Spada Lake during 1997.

(In 1979-80, Bradbury *et al.* (WDG 1982) felt rainbow "showed a definite preference for stream benthos, either preying on insect drift at the stream mouth, or actually entering the stream to feed. Mayfly larvae and large caddisfly larvae are especially important." These comments were based on a sample of 63 rainbow. Based strictly on frequency of occurrence, these food groups did not *predominate in* 1997, *nor* were there important differences between rainbow and cutthroat (Figures 98 and 99). However, in 1979-80, terrestrials, mayflies, and caddis comprised 65 percent of the stomach volume in rainbow, versus 29 percent in cutthroat (WDG 1982). By 1997, mayflies had practically disappeared from the diet of both species, and terrestrials plus caddis summed to roughly 30 percent (Figure 108). The reported difference between rainbow and cutthroat in 1979-80 for these food groups seemed to disappear by 1986.)

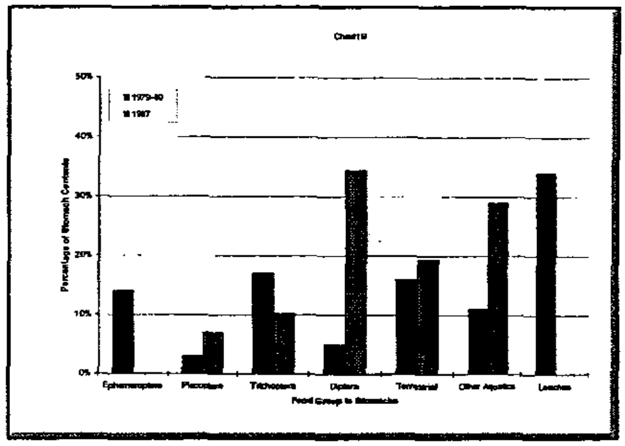


Figure 108. Average percentage (by volume) of each food group found in stomachs of trout sampled from Spada Lake during 1979-80 and 1997.

Volumetric percentages of each food group identified in stomachs did not vary substantially between Age 1, Age 2, or Age 3/Age 4 trout sampled in 1997 from Spada Lake (Figure 109). Prior to the stomach contents analysis, it was thought that small trout (Age 1) would depend more on Diptera,

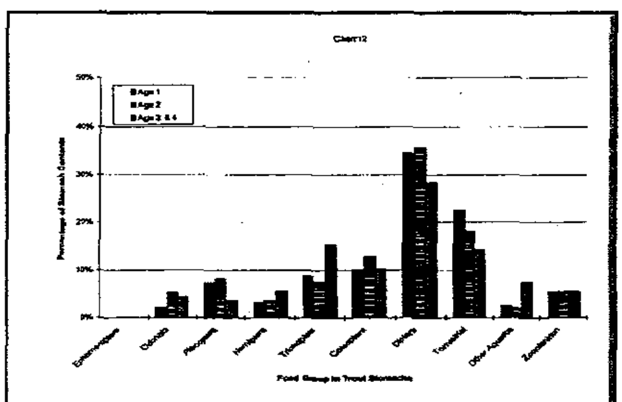


Figure 109. Average percentage (by volume) of each food group found in stomachs of cutthroat, rainbow, and hybrid trout (all species combined) sampled from Spada Lake during 1997.

zooplankton, and other small food items, compared to larger (older) trout. Similarly, it was thought that larger trout (Age 3 and Age 4) would predominately feed on terrestrial organisms, Odonata, and other large prey items. The uniform selection of different food items, regardless of prey size or trout age (Figure 109), was unexpected (especially Age 3 and Age 4 trout selectively preying on zooplankton).

The food group percentages plotted in Figure 109 are average values, and it was observed during stomach contents analyses that individual trout had highly variable diets. Many trout seemed to select a single prey type (e.g., aquatic snails or Odonata) and feed almost exclusively on one food type, ignoring other food items available in the reservoir.

Food group percentages in each trout stomach were plotted to see if there were any noticeable relationships between any food group and size of trout. There were no observable trends in these data. As an example of these graphs, Figures 110 through 112 show the relationships between trout length and stomach volume occupied by Coleoptera (aquatic beetles), terrestrial organisms, and zooplankton. There was a large amount of variability in consumption of all food types for all trout sizes sampled, and there were no apparent changes in overall trout diet with increases in trout length (age).

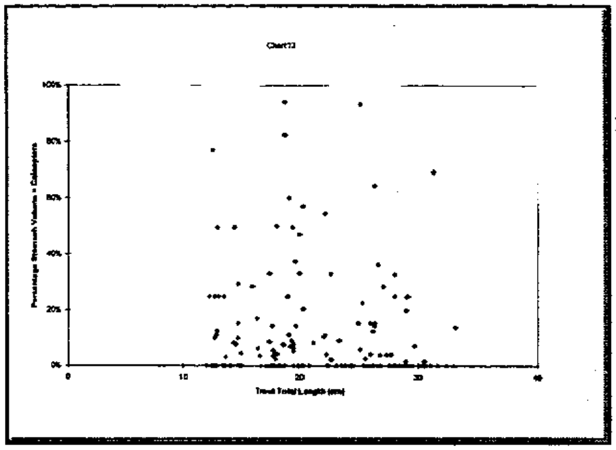


Figure 110. Relationship between trout length (all species) and stomach volume filled by Coleoptera.

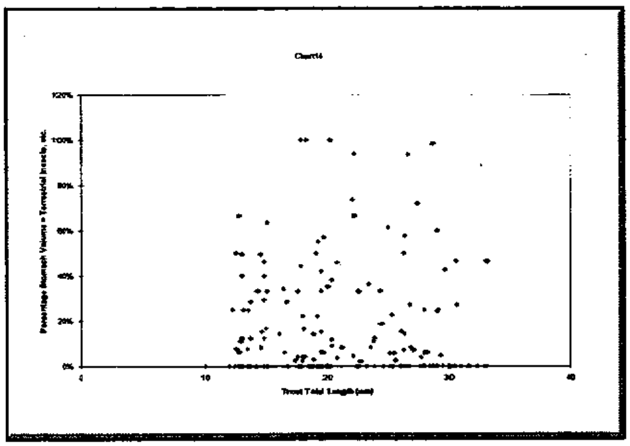


Figure 111. Relationship between trout length (all species) and stomach volume filled by terrestrial insects, spiders, centipedes, and worms.

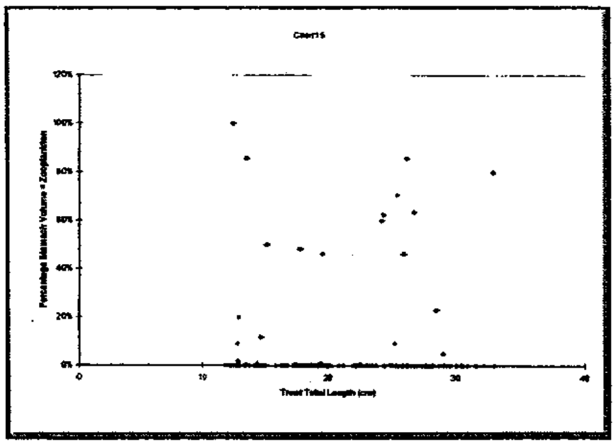


Figure 112. Relationship between trout length (all species) and stomach volume filled by zooplankton.

Selection for Zooplankton

Given the relative importance of dietary zooplankton as a vector for parasites (Trout Parasitism and Mortality), the 1997 stomach data were sorted into two age groupings, and the percentage of stomachs containing zooplankton noted for each group (these results are consistent with, and an adjunct to Figure 112):

	Age 1-2	Age 3-5	
Sample Size	123	37	
Percent of Stomachs with Some Zooplankton	12.2	10.8	Δ = 1.4%

There did not appear to be any important differences by age or species of trout, therefore, additional analysis pooled all ages and species.

Zooplankton was the only food item that was adequately monitored for abundance throughout the sampling period. A linear index of selection (Strauss 1979) for edible zooplankton was calculated on a monthly basis (Table 41) using the formula:

$$L = r_i - p_i$$

where r_i is the relative abundance of the prey item in the gut, and p_i is that prey item's relative abundance in the environment. This index has a value ranging from -1 to +1, with positive values indicating preference, and negative values indicating avoidance or inaccessibility. The expected value of L for random feeding is zero. It takes on extreme values only when the prey item is rare but consumed almost exclusively, or is very abundant but is rarely consumed (Strauss 1979). The latter case would apply if we had calculated L for *Holopedium*.

Table 41. Monthly indices of selection (Strauss' L) for *Daphnia* or *Epischura* in Spada Lake in 1997.

Sample (n): **Month**	**19** **May**	**22** **June**	**26** **July**	**28** **Aug**	**35** **Sept**	**30** **Oct**
Daphnia	-.01	-.02	-.56	-.34	+.45	-.60
Epischura	-.30	-.72	-.05	-.03	-.08	0.0

Epischura was never selected for by trout in Spada Lake (Table 41), but, in fact, was clearly selected against (avoided, or inaccessible, perhaps due to differing spatial distributions) during that plankter's June abundance increase. In the other months, its occurrence in the gut appeared to be almost random.

Daphnia first appeared in trout stomachs in July, therefore, the negative L values in May and June probably reflect low abundance (unavailability) in the environment. *Daphnia* appeared to be avoided in July, August, and October (Table 41). However, it was clearly selected for in the month of September. The negative *L* values in July may reflect an avoidance of *Daphnia* due to a relatively low abundance of mature individuals ≥ 1.2 or 1.3 mm in total length, or simply a relatively low abundance of *Daphnia* at that time (Figure 33). In August, when *Daphnia* peaked in abundance, its occurrence in the trout diet was well below random occurrence. Since only about one half of the *Daphnia* population was 1.2 mm or larger in August (Figure 34), its "avoidance" in that month may be due, in large part, to a relative scarcity of individuals large enough to elicit predation. The selection in September may be caused by a shift by rainbow to *Daphnia* 1.2 mm or larger, and/or a relative increase in *Daphnia* of this size in its overall population. Since *Daphnia* abundance had dropped substantially in September (Figure 33), we suspect that rainbow were actively preying on the larger remaining *Daphnia* individuals at that time. Future work (if any) should include more frequent measurements of *Daphnia* total length both in the lake population and in trout stomachs to explore this hypothesis.

Stage I v. Stage II Reservoir Effects

An important comparison was made between stomach content data from trout sampled in 1979-80 (WDG 1982) and 1997. The analysis required combining several food groups from the 1997 data to match categories for 1979-80 data. We observed that between–years variability in trout diets was much greater than between–species or between–ages variability; therefore, data for all ages of rainbow, cutthroat, and hybrid trout were combined within each sample period. This analysis was based on percent volume of each food type found in trout stomachs so did not include 1986 data which was limited to presence/absence of food types. The sample size for 1979-80 data was 126 trout, and sample size for 1997 data was 160. Sample periods and average trout lengths were similar between the studies.

The comparison of 1979-80 and 1997 trout stomach data for Spada Lake showed the following major differences between these years (Figure 108):

- Leeches constituted 34 percent (by volume) of trout diets in 1979-80, but were absent from the 1997 sample.
- Mayflies were a substantial component of trout diets in 1979-80, and only a minor part of trout diets in 1997.
- The percentage volume of Diptera (midges) in trout stomachs increased from 5 percent in 1979-80 to 34 percent in 1997.
- A substantial increase in the "Other Aquatics" category occurred from 1979-80 to 1997. The largest increase in this category was probably increased consumption of Coleoptera (aquatic beetles) in 1997.

Literature review conducted to enable interpretation of our findings yielded papers and reports that had a number of important consistencies. Chief among these is the fact that as reservoirs age, most exhibit dramatic reductions in invertebrate diversity, especially in the drawdown zone; certain invertebrates tend to be concentrated just below the point of maximal drawdown; and a few benthic invertebrate taxons tend to be favored, particularly the Tendipedidae and Chironomidae (Grimås 1961; Nilsson 1961; Paterson and Fernando 1969; Fillion 1967; Hunt and Jones 1972; Benson and Hudson 1975; Baxter 1977; Kaster and Jacobi 1978; Ploskey 1983). These research findings are supported by similar results in Pacific Northwest reservoirs (City of Seattle Dept. of Lighting 1973; Chisholm *et al.* 1989; May *et al.* 1988).

Leeches

The loss of leeches from the trout diet is truly unfortunate, as these organisms offer a substantially higher caloric reward than insects. We saw no leeches in the 160 stomachs examined, but did find four leeches in one Ekman grab taken at reservoir elevation 1426 in North Bay 1 (Secondary Production—Benthos; Results and Discussion). Thus, in at least some Spada Lake environments, low numbers of leeches still occur, even in the drawdown zone. More extensive benthos sampling in a multitude of habitat types around the reservoir may show that leeches are very restricted in distribution, and are generally in low abundance.

