

# Conditions for growth and survival of bull trout in Beulah Reservoir, Oregon

**Annual Report for 2002** 

James H. Petersen, Eric E. Kofoot, and Brien Rose

U.S. Geological Survey
Western Fisheries Research Center
Columbia River Research Laboratory
5501A Cook-Underwood Road
Cook, WA 98605

# **Prepared for the:**

U.S. Bureau of Reclamation Pacific Northwest Region 1150 North Curtis Road Boise, Idaho 83706-1234

August 25, 2003

# Table of Contents

List of Figures	3
List of Tables	5
Introduction	6
Study Design	7
Methods	8
Field studiesBioenergetic modeling	
Historical fish community in Beulah Reservoir	
Results	14
Field studies	
Bioenergetic modeling  Historical fish community in Beulah Reservoir	
Discussion	
Acknowledgements	38
References	39
Appendices.	42

List of Figures
Figure 1. Fyke net sampling at Beulah Reservoir in 2002
Figure 2. Daily water volume (acre feet *1000 <sup>-1</sup> ) of Beulah Reservoir from 1 October
2001 to 30 September 2002
Figure 3. Water temperature and dissolved oxygen in Beulah Reservoir during 2002 16
Figure 4. Species composition in gill net and fyke net samples collected at Beulah
Reservoir in 2002.
Figure 5. Length-frequency distributions of the most common species collected from
Beulah Reservoir in 2002. Note different scales on the abundance axes. The inset
graph for white crappie shows the same frequency distribution in more detail21
Figure 6. Maximum consumption estimates $(C_{max}; g \cdot g^{-1} \cdot d^{-1})$ for four size categories of
bull trout measured at four temperatures. Each point in A is the average of the four
highest daily estimates made over the three-week test period (see text). In B, points
are averages (±1 SE) of the three larger size groups combined (Adult, Large,
Medium; all fish >80 g; ●) and the Small size group (20 – 48 g; ○). Lines are
predicted $C_{\text{max}}$ for a 30-g and a 450-g fish using the fitted Thornton and Lessem
(1978) temperature models
Figure 7. Allometric relationship between bull trout size and maximum daily
consumption $(C_{max}; g \cdot g^{-1} \cdot d^{-1})$ . Panel A shows the fit to data collected at four
temperatures (7°, 10°, 13°, and 16°C), and panel B shows the fit to data for the 10°
and 13°C trials only. Lines are the least-squares fitted allometric equations27
Figure 8. Simulated temperature (left) and predicted consumption rate for a 30-g bull
trout (right) in Beulah Reservoir for April 18 and June 9, 1999. Segment number
refers to the water temperature model; Agency Valley Dam is at Segment 16 and
North Fork of the Malheur River is at Segment 1. Temperature simulations were
conducted by BOR (2002) and consumption rates (g·g <sup>-1</sup> ·d <sup>-1</sup> ) were based on the fitted
temperature model for bull trout in this study (see Table 7). The staircase in red is
the bottom of the reservoir
Figure 9. Total gillnet catch of common species collected in Beulah Reservoir between

1955 and 1970. Vertical lines indicate years (1955, 1961, and 1968) when the

	reserv	oir was drawn completely down.	Gillnet catches are the total number of fish
	collect	ted	32
Figu	ıre 10.	Average monthly water volume is	n Beulah Reservoir for July through October,
	1936 t	to 2002	33

# **List of Tables**

Table 1. Inclusive sampling dates at Beulah Reservoir during 2002
Table 2. Common and specific names of species or taxa mentioned in the text10
Table 3. Number of fish captured and number of sample sets fished at Beulah Reservoir
during 2002, by month
Table 4. Average CPUE (catch per hour of soak time for gill nets) for major taxa
collected at Beulah Reservoir in 2002. N is the total number of gill net sets per trip;
SD = standard deviation of the mean
Table 5. Average size of fish captured at Beulah Reservoir during 2002. N = sample size;
SD = standard deviation of the mean
Table 6. Average mass (g) and length (mm; FL) of 16 groups of bull trout used in
maximum consumption experiments. SD is in parentheses
Table 7. Preliminary parameter values estimated for the bull trout bioenergetics model.
Parameters in capital letters (e.g., CA and CQ) refer to the formulation in the
software of Hanson et al. (1997) for Consumption (their Equation 3), Respiration
(their Equation 1), and Egestion-Excretion (their Equation 2). Parameters with more
than one entry per line are values for small bull trout $(20-48\ g)$ and large bull trout
(>80 g), respectively. Single parameter values are assumed to apply to all sizes of
bull trout. Sources: Beauchamp and van Tassel (2001), Stewart et al. (1983), and this
study28

#### Introduction

The Bureau of Reclamation (BOR) constructed Agency Valley Dam on the North Fork of the Malheur River in 1934-35, creating Beulah Reservoir. The project is operated and maintained by the Vale Irrigation District for irrigation and downstream flood control. There is currently no formal agreement for a minimum pool level at Beulah Reservoir, but project operators of Agency Valley Dam and BOR are considering management alternatives. Although the project is not operated for fish and wildlife values, the reservoir supports a rainbow trout *Oncorhynchus mykiss* fishery and also seasonally harbors an adfluvial population of bull trout *Salvelinus confluentus* (Oregon Department of Fish and Wildlife [ODFW], unpublished data). Bull trout were listed by the USFWS as a threatened species throughout the Columbia and Klamath river basins in 1998, and Oregon has listed the North Fork Malheur River population "Of Special Concern".

Reasons for the decline of bull trout in the Malheur River likely include habitat degradation and fragmentation and downstream loss through entrainment at dams. The construction of dams in the Malheur River drainage isolated formerly connected bull trout metapopulations of the Snake River Basin. Migratory bull trout are important to the persistence and stability of the North Fork Malheur population because they may represent unique genetic resources and because large migratory individuals are more fecund than smaller, resident stream fish.

The BOR has initiated an investigation of alternatives for managing water levels in Beulah Reservoir. Water quality monitoring and modeling are underway to describe the seasonal distribution of dissolved oxygen and temperature relative to bull trout needs (BOR 2002). General limnological information is also being collected on a regular basis to describe algal and zooplankton standing crops under wet and dry year conditions. A Beulah Reservoir sedimentation survey was initiated in 2000 to provide updated capacity data, and a bathymetric map for use in developing a conservation pool. These investigations are to be completed by December 2004. Subadult or adult bull trout may reside in Beulah Reservoir for either all (subadults) or part (mature adults) of the year. During residence, bull trout are likely feeding on fish, including stocked rainbow trout, and will be exposed to temperatures, dissolved oxygen, and other conditions that might change with season or reservoir operation.

Recent water quality measurements indicated that Beulah Reservoir is a highly productive eutrophic reservoir (BOR 2002). Limnological data indicated that temperature and dissolved oxygen might be limiting factors on bull trout populations within the reservoir, especially during warm summer months and when reservoir water levels are low. During July-August of 2001, temperatures exceeded 15°C (Petersen and Kofoot 2002), which has been shown by Reiman and McIntyre (1993) and others to limit bull trout abundance. Dissolved oxygen levels decreased below levels described by Irving (1941) and Graham (1949) to cause physiological and behavior changes in brook trout *S. fontinalis*, a congener of bull trout. Adult and subadult bull trout may inhabit the reservoir during the fall, winter, and early spring but may exhibit an adfluvial behavior pattern to avoid potential stresses.

Studies during 2001 indicated potentially high abundances of available prey for bull trout (Petersen and Kofoot 2002). Redside shiners, rainbow trout, sucker *spp*., and northern pikeminnow (see Table 2 for scientific names) represented the majority of fish collected. Data also indicated a diverse range of size classes, which could potentially provide adequate food sources for all ages of bull trout. Limited samples from 2001 indicated potentially low abundances of benthic invertebrates in the reservoir.

During 2002, we continued to study the seasonal and interannual variations in prey availability for bull trout in Beulah Reservoir. Data will be integrated through an energetics model of bull trout with water quality work being done in the reservoir. Our long-term goal is to estimate the quality of habitat in the reservoir for bull trout growth and survival, and provide some guidance for reservoir operations and potential establishment of a conservation pool.

#### Study Design

Adult bull trout are presumed to be present in Beulah Reservoir during winter and early spring. They likely migrate to tributaries during early spring and return to the reservoir during late fall or early winter (Wayne Bowers, Oregon Department of Fish and Wildlife [ODFW], pers. comm.). No information has been available on the occurrence of subadult bull trout in the reservoir (Rick Rieber, BOR, pers. comm.), but subadult bull trout with an adfluvial life history commonly move downstream from tributaries and

7

spend part of their life in lakes or reservoirs (Rieman and McIntyre 1993). During their residence in Beulah Reservoir, both adults and subadults probably feed on small fish (Brown 1995), and possibly some benthic invertebrates. A major objective of this study is to quantify prey availability through time in the reservoir.

