Review Factors Limiting Trout Production in Spada Lake and of Data Gaps

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An Initial Assessment of Critical Information Gaps and Priorities

The following initial recommendations are based the information provided in Pfeifer et al. 1999 "*Spada Lake Biological Assessment and Sport Fishery Evaluation*" and on professional experience with temperate lake and reservoir food webs. Also, being mindful that more than 10 years have past since the last intensive sampling program, and because local climatic warming trends have been underway for decades, some data collection will be required to provide a current view of the food web, thermal regime and distribution patterns. Therefore, the following recommendations are intended to maximize the value and insights by synthesis of existing and new information rather than simply repeating previous studies.

Background and Summary of Relevant Points in Pfeifer et al. 1998:

The complete summary of the findings in the Biological Assessment of Spada Lake by Pfeifer et al. 1998 is replicated in the Appendix of this report with editorial comments noted and highlighted at the end of selected statements. Some of the more relevant points regarding limits to trout production include:

1. Trout production in Spada Lake appears to be limited by low growth conditions.

2. Trout yield is limited by a 12" minimum size limit, a low growth rate that prevents sufficient availability of large trout for harvest, and lack of information about trout abundance and recruitment.

3. Brown bullheads are relatively numerous and suspected to compete with trout for food, but no diet or quantitative abundance information is currently available to support these suspicions. Nonetheless, these are very plausible concerns and should be investigated. Moreover, most catfishes are capable of considerable piscivory when conditions are conducive, so the potential for brown bullheads to feed on trout should be examined.

4. The reported seasonal densities for edible sizes and taxa of zooplankton were relatively low. Based on their proportional contribution to the diet by weight, insects and benthic invertebrates like leeches contributed much more to the annual energy budget of trout than zooplankton. Marked changes in diet composition were reported between 1979-80 and 1997 (Pfeifer et al. 1998). Most notably, higher-energy prey like Ephemeroptera nymphs, Trichoptera larvae, and leeches were important prey for trout during 1979-80, but were absent or significantly reduced proportions of the diet in 1997. These prey all contained energy densities of approximately 4000 J/g live body weight. By 1997, these prey were replaced by much larger proportions of lower energy Dipterans (predominantly chironomid pupae; 3064 J/g) and other benthic invertebrates (generally lower and variable energy densities.

Growth can be affected by changing thermal regimes, particularly if the fish are forced to reside in temperatures that are either at the warmer or colder extremes of their thermal tolerance (Thornton and Lessem 1978). Any effect of any inter-annual variability in thermal regimes for Spada Lake is currently ambiguous, because: 1) thermal stratification patterns did not exhibit any clear trends over the period of record provided (1989-1995), and 2) uncertainty regarding the seasonal depth distribution of trout in relation to the vertical temperature profiles during summer (especially August-September) in recent years, compared to patterns reported by Stables et al. (1992) for summers in 1987 and 1988.

Evaluation of Production Limits

Growth can be retarded by limited food supply (either from low prey density or reduced access due to physical barriers or stressful conditions like high epilimnetic temperatures), poor food quality, poor spatial-temporal access to food resources during all or portions of the growing season, stressful environmental conditions (especially low DO or inappropriate temperatures), disease, or inter- and intra-specific competition. Each of these factors can act independently, but are more likely to operate synergistically on the trout population. For instance, energy-limited fish exhibit less growth and reproductive success; they are more prone to infection and mortality from disease.

When food supply is not limited, growth is relatively insensitive to thermal variation during the growing season, as long as temperatures remain within a range of 9-15^{o}C. However, thermal tolerances change under food-limited conditions, and the optimal temperature for growth contracts and shifts to a narrower range of cooler temperatures as food supply becomes more restrictive. As feeding rates decline, the upper thermal threshold for weight loss shifts to progressively lower temperatures. In Spada Lake, epilimnetic temperatures during summer become considerably higher than the optimal temperature for growth. For moderately to severely food-limited trout, summer epilimnetic temperatures could even exceed thermal tolerances (i.e., lead to weight loss over the short term or mortality at longer exposures) and potentially prevent or limit access to epilimnetic zooplankton and high energy terrestrial or adult aquatic insects at the surface.

To determine the relative importance of food supply, prey quality, and thermal regime on growth of trout in Spada Lake, bioenergetics model simulations were applied to diet, growth, and temperature conditions reconstructed or approximated for four different phases of reservoir operation: 1979-1980, 1986, 1992, and 1995-1997. The objectives of these simulations were to: 1) estimate the average annual feeding rate of trout in terms of total prey biomass consumed per individual trout and as a proportion of the theoretical maximum consumption rate for trout of the same size that experience the same thermal regime; 2) compare feeding (as a proportion of maximum consumption) and growth performance (age-specific growth rate and growth efficiency) of trout during the four phases of reservoir operation reported. Growth efficiency (GE) is a measure of growth in weight as a percentage of the weight of food eaten to generate that growth over some specified period (a year in this case), and thus provides a metric for how efficiently food was converted into somatic growth. High growth efficiencies are typically associated with feeding at moderate to high rates on high energy diets, or feeding at high rates on moderate to high energy diets. In both cases, more surplus energy is available to convert into growth after metabolic and waste losses have been satisfied.

Methods

The bioenergetics model simulations used average annual growth for ages 1, 2, and 3 cutthroat trout (**Figure 1**), using temperature (**Table 1**) and diet data (**Table 2**) that most closely approximated conditions during those years. Data limitations prevented inclusion of seasonal or size-based variation in diet within years, but diet composition varied among years in the simulations. When temperature data were not available for specific years in the simulation, data from the closest year was substituted. The diet composition data for 1986 were not in a compatible form for comparison to 1979-1980 and 1997. The diet composition for 1986 was modified (converted into assumed proportions of key prey categories in the diet by weight) based on reported changes in frequency of occurrence for mayflies, dipterans, leeches, and zooplankton between 1979-1980 and 1986 (Stables et al. 1990). The diet composition in 1992 was assumed to be similar to the diet reported in 1997.