The comments made by Bradbury *et al.* (1980) place the current dietary situation in perspective: "A large number of leeches were found in cutthroat trout stomachs taken in April and early May. Leeches have been found only in the shallow water areas of the lake, indicating that cutthroat feed in these areas in the spring..."

Since leeches prefer an organic substrate, we would not expect their abundance or distribution to improve in the drawdown zone.

Mayflies

We have no definite explanation for the reduction in importance of Ephemeroptera. Since members of this Order occupy both lentic and lotic habitats, we would need additional detail on the species available in the reservoir, in the tributaries, and found in the trout diet to interpret these changes.

Studies of cutthroat diets in Montana reservoirs showed little or no utilization of mayflies. Seattle Dept. of Lighting (1973) lumped mayflies, stoneflies, and caddisflies into a classic "EPT" group, and did not differentiate mayflies alone. The EPT group constituted up to 44 percent of the diet of Ross Lake rainbow, particularly the larger fish. If mayflies are grouped with stoneflies and caddisflies in Spada Lake, results are still unclear due to varying changes seen among the three groups (e.g., Figure 99).

More detailed sampling of the available invertebrates in Spada Lake, along with concurrent, and more detailed trout dietary analysis, would be needed to determine whether this reduction was unique to 1997, and whether this group represents an important loss of caloric input.

Midges

The increased utilization of midges is exactly what one would expect due to reservoir aging, increased relative abundance of these species in the drawdown zone, and concurrent loss of alternate prey species.

Coleoptera

We also do not have a solid explanation for the increase in "Other aquatics", notably aquatic beetles. However, this occurrence may reflect the need for the trout to search more earnestly in the extreme shallow, littoral areas where these species are concentrated.

Oligochaetes

Although these small worms are very numerous in Spada Lake (Secondary Production—Benthos; Results and Discussion), they are completely absent in the trout diet. This is in complete agreement with other studies on area reservoirs (Seattle Dept. of Lighting 1973; May *et al.* 1988; Chisholm *et al.* 1989). They are apparently too small and/or concealed within the bottom sediment, and are essentially unavailable as a trout food resource. (However, they may be important in the brown bullhead diet, which would then have aquatic ecosystem energy flow implications. It may be that considerable bullhead biomass is being supported at least in part by oligochaetes, and these fish may compete for other food resources needed by the trout.)

Pisidium

Freshwater clams have never been an important food item for Spada Lake trout, but they continue to enter the diet at a very low level. Clams are not considered of very high nutritive value, and they are currently distributed almost entirely below the average annual drawdown limit (Table 17), which is a classic response by this organism to frequent exposure and wave action.

Conclusions

Invertebrate conditions in Spada Lake appear to have followed a classic path, where larger invertebrates which are commonly preferred food for trout are eliminated from the drawdown zone (e.g., *Gammarus*, Trichoptera, Odonata, Hirudinea). Some forms concentrate just below the lower drawdown limit (e.g., clams), and are either generally unavailable to the trout due to depth, or are of little nutritive value.

Due to a combination of low natural fertility and competition with *Holopedium*, preferred cladoceran species (*Daphnia*) are only suitably abundant and large to elicit foraging for a few weeks out of the entire year.

Zooplankton occurred more frequently in rainbow stomachs than either cutthroat or hybrids. The largest increase in frequency of occurrence for this food group since 1986 also occurred with rainbow. This is not surprising since rainbow are well known to be more planktivorous than cutthroat.

Although almost all trout sampled were obtaining some food between early April and mid–October 1997, internal fat levels were extremely low, as was relative weight for most trout age groups. Only about six percent of all stomachs sampled in 1997 were judged to be full; a running biweekly mean of degree of fullness was always less than 50 percent. Although we cannot make a direct comparison of stomach fullness (or other measure of satiation) with 1979-80 dietary conditions, the drop in trout relative weights seen between 1986 and 1997 (Tables 35, 36) suggests that available food conditions have changed for the worse during Stage II.

Zooplankton abundance at the current time in Stage II is about equivalent to that seen in Stage I (Secondary Production — Zooplankton: Results and Discussion; Density and Standing Crop), with a possible drop of 20 percent in *Bosmina* (not a trout dietary item). However, the methods used in 1979-80 do not provide data directly comparable to 1997. This is somewhat academic since zooplankton has never been shown to be a major dietary item in Spada Lake trout. This is unfortunate, and should be rectified if possible, since zooplankton is a major dietary component in all other reservoirs with healthy trout populations (particularly rainbow).

Because of problems with comparability of data and methods between 1979-80 and 1997, we could not show a definite change in benthic invertebrate conditions one way or the other between Stages I and II (Secondary Production — Benthos: Results and Discussion). Therefore, we also cannot make any inferences as to the possible cause of the observed changes in occurrence of benthic invertebrate food groups.

Trout diets are currently based predominantly on midge larvae or pupae, supplemented with terrestrial insects and stone– or caddisfly nymphs, in that order of importance. Zooplankton (cladocerans) is less important throughout the year, except it is somewhat more important for rainbow, particularly during the July-September period.

Future Dietary Study Needs

Two key questions were not adequately answered by our work in 1997. These are:

1) Have trout dietary preferences changed? and

2) Are trout competing for scarce food with brown bullheads?

Strictly, food preference should be measured using an index such as that described by Strauss (1979). This has been accepted as a standard method (Bowen 1996). Hybrid indices such as an Index of Relative Importance are not meaningful, and should not be used; Bowen (1996) urges a focus on real measures of abundance in the environment and in guts, plus an assessment of food nutritive value. The challenge is to adequately measure the relative abundance of all potential dietary groups in the environment (Strauss 1979). Thus, it is necessary to sample all potentially important food groups and locations. The methods used by May *et al.* (1988) and Chisholm *et al.* (1989) are excellent examples. The benthic invertebrate samples need to be greatly expanded in spatial distribution, and in frequency. Sedimentation areas at the mouths of the major tributaries should receive particular attention. Since emerging aquatic and terrestrial insects are obviously important dietary components, both need to be measured in and on the reservoir. From these invertebrate abundance and timing data it may be determined whether trout are truly selecting any group(s) preferentially, and at what time.

Competition for available food with brown bullheads may be gauged through use of Schoener's index of dietary overlap (1971). An even more robust approach is to couple this index with principal component analysis (Litvak and Hansell 1990). Acquisition of a solid brown bullhead population estimate, plus these quantitative dietary measures, are needed to understand the degree to which the trout are competing with bullheads for relatively scarce food resources.

Very large sample sizes are often needed to obtain much confidence in abundance estimates. Our sample database is available for use by others to determine sample sizes in future studies, if any.

The question of whether trout are obtaining adequate nutrition, or whether an inadequate diet is contributing to high annual mortality, particularly for older fish, requires more detail (accuracy) in both dietary study and estimation of trout abundance. With respect to diet, methods outlined by Bowen (1996) and/or Cortès (1997) must be used as needed, with particular emphasis on autochthonous inputs, measures of insect emergence, diet overlap between bullheads and trout, nutritional value of dietary components, and minimization of regurgitation during fish sampling.

If resources are available for ecosystem modeling, a bioenergetics approach such as outlined by Cailliet and Simenstad (1982) or Adams and Breck (1990) should be used.

Trout Spawning Period and Age at Maturity

Methods

A total of 623 trout collected in the Spada Lake basin in 1995-97 were examined for gonadal condition, and rated according to the following scale:

0 = gonad undeveloped; sex undetermined
1 = immature; gonad slightly developed; sex determinable
2 = maturing; gonads enlarged and maturing; ripe within a few months
3 = running ripe; gametes easily expressed with slight hand pressure
4 = spawned out; testis flaccid and drained; ovary granular and diminished

A partial list of the database, excluding fish with a maturity rating of 0 or 1, appears as Appendix Table 16.

Spawning Period

We did not regularly walk the tributaries to look for spawning fish. A few tributary surveys were conducted in 1979-80, and the authors of WDG (1982) state: "We determined that trout of Spada Lake and its tributaries spawn in late February, March, and early April." It was not at all clear from that report how this determination was made. However, if one assumes that most of the trout in the reservoir are descendants of native rainbow or cutthroat, then a spawning period similar to that of winter steelhead of the lower Sultan River would be expected, particularly for the rainbow.

Our in–lake collections occurred as late as November 14, 1997, and as early as April 11 in both 1995 and 1997. Many of these fish were collected from nets set just off the mouths of the spawning tributaries. We approximated the end point of the spawning period by noting the latest date when running ripe fish were taken in these areas. The beginning of the spawning period was not determined, although fish with near–ripe gonads were collected in mid–November 1997 (Appendix Table 16).

Age at Maturity

Reading of scales collected in 1986, 1995, 1996, and 1997 included recording of "spawning checks" on data forms. However, these data were considered highly subjective due to indistinct (or lacking) spawning checks on many mature trout, other irregularities on scales which appeared to be similar in appearance to typical "spawning checks," and reduced numbers of circuli and closer spacing of circuli (slower growth) as trout aged. These factors substantially reduced confidence in identification of spawning checks, and these data are not reported. An independent evaluation of the scale collection by an aging expert within WDFW resulted in a similar judgment (John Sneva, pers. comm. 1998). Review of the lab data sheets showed that "spawning checks" (and/or similar scale patterns) were recorded most often for Age 2+ and Age 3+ trout from Spada Lake. Pentec (1993) stated that the age of first spawning for trout from Spada Lake was 2–year–olds, with most trout spawning at Age 2+ or Age 3+. Data from trout collected in 1986 and 1995-97 are consistent with these observations.

While we could not identify trout length at first spawning from scales with confidence, we were quite confident of our ability to gauge sexual maturity from gonad condition, and make age determinations from scales collected from these fish. We assumed that all mature trout with a total age of 2.0 (life history designations of 2.0 or 1.1, mostly the latter) were maiden spawners. Trout with a total age of 3.0 were more problematic (life history designations of 2.1 or 1.2), but it seems likely that most, if not all of these were also initial spawners. We assumed that many mature trout with a total age of 4.0 were repeat spawners, and their lengths and ages were not used to estimate average length or age at maturity. Uncertainty regarding the proportion of Age 4 or Age 4+ trout which are maiden spawners is the largest source of error in our estimates of length or age at maturity. However, fish of this age probably represent only about four percent of the overall trout population (Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock).

The database of all trout which had been rated for a maturity of 3 was sorted, by species, yielding 30 cutthroat, 18 hybrids, and 22 rainbow. Four of the cutthroat, 1 of the hybrids, and 4 of the rainbow were either Age 4, or of a length which made them likely to be Age 4; these records were deleted from this analysis. Ten of the cutthroat, 9 of the hybrids, and 11 of the rainbow in this data set were not aged using scales. However, their lengths placed them well within the upper range of Age 3 fish, and were assumed to be Age 3 or younger. These unaged fish were assumed to be at initial maturity. This approach resulted in the data shown in Table 42.

Table 42. Total length (mm) of sexually mature trout collected in the spring in Spada Lake, 1995-97.

Species	Age	Total Length	Species	Age	Total Length	Species	Age	Total Length
CT		278	RB		190	HYB		230
CT		202	RB		300	HYB		237
CT		192	RB		200	HYB		246
CT		236	RB		209	HYB		255
CT		266	RB		231	HYB		271
CT		267	RB		288	HYB		187
CT		284	RB		180	HYB		192
CT		294	RB		185	HYB		188
CT		240	RB		187	HYB	1.2	315
CT		195	RB		192	HYB	2.0	202
CT	1.1	181	RB		208	HYB	1.2	235
CT	1.2	234	RB	1.2	181	HYB	1.2	263

Table 42 continued

Species	Age	Total Length	Species	Age	Total Length	Species	Age	Total Length
CT	1.2	246	RB	1.1	181	HYB	1.2	320
CT	2.1	249	RB	1.2	227	HYB	1.2	268
CT	1.2	257	RB	1.2	237	HYB	2.0	167
CT	1.2	265	RB	2.1	265	HYB	1.1	257
CT	1.2	273	RB	1.2	304	HYB	1.2	302
CT	1.2	296	RB	1.1	186			
CT	1.2	302						
CT	2.1	264						
CT	1.2	279						
CT	1.2	290						
CT	1.2	283						
CT	1.2	293						
CT	1.2	299						
CT	1.2	313						
Means:	2.94	261		2.71	220		2.67	243

Length at Maturity

The length frequency of all mature (rating = 3) trout collected in the spring of 1995, 1996, and 1997 was plotted by species to characterize the distribution.

