Henry M. Jackson Hydroelectric Project
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Factors Limiting Trout Production in Spada Lake
Final Technical Report for
Revised Study Plan 16: Spada Lake Trout Production

Prepared for:
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1.0 Introduction

Trout production in Spada Lake declined from previous periods of relatively high production during the 1970s through early 1990s to a lower productivity regime in the mid-1990s (Pfeifer et al. 1998) and remains low under current conditions (Meridian Environmental and Shuksan Fisheries Consulting 2008). The higher productivity during the earlier regime was likely fueled in part by inundation when the reservoir was enlarged; however, the actual processes that currently limit trout production could involve temperature, food supply, predation, disease, or some combination of these factors. Some of the conclusions drawn from past research including Pfeifer et al. (1998) and Beauchamp (2006) that relate to current hypotheses about trout production in Spada Lake 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). Currently, the effects of inter-annual variability on thermal regimes in Spada Lake seem 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.

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 9-14^{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, Beauchamp (2006) used bioenergetics model simulations combined with existing data on diet, growth, and temperature conditions that were 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. Similar analyses were required to evaluate the current growth conditions for trout and to compare the current situation to previous production regimes in Spada Lake.

Prior to this study, the specific factors that currently limit trout production in Spada Lake remained undetermined. Consequently a field sampling effort was mounted during April-November 2007 to measure key data on limnological conditions (temperature, zooplankton), and fish populations (size structure, distribution, diet, and abundance of trout and other fishes) to assess the current physical and biological characteristics of the reservoir fish community (Meridian Environmental and Shuksan Fisheries Consulting 2008). These data were targeted to provide inputs into a bioenergetically-based food web model that would be used to determine what processes limit trout production. This report summarizes the diet, stable isotope, and size-age data that were analyzed from samples collected by Meridian Environmental and Shuksan Fisheries Consulting 2008. Collectively, these data and analyses were synthesized into the bioenergetics modeling analysis.

The objectives of this study were to: 1) describe the trophic interactions of trout and brown bullhead based on diet and stable isotope analyses; 2) assimilate these and supporting field data from Meridian Environmental and Shuksan Fisheries Consulting (2008) into a bioenergetics modeling framework; and 3) use bioenergetics simulations to determine whether food supply, food quality, thermal regime, or density-dependent growth from inter- or intra-specific competition limit trout production.

2.0 Methods

2.1 Diet Analysis

Monthly changes in diet composition were measured for cutthroat, hybrid, and rainbow trout and brown bullheads from April through November 2007. Diet composition was summarized by 100-mm size classes for each species, based on an initial examination of length frequency histograms for the fish and a preliminary examination of diet patterns by size. When possible, the contents from 5-10 non-empty stomachs were examined from each month x species x size class combination. Insects were identified to order and life stage (larval, pupal, or adult); other benthic invertebrates were identified to class or order as appropriate; and zooplankton were identified to genus. These taxa were allocated into functional groups for bioenergetics analysis and included: chironomid pupae, other aquatic forms of insects, terrestrial or adult forms of aquatic insects (i.e., neustonic prey that required foraging on organisms in the surface film), zooplankton (almost exclusively *Daphnia*), other aquatic invertebrates (primarily oligochaetes, amphipods, and gastropods), and fish (juvenile trout and brown bullheads).

Prey were separated into taxa, and blotted-dry wet weights were recorded individually for each stomach sample. These wet weights were converted into proportional weight contributions to the diet of individual fish, and the proportions from non-empty stomachs were averaged for each month x species x size class combination (**Table 1**).

Table 1. Scale-based fork length and corresponding weight at age for cutthroat trout. The weights for adjacent age classes were used as the initial and final weights in the bioenergetics model simulations.

Scale Age	Avg FL	SD	N	Initial Wt (g)	Final Wt (g)	Spawning % Wt loss
1	129	14		25	56	0%
2	172	46	6	56	129	0%
3	233	20	17	129	147	8%
4	245	22	16	147	210	8%
5	279	9	2	210		

2.2 Stable Isotope Analysis

Because diet analysis provides only a snapshot of feeding over the prior 12-36 hours, these results might not detect rare, but important events like fish predation. Stable isotope analysis provides a more time-integrated signal of past feeding history over approximately the prior six months and can determine the trophic position (e.g., herbivore, primary or secondary consumer, based on $\delta^{15}N$ values), and the primary energy pathway through which carbon flows through the food web to that consumer (i.e., benthic versus pelagic prey, based on $\delta^{13}C$; Peterson and Fry 1987; Post 2002; McIntyre et al. 2006). Fish were taken from the October sampling period to ensure that the younger trout that recruited to the reservoir over the summer were included and to measure the isotopic signal during or after the primary growth period for the year. Up to 1 g of skinless dorsal muscle tissue was dissected from the sample fish. Muscle tissue was rinsed in deionized water, and all samples were dried at approximately 60ºC, ground into powder, and homogenized. A 1.0 mg ± 0.2 mg sample was weighed on a Cahn electrobalance, precise to 0.001 mg, and sent to the Colorado Plateau Stable Isotope Laboratory for analysis.

Stable isotope signatures for trophic level and energy pathway were examined as a function of body size to determine whether ontogenetic shifts in food habits were evident (e.g., piscivory by larger trout, or shifts between benthic and pelagic feeding modes; McIntyre et al. 2006). The $\delta^{15}N$ and $\delta^{13}C$ of individuals from the different species were plotted together to determine whether feeding niches were separate or overlapping. A full trophic level difference in feeding (e.g., herbivore to primary carnivore or primary to secondary carnivore) is typically represented by an increase of 3-3.4‰ in $\delta^{15}N$, whereas a smaller difference would indicate a mixed diet of prey from different trophic levels. More negative $\delta^{13}C$ values suggest a higher reliance on pelagic-origin prey (e.g., phytoplankton-based energy pathway), whereas higher $\delta^{13}C$ values indicate greater contributions of terrestrial or benthically-derived prey (e.g., periphyton-, macrophyte-, or riparian-based energy pathway).

2.3 Bioenergetics Modeling

Bioenergetics model simulations can estimate the feeding rate and total biomass of prey that must be consumed in order to satisfy the observed growth rates for each age class of trout, given the diet composition and thermal regime experienced by each age class used in the simulations. Because data were incomplete for hybrid and rainbow trout, the model simulations focused on cutthroat trout. Simulations for each age class started on April 1 (simulation day 1) and ran for 365 d. April 1 was selected as a convenient starting date, because it likely corresponded with completion of the previous annulus on scales (based on the seasonal thermal regime in the reservoir) and coincided with the start of sample collection for the model inputs. Based on monthly length frequency data (Meridian Environmental and Shuksan Fisheries Consulting 2008), peak recruitment of age-1 trout into the reservoir occurred around July 1 (day 90 of the simulation), so simulations for age-1 trout extended from July through March.

The average annual growth of ages 1-4 cutthroat trout were used to fit consumption rates. For length (mm) at age was estimated from scales (N=41; **Table 1**) and otoliths (N=45) and were compared to seasonal length frequency histograms for cutthroat trout and all trout combined. Fork lengths (FL in mm) for cutthroat trout were converted to weight (Wt in g) at each annulus using a length-weight regression (r^2 = 0.983; N = 299; P < 0.00001):

$$Wt(g) = 0.0000418 \cdot FL(mm)^{2.7408}.$$

The weight at the age-1 annulus was used as the initial weight and weight at the age-2 annulus was used as the final weight for age-1 trout in the bioenergetics model simulations. Similarly, the starting weights for subsequent year classes were used as the final weights for the previous year classes (**Table 1**).

Monthly diet composition for the 100-199 mm FL size class was assigned to age-1 cutthroat trout, and the diet composition for 200-299 mm trout was assigned to all older age classes. Over the entire sampling period, only 1-2 non-empty stomachs were available for cutthroat, hybrid, or rainbow trout ≥ 300 mm FL. Since the diets and stable isotope values for these larger trout were similar to the 200-299 mm size class, the diets were pooled together for these two size classes. The diet composition inputs to the model were aggregated into functional groups and assigned energy density values (J/g) based on bomb calorimetry measurements of similar prey taxa from other waters in the Pacific Northwest (**Table 2**).