Model simulations were run from 1 January through 31 December separately for ages 1-3 for each reservoir period. The model accounted for energy losses from spawning for age-3 cutthroat trout by removing an average 8% body mass, for males and females combined, on 1 May (simulation day 121), an approximation of the median spawning date for cutthroat trout in the Spada Lake basin (Pfeifer et al. 1998).

Since the ambient thermal regime did not differ much among the simulation periods, lower and higher temperatures were applied to the 1995-1997 simulations. To examine the sensitivity of annual consumption rate and growth efficiency to thermal variability, temperatures were changed ± 1^{o}C in April and ± 2^{o}C during May-November for ages 1-3 cutthroat trout during the 1995-1997 simulations. Growth rates were constrained to the same observed starting and final weights as in the nominal simulations (Table 3), so sensitivity was evaluated in terms of changes in consumption rate and growth efficiency in response to the lower and higher thermal regimes.

Results

Although cutthroat trout grew faster during 1979-1980 and 1986 (**Figure 1**), their feeding rates (47-60% of maximum consumption rates) were similar to or even lower than feeding rates during the 1992 and 1995-1997 simulations (52-63%) when growth was slower (**Table 3**). Across all years, annual per capita consumption rates ranged 571-914 g/yr for age-1, 1360-1908 g/yr for age-2, and 1973-3363 g/yr for age-3 cutthroat trout.

Growth efficiency was considerably higher (GE = 5-13%) for most age classes during the 1979-1980 and 1986 phases than during the later years (GE = 4-11%; **Table 3**). Higher growth efficiency during the earlier phases of the reservoir also corresponded to higher dietary proportions of high-energy prey like Ephemeroptera and leeches. These results suggest that higher growth rates during the earlier years resulted from higher prey quality rather than from a higher feeding rate. Similar feeding rates suggest that the supply of available prey was similar among years, but the prey community shifted from high-energy prey like Ephemeroptera and leeches to predominantly lower-energy organisms like chironomid pupae.

Because trout can behaviorally adjust their depth to modify their thermal exposure, thermal regimes experienced by trout were likely similar among years and were unlikely to account for the differences in growth rates. However, consumption and growth performance were moderately sensitive to a ± 2°C shift in temperature during the growing season (Figure 2). To achieve the same annual growth rate, all three ages of cutthroat trout needed to feed at slightly higher rates as temperature increased, with a somewhat larger increase required between the nominal and higher temperature regimes (Figure 3A). Over the 4°C range in thermal experienced spanned by the sensitivity analysis, the three age classes only needed to increase from 49-51% of their maximum feeding rates at the low thermal regime to 57-59% of their maximum feeding rates at the high thermal regime. The annual per capita biomass of prey consumed by trout of each age also increased modestly from the low to high thermal regimes (Figure 3B), whereas growth efficiency declined considerably with increasing temperatures (Figure 3C).

Conclusions

The work by Pfeifer et al. (1998) and the supplemental analyses here provide compelling evidence for food limitation, exacerbated by *Diphyllobothrium* parasitism, are the primary factors currently limiting production of trout in Spada Lake. Although feeding rates are similar to periods when trout growth and yield to the fishery were much higher, the energetic quality of prey has declined. Interannual variability in thermal regimes have probably not been a cause for declining growth to date, but could become a very important limitation under continuing warming trends by both increasing metabolic costs (reducing growth efficiency) and preventing access to epilimnetic prey like zooplankton and high-energy adult or terrestrial insects in the surface film.

Competition for prey becomes important in food-limited systems. Intra- and inter-specific density dependent effects on growth by trout become an important consideration as well as competition by brown bullhead. Under such conditions, adding more of the same species would intensify competitive effects, reduce growth, and increase mortality. Instead, reducing competition by increasing harvest should increase both yield to the fishery and productivity of the trout populations. For instance, a slight reduction in minimum size limit to 11” total length (27.5 cm) would provide anglers with access to considerably more harvestable-sized trout while keeping the minimum size limit above the average spawner size for cutthroat trout (26.5 cm) and rainbow trout (22.0 cm). Such a change would moderately reduce the spawning population, and would likely lead to a smaller, but more productive and resilient population (e.g., fewer trout but with higher growth rates and larger lipid reserves).

The loss of energy-rich leeches and significant reduction of mayfly naiads in the diet suggest a significant shift in the benthic community, wherein these species have either declined dramatically, or have become spatially or behaviorally inaccessible to trout. The energy subsidy from high-energy prey like terrestrial insects (4000-8000 J/g) could also be extremely important, but their proportions changed only slightly between phases (proportions of terrestrial insects actually increased slightly in trout stomachs during 1997). Magnitude of this input to the lake is not currently known (sampling the availability of insects in the surface film with neuston nets would be required), and access to these prey could be reduced during summer, because high epilimnetic temperatures might deter surface feeding by trout. High temperatures would be more of a deterrent for cutthroat trout than rainbow trout (e.g., Stables et al. 1992), and would deter larger individuals more than smaller fish of either species due to weight-dependent changes in metabolic costs and consumption limits.

It might be fruitful to explore food web manipulations with trace nutrients and/or essential fatty acids rather than conventional N:P fertilization schemes to customize the energy pathways in favor of desirable invertebrates, zooplankton, and fish. Introducing new species that fill alternative niches might have some merit, but should be considered very cautiously within the context of ecological risk to the Spada Lake and greater Snohomish River basins versus probability and potential magnitude for success.

