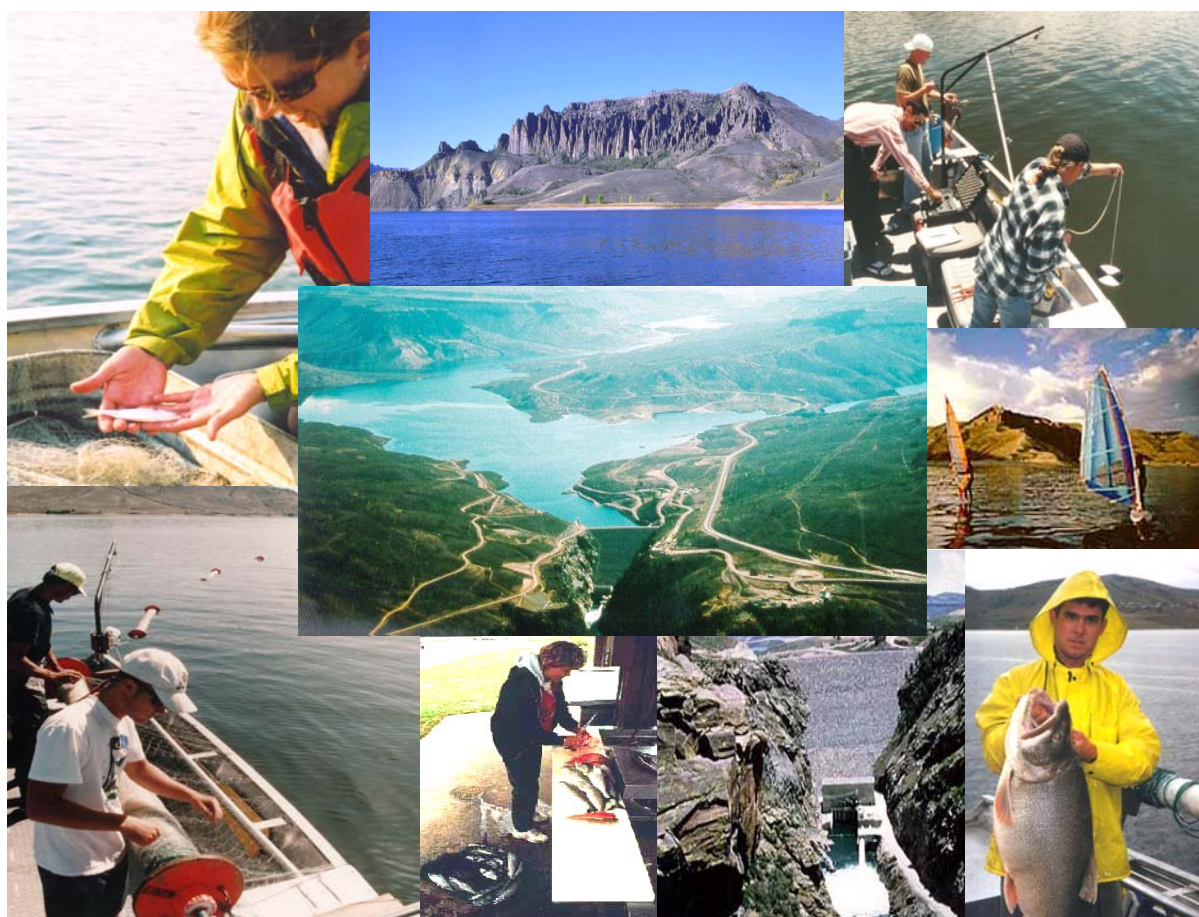


RECLAMATION

Managing Water in the West

A synthesis of the “Ecological Effects of Reservoir Operations at Blue Mesa Reservoir” Project

RESERVOIR AND FOOD WEB DYNAMICS AT BLUE MESA RESERVOIR, COLORADO, 1993-2002



**U.S. Department of the Interior
Bureau of Reclamation
Technical Service Center
Ecological Planning and Assessment Group
Denver, Colorado**

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Prepared for:

**U.S. Department of the Interior
Bureau of Reclamation**

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Cover photos (clockwise from top): Dillon Pinnacles (National Park Service), CSU students making limnological measurements (B. Johnson), sailboarders in Cebolla basin (National Park Service), large lake trout captured for growth, diet and stable isotope analyses (B. Johnson), Blue Mesa dam and outlet works (Bureau of Reclamation), happy angler with a nice catch of kokanee (B. Johnson), CSU students doing vertical gill net survey (B. Johnson), Alissa Gigliotti, CSU undergrad, with an age-0 kokanee, center: aerial view of Blue Mesa Reservoir (Reclamation).



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ABSTRACT

Historically, the Blue Mesa Reservoir (BMR) fishery has generated a multi-million dollar annual input to local and state economies. The fishery has attracted anglers from 49 states and kokanee usually comprise over 80% of the catch. Changes to the seasonal pattern of hypolimnetic releases beginning in 1993 prompted this study to investigate the effects of dam operations on this important fishery, as well as the limnology and food web of BMR during 1993-2003. The study coincided with a period of drought with generally declining inflows; thus, it was necessary to consider hydrologic conditions as a covariate with dam operations. The reservoir was mesotrophic (mean TSI = 42) during the study period, decreasing only slightly from that reported in the past. Water clarity increased since 1975 and it appears that algal biomass may be declining in the reservoir. The crustacean zooplankton assemblage of BMR was a key link between primary production and fish and consisted mainly of two copepod taxa (a cyclopoid and a calanoid), and two *Daphnia* species (*D. pulicaria* and *D. galeata*). Energy produced in the pelagic food web supported kokanee, rainbow trout and juvenile lake trout to varying degrees. Diet and stable isotope analysis showed that benthic pathways were also important to fish production. Benthic production supported rainbow trout and small lake trout, and larger lake trout relied on fish biomass originating from both pelagic and benthic pathways. Modeling predicted that the new dam operation regime would have virtually no effect on reservoir thermal structure under normal hydro-meteorological conditions, compared to the historic operating pattern. It was not possible to evaluate the direct effects of new dam operations on zooplankton dynamics because of the lack of historical data but entrainment of *Daphnia* through the dam during summer was not significant relative to the standing stock in the reservoir. There was conflicting evidence about the intensity of fish entrainment at BMR but year-round studies are lacking. However, kokanee and rainbow trout survival declined steadily after dam operations changed. Factors unrelated to dam operations could account for a significant portion of the observed mortality of both rainbow trout and kokanee. Lake trout predation alone was sufficient to account for the decline in rainbow trout survival. Predation, losses to irrigation ditches, and harvest could not entirely explain kokanee declines. New dam operations did not appear to affect food availability, growth or body condition of age-1 and older kokanee in BMR. There was no evidence to suggest that new dam operations affected growth of rainbow trout either. Changes to reservoir thermal structure caused by new operational modes such as surface spills and use of a TCD, were predicted to affect kokanee growth and risk of predation from lake trout. If water was released via the spillway instead of the hypolimnetic outlet, kokanee growth was predicted to decline due to cooler conditions and decreased zooplankton productivity. Modeling showed a TCD would also result in cooler conditions and predation risk to kokanee from lake trout would be higher if a TCD were installed. Overall, while changes to withdrawal depth may affect the reservoir's food web and fishery, the reservoir appeared to be resistant to changes in the release regime from the hypolimnetic outlet. Thus, water managers at BMR have considerable latitude for changing hypolimnetic release patterns without affecting physicochemical conditions or productivity of the reservoir.

ACKNOWLEDGEMENTS

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1 INTRODUCTION

1.1 Background

Historically, large dams in the arid western United States have been operated to capture spring runoff and then release that water for irrigation and hydropower generation during summer. This operational pattern has had dramatic effects on river hydrographs, reducing the amplitude of spring peak flows, dampening seasonal variation, and increasing daily variation in flows downstream of the dam (Ward and Stanford 1979; Petts 1984). River regulation has had adverse effects on riverine biota (Poff et al. 1997), including disruption of spawning and recruitment of endangered fishes (Tyus 1991, Stanford 1994). These effects have prompted ecologists to advocate for new dam operations to restore more natural hydrographs below dams to mitigate some of these ecological impacts.

Construction of Blue Mesa Reservoir (BMR), the upstream-most reservoir of the Aspinall Unit of the Colorado River Storage Project, changed the flow regime in the lower Gunnison River and in the upper Colorado River and habitat for fishes (Stanford and Ward 1984; McAda and Kaeting 1990). This area is now considered critical habitat for endangered Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *Gila cypha*, bonytail *G. elegans*, and razorback sucker *Xyrauchen texanus*. Because the changes to the flow regime were considered harmful to these species (see McAda 2003) Reclamation implemented new dam operations beginning in 1993. Flow recommendations for recovery of endangered fish continued to be developed during subsequent years (McAda 2003). These recommendations sought to create and maintain habitat for all life stages of the endangered fishes; a major component of the recommendations was the creation of spring peak flows by altering the timing and magnitude of releases from the dam.

Because very little was known about how BMR itself might respond to changes in release patterns, fishery managers expressed concern that new dam operations might jeopardize the extremely popular and economically important sport fishery in the reservoir (Figure 1). Blue Mesa Reservoir has been cited as one of the most productive kokanee *Oncorhynchus nerka* fisheries anywhere (R. Behnke, CSU, personal communication) and the population provides up to 86% of the State's kokanee egg supply used in the hatchery system (Dan Brauch, CDOW, personal communication). Visitation at the Curecanti National Recreation Area (CNRA) is approximately one million visitors annually (National Park Service (NPS) 2003) and many of those people are seeking fishing recreation. The fishery was valued at \$5.43 million with \$2.64 million in actual expenditures in 1987 (Johnson and Walsh 1987). Clearly, negative impacts of new dam operations on the sport fishery could have serious implications for the CNRA, the local economy, and for kokanee management statewide.

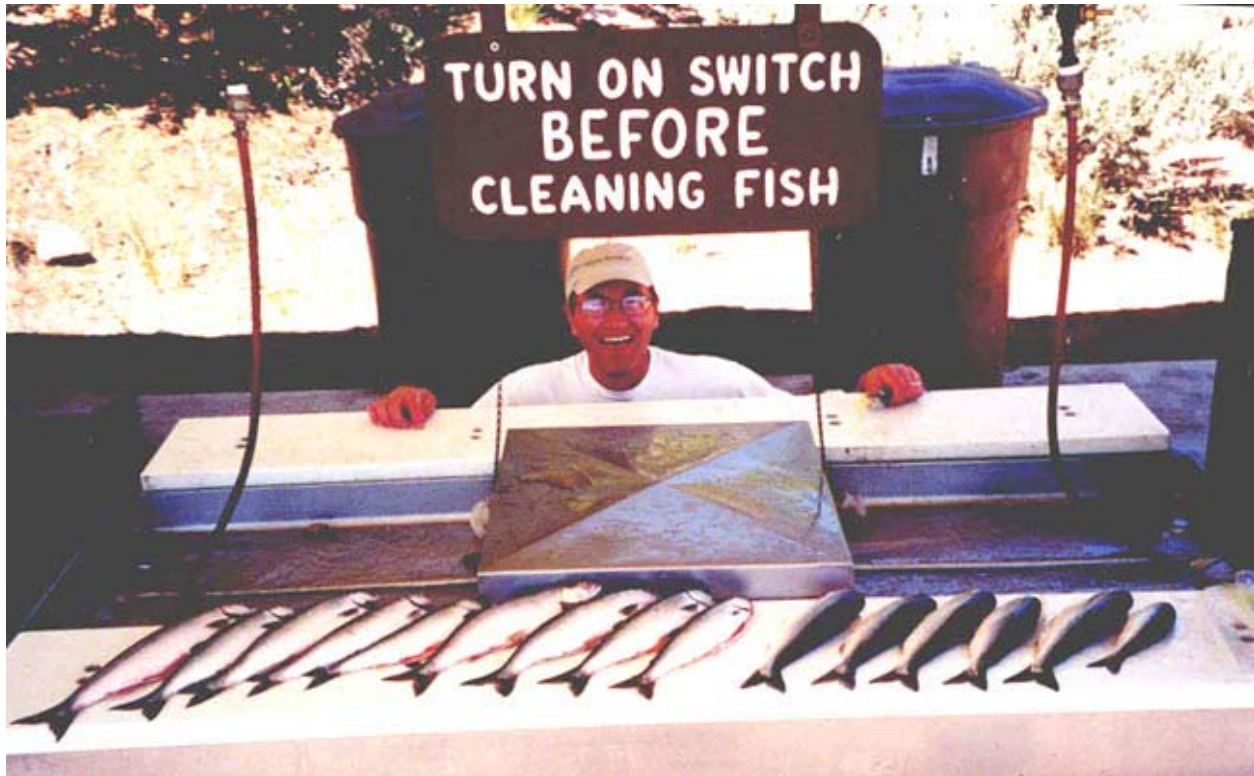


Figure 1. Ron Sutton (Reclamation) with a nice catch of kokanee from Blue Mesa Reservoir (photo: Brett Johnson).

Dam operations interact with hydro-meteorological conditions to affect reservoir characteristics through a variety of direct and indirect mechanisms (Figure 2). Natural inflow and release patterns alter water residence time with implications for nutrient loading and availability to primary producers. Large releases may increase entrainment of the biota, reducing zooplankton production and fish recruitment. Water level fluctuations have been shown to negatively impact fish reproduction in reservoirs (Ploskey 1986). Together, these factors affect energy available to the pelagic food web, and ultimately fish biomass, production and yield.

Reservoir thermal structure is also affected by dam operations and hydro-meteorology. Thermal structure is a critically important ecological factor in aquatic systems because it determines physiological rates of primary producers and poikilothermic (cold-blooded) animal inhabitants. In addition, thermal structure controls internal nutrient cycling by altering water column stability. Thermal stratification can either segregate or aggregate predators and prey and competitors, depending on the thermal preferences of each. Stratification can provide a thermal refuge for prey in the epilimnion or hypolimnion, or it may intensify species interactions by concentrating animals in a subset of the reservoir's volume. Thus, temperature drives production of food organisms as well as predator and prey consumption rates, with profound implications for reservoir productivity and sport fish yield.

This study sought to provide a better understanding of the mechanisms and pathways by which reservoir operations at BMR impact reservoir productivity and the quality of the fishery the reservoir supports. That knowledge contributes to our understanding of ecological and fishery implications of alternative reservoir operation strategies in the future and in other reservoirs. Our approach was to examine some key indicators of ecosystem change: limnological conditions and fishery characteristics. These indicators are related to dam operations and hydro-meteorological conditions, and alternative explanations for changes to the reservoir food web that coincided with new dam operations were examined.

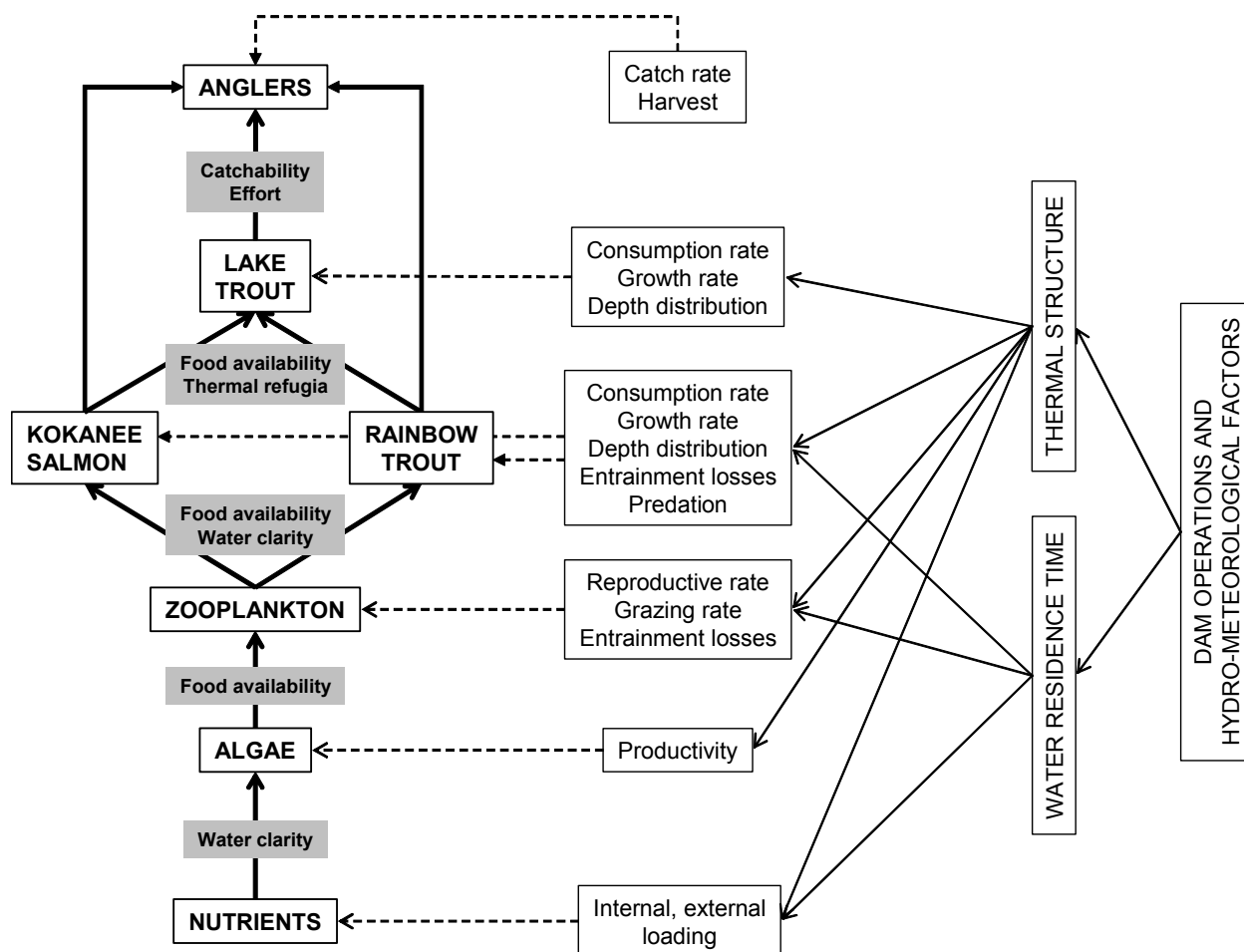


Figure 2. Mechanisms relating dam operations and hydro-meteorological factors to reservoir physical conditions (temperature and water residence time), and the influences of these conditions on a coldwater reservoir food web such as that in Blue Mesa Reservoir. Thin solid arrows represent physical effects and their corresponding effects on population dynamics. Dashed arrows represent how population dynamics affect biomass and production in food web components. Heavy solid arrows represent

flow of energy and biomass through the food web; gray boxes represent factors controlling linkages among trophic levels.

1.2 Site Description

BMR (Figure 3) is a mesotrophic impoundment in southwestern Colorado. With a storage capacity of $1.160 \times 10^9 \text{ m}^3$ (Table 1), it is the largest reservoir in the state. The earthen dam forming BMR was constructed to store and control large spring flows, and rises 104 m above the streambed of the river (Reclamation 1975). The dam was completed in 1965. Two 40,000 kW generating units operate at the base of the dam. The penstocks are located 50 m below the surface at full pool. Blue Mesa is the upstream-most of three reservoirs in the Aspinall Unit of the Colorado River Storage Project, providing flood control and water for irrigation, power generation, and recreation.