Drawdowns and pool-level manipulations can presumably have effects on temperature and the available preyfish within the reservoir, which could greatly influence growth and survival of bull trout. Temperatures in the reservoir could stratify creating very different environments for bull trout across short distances. Energetics models (e.g., Brandt and Kirsch 1993; Labar 1993; Petersen and Kitchell 2000) have been used to synthesize temperature, diet, water quality, and variations in forage base for a variety of fish species, and to address specific management questions. Such a model for bull trout could be used to estimate changes in specific or total reservoir habitat, and predict the expected growth rates with different management scenarios. Beginning with parameters from Arctic char *S. alpinus*, brook trout, lake trout *S. namaycush*, and other cold-water species in the genus *Salvelinus*, a preliminary bioenergetics model has been developed (Hanson et al. 1997; Beauchamp and van Tassel 2001). We plan to improve this model by identifying sensitive parameters (Petersen and Kofoot 2002) and conducting laboratory studies to refine specific parameters.

#### Methods

#### Field studies

Water quality and fish sampling were conducted from early April to late July on five trips (Table 1). Sample times were assigned a trip number that corresponded to the time of sampling (i.e., samples collected on 29 April 2002 were assigned to the early May trip). Sampling efforts lasted from two to five days.

# Water quality

Water quality parameters were measured at the deepest part of the reservoir. Contour elevation maps of Beulah Reservoir, provided by the Bureau of Reclamation in Boise, ID, indicated an area of deepest water from near the dam face extending north along the original thalwag to approximately mid-reservoir. During the spring, when the water level was near its seasonal peak, we physically located this deep area using a boat

and an electronic depth sounder. We recorded GPS coordinates at several of the deepest locations using a PLGR+96 GPS unit. During subsequent monthly sampling visits to Beulah Reservoir, we returned to these locations to collect water quality data.

Dissolved oxygen (ppm) and water temperature (°C) data were collected with a YSI (Yellow Springs Instruments) model 57. Data were collected at 1-meter intervals from the surface to 14 meters in depth when possible. Surface measurements were taken at approximately 10 cm below the water surface. Turbidity data were collected at about 10 cm below the water surface, and at 1, 5, 10, 15, and 20 m, depth permitting. A Van Dorn water sampler was used to collect unmodified water samples at depth. Turbidity samples were processed with a HACH 2100P turbidity meter and data were recorded in Nephelometric Turbidity Units (NTUs). Data collected during a single sampling period were combined and then averaged by depth interval.

#### Fish sampling

Fish were sampled with experimental gill nets and fyke nets. Each gill net had six panels (6.1 m long by 3.0 m deep) with stretch mesh sizes of 8.9, 7.6, 6.3, 5.1, 3.8, and 2.5 cm (3.5, 3.0, 2.5, 2.0, 1.5, and 1.0 inches). To sample day, crepuscular, and dark periods, gill nets were generally set and fished on the bottom from late afternoon through early night hours. Two to four nets were set in a series, and a set ranged from 0.5 to 2.5 hours. Fyke nets equipped with two wings were fished for 16 to 48 hours. During April, fyke nets were set with one wing extending to shore and the second wing extending towards deeper water. The wings were set at approximately 45 degrees to the shore to increase the probability of fish being led towards the trap. Whenever necessary the open end of the fyke net was fished towards the downwind side of the reservoir to minimize problems with debris. During May-July, Fyke nets were set with a center lead extending to shore and wings angled off each side. Occasionally, especially when water temperatures were warm, nets were fished offshore, in deep water. Fish captured were identified (see Table 2 for common and scientific names used in this report) and measured (fork length FL; nearest mm). The number of hours fished per set was rounded to the nearest 0.1 h, and catch per unit of effort (CPUE) was calculated as the number of fish caught per hour of fishing.

Table 1. Inclusive sampling dates at Beulah Reservoir during 2002.

Trip Number	Month designation	Start date	End date	
1	April	2-Apr	4-Apr	
2	Early May <sup>1</sup>	29-Apr	8-May	
3	Late May	28-May	30-May	
4	June	24-Jun	26-Jun	
5	July	22-Jul	25-Jul	

<sup>&</sup>lt;sup>1</sup>1 May-5 May not sampled

Table 2. Common and specific names of species or taxa mentioned in the text.

Common name	Scientific name or taxa
Northern pikeminnow	Ptychocheilus oregonensis
Redside shiner	Richardsonius balteatus
Rainbow trout	Oncorhynchus mykiss
Bull trout	Salvelinus confluentus
Mountain whitefish	Prosopium williamsoni
Sculpins	Cottidae
Bridgelip sucker	Catostomus columbianus
Largescale sucker	Catostomus macrocheilus
White crappie	Pomoxis annularis



Figure 1. Fyke net sampling at Beulah Reservoir.

### Bioenergetic modeling

#### Laboratory experiments

Experimental methods were modified from Stewart et al. (1983) and Hartman and Brandt (1995). Smaller bull trout (20 to 350 g) for the experiment were collected with a screw trap on the Metolius River, OR during April and May 2002, while larger bull trout (>350 g) were collected by angling in Lake Billy Chinook, OR during August 2002. The fish were transported in large tanks and held at the USGS Columbia River Research Laboratory, Cook, WA, until consumption experiments, which were conducted in September and October. Small bull trout (7 to 13 per tank) were held in 76-cm diameter circular tanks with 11°C well water at a flow rate of 2 L/min. Large bull trout (10 fish per tank) were held in 1.5-m diameter circular tanks at 11°C, with a flow rate of 6 L/min. Prior to temperature acclimation and the start of the experiment, all bull trout were fed live

prey (juvenile chinook salmon *Oncorhynchus tshawytscha* or goldfish *Carrassius auratus*) at least twice a week.

Consumption experiments were conducted in 60-cm diameter tanks with flow-through water at a rate of 2 L/min. Temperature was maintained with a head box that had a controller regulating the amount of hot water coming in from a heat exchanger. The hot and cold-water mixture was pumped through a cracking column to remove excess dissolved gas and then was pumped to the treatment tanks. Fish were acclimated to a given temperature for at least two weeks prior to conducting the feeding experiment. During the acclimation period, fish were fed a maintenance ration on Monday, Wednesday, and Friday.

To stock an experimental tank, bull trout were lightly anesthetized with MS-222, weighed (nearest 0.1 g), measured (FL, nearest mm), and sorted into four size groups (Small, Medium, Large, Adult) and four temperature categories (7°, 10°, 13°, and 16°C). Ages were not available for the fish tested, but approximate ages would be: Small - Age 1; Medium – Age . Fish were tested over a broad range of sizes so data would be applicable to bull trout in a variety of systems. The number of bull trout in each tank varied from one to three, depending on the availability of fish in a particular size range and the need to stock fewer large fish per tank.

Experiments were conducted over three weeks, with a series of trials being conducted each week. To begin an experiment, bull trout were removed from an experimental tank, lightly anesthetized, quickly weighed, and replaced. Bull trout were starved for two days and then fed an excess ration of preyfish for one hour at 0800 and again at about 1500 h. This daily routine (2 feeding periods) was repeated for 4 days in a given week. Estimates of the maximum amount of food necessary to satiate predators during a 1-h period (feeding bout) were based on laboratory experiments with lake trout (Stewart et al. 1983), since data were not available for bull trout. Preliminary experiments were conducted with bull trout to assure that excess food was given. When the experiment was repeated the second and third weeks, tanks contained only one bull trout. For the third week of the experiment, Adult size bull trout replaced the small juvenile bull trout. Water temperature was measured during each feeding period.

Because of the extreme range in the size of the predators, we could not offer them the same prey. Small predators (<50 g) were fed goldfish (~1 g each) and larger predators (>80 g) were fed juvenile chinook salmon (10 to 11 g each). The number of prey fish per tank ranged from two to15, depending upon preliminary experiments, predator size, and prey size. Prey were weighed (wet weight; nearest 0.1 g) before adding them to an experimental tank, and all prey were removed and weighed after each 1-h feeding bout.