Filling Existing Data Gaps

Frequent Vertical Temperature Profile Measurements. Temperature profiles should be recorded every 1-14 days throughout the year. With significant increasing and consistent trends in water temperature reported for local lakes (e.g., Lake Washington; Winder and Schindler 2004), frequent temperature profile monitoring becomes essential for tracking changes in the timing, duration, depth, and magnitude of thermal stratification. Thermal regime drives most biological rates in aquatic systems, and can alter spatial-temporal distribution patterns that significantly affect access to food, or refuge from predation or environmental stressors. Monitoring can be accomplished most economically with a couple strings of temperature loggers that record integrated daily average temperatures at specified depths (every meter over 0-15 m, every 5 m from 15 m to bottom), or by measuring vertical temperature-DO profiles, Secchi depths, etc. biweekly with a field crew.

Population abundance of trout and brown bullheads. Species-specific trout abundance estimates are needed to evaluate recruitment, potential harvest, and fishing mortality, estimate seasonal carrying capacity, and reproductive capacity. Estimates of brown bullhead are potentially important if they act as either significant predators or competitors for trout. Concurrent estimation of trout and brown bullheads would be more cost-effective, even using separate methodologies due to economies of scale.

Recommendation: A 2-pronged population assessment study should be undertaken for trout involving a mark-recapture experiment and a targeted quantitative hydroacoustic study.

-The mark-recapture study would involve trapping and marking age-1 downstream migrants and upstream/downstream migrating spawners in 2-3 of the major spawning tributaries during February-May. The marked fish would be allowed to redistribute into the lake until the recapture period started in June. By using migrants and spawners from one or more streams fish should be accessible for live capture, marking and release in larger numbers than might be feasible from lake sampling alone. The recapture period would be conducted during June-July (or June-October if needed) when fish captured with gill nets and/or from a creel survey would be examined for marks. The recapture period would satisfy the requirement for random sampling at either the mark or recapture phase of the experiment.

Brown bullhead would also be assessed via mark-recapture, but both mark and capture methods would likely differ partially or completely from trout sampling methods. The fish examined during the recapture phase would also provide biological material for age-growth, diet analysis, stable isotope analysis, temporal energy density dynamics, and bioenergetics modeling (listed below).

-Hydroacoustic assessments for trout (Kubecka et al. 1994; Kubecka and Wittingerova 1998; Yule 2000) differ significantly from the more common surveys for kokanee or juvenile sockeye salmon, because trout depth distribution and diel movement and behavior patterns (Stables et al. 1994) diverge considerably from that of salmon (Beauchamp et al. 1997). Shallower orientation by trout often requires side-looking or side- and down-looking transducers towed along transects in mobile daylight surveys (Yule 2000). The hydroacoustic estimate can be conducted concurrently with the mark-recapture estimate and would provide an independent estimate of trout inhabiting the pelagic waters of the lake. Meanwhile, the net sampling used during the recapture phase would provide species verification of pelagic targets (i.e., differentiate among species of trout and pelagic brown bullheads).

Quantitatively Evaluate the Factors Affecting Growth and Survival of Trout: Determining the Relative Importance of Thermal Regime, Food Supply, Food Quality, and Trophic Interactions

The existing information on age and growth, diet, thermal regime, fish distribution, and zooplankton densities can be assimilated into bioenergetics model simulations of conditions during previous and current reservoir stages. These simulations estimate the biomass of each major prey group consumed for each species and age class of trout through the year and the resulting growth efficiency. These simulations account for temporal changes in temperature, body mass, diet, and prey quality (modeled on a daily time step) and identify which of these factors, if any, contribute most to growth limitation (Beauchamp et al. in press). These simulations estimate daily feeding rate which can be compared to the maximum physiological consumption rate for trout of the same size that experience the same thermal regime. This proportion of maximum consumption provides a useful indicator for whether feeding rate (which implies that accessible food supply is limiting) is the primary factor limiting growth.

When coupled with information on abundance and size structure of the consumers and major prey taxa, bioenergetics simulations can evaluate how food supply compares to consumption demand through different months or seasons to determine if particularly severe bottlenecks in food supply occur (temporal carrying capacity) during specific life stages or only under certain environmental conditions. This approach can quantitatively identify periods when specific segments of the predator and prey populations interact most strongly (Beauchamp et al. 1995; 2004; Baldwin et al. 2000). These models can also simulate responses to potential management scenarios (stocking or harvest strategies), or different environmental conditions (e.g., changing thermal regime due to climate or reservoir operations). The potential role of cannibalism by trout (Baldwin et al. 2000) and predation or competition by brown bullheads in regulating growth and survival of trout can be addressed within this modeling framework if supplemented by some targeted stable isotope analysis or diet analysis (see below).

The existing raw diet data from 1997 (Pfeifer et al. 1998) and 1970-1980 (Bradbury et al. 1982) should be re-analyzed to determine the proportional contribution by <u>volume</u> of each major prey group for different size/age classes for each species of trout by month or season. Although prey volumes were measured in both 1997 and 1979-1980, these data were only presented in unreadable graphs (Figures 106-109). Also, since the data were pooled over the entire sampling season, any temporal variability was obscured. Diet data should be re-analyzed by season and size class for each species of trout.

Using Stable Isotope Analysis for Detecting Piscivory and Quantifying Major Energy Pathways That Support Trout Growth

Piscivory can be a major factor regulating fish populations, but can go largely undetected under routine sampling programs, unless sampling regimes or analytical techniques are specifically designed to address this topic via either intensive temporal diet sampling (Beauchamp et al. 1992; Baldwin et al. 2000), or through elevated $\delta^{15}N$ signatures, using stable isotope analysis (SIA; McIntyre et al. 2006). Diet data and stable isotope data are complementary in that diet data captures feeding patterns over the previous 4-20 hours (depending on temperature and sampling method), whereas SIA captures the integrative history of general food types over the previous 6-12 months. Diet analysis enables identification of specific prey taxa, but requires relatively large sample sizes to capture a representative view of short-term feeding patterns. In contrast, SIA characterizes prey groups that share similar trophic position (e.g., primary consumer versus piscivore) and energy pathway (e.g., benthic invertebrates versus pelagic zooplankton) and records this in proportion to the biomass contribution of these prey over the previous 6-12 months, depending on how much fast the consumer's body mass changed over that period. Tissue samples from different sizes of brown bullheads and trout, and composite samples for representative prey could undergo SIA to look for evidence of piscivory. By mapping $\delta^{15}N$ and $\delta^{13}C$ signatures of consumers and potential prey, the relative importance of pelagic-, benthic-, or terrestrial-origin prey (e.g., zooplankton versus insects) and fish versus invertebrate prey can be inferred from the integrated feeding history of the organisms, expressed as isotopic coordinates on a $\delta^{15}N$ versus $\delta^{13}C$ plot.