The land immediately surrounding the reservoir is dominated by a sagebrush and grassland community. Development along the shores is minimal; most of the reservoir is within the NPS's Curecanti National Recreation. The watershed drains an area of 10,269 km² (Figure 4); about 60% of that area is forested and only 0.14% of that is developed (Gurdak et al. 2002). Historically, the dominant land use in the watershed was ranching and mining. Most of the annual inflow occurs during spring in a pattern characteristic of a snowmelt hydrograph (Van Steeter and Pitlick 1998); approximately 57% of the total inflow comes from the Gunnison River with the Lake Fork Arm of the Gunnison and Cebolla Creek providing most of the remaining inflow (Cudlip et al. 1987). The regional climate is semi-arid with about 26 cm of precipitation annually.

Summer limnological conditions in BMR vary annually and spatially, but in general the reservoir stratifies every summer, beginning in early May and surface temperatures in August reach 19-20°C. Hypoxia occurs in the hypolimnion, especially by September. Fall mixing usually occurs during late October or early November. Summer conductivity averages about 200 µS/cm; Secchi depth in July has averaged about 4.1 m since 1983. Epilimnetic chlorophyll in August has varied between 1 µg/liter and 6 µg/liter since 1975. TSI (mean of phosphorus, Secchi and chlorophyll; Carlson 1977) ranged 30-55 during 1994-2002, and is indicative of oligotrophic or mesotrophic conditions. The primary macrozooplankton include the cladocerans *Daphnia pulcaria* (*pulex* and *Daphnia galeata mendotae*) (Figure 5), *Bosmina* spp., *Ceriodaphnia* spp., the cyclopoid copepod *Diacyclops* spp. and the calanoid *Diaptomus* spp.



Figure 3. Map of Blue Mesa Reservoir and vicinity (NPS).

Table 1. Morphometric characteristics of Blue Mesa Reservoir and dam, Gunnison County, Colorado (measurements refer to reservoir at full pool). Data sources shown in footnotes.

Parameter	Value	Units	Source
Surface area	3,793	ha	1
Total capacity	1.160×10^9	m ³	1
Active capacity	9.232×10^8	m ³	1
Inactive capacity	1.000×10^8	m ³	1
Dead storage	1.372×10^8	m ³	1
Length	42	km	3
Maximum depth	101	m	6
Mean depth	27.9	m	5
Surface elevation	2,292	m	1
Top of dead storage	2,242	m	1
Penstock elevation	2,242	m	1
Maximum discharge (penstocks)	142	m ³ /s	1
Maximum discharge (spillway)	962	m ³ /s	1
Approximate hydraulic retention time	0.8	y	2, 4
Drainage basin area	8,894	km ²	1

Sources: ¹Reclamation (1999); ²Johnson et al. (2004); ³Cudlip et al. (1987); ⁴Bauch and Malick (2003); ⁵USEPA (1977); ⁶ Reclamation (1975).

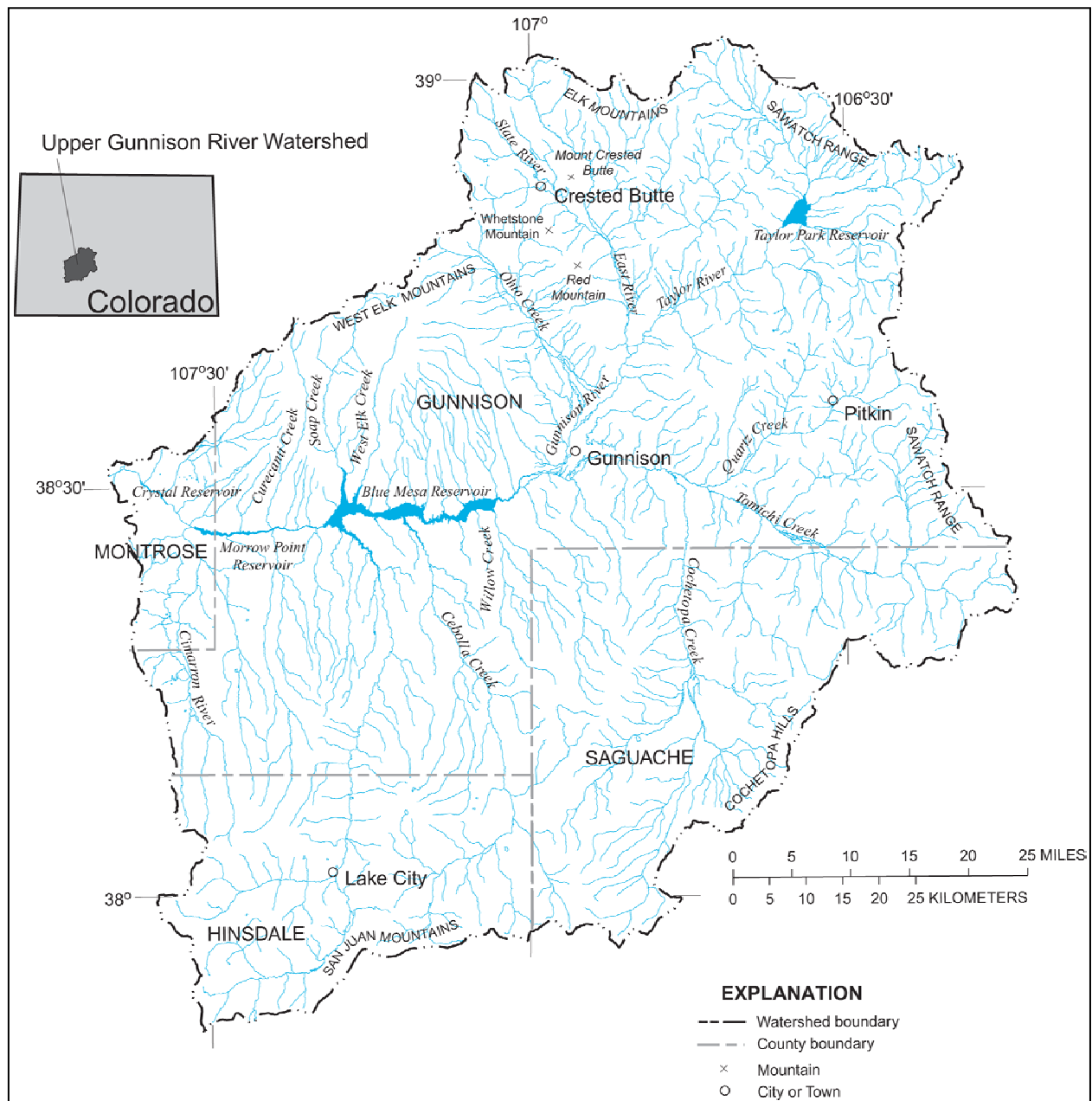


Figure 4. The watershed of Blue Mesa Reservoir (Gurdak et al. 2002).



Figure 5. *Daphnia pulicaria* (left) and *Daphnia galeata mendotae* (right), the primary food of kokanee in Blue Mesa Reservoir (photo: University of Wisconsin, Center for Limnology).

Wiltzius (1978) reported that for at least 80 years prior to the construction of the Aspinall Unit, the upper Gunnison River was a world-renowned trout fishery, first consisting entirely of Colorado cutthroat trout *Oncorhynchus clarki pleuriticus* and later of rainbow and brown trout. After impoundment, the fish community in BMR has consisted primarily of kokanee *Oncorhynchus nerka*, rainbow trout *O. mykiss*, lake trout *Salvelinus namaycush*, brown trout *Salmo trutta*, longnose sucker *Catostomus catostomus*, and white sucker *Catostomus commersoni*. Coho salmon *O. kisutch* were stocked shortly after the reservoir filled but those attempts to establish the species were unsuccessful (Wiltzius 1971). Cutthroat trout *O. clarki* continue to be stocked periodically but are rarely seen in the reservoir; longnose dace *Rhinichthys cataractae* are present and

northern pike *Esox lucius* and yellow perch *Perca flavescens* invaded the reservoir, apparently in the late 1990s. The reservoir supports an extremely popular and productive kokanee fishery. For example, in 1993, BMR received over 612,000 angler-hours of fishing effort (ice and openwater angling; S. Hebein, CDOW, personal communication). About 340,000 fish were harvested, of which 75.3% (255,772 fish) were kokanee salmon, and 18.5% (83,898 fish) were rainbow trout. Angler caught kokanee were among the largest in Colorado with a mean length of 320 mm.

1.3 Previous Research

BMR has been the subject of a number of previous investigations focusing mainly on its water quality and fishery. There have also been several studies monitoring the water quality of the inflows (reviewed in Bauch and Malick 2003). Wiltzius (1971, 1974, and 1978) studied the pre-dam conditions in the Gunnison River, and changes to water quality characteristics and response of fish populations to impoundment and stocking of the reservoir.

The U.S. Environmental Protection Agency (USEPA; 1977) conducted a water quality study during 1975, as part of the National Eutrophication Survey. They found the reservoir to be mesotrophic, that the system was nitrogen-limited and that nearly all the nutrient loading was from non-point sources. Reservoir limnological characteristics during 1965-1985 were summarized by Cudlip et al. (1987); they reported that the reservoir did not experience the usual pattern of trophic upsurge shortly after impoundment followed by trophic decline. Rather, the reservoir remained mestrophic during that time period.

Stanford and Ward (1984) evaluated the physicochemical and biotic effects of the operations of the Aspinall Unit on the Gunnison River. They found that the dams disrupted the characteristic longitudinal gradients in natural rivers predicted by the River Continuum Concept (Vannote et al. 1980), and instead there was a serial discontinuity (Ward and Stanford 1983) in river attributes. McAda and Kaeting (1990) reported on changes to the native fish community after construction of the Aspinall Unit.

In spring and summer of 1994-1996 Mueller and Hiebert (1997) conducted a study of fish entrainment through the powerplant of the Blue Mesa Dam. Most of the fish sampled in the sieve net in the outlet of Blue Mesa Dam were small (age-0) kokanee but fish transport rates were estimated to be <4% of the annual fingerlings stocked into BMR.

The NPS has conducted a wide variety of studies of BMR and adjacent aquatic ecosystems. A water resources scoping report (NPS 1995) developed water resources objectives and identified water resources related issues and concerns. A water resources management plan (Cudlip et al. 1996) was developed, describing water resources of the Curecanti National Recreation Area and management alternatives

addressing watershed-related issues. A massive compendium of water quality data for the Curecanti National Recreation Area was created from USEPA databases (NPS 1998a; 1998b). Bauch and Malick (2003) presented results of an intensive water quality investigation conducted in 1999, examining the Aspinall Unit's inflow, outflow and reservoir characteristics. Also included was a retrospective analysis of water quality in BMR during 1975, 1983-1985, and 1998. Trophic state indices based on phosphorus, chlorophyll and Secchi depth were characteristic of mesotrophic conditions in 1999, and nutrient loading and the trophic status had not changed in the preceding 25 years.

Martinez (1994-2003) supplemented work performed by Colorado State University (CSU) throughout the project and continued limnological sampling during 1998-2000 when CSU was not working on the reservoir. His work included standardized temperature-dissolved oxygen profiles and zooplankton species composition, size structure, and abundance. Martinez also conducted whole-reservoir hydroacoustics surveys during 1994-2003, sampled kokanee from the spawning run at Roaring Judy Hatchery for otoliths each year, and conducted annual sampling to look for *Mysis relicta*.

Gurdak et al. (2002) analyzed water quality data for the Upper Gunnison River watershed during 1969-1999. Despite population growth, development, and land use changes during the study period, there were no temporal trends in either nitrate or total phosphorus in surface waters of the watershed. Chlorophyll concentrations in the reservoir were found to be typical of unenriched to moderately enriched waters, consistent with the findings of USEPA (1977) and Cudlip et al. (1987).

Historic data on the hydrology of the Gunnison River before and after the construction of the Aspinall Unit was examined by McAda (2003) to evaluate the effects of the dams on endangered fish habitat in the Gunnison and Upper Colorado rivers. The report provided biologically based, seasonal flow recommendations for the Gunnison River for the benefit of native fishes. Flow recommendations were used to assist in the development of dam operations plans to simulate a more natural hydrograph downstream to improve habitat for native fishes. These recommendations were a function of runoff conditions in the Gunnison basin; more water was to be released from Aspinall dams during years with high runoff, and less during drier years.

1.4 Approach

Environmental impact assessments are most convincing when inferences about causation are derived from experimentation. True experiments have replication, randomly applied treatments, and control of confounding variables. Because anthropogenic disturbances are not usually applied to systems at random, and they may not be replicated across similar but independent systems, impact assessment through experimentation can be extremely difficult. Further, treatment size (magnitude of disturbance) is usually constrained by socioeconomic and practical considerations and are not subject to manipulation for scientific purposes. While before-after-control-impact (BACI) designs (Stewart-Oaten et al. 1986) allow for an experimental framework for

impact assessment, this design requires that a control system can be identified and studied simultaneously. Unfortunately, in the case of new dam operations at BMR, a suitable control was not available given the unique nature of the reservoir. Blue Mesa Reservoir is distinguished as the largest reservoir in Colorado with one of the most productive kokanee fisheries in the world, and as it is the only large, coldwater reservoir in the state without *Mysis relicta*. These issues necessitated an observational study.

Adopting an observational rather than experimental approach, we hypothesized how impacts of new dam operations would be manifested, implemented a rigorous sampling program and developed simulation models to address the hypotheses. We then compared our after-impact data with past studies on the reservoir. Our approach was fivefold: (1) assemble historic datasets on dam operations, hydrology and limnology at BMR, (2) conduct a standardized limnological assessment program at sites throughout the reservoir, measuring physicochemical and biological parameters, (3) conduct a fisheries assessment program, (4) examine relationships among dam operations, hydro-meteorology, and reservoir characteristics and consider alternative hypotheses to explain changes in characteristics that coincided with new dam operations, and (5) develop simulation models to predict thermal and fish bioenergetic responses to new operation scenarios.

1.5 Methods Overview

Sampling was conducted during 1993-1997 and 2001-2002. We focused on laboratory experiments and modeling during 1998-2001. To ensure comparability across years sampling sites and methods were standardized beginning in 1993, as well as when new parameters were added. We established three main sampling sites at mid-basin locations (Sapinero, Cebolla and Iola; Figure 6). These sites were not selected at random, but rather their locations were assumed to represent each basin's overall characteristics. This assumption is most supportable for physicochemical measures since wind mixing results in homogenization of these features, particularly in the epilimnion where the bulk of the reservoir's biological production occurs.

Sampling dates varied somewhat across years, but we conducted all sampling during the growing season (May-September). When gathering data from studies conducted by other researchers prior to 1993, efforts were made to select only those data where sampling dates and methods were comparable. For many analyses, yearly means (generally consisting of samples during May-September) are presented along with a measure of sampling variability, such as standard errors. It was assumed that these variances approximated those from a randomized sampling program. Annual variations in climate also made temporal comparisons across years difficult. Strong seasonality, non-random site selection and lack of consistency in sampling dates and sampling intensity among years made statistical analysis of many parameters problematic.

The computer simulation models we developed sought to (1) to predict the relative effects of dam operations and hydro-meteorologic variability on reservoir thermal structure (CE-THERM), and (2) to predict how the kokanee population would respond

to changes in its thermal environment, food availability, and overlap with predators that could arise from changes in dam operations and hydro-meteorologic factors (bioenergetics-based foraging model).

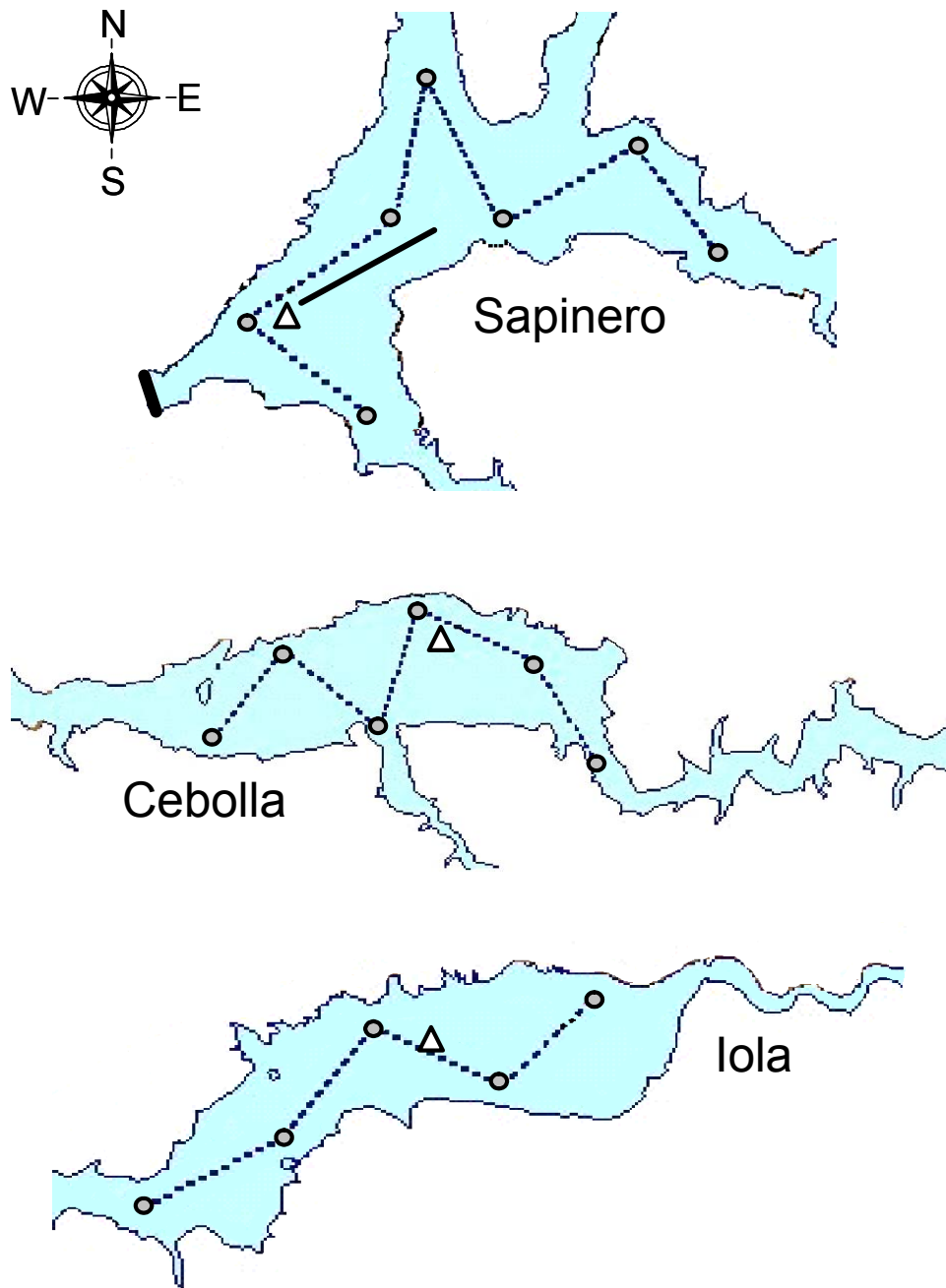


Figure 6. The three basins of Blue Mesa Reservoir showing locations of limnology and vertical gill net stations (triangles), hydroacoustics transects (connected circles), and the location of the diel fish distribution survey (heavy line in Sapinero basin).