Results and Discussion

Spawning Period

We confirmed that spawning occurs at least as early as late February in at least Williamson Creek. Seventeen redds were observed in the lower mile or so of Williamson Creek on 18 February 1998. (Of these, about four were in the drawdown zone.) The end of spawning may be as late as the first week in June, based on ripe fish collected near tributary mouths in 1997:

Species	Number Collected	Number Ripe	Percent Ripe	Date
Rainbow	12	3	25.0	9 May
	21	8	38.1	23 May
	48	3	6.3	6 June
	3	0	0.0	20 June
Cutthroat	7	4	57.1	9 May
	9	1	11.1	23 May
	10	0	0.0	6 June
	2	0	0.0	20 June

Species	Number Collected	Number Ripe	Percent Ripe	Date
Hybrids	8	4	50.0	9 May
	11	3	27.3	23 May
	14	1	7.1	6 June
	2	0	0.0	20 June

Age and Length at Maturity

All trout species collected in 1997 had a mean age at maturity less than 3.0, which is a reduction from past years:

Sample Year	Species	Mean Age	n
1979	Cutthroat	3.09	23
1980	Cutthroat	3.40	22
1992	Cutthroat	3.02	85
1997	Cutthroat	2.94	16
1992	Rainbow	3.18	39
1997	Rainbow	2.71	7
1997	Hybrids	2.67	9

The slight reduction in mean age seen in cutthroat is probably not significant; most fish still mature at Age 3. The greater proportion of rainbow and hybrids maturing at Age 2 is much more worrisome, as this translates into reduced fecundities and potential recruitment. What is more, the proportion of the fish population as hybrids has increased to an average of 27.6 percent in recent years (Fish Relative Abundance, Length Frequency, and Sex Ratio: Results and Discussion, and 1992 and 1995 creel survey data). The mean age reduction seen in rainbow and hybrids may be due to the small sample sizes, which, again, underscores the need to develop ways to either truth spawning checks on scales or collect larger samples of known spawners.

The lengths of ripe trout collected in the spring in Spada Lake are shown in Figures 113 through 115. Breaks in the distributions reflect Age 2 and Age 3 fish, with 17 through 21 cm fish generally being Age 2. Arithmetic mean lengths and age at maturity, by species, are provided in Table 42. Mean lengths ranged from a high of 26.1 cm for cutthroat to a low of 22.0 cm for rainbow. Hybrids had an intermediate total length value of 24.3 cm.

It is important to note that these lengths are from fish which were presumed to be ready to ascend the tributaries to spawn, i.e., their total lengths were essentially equivalent to length at spawning which would otherwise be determined from scale spawning checks. There are no data from past years which were collected in this manner (ripe fish in the spring) which would allow direct, historic comparisons. Length at spawning in earlier years was reported by Pentec (1993) based on perceived spawning checks on historic scale collections. We are not confident that those determinations were accurate.

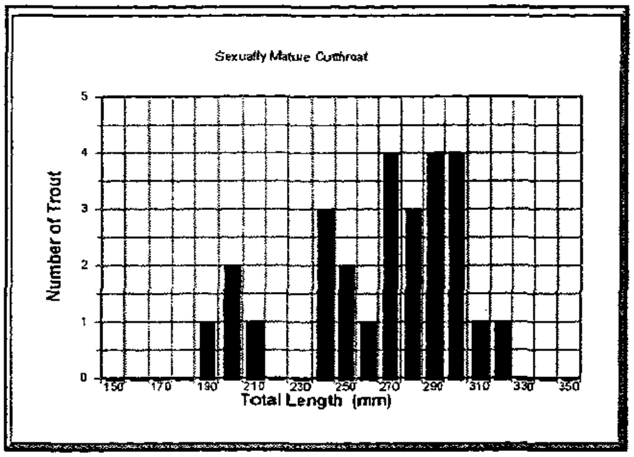


Figure 113. Length frequency of sexually mature cutthroat from Spada Lake in 1997.

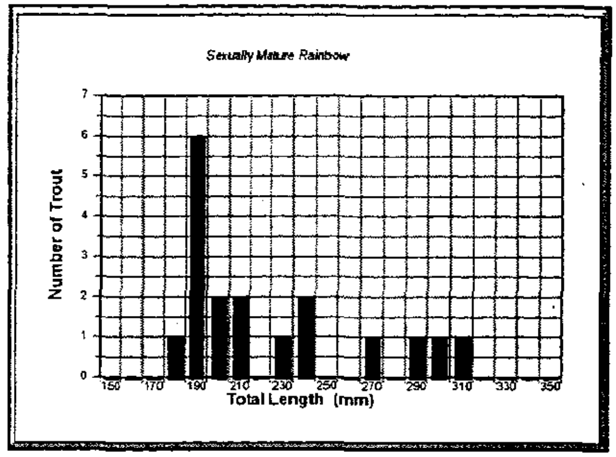


Figure 114. Length frequency of sexually mature rainbow from Spada Lake in 1997.

Because of differences in the methods used to estimate mean length at maturity, we cannot state, with certainty, whether there has been a significant change in this measure between Stage I and Stage II. The available data, based on a limited sample of ripe fish (rather than the preferred method of field truthed scale analysis), when compared with data found in Table 18 of Pentec (1993), suggests either no change, or an increase in the mean length at first maturity.

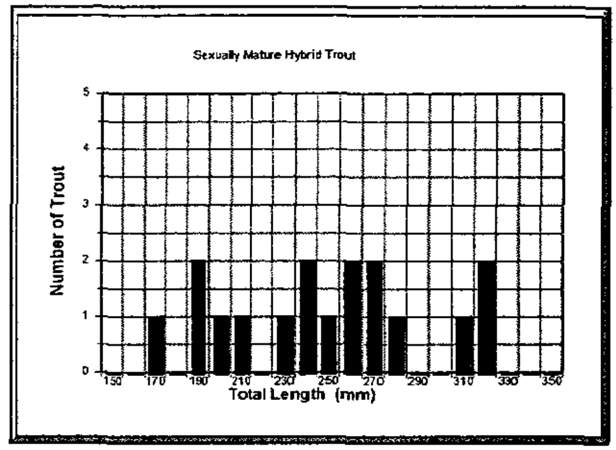


Figure 115. Length frequency of sexually mature hybrid trout in Spada Lake, 1997.

The current (1998) 12" (305 mm) minimum length for harvest of trout from Spada Lake clearly protects nearly all first–time spawners.

Conclusions

The spawning period of trout in Spada Lake is approximately mid–February through the first week in June. Cutthroat spawning may end a week or two earlier than rainbow or hybrid trout. These approximations should be verified by actual foot surveys and fish collections in the spawning streams.

Most cutthroat mature at Age 3. A majority of rainbow also mature at Age 3, but their mean age at maturity was 2.7 in 1997. There appears to have been a reduction in the mean age at maturity, particularly for rainbow and hybrids. The sample size leading to this conclusion was small, but if real, this reduction would translate into a somewhat smaller potential egg deposition and resultant fry recruitment.

Changes in length at first maturity in 1997 versus past years could not be demonstrated, largely due to differences in the methods used to document age and length at spawning. The mean length of ripe cutthroat collected off tributary mouths in the spring was 26.1 cm; a similarly–collected value for rainbow was 22.0 cm.

Trout Parasitism and Mortality

One of the principal concerns prompting our work in 1995-97 was the apparent lack of trout over 12" in the Spada Lake sport fishery. The causes of this lack of older fish could include angler overharvest, a natural reduction in growth rates due to reservoir aging, inaccessibility of older trout due to behavioral differences, mortality due to parasitism, or some combination of these factors.

Earlier investigators (WDG 1982) had noted "the presence of a cestode parasite in many rainbow collected from Spada Lake" in 1979-80. Pentec (1993) speculated that "high" parasitism by *Diphyllobothrium* could be a cause of what they perceived to be size–selective mortality in older rainbow. The Pentec report authors discounted the fishery as a source of size–selective mortality since it was not perceived in cutthroat scale data, only rainbow, and both trout species were deemed equally vulnerable to the fishery. They further noted that "cutthroat were relatively free of this parasite", and opined that "Spada Lake rainbow are destined for a relatively short life and are less suited to Spada Lake than the cutthroat trout."

Based on this information and opinion, we set out to determine the relative infection intensity of *Diphyllobothrium* in cutthroat versus rainbow. We also wished to know more about the timing of the infection, and whether it is a significant source of mortality to either trout species.

Methods

Trout were collected from Spada Lake for preliminary parasitism evaluation by gillnetting in April 1995 and October 1996. Eighteen trout taken on the latter date were necropsied for a total count of *Diphyllobothrium* plerocercoids (as well as other parasites) in order to assess the condition of the trout population as it entered the winter.

In 1997, trout samples were collected from Spada Lake approximately biweekly from April 11 through November 14. From 15 to 99 trout were taken by gillnet on each sample date from a variety of locations around the reservoir (Fish Relative Abundance, Length Frequency, and Sex Ratio):

Date	Total Trout Sample	Total Trout Necropsied
11 Apr	54	54
25 Apr	29	28
9 May	27	26
23 May	41	41
6 June	73	32
21 June	59	35
2 July	29	29
17 July	53	40
5 Aug	19	18
19 Aug	15	15
9 Sept	31	30
24 Sept	43	43
10 Oct	99	40
14 Nov	29	29

Each fish sample's location on the lake and in the water column was noted. All trout were kept cool and shaded when removed from the gear, until they were dissected (fish were kept on ice in the warmer months). All trout inspected for parasites were weighed and measured as previously described for the general fish biological workup (Fish Relative Abundance, Length Frequency, and Sex Ratio: Methods and Trout Age, Growth, and Condition: Methods). The amount of visceral fat on the stomach, pyloric caecae, and integuments was observed and recorded for each trout (See Fish Relative Abundance: Methods).

Stomachs were taken from many of the trout necropsied for parasite loads in order to look for correlations between zooplankton consumption and cestode infection (Trout Food Habits).

Between 15 and 54 trout per biweekly outing were given a detailed necropsy to enumerate all parasites. Individual plerocercoids were teased from their cysts, or from the stomach or intestine wall using fine forceps under a low power magnifier lamp. A sub-sample of larger plerocercoids were retained in alcohol for later taxonomic examination. All caecae and stomach/intestine surfaces and folds were carefully teased apart and examined. Care was taken to assure that any plerocercoids that had broken out of their cysts and were ambulatory in the coelom were accounted for. The number of trout tapeworms (*Proteocephalus salmonidicola*) present in the caecae were grossly enumerated per the scheme described in Fish Relative Abundance, Length Frequency, and Sex Ratio: Methods. All *Eubothrium salvelini* tapeworms were counted individually, as were any occasional free nematodes. No other macroparasites were seen.

Parasite prevalence, infection intensity, and plerocercoid dispersion were calculated as necessary to compare these measures among the trout species, and for varying time frames and trout life histories. Prevalence is the number of host species infected divided by the number of hosts examined, expressed as a percentage; infection intensity is the number of plerocercoids in each infected host (Margolis *et al.* 1982); and dispersion is the variance to mean ratio (s^2/x) of parasite numbers/host (Anderson and Gordon (1982)). See the latter paper (p. 375) for an excellent explanation of dispersion.

Results and Discussion

Necropsies

The cestode plerocercoids were tentatively identified as *Diphyllobothrium ditremum* (Creplin 1825) using descriptions by Andersen *et al.* (1987) and Andersen and Gibson (1989). No plerocercoid from Spada Lake trout exceeded 20 mm in length. Two other adult cestodes were found in the fish. *Proteocephalus salmonidicola* (commonly called trout tapeworm) were common inside the pyloric caecae and lower intestine; an occasional *Eubothrium salvelini* was found in the same location.

The gross pathology of the fish harboring *D. ditremum* plerocercoids was similar to that described by Sharp *et al.* (1989), and Weiland and Meyers (1989). One notable exception to the latter paper is that plerocercoids were seldom found in the livers of trout from Spada Lake. Visceral adhesions were not common, but did occur occasionally.

Infection Prevalence

We analyzed the plerocercoid data under the basic premise that all trout obtained their infections by consuming procercoid–bearing copepods *in the reservoir* (Duguid and Sheppard 1944; Hickey and Harris 1947; Thomas 1947; Meyer and Vik 1963; Vik 1964; Freeman and Thompson 1969; Johnson 1975; Henricson 1978; Curtis 1984; Berube and Curtis 1986; Amundsen and Kristoffersen 1990; Knudsen and Klemetsen 1994; Pasternak *et al.* 1995). We assumed that the probability of infection, or reinfection, increases with the length of reservoir residence time, and that all trout species spend little or no time in the tributaries once they enter the reservoir environment. Therefore, we stratified the plerocercoid count data based on trout life history determined from scale analysis.

(Some infections by some species of *Diphyllobothrium* can be acquired by consumption of fish which contain viable procercoid–bearing copepods in their stomachs—commonly threespine sticklebacks (Curtis 1984). We are confident this mode of transmission does not occur to any appreciable degree in Spada Lake. No fish or fish remains were reliably identified in any of 160 stomachs examined in 1997, nor in any of hundreds of stomachs sampled in earlier studies on the reservoir. Based on experimental feeding of infected char to rainbow, Halvorsen and Wissler (1973) concluded that *D. ditremum* could not use paratenic hosts to any significant extent.)