The SIA results would be combined with existing and/or new diet data to provide input into bioenergetics simulations to estimate trout mortality due to predation, and estimates of seasonal supply and demand of major food sources supporting trout growth. These simulations would form the basis for evaluating options regarding harvest management and/or efficacy of potential enhancement measures.

Neuston and Zooplankton Sampling

Insects contribute much more to the annual energy budget of trout than do zooplankton, but these processes can be dynamic. Zooplankton sampling should be repeated to update information on species and size composition, and density of edible taxa. The value of gelatinous *Holopedium* as a food source (edibility, energy density, selectivity by planktivores), and their ecological role in the food web are not understood very well.

The energy subsidy from terrestrial insects could be extremely important, but the magnitude of this input is not currently known. The seasonal availability and biomass of insects in the surface film should be sampled with neuston nets. Adult insects contain low water content and often high lipid concentrations, and are thus very high-energy prey in terms of their energy density (Joules/g live body mass). Knowing their source (terrestrial or aquatic) can provide considerable insight into projected contributions of these prey groups, based on land use and climatic trajectories.

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Table 1. Thermal experience from used in model simulations. Source: appendix Fig 2-9 in Pfeifer et al 1998. The low- and High-temperature regimes were used to examine the sensitivity of trout consumption and growth efficiency (see text for details)

Start Month	Day	Temp 1989	Temp 1995	Low-Temp regime	High-Temp regime
Jan	1	3.0	5.0	5.0	5.0
Feb	32	3.0	3.0	3.0	3.0
Mar	60	3.0	4.0	4.0	4.0
Apr	91	5.0	5.0	4.0	6.0
May	121	9.0	8.0	6.0	10.0
Jun	151	12.0	12.0	10.0	14.0
Jul	181	14.0	13.0	11.0	15.0
Aug	211	15.0	14.0	12.0	16.0
Sep	241	16.0	15.0	13.0	17.0
Oct	272	15.0	13.5	11.5	15.5
Nov	303	11.5	13.3	11.3	15.3
Dec	334	8.0	9.5	9.5	9.5
End	365	7.5	8.0	8.0	8.0

Table 2. Annual diet composition for cutthroat trout during four reservoir phases. The diet composition from 1997 was modified for the 1986 and 1992 cohorts, based on changes in frequency of occurrence for mayflies, dipterans, leeches, and zooplankton in 1979-80 versus 1986 (Stables et al. 1990). Energy density (J/g wet weight) of prey are listed at the bottom.

Diet 1979-80								
Day	Mayfly	Stonefly	Caddis	Dipteran	Terrestrial	Other Aq. Inverts	Leeches	Zoopl
1	0.14	0.03	0.17	0.04	0.17	0.11	0.34	0
365	0.14	0.03	0.17	0.04	0.17	0.11	0.34	0
Diet 1986								
Day	Mayfly	Stonefly	Caddis	Dipteran	Terrestrial	Other Aq. Inverts	Leeches	Zoopl
1	0.07	0.03	0.17	0.34	0.17	0.11	0.02	0.09
365	0.07	0.03	0.17	0.34	0.17	0.11	0.02	0.09
Diet 1997								
Day	Mayfly	Stonefly	Caddis	Dipteran	Terrestrial	Other Aq. Inverts	Leeches	Zoopl
1	0.00	0.07	0.10	0.34	0.20	0.29	0.00	0
365	0.00	0.07	0.10	0.34	0.20	0.29	0.00	0
Energy density (J/g Wet Wt)								
Day	Mayfly	Stonefly	Caddis	Dipteran	Terrestrial	Other Aq. Inverts	Leeches	Zoopl
1	3076	4272	4272	3064	5000	2788	4745	3600
365								3600

Table 3. Simulation results for annual growth and consumption of cutthroat trout ages 1-3. Jan 1 is day 1 of simulation. Cutthroat trout spawn at age 3 on May 1 (day 121) and lose 8% body weight as an average gonadal loss for males and females combined.

Year	Age	Wt	Prop. Max consumption	C (g/yr)	G (g/yr)	Growth Eff. (G/C)	Spawn loss %BWt	Diet	Temp
1979-80	1	17.8	0.468	571	73.8	13%		1979-80	1989
	2	91.7	0.517	1536	156.1	10%		1979-80	1989
	3	247.8	0.576	3063	256.0	8%	8%	1979-80	1989
	4	503.8							
1986	1	16.8	0.575	781	98.1	13%		1986	1989
	2	114.9	0.583	1908	153.0	8%		1986	1989
	3	267.9	0.602	3053	161.1	5%	8%	1986	1989
	4	429.1							
1992	1	27.9	0.55	914	98.8	11%		1997	1995
	2	126.7	0.544	1844	121.8	7%		1997	1995
	3	248.5	0.626	3363	222.5	7%	8%	1997	1995
	4	471.0							
1995-97	1	15.3	0.527	636	72.4	11%		1997	1995
	2	87.7	0.516	1360	91.6	7%		1997	1995
	3	179.3	0.524	1973	81.3	4%	8%	1997	1995
	4	260.6							