Data analysis – Total prey consumption for a trial was the difference between starting and ending prey masses. Daily specific consumption was the sum of the two feedings per day, divided by the total predator mass at the start of the period (Hartman and Brandt 1995). Maximum consumption, or C<sub>max</sub>, for a size group and temperature treatment was the average of the four highest observed daily consumption values (Stewart et al. 1983; Hartman and Brandt 1995). We examined the average consumption by temperature and size group to determine the temperature at which maximum consumption occurred. Allometric models for maximum consumption were fit with linear least-squares regression (Hartman and Brandt 1995, e.g.). Maximum consumption was described as a function of temperature using the Thornton and Lessem (1978) model.

#### Simulations in Beulah Reservoir

We conducted two simulations with preliminary model parameters to demonstrate the potential change in feeding conditions within the reservoir. We used predicted temperatures for April 18, 1999 and June 9, 1999 in these simulations, which were provided by Alan Harrison (BOR, Denver). These dates were selected to demonstrate seasonal effects and specific differences. For each day, temperatures were predicted longitudinally in the reservoir in a series of segments (16) from the upper reservoir (inflow; North Fork of the Malheur River) to the dam (outflow; see BOR 2002). Each segment has divided into 0.5-foot depth intervals. For each spatial cell, we estimated potential consumption rate for a 30-g bull trout (chosen because of the variation of smaller fish to temperature; see Results) using the allometric and temperature portions of the bioenergetics model derived below.

#### Historical fish community in Beulah Reservoir

Fisheries data were copied from the files of the Oregon Department of Fish and Wildlife (Burns office) with the help of Wayne Bowers. We copied data sheets and reports on fish collection efforts in Beulah Reservoir during the 1950s through the 1970s. If available, we also collected information on effort and physical conditions during these years. Data are summarized here, and put into the context of management efforts that were ongoing during these earlier periods. We also collected and summarized reservoir level data from 1936 to the present (Hydromet records).

#### **Results**

## Field studies

During 2002, Beulah Reservoir filled to a maximum of about 47,000 acre-feet in early May and had a minimum of 0 acre-feet from 10 August 2002 through 30 September 2002 (Figure 2). Water temperature and dissolved oxygen conditions in Beulah Reservoir are summarized in Figure 3. Average water temperature at the surface increased from about 13°C in April to over 25°C in June. During the April, early May, and June sampling periods, there was of a slight thermocline in the upper water column. During the late May and July sampling periods, water temperature decreased gradually with depth.

Dissolved oxygen (DO) was highest in surface waters during early May and lowest during June and July. During July, DO ranged from >6 ppm at the surface to <2.5 ppm near the bottom of the reservoir at 10 m of depth (Figure 3).

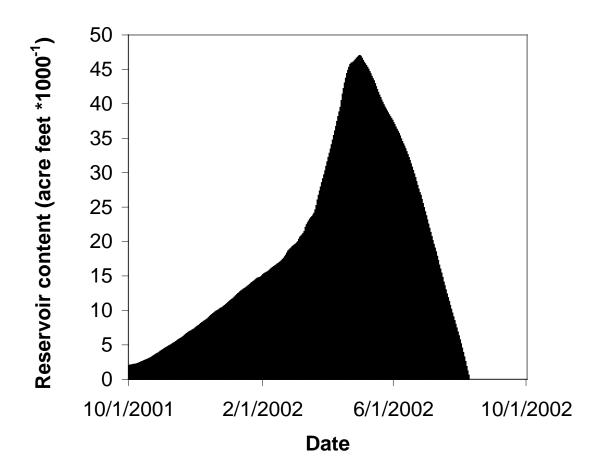


Figure 2. Daily water volume (acre feet \*1000<sup>-1</sup>) of Beulah Reservoir from 1 October 2001 to 30 September 2002.

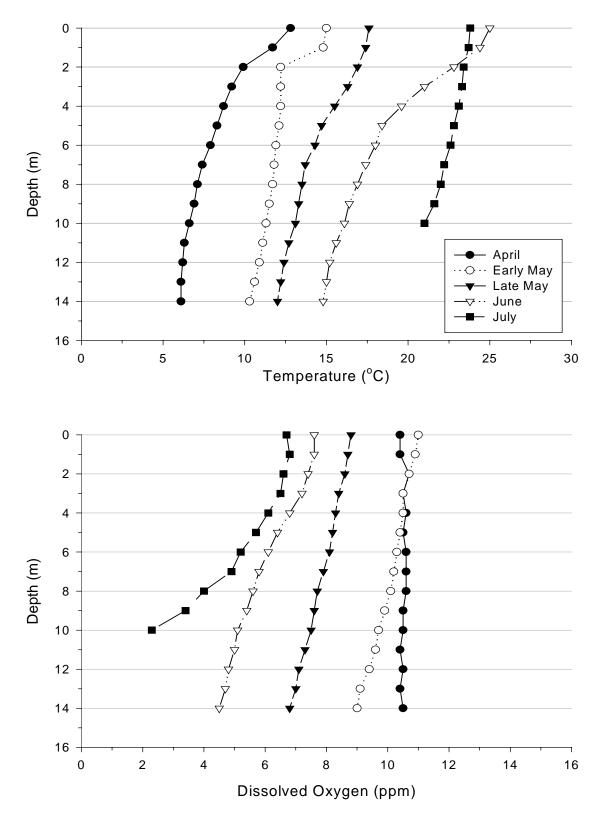


Figure 3. Water temperature and dissolved oxygen in Beulah Reservoir during 2002.

Gill net sampling was distributed throughout Beulah Reservoir, but the majority of the effort was concentrated in the northern half of the reservoir. During July, when the reservoir level was lowest, sampling efforts were concentrated in the deepest water, at the southern third of the reservoir and along the thalweg of the old river. Fyke net sampling was primarly distributed along the shorelines in water less than 2 m deep.

We collected 227 fish in gill nets and 322 fish in fyke nets during sampling in 2002 (Table 3; Figure 4), although none of the fish captured were bull trout. Northern pikeminnow and largescale suckers were the most common species collected with gill nets, each representing 30.4% of the catch, while rainbow trout and mountain whitefish were the third and fourth most common species, respectively. The most common species collected with fyke nets were white crappie (42.9%), redside shiners (24.2%) and northern pikeminnow (18.6%; Figure 4).

CPUE numbers are summarized in Table 4. CPUE numbers showed few strong patterns through the seasons considering the variation in catch. Mountain whitefish had the highest CPUE during April and were not collected after the May sampling period. Rainbow trout CPUE numbers were highest in July and lowest during April. Northern pikeminnow and largescale sucker had highest CPUEs in early May.

The sizes of fish captured in Beulah Reservoir are summarized in Table 5 and Figure 5. Rainbow trout were the largest fish collected (mean FL = 356 mm; range 74-535 mm) during 2002 sampling periods. Sucker *spp.*, northern pikeminnow, rainbow trout, redside shiners and white crappie were collected over a wide variety of size classes (Figure 5). Smaller fish were generally captured with fyke nets. Length frequency data indicated the occurrence of a variety of age classes for all species except sculpins (Figure 5).

We collected a few bottom samples during May and June using a van Veen dredge, but observed very low numbers of invertebrates. Most samples included only dark mud with no obvious macroinvertebrates.

Table 3. Number of fish captured and number of sample sets fished at Beulah Reservoir during 2002, by month.

			Month			
	April	Early May	Late May	June	July	Total
Bridgelip sucker	2		2	4	5	13
Largescale sucker		2		2	6	10
Northern pikeminnow	4	8	10	16	22	60
Rainbow trout	1	8	4		1	14
Redside shiner	26	26	13	10	3	78
Cottidae					3	3
Sucker spp. 1			1		5	6
White crappie				2	136	138
Fyke net sets <sup>2</sup>	4	12	3	6	9	34
Bridgelip sucker	1	6	2	2	2	13
Largescale sucker	19	38	2	2	8	69
Mountain whitefish	16	3	1			20
Northern pikeminnow	7	17	32	2	11	69
Rainbow trout	3	11	10	4	14	42
Redside shiner		2	4		1	7
Sucker spp. 1		1	2	1		4
White crappie	3					3
Gill net sets	25	16	21	13	18	93

<sup>&</sup>lt;sup>1</sup> Unidentified suckers <sup>2</sup> Number of days nets soaked

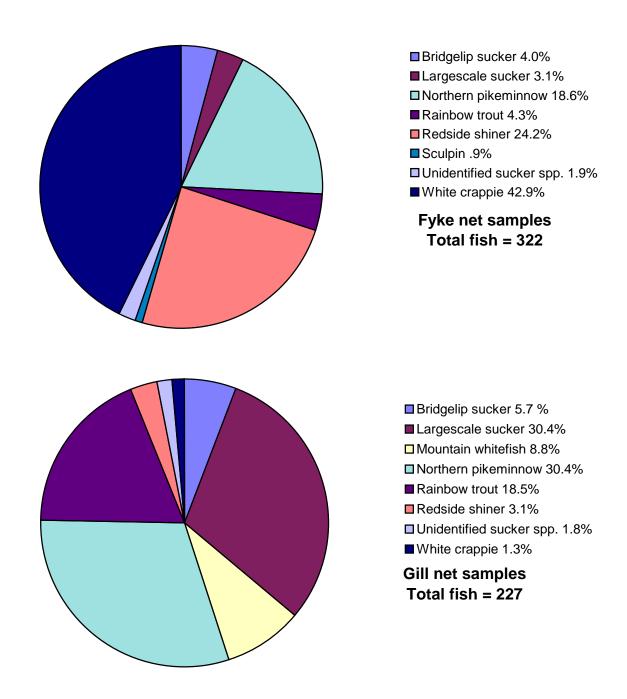


Figure 4. Species composition in fyke and gill net samples collected at Beulah Reservoir in 2002.