Figures 116 through 119 plot the prevalence of *Diphyllobothrium* in each species of trout by length of reservoir residence time, beginning with new immigrants (up to one year in the lake). For the first two years of reservoir rearing, cutthroat had a consistently equal or lower prevalence than rainbow or hybrid trout (with one minor exception in the fall for 2–year fish—Figure 117). Two or more years of lake rearing is associated mainly with trout of Age 3 or older (Trout Age, Growth, and Condition: Methods), therefore, Figures 116 and 117 represent the bulk of the trout in the reservoir.

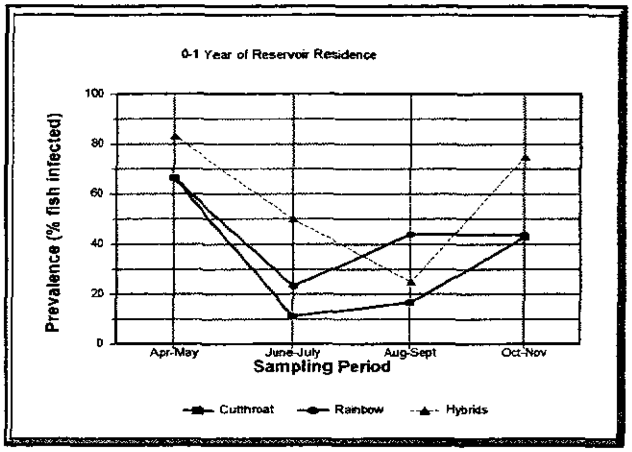


Figure 116. Seasonal prevalence of *Diphyllobothrium* in trout with less than one year of residence in Spada Lake, 1997 sampling season.

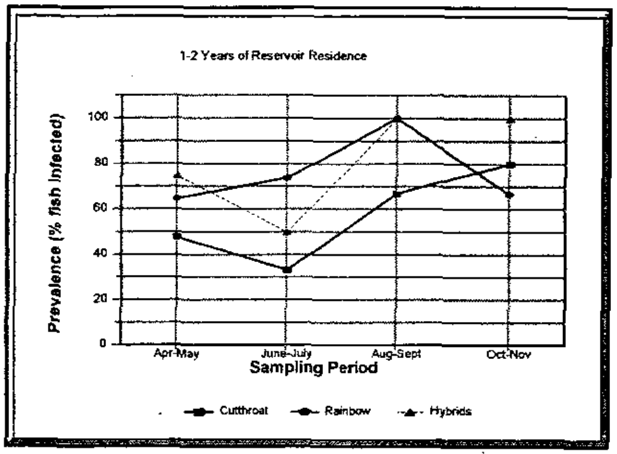


Figure 117. Seasonal prevalence of *Diphyllobothrium* in trout with 1 to 2 years of residence in Spada Lake, 1997 sampling season.

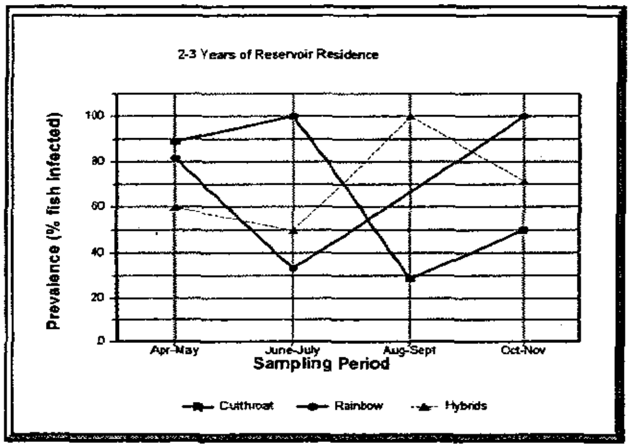


Figure 118. Seasonal prevalence of *Diphyllobothrium* in trout with 2 to 3 years of residence in Spada Lake, 1997 sampling season.

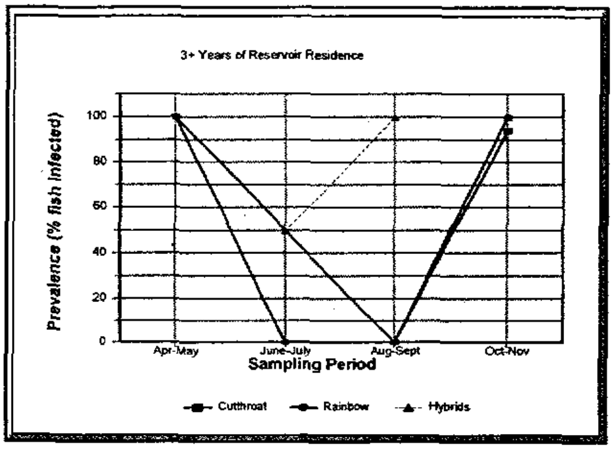


Figure 119. Seasonal prevalence of *Diphyllobothrium* in trout with more than three years of residence in Spada Lake, 1997 sampling season.

Although the pattern is not wholly consistent among the three trout species, prevalence often drops to some degree (sharply for first–year residents) between April-May and June-July (Figures 116 through 119). In the case of first–year reservoir residents, the drop in June-July is probably due, perhaps in large part, to immigration of uninfected fish from the tributaries (Figure 116). For trout in their second or greater year of reservoir residence, there is a less consistent pattern, and the cause/s of reduced prevalence is largely a matter of speculation. One possible cause of reduced prevalence in early summer is mortality of fish bearing moderately heavy parasite burdens in the spring due to maturation and emergence of plerocercoids from their cysts as the reservoir warms in May-June (Becker and Brunson 1967). This did not seem to be the case for rainbow (Figure 117). Becker and Brunson (1967) noted an apparent higher susceptibility in cutthroat, and this is suggested by the reduced prevalence in June-July for that species (and hybrids). Cestode prevalence in second–year lake residents generally built to seasonal highs of 68 to 100 percent by late summer or early fall.

Trends are no longer apparent for fish which have resided in the lake for more than two years (Figures 118 and 119), mainly due to low sample sizes and high variability in plerocercoid counts. In general, cutthroat or rainbow which have survived through two full years of reservoir rearing enter their third year with prevalence levels of 80 to 100 percent. Again, drops in prevalence in mid–summer may represent mortality due to lake warming and emergence of encysted worms. The three zero values for June-July and August-September in Figure 119 represent single samples for aged fish, i.e., very low, and probably unrepresentative samples.

Near–complete prevalence of the cestode in fish which are Age 4 or older is not unexpected; it is common for older animals, or hosts which have been exposed to a parasite, to accommodate a low to moderate parasite load (heterogeneity in host susceptibility to infection or mortality; Anderson and Gordon 1982).

By the October-November sampling period, virtually all trout species, regardless of length of reservoir residence, had *Diphyllobothrium* prevalence levels of 50 percent or more.

The shape of the prevalence (and infection intensity) curves presumably reflects the timing of infection, i.e., when the trout are feeding on procercoid–bearing copepods. Cyclopoid copepods are generally listed as the intermediate host for *Diphyllobothrium* in all of the literature which we reviewed, with the exception of Knudsen and Klemetsen (1994) who stated that "all copepod species are considered to be first intermediate hosts of *Diphyllobothrium* spp." They gave no citations or data in support of that statement. (There is no evidence, and little likelihood that the only other mechanism of infection, piscivory on small fish with viable infected copepods in their stomachs, ever occurs in Spada Lake.) Although we only documented selection for zooplankton (daphnids) in September (Table 41, Trout Food Habits: Results and Discussion), the plerocercoid prevalence and infection upswings in the late summer or fall (Figures 116 and 117) would correlate with the larger pulses of *Daphnia* and *Epischura* in August and early September, respectively (Figures 33 and 34, Secondary Production—Zooplankton: Results and Discussion).

Given the water temperatures in August and September, ingested procercoids could metamorphose into a plerocercoid relatively rapidly (Becker and Brunson 1967). Thomas (1947) experimentally fed *Diaptomus* infected with procercoids to 48 guppies; three fish dissected five days later were "found to contain plerocercoids in the stomach walls and mesenteries." The September increase in prevalence and infection intensity shows clearly in a monthly summary figure for all first–year resident trout combined (Figure 124).

Infection Intensity

The pattern of infection intensity over the course of the sampling season varied significantly for trout with less than a full year of reservoir residence when compared with the others (Figures 120 through 123).

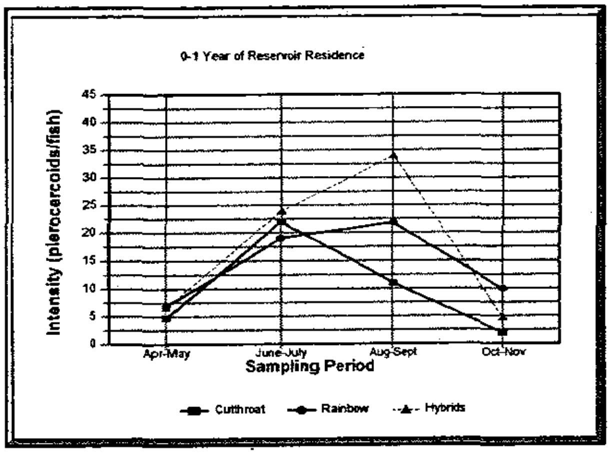


Figure 120. Seasonal intensity of *Diphyllobothrium* in trout with less than one year of residence in Spada Lake, 1997 sampling season.

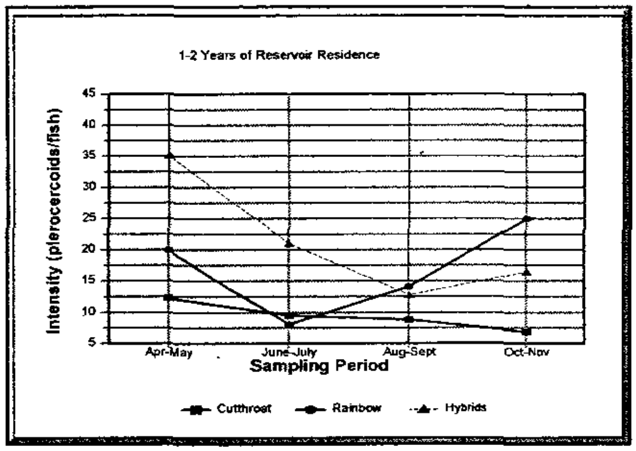


Figure 121. Seasonal intensity of *Diphyllobothrium* in trout with 1 to 2 years of residence in Spada Lake, 1997 sampling season.

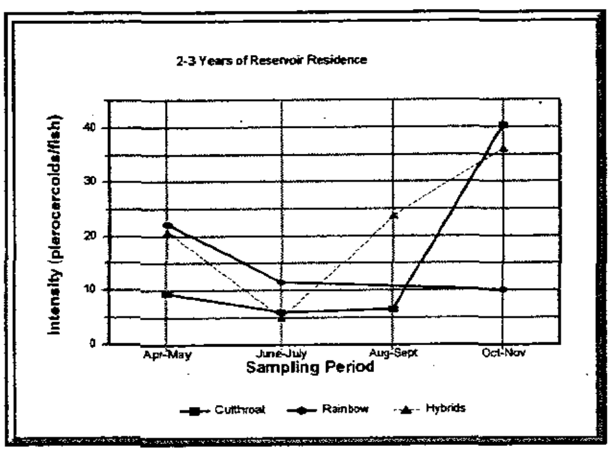


Figure 122. Seasonal intensity of *Diphyllobothrium* in trout with 2 to 3 years of residence in Spada Lake, 1997 sampling season.

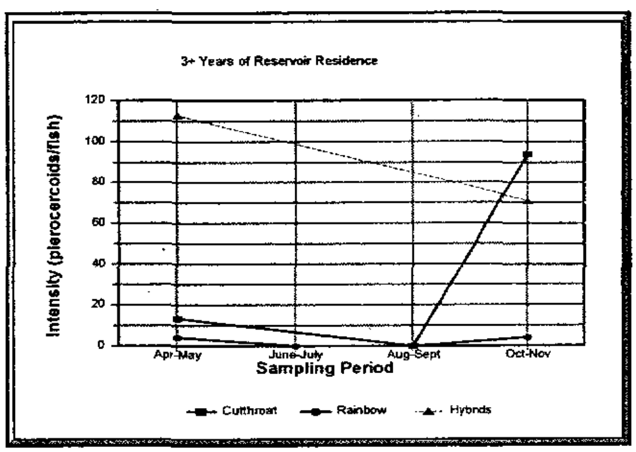


Figure 123. Seasonal intensity of *Diphyllobothrium* in trout with more than 3 years of residence in Spada Lake, 1997 sampling season.

Trout spending their first year in the lake built plerocercoid numbers through July (or August-September for hybrids), then either leveled, or dropped going into the fall (Figure 120). Since the trout do not shed their plerocercoids, a reduced intensity in the sample represents mortality in the host population (Lopukhina *et al.* 1973; Henricson 1978; Anderson and Gordon 1982). Figure 120 suggests that cutthroat may suffer more rapid mortality, i.e., succumb at a lower infection intensity, than rainbow or hybrids. However, all three species exhibited a sharp decline in intensity by the October-November period; this decline may represent mortality.