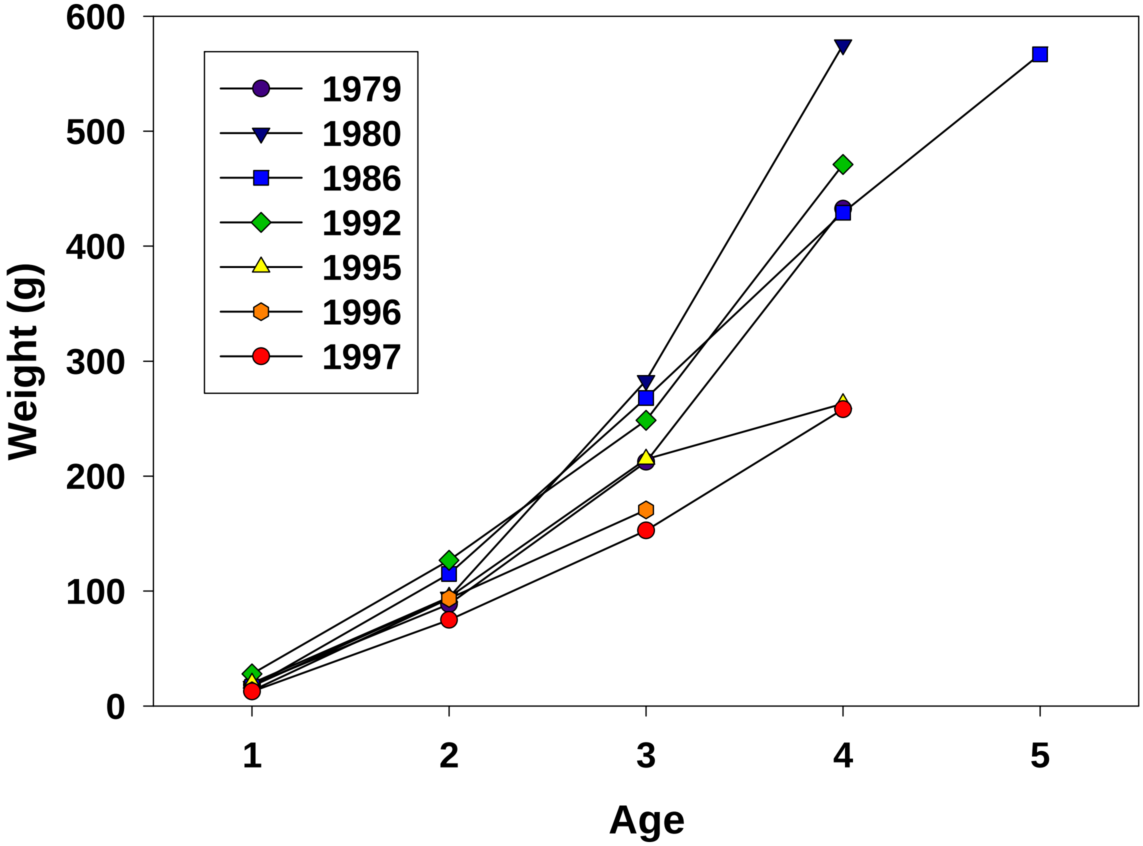

Figure 1. Weight-at-age for cutthroat trout during 1979-1980 (before enlargement of the reservoir in 1984), 1986 (during the early reservoir effect), 1992, and 1995-1997. Note that faster growth was observed during the years prior to the most recent surveys in 1995-1997.

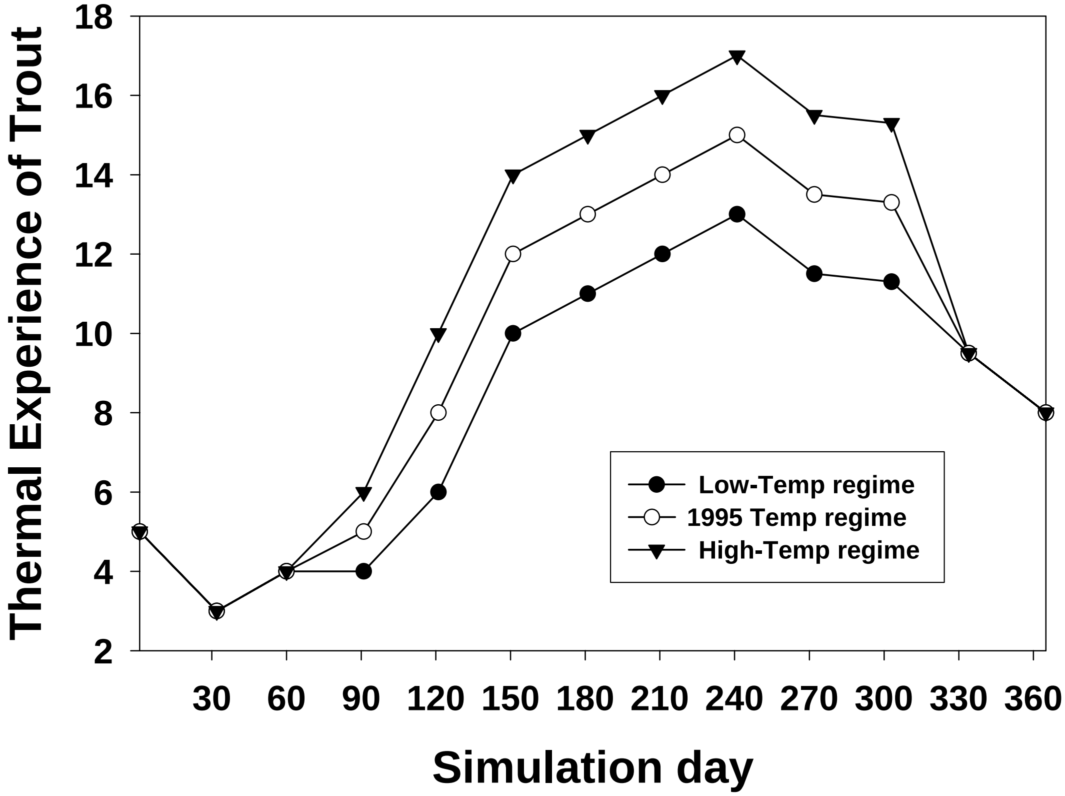

Figure 2. Low- nominal, and high temperature regimes used to examine the sensitivity of cutthroat trout consumption and growth efficiency to different thermal experience.