Table 4. Average CPUE (catch per hour of soak time for gill nets) for major taxa collected at Beulah Reservoir in 2002. N is the total number of gill net sets per trip; SD = standard deviation of the mean.

Month	Northern		Rainb	Rainbow		escale	Mou	Mountain		
(trip number)	pikemin	now	trout		suck	er	whitefish			
	Mean	SD	Mean SD Mean SD		Mean SD		Mea	n SD		
April (1)	0.4	0.8	0.1	0.4	0.6	1.1	0.6	0.9	25	
Early May (2)	0.7	1.1	0.4	0.5	1.7	2.3	0.1	0.2	16	
Late May (3)	1.5	1.5	0.5	1.3	0.1	0.3	0	0.1	21	
June (4)	0.1	0.3	0.3	0.4	0.1	0.3	0	0	13	
July (5)	0.5	0.9	0.7	1	0.5	1.1	0	0	18	
All months	0.7	1.1	0.4	0.9	0.6	1.3	0.2	0.5	93	

Table 5. Average size of fish captured at Beulah Reservoir during 2002. N = sample size; SD = standard deviation of the mean.

Species / taxa	Fork length (mm)						
	Mean	Minimum	Maximum	SD	N		
Bridgelip sucker	231	108	375	69	26		
Largescale sucker	350	131	458	78	79		
Mountain whitefish	302	184	356	41	20		
Northern pikeminnow	230	27	385	80	129		
Rainbow trout	357	74	535	108	56		
Redside shiner	62	32	90	12	84		
Sculpin	36	33	38	3	3		
Unidentified sucker spp.	80	40	119	29	9		
White crappie	41	21	111	14	140		

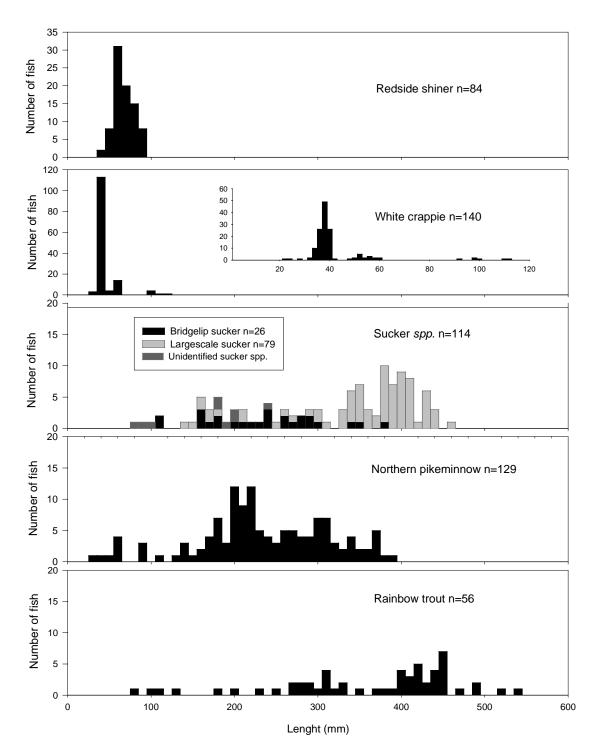


Figure 5. Length-frequency distributions of the most common species collected from Beulah Reservoir in 2002. Note different scales on the abundance axes. The inset graph for white crappie shows the same frequency distribution in more detail.

#### Bioenergetic modeling

# <u>Laboratory experiments</u>

Averages sizes for the four groups (called Adult, Large, Medium and Small) of bull trout were: Adult: 416 g, Large: 339 g, Medium: 128 g, and Small: 31 g (Table 6). See Table 6 for corresponding lengths. Approximate ages of size groups were: Adult – 4+ yrs; Large – 3 yrs; Medium – 2 yrs; Small – 1to 2 yr. The average mass of bull trout in a size group was not significantly different for the temperatures tested (ANOVA's, P>0.5). Average water temperatures for the four treatments were: 7.1°C (range 6.6 to 7.4°C), 10.1°C (range 9.9 to 10.5°C), 13.0°C (range 12.7° to 13.3°C), and 16.0°C (range 15.8° to 16.2° C). Actual temperatures were used in modeling feeding responses, rather than the treatment mean.

The time that preyfish were exposed to predators in trials ranged from 56 minutes to 69 minutes, with an average exposure of 61 minutes. We observed no effect of the number of predators in a tank on feeding results (ANOVA; P > 0.2). All prey were eaten in a small number of the trials (6%; 16/288). Nine of the 16 trials with all prey eaten occurred after fish had been starved over the 2-d period prior to the start of experiments for a given week.

Table 6. Average mass (g) and length (mm; FL) of 16 groups of bull trout used in maximum consumption experiments. SD is in parentheses.

Adult
Temp-

Temp- era- ture group	Predator size group											
(°C)				I	Large			Medium			Small	
	Mass	Length	N	Mass	Length	N	Mass	Length	N	Mass	Length	N
7	411 (46)	326 (11)	8	357 (173)	306 (44)	24	129 (37)	226 (20)	24	25 (6)	137 (9)	16
10	421 (40)	329 (10)	8	341 (156)	302 (41)	24	135 (59)	227 (30)	24	29 (6)	143 (10)	16
13	421 (40)	329 (10)	8	344 (175)	301 (46)	24	119 (32)	221 (18)	24	35 (15)	150 (20)	16
16	411 (46)	326 (11)	8	315 (123)	296 (35)	24	130 (47)	225 (25)	24	35 (13)	149 (19)	16

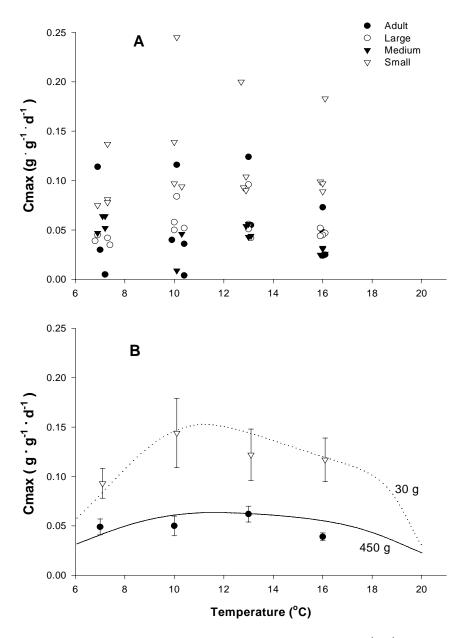


Figure 6. Maximum consumption estimates  $(C_{max}; g \cdot g^{-1} \cdot d^{-1})$  for four size categories of bull trout measured at four temperatures. Each point in A is the average of the four highest daily estimates made over the three-week test period (see text). In B, points are averages ( $\pm 1$  SE) of the three larger size groups combined (Adult, Large, Medium; all fish >80 g; •) and the Small size group (20-48 g;  $\circ$ ). Lines are predicted  $C_{max}$  for a 30-g and a 450-g fish using the fitted Thornton and Lessem (1978) temperature models.

Temperature appeared to have a relatively small effect on  $C_{max}$  for most size groups tested (Figure 6). Replicates had a fairly wide range and there was overlap between results for size groups at each temperature (Figure 6A). Individual replicate values of  $C_{max}$  ranged from 0.01 to 0.25 g·g  $^{-1}$ ·d $^{-1}$  (Figure 6A). In a two-way ANOVA of temperature and size, temperature did not have a significant effect on  $\log_e$ -transformed  $C_{max}$  (P > 0.3 for a temperature effect), although size was significant (P < 0.05). Using Tukey's multiple comparison's test,  $C_{max}$  estimates were not different among Medium, Large, and Adult bull trout (P > 0.05), but  $C_{max}$  values for the Small group were significantly different from the other three size groups (P < 0.05). We pooled fish from the Medium, Large, and Adult size groups for most analyses below.