We believe that the late summer to fall drop in intensity in first–year lake residents is due to mortality for two reasons. First, hosts with no prior exposure to a parasite commonly experience greater mortality than older, longer–exposed individuals. In our case, new lake immigrants are, for the most part, also small fish, and plerocercoid damage may be proportionately greater for each larva present in smaller fish (Hoffman and Dunbar 1961; Becker and Brunson 1967). Second, *Diphyllobothrium* burdens of 20 to 30 or more are adequate to cause mortality in salmonids (Weiland and Meyers 1989), particularly those in poor condition (Knudsen and Klemetsen 1994).

The general pattern of infection intensity for fish in their second or third year of lake rearing (Figures 121 and 122) was survival through the winter with between 10 and 35 plerocercoids, followed by two to four months of mortality, then a rebuilding of parasite numbers in the late summer or fall. The relatively low infection intensity seen in the cutthroat in April-May may again reflect a somewhat lower tolerance to the parasite. (Dietary analysis failed to show important differences in diet between the three trouts—Trout Food Habits: Results and Discussion). Cutthroat were also exceptional in that they showed just a gradual decline in infection over the course of the season for fish in their second year of lake residence, and no upswing in October-November. One possible explanation for this is a lack of late summer feeding on zooplankton by this age group of cutthroat.

An observation regarding cutthroat infection *intensity* that is consistent with *prevalence* was the fact that cutthroat were either equivalent to rainbow or hybrids, or had lower infection intensities in the first two years of lake rearing (Figures 120 and 121). (The largest, oldest trout collected in 1997 was an Age 6+, 57 cm cutthroat that was carrying only three plerocercoids.)

Infection intensity sample sizes are very small for fish with more than three years of lake residence (Figure 123), and are shown for completeness only.

Figure 124 presents a more detailed, monthly plot of both intensity and prevalence for all trout combined which were experiencing their first year of reservoir residence. This figure clearly shows the level of trout vulnerability to *Diphyllobothrium* infection in Spada Lake. (Although we did not measure and record plerocercoid total lengths, recent infections were obvious in our dissections, with the plerocercoids of many of the newly recruited trout emerging as very tiny worms in the outer stomach musculature or serosa.)

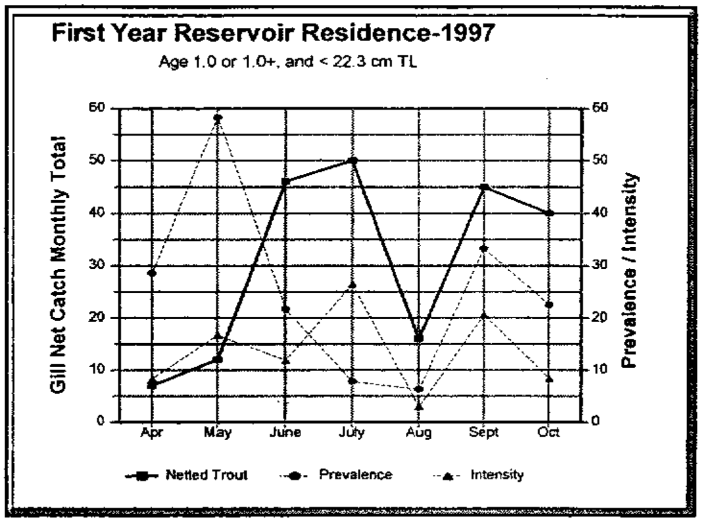


Figure 124. Relationship between entry of trout from tributaries of Spada Lake and the prevalence and intensity of *Diphyllobothrium* infection in 1997.

Immigrant Age 1.0 trout from the tributaries became numerous in our gillnet sets in early June, with total catches jumping from less than 10 per month to 40 or 50 (Figure 124). (August was an exception, with fish apparently moving offshore, away from most of our gear.) The prevalence of the parasite in the immigrant trout population peaked rapidly at about 58 percent in May, and probably reflects feeding on either littoral cyclopoid copepods (e.g., *Microcyclops*), or on *Epischura*. Prevalence declined steadily to a low of about 7 percent in August (which may be partly an artifact of the low sample size of 16 fish), then rebounded to 34 percent in September. The secondary peak may also be related to feeding on the late summer pulse of *Epischura*, or other copepod vector/s. Infection intensity levels for these new immigrants followed a roughly similar pattern, but with initial peak intensity lagging behind peak prevalence by a month or two.

General Discussion of *Diphyllobothrium* Dynamics

We used the conceptual model of Anderson and Gordon (1982) to interpret the distributional patterns of infection intensity and dispersion (the variance of parasite numbers/host divided by its mean), for all trout combined, collected from Spada Lake in 1997. This model predicts that dispersion will equal unity if parasites are acquired in a random fashion. Factors which will cause dispersion to <u>increase</u> from unity include heterogeneity in host susceptibility to infection, direct parasite reproduction within the host, or heterogeneity in the ability of hosts to kill or neutralize parasites, whether by immunological or other types of responses. Heterogeneity examples include a greater ability of some fish species to tolerate *Diphyllobothrium*, the ability of older fish to tolerate a heavier parasite burden than younger fish, or feeding behaviors which reduce the probability of acquiring an infection from copepods. Factors which will cause dispersion to <u>decrease</u> from unity include parasite mortality, density–dependent processes, or parasite–induced host mortality (with the host death rate positively correlated with the parasite burden) (Anderson and Gordon 1982).

Of these factors, those likely to be relevant to Spada Lake include the likelihood that older trout are either more resistant to new infection, or can tolerate a greater parasite burden and associated parasite–induced mortality than younger fish. These would tend to work against each other to an unknown degree.

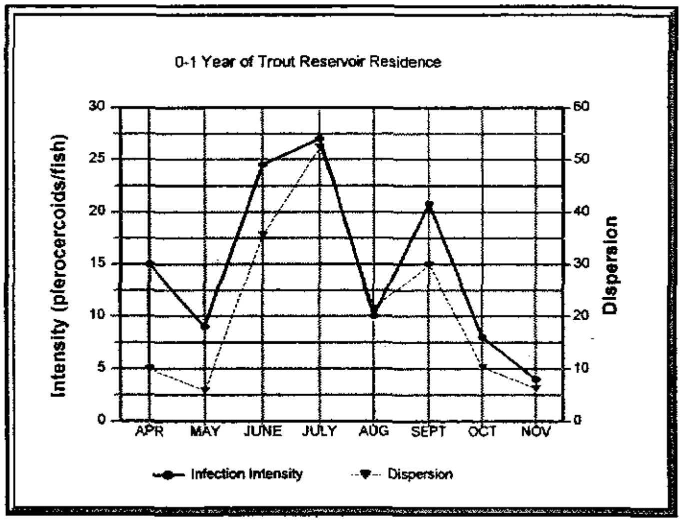


Figure 125. Intensity and dispersion of *Diphyllobothrium* infection in trout with less than one year of residence in Spada Lake in 1997.

Parasite–induced host mortality tends to produce curved, or domed age–intensity curves with a descending right–hand limb. Figures 120 and 125 are classic examples (conforming closely to Anderson and Gordon's (1982) model), and strongly suggest that all three trout species suffer appreciable mortality from *Diphyllobothrium* in their first year of residence in Spada Lake.

Domed age–intensity curves, concomitant with a decline in dispersion of parasites in those hosts exposed to the parasite for a longer time period, can provide evidence of host mortality where the rate of mortality is positively correlated with the parasite burden (Anderson and Gordon 1982). Figure 125 seems to meet these criteria well for trout experiencing their first year of rearing in Spada Lake. (Note that these trout were not all of the same total age, or year class.) The secondary peak in intensity (and to a lesser degree in dispersion) in September may reflect a second period of planktivory, with the first occurring in June.

If, however, uninfected trout recruit to the reservoir over the course of the summer, rather than predominantly in the spring, a decline in intensity, and probably also dispersion, would be expected. May *et al.* (1988) reported that 99 percent of all cutthroat immigration to Hungry Horse Reservoir (MT) from Hungry Horse Creek occurred in a six–week period from mid–June through July. Since we first netted Age 1.0 fish in early May, immigration may be a month or so earlier in this system, which, if similar to Hungry Horse Creek, would put most of the immigrants into Spada by the end of June. Actual trapping on Williamson Creek, Elk Creek, etc. is highly recommended to complete our understanding of trout life history in this system.

One way to test the hypothesis that the observed drop in infection intensity is not due to immigration of uninfected fish, would be to track marked downstream migrants after they enter the reservoir environment. Support for the interpretation that mortality occurs in the first–year residents comes from a general drop in dispersion in second–year residents from June through

November (Figure 126) which, if scale analysis is correct, should not be subject to the error of uninfected trout immigration.

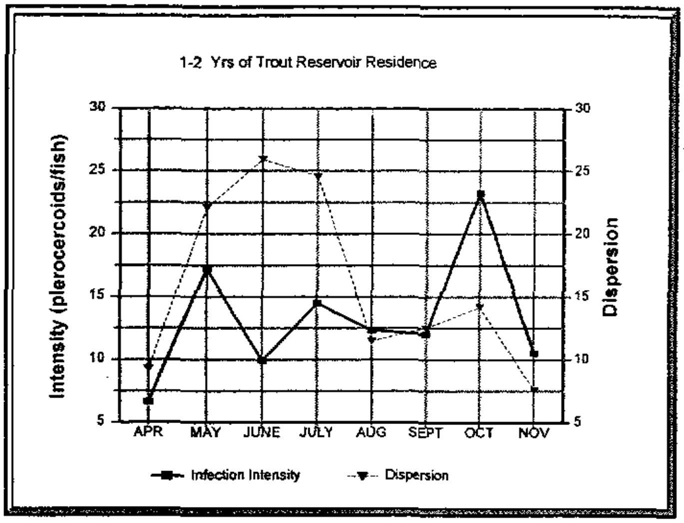


Figure 126. Intensity and dispersion of *Diphyllobothrium* infection in trout with 1 to 2 years of residence in Spada Lake in 1997.

The pattern in first–year residents is less–well demonstrated for fish in their second year of reservoir rearing (Figure 126). For these, infection intensity tended to build to a peak in October, then returned to an approximate season–long average of 10 to 12 plerocercoids/fish going into the winter. Dispersion, however, peaked in June, then fell more or less continually through mid–November. The decline in dispersion in Figure 126 may reflect actual mortality, but we never saw any empirical evidence of it in or on the lake (nor would we ever expect to, given its size, lack of gulls and other scavengers, etc.).

The shape of the intensity/dispersion curves for the oldest trout (Figure 127) was unlike that seen for any of the other groups in relation to season. However, dispersion was closely correlated with infection intensity, as was seen in the first–year lake residents (Figure 125). We interpret Figure 127 as follows. Larger, older trout did not feed on zooplankton in the spring, therefore, did not show an increase in infection intensity in June-July. As the lake warmed, some older trout succumbed to tissue damage caused by parasite activity, hence dispersion and infection intensity waned through August. Some older fish utilized the late summer zooplankton bloom (presumably *Epischura;* see Trout Food Habits: Results and Discussion, and below), resulting in increased infection levels in the fall.

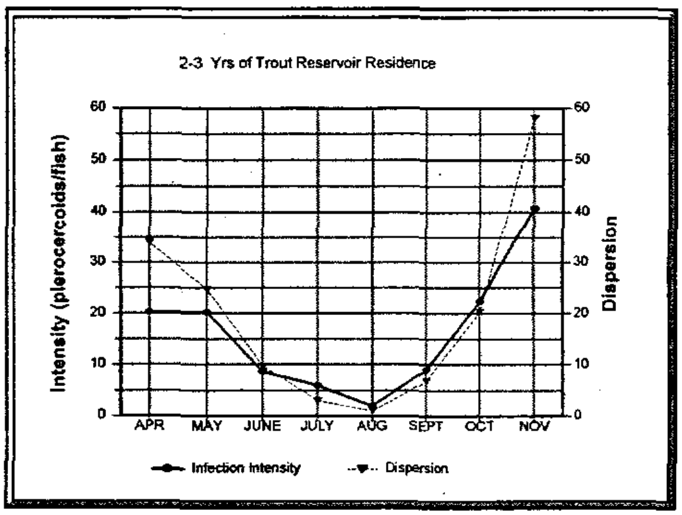


Figure 127. Intensity and dispersion of *Diphyllobothrium* infection in trout with 2 to 3 years of residence in Spada Lake in 1997.

Overall, interpretation of these statistics is complicated by the fact that decreases in infection intensity and dispersion in older fish can be associated with factors such as changes in feeding behavior or habitat utilization, or the acquisition of acquired immunity. Also, chance effects can have a major effect on age–related patterns in these parameters when the size of the cohort falls to a low level, which is definitely the case with older trout in Spada Lake. In other words, declines in intensity or dispersion can be caused by small sample sizes (and they are small for Figure 127), which themselves may be a consequence of the relative scarcity of older hosts in the population (Anderson and Gordon 1982).