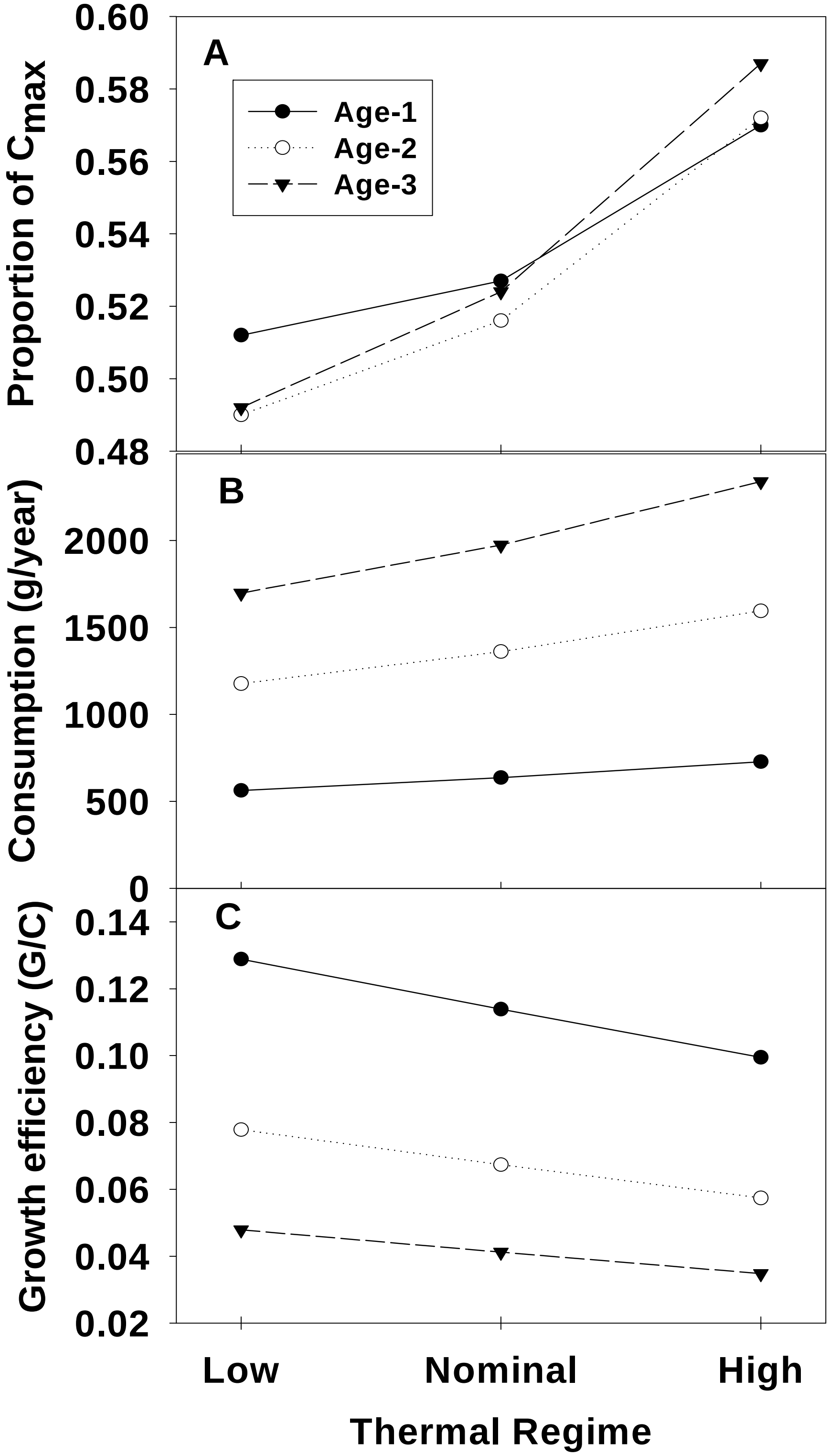

Figure 3. Sensitivity of trout to different thermal regimes in terms of A. feeding rate as a proportion of maximum consumption, B. annual consumption, and C. growth efficiency.

APPENDIX

Summary of Findings excerpted from Pfeifer et al. 1998 Biological Assessment of Spada Lake

Sport fishery creel surveys were conducted on Spada Lake in 1979-80, 1985 through 1989, 1992, and 1995. Fish sampling occurred on the lake and in the tributaries between 1995 and 1997, with most fish being sampledfrom the lake in 1997. The reservoir was sampled quantitatively for zooplankton between early April and mid-November of 1997. This report is a synthesis of these surveys, and makes recommendations for future management of the reservoir and its fishery.

Individual report segments end with a listing of conclusions that are specific to each unit. This report segment is a more general overview of the project's conclusions. The reader should review individual report segments for more detail.

Creel Survey

Catch. Harvest, and Effort

-Total game fish harvest increased five or six-fold (20,243 trout) after the raising of Culmback Dam (Project Stage II), but decreased to 2.1 percent of its 1985 level in 1995 (422 trout).
-A 78% drop in harvest between 1989 and 1995 was not caused by a change in regulations.
-Sharply reduced harvest rates are attributed to a scarcity of legal-sized fish (≥12 inches).
-Catch rates have held fairly constant since 1986, since the number of trout <12 " appears to be relatively high, and total catch includes fish voluntarily released.
-Angler effort (number of trips) on the lake has declined almost continuously since 1985. -Effort in 1995, the last surveyed season, was lower than during Stage I, at just over one trip per surface acre, or 2002 trips in 1995. The 1995 effort level was 15.4 percent of that seen in 1985.