2 HYDROLOGIC CONDITIONS AND RESERVOIR OPERATIONS

2.1 Overview

Dam operations can have a variety of hydrologic effects on reservoirs. Release patterns affect elevation, storage, and water residence time. These in turn can alter reservoir thermal structure, water column stability, and internal nutrient loading. Variation in these physicochemical features may affect reservoir biota by changing physiological rates, primary production, distribution patterns of organisms, and prey availability; these were all characteristics of interest in our study. To compare inflow and outflow patterns before and after new operations were implemented we assembled a dataset on key hydrologic variables measured from the time of impoundment (1965) to the end of our study (2002)

Physicochemical conditions in reservoirs are also sensitive to climatic and hydrologic factors which are stochastic and exhibit considerable inter-annual variability. Because the primary goal of this study was to determine the effects of new dam operations on abiotic and biotic conditions in the reservoir, it was essential to parse out the relative importance of dam operations and hydro-meteorological factors. We developed scenarios with the computer simulation model, CE-THERM (Johnson et al. 2004), and used the model to compare thermal effects of “traditional”, “new”, and “extreme” dam operation regimes. We also used the model to conduct a sensitivity analysis to evaluate the relative importance of dam operations versus hydrology and meteorology on the reservoir’s thermal structure.

2.2 Methods and Data Analysis

Reservoir water operations data (unregulated inflow, power and non-power releases, elevation, storage) were obtained from Reclamation web databases and monthly reservoir reports, United States Geological Survey (USGS) Water Resources Bulletins, and CDOW Research Reports (Wiltzius 1974). Exceedance probabilities, P (%), were computed from unregulated inflows (sum of April-July) into BMR by McAda (2003). Exceedance probabilities were then used to classify hydrologic conditions during 1965-2002 into six categories: Dry (90-100%), Moderately Dry (70-90%); Average Dry (50-70 %); Average Wet (30-50%); Moderately Wet (10-30%); and Wet (0-10%). Water residence time (hydraulic retention time) was computed as mean annual reservoir content in a year divided by total annual unregulated inflow for that year. Annual and long term means (1965-1992) of hydrologic variables were compared to the means of those variables during 1993-2002. Effects of inflow, outflow, as well as meteorologic conditions were evaluated with the thermal model, CE-THERM (USACE 1995).

CE-THERM is a one-dimensional model of reservoir thermal structure. The model is an independent model within CE-QUAL-R1, a reservoir water quality model developed by

the U.S. Army Corps of Engineers (USACE) at the Engineering Research and Development Center. The model simulates reservoir thermal dynamics over a series of stacked vertical layers (Figure 7). Each layer is longitudinally homogeneous. Mass balance and heat budget calculations are made for each layer. The heat budget includes heat flux from insolation (long and short wave radiation), tributary inflows, outflows, and fluxes due to evaporation and conduction. Internal fluxes among layers include entrainment and diffusion processes.

To implement the model, we assembled several kinds of input data, including the reservoir's bathymetry, latitude and longitude, discharge depth and configuration of the outlet works (Johnson et al. 2004). An air turbidity constant was specified to simulate light attenuation due to dust in the atmosphere. Initial reservoir conditions (starting elevation, water transparency, temperature profile, and total dissolved solids (TDS)) were gathered from the reservoir. Daily values for the quantity, temperature, and TDS of inflows, as well as meteorologic data (cloud cover, air temperature, dew point, barometric pressure and wind speed) were used to perform simulations on a daily time step. Finally, we developed a variety of outflow regimes. With this information, the model calculated the temperature profile and water budget for each day. We calibrated the model using reservoir conditions, hydrologic and meteorologic data from 1994. We then validated the model by predicting thermal conditions in 1996 using hydro-meteorologic data from that year, and comparing those predictions to the thermal conditions actually observed.

Reservoir operation regimes ("traditional", "new", and "extreme") were developed through consultations with Reclamation hydrologists and U.S. Fish and Wildlife Service (USFWS) biologists. The traditional regime (Figure 8) emphasized stable releases for hydropower generation (57 cms maximum), while attempting to fill the reservoir by about July 15. Given a May 1 starting elevation and historical inflows, the volume above that necessary to reach the fill target was computed and released evenly over the simulation period. Regardless of inflows, releases of at least 8.5 cms were maintained for instream flow requirements. After July 15, releases increased if necessary to meet downstream user allocations (totaling 37 cms). Traditionally, operators have tried to draw the reservoir down to 2,283 m by December 31 to allow them to capture the following spring's runoff and to prevent ice damage along the river above the reservoir.

Under new operations, we assumed that inflows greater than the quantity needed to achieve the in-reservoir goals would be used to generate an 8-day "spring peak hydrograph" downstream. The peak was generated using a 4-day ramping up period with flows increasing at ≤ 14 cms/day, followed by a 4-day period of flows decreasing at ≤ 11 cms/day. Average releases before July 15 needed to be lower than under traditional operations so that the spring peak could be generated (Figure 8). After July 15, releases did not differ under traditional and new operations regimes.

We also simulated an "extreme" operational scenario that simulated the farthest departure from traditional operations that could occur without removing the dam, i.e., a "run-of-the-river" operating policy. This scenario used average climatic conditions,

including the average starting elevation with the associated initial temperature profile, and average inflows. Outflows were adjusted so that the starting elevation was maintained throughout the simulation.

Simulations were of six month duration from May 1 through October 31 because that was the period in which operational policies were expected to change, and because this is the period that the reservoir exhibits thermal stratification. Boundary conditions were therefore required for May 1. This required adjusting the model's initial water temperature profile based on measured water temperatures on May 24, 1994 and May 21, 1996 to May 1. We accomplished this by adjusting an initial profile on May 1 until the modeled profile on May 21 matched the mean of the measured profile on May 21 and May 24 for the two years.

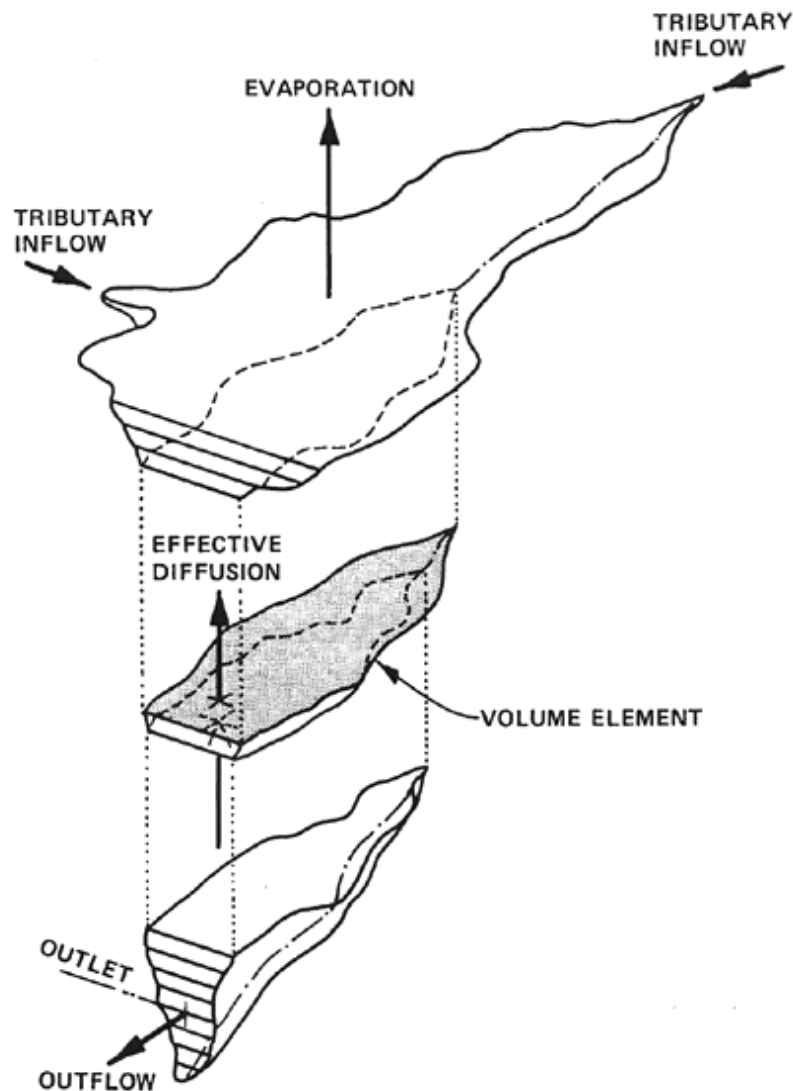


Figure 7. One dimensional representation of a reservoir as modeled by CE-THERM. From USACE (1995).

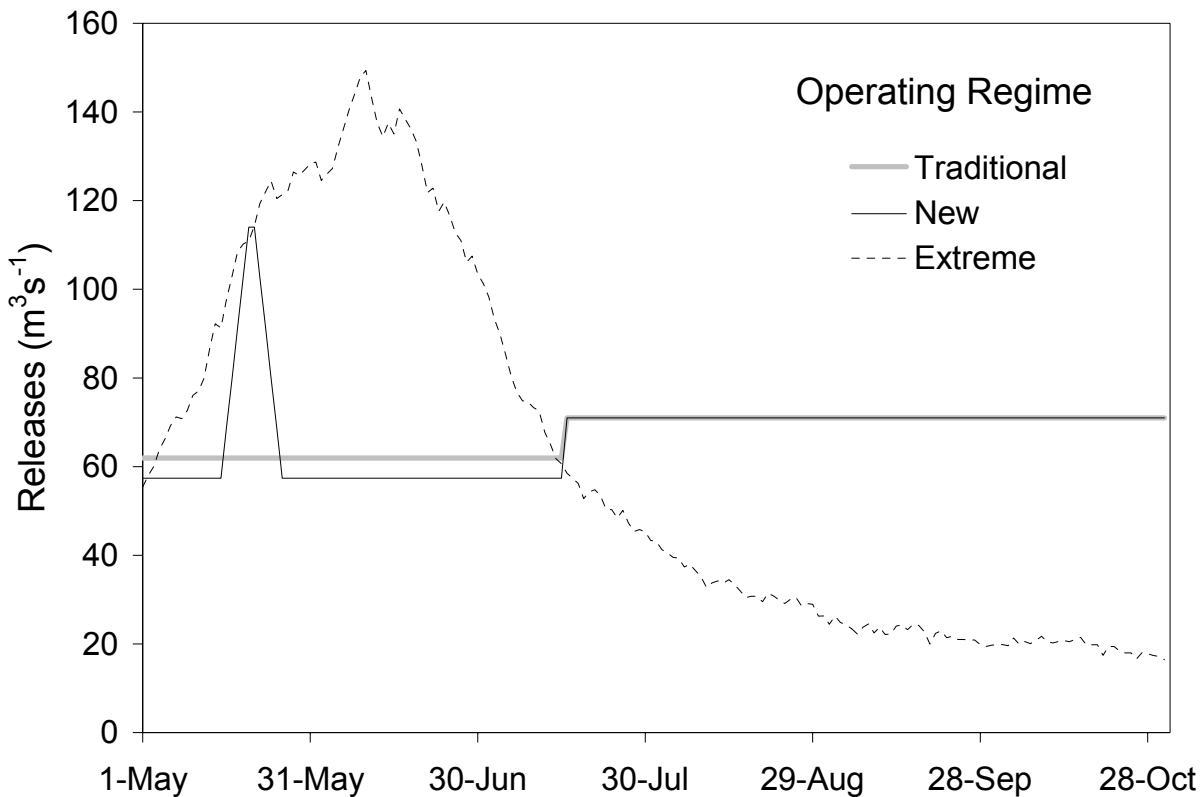


Figure 8. Release patterns under three operating regimes at Blue Mesa Reservoir, simulated with CE-THERM.

To conduct the sensitivity analysis, we computed average daily values for all input variables over the period of record, along with their standard deviation (SD). Then we manipulated the inputs, one variable at a time, by ± 1 SD and ran the model from May 1 through October 31. Because some model inputs were dependent on the manipulated inputs (e.g., stream temperatures were computed from air temperatures and inflow volumes, starting elevations were based on inflow quantities, and target fill elevations were based on starting elevations), dependent inputs were adjusted as necessary in each simulation using the same relationships used to compute the dependent inputs in the baseline run (Johnson et al. 2004).

Average daily inflows and SD were computed from Reclamation records measured during 1969-1997. Starting elevation, stream temperatures, and reservoir outflows were adjusted according to simulated inflows. Average starting elevation (May 1) and SD were computed from Reclamation records measured during 1969-1997. Average daily air and dew point temperatures and their SD were computed from Colorado Climate Center records measured during 1900-1997. Corresponding inflow water temperatures were adjusted according to simulated air temperatures. Daily cloud cover averages and SD were determined from data over 1992-1997. Sensitivity of model parameters was assessed by computing the average root mean squared error (RMSE) between water

temperature profile predictions under baseline conditions with temperatures predicted from "1 SD scenarios:

$$(2) \quad \text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (T - T_{\text{avg}})^2}{n}}$$

This metric is essentially a measure of the average departure of water temperature profiles in simulations with the baseline temperature profile. Larger RMSE values indicate larger differences between the temperature profiles.

2.3 Results and Discussion

Reservoir Hydrology

The mean total unregulated inflow during WY 1965-2002 was 983,000 ac-ft per year (Figure 9). Mean annual inflow was slightly lower than the long term mean during WY 1965-1992 and slightly higher during the study period (WY 1993-2002); however, the WY 1993-2002 mean was heavily influenced by very high inflows in 1995, and the difference in mean annual inflow between the two periods was not significant ($t = 0.15$, $p = 0.90$). Interannual variance in inflow was high during the study period, with one of the highest and one of the lowest inflows on record since the dam was built. Using P to categorize inflow each year into hydrologic categories showed that there were slightly more dry years during the present study compared to the period before WY 1993 (Figure 10). Overall, P showed a strong increasing trend through time (1975-2002; $r = 0.70$, $p < 0.0001$). In the three previous studies available, the inflow was below average (Wiltzius 1974), slightly above average (EPA 1977), and above average (Cudlip et al. 1987). The seasonal pattern of inflows, though highly variable among years, was nearly identical before and after the operational change.

Mean annual content (storage plus dead storage) showed an increasing trend during the period before new operations (Figure 11). The mean annual content during that period was 659,425 ac-ft compared to 713,797 ac-ft during WY 1993-2002. With the exception of the severe drought of 2001-2002, reservoir content was above the long term average during the study period. Mean water residence time since impoundment was 0.79 years, with a mean of 0.77 years before new operations and 0.84 after (Figure 11). Water residence time was highest in drought years of 1977, 1981, 1990 and 2002.

Mean daily releases were quite similar in the two periods, with a mean of 1,370 cfs during WY 1965-1992 and a mean of 1,381 during WY 1993-2003. However, when scaled to the year's inflow, the seasonal pattern of releases differed considerably among the periods (Figure 12). Releases were more consistent among months before WY1993 and there were large seasonal changes in releases after. In general, a higher fraction of the annual inflow was released during winter before new dam operations began and more was released during summer after new dam operations. There was no correlation ($r = 0.26$, $n = 32$) between P and the proportion of the year's discharge

released during May-July. The mean proportion of the total annual discharge released during May-July was 0.27 (SE = 0.02, n = 23) before new operations and 0.33 (SE = 0.02, n = 9) after.

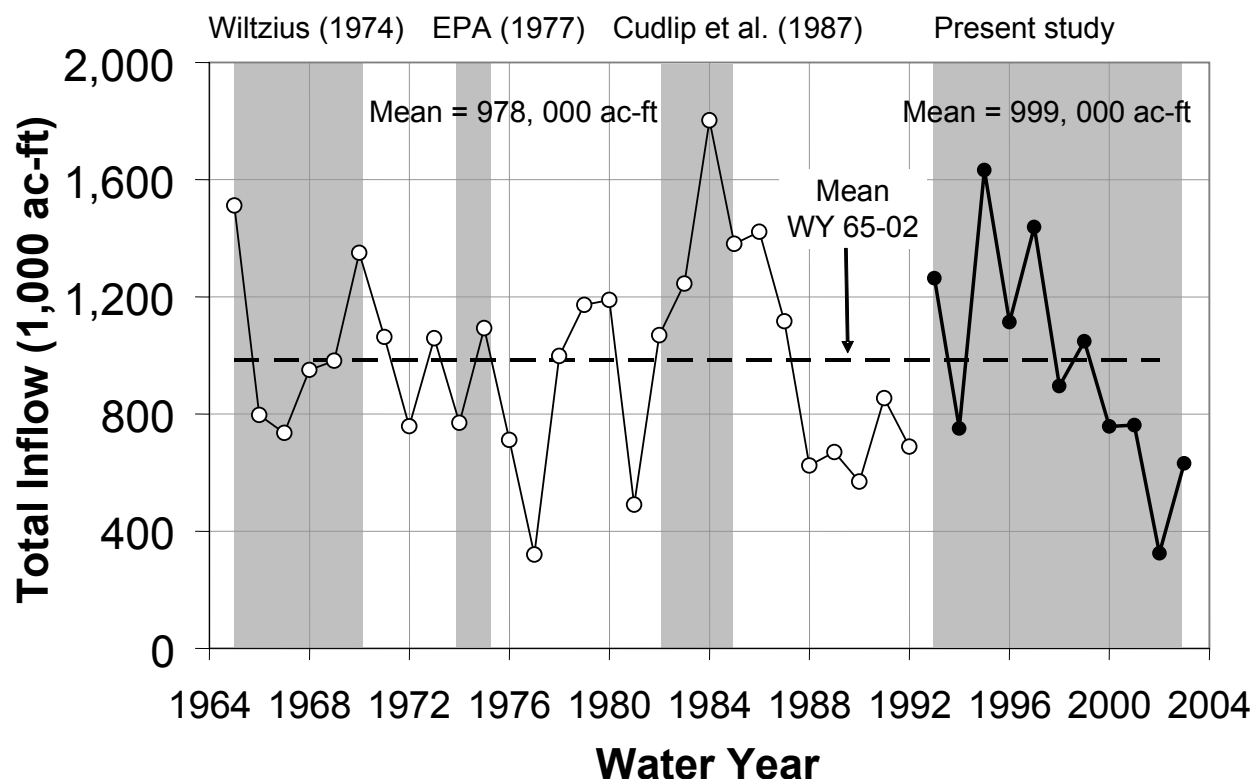


Figure 9. Total annual inflow to Blue Mesa Reservoir since the dam was completed in 1965. Shaded areas represent years when intensive studies were conducted. The heavy line shows inflows during the period of study after dam operations changed, with a mean of 999,000 ac-ft, and the thin line the inflows before dam operations changed, with a mean of 978,000 ac-ft. The dashed line shows the mean inflow since 1965.

Mean annual surface elevation before operations changed was 7,484 ft above sea level (ASL) and after, the mean was eight feet higher, or 7,492 ft ASL (Figure 11). The proportion of years when the reservoir approached the top of active storage (7,519 ft ASL) was lower before operations changed (36%) than after (50%), probably as a result of somewhat higher annual inflows and lower releases before runoff in the new operations period. Though highly variable, surface elevations were higher throughout the year after new operations, with the largest difference occurring in late winter and spring (Figure 11)

Modeling New Reservoir Operations

Measured temperature profiles from dam and mid-Sapinero stations under high discharge conditions (1995) were nearly indistinguishable (Johnson et al. 1996). Further, mean epilimnion temperatures (0-10 m) measured in July over eight years differed on average by only 0.9°C between Sapinero and Iola basins (Table A2, A3, A4), confirming the applicability of a one-dimensional model.