Anderson and Gordon (1982) emphasize that in general, it is difficult to detect the presence of parasite–induced host mortality from field data, but that *Diphyllobothrium*/trout associations may lend themselves to this type of analysis better than most. Although we saw no direct evidence of mortality due to *Diphyllobothrium* (unlike that reported in Becker and Brunson 1967), we believe the patterns of Figures 125 and 126 reflect late summer mortality in fish spending their first or second year in the lake, particularly their first. The high average counts of plerocercoids and increasing dispersion shown in Figure 127 reflect the ability of the older trout to tolerate plerocercoid counts of up to 113 and 185 (Appendix Table 17).

Evaluation of Putative Parasite–induced Mortality

There is some controversy in the literature as to whether the smaller *D. ditremum* causes mortality in salmonids when compared with *D. dendriticum* (the latter known earlier as various species, including *cordiceps, sebago*, and *ursi* (Andersen *et al.* 1987)). Henricson (1977) categorically states that "there are no reliable reports of *D. ditremum* causing a high mortality in fish." However, his conclusion was felt by others to be confounded by the high incidence of the much larger, much more damaging plerocercoids of *D. dendriticum* in his heavily–parasitized char. The two cestodes are commonly found together in the same fish in many lake systems. *D. ditremum* does not have as great a power of migration through host tissues as *D. dendriticum* (Halvorsen and Andersen 1984). Nevertheless, in lakes where *D. ditremum* is the sole cestode species, or greatly outnumbers *D. dendriticum*, trout or char mortality has been documented (Becker and Brunson 1967; Halvorsen and Andersen 1984).

Weiland and Meyers (1989) clearly showed that indeed, *D. ditremum* can cause mortality, at least in coho (*Oncorhynchus kisutch*). The average number of worms causing ascites and mortality in their study ranged from 28 to 32, versus 11 in subclinically parasitized fish (Weiland 1988). Our figures generally plot mean plerocercoid levels; counts of 30 or more in individual fish were not at all uncommon (Appendix Table 17).

Of great practical significance in our case are the observations and citations of Knudsen and Klemetsen (1994) who compared char mortality rates in Lake Takvatn, Norway. Mortality was high in the early 1980s when "the charr population was stunted and in poor condition", but following a stock depletion program, char densities were reduced which improved their growth and condition, and resulted in a "general impression from (their late 1980s) results that host mortality caused by the three parasite species in Takvatn is low." They go on to state that "charr in better physiological condition may be better able to tolerate higher densities of parasites."

Since trout in Spada Lake grow quite slowly and are in poor condition (Trout Age, Growth, and Condition), we believe our data on infection intensity and dispersion are indirect evidence of mortality.

Of the studies we reviewed on *Diphyllobothrium* population dynamics which were published after 1976, most associated declines in infection intensity and dispersion with host mortality, but no authors used these statistics to estimate mortality in a direct quantitative way. A common presumption is that short–term declines in prevalence or intensity of infection reflect mortality since cestode larvae are long–lived in trout hosts (Lopukhina *et al.* 1973). This assumes that infected and non–infected hosts are sampled with equal probability. We feel relatively safe in making that assumption for trout in their second or greater year of lake residence, but the observed infection rate of first–year residents could be affected by immigration of clean fish from the tributaries over the course of the summer.

Earlier we estimated total annual mortality at 45.2 percent, and an instantaneous rate of natural mortality of .601 (Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock). However, these were based on overall trout community age composition from scale data, and are not apportioned to specific trout species or age groups. Both would be necessary to determine in a more quantitative way whether rainbow or cutthroat exhibited differential mortality to the parasite in their first year of lake residence.

Unfortunately, we are not aware of any method to directly estimate mortality due to *Diphyllobothrium* in a large open lake system. A test application of the method of Lopukhina *et al.* (1973) quickly revealed violation of at least one of two critical assumptions, viz.: the trout population being sampled does not experience immigration or recruitment of uninfected individuals, and the proportion of infected (or uninfected) individuals is sampled in an unbiased manner. Example: rainbow in their second year in the reservoir which were sampled in the August-September period exhibited 100 percent infection (Fig. 117), but only 68 percent in October-November. Theoretically, there could be no "immigration" of fish in their second year of lake rearing. The infection rate was probably not 100 percent in August-September, and we failed to sample uninfected fish of this life history group. This sampling error was easy to make since sample sizes of older fish was unavoidably small.

Internal Fat, Condition, and Infection Intensity

Plerocercoid counts varied greatly among most fat content categories as shown in the following table. Nevertheless, there is a negative relationship between mean cestode counts and internal fat content, as shown in Figures 128 through 132.

	FAT CONTENT				
	NONE	TRACE	LIGHT	MODERATE	HEAVY
Trout Sample Size	236	129	131	33	4
Worm Count Range	0 - 185	0 - 76	0 - 136	0 - 37	-----
Mean	10.62	6.04	6.91	2.64	0.0

Figure 128 illustrates that for all trout species combined, and for all months and trout life histories, only fish with no plerocercoids contained "heavy" fat accumulations (n = 4 among 533). For all of the rest, fat content dropped to trace or non–existent levels when mean cestode counts were any more than five or six.

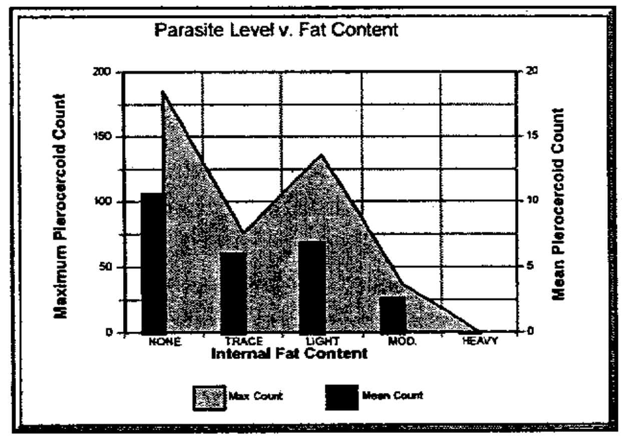


Figure 128. The relationship between internal fat content and the mean and maximum count of *Diphyllobothrium* plerocercoids in Spada Lake trout in 1997.

The negative correlation between the mean plerocercoid count (shaded areas) and fat content was very consistent, even when the data were categorized for differing seasons or trout maturity stages (Figures 129 through 132), with one exception. For fish which were running ripe when captured in the spring months, fish with light fat levels seemed to be tolerating a higher level of infection. This may have been caused by the very low sample size for fish with light or trace levels. None of the fish in these life history classifications contained heavy fat reserves.

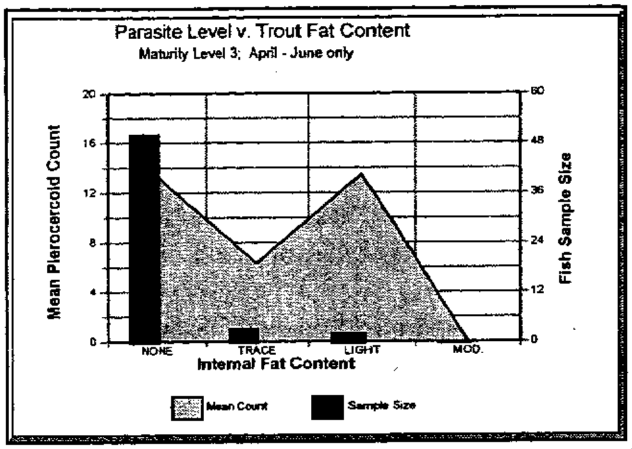


Figure 129. The relationship between internal fat content and the mean count of *Diphyllobothrium* plerocercoids in mature Spada Lake trout in 1997.

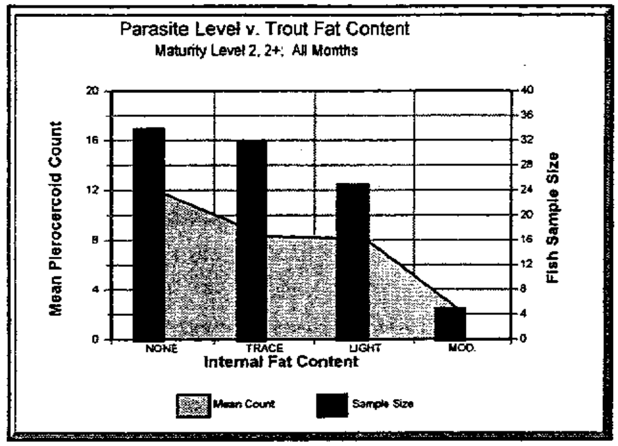


Figure 130. The relationship between internal fat content and the mean count of *Diphyllobothrium* plerocercoids in near–mature Spada Lake trout in 1997.

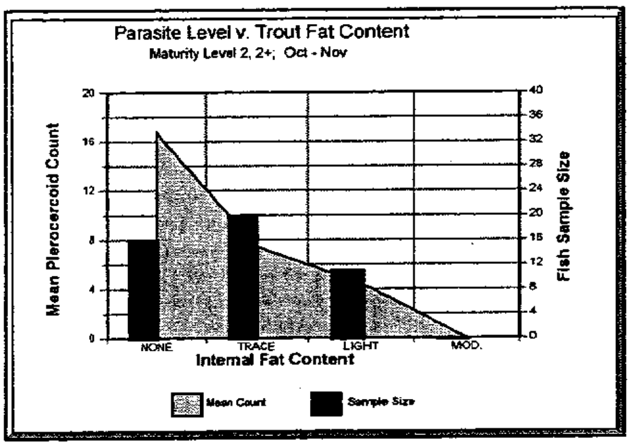


Figure 131. The relationship between internal fat content and the mean count of *Diphyllobothrium* plerocercoids in near–mature trout sampled from Spada Lake in October-November, 1997.

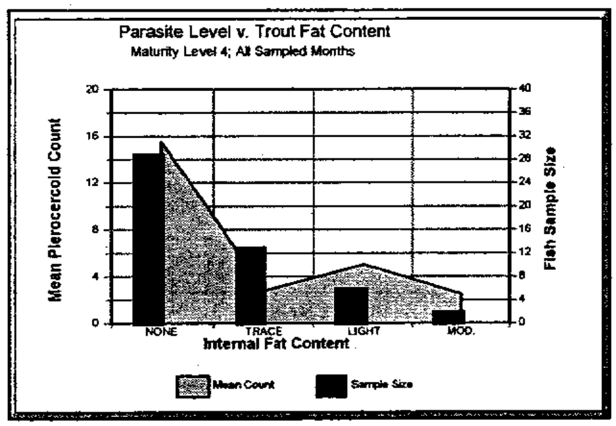


Figure 132. The relationship between internal fat content and the mean count of *Diphyllobothrium* plerocercoids in recently–spawned trout sampled from Spada Lake in October-November, 1997.

Trout which were near–ripe, and collected in the fall a few months before spawning, are represented by Figure 131. None of these fish were going into the stressful winter and spawning period with even moderate fat levels. Fat reserves were slim to none for fish with an average of eight plerocercoids or more, and by fall mean counts were relatively high (17) for ripening fish with no fat.

Of 50 trout which had survived the rigors of spawning, 8 exhibited light or moderate internal fat, but again those with more than 5 or 6 worms had trace fat levels, or none (Figure 132).

Regression analysis showed that there was no statistically significant relationship between trout relative weight (W_r) and infection levels in individual fish (Figures 133 through 135). This suggests that while internal fat is often negatively correlated with infection, many fish are nevertheless able to build a level of condition that overrides the fat:infection relationship. We did not see a consistent decline in W_r with increasing plerocercoid counts. More intensive data analysis with further stratification by trout life history group might reveal relationships that our brief analysis did not. Factor analysis would be a particularly beneficial approach.

One potentially important pattern did emerge, however, and is consistent with findings noted elsewhere in this report (e.g., Table 35). When cutthroat and rainbow are compared, only cutthroat exhibited relative weights greater than 100 (the "average" level for populations range wide)(Figures 133 and 134), and all of the fish with a $W_r > 100$ except one had no plerocercoids (Figures 134 and 135). This suggests that even slight *Diphyllobothrium* infection levels in Spada Lake trout result in sub-standard physical condition, particularly for rainbow.