Table 2. Monthly diet composition by weight and size class for cutthroat trout in Spada Lake during April 2007 to March 2008. April 1st is Day 1 of the simulation and March 31st is day 365. Diet proportions in the model are interpolated daily from one entry to the next in the table below. Diets in November were assumed to shift back to the observed April diet by January 1st (day 270), except that the proportions for adult or terrestrial insects were re-allocated to the most likely category for winter feeding, like aquatic forms of insects. The corresponding energy density (J/g wet weight) for each prey category is listed at the bottom of each table.

100-199 mm FL Cutthroat trout

Day	Chironomid Pupae	Aquatic Insects	Adult or Terrestrial Insects	Zoo-plankton	Other Aquatic Inverts.	Fish
1	0.58	0.26	0.16	0.00	0.00	0.00
30	0.43	0.23	0.29	0.00	0.05	0.00
60	0.01	0.52	0.29	0.00	0.18	0.00
90	0.51	0.23	0.08	0.18	0.00	0.00
120	0.00	0.01	0.25	0.74	0.00	0.00
150	0.09	0.28	0.29	0.32	0.02	0.00
180	0.00	0.36	0.00	0.30	0.34	0.00
210	0.01	0.19	0.17	0.49	0.14	0.00
270	0.58	0.26	0.00	0.05	0.11	0.00
365	0.58	0.26	0.16	0.00	0.00	0.00
J/g:	3064	4272	4993	1930	2788	5000

200-299 mm FL Cutthroat trout

Day	Chironomid Pupae	Aquatic Insects	Adult or Terrestrial Insects	Zoo-plankton	Other Aquatic Inverts.	Fish
1	0.60	0.37	0.03	0.00	0.00	0.00
30	0.25	0.41	0.31	0.00	0.03	0.00
60	0.01	0.70	0.01	0.00	0.23	0.05
90	0.26	0.70	0.03	0.00	0.01	0.00
120	0.08	0.08	0.47	0.33	0.04	0.00
150	0.08	0.17	0.33	0.05	0.17	0.20
180	0.01	0.09	0.54	0.35	0.01	0.00
210	0.01	0.33	0.21	0.41	0.04	0.00
270	0.58	0.37	0.00	0.05	0.00	0.00
365	0.60	0.37	0.03	0.00	0.00	0.00
J/g:	3064	4272	4993	1930	2788	5000

Thermal experience of cutthroat trout was estimated by combining data on seasonal vertical distribution from gill net CPUE data and hydroacoustic data during peak thermal stratification (Meridian Environmental and Shuksan Fisheries Consulting 2008) with monthly vertical temperature profiles (**Table 3**).

Table 3. Thermal experience of trout during 2007, based on monthly vertical temperature profiles with the temperature experienced by trout estimated by averaging the temperatures over their modal depth distribution.

Month	Day	Thermal experience	Modal Depth (m)
Apr	1	5.5	1-15
May	32	10.0	1-5
Jun	60	12.6	1-10
Jul	91	14.9	1-15
Aug	121	16.6	1-15
Sep	151	15.7	1-15
Oct	181	10.5	1-15
Nov	211	8.2	1-15
Dec	241	4.4	1-15
Jan	272	2.6	1-15
Feb	303	2.4	1-15
Mar	334	2.7	1-15
Mar31	365	3.2	1-15

3.0 Results

3.1 Diet Composition

Cutthroat trout fed predominately on aquatic and terrestrial insects, zooplankton, benthic invertebrates, and only rarely on fish prey (**Table 4**). Aquatic forms of insects (i.e., larvae, naiads, pupae) were important to all size classes of trout throughout the year, representing 11-70% of the diet by weight. In addition to the other aquatic insects, chironomid pupae contributed heavily to the diet during April-May and again in July. Adult and terrestrial insects were important to smaller cutthroat trout (100-199 mm) during the spring and sporadically during summer and fall, whereas these were particularly important to larger trout during May (25%) and August-November (21-53%). *Daphnia* contributed 18-49% of the diet for smaller trout during July-November. *Daphnia* were also important to larger trout during August (33%) and October-November (35-41%), but were supplanted by benthic invertebrates and fish prey during September.

Most of the sampled brown bullheads fell within the 100-199 mm size range which pre-empted the opportunity to detect size-dependent diet differences (**Table 4**). This size class of brown bullheads fed heavily on other aquatic invertebrates during most of the year, but appeared to feed exclusively on *Daphnia* during September. Aquatic insects were important during July and November.

Table 4. Monthly proportional diet composition by weight and sample size of non-empty stomachs examined for each size class of cutthroat trout, hybrid trout, rainbow trout, and brown bullhead sampled during April-November 2007.

Species & Size class	Month	N	Chiro-nomid Pupae	Aquatic Insects	Adult-Terrestrial insects	Zoo-plankton	Other Aq Inverts	Fish
Cutthroat trout								
100-199	Apr	5	0.58	0.26	0.16	0.00	0.00	0.00
	May	10	0.43	0.23	0.29	0.00	0.05	0.00
	Jun	5	0.01	0.52	0.29	0.00	0.18	0.00
	Jul	5	0.51	0.23	0.08	0.18	0.00	0.00
	Aug	4	0.00	0.01	0.25	0.74	0.00	0.00
	Sep	6	0.08	0.28	0.29	0.32	0.02	0.00
	Oct	5	0.00	0.36	0.00	0.30	0.34	0.00
	Nov	5	0.01	0.19	0.17	0.49	0.14	0.00
200-299	Apr	10	0.60	0.37	0.03	0.00	0.00	0.00
	May	12	0.25	0.41	0.31	0.00	0.03	0.00
	Jun	5	0.01	0.70	0.01	0.00	0.24	0.05
	Jul	6	0.26	0.70	0.03	0.00	0.01	0.00
	Aug	5	0.08	0.08	0.47	0.33	0.04	0.00
	Sep	5	0.08	0.17	0.33	0.05	0.17	0.20
	Oct	5	0.01	0.09	0.54	0.35	0.01	0.00
	Nov	5	0.01	0.34	0.21	0.41	0.04	0.00
300-350	May	1	0.00	1.00	0.00	0.00	0.00	0.00
Hybrid trout								
100-199	Apr	7	0.58	0.40	0.00	0.00	0.02	0.00
	May	11	0.35	0.38	0.23	0.00	0.04	0.00
	Jun	5	0.03	0.47	0.36	0.00	0.13	0.00
	Jul	7	0.42	0.30	0.14	0.14	0.00	0.00
	Aug	4	0.11	0.25	0.01	0.62	0.00	0.00
	Sep	6	0.12	0.34	0.14	0.18	0.22	0.00
	Oct	5	0.01	0.16	0.24	0.34	0.24	0.00
	Nov	5	0.02	0.30	0.06	0.38	0.24	0.00
200-299	Apr	8	0.27	0.50	0.23	0.00	0.00	0.00
	May	6	0.24	0.09	0.63	0.00	0.04	0.00
	Jun	5	0.04	0.49	0.46	0.00	0.00	0.00
	Jul	4	0.56	0.23	0.20	0.00	0.00	0.00
	Aug	1	0.00	0.05	0.68	0.25	0.02	0.00
	Oct	5	0.10	0.25	0.55	0.05	0.05	0.00
	Nov	5	0.01	0.36	0.25	0.11	0.27	0.00
300-350	Jun	1	0.00	0.48	0.52	0.00	0.00	0.00

Table 4--Continued.