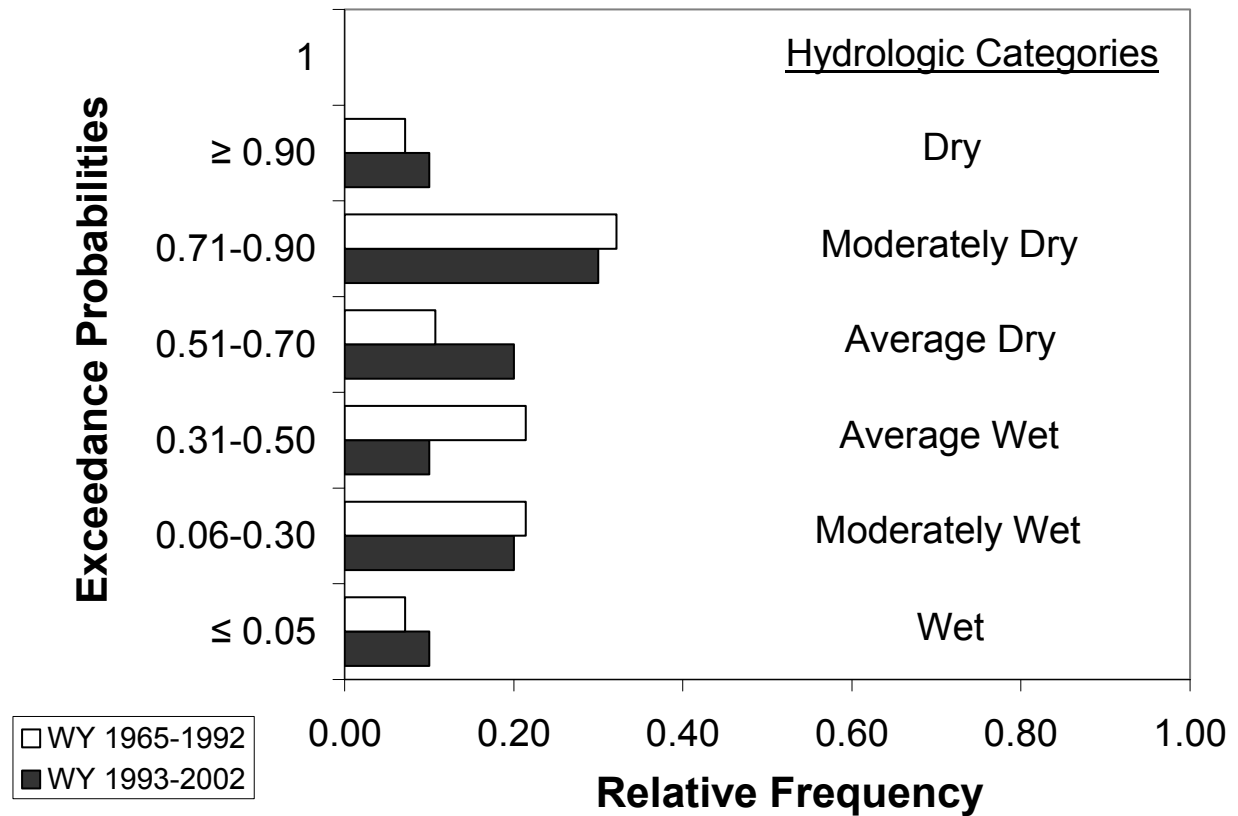


Figure 10. Relative frequency of various levels of inflows shown as exceedance probabilities, grouped into hydrologic categories. Exceedance probabilities from McAda (2003).

Simulated operating regimes were necessarily simplified and generalized to input to CE-THERM. Because the operational rules that were specified (fill target and minimum release requirements) governed both the traditional and new operations, and these constraints took precedence over goals for new release regimes, the “new” operations did not differ greatly from “traditional” operations in most simulations. In wet years operations were dominated by flood control considerations. In dry years new operations did not generate a spring peak because inflow was insufficient for in-reservoir requirements, and further, peak releases during dry years would be contrary to the goal of changing dam operations to mimic a more natural hydrograph. Thus, only in years of intermediate inflow did the release regime differ between traditional and new operations scenarios (Johnson et al. 2004).

The new operational regime had little influence on reservoir thermal structure; the RMSE of profiles between traditional and new operations was $\leq 0.31^{\circ}\text{C}$ (Johnson et al. 2004). This is likely because the new operations simulations constituted a relatively

minor departure from traditional operations. Operations were identical in both dry and wet years, and after July 15 in average years because of the in-reservoir and downstream objectives we specified. We hypothesized that larger departures from the traditional operating pattern would have a greater effect on thermal profiles. However, the extreme operational regime, equivalent to a “run of the river” policy, warmed the temperature profiles only slightly, with an average RMSE of 0.56°C. Thus, changes to hypolimnetic release patterns alone appeared to have very little effect on the thermal structure of BMR. Although modeled operations scenarios may not be deemed realistic by hydrologists and dam operators familiar with the BMR system, the finding that operations had little influence on thermal structure is robust since even the extreme operations scenario produced only slight warming of the reservoir. It appears that water managers at Blue Mesa Reservoir have considerable latitude for implementing new operations without negative thermal consequences to the reservoir.

Perturbations to hydrologic and meteorologic inputs produced much greater changes to temperature profiles than did changing reservoir operations. Reservoir temperatures were most sensitive to inflow, starting elevation, and air temperature. A ± 1 SD change in these inputs produced changes to thermal profiles that were much greater than those produced by new operations, and greater than even those produced by extreme operations (Figure 13). One of the reasons the model was particularly sensitive to hydro-meteorologic inputs was because many of them individually affected other inputs as well. For example, changing air temperatures or inflow quantities also changed inflow temperatures.

Inflow quantity was by far the most influential variable affecting thermal profiles. A ± 1 SD deviation from average inflow produced a deviation in temperature profiles of approximately 1.5°C from the baseline conditions (Figure 13). Predicted temperature profiles revealed that the largest effect of meteorologic variables and operations occurred in the top 40 m of the reservoir (Johnson et al. 2004). The opposite was true for hydrologic variables, which generally showed the smallest effect on temperatures in the top 10 m of the reservoir.

Modeling performed in associated studies suggested that both spillway releases (Saito and Koski in review) and installation of a TCD to increase release temperatures (Amy Cutler, Reclamation, personal communication) would affect reservoir thermal structure. When some water was released over the spillway to supplement releases through the hypolimnetic outlet the epilimnion became thinner and metalimnetic temperatures decreased. A TCD was also predicted to lower reservoir temperatures significantly at depths of 5 – 60 m. In August, the 10 °C isotherm was almost 20 m shallower with a TCD.

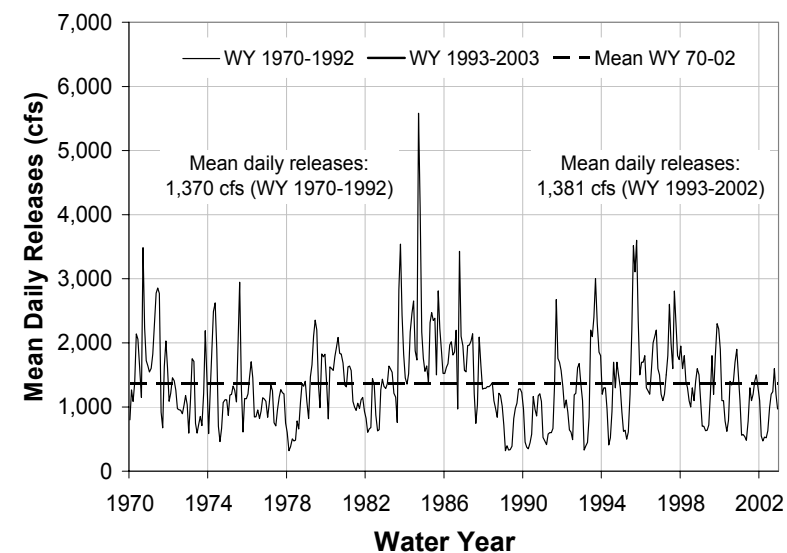
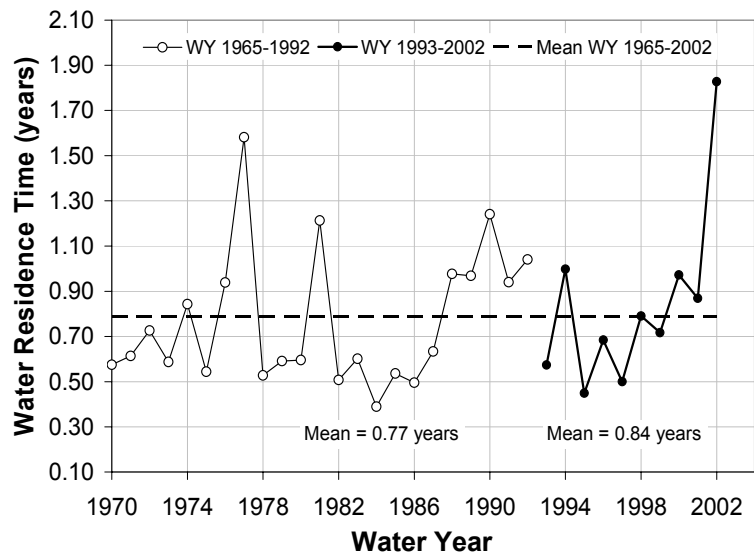
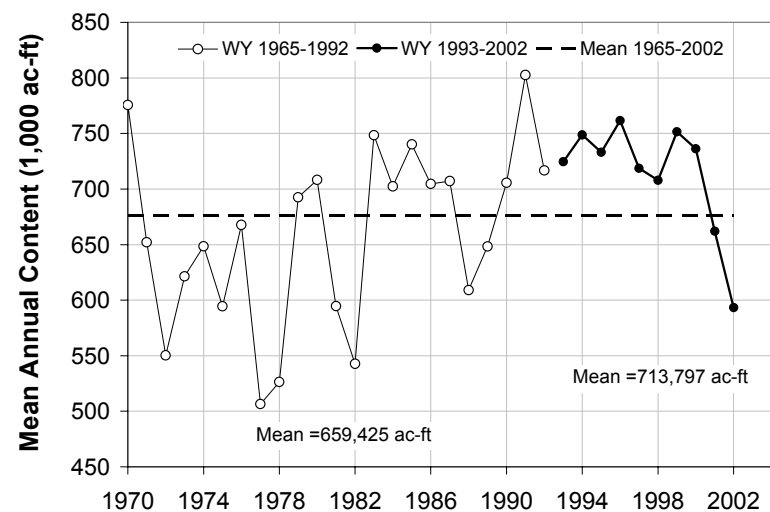
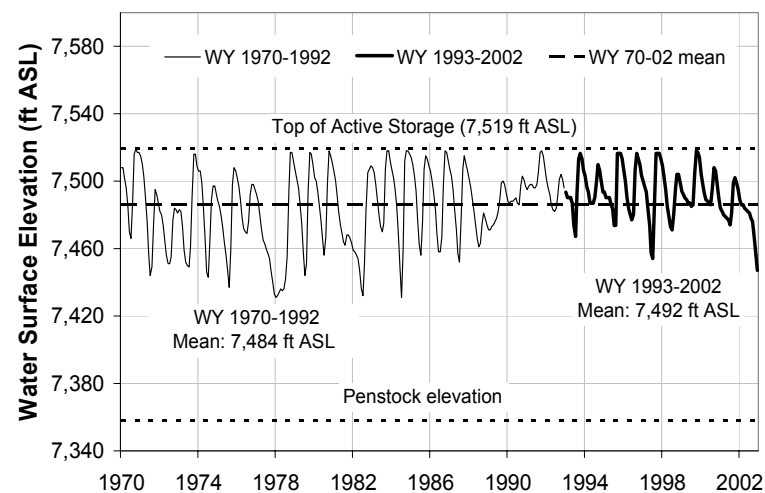


Figure 11. Surface elevation (top left), mean annual content (top right), water residence time (lower left), and mean daily releases (lower right) at BMR during 1970 to 2002.

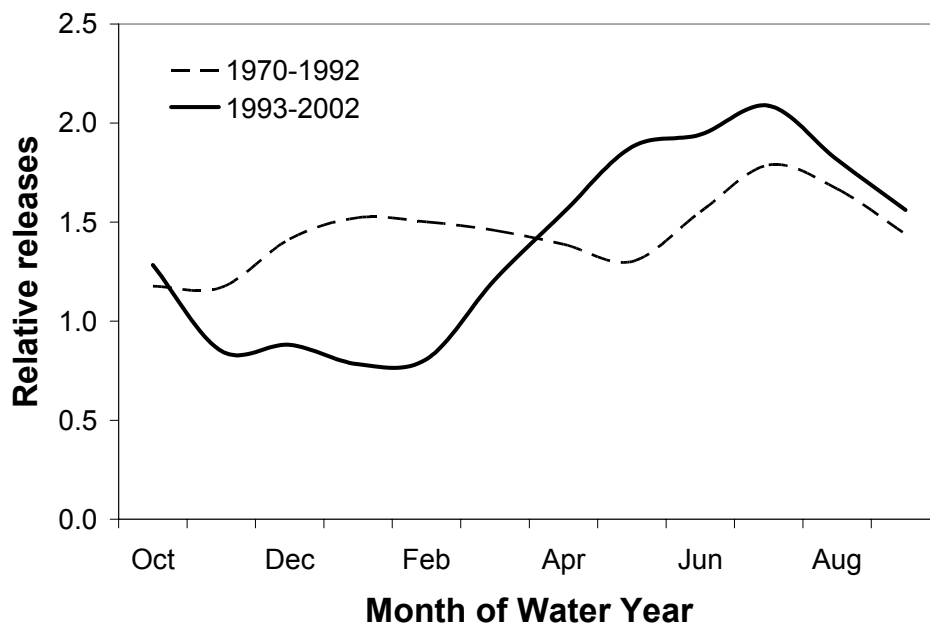


Figure 12. Relative mean daily releases during each month in 1970-1992 and in 1993-2002. Releases (CFS) were scaled by dividing each by the annual inflow (1,000s of ac-ft).

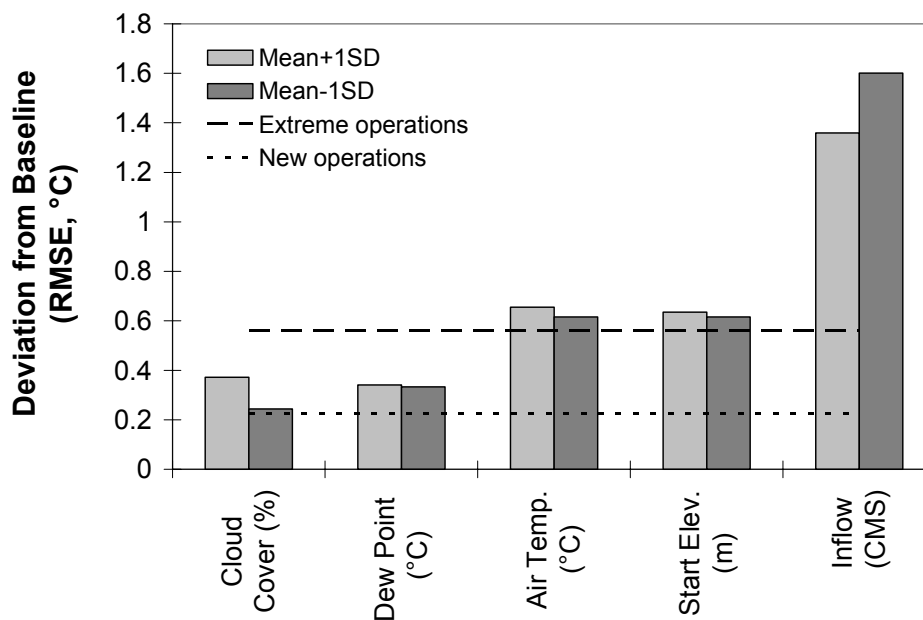


Figure 13. Deviation (mean RMSE) of temperature profiles from baseline run resulting from changes (mean $\pm$ one standard deviation, SD) in hydrologic and meteorologic input conditions. Change in temperature profiles resulting from new operations under average meteorologic and hydrologic conditions (dotted line), and the change in temperature profiles resulting from extreme operations under average meteorologic and hydrologic conditions (dashed line) are also shown.

2.4 Summary

- This study coincided with a period of drought with generally declining inflows during 1993-2002. Despite the drought mean annual surface elevation and reservoir content were slightly higher during 1993-2002 than before.
- Water residence time generally increased during this period.
- Mean daily releases were similar before and after 1993 but the seasonal pattern of releases changed considerably beginning in 1993.
- Before 1993 releases were generally higher during winter and lower during spring than after that date.
- CE-THERM proved to be a useful tool for evaluating effects of alternative dam operation regimes on reservoir thermal conditions, while controlling for potentially confounding hydro-meteorological variables.
- The CE-THERM model underwent a thorough calibration and validation process that showed that the model captured the essential physical elements of the BMR system accurately.
- The model predicted that hypolimnetic release patterns that approximated the new dam operation regime implemented starting in 1993 would have virtually no effect on reservoir thermal structure under normal hydro-meteorological conditions, compared to the historic operating pattern.
- Even an extreme operation scenario, with a run-of-the-river hypolimnetic release pattern, produced small changes in predicted thermal regime of the reservoir relative to those induced by the climatic and hydrologic variables.
- The average difference in temperature profiles between baseline runs and either of the new operations were similar in magnitude to those arising from model prediction errors quantified during calibration and validation. This suggests that realistic changes to the seasonal pattern of hypolimnetic releases at Blue Mesa Reservoir may produce changes in thermal regime that are too small to model accurately and are probably of limited ecological significance.
- In contrast to our findings regarding effects of hypolimnetic releases, other work showed that releases over the spillway or through a TCD would produce ecologically important changes to the reservoir's thermal regime, creating a shallower and cooler epilimnion.

3 LIMNOLOGICAL CONDITIONS

3.1 Overview

It was hypothesized that changes to the reservoir's water budget arising from new dam operations might alter physicochemical characteristics of the reservoir by affecting water residence time, temperature and oxygen stratification and nutrient loading, as well as increasing turbidity induced by exposure of alluvial deposits. Changes in these physicochemical parameters would be expected to affect primary production, zooplankton dynamics, fish diet and growth rates and predator-prey interactions between kokanee and lake trout. A limnological sampling program was devised to provide the data necessary to compare contemporary conditions to historic (before dam operations changed) conditions. The goal was then to evaluate changes in abiotic and biotic characteristics in the reservoir associated with the change in dam operations beginning in 1993, and consider alternative explanations for those changes. In 2002, we added a new objective to look at the impacts of the 2001-2002 drought on the reservoir. Record low inflows to BMR and continuing downstream obligations for instream flows and other uses in 2002 resulted in plummeting lake levels. The drought presented a valuable opportunity to learn more about how reservoir ecosystems respond to such climatic forcing and associated water management actions necessitated by severe demands on water resources.

3.2 Methods and Data Analysis

The relatively short period of record in the limnological database and high variability in hydro-meteorologic conditions precluded statistical trend analysis of limnological characteristics, but these variables were evaluated in light of annual variation in inflow to the reservoir.

Physicochemical Limnology

Several previous studies measured physicochemical parameters providing a longer time series than was available for biological limnology parameters. Historic data on temperature, dissolved oxygen profiles, Secchi depth, conductivity and phosphorus concentrations were obtained from Wiltzius (1971), USEPA (1977), Cudlip et al. (1987), Johnson et al. (1994-1997), and NPS (M. Malick, personal communication). For seasonal comparisons, efforts were made to match up data among years according to sampling date as much as possible.

Vertical profiles of temperature and dissolved oxygen were recorded at mid-basin reference stations (Figure 6; Table A1) during 1993-1998 and in 2001, 2002. Temperature and dissolved oxygen profiles were obtained using an YSI Model 52 digital meter with 60 m probe cable. Measurements were taken at one meter intervals from 0 to 20 m and at 5 m intervals from 20 to 55 m of depth. Inflow and outflow temperatures were measured with temperature loggers set in four tributaries and in the tailrace below

the Blue Mesa Dam in 1996. In 1997 and 2002 we recorded temperatures only in the Gunnison River about 3 km upstream from the reservoir.