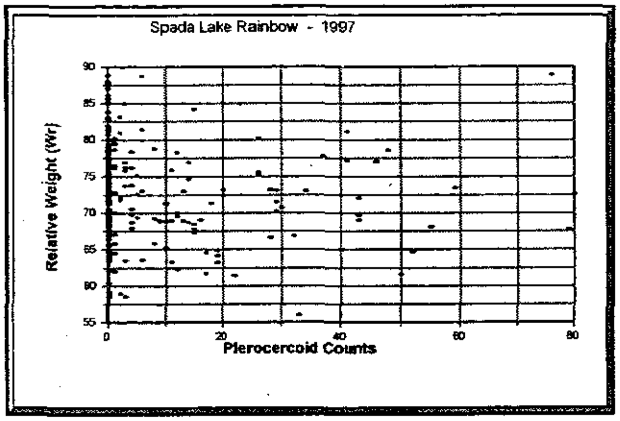


Figure 133. The relationship between relative weight (W_r) and *Diphyllobothrium* infection intensity in Spada Lake rainbow in 1997.

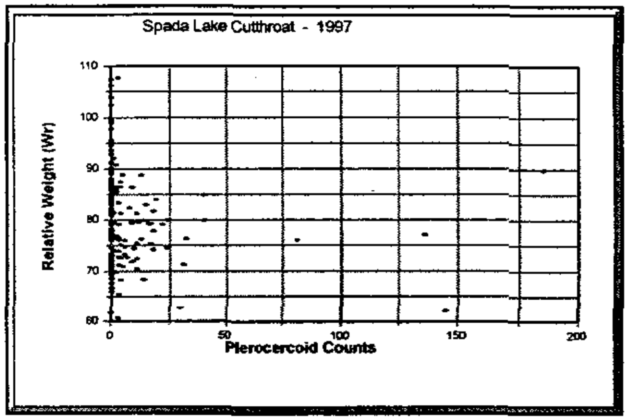


Figure 134. The relationship between relative weight (W_r) and *Diphyllobothrium* infection intensity in Spada Lake cutthroat in 1997.

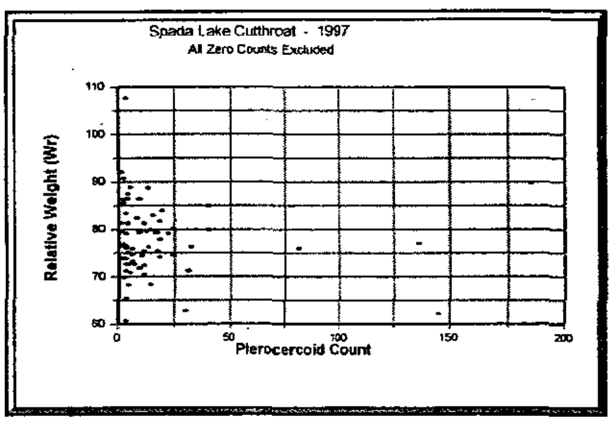


Figure 135. The relationship between relative weight (W_r) and *Diphyllobothrium* non-zero infection intensity in Spada Lake cutthroat in 1997.

The Diphyllobothrium Life History Conundrum

<u>First Intermediate Host</u>

All literature which we reviewed specify pelagic calanoid or cyclopoid copepods as the first intermediate host of *Diphyllobothrium* in general, or *D. ditremum* specifically (Vik 1964). However, we were astounded to find these relatively high infection levels in trout when the classically–cited copepod species occurred at only trace or rare levels in Spada Lake in 1997 (Tables 11 through 13, Secondary Production—Zooplankton: Results and Discussion).

All of the zooplankton samples were examined for procercoids in the enumeration split (Secondary Production — Zookplankton: Methods). Drawings of the larva from Hutchinson (1967) were used as identification sources. No free specimens were observed. Since survival of the procercoid is only a few days outside of a host, this finding was anticipated.

When Spada Lake was first formed (Stage I), there were many cyclopoid copepods present in the plankton (WDG 1982). Its copepod population has apparently changed as the number of cyclopoids has dropped to a seasonal maximum of less than 50/m^3 for all species of this taxon combined (Secondary Production — Zooplankton: Results and Discussion). Nor were there diaptomids present in the 1997 zooplankton other than a few, very rare "wash–ins." The question arising from this evidence is, how do the fish acquire their cestode infection?

In our opinion, cyclopoids and diaptomids were present in insufficient numbers in the Spada Lake plankton to cause the observed level of parasitism. By comparison, the number of *Epischura* in the lake's top sampling stratum was over 100 individuals/m^3 for 10 of the 16 plankton sampling trips. Furthermore, none of 8 trout stomachs given <u>detailed</u> examination for zooplankton species had cyclopoids in them, while 1 of the 8 had <u>only</u> *Epischura* in it, and there was a single specimen of *Epischura* in another 1 of the 152 other stomach samples. Although *Epischura* has not been documented as carrying *Diphyllobothrium* to our knowledge, the coracidium cannot live long after hatching without occupying its first host, and the only possible alternate euplanktonic host to *Epischura* in Spada Lake is *Daphnia rosea*. *Epischura* is less different from cyclopoids or diaptomids than is *Daphnia*, so is a more probable intermediate host. In addition, the seasonal infection rate in trout demonstrated a double pulse (Figure 124), a phenomenon only observed for the *Epischura* population.

Copepods other than *Epischura* appeared to play an extremely minor role in the trout diet, but the *D. ditremum* infection rate was high. Halvorsen and Andersen (1984) reported a similar problem, and "suspected that copepods (were) under–represented in the (stomachs) relative to their actual uptake rate because of rapid disintegration in the fish stomach." We do not believe this was a significant source of error in our study since stomachs were preserved soon after fish were taken from the lake, and we did not note a high percentage of well–digested plankton material in many stomachs.

Determination of the actual intermediate host for *Diphyllobothrium* in Spada Lake is largely an academic exercise from a fishery management standpoint. There is no question that the fish acquired new infections in 1997; the only question is from which plankter. We do, however, feel this is an exceedingly interesting question given the apparent rarity of these circumstances as judged by the literature. Academics interested in pursuing this question should review Johnson (1975) to gain an appreciation of the type and amount of work that would be involved.

Final Host Identification and Abundance

Vik (1964) lists cormorants, a heron, gulls, and mergansers as final hosts for *D. ditremum*. His list is expanded with two mammals (cats and mice) for *D. dendriticum*. In a later review, Halvorsen (1970) said "results indicate that *D. dendriticum* is linked with gulls and *D. ditremum* with loons and mergansers." Other species of *Diphyllobothrium* have been identified in one or more species of loon, pelican, magpie, black and grizzly bear, seal, dog, fox, vole, hamster, and man (Vik 1964; Curtis 1984; Andersen and Vik 1987; Amundsen and Kristoffersen 1990). Janicki and Rosen (1917) and Tarassov (1934) (cited from Vik 1964) list "several piscivorous mammals" as final hosts for *D. latum*. Given this list, we presume that one or more of the piscivorous birds are likely final hosts at Spada Lake. We would also recommend sampling otters to see whether they should be included since this was the only species for which strong circumstantial evidence exists of trout consumption in the reservoir, even if the fish were artificially confined in gillnets (below).

The following species were observed at or on Spada Lake which have life histories including piscivory, although we failed to observe it directly: western grebe, hooded merganser, western gull, great blue heron, and river otter. It's definitely possible that one of these species, or one not on this list, was at the lake at times we were not. Chubb (1980) noted that in northern areas in Sweden and many parts of Norway the definitive hosts were present at habitats for only part of each year. The actual final host/s for *D. ditremum* in Spada Lake remains unresolved.

Diphyllobothrium Control Considerations

Final Host Control

We did not attempt to make accurate counts of fish–eating birds or mammals at or near the reservoir. It quickly became obvious that a major effort would be required to obtain any confidence in a final host population estimate (assuming the final host/s was identified). One bald eagle was seen occasionally on roost trees near the mouth of Williamson Creek. A few black bear were seen on the south shore road during the tenure of our field work, but none were seen at or by the lake. River otters are known to be resident near the lake's eastern end, and we experienced net robbing by one or more of these animals on two occasions. An occasional gull or heron was seen, but never as many as a dozen, and on only a few of our 17 trips to the lake. A very small number of grebes and mergansers (<10) were seen, again on an irregular basis.

We were also perplexed by the abundance of the cestode in the trout given the apparent dearth of likely host species, at least on the 17 trips made between early March and mid–November. The number of defecations needed to "seed" a lake the size of Spada is unknown to us, but one possibility is that introductions of cestode eggs occur through defecations by birds which spend most of their time on other lakes in the vicinity (Becker and Brunson 1967). Virtually all of the lakes in the general area support *Diphyllobothrium* (WDFW file records). Therefore, it may only require brief visitations by an otherwise very numerous gull, merganser, or cormorant population to seed the lake. It is not necessary that a final host obtain plerocercoids from fish in the reservoir. This seems a more plausible mode of current reservoir seeding, lacking a more exhaustive census of potential final hosts on or around Spada Lake.

Changed Fish Species Composition or Balance

Prevalence of the cestode was lower in cutthroat for certain life history stages (Figures 116 and 117), but this was offset to some degree by what appeared to be a higher level of mortality in cutthroat versus rainbow or hybrids (Figure 120). The range in relative weight was also higher for cutthroat which were uninfected when compared with rainbow (Figures 133 and 134). While cutthroat are very clearly quite vulnerable to the parasite in Spada Lake, these results offer some slight hope that shifting the species balance towards cutthroat may result in improved survival of harvestable trout.

Eastern brook char are already established in the basin above Culmback Dam (Description of the Study Area — Fish Species and Brief Life History). Although this species is not immune to this parasite, we have generally observed lower infection levels in brookies than in rainbow, even when in sympatry. Char survival to older ages than rainbow also seems to be the rule rather than the exception in these instances (WDFW Region 4 file data).

Fasten (1922) also noted a "striking" difference in *Diphyllobothrium* infection rates between brook char and cutthroat in Lost Lake, near Snoqualmie Pass. From the description of the size of the plerocercoids, it's likely that his samples were *D. ditremum*. Bangham and Adams (1954) examined 110 brook char from British Columbia waters and found no *Diphyllobothrium* in 94 infected fish. They cite one study from California where *Diphyllobothrium* sp. was "rare" in 31 eastern brook examined. When conditions are right, eastern brook can nevertheless develop large epizootics and mortality from *Diphyllobothrium* (Simms and Shaw 1931). In this Oregon case history, however, the cestode was "tentatively identified as *D. cordiceps*", which has since been shown to be *D. dendriticum* (Andersen *et al.* 1987), a much more invasive and destructive species.

The obvious and extreme brown trout mortality reported by Fraser (1960) indicate this species is probably no more resistant to *D. ditremum* than our native rainbow or cutthroat. The English case history involved heavy piscivory on threespine sticklebacks, however. Brown trout are also vulnerable to losses from *D. dendriticum* (Rahkonen *et al.* 1996).

Becker (1966) stated that "no salmonid species appears immune to infection by *Diphyllobothrium*." However, in some circumstances coho carry lower infection intensities, and contribute to the sport fishery, even in lakes where rainbow mortality to *Diphyllobothrium* is high (Becker 1966; Becker and Brunson 1967; Starkey 1970). Coho have previously been illegally stocked into Spada Lake (Description of the Study Area — Fish Species and Brief Life History), but the number stocked was unknown. Thus, we cannot objectively evaluate the low–level appearance of this species in past creel surveys (Pentec 1993).

Effect a Dietary Shift

Any ecological change within the reservoir that would result in less consumption of copepods by salmonids would reduce the prevalence of *D. ditremum*. Whether this is feasible in Spada seems highly problematic. In some systems abundance reduction of one fish group resulted in a dietary shift in another such that *D. ditremum* prevalence dropped overall (Amundsen and Kristoffersen 1990).

Benthic and terrestrial insects have historically been the trout dietary mainstay in Spada Lake. Since we presume that little can be done to appreciably increase the abundance of these food resources, particularly in the drawdown zone, reducing competition from brown bullheads may create some alternate prey for trout, resulting in less consumption of copepods. An alternative is to provide a greater supply of large daphnids, such as can be accomplished with fertilization (Langeland 1982; Budy *et al.* 1998). Yet another possibility is creation of increased vegetation in the drawdown zone, which can serve as an attachment substrate for invertebrate food resources (Ploskey 1983).

The case history of Amundsen and Kristoffersen (1990) offers evidence that some parasite control may be attained by reducing the number of the intermediate hosts (whitefish in their case). While our interim trout population density estimate was quite low (Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock), we had very little confidence in the estimate. If a more robust estimate is developed from a marked fish experiment, this approach can be given greater scrutiny. In some cases, if a reduction in fish density is large enough, a change in the species composition of the zooplankton community from copepods towards cladocerans may occur because of a reduced effect of selective predation on the larger cladocerans (Brooks and Dodson 1965).

Swedish lake managers have achieved some success in reducing *Diphyllobothrium* infection rates and resultant mortality in arctic char by introducing *Mysis relicta*, which provided an alternate food resource from copepods (Hammar and Henricson 1982; Hammar *et al.* 1983). Because of the extreme ecological disruption new invertebrate species introductions can cause (Richards *et al.* 1975; Li and Moyle 1981; Northcote 1991), this option will require considerable further study.

Conclusions

Diphyllobothrium ditremum was tentatively identified as the cestode present in Spada Lake trout.