Species & Size class	Month	N	Chironmid Pupae	Aquatic Insects	Adult-Terrestrial insects	Zoo-plankton	Other Aq Inverts	Fish
Rainbow trout								
50-99	June	1	0.00	1.00	0.00	0.00	0.00	0.00
100-199	Apr	9	0.62	0.34	0.04	0.00	0.01	0.00
	May	10	0.09	0.47	0.35	0.00	0.10	0.00
	Jun	6	0.06	0.12	0.17	0.00	0.66	0.00
	Jul	6	0.57	0.31	0.12	0.00	0.00	0.00
	Aug	4	0.00	0.12	0.14	0.73	0.00	0.00
	Sep	6	0.21	0.49	0.10	0.02	0.19	0.00
	Oct	5	0.00	0.16	0.08	0.66	0.09	0.00
	Nov	5	0.02	0.17	0.24	0.51	0.07	0.00
200-299	Apr	7	0.65	0.25	0.00	0.00	0.11	0.00
	May	8	0.12	0.45	0.34	0.00	0.09	0.00
	Jun	1	0.00	0.00	0.00	0.00	1.00	0.00
	Jul	3	0.45	0.36	0.00	0.18	0.02	0.00
	Sep	3	0.01	0.03	0.75	0.16	0.06	0.00
	Oct	2	0.01	0.33	0.66	0.00	0.01	0.00
	Nov	2	0.00	0.74	0.18	0.00	0.08	0.00
300-350	Apr	1	0.00	1.00	0.00	0.00	0.00	0.00
	May	1	0.00	1.00	0.00	0.00	0.00	0.00
Brown bullhead								
50-99	May	1	0.00	0.01	0.00	0.00	0.99	0.00
100-199	May	5	0.00	0.07	0.00	0.00	0.92	0.00
	Jul	5	0.18	0.54	0.01	0.00	0.28	0.00
	Sep	6	0.00	0.00	0.00	1.00	0.00	0.00
	Nov	6	0.00	0.34	0.00	0.04	0.62	0.00

3.2 Stable Isotope Analysis

The range in average $\delta^{15}N$ signals (from 5.5‰ to7.6‰) across all sizes of brown bullheads, trout, and largescale suckers *Catastomus macrocheilus* spanned less than one full trophic level ($\delta^{15}N$ 3.0-3.4‰; **Figure 1**). Brown bullheads showed significantly higher trophic position ($\delta^{15}N$) than all species of trout (ANOVA and two-sample t-tests, $P < 0.002$). Brown bullheads overlapped considerably in carbon source ($\delta^{13}C$) with cutthroat ($P = 0.40$) and rainbow trout ($P = 0.07$), but differed from large hybrid trout (P = 0.02). In general, trout diverged somewhat from brown bullheads with lower $\delta^{15}N$ and higher (less negative) $\delta^{13}C$, suggesting a heavier reliance on benthic invertebrates by trout, and a slightly higher tendency toward pelagic carnivory (higher $\delta^{15}N$ and lower $\delta^{13}C$) by brown bullheads. Both small and large largescale suckers focused on lower trophic-level benthic invertebrates.

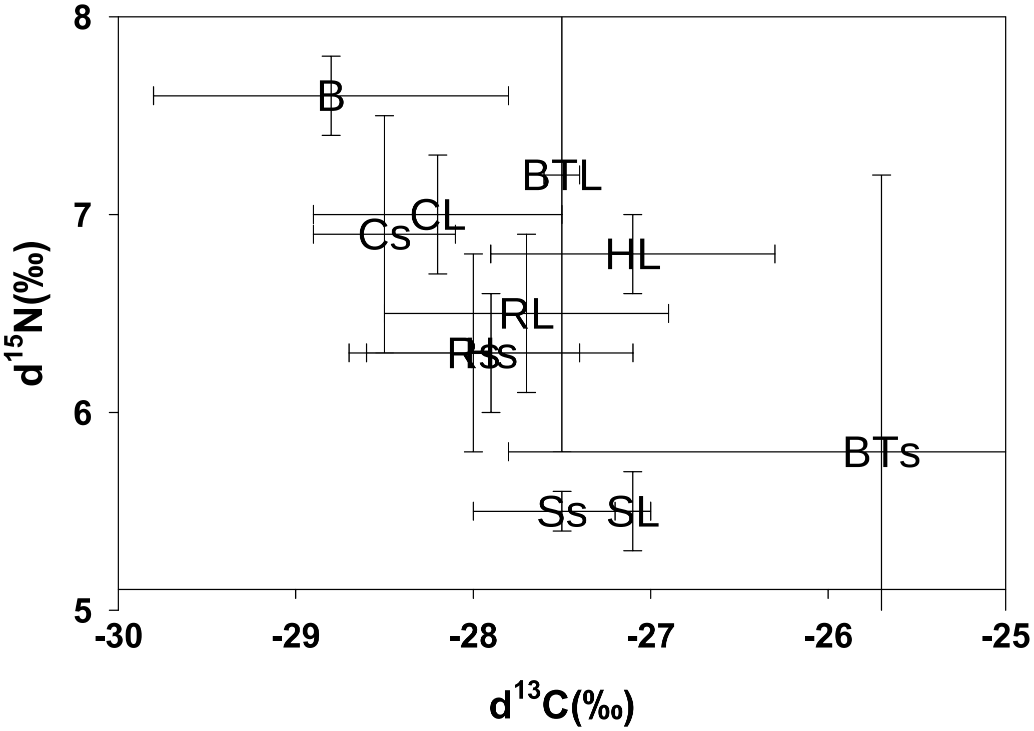

Figure 1. Average (± 2SE) stable isotope values $\delta^{15}N$ and $\delta^{13}C$ for brown bullheads (B, 100-199 mm), small (100-199 mm FL) cutthroat Cs, hybrid Hs, rainbow Rs, and brook trout BTs, large (200-299 mm FL) cutthroat CL, hybrid HL, rainbow RL, and brook trout BTL, and small Ss and large SL largescale suckers in Spada Lake sampled during 2007.

Small and large trout of all three forms generally clustered at intermediate values for $\delta^{15}N$ and $\delta^{13}C$ (**Figure 1**). The small differences in $\delta^{15}N$ (0.1-0.5 ‰) between smaller and larger trout of the same species was much smaller than the 3.0-3.4‰ difference expected between two trophic levels. Thus, the patterns in $\delta^{15}N$ showed no evidence for a significant shift toward piscivory by larger trout and corroborated the findings from the diet analysis. Although all trout forms exploited somewhat similar food resources, some interspecific differences suggested a mild degree of trophic segregation. Cutthroat trout differed significantly in $\delta^{15}N$ from hybrid (P = 0.02) and rainbow trout (P = 0.004), but only differed significantly in $\delta^{13}C$ from larger hybrid trout ($P = 0.04$). Rainbow and hybrid trout strongly overlapped in both $\delta^{15}N$ and $\delta^{13}C$ ($P > 0.30$). Only four brook trout were encountered, so estimates of average $\delta^{15}N$ and $\delta^{13}C$ were highly variable. Nonetheless, large brook trout overlapped with all other trout forms and sizes, whereas small brook trout exhibited signals indicative of feeding heavily on lower trophic level (mostly herbivorous) insects and other benthic invertebrates.

3.3 Growth

Growth was high during the periods before (1979-1980), during reservoir enlargement (1986), and for at least six years after (1992) producing 400-600 g age-4 or 5 fish, but growth rates declined markedly by the mid-1990s and worsened by 2007 (**Figure 2**). The weight-at-age of cutthroat trout was smaller in 2007 than for all of the previous years on record, especially for the older age classes (ages 4-5; **Figure 2**). During 2007, very few trout larger than 300 mm FL were encountered despite intensive net sampling throughout the growing season (**Figure 3**). A pulse of smaller trout FL<150 mm during summer (primarily late June-early July) indicated peak recruitment of age-1 trout into the reservoir.