Figure 14. CSU personnel (Cory Counard (bottom), Mike Wise and Glenn Szerlong (top)) making limnological measurements at Blue Mesa Reservoir (photo: Brett Johnson).

Secchi depth measurements were made every year with a standard 200 mm white and black limnological Secchi disc (Wetzel and Likens 1991) by averaging two replicate readings taken on the shaded side of the boat. Historic Secchi measurements were also available from USEPA (1977), and Cudlip et al. (1987). Turbidity measurements were made at the surface during 2001, 2002 using a LaMotte model 2020 turbidimeter. Conductivity measurements were made with an Oakton conductivity meter with automatic temperature correction during 2001, 2002. During 1998, 2001, and 2002 light profiles were obtained with a LI-COR photometer and LI-COR terrestrial type SA: LI-190 deck cell, and underwater type SA: LI-193SA spherical quantum sensors (Johnson and Andre 1998). Underwater light intensity was computed in 1 meter depth intervals using the formula: $[(\text{deck cell measurement})/(\text{underwater measurement})]*100\%$.

Trophic State Index (TSI; Carlson 1977) was computed by month, basin and year based on total phosphorus concentration (TP; $\mu\text{g/L}$): $\text{TSI}_{\text{TP}} = 14.42 \cdot \ln(\text{TP}) + 4.15$, Secchi depth (SD; m): $\text{TSI}_{\text{SD}} = 60 - (14.41 \cdot \ln(\text{SD}))$, and chlorophyll-a (CHL; $\mu\text{g/L}$): $\text{TSI}_{\text{CHL}} = 9.81 \cdot \ln(\text{CHL}) + 30.6$ data gathered during 1994-2002 (CSU and NPS sources). A mean TSI was then computed from the three indices.

Biological Limnology - Chlorophyll

Chlorophyll data were gathered from three previous studies: USEPA (1977), Cudlip et al. (1987), and Bauch and Malick (2003). We collected chlorophyll samples during 1994-1996; water samples were taken at different depths each year to test various hypotheses about vertical distribution of chlorophyll. In 1994, samples were collected with 5-m and 10-m integrated water column samplers. In 1995, we collected water samples with only the 10-m water column sampler. In 1996, samples were obtained using either a van Dorn sampler (at depths of 1, 2, 4, 6, 8, 10, 12, 14, 17.5 and 25 m) or a 10-m integrated water column sampler. Some 10-m integrated samples in 1995 and 1996 were pre-filtered through a 35 μm mesh sieve to separate them into edible and inedible (to *Daphnia*) fractions of total chlorophyll concentration.

All water samples were filtered through glass microfiber filter paper (Whatman GF/F) using a vacuum pump. The filter papers were frozen on dry ice and stored frozen until the chlorophyll was extracted and processed. Samples were analyzed for chlorophyll-a by the 24-hr methanol extraction (Holm-Hanson and Riemann 1978, Marker et al. 1980, Riemann 1980) and fluorometry method (Lind 1979, Axler and Owen 1994) using a Turner Designs Model 450 fluorometer.

Biological Limnology – Zooplankton

As far as we know, no historical data on zooplankton species composition or density exist. The first zooplankton collections were done by CSU, beginning in 1993. Because of the lack of historical data for BMR, we began our work on zooplankton dynamics by answering some basic questions about species composition and distribution and behavior in the reservoir. Our first objective was a description of the taxa present and their spatial distribution and temporal dynamics. Our interest was primarily in *Daphnia* spp. because they are preferred by planktivorous fishes. Zooplankton sampling was most intensive during 1994 and 1995 when 270 and 229 samples, respectively, were taken.

We collected zooplankton by the same method every year, making oblique tows using a Wildco model 37-315 Clarke-Bumpus plankton sampler (Lind 1979) with 130-mm diameter opening (Figure 15) during summer 1993-1997 and 2001-2002; Martinez (2000, 2001, 2003) collected zooplankton during 1998-2000 and 2002. The standard protocol used a 153- μm mesh net; in 1996 and 1997 we also gathered samples with a 500 μm net to select for large *Daphnia*, the zooplankters prevalent in the kokanee diet.

Sampling sites varied somewhat among years, but the three mid-basin sites were maintained in all years except 1997 when only the Sapinero site was sampled. In general, we were interested in the vertical distribution of zooplankton in the water column. Thus, sampling was stratified by depth, though the particular strata differed among years given the variety of sampling objectives over the course of the project. In 1993, we collected two or three replicate samples from 0-5 m, 5-10 m, 10-20 m, and 20-30 m depth strata. Depth strata were changed in 1994 to provide more vertical resolution within the epilimnion; two or three replicate samples taken at each of four depth strata: 0-5 m, 5-10 m, 10-15 m, and 15-30 m. We sampled these same depth strata in May 1995; thereafter, we took replicate samples from 0-10 m, and 10-30 m.



Figure 15. Randy Oplinger, CSU undergraduate assistant, operates the Clarke-Bumpus metered plankton sampler (photo: Brett Johnson).

In 1996 and 1997, we continued to sample the 0-10 m stratum with the 153- μ m net, but we sampled the 0-5 m, 5-10 m, 10-15 m (and 15-20 m, and 20-30 m in 1996) strata with the 500- μ m net. Martinez (2000, 2001) sampled 0-10 m in 1998 and 1999, and the 0-5 m and 0-10 m strata in 2000. During 2001-2002, CSU made a single tow in the 0-5, 5-10, 10-15, and 15-30 m depth strata at each of six stations during five sampling periods

from April-August (Table A1). Only samples from comparable sites and depth strata were used in inter-annual comparisons; data were summed if necessary to obtain zooplankton density estimates in the 0-10m stratum.

We examined the magnitude of horizontal patchiness at three spatial scales in the reservoir 1994 and 1995 (Wise (1997)). We took replicate samples within a single station (approximately a 500 m scale), samples at six randomly selected stations within Sapinero basin, and samples from representative stations in each of the three basins.

Samples were usually taken between 0730 and 1030 h; samples were preserved in 8% sugared, buffered formalin or 70% ethanol. Diel variation in zooplankton depth distribution was assessed in 1993 and 1994. In 1993, we sampled during mid-day and in July, we repeated these samples during the night, at least 1 hr after sunset at five sites that spanned the length of the reservoir. Sixty-three samples were collected at night and 88 samples during the day at 0-5 m, 5-10 m, 10-20 m, and 20-30 m strata. In 1994, we repeated the diel study but modified our methods to increase the temporal and spatial resolution in the data. We sampled at discrete depths (1 m, 3 m, 6 m, 12 m, and 15 m) during the light transition periods around dawn and dusk. Sampling was conducted on 7 July, 1994 (new moon) at the Cebolla limnology station. Time did not allow us to take replicated samples so we made longer horizontal tows than usual to minimize sampling error due to small scale patchiness in density.

Samples collected with the 500- μ m mesh net were processed in the same fashion as the 153- μ m mesh net. However, only *Daphnia* were counted and measured. Egg counts were also recorded. Subsampling was terminated when 50 measurable *Daphnia* had been encountered, or three aliquots examined. When a sample contained low numbers of *Daphnia*, total counts were made using a plexiglass plankton wheel mounted on a dissecting scope. *Daphnia* were then placed in a Sedgwick-Rafter counting cell and measured under the compound microscope.

Samples collected with the 153- μ m net were identified and enumerated in the same manner in all years. *Daphnia* were identified to species, while copepods and other cladocerans were identified to genus. Each sample was diluted to provide approximately 50-60 *Daphnia* per 1-ml aliquot subsample and subsamples were then placed in a Sedgwick-Rafter counting cell where all macrozooplankton taxa were identified and enumerated (Lind 1979) under a compound microscope. Three aliquots were examined per sample. Body length measurements and egg counts were made only for *Daphnia* species. Up to 25 individuals for each of *Daphnia pulicaria* and *D. galeata* were measured for each sample. Subsampling was terminated if 25 measurable *D. pulex* were encountered before the third aliquot.

We identified copepods to Genus based on gross morphological characteristics. We did not identify copepods beyond the Genus level because functional roles and use by fishes do not differ among species within a Genus, identification to the species level requires extremely laborious procedures for examinations of minute body structures, and our microscopes did not have the required level of magnification. Zooplankton

densities were computed as number of organisms per liter using the number of revolutions measured by the Clarke-Bumpus sampler, the calibration factor (liters filtered per revolution) and the dilution volume from which we took 1-ml aliquots.

Effects of Drought

Hydrologic variables (inflow, outflow, water residence time, and surface elevation) measured in 2002 were compared to the long term mean, and to those from 1995, when there was unusually high inflow to the reservoir. Surface temperature and Secchi depth in 2002 were compared to those measured in 1994 and 1995. We also compared inflow temperatures in 1997 and 2002.

We used field measurements, data analyses, and computer modeling to evaluate drought effects. We placed temperature loggers at two locations on the Gunnison River (Cooper Ranch Picnic Area, and about 0.5 km downstream) and at one location in the Lake Fork of the Gunnison River upstream of BMR to measure tributary temperatures. We conducted an ultrasonic telemetry survey to establish locations of lake trout in the reservoir during late summer when thermal effects of the drought were most intense. We accessed web-based databases to obtain hydrological and meteorological data necessary for input to CETHERM model. We used vertical gill nets to sample the pelagic fish assemblage in August and assess depth distribution and body condition (Fulton's condition factor k). We used bioenergetics-based foraging models (e.g., Stockwell and Johnson 1997, 1999) to evaluate energetic challenges faced by kokanee under warmer reservoir conditions.

Saito and Gebeyehu (2003) modified the CE-THERM model calibrated to "normal" reservoir conditions to evaluate the effects of drought on thermal stratification. Measured values for inputs from 2002 were gathered from various sources and included daily inflow, outflow and reservoir elevation data. Meteorologic data at 20 minute intervals were obtained and converted to daily values. Stream temperatures were obtained from temperature loggers placed in the Gunnison River and the Lake Fork of the Gunnison River. The air-stream temperature function in Johnson et al. (2004) was also used in drought simulations. Reservoir morphometry needed to be adjusted for low water conditions. The Reclamation area-elevation polynomial did not perform well in water budget calculations under drought conditions, overestimating area and content when elevations dropped below 50% of maximum. A power function was fit to Reclamation area-elevation data that provided a much better fit:

$$\text{AREA} = 824.80 * Z(I)^{2.365}$$

where $Z(I)$ is the water surface elevation above the bottom of the reservoir. Water residence time was computed as the reservoir content on a day divided by that day's inflow. Quantification of differences between measured and predicted temperature profiles was done by computing the RMSE. Finally, to evaluate the effects of drought against baseline conditions (historical average) plots of the two were prepared and RMSE computed for each set of profiles.

3.3 Results and Discussion

Physicochemical Limnology

Reservoir temperatures were consistent among years. Temperature of the 0-10 m stratum (approximating epilimnion temperatures) was about 9°C in mid May and peaked at about 18-19°C between late July and late August (Figure 16; Table A2, A3, A4). The mean difference in epilimnion temperature between Sapinero and lola basins in July was 0.9°C during 1993-2002, suggesting that surface temperatures in July do not vary significantly from upstream to downstream in the reservoir. Across years, hypolimnetic temperatures (at 50 m) averaged 6°C ranged 4-9°C during May-September in Sapinero and averaged 7°C and ranged 5-10°C in Cebolla basin during the same period. No temperatures were available for lola basin because of its low maximum depth. Hypolimnetic temperatures were lower in low inflow years and higher in high inflow years. Simulations with CE-THERM showed that, given equal starting conditions in May, BMR's thermal structure is relatively insensitive to changes in dam operations so any differences among years were likely due to hydrometeorologic factors or differences in stratification in spring.

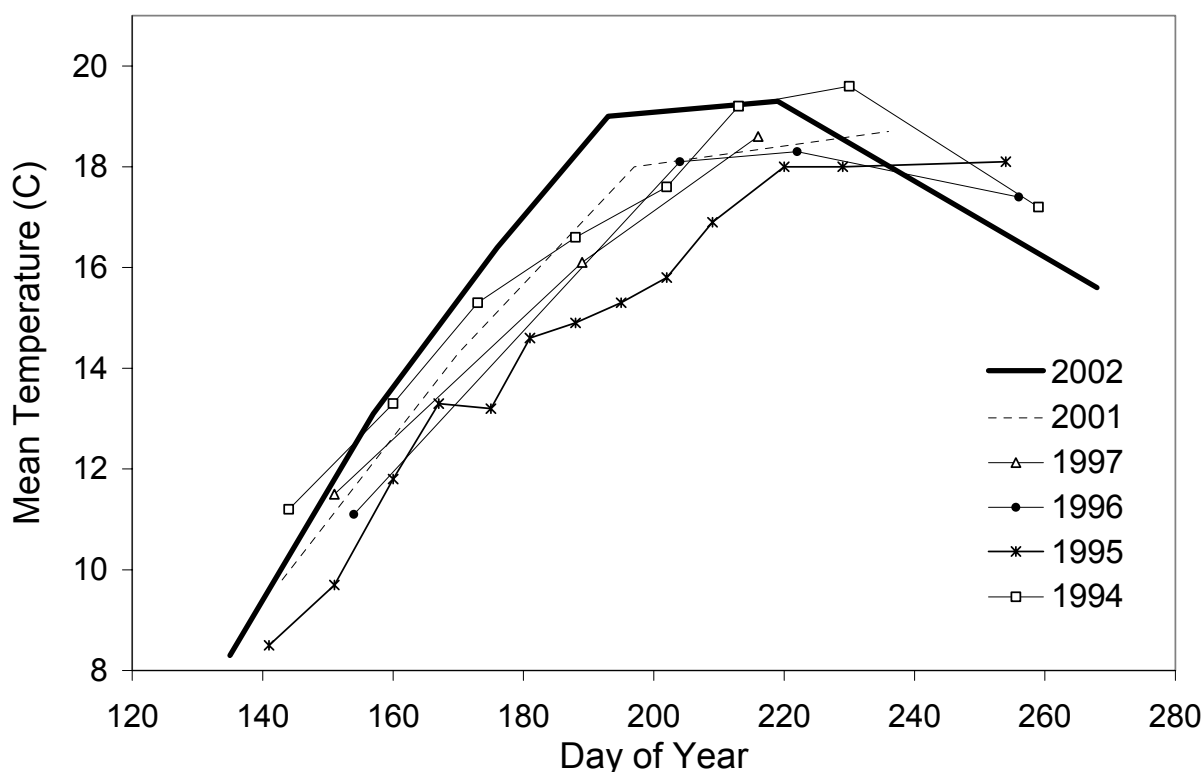


Figure 16. Surface temperature (°C at 2 m depth) of BMR measured at Sapinero basin during summer 1994-2002.

Dissolved oxygen concentration at 50 m, across all years, averaged 7.5 mg/L and ranged 2-10 mg/L in Sapinero basin during May-September, and an average of 6.2

mg/L and a range 2.9-8.3 mg/L in Cebolla during the same period. Dissolved oxygen measurements in Cebolla showed a metalimnetic dissolved oxygen minimum in some years. In some years, in both Sapinero and Cebolla basins, the dissolved oxygen concentration at depths below 35 m in September was less than 3.0 mg/L, the acute lethal level for salmonids (USEPA 1986). Dissolved oxygen concentrations were below the 4.0 mg/L minimum established by USEPA at depths greater than 18 m in September of some years. Low dissolved oxygen concentrations in the hypolimnion would pose the greatest hardship for lake trout since their low temperature preference (10°C) drives them into deeper water as the summer progresses.

Conductivity measurements were most numerous for Sapinero basin; analyses were restricted to that basin. Average summer (May-September) conductivity (data from all previous studies since 1966) was not correlated with inflow ($r = 0.37$, $n = 15$, $p = 0.17$). Conductivity averaged by year did not differ before and after new operations ($r = -0.18$, $p = 0.86$). Mean turbidity in both years in which data were available was quite low (2001: 1.7 NTU, 2002: 1.6 NTU). There were no historical data on turbidity, and it was not possible to evaluate the effect of rapid changes in reservoir level on turbidity.

Mean annual Secchi depth during 1994-2002 (all months combined) was 4.0 m, but this value may have been influenced by differences in months sampled during the study (Figure 17). During 1975-2002 Secchi depth showed a strong increasing trend through time ($r = 0.76$, $p < 0.0001$). Correlations were generally higher in June and July and in Cebolla and Sapinero, and lowest in May and September and in Iola. In drier years the reservoir was clearer than in wetter years and the effect was stronger closer to the dam. Mean Secchi depth (by year) in historic data was significantly lower than in the current study ($p < 0.001$). This difference could be due to the trend towards decreasing inflow through all years. But, when years with equal P are selected mean Secchi depth across all basins was 2.6 m during 1973-1985 and 3.6 m during 1993-2002, suggesting that water clarity may have increased in wet years since 1985. Seasonally, Secchi depth tended to be low in May, and, with the exception of 1994 and 1995, maximal in July (Figure 18). Mean monthly (May-September) Secchi depth during 1975-2002 was positively correlated to P in each basin (Table 2).

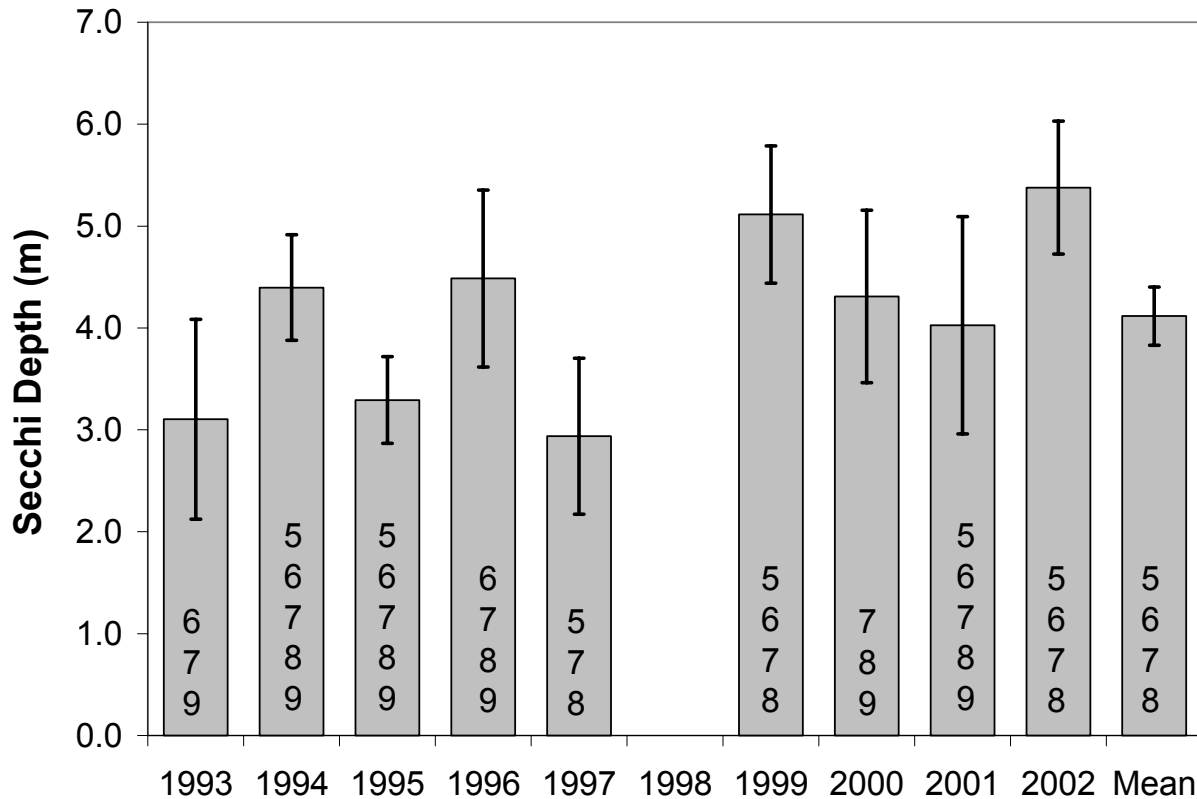


Figure 17. Annual and overall mean Secchi depths measured at standardized limnology stations at Blue Mesa Reservoir. The numbers in each bar show the months where measurements were taken.