Rainbow, cutthroat, and their hybrids were found to be infected with *D. ditremum*. Prevalence of the parasite varied seasonally in all three trouts; declines in prevalence over the course of the summer within a single species and age group is interpreted as mortality. Prevalence levels ranged from 10 to 100 percent overall, but was between 50 and 100 percent by mid–November.

Infection intensity varied greatly, with plerocercoid counts ranging from 0 to 185 in individual fish. First–year reservoir residents built to a mean mid–summer peak of 27 plerocercoids/fish, but declined to a fall level of 4/fish. Infections in second–year lake residents ranged from 7 to 23/fish overall, but the range was limited to 10 to 14 for most of the season. Oldest trout exhibited the largest range in mean monthly counts at 2 to 41/fish; the maximum was seen at the end of the season, in mid–November.

Patterns of intensity over the sampling period varied between the trout life history groups, with first–year reservoir residents potentially suffering greatest mortality. Dome–shaped intensity curves were taken as evidence of mortality, particularly in the late summer.

Cutthroat tended to exhibit lower infection intensities than either rainbow or hybrid trout. When considered on a seasonal basis, this difference may also indicate a greater susceptibility to mortality from *D. ditremum* in cutthroat versus the other two forms.

The infection intensities observed are sufficient to cause mortality, particularly for trout in relatively poor condition. Relative weight reached or exceeded 100 only in trout that harbored no plerocercoids. There was a generally consistent negative relationship between plerocercoid counts/fish and the amount of internal body fat grossly observed. Fat content dropped to trace or non–existent levels in trout bearing more than five or six plerocercoids.

Euplanktonic cyclopoid or calanoid copepods are normally found to be the first intermediate host of *D. ditremum*. Their near–absence in the lake's pelagic zone, and absence in trout stomachs led us to believe that *Epischura* fills the role of first intermediate host in Spada Lake. This has not been confirmed by detection of procercoids in *Epischura*.

The final host for *D. ditremum* in Spada Lake was not confirmed, and could be one or more species of piscivorous bird, or mammal. The most likely candidates are gulls, mergansers, or otters, in decreasing order of probability. It's likely that the final host for the cestode is one or more bird species that is part of a larger regional population, members of which visit Spada Lake infrequently, or at a time and place not observed by us. Direct control is not deemed practicable for any final host in this system.

Options with the most promise for indirect control of the parasite in the fish community include a change in the fish species mix, with one or more carefully–considered introductions, and lake fertilization or other enhancement of the invertebrate prey base to effect a dietary shift away from copepods. A dietary shift may be facilitated by control of brown bullheads, if the latter are shown to be a major competitor for relatively scarce food resources.

Fish Harvest (Yield) and Recreational Use Levels

Methods

Estimates of annual yield from the Spada Lake sport fishery are provided in Table 43. The values are the product of the estimated weight from the mean length of all creeled trout in $Year_x$, and the estimated total number of trout harvested in $Year_x$. The reservoir area used to calculate weight/area was based on a full pool condition (756.8 ha).

Table 43. Estimates of annual sport fishery yield from Spada Lake, Snohomish County, Washington, 1979 through 1995.

Year	Kg	Kg/ha	Lbs	Lbs/acre	
1979	754	2.42	1662	2.16	Stage I
1980	616	1.98	1358	1.76	
1985	4899	6.47	10,800	5.78	
1986	2596	3.42	5723	3.06	
1987	2513	3.32	5540	2.96	
1988	402	0.53	886	0.47	Stage II
1989	533	0.71	1176	0.63	
1992	258	0.34	569	0.30	
1995	52	0.07	115	0.06	

Shaded data represents years of theoretical overfishing (the trout population was artificially enhanced by stocking through 1979). See Table 45.

Predicted Stage I sustainable annual yield from MEI: 1.46 kg/ha, 456 kg/yr.

Predicted Stage II sustainable annual yield from MEI: 1.12 kg/ha, 844 kg/yr.

Several models have been developed that relate lake or reservoir morphometry and chemical conditions to fishery yield (Rigler 1982). Those that are most applicable to Spada Lake are presented in Table 44.

A morphoedaphic index (Ryder 1965) was calculated for Spada Lake based on its mean conductivity of 20.6 μS/cm (Everett Water Department file data). Conductivity was converted to total dissolved solids (TDS) by multiplying by 0.65 (APHA 1971), yielding an estimated value of 13.39 mg/*L*. Mean depths in Stage I (13.55 m) and Stage II (24.98 m) resulted in an MEI of

0.988 for Stage I, and 0.536 in Stage II. (Comparable MEIs from area reservoirs are listed in Table 14, Secondary Production—Zooplankton: Results and Discussion.)

Results and Discussion

Ryder (1965) presented two models, one for natural lakes with fairly intensive fisheries, and one for lakes in which the fishery is restricted in some fashion. The yield levels for the latter model are nearly 100 percent lower than that predicted for full–fisheries. However, it is interesting that the yield predicted for Spada Stage II (0.068 kg/ha, Table 44) is almost exactly that documented on Spada in 1995 (0.07, Table 43). Whether this is just a coincidence probably relates to whether the lack of fish over 12" in Spada Lake is similar to the conditions in Ryder's 11 "restricted fishery" lakes. Jenkins (1982) presented an updated model using Ryder's original data set, with logarithmic transformations. Stables *et al.* (1990) chose to use this equation to represent Spada's potential yield. Two of these three natural lake models, including that used by Stables *et al.* (1990), predict an annual yield of roughly 1.0 kg/ha. Henderson *et al.* (1973) state that "once a reservoir is stabilized...with only minor fluctuations in depth and nutrients, the MEI may be used as described for natural lakes."

Models developed specifically for reservoirs were reported by Jenkins (1977) and Jenkins (1982). The latter paper's model gave the highest values for potential Stage II yield, at 5.77 kg/ha. This would presumably represent the upper end of the range of potential fishery yield in Spada under liberal regulations. His earlier 1977 model is particularly interesting, and probably most applicable, in that it offers a multi–variate approach that includes elements for length of growing season and reservoir age. Its output, 1.3 kg/ha, is very close to that of two of the other four models.

In most of the models the change in potential yield declines roughly 24 percent from Stage I to Stage II on a unit area basis. This is caused by a major enlargement of the reservoir's volume and mean depth, with no concomitant increase in the edaphic factor (TDS). Thus, while the lake surface area available for anglers was increased 240 percent, in fact, reservoir enlargement only increased potential annual yield by 76 percent (466 kg to 820 kg).

All indicators point to a very low level of potential production, particularly the thrice–annual turnover rate and extremely low conductivity (TDS). We assume a potential mean annual yield of 1.15 kg/ha (1.03 lbs/ac) for planning purposes. This equates to about 820 kg annually if a mean summer–fall reservoir elevation of 1445 ft (714 ha) is assumed (Figure 8).

The mean weight of harvested rainbow and cutthroat combined in 1995 was 232.5 g. If the current 12" minimum size were to remain in effect, 3527 fish of this weight could theoretically be harvested annually at 1.15 kg/ha (8.4 times the 422 estimated in 1995; Pfeifer 1996a). Given the dearth of fish of this size (Figure 54), attainment of this yield level is unlikely on a regular basis. It is also important to note that almost 58 percent of all fish checked in the 1995 creel

Table 44. Estimates of potential sport fishery yield (kg/ha/yr) from Spada Lake for Stage I and II.

Authority	Modeled Water Type	Model /2	Predicted Annual Harvest (Yield) /1		
			Stage I	Stage II	% Change
Ryder (1965)	Natural lakes /3	H = 2.094 (X ^0.44610)	1.374	1.045	-24.0
Ryder (1965)	Natural lakes /4	H = 0.1357 (X ^0.4435)	0.090	0.068	-24.4
Jenkins (1982)	Natural lakes	log H = 0.168 + 0.446 (log MEI)	1.464	1.115	-23.8
Jenkins (1982)	Reservoirs	log H = 0.925 + 0.563(log MEI) - 0.149(log MEI)^2)	8.320	5.770	-30.7
Jenkins (1977)	Reservoirs /5	H = 0.3994 - 0.1519(log ha) + 0.2027(log TDS) + 0.9796(log days) - 0.3055(log age)	1.646	1.296	-21.3

/1 All model outputs were converted to kg/ha/yr.
/2 H = fishery yield (units/area/time); X = morphoedaphic index.
/3 Moderately to intensively fished natural lakes.
/4 Restricted fisheries in natural lakes.
/5 TDS = total dissolved solids in mg/L; ha = reservoir area; days = growing season; age = reservoir age in years (Stage II).

survey were "illegal," i.e., <12" in total length (Background—Creel Surveys and Fishery Performance and Pfeifer 1996a), therefore, the mean weight of 232.5 g is probably less than it would have been if all of the trout had been ≥ 12". A larger mean weight would equate to a lower potential harvest number.

Table 45 presents some "what if" scenarios that estimate the potential number of trout harvestable at Age 2, 3, and 4 at differing exploitation rates by age class. In actual practice, the fishery would need to be monitored to assure that the annual harvest did not exceed the theoretical yield greatly, as may have happened in the past (Table 43). Modeling of various fishery scenarios should also be performed to estimate probable impacts on the spawning stock (e.g., Taylor 1981; Beamesderfer 1988). However, several of the parameters needed for these models are poorly measured, if at all, in Spada Lake, such as egg–to–fry survival, recruitment, and total trout population size. These deficiencies must be rectified if optimum, long term management of the wild trout fishery in Spada Lake is to be assured.

Table 45. Exploratory trout harvest totals from Spada Lake given a yield ceiling of 820 kg (1.15 kg/ha). The 1997 length:weight relationship was used to estimate mean weights. All weights are in grams.

	Age 2		Age 3		Age 4		Age 5		Total	Total
Scenario	Number	Mean Wt.	Number	Mean Wt.	Number	Mean Wt.	Number	Mean Wt.	Weight	Harvest
1	3000	80	2700	160	400	224	100	557	817,300	6200
2	2900	80	3200	160	350	224	0	557	822,400	6450

Scenario 1: Trout are caught in proportion to their abundance by age class in 1997.

Scenario 2: All trout larger than 12.0 inches are released; some high–grading for Age 3 or 4 occurs.

The numbers caught in each age class in Table 45 were arbitrarily set to conform to the proportions of these ages seen in the whole–season gillnet catch in 1997, and to sum to a total yield of approximately 820 kg. The total harvest is roughly equivalent in each case, with 250 more younger trout substituting for Age 5 and larger Age 4 trout if a 12" maximum size limit were imposed.

One of the current management objectives for Spada is an effort level of 2.75 trips/acre (5140 trips/yr; Background — Relationships to Current Fishery Management Goals and Objectives). That effort level equates to about 1.25 trout/trip given a cap on harvest of 6200 to 6450. Less than two harvested trout per outing on Spada is probably unacceptable to most anglers (Braaten 1970), and likely explains much of the drop in use levels in recent years. If a harvest level ≥ 2.0 trout/angler is set as the goal, then a total harvest of 6450 would support 3225 trips, or 1.73 trips/ac. This is roughly equivalent to the angler effort level seen in 1992 (Table 3), and may be a peak level of *harvest* on naturally–produced trout in the reservoir.

If our second trout population estimate of 10,162 is accurate, then Scenario 1 and 2 harvest levels of around 6400 would be far too high, taking virtually all of the Age 2 to Age 4 cohorts extant (Tertiary Production — Estimates of Trout Immigration, Mortality, Population Size, and Standing Stock: Results and Discussion). This must be resolved by close monitoring of any new regulation/s, and re–assessing the trout population size through a mark-recapture estimation procedure. The relative contribution of wild versus hatchery trout would be a side benefit of such a test.

There appears to be few, if any harvestable trout older than Age 3 under current rearing conditions in Spada Lake. Therefore, assuming no supplemental stocking, most improvements in harvest rates must come from trout less than Age 4. The challenge is to allow some harvest of these fish, most of which will succumb to some form of natural mortality, without an unacceptable reduction in the spawning escapement.

Conclusions

Potential yield has been reduced about 24 percent from Stage I to Stage II on a per unit area basis. Reservoir enlargement resulted in an estimated 76 percent increase in annual yield (466 kg to 820 kg).

Sustainable yield (harvest) from Spada Lake is estimated as 1.15 kg/ha (1.03 lbs/ac).

If the current 12" minimum size remains in effect, regular attainment of even this very low yield level is highly unlikely.

A preliminary estimate of harvestable trout suggests that between 6200 and 6450 fish, ranging from Age 2 to Age 5, may be taken and remain below the maximum sustainable yield level. However, additional trout life history information is needed to enable modeling of various fishery strategies, and help assure that escapement levels are not reduced to an unacceptable level.

Attainment of a mean 2.0 trout/completed angler harvest level would cap effort levels at 1.73 trips/ac, or 3225 trips/yr (disregarding anglers who voluntarily choose to practice strict catch–and–release).