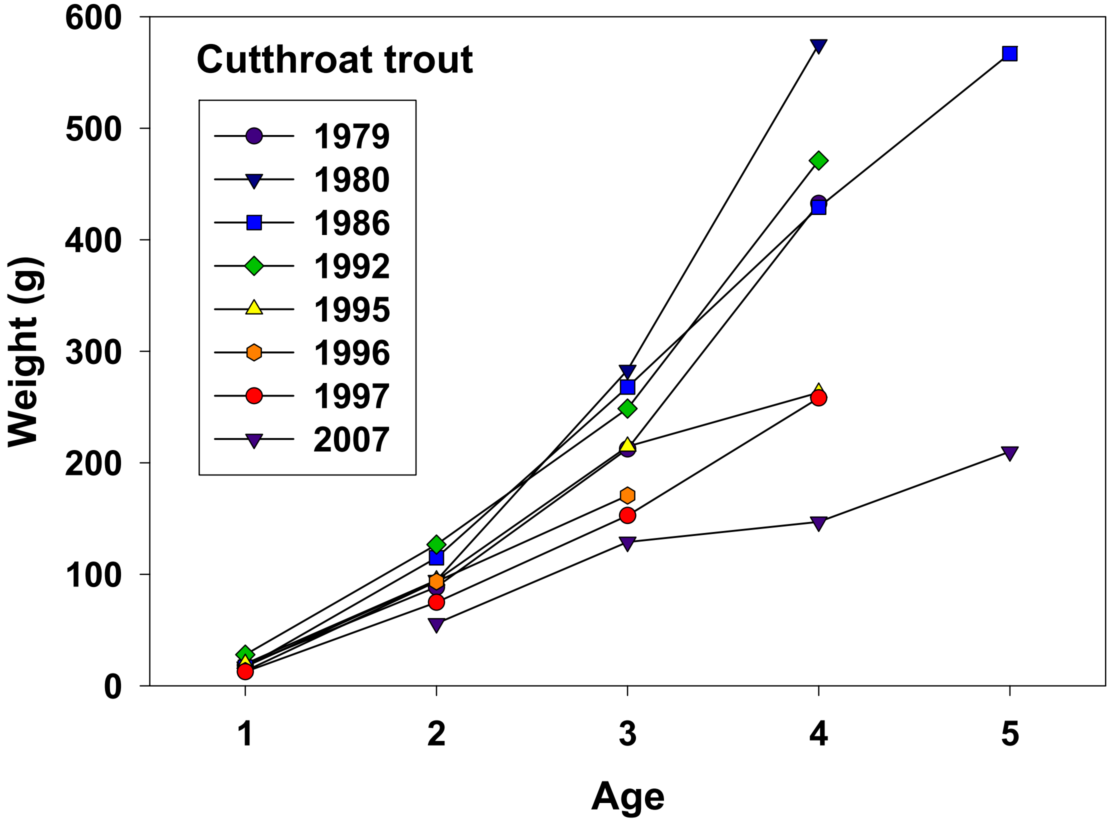

Figure 2. Weight-at-age for cutthroat trout during 1979-1980 (before enlargement of the reservoir in 1984), 1986 (during the early reservoir effect), 1992, 1995-1997, and 2007. Note that growth has been consistently lower since 1992, with weight at age declining first for older ages in 1995, then declining for progressively younger ages during 1996-1997 and 2007.

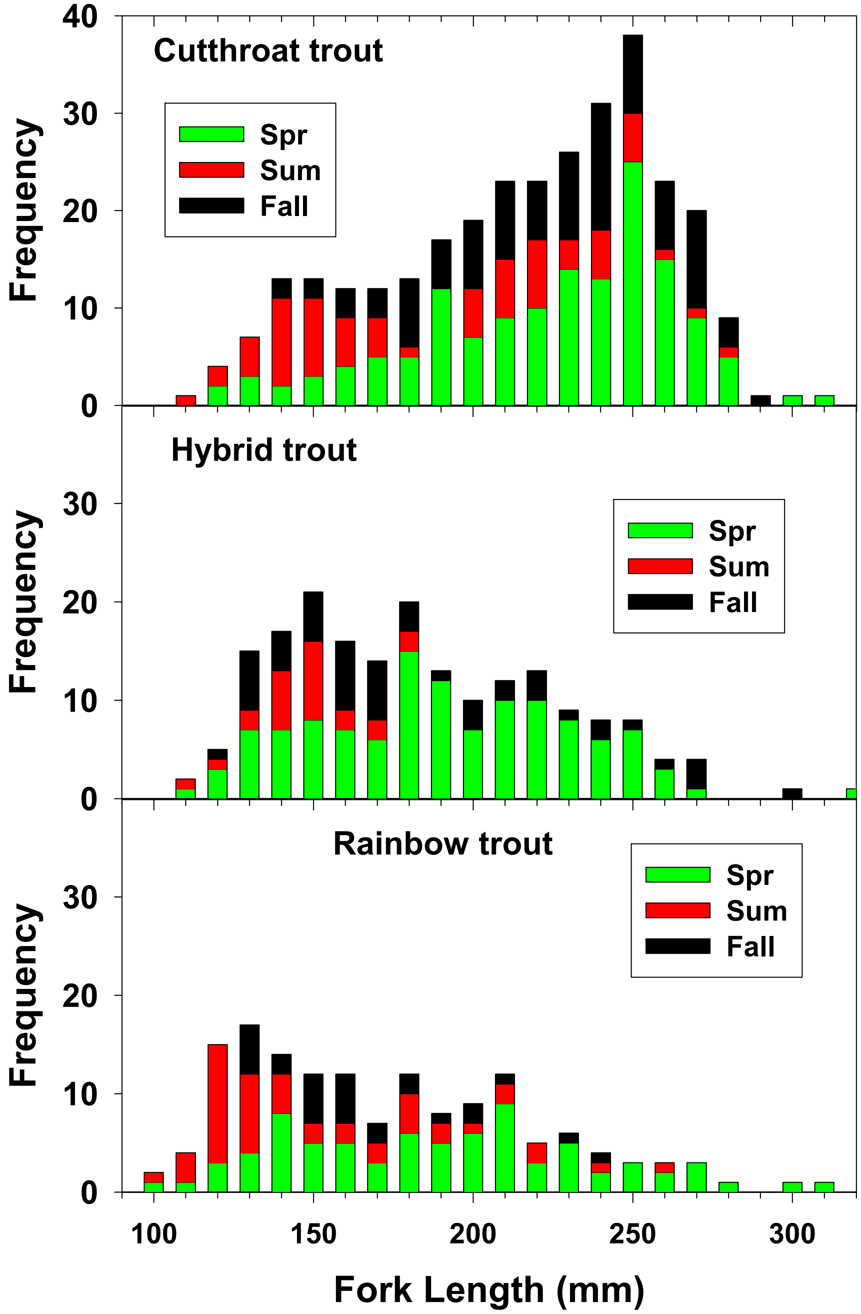

Figure 3. Seasonal length frequency histograms of cutthroat, hybrid and rainbow trout sampled in Spada Lake during 2007 (data from Meridian Environmental and Shuksan Fisheries Consulting 2008). Note the pulse of smaller trout FL<150 mm during summer (July), which indicates peak recruitment into the reservoir of age-1 trout.

3.4 Temperature Regime and Vertical Distribution of Trout

Temperatures were extremely cold (<3.5°C) during winter 2007 and January-April 2008 (**Table 5**). The water column warmed during spring with pronounced surface warming during May and June, followed by strong thermal stratification during July-September. Depths where temperatures exceeded optimal temperatures for trout growth (>15°C, when food supply is abundant) occurred at 0-6 m in July and 0-10 m in both August and September. During May (both years), trout concentrated in the upper 0-5 m where 10°C water was considerably warmer than the rest of the water column. Despite sub-optimal warm epilimnetic temperatures, trout occupied the upper water column (0-15 m or 0-20 m) throughout the growing season (Meridian Environmental and Shuksan Fisheries Consulting 2008).

Table 5. Monthly vertical temperature profiles for Spada Lake during March 2007-May 2008. The yellow-shaded cells indicate depths where temperatures exceeded optimal temperatures for trout growth if food supply was unlimited. When feeding rates decline below 50% of the maximum rate (50% Cmax), optimal growth conditions and thermal tolerances shift toward cooler temperatures. The assumed modal depths occupied by trout and resulting thermal experience are indicated on the rows below the temperature profile values.