Because of the lack of an obvious temperature effect on feeding across the temperature range tested here, we first estimated allometric relationships using all four temperatures (Figure 7A). The intercept and slope of the fit were 0.324 and -0.367, respectively. To examine the allometric effect on  $C_{max}$ , most authors have used results of feeding experiments at temperatures where fish are assumed to feed at a maximum rate (Stewart et al. 1981; Hartman and Brandt 1995). Selong et al. (2001) suggested that bull trout may have an optimum feeding and growth response at  $10^{\circ}$  to  $13^{\circ}$ C, so we also fit allometric equations for this restricted temperature range (Figure 7B). The intercept and slope of the fit for this smaller dataset were 0.394 and -0.387, respectively. Allometric equations provided significant fits to both datasets (P < 0.05; Figure 7) and the  $r^2$  values were similar (0.24 to 0.27).

We observed a slight reduction in C<sub>max</sub> for both size groups at 7° and at 16°C, compared to the trials at 10° and 13°C (Figure 6B), suggesting lower rates of feeding at either higher (>16°C) or lower (<7°C) temperatures than were tested. We fit the Thornton and Lessem (1978) temperature model to the Cmax data, making some assumptions about patterns beyond the temperature range that we tested. First, we assumed that bull trout in both size groups would have reduced feeding at colder temperatures, and that feeding would be about 10% of the maximum possible consumption at 2°C. Second, we needed to approximate how C<sub>max</sub> will change at temperatures above 16°C. Selong et al. (2001) estimated that the upper incipient lethal temperature for juvenile bull trout was 20.9°C with a 60-d acclimation period. Growth

rate of age-0 bull trout declined rapidly above  $16^{\circ}$  C and was about 25% of the maximum rate (which was at ~13° C) by the time temperature had risen to  $20^{\circ}$ C (Selong et al. 2001). Based on these results in other studies, we assumed that  $C_{max}$  would decline rapidly above  $16^{\circ}$  C and  $C_{max}$  would be about 10% of its maximum when temperatures were  $21^{\circ}$  C. Finally, we assumed that the response of both small and large bull trout size groups would be similar at low and high temperatures (e.g., see parameter sets listed in Hanson et al. 1997). These assumptions allowed us to approximate the seven parameters of the Thornton and Lessem temperature model (Table 7).

Parameters of the Thornton and Lessem (1978) model were fit by iteratively selecting values and evaluating the fitted line to the data and the assumptions (Hartman and Brandt 1995). Preliminary parameter estimates are given in Table 7. Since we pooled the Medium, Large, and Adult groups together, there are two estimates, one for fish 20 to 48 g fish (Small) and one for fish >80 g (pooled sizes).

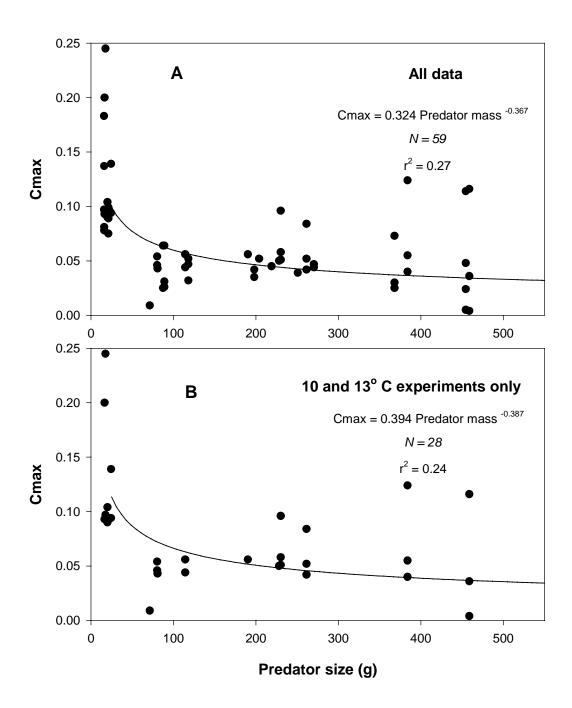


Figure 7. Allometric relationship between bull trout size and maximum daily consumption ( $C_{max}$ ;  $g \cdot g^{-1} \cdot d^{-1}$ ). Panel A shows the fit to data collected at four temperatures (7°, 10°, 13°, and 16°C), and panel B shows the fit to data for the 10° and 13°C trials only. Lines are the least-squares fitted allometric equations.

Table 7. Preliminary parameter values estimated for the bull trout bioenergetics model. Parameters in capital letters (e.g., CA and CQ) refer to the formulation in the software of Hanson et al. (1997) for Consumption (their Equation 3), Respiration (their Equation 1), and Egestion-Excretion (their Equation 2). Parameters with more than one entry per line are values for small bull trout (20 - 48 g) and large bull trout (>80 g), respectively. Single parameter values are assumed to apply to all sizes of bull trout. Sources: Beauchamp and van Tassel (2001), Stewart et al. (1983), and this study.

Parameter	Parameter description	Parameter values
	Consumption, C <sub>max</sub>	
CA	Intercept: $C_{\text{max}}$ at $(\theta_{2} + \theta_{3})/2$	0.394
CB	Coefficient: C <sub>max</sub> versus weight	-0.387
$\theta_1$	Temperature for K1 (Thornton and Lessem 1978)	4, 2.5
$\theta_2$	Temperature for K2 (Thornton and Lessem 1978)	15.5, 14.0
$\theta_3$	Temperature for K3 (Thornton and Lessem 1978)	17, 14.5
$\theta_4$	Temperature for K4 (Thornton and Lessem 1978)	20.0, 20.0
$K_1$	Proportion of $C_{max}$ at $\theta_1$	0.1, 0.1
$K_2$ , $K_3$	Proportion of $C_{max}$ at $\theta_2$ , $\theta_3$	0.98, 0.98
$K_4$	Proportion of $C_{max}$ at $\theta_4$	0.3, 0.4
	Metabolism, R	
RA	Intercept: R (g O <sub>2</sub> d <sup>-1</sup> )	0.00463
RB	Coefficient: R versus mass	-0.295
RQ	Coefficient: R versus temperature	0.059
RTO	Activity coefficient	0.0232
RK1	Swimming speed intercept	1
RK4	Swimming speed slope	0.05
RTL	Cuttoff temperature for activity change	11
SDA	Specific dynamic action	0.172
ACT	Activity	11.7
Bact	Temperature dependence coefficient	0.041
	Egestion	
FA	Proportion of consumption egested	0.212
FB	Temperature coefficient for egested	-0.222
FG	Feeding level (p-value) coefficient	0.631
UA	Proportion of (consumption - egested)	0.31
UB	Temperature coefficient for excretion	0.58
UG	Feeding level (p-value) coefficient	-0.299

## Simulations in Beulah Reservoir

The dates selected for simulations were fairly representative of spring and early summer, although water temperatures appeared to vary considerably between days, especially in the spring. These variations appeared to be due to thermal warming and some variations in the temperature of the input flow. On April 15, for example, inflow temperatures at the upper end of the reservoir were about 2°C cooler than on April 18, and there was little surface warming in the reservoir.

On April 18, inflow temperatures at the north end of Beulah Reservoir were predicted to be about 10°C and there was gradual warming of surface water as it flowed toward the outfall (Figure 8). Deeper water showed little variation, ranging from about 6-7°C. The slight surface warming caused predicted consumption rate to vary over 10-fold from the cold bottom water to the moderately warm surface water (Figure 8).

On June 9, inflow water from the river was cooler than much of the water in the reservoir, averaging about 12.5°C (Figure 8). Surface water in the central part of the reservoir ranged from 16-17°C. In front of Agency Valley Dam, surface water was 16°C and bottom water was <11°C (Figure 8). Potential consumption rate was high throughout the reservoir on this date, generally being >0.12 g·g <sup>-1</sup>·d<sup>-1</sup>, with some variation between surface and bottom (Figure 8).