Table 2. Pearson correlation coefficients (r) between P and Secchi depth (m) by month in three basins of BMR Reservoir since 1975. The number of years measurements occurred during 1975, 1983-1985 and 1993-2002 is shown as n and significant ($\alpha=0.05$) correlations are in bold.

	Sapinero			Cebolla			Iola		
	n	r	p	n	r	p	n	R	p
May	8	0.50	0.21	7	0.90	0.006	7	0.83	0.022
Jun	10	0.86	<0.001	10	0.81	0.005	10	0.82	0.004
Jul	13	0.82	<0.001	12	0.84	0.001	12	0.65	0.021
Aug	12	0.66	0.38	11	0.66	0.026	11	0.38	0.245
Sep	10	0.36	0.30	10	0.26	0.461	10	0.08	0.820

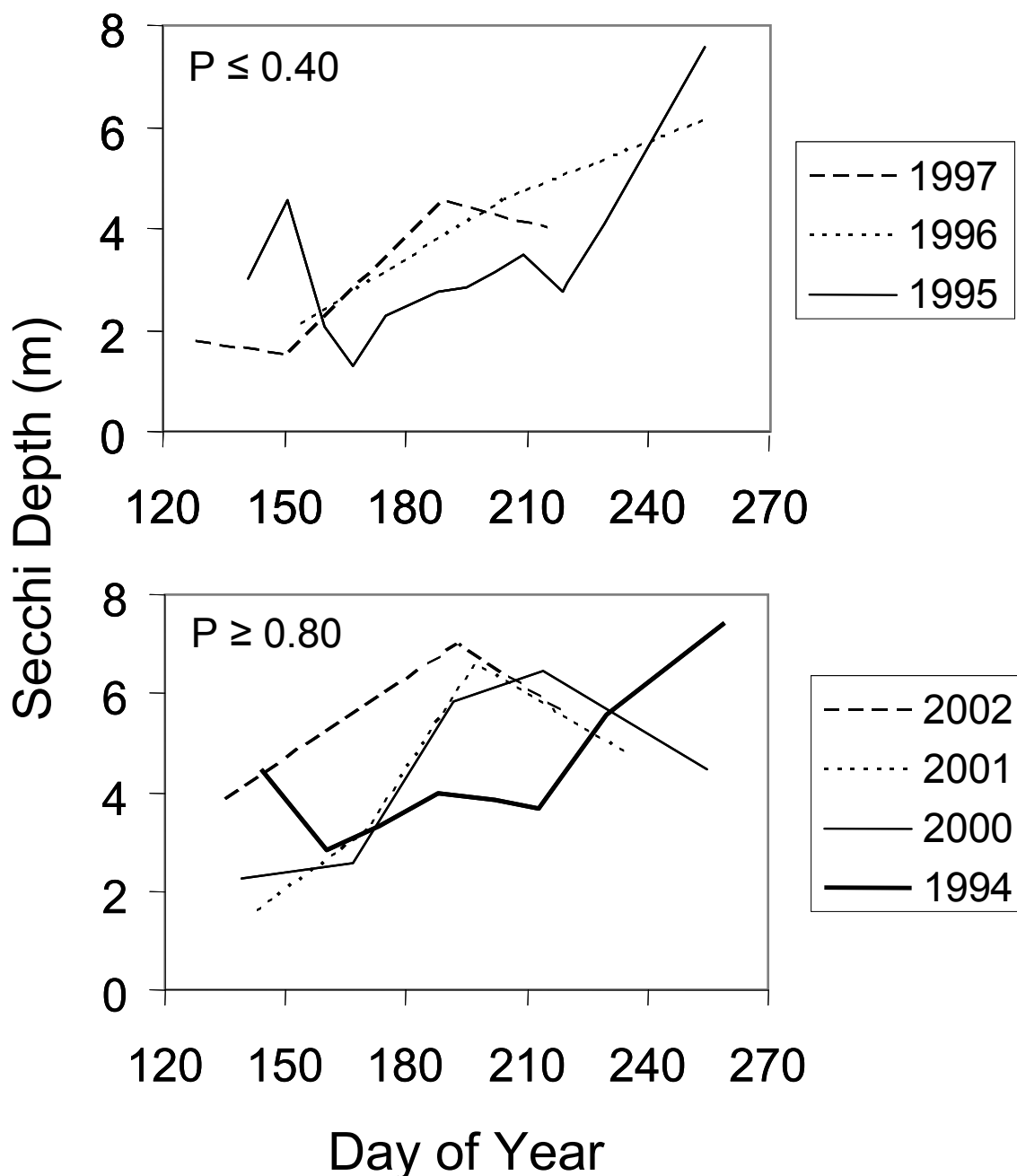


Figure 18. Secchi depth measured at Sapinero basin, BMR during summer 1995-1997 (exceedence probability ≤ 0.4) and summer 1994 and 2000-2002 (exceedence probability ≥ 0.8)

Biological Limnology - Chlorophyll

During 1994-1996, chlorophyll-a concentrations peaked in early June and declined steadily for the remainder of the growing season (Johnson et al. 1997). Chlorophyll-a concentration did not vary much by depth; in chlorophyll-depth profiles it appeared that chlorophyll was slightly more concentrated in the top 10 m of the water column, but the

pattern was not statistically significant. There was no indication of a metalimnetic chlorophyll-a peak in any basin during 1994-1996.

A weak downward trend in chlorophyll-a concentrations at Iola basin was detected in NPS data during 1988-1996 by Gurdak et al. (2002); concentrations were characteristic of mesotrophic conditions. Using all years in our dataset (1975, 1983-1985, 1994-1996, 1999, 2002) for Sapinero basin, we found a stronger negative trend with time. Correlation between August chlorophyll-a concentration and year was -0.86 ($p < 0.05$). Using August data from all basins ($n = 24$) from the same period of years the correlation between chlorophyll and year was also strong ($r = -0.65$, $p < 0.001$; one outlier was eliminated). Thus, it appears that algal biomass may be declining in the reservoir. Nitrate and total phosphorus concentrations in tributaries did not show any trend during 1988-1996 (Gurdak et al. 2002), but nitrogen limitation in summer has been observed before at BMR (Bauch and Malick 2003). August chlorophyll-a concentrations among all basins were significantly lower ($p = 0.02$) after dam operations changed (mean = $2.4 \mu\text{g/L}$) than before (mean = $3.2 \mu\text{g/L}$).

Unlike Secchi depth, chlorophyll-a concentration was not correlated with P ($r = -0.27$, $p = 0.49$). Thus, it appears that the effect of inflow on water clarity may have been primarily due to inorganic turbidity in high inflow years rather than from algal production. During 1994-2002 (including NPS data) chlorophyll-a concentration was not correlated with Secchi depth, suggesting that 1) algae are not limited by water clarity, and 2) water clarity in BMR is generally dependent on factors other than algal concentration.

Data for computing Trophic State Index (TSI) were most available for Iola basin Table 3). Iola basin, being the most upstream basin, is usually more productive than the others. Thus, mean TSI computed from all dates for Iola basin was slightly higher (47) than for Cebolla (38) or Sapinero (40) basins. The overall average TSI for the reservoir was approximately 42, indicative of mesotrophic conditions (TSI of 40-50 is the range describing mesotrophy; Carlson 1977). The TSI was originally developed for natural temperate lakes; all three predictors of the TSI are aimed at quantifying the biomass of algae present. Chlorophyll-a is most closely related but algae biomass is also correlated with Secchi depth and phosphorus concentration. In the case of BMR, chlorophyll is probably the most accurate indicator of trophic state.

As has already been shown above, chlorophyll-a was not correlated with Secchi depth or inflow, suggesting that water clarity in the reservoir is primarily a function of inorganic turbidity, and thus, Secchi depth would be a poor predictor of trophic state. Phosphorus concentration has been shown to correlate well with algal biomass in lakes all over the world (Schindler 1978) and phosphorus is generally regarded as the primary limiting nutrient for algal production. However, USEPA (1977) and Bauch and Malick (2003) reported that algae were usually nitrogen limited in BMR. Hence, total phosphorus concentration should also be less useful as a predictor of trophic state at BMR. Despite these caveats, the mean TSI computed from chlorophyll concentration from all months and basins lumped by year was 41, again, indicative of mesotrophic conditions in the 1990s. So, while we found a significant downward trend in chlorophyll concentration

since 1975, and chlorophyll concentration was on average lower after new dam operations than before, the reservoir would still be classified as mesotrophic.

Table 3. Trophic state index (Carlson 1977) of Iola basin during May and August 1997-2002 computed from three metrics- Secchi depth, chlorophyll-a concentration (CHL), and total phosphorus concentration (total P). Data were collected by CSU or by NPS.

Year	Secchi (m)	TSI (Secchi)	Chl (mg/m ³)	TSI (CHL)	total P (mg/m ³)	TSI (P)	mean TSI
May							
1994	2.1	50	3.7	43	242.5	83	59
1995	1.3	56	2.3	39	70.0	65	53
1996	2.8	45	7.8	51	37.5	56	51
1997	--	--	22.8	61	103.0	71	66
1998	1.0	60	3.4	43	63.0	64	55
1999	2.0	50	2.9	41	3.0	20	37
2000	2.5	47	3.0	41	42.0	58	49
2001	1.5	54	--	--	--	--	54
2002	2.5	47	2.6	40	28.4	52	46
Mean	2.0	51	6.1	45	73.7	59	52
August							
1994	6.8	32	2.5	40	206.5	81	51
1995	3.8	41	2.3	39	20.0	47	42
1996	5.8	35	2.9	41	20.0	47	41
1997	3.5	42	7.0	50	38.0	57	49
1998	6.1	34	9.4	53	44.0	59	48
1999	4.8	38	1.7	36	2.0	14	29
2000	5.8	35	1.3	33	70.0	65	44
2001	4.5	38	11.1	54	14.0	42	45
2002	3.0	44	7.7	51	40.4	57	51
Mean	4.9	38	5.1	44	50.5	52	45

Biological Limnology - Zooplankton

The crustacean zooplankton assemblage of BMR (Figure 19) consisted mainly of two copepod taxa, a cyclopoid (*Diacyclops*) and a calanoid (presumed to be *Leptodiaptomus*). Two Daphnids, *Daphnia pulicaria* (*pulex*) and *Daphnia galeata mendotae*, were the most abundant cladocerans. Other cladocerans include *Bosmina* and *Ceriodaphnia*, both of which are smaller than the *Daphnia*, and less preferred as food by fish. In most years, *Diacyclops* was numerically most abundant, comprising about 50% of the density of all plankters in the 0-10 m stratum (Johnson et al. 1997). *Daphnia* spp., most of which were *D. pulicaria*, constituted about 25% of the total.

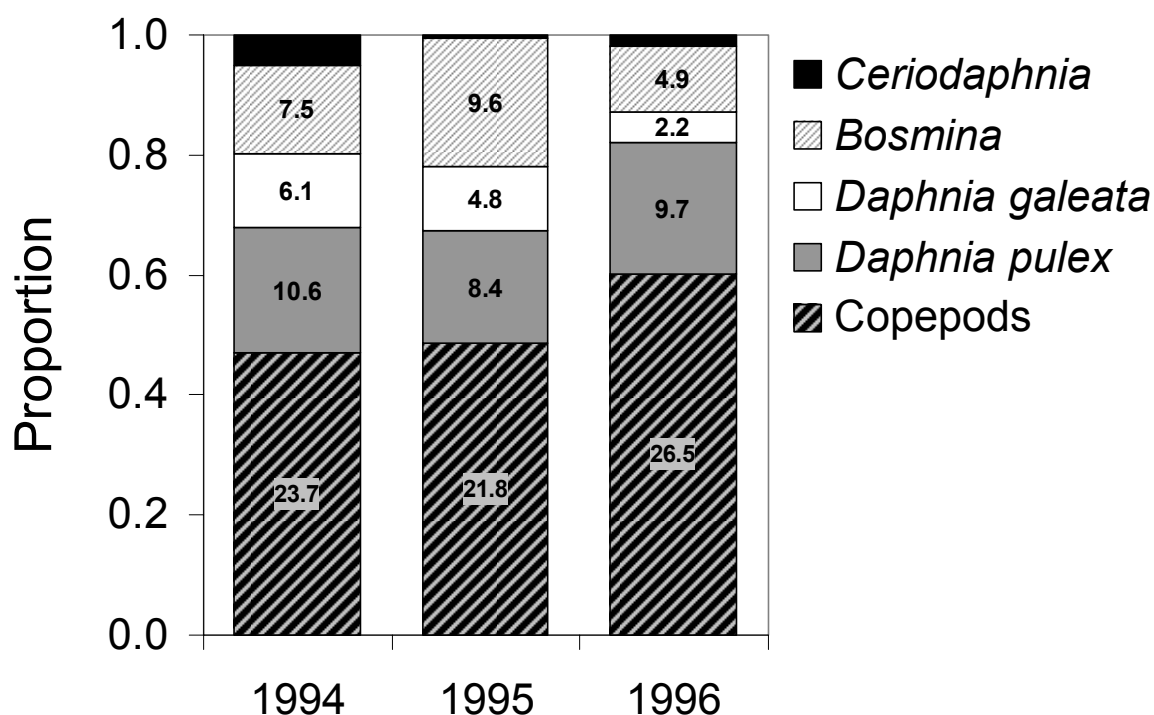


Figure 19. Relative species composition of crustacean zooplankton sampled by oblique tows with a Clark-Bumpus metered plankton sampler from the surface to 10 m and back to the surface during May-September, 1994-1996, at Sapinero basin of BMR. Numbers on each bar are animals/L.

Zooplankton are known to exhibit diel vertical migrations (DVM) in many systems (Horne and Goldman 1994). The presence of this behavior in BMR would affect food availability for kokanee and rainbow trout, and affect the planktivores' thermal experience. Work in 1993 and 1994 documented weak, small-scale DVM of *Daphnia*, on the order of < 5 m (Figure 20). The temporal pattern of the DVM was unexpected, with the *Daphnia* inhabiting shallower water during the day than at night (Johnson et al. 1994, 1995). Thus, predation avoidance does not appear to be the mechanism driving DVM in BMR. There was no difference in *Daphnia* length distributions across depths during day and night samples suggesting that the whole population migrated

synchronously. Given the small magnitude of DVM of *Daphnia*, further investigation of the phenomenon was not performed after 1994.

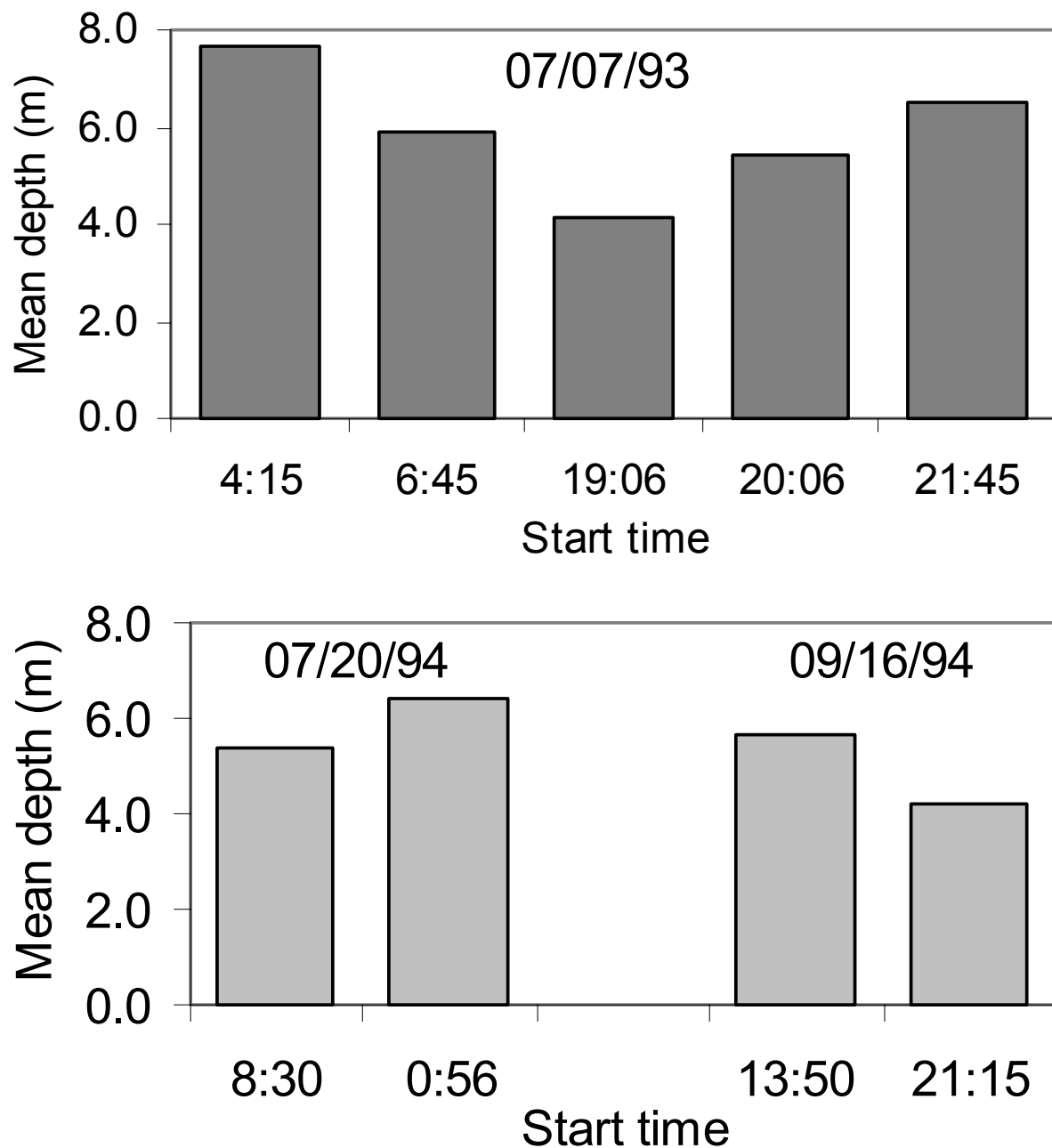


Figure 20. Mean depth of *Daphnia pulex* sampled throughout the day (military time) in July 1993, and July and September 1994. Samples were collected with a Clarke-Bumpus net. In 1993 we sampled at 1, 3, 5, 9, 12, and 15 m, and in 1994 we sampled 0-5 m, 5-10 m, 10-20 m, and 20-30 m depth strata.