	2007										2008				
	Months:														
Depth(m)	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5
0		6.6	10.7	14.7	19.6	19.5	17.7	11.1	8.3	4.3	2.3	0.1	0.5	2.1	8.1
1	3.6	5.9	10.6	14.7	19.5	19.5	17.7	11.1	8.4	4.4	2.6	1.7	2.6	3.2	7.8
2	3.6	5.8	10.2	14.3	19.1	19.3	17.6	11.0	8.4	4.4	2.5	2.0	2.6	3.1	7.4
3	3.5	5.7	10.0	13.9	18.6	19.2	17.5	10.9	8.3	4.3	2.5	2.2	2.5	3.1	7.0
4	3.5	5.6	9.7	13.5	17.9	19.1	17.4	10.9	8.3	4.3	2.5	2.4	2.6	3.1	6.5
5	3.5	5.5	9.4	13.0	16.8	18.9	17.4	10.9	8.3	4.3	2.5	2.5	2.6	3.1	6.1
6	3.6	5.6	9.1	12.5	15.8	18.6	17.4	10.9	8.4	4.4	2.6	2.6	2.7	3.2	5.8
7	3.5	5.4	8.6	11.8	14.7	17.7	17.0	10.7	8.2	4.3	2.5	2.4	2.6	3.1	5.3
8	3.6	5.4	8.3	11.4	14.1	16.9	15.8	10.7	8.3	4.4	2.6	2.5	2.7	3.2	5.2
9	3.6	5.3	7.9	11.0	13.5	16.1	16.2	10.6	8.3	4.5	2.7	2.6	2.8	3.3	5.1
10	3.5	5.1	7.5	10.5	12.8	15.1	15.3	10.4	8.2	4.4	2.6	2.6	2.7	3.2	4.9
11				10.1	12.1	14.2	14.2	10.2	8.2	4.4	2.6	2.5	2.7	3.2	4.8
12	3.5	5.0	6.8	9.8	11.7	13.4	13.5	10.1	8.2	4.4	2.7	2.6	2.7	3.2	4.7
13	3.5	5.0	6.5	9.4	11.2	12.5	12.0	9.9	8.1	4.4	2.6	2.6	2.7	3.2	4.6
14	3.4	4.9	6.2	9.0	10.7	11.6	10.6	9.7	8.0	4.4	2.6	2.6	2.7	3.2	4.5
15								9.4	7.9	4.3	2.6	2.5	2.7	3.2	4.4
20	3.5	4.7	5.3	6.5	7.7	7.4	6.8	8.4	7.7	4.4	2.7	2.7	2.8	3.3	4.3
25	3.5	4.6	5.0	5.6	6.3	6.5	6.4	7.3	7.4	4.4	2.8	2.8	2.9	3.3	4.2
30	3.4	4.5	4.8	5.3	5.9	6.2	6.0	6.6	6.9	4.4	2.8	2.9	2.9	3.4	4.1
35	3.4	4.5	4.7	5.1	5.6	5.8	5.7	6.2	6.5	4.4	2.8	2.9	2.9	3.4	4.0
40	3.5	4.5	4.6	5.0	5.4	5.6	5.6	6.0	6.4	4.5	2.9	3.1	3.0	3.5	4.1
45	3.5	4.6	4.6							4.4	2.9	3.0	2.9	3.4	4.0
50	3.4	4.5	4.5	4.6	4.9	5.1	5.3	5.7	6.0	4.4	2.8	2.8	2.8	3.3	4.0
55	3.3	4.4	4.4	4.5	4.8	5.0	5.3	5.6	6.0	4.3	2.8	2.9	2.8	3.3	3.9
60	3.4	4.5	4.5							4.4	2.9	3.0	2.9	3.4	4.0
64	3.4	4.5	4.5							4.4	3.2	3.2	3.1	3.4	4.0
Vertical Distribution	1-15	1-15	1-5	1-10	1-15	1-15	1-15	1-20	1-20	1-20	1-20	1-20	1-20	1-15	1-5
Thermal experience	3.5	5.5	10.0	12.6	14.9	16.6	15.7	10.5	8.2	4.4	2.6	2.4	2.7	3.2	7.0

3.5 Bioenergetics Simulations of Seasonal Feeding Rate, Consumption, Growth, and Growth Efficiency

Model simulations indicated that cutthroat trout fed at a moderate rate of 46-63% of the maximum theoretical rate (C_{max}), but annual growth efficiencies (GE) were quite low at 1.5-7.2% (**Table 6**), compared to more typical GE ≥10% expected for this size range of trout. Although per capita annual consumption rates C increased with age, growth and growth efficiency declined markedly when fish matured and incurred spawning losses at ages 3 and 4. Unlike years before the mid-1990s, growth rates declined well before trout achieved 300 mm FL and 300 g weight. In fact, even age-5 cutthroat trout averaged only 279 mm FL and 210 g.

Table 6. Simulated consumption (C in g) and growth efficiency (GE = g growth/g consumption) from bioenergetics model fits of annual growth increments to observed size-at-age for cutthroat trout sampled during 2007. Feeding rate is expressed as a percentage of the maximum theoretical consumption rate (C_{max}) for a fish of the same body mass that experienced the same thermal regime.

Scale Age	Initial FL (mm)	Final FL (mm)	Initial Wt (g)	Final Wt (g)	%C_{max}	C (g)	G (g)	GE	Spawning % Wt loss
1	129	172	25	56	63%	433	31	7.2%	0%
2	172	233	56	129	52%	1064	72	6.8%	0%
3	233	245	129	147	46%	1240	19	1.5%	8%
4	245	279	147	210	52%	1674	62	3.7%	8%

The simulated growth trajectories for age 2-4 cutthroat trout exhibited relatively fast initial growth during spring with increasing water temperature, followed by slower growth by ages 1-2 and weight loss by ages 3-4 during peak summer stratification in July-September, a second pulse of faster growth by all ages during fall, then weight loss during winter (**Figure 4a-b**). Population-level consumption by newly-recruiting age-1 cutthroat trout peaked during summer at 1,437 kg of prey when they fed primarily on *Daphnia* followed by aquatic forms of insects and terrestrial or adult aquatic insects (neuston); consumption on a similar prey composition declined to 1,088 kg of prey in fall, and very low (346 kg) during winter (**Figure 4c; Table 7**). Population-level consumption for age 2-4 cutthroat trout was relatively high during spring (4,602 kg), and corresponded with increasing water temperatures and relatively fast growth while feeding predominantly on aquatic forms of insects and chironomid pupae (**Figure 4a,b,d;**

Table 7). Although consumption peaked during summer (5,660 kg), growth decelerated or declined for age 2-4 cutthroat trout during summer stratification; approximately half of the food biomass consumed was relatively high-energy terrestrial or adult insects and some fish, but a significant fraction of the diet was also composed of much lower-energy *Daphnia*. Growth rates increased as temperatures declined during fall, despite lower consumption (3,642 kg) and a similar diet composition to the summer. Population-level consumption rates for age 2-4 trout were lowest during winter (1,330 kg).