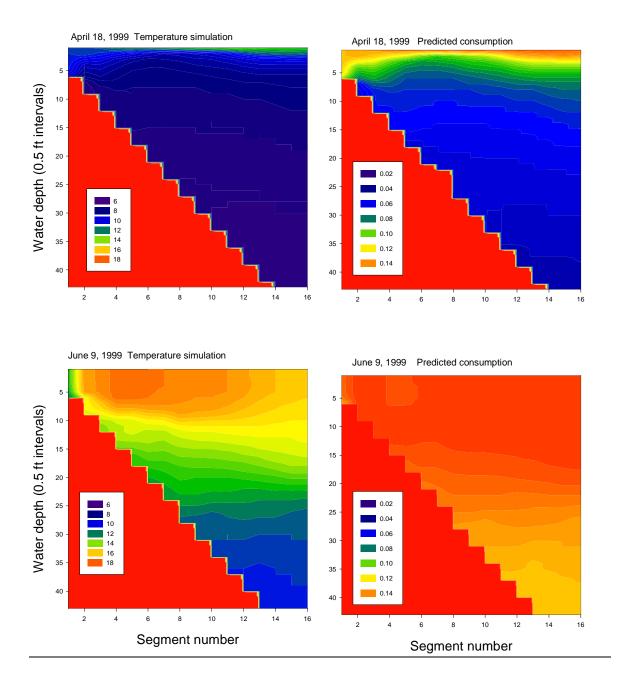


Figure 8. Simulated temperature (left) and predicted consumption rate for a 30-g bull trout (right) in Beulah Reservoir for April 18 and June 9, 1999. Segment number refers to the water temperature model; Agency Valley Dam is at Segment 16 and North Fork of the Malheur River is at Segment 1. Temperature simulations were conducted by Alan Harrison (BOR, Denver; BOR 2002) and consumption rates (g·g -¹·d⁻¹) were based on the fitted temperature model for bull trout in this study (see Table 7). The staircase in red is the bottom of the reservoir.

## Historical fish community in Beulah Reservoir

Beulah Reservoir was sampled fairly regularly by gillnet fishing during 1955 through 1970; since 1970, sampling has been less regular so we did not attempt to summarize those data. Methods appeared to vary somewhat from year to year, and from decade to decade, so we can only give a general summary here. In particular, the amount of effort expended during sampling periods (hours of gillnet fishing, number of gillnets fished, etc.) was not always available so we could not compute catch-per-unit-of-effort. This limits our interpretation to general patterns only, and makes comparisons about abundance between years difficult. Most sampling occurred during the spring to early summer months, which are the data summarized here.

Datasheets and reports generally included the number of individuals collected per species, and for some surveys, the size or total weight. Lengths of fish were occasionally measured. The location of gillnet sets was given only in a general sense (e.g., "north end of reservoir"). Stocking records and some creel census numbers are available in the data sheets, although we did not attempted to summarize this information.

Between 1955 and 1970, Beulah Reservoir was emptied three times (1955, 1961, and 1968; Figure 9) and was treated with rotenone in attempts to remove "trash fish", probably sucker species and northern pikeminnow (called "squawfish" in older data sheets). Gillnet catches of common species tended to be zero or very low for two to four years following a drawdown and rotenone treatment (Figure 9). The relative abundance of common species increased fairly rapidly in 1957-1960 and in 1966-1967, although there was considerable year-to-year variation. Largescale suckers (called "coarse-scale sucker" in old data sheets) seemed to show an especially large increase in numbers, although specific conclusions are difficult without knowing the amount of effort that was expended per year. Some species also showed declines that were apparently unrelated to drawdown or rotenone poisoning, such as the decline in bridgelip sucker (presumably called "fine-scale sucker") catch between 1958 and 1961 (Figure 9).

Since 1936, Beulah Reservoir was drawn down to minimum water levels in summer months during several years (Figure 10). Besides the three years mentioned above (1955, 1961, and 1968;), water levels were at a minimum for at least one month in 1950, 1973, 1977, and for several years between 1987 and 1994 (Figure 10).

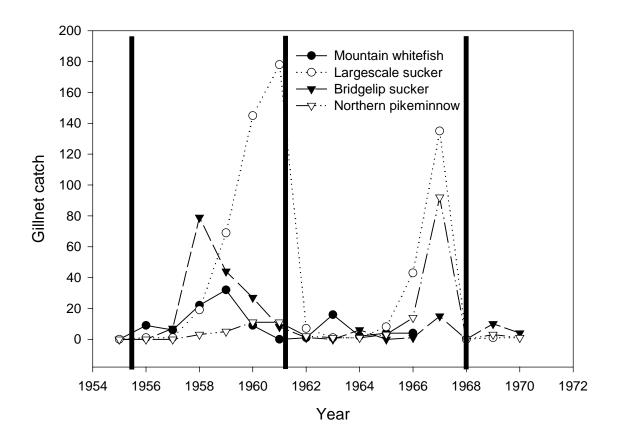


Figure 9. Total gillnet catch of common species collected in Beulah Reservoir between 1955 and 1970. Vertical lines indicate years (1955, 1961, and 1968) when the reservoir was drawn completely down. Gillnet catches are the total number of fish collected.

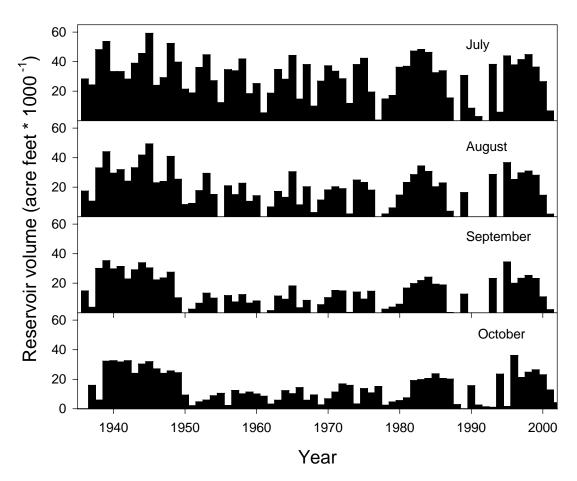


Figure 10. Average monthly water volume in Beulah Reservoir for July through October, 1936 to 2002.

#### **Discussion**

During fish sampling of 2001 and 2002, bull trout were not detected in Beulah Reservoir, although 1,330 and 549 individuals of other species were collected during the two years, respectively. The methodology used during 2001 and 2002 was successful in capturing bull trout in Beulah Reservoir in past years (e.g., ODFW data). The lack of bull trout collection may indicate that their numbers are extremely low or that bull trout are migrating out of the reservoir prior to sampling efforts. Based on temperatures observed and preferences noted in the literature for bull trout (see Selong et al. 2001 for a summary), it may not be too surprising that none were captured. Saffel and Scarnecchiea (1995) noted sharp declines in bull trout abundances when temperatures were >13.9°C. Many other authors have concluded that temperatures in excess of 15°C limit bull trout distributions (Rieman and McIntrye 1993 and references within). In Lake Billy Chinook, OR, the CPUE of bull trout (by size classes) was zero during July-September and was zero or relatively low during June in the reservoir habitat; CPUEs were generally higher in the river and transitional zones (Beauchamp and van Tassel 2001; their Table 4).

The relative abundance and composition of other species collected in Beulah Reservoir changed somewhat in 2002 compared to the findings of 2001. The most obvious of these changes were the decrease in overall CPUE, the occurrence of mountain whitefish, increases in the collection numbers of white crappie, and change in percent composition of different species, which are discussed below. Mountain whitefish may be an important food source for bull trout in some reservoir systems (T. Salow, Bureau of Reclamation, pers. comm..).

Overall gillnet CPUE decreased from 5.9 fish per hour during 2001 to 0.7 fish per hour during 2002. Extremely high catches in 2001 were likely due to our sampling during low water periods. During our major sampling efforts in July and August of 2001, Beulah Reservoir contained about 2000 acre-feet of water, about half the amount of water during June and July of 2002 when we sampled. Increased catch numbers during the low water periods of 2001 likely caused relatively high densities of fish in the deep-water regions of the reservoir where fish sampling efforts were concentrated. During sampling trips of 2002, high water may have caused fish to be more dispersed throughout the reservoir, lowering average fish density and CPUE. The extremely low CPUE of white

crappie may have been caused by their nearshore distribution, limiting their susceptibility to bottom gillnet sampling.

Mountain whitefish, which were not collected during 2001, represented 8.8% of the gill net catch in 2002, with a seasonal CPUE of 0.2 fish per hour. All 20 of the mountain whitefish collected during 2002 were captured during April (N=16) and May (N=4). Considering that fish sampling during 2001 did not begin until May, mountain whitefish may have used the reservoir during 2001 but migrated out prior to the beginning of sampling efforts. Similar to bull trout, mountain whitefish may use the reservoir during the winter and spring periods, then seek refuge in the cooler river water during the summer months.