Daytime depth distribution of *Daphnia* was very consistent among years. *Daphnia* were most abundant in the top 10 m of the water column. The mean percentage of the population in the 0-10 m stratum was 85% (Figure 21). Only about 4% of the total *Daphnia* abundance was located below 15 m. Phytoplankton (as measured by chlorophyll-a concentration), the primary food of *Daphnia* (Kerfoot et al. 1988), appeared to be somewhat more concentrated in the epilimnion, but that pattern was not statistically significant. *Daphnia* may be seeking warmer epilimnetic waters in part to maximize food availability, but also to benefit from increased reproductive rates in warmer water (Gabriel 1987). Given their distribution in well-lit surface waters and a reverse DVM pattern it does not appear that *Daphnia* behavior or distribution is driven by predation avoidance in BMR. Their epilimnetic distribution implies that the *Daphnia* would not be subject to entrainment from the hypolimnetic release, and thus, increased spring and early summer withdrawals should not have a direct effect on *Daphnia* populations. Sampling the dam outflow in 1994 (Johnson et al. 1995) showed that 1) *Daphnia* were a small fraction of the plankton entrained (a maximum of 14% in May, only trace amounts in June-July), 2) species composition of the zooplankton in the outflow was most similar to reservoir samples taken at depths of 30-55 m, and 3) rough calculations suggested that during the period of maximum *Daphnia* entrainment <0.06% of the biomass of the reservoir was lost through the dam each day. Shallower releases from a TCD or spills would cause much higher losses of *Daphnia*.

Factors that lower epilimnetic temperatures, for example, a TCD, can be expected to negatively impact *Daphnia* production by increasing egg development time and thereby depressing reproductive rates. Given that CE-THERM simulations showed that altering the pattern of withdrawals from the hypolimnetic outlet would have very limited effects on reservoir temperatures, increased spring releases should not alter *Daphnia* production via temperature effects.

Zooplankton are also known to be distributed patchily in the horizontal dimension (Pinel-Alloul 1995). Intensive sampling at several spatial scales in 1994 and 1995 showed that the coefficient of variation (CV) of mean *Daphnia* density was lowest among samples within a station (about 22%), and was significantly higher at stations within a basin (about 36%). Variance among samples from standardized stations among basins was not different from that among random stations within one basin. Thus, horizontal patchiness in zooplankton density was greater at larger spatial scales, but similar within a basin and across basins. *Daphnia* density did not differ among stations within Sapinero basin, but inter-basin differences existed, especially during May-July (Wise 1997).

It was not possible to evaluate the actual effects of new dam operations on zooplankton dynamics because of the lack of historical data. Mean *Daphnia* density, across all months and all years, was 10 animals/L and ranged 5-25 animals/L (Figure 22). *Daphnia* density typically peaked in June (Figure 23) and in general *Daphnia* density peaked earliest in Sapinero basin and latest in Iola basin (Wise 1997). There was no relationship between *Daphnia* density and P of inflow ($r = 0.05$, $n = 10$). However, as with any retrospective analyses, it is difficult to account for confounding variables that

may have obscured any such relationship. Density of cyclopoid copepods (mainly *Diacyclops*) was highly variable but appeared to exhibit a declining trend over the term of the study ($r = -0.67$; Figure 22). *Diacyclops* was the most abundant taxon in the samples from the outflow (Johnson et al. 1995).

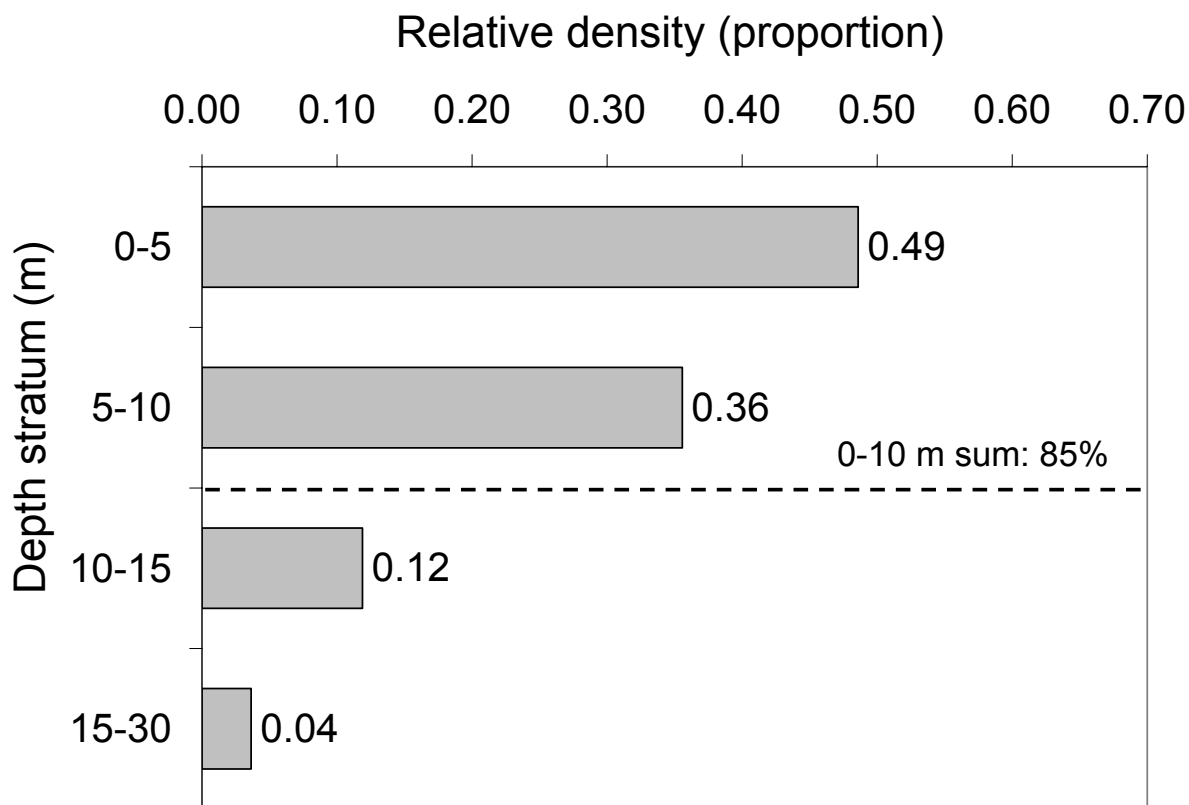


Figure 21. Average vertical distribution of *Daphnia* in four depth strata sampled at BMR during 1994, 2001 and 2002. The numbers at right of each bar show the proportion found in each stratum. On average, 85% of the total *Daphnia* density was found in 0-10 m.

The mean length of *Daphnia pulicaria*, across all months and years, was 1.25 mm (SD = 0.16, $n = 43$). The mean length increased from May to September each year (Figure 24). Among years, mean lengths of *D. pulicaria* were similar and the range of lengths (SD) was very similar each year as well. Reasons for the unusually low mean lengths of *Daphnia* sampled in 2002 are unknown. Typically, a decline in cladoceran size suggests an increase in planktivory (Brooks and Dodson 1965).

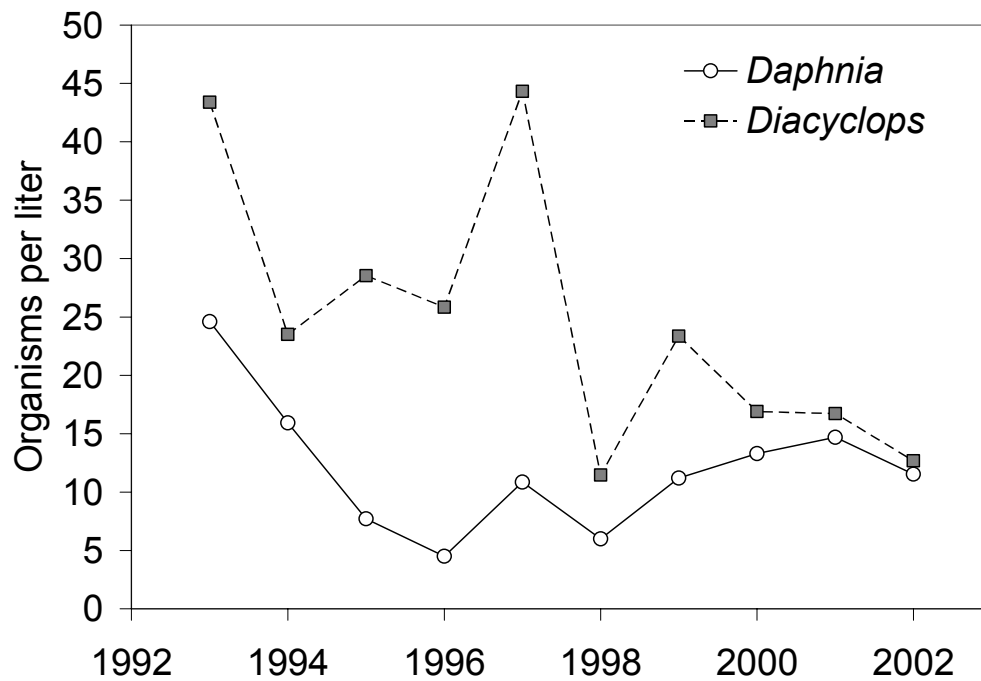


Figure 22. Mean density of all species of *Daphnia* and *Diacyclops* sampled from 0-10 m at Sapinero basin, BMR during July 1993-2002.

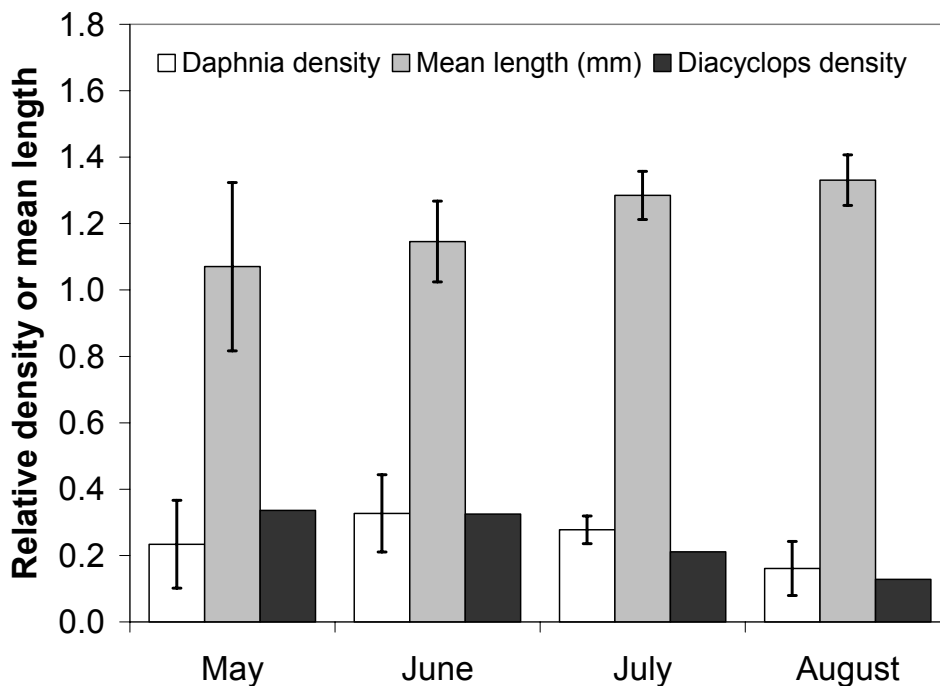


Figure 23. Seasonal variation in relative density and mean length (mm) of *Daphnia*, and relative density of *Diacyclops* sampled from Sapinero basin at BMR during May-August 1994-1995, and 2000-2002.

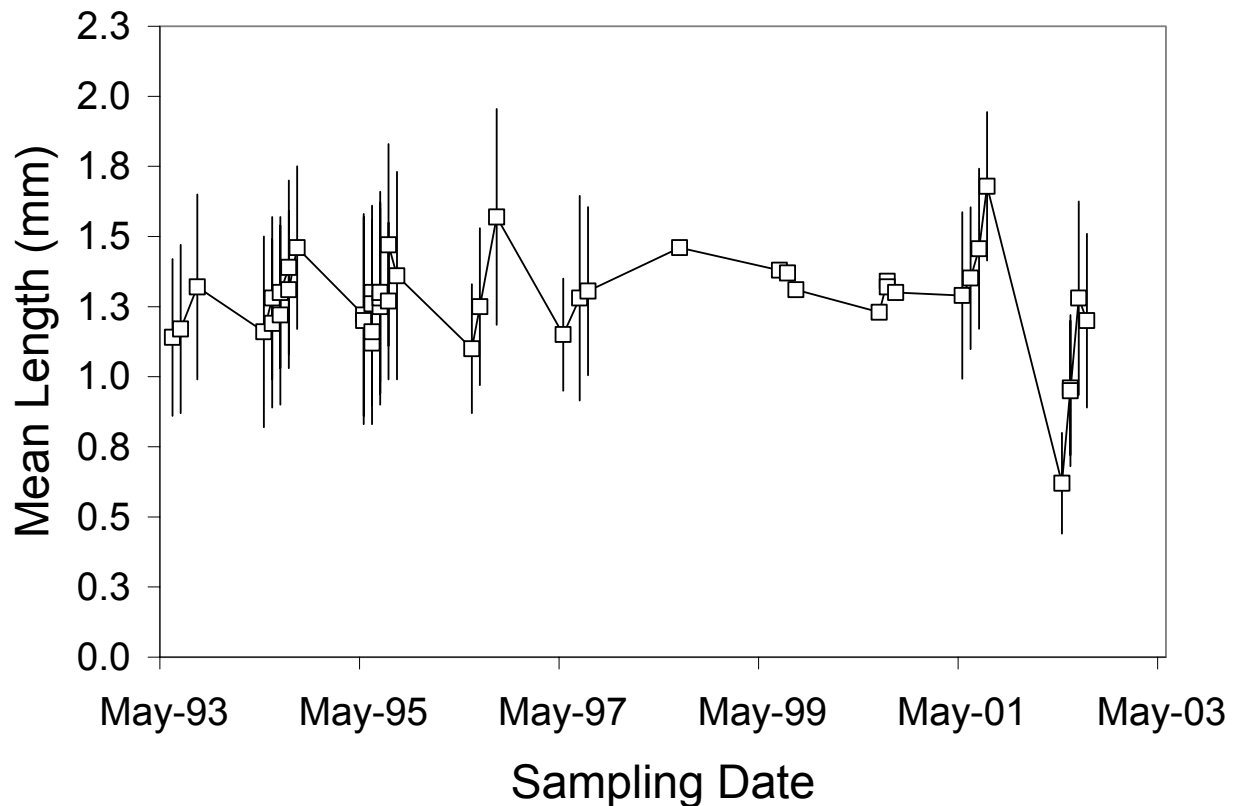


Figure 24. Mean length (mm) of *Daphnia pulex* sampled from Sapinero basin of BMR in May-September 1993-2002. Error bars show ± 1 standard deviation (not available in 1998-2000).

Surveys for *Mysis relicta* were performed by Pat Martinez at 15 stations across the entire reservoir, during summer 1993, 1996, 1998, and 2002. None were detected despite an abundant population in Taylor Park Reservoir, about 70 km upstream of BMR. Martinez (2002) speculated that fish predation and turbulence in the river below Taylor Park Reservoir has precluded the invasion of *Mysis* into BMR. It is fortuitous that *Mysis* have not invaded BMR. The ability of *Mysis* to decimate zooplankton populations, resulting in reduced growth rates of kokanee, and increased mortality from lake trout is well documented in the literature (Nesler and Bergersen 1991). Invasion of the reservoir by other crustaceans also has the potential to seriously disrupt the zooplankton assemblage and thus pose a significant threat to the system's kokanee population. *Bythotrephes*, *Cercopagis pengoi*, and *Daphnia lumholtzi* are exotic zooplankters that have invaded many systems both to the east and west of Colorado. These organisms either prey on other cladocerans or eliminate them by competition, and their spiny morphology defends them from fish predation, thus reducing food for kokanee and trout.

Effects of Drought

Hydrological effects of drought were most obvious when compared to reservoir hydrology in 1995 (an unusually wet year) or to the long term average (Figure 26). Inflow to BMR in spring 2002 was well below even the unusually dry conditions in 2001, and far below the long term average, and the average inflow during the preceding years of study (1993-2000). Reservoir surface elevation at BMR declined continuously during May-September 2002. This pattern has not been observed previously and was indicative of the extremely dry conditions in the basin in 2002.



Figure 25. Two views of Sapinero basin of Blue Mesa Reservoir showing summer surface elevation under drought (left) and more normal (right) hydrologic conditions.

Daily temperatures of the Gunnison River near the Cooper Ranch picnic area were 3-4 °C warmer during most of the summer 2002 than during summer 1997 (Johnson et al. 2002). By mid-August, stream temperatures in 1997 and 2002 were similar. We did not have stream temperature data from any other years to compare with those measured in 2002. The increase in stream temperatures during low discharge was not unexpected (Bartholow 1989).

Temperature at 2 m and average epilimnion temperatures at Sapinero basin in mid summer 2002 were the highest observed since 1994 (Johnson et al. 2002). Thickness of the epilimnion (depth at which temperature changed by $>0.5^{\circ}\text{C}/\text{m}$) was variable each year, but was greatest in 2002 on most dates compared to other years back to 1994. Secchi depth at Sapinero basin was also higher than observed in any other year since 1994. *Daphnia* abundance in 2002 was not significantly different from previous years. LaBounty and Sartorius (1981) found that nutrient loading from inflows, chlorophyll-a concentration and zooplankton density were all depressed during two years of drought at Twin Lakes, CO, and Seminoe Reservoir, WY.

It is difficult to attribute differences in some reservoir limnological conditions in 2002 to the drought since other weather variables during summer can also influence reservoir conditions. Drought in Colorado is strongly related to winter snowpack and subsequent stream flows during melting. Effects of low snowpack on water supplies are compounded by warm, dry conditions in summer but snowpack and summer weather

are rather independent (Nolan Doesken, CSU, personal communication). Thus, summer air temperatures and insolation may be high or low in drought years and these variables affect the reservoir's thermal regime. Further, the generality of our findings in 2002 is difficult to assess because there are no extreme drought years represented in any of the previous studies. Prolonged droughts occurred in 1977 and 1981, with 1988-1992 unusually dry also. Unfortunately, data are very scarce for these periods. We evaluated general drought effects on temperature by controlling for the confounding effects of weather in simulations with CE-THERM.

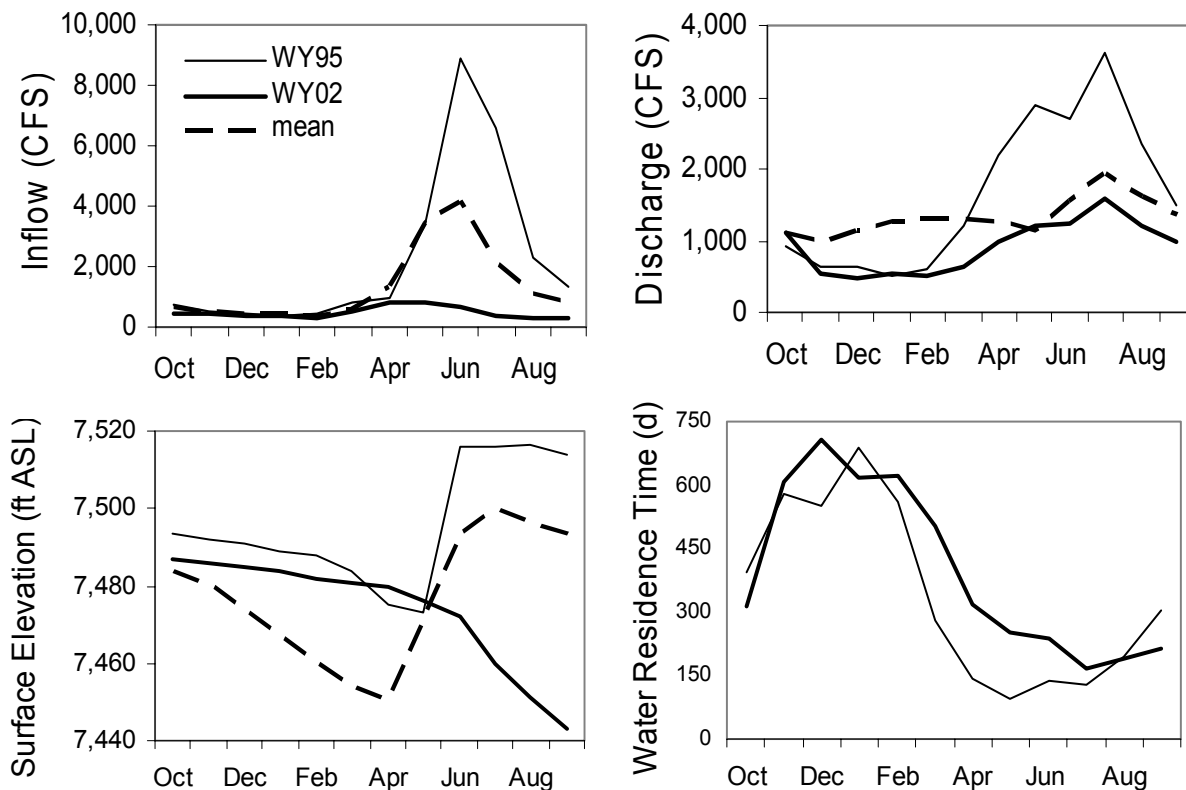


Figure 26. Hydrologic characteristics of BMR during a year of very high inflow (exceedance probability, $P = 0.05$) and a year of very low inflow ($P = 0.95$) compared with the long term mean (1969-1993).