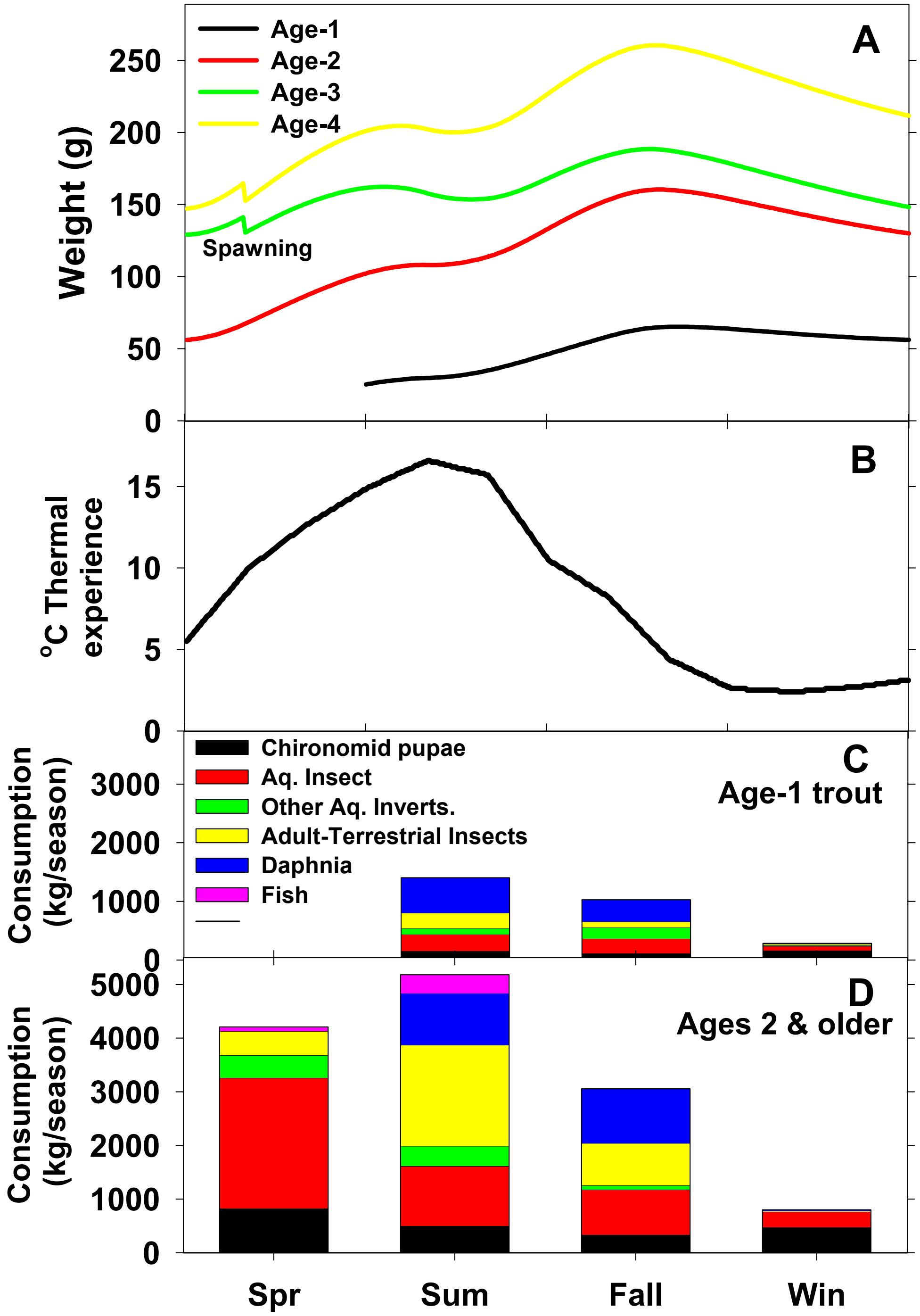

Figure 4. A. Simulated daily growth trajectories for each age class of cutthroat trout exposed to the temperature regime (panel B). The resulting seasonal population-level consumption on each major prey category are presented for C. age-1 cutthroat trout and D. ages 2-4 cutthroat trout.

Table 7. Seasonal, population-level consumption rates (kg prey eaten/season) by age class for all trout in Spada Lake, based on size-specific diet composition and growth of cutthroat trout.

Age	Season	Nt	Mean Wt (g)	Chiro-nomid Pupae	Aquatic Insects	Other Aq Inverts	Adult-Terrestrial insects	Zoo-plankton	Fish	Total food (kg)
1	Sum	6,660	33	155	285	101	266	597	-	1,437
	Fall	6,024	60	117	252	189	100	372	-	1,088
	Win	5,437	59	166	74	15	23	7	-	346
				437	611	305	389	976	-	2,718
2	Spr	4,967	78	269	825	143	145	-	28	1,487
	Sum	4,607	113	186	406	141	703	360	129	2,039
	Fall	4,273	153	134	332	30	309	397	-	1,356
	Win	3,955	141	189	118	-	5	8	-	460
				778	1,681	315	1,162	765	157	4,858
3	Spr	3,661	144	288	829	142	156	-	27	1,586
	Sum	3,396	159	161	353	118	588	302	106	1,786
	Fall	3,150	183	99	249	23	235	301	-	1,090
	Win	2,916	162	137	86	-	4	6	-	395
				686	1,517	282	983	609	133	4,210
4	Spr	2,699	171	269	784	134	145	-	26	1,529
	Sum	2,503	206	160	349	119	590	303	107	1,835
	Fall	2,322	251	104	260	24	244	313	-	1,196
	Win	2,149	228	146	92	-	4	6	-	476
				679	1,484	276	984	622	133	4,178
Total 1-4	Spr	17,987	426	980	2,723	519	713	597	81	6,039
	Sum	16,530	537	623	1,360	566	1,981	1,338	343	6,748
	Fall	15,181	646	504	915	92	811	1,018	-	3,987
	Win	9,020	531	909	907	305	401	996	-	4,049
				2,142	4,682	873	3,128	1,996	423	13,246

The weight loss or depressed growth during summer compared to improved growth rates in fall, despite a lower feeding rate and similar energy composition of the diets during fall, suggests that warm epilimnetic summer temperatures and a limited supply of high-energy food combined to limit overall growth of trout in Spada Lake under current conditions. The effect of a slightly lower thermal experience on growth was explored by assuming that a either cooler temperature regime or behavioral thermoregulation exposed trout to summer temperatures $\leq 14^{o}$C while diet composition, feeding rate as a proportion of C_{max}, and initial weight remained the same (**Figure 5a-b**). By limiting thermal exposure to 14^{o}C instead of ranging from $14\text{-}16.6^{o}$C over the summer (**Figure 5b**), relatively high growth rates were maintained over the summer and the final weight on day 365 (March 31st) increased from 147 g to 173 g for age 3 trout and from 210 g to 245 g for age 4 trout (**Figure 5a**). The larger body size and cooler temperatures led to both age classes eating 7% more food under the cooler scenario, but this translated into 17-18% higher final weights, and growth efficiency also improved from 1.5% to 3.4% for age 3 and from 3.7% to 5.5% for age 4 trout.