The catch of white crappie in 2002, captured in limited numbers during 2001, increased considerably during 2002. During 2002, 141 white crappie were collected from Beulah Reservoir, ranging in size from 21 to 111 mm FL (mean 47 mm). Three white crappie were collected in April, two were caught in June, and the remainder (136) were collected during July sampling. For the first time in Beulah Reservoir, length frequency data indicated the possibility of two age classes of white crappie in the reservoir (age-0, 21-62 mm FL and age-1, 97-111 mm FL). Although scales were not collected for exact age interpretation, fish lengths were comparable to age-0 lengths described by Trautman (1957), 25-97mm FL. Wydoski and Whitney (1979) stated that white crappie reached reproductive maturity at ages of 2-3 years, about 180-200 mm FL. None of the fish collected during 2002 fell into these size classes. This may suggest that white crappie are reproducing in Beulah Reservoir at a smaller size, or that older, reproductive white crappie are in the reservoir but were not collected.

The percent composition of fishes collected in fyke nets changed noticeably between 2001 and 2002, whereas the composition of gill net catches varied less between these years. Possibly the most significant change was the 42.9% increase in fyke net catch of the white crappie during 2002 compared to 2001. The addition of the high numbers of white crappie to the sample caused a decrease in the percent composition of other fish species within the reservoir. Percent composition of gill net catch and fyke net catch without white crappie in the data set showed only minor variations in catch percentages between years. For example, northern pikeminnow percent composition decreased from

40% during 2001 to 18.6% during 2002. However, with white crappie numbers removed from the sample set, 2002 percent composition of northern pikeminnow would have equaled 33% of the fyke net catch, a percentage similar to 2001 findings, indicating that their abundance was similar between the two years.

The historical catches of various species in Beulah Reservoir provide a rough indication of the recovery period for some species following a drawdown to river level. In general, there appeared to be a lag of 1-3 years before some species showed up in gill net catches in Beulah Reservoir. We have, however, little information on the abundance of smaller sized fishes in the recovering reservoir, which might provide food for bull trout during fall, winter, or spring. Considering that the reservoir has been drawn down to a minimum level during several years since 1936, past and recent data suggest that the fish community is fairly resilient to this type of management.

Variations in water quality findings were difficult to compare between 2001 and 2002 due because sampling periods differed between years. Water quality sampling during 2001 was carried out from July through November. Sampling in 2002 was only during April-July since the reservoir was drained in August. The July surface temperatures exceeded 24°C during 2001 compared to 22°C in 2002. Temperature readings near the bottom of the reservoir exceeded 20°C during both years of field studies. During the months of July through September of most years, water temperatures throughout the reservoir likely exceed 15°C, a temperature shown by Reiman and McIntyre (1993) and others to limit the distribution of bull trout.

From the laboratory experiments that we conducted, preliminary estimates for the allometric parameters for maximum consumption rate were 0.394 (CA) and –0.387 (CB). These values differ considerably from the parameters used by Beauchamp and van Tassel (2001) in their bioenergetic analysis of bull trout in Lake Billy Chinook, OR (CA=0.059; CB=-0.307). The parameters used by Beauchamp and van Tassel (2001) were originally derived from laboratory experiments with lake trout (Stewart et al. 1983), and the assumption was that they could be applicable to a congener. Sweka and Hartman (2001) recently estimated consumption rate parameters CA (0.130) and CB (-0.201) for a congener of bull trout, brook trout. Experiments with brook trout, however, were conducted at only one temperature (12.0 °C) and with relatively small individuals (avg. 37)

g). Although brook trout, bull trout, and lake trout are congeners, the differences in the derived parameters for the three species suggest differences in their allometric response, and that parameters for one species may not be especially useful in other bioenergetic models. The parameter values that we developed for CA and CB are within the range observed for other cool- or cold-water species such as walleye *Stizostedion vitreum*, salmon, and steelhead (Hanson et al. 1997).

The temperature parameters for bull trout that we derived were fit to a relatively few data points (four temperatures) and we had to make some assumptions about changes in feeding rates below 7°C and above 16°C. The bioenergetics models for congeners that have been developed, such as for lake trout, did not use the Thornton and Lessem temperature model so they can not be compared directly to our results. Beauchamp et al. (1989) fit a Thornton and Lessem model to sockeye salmon and their estimates for K<sub>1</sub>, K<sub>4</sub>,  $\theta_1$ ,  $\theta_2$ ,  $\theta_3$ , and  $\theta_4$  can be compared to our values. For adult sockeye salmon and adult bull trout, these six parameter values were, respectively: 0.58 vs. 0.1, 0.5 vs. 0.4, 3 vs. 2.5, 20 vs. 14.0, 20 vs. 14.5, and 20 vs. 24 (Beauchamp et al. 1989; Table 7). Parameters K<sub>2</sub> and K<sub>3</sub> were 0.98 for both species, largely by convention for the Thornton and Lessem formulation. The main difference between the models for these two species is that maximum consumption stays at a higher rate at increased temperatures in the sockeye model, compared to the bull trout model. A Thornton and Lessem temperature model for steelhead (Rand et al. 1993) also tended to predict somewhat higher rates of maximum consumption at high temperatures than for our bull trout model. The assumptions that we made regarding the decline in maximum consumption at higher temperatures, in particular, may need additional data to corroborate.

The difference between consumption parameters for bull trout and congeners that we observed in these experiments may suggest that other important parameters, such as resting respiration rate or activity, should also be empirically derived rather than borrowed. The model for bull trout is based on the lake trout parameter set where activity is a function of swimming speed, and swim speed is a function of mass and water temperature below a cutoff temperature (Stewart et al. 1983). The activity coefficient in this model ranges from about 1.4 at low temperature and small size to 1.9 at high temperature and large size (Stewart et al. 1983). Some studies have suggested that activity

is underestimated in many bioenergetic model formulations (e.g., Boisclair and Leggett 1989; Ney 1993; Rowan and Rasmussen 1996). Rowan and Rasmussen (1996) estimated that the activity multiplier for lake trout might be as high as 4 or 5 for mature fish, which could translate into an underestimate of consumption by roughly half. Relatively few field studies have been done to estimate how activity influences field estimates of consumption or growth. If activity is under-estimated in the bull trout model, predictions about the needed prey base to support a bull trout population could also be underestimated. Past or ongoing radio telemetry studies with bull trout might be useful in deriving a better estimate for the activity parameter, and more accurate bioenergetic predictions.

The simulations of predicted consumption rate in Beulah Reservoir on April 18 and June 9 were conducted as a demonstration of the bioenergetics model, and how the model can be combined with physical data or models. These simulations showed that predicted or "potential" consumption rate can vary over 10-fold throughout the reservoir based upon temperature alone, and that variations occur vertically and longitudinally in the reservoir. Predicted temperatures are available for April 13, 1999 to December 28, 1999 (BOR 2002), so simulations could be conducted for any period. Patterns of potential consumption rates have been used to explore the effects of complex habitats in various other aquatic system such as Chesapeake Bay, Oneida Lake NY, and the Gulf of Mexico (e.g., Brandt et al. 1992; Breitburg et al. 1999; Rose 2000).

#### Acknowledgements

Wayne Bowers and Rick Rieber offered helpful comments on the study. Dave Beauchamp provided many useful suggestions and also loaned nets for the study. Jon Martin, Jon Kirby, Sarah Rose, Greg George and Brian Sharp from the USGS / Columbia River Research Laboratory assisted with the fieldwork. Tammy Salow and Dena Gadomski reviewed drafts of the report and provided many helpful suggestions. This study was funded by the Bureau of Reclamation, Pacific Northwest Region, administered by Rick Rieber, which we appreciate.