Water Quality

-Dissolved oxygen in the reservoir is at near-saturation levels for much of the year (based primarily on samples taken near the dam), but a zone of reduced oxygen content occurs in the old river channel just upstream of the dam. The dimensions of this zone are poorly documented, but are probably not large.
-The lake is isothermal at about 3°C in mid-winter, and warms to 21°-22 °C by early August.
-The thermocline is only weakly developed due to the reservoir's very high turnover rate (3.41/yr).
-A metalimnion occurs between ***6*** and 9 meters (20 to 30 feet).

Spada Lake Fishey Study: 1995-97

-The 1997 heat budget (20,320 cal/cm2) was the highest in the years 1989 through 1997, but was nevertheless below both median and mean values for lakes of similar size, elevation, and latitude.
-Mineral turbidity is an important occurrence, particularly in the spring. Secchi transparency begins with a low of about 1.5m (5 ft) at that time, peaks in late June at about 4.9m (16 ft), and diminishes during a late August-September phytoplankton pulse to about 2.7m (9 ft). NOTE-These turbidity levels suggest that piscivory by visually-feeding trout should be minimal, but probably does not affect foraging by brown bullheads which rely heavily on chemo-reception and other sensory mechanisms besides vision.
-The euphotic zone was estimated to range from 13.7m (45 ft) in June to 7.6m (25 ft) in September. The mean monthly euphotic zone between June and September was 9.3m (30.4 ft).
-These estimates suggest Spada Lake is roughly equivalent to other reservoirs that were highly oligotrophic and unproductive.
-Historic and present conductivity levels in Spada Lake average 20.6 µS/crn.
-Water column pH values ranged from 6.1 to 7.4, and averaged 6.68.

Secondary Production

Zooplankton

-Of 12 cladocerans identified from Spada Lake, only ***Daphnia rosea*** was seasonally important in the trout diet.
-***Epischura nevadensis*** was the only copepod eaten, and ***then*** only occasionally.
-***Holopedium gibberurn*** **was** the numerically most important plankter, but did not contribute to the trout diet in a meaningful way.

-***Holopedium*** constituted 75 to 95 percent of the plankton for much of the year. ***Daphnia*** and ***Epischura*** were the only important edible species.
-Cyclopoid copepods were far less abundant in Stage **I1** than in Stage I, probably due to reservoir aging.
-Although comparisons with Stage I were very difficult due to differing methods, ***Holopedium*** appeared to be roughly 70% less abundant, ***Daphnia*** is approximately unchanged, and ***Bosmina*** is about 20% of its Stage I density.

-Total crustacean zooplankton density in the reservoir's top 15 feet (12,500 to 16,000 individuals/m3), when used as **an** indirect measure of primary production, is similar to, or higher than that seen in other area lakes and reservoirs having similar putative low potential production.
-The growing season extended from early May through mid- or late October.
-The mean density of edible zooplankton was 1440/m^3. The mean percent of edibles between mid-July and mid-October was 3.1% of the total crustacean zooplankton, which is representative of an oligotrophic system.
-The overwhelming abundance of ***Holopedium*** relative to ***Daphnia,*** plus the near-absence of ***Diaptomus,*** may be a reflection of excessive planktivory. The fish population (trout plus brown bullheads) is probably too numerous for the level of planktonic secondary productivity. NOTE- Total consumption demand by fish on zooplankton cannot be assessed adequately without reasonable estimates of consumer abundance and diet data that are stratified into monthly or seasonal stanzas.
-Low phytoplankton (primary) production is the ultimate cause of food shortages.
Daphnia was clearly the most important rainbow and cutthroat dietary species. However, due to its small size, only about one half of the *Daphnia* in Spada are suitable as trout food.
-Spada Lake in Stage II is oligotrophic, and is expected to remain at that level. Nutrients added by soils flooded in 1985 have probably been exhausted due to ongoing sedimentation into the deeper parts of the reservoir, and earlier removal in intensive fisheries in the mid- to late 1980s.
NOTE-Might be fruitful to explore food web manipulations with trace nutrients and/or essential fatty acids rather than conventional N:P fertilization schemes to customize the energy pathways to favor desirable invertebrates, zooplankton, and fish. Dr. Mike Brett at UW Civil Engineering, would be an excellent resource for this.

Benthos
-Chironomid densities in the drawdown zone appeared to be roughly equivalent to Stage I levels.
-Oligochaete densities appeared to be higher in Stage II, but these invertebrates were not eaten by trout.
-Both midges and segmented worms may be at above-average levels in Spada when compared with other area reservoirs.
-Leeches and clams are minimally present in the trout diet, but are still present in certain zones or locations within the reservoir. NOTE-Loss of energy-rich leeches and mayfly naiads in the diet suggest a significant shift in the benthic community wherein these species have either declined dramatically, or are no longer spatially or behaviorally accessible to trout.
-There was no apparent loss or gain of invertebrates species between Stages I and II, given the very low level of sampling to date.
-Benthic sampling data collected in 1997 should be used to design more complete surveys in future years.

Tertiary Production

-One half of all trout collected were rainbow; somewhat less than one third were cutthroat, and about one fifth were hybrids. A subsample of those fish ≥12" yields species proportions very similar to that seen in the 1986 and 1992 sport fisheries.
-Horizontal gill net catch per unit effort was higher than for vertical gillnets in four of six sampling months. Floating gill nets out-fished sinking horizontals set from the shore's edge.
-Brown bullheads were collected in all gear types, even offshore, but most were taken in the horizontal nets set from shore.
-Trout were always taken from near the surface in vertical nets, but their maximum collection depth increased as the reservoir warmed, then retracted towards the surface in the fall. The deepest trout collected was at 68 ft (20.7m). There was no evidence that older, larger trout preferred deeper water.