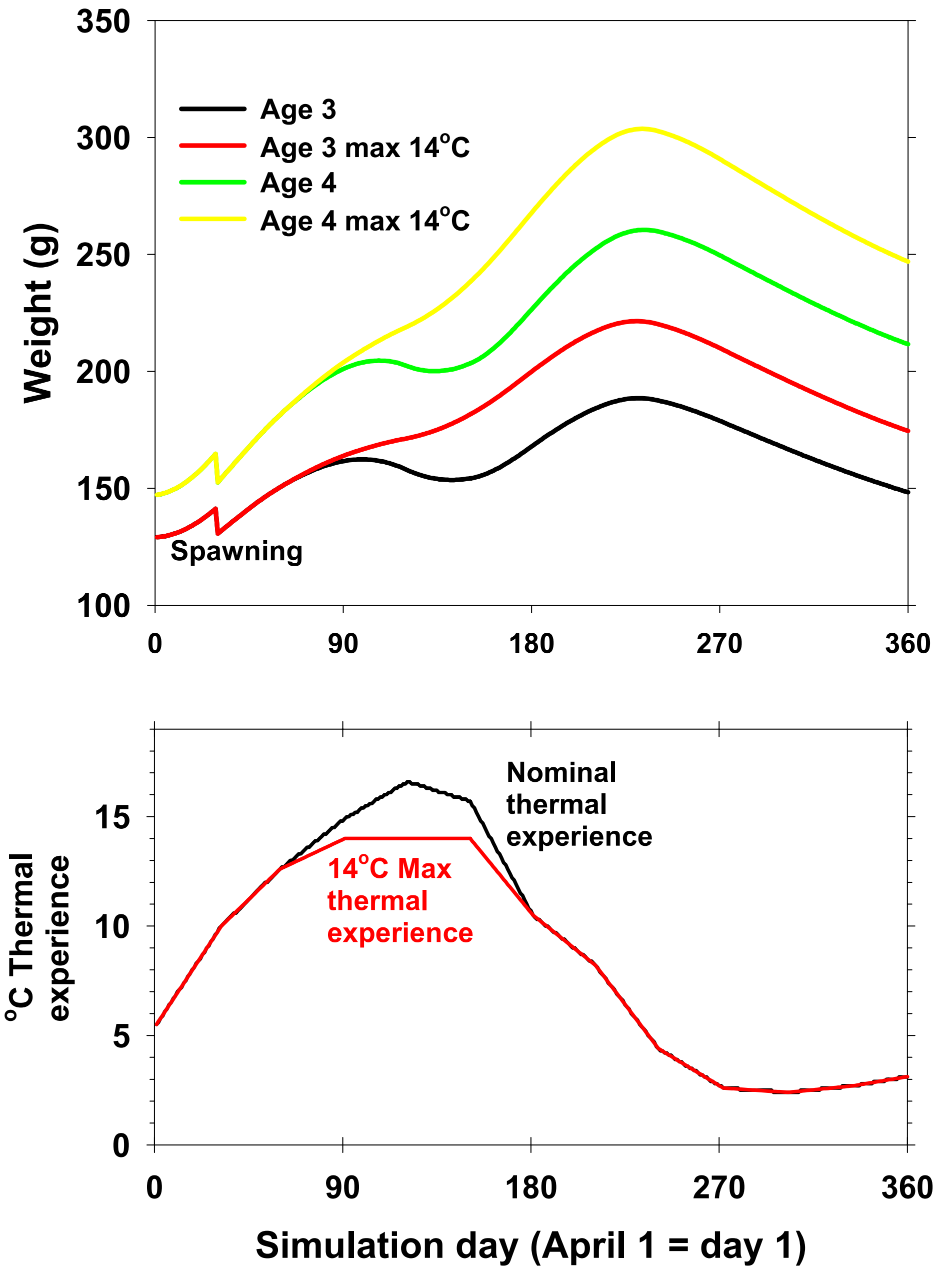

Figure 5. A. Simulated growth trajectories for age 3 and 4 cutthroat trout under nominal diet and temperature conditions as in the previous figure compared to growth when summer thermal experience does not exceed 14°C. B. Thermal experience used under each growth scenario.

The *Daphnia* bloom occurred late and was highly concentrated in August (**Figure 6a**). The average monthly supply (biomass) of *Daphnia* ranged from 157 kg in July up to 117,667 kg in August and back down to 3,283 kg by October. The monthly population-level consumption demand by trout was not detected until July and was fairly constant at 500-550 kg per month during summer, peaked at 810 kg in October and declined to 485 kg by November (**Figure 6a**). The patterns of monthly population-level consumption demand C by trout versus the supply of *Daphnia* biomass B were expressed as a ratio C/B. A consumption to biomass ratio (C/B) of 0.25 would suggest that trout ate 25% of the *Daphnia* biomass in the reservoir during that month, if no additional production of Daphnia occurred (i.e., no ovigerous females were present in the samples). Because these C/B ratios do not account for *Daphnia* production, they represent an overestimate of the actual consumption demand to prey supply relationship. Trout consumption approached 25% during July and October, and 7% in September, but was less than 1% during the peak *Daphnia* bloom in August the rest of the growing season (**Figure 6b**). Thus, trout consumption alone did not impinge on the carrying capacity of the lake for planktivores. Brown bullheads also consumed *Daphnia* during September, but the extent to which they affected the zooplankton forage base could not be evaluated with the existing data.

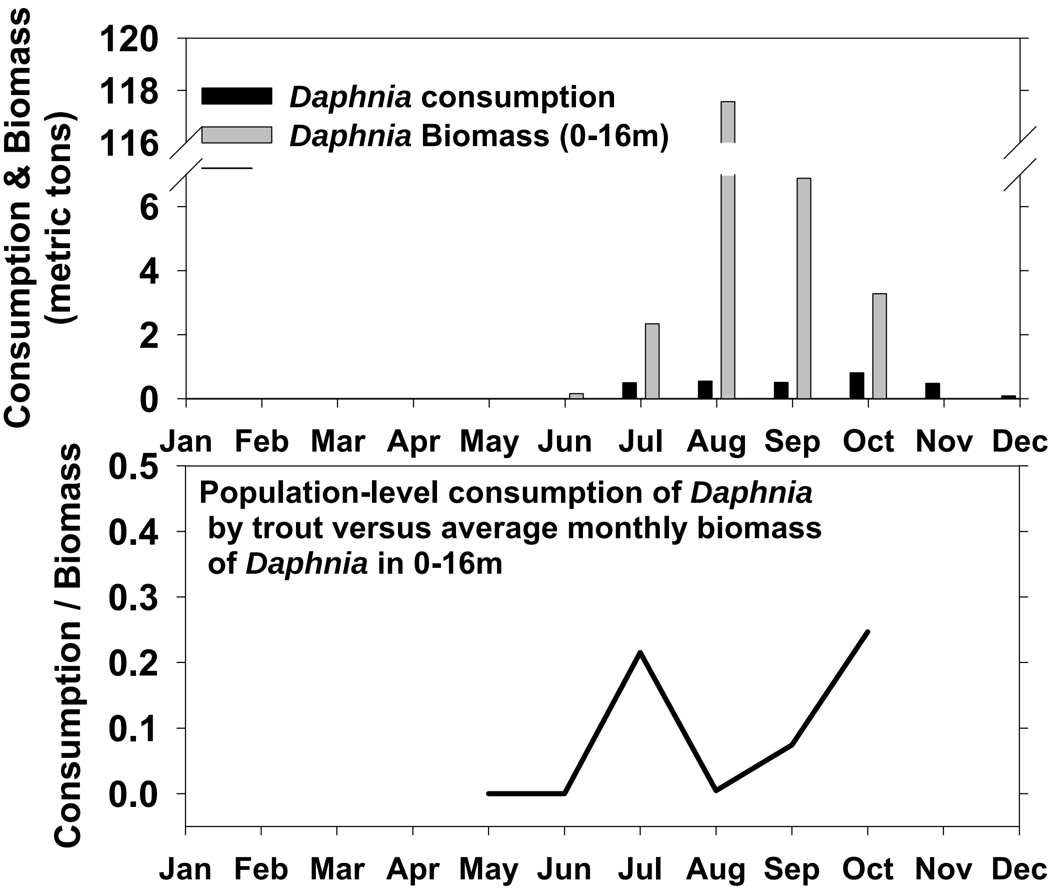

Figure 6. A. Comparison of monthly population-level consumption by trout on Daphnia versus the average monthly biomass of Daphnia in Spada Lake. B. The monthly ratio of trout consumption of *Daphnia* to *Daphnia* biomass in the 0-16m depths of Spada Lake during 2007. A proportion of 0.25 suggests that trout ate 25% of the *Daphnia* biomass in the reservoir during that month. These proportions do not account for additional Daphnia production, so they represent an overestimate of the actual consumption demand to prey supply relationship.

4.0 Discussion

Based on field data collected in 2007, the bioenergetic model simulations suggest that a combination of warm summer epilimnetic temperatures and a shift to lower energy content prey primarily limit growth and production of trout in Spada Lake compared to periods before and shortly after the reservoir enlargement and inundation of shorelines in 1985-1986. Although cutthroat trout grew faster during earlier regimes, their feeding rates in bioenergetics modeling simulations (47-58% C_{max} during 1979-1980 and 58-60% C_{max} during 1986) were similar or lower than feeding rates during 1992 and 1995-1997

(52-63% C_{max}) when growth was slower (Beauchamp 2006). During 2007, cutthroat trout fed at similar rates (46-63% C_{max}), but grew slower than all previous years. Growth efficiency was considerably higher (8-13%) during 1979-1980 and 1986 (5-13%) compared to more recent years like 1992 (7-11%), 1995-1997 (4-11%) and 2007 (1.5-7%). The most evident change in growing conditions has been the decline in the composite energy density of the diet for trout over time, starting with a high-energy averaging 4178 J/g in 1979-1980, 3687 J/g in 1986, 3577 J/g in 1997, and 3709 J/g during 2007 (**Figure 7**). The composite energy density of prey in 2007 was only 89% of the energy density of the diet eaten in 1979-1980. Current feeding rates would need to be 13% higher than in 1979-1980 (i.e., 52-65% C_{max}) to compensate for a lower energy diet in order to achieve the same growth rates as in 1979-1980, assuming a similar thermal regime.