#### References

- Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Trans. Am. Fish. Soc. 118:597-607.
- Beauchamp, D. A., and J. J. van Tassel. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Trans. Am. Fish. Soc. 130:204-236.
- Boisclair, D., and W. C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. 46:1859-1867.
- BOR (U.S. Bureau of Reclamation). 2002. Beulah Reservoir Water Quality Modeling Study, Vale Irrigation Project, Oregon. Denver, CO.
- Brandt, S. B., D. M. Mason, and E. V. Patrick. 1992. Spatially-explicit models of fish growth rate. Fisheries 17:23-31.
- Brandt, S. B., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Trans. Am. Fish. Soc. 122:845-869.
- Breitburg, D., K. Rose, and J. Cowan. 1999. Linking water quality to larval survival: predation mortality of fish larvae in an oxygen-stratified water column. Mar. Ecol. Progr. Ser. 178:39-54.
- Brown, T. G. 1995. Stomach contents, distribution, and potential of fish predators to consume juvenile chinook salmon in the Nechako and Stuart rivers, B. C. Can. Tech. Rep. Fish. Aquat. Sci., no. 2077, 47 pp.
- Davis, J.C. (1975). Minimal Dissolved Oxygen Requirements of Aquatic Life with Emphasis on Canadian Species: a Review. J. Fish Res. Board Can. 32 (12): 2295-2332
- Graham, J. H. 1949. Some effects of temperature and oxygen pressure on the metabolism and activity of the speckled trout, *Salvelinus fontinalis*. Can. J. Res. 27: 270-288 (cited from Davis 1975)
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin-Madison, Sea Grant Institute, Madison, Wisconsin.
- Hartman, K. J., and S. B. Brandt. 1995. Comparative energetics and development of bioenergetics models for sympatric estuarine piscivores. Can. J. Fish. Aquat. Sci. 52:1647-1666.
- Irving, L., C. Black, and V. Stafford. 1941. The influence of temperature upon the combination of oxygen with the blood of trout. Biol. Bull. 80:1-17 (cited from Davis 1975)
- Labar, G. W. 1993. Use of bioenergetics models to predict the effect of increased lake trout predation on rainbow smelt following sea lamprey control. Trans. Am. Fish. Soc. 122:942-950.

- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122:736-748.
- Petersen, J.H., and D. L. Ward. 1999. Development and corroboration of a bioenergetics model for northern squawfish feeding on juvenile salmonids in the Columbia River. Trans. Am. Fish. Soc. 128:784-801.
- Petersen, J. H., and J. F. Kitchell. 2000. Climate regimes and water temperature changes in the Columbia River: bioenegetic implications for predators of juvenile salmonids. Can. J. Fish. Aquat. Sci. 58:1831-1841.
- Petersen, J. H., and E. E. Kofoot. 2002. Conditions for growth and survival of bull trout in Beulah Reservoir, Oregon. Annual Report for 2001. Report to the U.S. Bureau of Reclamation, Pacific Northwest Region, Boise, Idaho. 43 p.
- Rand, P. S., D. J. Stewart, P. W. Seelback, M. L. Jones, and L. R. Wedge. 1993.Modeling steelhead population energetics in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. 52:1546-1563.
- Reed, J.R., and W.D. Davies. 1991 Population Dynamics of Black and White Crappie in Weiss Reservoir, Alabama: Implications for the Implementation of Harvest Regulations. North American Journal of Fisheries Management 11:598-603
- Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. General Technical Report INT-302, U.S. Forest Service, Ogden, Utah.
- Roach, L.S., and I.M. Evans. 1948. Growth of game and pan fish in Ohio. 2. Ohio Div. Conserv. Sec. Fish Manage., Fish Manage. Rep. 29 p. (Referenced from Scott and Crossman 1973).
- Rose, K. A. 2000. Why are quanitative relationships between environmental quality and fish populations so elusive? Ecol. Applic. 10:367-385.
- Rowan, D. J., and J. B. Rasmussen. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (<sup>137</sup>Cs). Can J. Fish. Aquat Sci. 53:734-745.
- Saffel, P. D., and D. L. Scarnecchia. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. Northwest Science 69:304-317.
- Scott, W.B. and E.J. Crossman (1973) Freshwater Fishes of Canada. Fisheries Research Board of Canada, Ottawa Canada. 966 p.
- Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Burrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Trans. Am. Fish. Soc. 130:1026-1037.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: Application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.

- Sweka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. Can. J. Fish. Aquat. Sci. 58:386-393.
- Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. Soc. 107:284-287.
- Trautman 1957. The fishes of Ohio with illustrated keys. Ohio State University Press, Columbus Ohio. 683 p. (Referenced from Scott and Crossman 1973)
- Wydoski, R. S., and R. R. Whitney. 1979. Inland Fishes of Washington. University of Washington Press, Seattle.

# Appendices.

Appendix 1. Catch (number of individual fish) in gill nets by species in Beulah Reservoir during 2002. MWF = mountain whitefish; NPM = northern pikeminnow; WCR = white crappie; LSS = largescale sucker; BLS = bridgelip sucker; RBT = rainbow trout; RSS = redside shiner.

									RSS
4/2/02	4	36	0	0	0			0	0
	5	43	0	0	0			0	0
	6	47	1	0	0			0	0
	7	54	0	1	0	0	0	0	0
	8	58	0	0	0			0	0
	9	60	0	0	2	0	0	0	0
4/3/02	15	57	0	0	0			0	0
	16	67	0	0	0			0	0
	17	75	0	2	0			0	0
	18	47	0	0	0	0			0
	19	61	1	1	0	1	0		0
	20	67	1	0	0	1	0		0
	21	65	0	0	0			0	0
	22	54	1	2	0	3	0		0
	23	56	1	0			0	0	0
	24	51	0	0	0			0	0
4/4/02	30	59	2	0	0	1	1		0
	31	73	1	1	1	2	0		0
	32	62	0	3	0			0	0
	33	61	3	0	0			0	0
	34	57	0	0	0	1	0	1	0
	35	67	3	0	0	0	0	2	0
	36	64	1	0	0	1	0	0	0
	37	71	0	0	0	5	0	0	0
	38	51	1	0	0	1	0	0	0
5/6/02	47	90	0	0	0	1	1	0	0
	48	99	0	2	0	1	2	0	0
	49	122	1	0	0	1	1	0	0
	50	64	0	1	0	0	0	0	0
	51	59	0	1	0	0	0	0	0
	52	54	0	0	0	0	0	0	0
5/7/02	54	63	0	0	0	3	1	1	0
	55	79	0	1	0	3	0	1	0
	56	110	0	4	0	2	0	1	1

									RSS
5/7/02	57	79	0	0	0	0	1	0	0
3/1/02	58	64	0	0	0	1	0	0	1
	59	50	0	0	0	1	0	0	1
5/8/02	62	64	0	2	0	9	0	1	0
	63	97	1	6	0	8	0	2	0
	64	141	1	0	0	7	0	2	0
	65	86	0	0	0	1	0	2	0
5/28/02	66	63	0	3	0	0	0	0	0
	67	65	0	4	0	0	1	0	0
	68	39	0	1	0	0	0	0	0
	69	46	0	1	0	0	0	0	1
	70	50	0	0	0	0	0	0	0
	70	58	0	0	0	0	0	0	0
5/29/02	77	51	0	4	0	0	0	5	0
3/29/02	78	75	0	2	0	0	0	1	1
	79	90	1	4	0	1	0	2	0
			0		0	0		0	0
	80	56		0			0		
	81	51	0	1	0	0	0	0	0
	82	54	0	0	0	0	0	0	0
5/30/02	84	58	0	3	0	0	0	0	0
	85	61	0	0	0	1	0	1	1
	86	77	0	4	0	0	1	0	0
	87	56	0	2	0	0	0	0	1
	88	61	0	3	0	0	0	0	0
	89	60	0	0	0	0	0	0	0
	90	61	0	0	0	0	0	1	0
	91	51	0	0	0	0	0	0	0
5/0.4/0.0	92	42	0	0	0	0	0	0	0
6/24/02	96	69	0	1	0	0	0	1	0
	97	81	0	0	0	1	0	0	0
	98	55	0	0	0	0	0	0	0
	99	51	0	0	0	0	0	1	0
6/25/02	104	115	0	1	0	0	1	1	0
	105	86	0	0	0	0	0	0	0
	106	59	0	0	0	0	0	0	0
	107	62	0	0	0	0	0	0	0
	108	64	0	0	0	0	0	1	0
	109	62	0	0	0	0	0	0	0
	110	67	0	0	0	1	1	0	0
	111	49	0	0	0	0	0	0	0
	112	49	0	0	0	0	0	0	0

			1				1	1	1
					<u> </u>		<u> </u>		
									RSS
7/23/02	123	60	0	0	0	0	0	1	0
	124	68	0	0	0	1	0	0	1
7/23/02	125	75	0	1	0	0	0	1	0
	126	55	0	0	0	0	0	0	0
	127	61	0	0	0	0	0	0	0
	128	63	0	0	0	0	0	0	0
	129	58	0	0	0	0	0	0	0
	130	55	0	2	0	4	0	0	0
	131	63	0	2	0	0	0	0	0
7/24/02	137	93	0	2	0	0	0	2	0
	138	107	0	0	0	0	0	1	0
	139	102	0	2	0	1	1	4	0
	140	47	0	0	0	0	0	1	0
	141	47	0	0	0	0	0	0	0
	142	37	0	0	0	0	0	2	0
	143	44	0	0	0	0	0	0	0
	144	57	0	0	0	0	1	0	0
	145	50	0	2	0	2	0	2	0