Length Frequencies
-Length frequencies of trout collected correlated closely with length-at-age data. Most trout sampled were Age 1 to 3, with older trout being relatively scarce. Trout larger than 32 cm (12.5") were rare.

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

Trout Immigration, Mortality, Population Size, and Standing Stock
A preliminary, indirect estimate of immigration in 1997 ranged from 0.56 to 2.5 trout/acre. A more definitive assessment needs to be made, either by mark-recapture methods, or tributary trapping. Note-This is highly recommended

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

Population Size
Two trout population estimates were made, one based on gillnet catch per unit effort, the other on the relationship between angler catch rate and trout density (Ross Lake model). These ranged from 2,269 to 10,162. The latter figure is more reasonable, but may still be low, at 5.4 trout/acre. Note-Too much uncertainty surrounding these estimates to consider extrapolating per capita consumption estimates by different ages of trout up to a size-structured, population-level consumption estimate for key prey.

Standing Stock
-Based on the larger trout population estimate and the 1ength:weight relationship, trout standing stock in 1997 was estimated as a little less than 1.0 lb/acre.
-Based on Spada's water chemistry and morphometry, and models from other reservoirs, standing stock should be closer to 40 lb/acre.
-The difference is probably due to an erroneous trout population estimate, and/or the lack of an estimate of brown bullhead biomass.

Trout Age, Growth, Condition, and Internal Fat
Age and Growth
-Annual incremental growth of trout Age 3 or older was significantly lower in 1997 than five years earlier.
-Trout growth rates in Spada are lower than most other area reservoir trout populations.
-Relative weights of both rainbow and cutthroat were almost universally below the median, or "good" value of 100 established for this index. Only rainbow showed a slight increase in relative weight over the summer.
-The 1997 trout samples showed sharp declines in both relative weight and relative condition (two separate indices) after 11 to 12 years of reservoir aging.
-Ninety three percent of all trout sampled from Spada Lake in 1997 held little or no internal fat.
-Both rainbow and cutthroat showed a decrease over the summer in the percentage of fish with no fat, but 55 percent of all trout in late October to early November had little or no internal fat.
NOTE-All of the relative weight and fat index results provide compelling evidence for a food-limited population.

Trout Food Habits
-Larger invertebrate food resources in Spada Lake have been reduced or eliminated in the drawdown zone.
-Preferred cladoceran zooplankton species *(Daphnia)* are only suitably abundant and large enough to elicit a trout feeding response for a few weeks of the year.
-Zooplankton occurred more frequently in rainbow stomachs than in cutthroat or hybrids.
-Although almost all trout were obtaining.some food between early April and mid-October, internal fat levels were extremely low, as was relative weight for most trout age groups.

-Only about 6% of all stomachs sampled were judged to be full; a running biweekly mean of degree of fullness was always less than 50 percent.
-Trout diets are currently based predominantly on midge pupae or larvae, supplemented with terrestrial insects and stone- or caddisfly nymphs. Zooplankton (cladocerans) is less important throughout the year, except it is somewhat more important for rainbow, particularly during the July-September period.

Spawning Period and Age at Maturity
-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.
-Most cutthroat mature at Age 3 in Spada Lake, as do a majority of the rainbow. There appears to have been a reduction in mean age at maturity, particularly for rainbow (2.7) and hybrids.
-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 trout collected off stream mouths in spring 1997 was 26.1 cm for cutthroat, and 22.0 cm for rainbow.

Trout Parasitism and Mortality
-Rainbow, cutthroat, and their hybrids were infected with ***Diphyllobothrium ditremum*.**
-Prevalence of the parasite varied seasonally in all three trouts, ranging 10-100% overall, but was 50-100% in mid-November.
-Declines in prevalence within a single species and age group over the summer was interpreted as mortality.
-Infection intensity varied greatly, with plerocercoid counts ranging 0-185 per fish.
-First-year reservoir residents built infections to a mean mid-summer peak of 27 Plerocercoids per fish, but declined to 4/fish in fall.
-Patterns of intensity over the sampling period varied between the trout life history groups, with first-year reservoir residents potentially suffering greatest mortality.
-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.
-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 correlation between plerocercoid counts/fish and the amount of internal body fat. Fat content dropped to trace or non-existent levels in trout bearing more than five or six plerocercoids. NOTE-Regress fat content as a function of plerocercoid count and body weight or body length.
-The final host for ***D. ditremum*** in Spada Lake was not confirmed, and could be one or more species of piscivorous bird or mammal.
-Options with the most promise for indirect control of the parasite in the fish community include a change in the fish species mix, 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
Fisherv Yield
-Estimated fishery yield (annual weight of trout harvested per unit area) nearly tripled at the outset of Stage II, but then declined to 3.2% of the level seen in 1979-80 (Stage I), and 1.1 percent of that seen in 1985.
-Current Stage II water chemistry and reservoir morphology suggest a sustainable annual yield of 1.15 kg/ha (1.03 lb/acre). This represents an estimated 24% reduction from Stage I on a per unit area basis, but reservoir enlargement in Stage II increased overall potential yield 76% from Stage I.
-Attainment of 1.15 kg/ha in the fishery is nearly impossible under the current 12" minimum size regulation. Harvest of smaller, younger age classes of trout will allow an increase in fishery yield, but the negative impact on spawning escapement cannot be assessed without a more accurate trout population estimate, and/or additional trout life history information to allow modeling of various fishery strategies.-NOTE-This is a Key conclusion. A slight reduction in minimum size limit to 11” total length would provide access to considerably more harvestable-sized trout while remaining above the average spawner

size. Such a change would probably moderately reduce the spawning population, and would likely lead to a smaller, but more productive and resilient population (e.g., fewer trout but with higher growth rates and larger lipid reserves).

Recreational Use (Fishing Effort) Levels

Harvest of a preliminary estimate of 6,450 younger trout would cap effort levels at 1.73 tripstacre, or 3,225 txipslyr if all parties harvested two trout per outing.