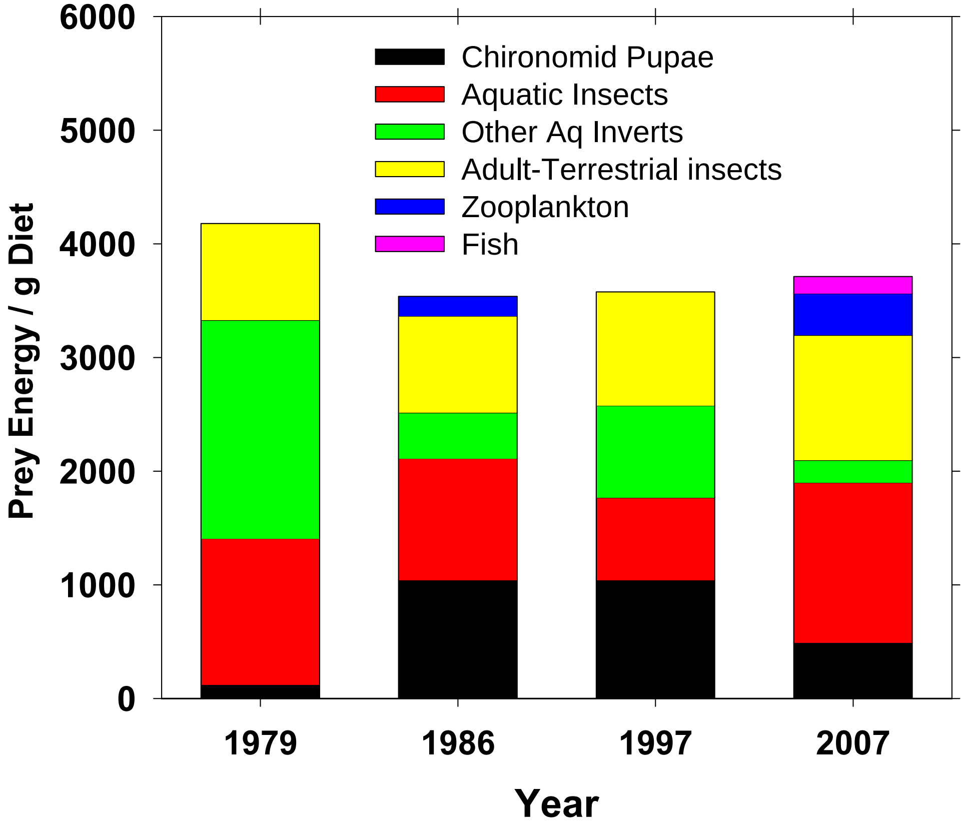

Figure 7. The average contribution of major prey categories to the annual energy budget of cutthroat trout during different production regimes in the reservoir. Values were standardized to represent the Joules of energy contributed by each prey category to an average gram of the composite annual diet during each year.

In earlier years, the ability to forage on high-energy prey like leeches at deeper, cooler depths afforded the combined benefits of higher energy intake (even at somewhat smaller ration sizes), lower metabolic costs, and higher growth efficiency. Higher growth efficiency during the earlier regimes of the reservoir coincided with higher dietary proportions of high-energy aquatic invertebrates like leeches which were nearly absent from the diets in 2007. Although adult and terrestrial insects in the neuston are high-energy prey, trout must feed in the warm surface temperatures to access these prey during summer stratification. The cooler summer growth scenario demonstrated that prolonged exposure to the warmer epilimnetic temperatures imposed significant growth penalties on trout. These results suggest that higher growth rates during the earlier years resulted from higher prey quality rather than from a higher feeding rate, but that higher growth and growth efficiency were mediated by the thermal environment and depth distribution of key prey.

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 terrestrial insects was an important component of the annual energy budget for trout in 2007, but also imposed higher metabolic costs on growth. If regional climatic warming trends continue, 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.

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 potential competition with brown bullhead. Under such conditions, adding more of the same species through stocking would intensify competitive effects, reduce growth, and increase mortality. Instead, reducing competition by modestly increasing harvest should increase both yield to the fishery and productivity of the trout populations. For instance, a reduction in minimum size limit to 11” total length (275 mm TL, which is approximately 250 mm FL) 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 (265 mm), and rainbow trout (220 mm). Such a change would moderately reduce the spawning population, and likely lead to a smaller, but more productive and resilient population (e.g., fewer trout but with higher growth rates and larger lipid reserves).

5.0 References

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Appendix A

Response to Stakeholder Comment on Draft Report

Comment from Julie Sklare, City of Everett – Email Date 8/7/08	**Response**
My main comment / question centers around the parasite issue. The Phase 2 Field Studies Technical report from MEI states that that a high percentage of the trout in Spada Lake have some level of parasite infection (Diphyllobothrium) with the rate of occurrence and load higher in larger trout. The bioenergetics model looks only at the impact of food supply, prey quality and thermal regime on growth. Since the parasitic infection affects growth, I'm curious how that factors into the model and the conclusions of the report.	The model does not account for loss of growth due to parasite loading. Unfortunately, we can only speculate about how much energy is diverted by parasites. Other lowland lakes in western Washington support very high growth rates for trout despite high parasite loads (not necessarily Diphyllobothrium). For instance, rainbow trout in L. Washington grew from 100 mm FL to 300 mm FL from May to December, despite 10's to 100's of parasitic worms in the visceral cavity.

-----Original Message-----
From: Dave Beauchamp [mailto:davebea@u.washington.edu]
Sent: Thursday, August 07, 2008 4:28 PM
To: Binkley, Keith
Subject: Re: Comments to Spada Lake Report

HI Keith,
You're right-my recommendation was based on older regulations. I wouldn't change your current regulations. Lake productivity is the issue. Trout are reproducing, but not growing, so shifting back to a larger minimum size limit would reduce both the fishery yield and reduce growth. Might consider removing the slot and just use a minimum 8" size limit. The fish larger than 12" are very scarce (because of the slow growth rate-they top out at a smaller size) and probably don't contribute significantly to reproduction, so the psychological benefit of potentially catching a larger trout probably outweighs the ecological consequences. Best regards, Dave

David A. Beauchamp
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On Thu, 7 Aug 2008, Binkley, Keith wrote:

> Hi Dave - No comments were received within the 30 day time frame.
> That does not mean some still won't come in. One thing I missed on my
> review relates to the final paragraph in the report, specifically the
> portion in bold. The current regulations have a slot with minimum
> size of 8" and a maximum size of 12". I believe your recommendation
> to reduce the minimum size limit to 11" are based on the old
> regulations. The regulations changed after the Pfeiffer report was
> released. With that said, would you suggest an alternative
> modification to the regulations? Maybe a 10" / 14" slot? Anglers, of
> course, want us to increase the maximum size limit. They would
> probably prefer that we return to the old regulations. Thanks for
> your input.
>
> Keith
>

> “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 potential competition with brown bullhead. Under such conditions, adding more of the same species through stocking would intensify competitive effects, reduce growth, and increase mortality. Instead, reducing competition by modestly increasing harvest should increase both yield to the fishery and productivity of the trout populations. For instance, a reduction in minimum size limit to 11" total length (275 mm TL, which is approximately 250 mm FL) 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 (265 mm), and rainbow trout (220 mm). Such a change would moderately reduce the spawning population, and likely lead to a smaller, but more productive and resilient population (e.g., fewer trout but with higher growth rates and larger lipid reserves).”