The fit between stream temperatures, and reservoir temperature profiles predicted by CE-THERM and those measured in 2002 was not as good as in validation simulations by Johnson et al. (2004) but still reasonably close (Saito and Gebeyehu 2003). The fit between modeled and observed stream temperatures was $r^2 = 0.64$ using 2002 data and $r^2 = 0.98$ using data presented in Johnson et al. (2004). Because Johnson et al. (2004) found that reservoir thermal structure was most sensitive to inflow and air temperatures, a new multiple regression fit to 2002 air and stream temperature data might improve the modeled stream temperature inputs and therefore, the accuracy of predicted reservoir temperature profiles. The overall average RMSE for all predicted

temperature profiles in the reservoir was 1.02°C and the model captured the shape of the temperature profiles very well. In general, the model predicted that under drought conditions the hypolimnion was cooler and the epilimnion was warmer than baseline conditions. The baseline predictions in late July agreed well with the measured profile on 08/04/99, a year with inflow equal to the long term average. The model accurately predicted the observed differences in metalimnetic temperatures between normal and drought conditions (Figure 27), boosting our confidence in the model's validity.

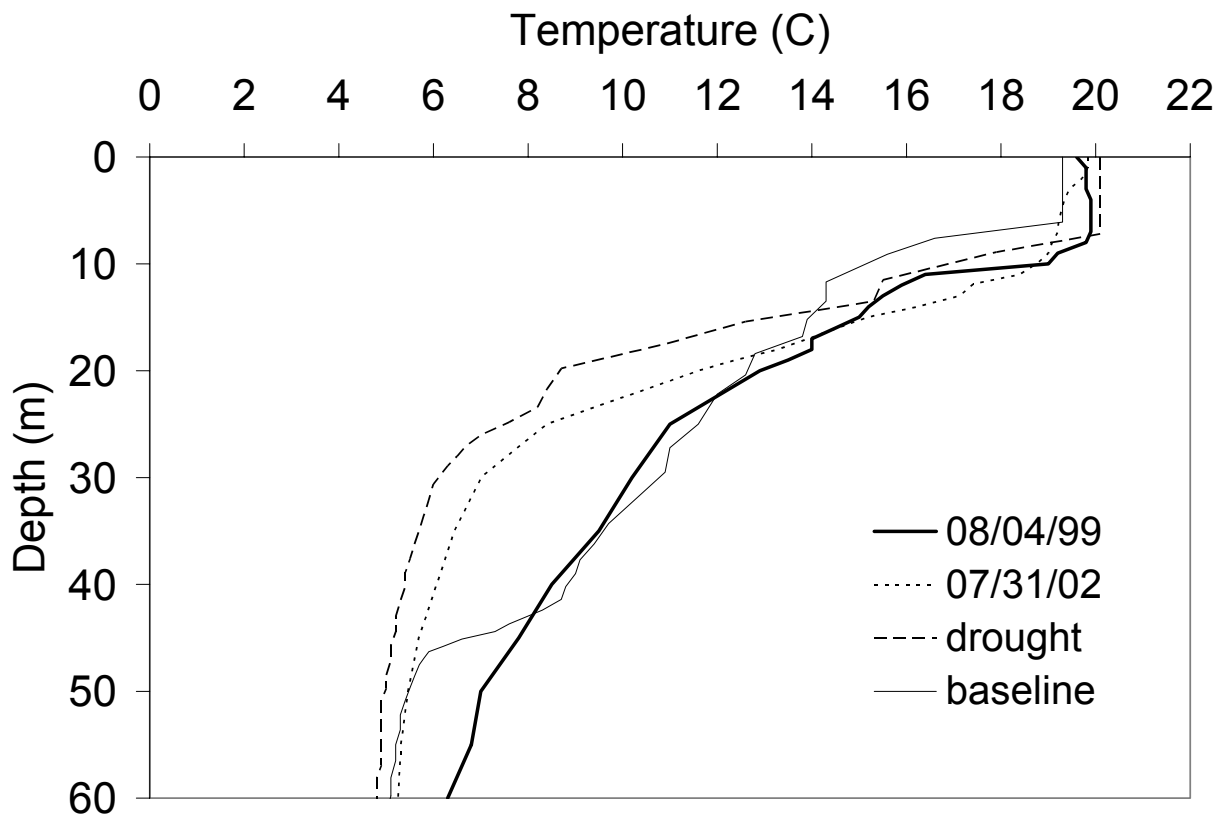


Figure 27. Temperature profiles measured on two midsummer dates in 1999 ($P = 0.60$) and 2002 ($P = 0.05$) and two profiles predicted by CE-THERM for drought and baseline hydrologic conditions.

In addition to the effects on temperature profiles, a large increase in water residence time under drought versus baseline conditions was predicted. This increase was likely due to reduced inflow and outflow, and increased flushing time of the reservoir. Computed water residence times using actual hydrologic data for the 1977 and 2002 droughts were the highest on record. Again, this supports the accuracy of the CE-THERM simulations and indicates that droughts increase water residence time significantly at BMR.

3.4 Summary

- Epilimnetic temperatures usually reached 18-19°C in midsummer and the temperature of the hypolimnion was 6-7°C throughout May-September, but hypolimnetic temperatures were somewhat lower in years of low inflow.
- Dissolved oxygen concentration dropped below 3.0 mg/L (the acute lethal concentration for salmonids) in Sapinero and Cebolla basins at depths > 35 m by September in some years.
- Average summer conductivity (1966-2002) was not correlated with inflow and conductivity did not differ before and after new operations.
- Secchi depth was lower before 1993 than after, even after controlling for differences in inflow.
- Secchi depth showed an increasing trend during 1993-2002; this was believed to be the result of declining inflows during the period.
- There was a strong negative trend in chlorophyll concentration in Sapinero basin since 1975. August chlorophyll-a concentrations among all basins were significantly lower ($p = 0.02$) after dam operations changed (mean = 2.4 µg/L) than before (mean = 3.2/µg/L). Thus, it appears that algal biomass may be declining in the reservoir.
- Chlorophyll concentration was not correlated with P indicating that the declining trend in chlorophyll measurements since 1975 could be due to reduced nutrient availability.
- Trophic state indices computed from nutrients, Secchi depth, and chlorophyll concentration during 1994-2002 were characteristic of mesotrophic conditions (mean TSI = 42).
- It was not possible to evaluate the actual effects of new dam operations on zooplankton dynamics because of the lack of historical data.
- During 1993-2002, the crustacean zooplankton assemblage consisted mainly of two copepod taxa (a cyclopoid and a calanoid), and two *Daphnia* species (*D. pulicaria* and *D. galeata*).
- Mean *Daphnia* density, across all months and all years, was 10 animals/L and ranged 6-18 animals/L.

- *Daphnia* were always more abundant in the top 10 m of the water column than in deeper water. The mean relative density of the *Daphnia* population in the 0-10 m stratum was 85% and only about 4% below 15 m.
- We observed weak diel vertical migrations of *Daphnia* but these occurred over a small depth range (< 5 m).
- Entrainment of *Daphnia* through the dam during summer was not significant relative to the standing stock in the reservoir. Few *Daphnia* were entrained because they were distributed much shallower than the depth of the intake structure.
- Density of cyclopoid copepods (mainly *Diacyclops*) was highly variable but appeared to exhibit a declining trend over the term of the study. *Diacyclops* was the most abundant taxon in samples taken from the outflow.
- Extreme drought resulted in a continuous decline in surface elevation during the entire 2002 water year.
- Inflow temperatures were 3-4°C higher in 2002 than in previous years.
- Reservoir surface temperatures and depth of the thermocline were also greatest in 2002.
- In general, the CE-THERM model accurately predicted that under drought conditions the hypolimnion would be cooler and the epilimnion warmer than baseline conditions.
- The model also correctly predicted the observed differences in metalimnetic temperatures between normal and drought years.
- Both modeling and calculations from hydrologic data showed that drought increased the water residence time of the reservoir significantly.
- Invasion of the reservoir by non-native species poses a significant threat to the stability of the food web and sustainability of the sport fishery in BMR.
- *Mysis relicta* have not been detected in BMR in periodic monitoring by CDOW; *Mysis* are capable of decimating cladoceran zooplankton populations, resulting in reduced growth rates of kokanee,
- Other crustaceans also have the potential to seriously disrupt the zooplankton assemblage and thus pose a significant threat to the system's kokanee population. *Bythotrephes*, *Cercopagis pengoi*, and *Daphnia lumholtzi* are exotic zooplankters that either prey on other cladocerans or eliminate them by competition, and they are not fed on by fish.

- Recently introduced yellow perch may compete with kokanee for food; zooplankton prey may become very scarce if predaceous crustaceans invade the system resulting in poor growth rates and survival of planktivorous fishes.

4 THE FISHES AND FISHERY

4.1 Introduction

The sport fishery at BMR is one of the largest and most valuable in Colorado, and kokanee are the centerpiece. Rainbow trout are also an important component of the fishery because that species is typically more accessible to shore-based anglers than kokanee. In recent years approximately 1 million rainbow trout and nearly 3 million kokanee have been stocked each year to sustain the fishery.



Figure 28. A successful angler cleaning a catch of kokanee from BMR. The reservoir's kokanee fishery has been called one of the best anywhere (photo: B. Johnson).

Kokanee comprise over 80% of the catch, and in 1993 for example, anglers fished 350,000 hours, primarily for kokanee. Historically, the BMR fishery has generated a

multi-million dollar input to local and state economies annually, and the actual economic value of the fishery is much higher (Johnson and Walsh 1987). The kokanee fishery is thought to be one of the primary factors driving visitation at the Curecanti National Recreation Area (M. Malick, NPS, personal communication). Eggs taken from Blue Mesa Reservoir's kokanee population are also critical to sustaining kokanee fishing throughout the state. In recent years BMR has provided nearly 90% of the entire state's supply of kokanee eggs. The management objective at Blue Mesa has been to maintain kokanee and rainbow trout populations for fishing recreation and to maintain the kokanee population to provide an egg supply for the hatchery system.

Because little was known about potential in-reservoir impacts of increased spring releases from BMR (and western reservoirs in general), fishery managers at BMR expressed concern that these new operations could jeopardize the reservoir's sport fishery, kokanee in particular. A primary motivation for the present study was the need to address that concern.

Adverse effects of dam operations on fish populations can be manifested in a number of ways. In general, those effects occur via changes to population parameters such as growth, recruitment, emigration and survival. Evidence of effects on growth can include changes to annual growth increments, body condition and diet. Recruitment, the addition of new individuals to the population, is controlled by reproductive output or stocking, and the subsequent survival of the young. Changes to recruitment can be evident in the abundance and size-age structure of the population. Emigration through the dam (entrainment) causes losses to the reservoir fishery above the dam, and may be measured directly by sampling, or assessed indirectly from the spatial distribution of the fishes. Finally, changes to survival can be due to mortality during any life stage, and the agents of mortality can be expected to change with fish size. In general, survival can be reduced by size-dependent mortality associated with growth and predation. It is difficult to measure survival directly but growth during the first year of life, quantification of predation risk and predator consumption demand, and sport fishery harvest provide useful indicators.

Water level fluctuations resulting from dam operations have been shown to affect fish populations through a variety of direct and indirect mechanisms. Recruitment of shore-spawning fishes is adversely affected by the loss of habitat (Irwin and Noble 1996; O'Brien 1990) and reduction in the survival of eggs and young fish (Kohler and et al. 1993; Ploskey 1986). Drawdown can aggregate predators and prey and competitors, and it may intensify species interactions by concentrating animals in a subset of the reservoir's volume (Jenkins 1970; Stockwell and Johnson 1997). Water level fluctuations can also adversely affect food availability for fishes produced in the littoral and pelagic zones. Short duration drawdowns that prevent colonization and subsequent inundation of terrestrial vegetation (Ploskey 1986) are particularly detrimental to littoral communities. Benthic aquatic organisms such as periphyton, macrophytes, aquatic insects and decapods may be eliminated by periodic drawdown and dessication with implications for food availability for benthivorous fishes (Ploskey 1986; Siegfried 1984). Water level fluctuation, as well as water residence time, have the potential to alter physicochemical characteristics of the water column, including

nutrients, turbidity levels and thermal profiles (Thornton et al. 1990), and thus, can have far-reaching effects on the reservoir's food web and fishery. Such changes may affect algal production (Kimmel et al. 1990) zooplankton productivity (Marzolf 1990), fish bioenergetics (Stockwell and Johnson 1997), the amount of light available for predators (Hardiman et al. 2004; Koski 2004; Koski and Johnson 2002) and predation risk from piscivores (Koski 2004)

Of course, other factors that may be independent of dam operations can also negatively affect fish populations and community interactions. Gradual reductions in ecosystem productivity may occur as a reservoir ages (Kimmel and Groeger 1986; Ryder 1978) and land use changes in the watershed can also be detrimental to reservoir fishes (Kimmel and Groeger 1986). Changes in the number of fish stocked or early mortality of those fish affect recruitment and year class strength. For fish such as kokanee that are often stocked upstream of reservoirs, predation or losses to irrigation diversions occurring as the fish migrate downstream to the reservoir can be important factors reducing survival and therefore recruitment. Reservoir conditions can be sensitive to hydrologic and weather conditions (Johnson et al. 2004; Nowlin et al. 2004), as well as dam operations. Short term variations in climate can be detrimental if they affect habitat quality, food production, or predator-prey interactions (Koski 2004). Changes in the number of piscivores, either via recruitment or management strategies that foster the expansion of those species, can lower the survival of other sport fishes preyed upon by piscivores. Sport fishery harvest can also be an important source of mortality to fishes that can be independent of dam operations.

Predicting how fish populations (and the sport fisheries they support) will respond to changes in dam operations requires a solid understanding of demographic processes and behavior of the fishes. Without controlled experiments, conclusions regarding how dam operations might be responsible for changes in reservoir communities and fisheries are tentative and subject to the confounding effects of uncontrolled variables (Stein et al. 1996). Hence, assessment of the potentially confounding effects of hydro-meteorological conditions, the sport fishery harvest, and fishery management policy on the fish assemblage was critical to the present study.

An important side benefit of this project was a wealth of information useful to fishery managers at BMR and in other Colorado reservoirs. Thus, analyses and recommendations presented in this report include those of interest to fishery managers.

4.2 Methods and Data Analysis

Overview and Approach

In general, our fishery investigations were undertaken to 1) determine if changes in the fishery coincided with changes in dam operations, 2) gain a mechanistic understanding of the community that would allow us to assess the extent to which dam operations may be responsible for such changes, and 3) investigate alternative explanations for

changes that were not due to dam operations. Our approach included intensive field studies to track changes in the food web and gather inputs for simulation models. We used simulation modeling to investigate the relative importance of a variety of factors affecting the fishery, including limnological characteristics, food availability and predation. We also performed laboratory experiments to refine simulation models. Creel survey data from CDOW provided measurements of the intensity of fishing mortality and an indication of fish population trends. Findings from these studies were compared to results of studies conducted prior to the change in operations in 1993.

The focus of our fishery investigations was on the potential detrimental effects to the kokanee and rainbow trout populations since these species drive the overwhelming majority of the BMR fishery's fishing effort, catch and harvest.

Overall objectives for our fish and fishery investigations at BMR included the following:

1. Gain an understanding of the spatial distributions of fish populations, on diel, seasonal and inter-annual time scales to aid in the interpretation of changes in growth, recruitment, emigration and survival that may be linked to dam operations or other factors.
2. Determine if changes to food availability for sport fishes coincided with new dam operations. Examine growth rate and body condition of kokanee and rainbow trout before and after new operations were implemented. Conduct laboratory experiments and simulation modeling to predict how kokanee growth could respond to changes in the physicochemical environment induced by a variety of dam operation scenarios and by hydrometeorological factors.
3. Conduct diet and stable isotope studies to understand the food base supporting kokanee and trout production, and to assess the degree of diet overlap among various fish species. Determine the predation pressure exerted by lake trout on other fishes.
4. Evaluate potential factors that contributed to trends in recruitment and survival, primarily of kokanee, in BMR: stocking rates, survival during the river transit stage immediately post-stocking, entrainment, predation, and harvest in the sport fishery. Evaluate how dam operations and climate might affect risk of predation by lake trout.

Methods-- Field Sampling and Analysis

Post-stocking Dispersal

We studied the timing of the migration of stocked kokanee fry from Roaring Judy Hatchery (Figure 29) to Blue Mesa Reservoir in 2001 (Hardiman and Johnson 2001). To determine size structure of the stocked cohort, we took samples of 15 individuals from each of the hatchery's 22 large holding tanks plus two smaller tanks, which housed fish thermally marked in January. We measured lengths and weights and preserved

them in 70% ethanol. Stocking in 2001 proceeded as it had in the past: fish were stocked at night during the new moon in April to reduce predation losses under cover of darkness. An enhanced flow of approximately 200-300 CFS in the Taylor River was released from Taylor Park Reservoir to speed travel times to the reservoir and minimize predation exposure and entrainment into irrigation ditches. The release from Roaring Judy Hatchery (ROJ) started at 1900 h on April 20, 2001 and finished at 1945 h on the same night. Fish were flushed from the hatchery raceways into a drainage system of pipes and ditches that lead to the East River. Fish entered the East River from the hatchery ditch outlets at approximately 2015 h that evening. Five sites were sampled along the riverine migration route (Figure 30). The sites were selected based on ease of access and efficiency of sampling. The first three sites were about 4 miles apart, and the last site was another eight miles downstream, about 4 miles upstream from the reservoir. The first site was at Almont in the East River just above the confluence with the Taylor River (where it becomes the Gunnison River). We sampled with seines measuring 6' x 12', each with a 4' x 4' x 2' bag; mesh size was 1/8" (delta type). We used a passive seining technique, holding the seine at a fixed location in the mainstream river channel, because river flows were too great for a more active seining method. Seines were held in position for 2 min. We employed longer (5 min) sampling times as the catch decreased. Sites were sampled approximately every 3 hours to assess the timing of the migration.



Figure 29. Colorado Division of Wildlife's Roaring Judy Fish Hatchery raises almost 3 million kokanee fry per year, most of which are stocked into BMR. The hatchery is ramping up production of catchable rainbow trout, some of which are destined for BMR (photo: B. Johnson).

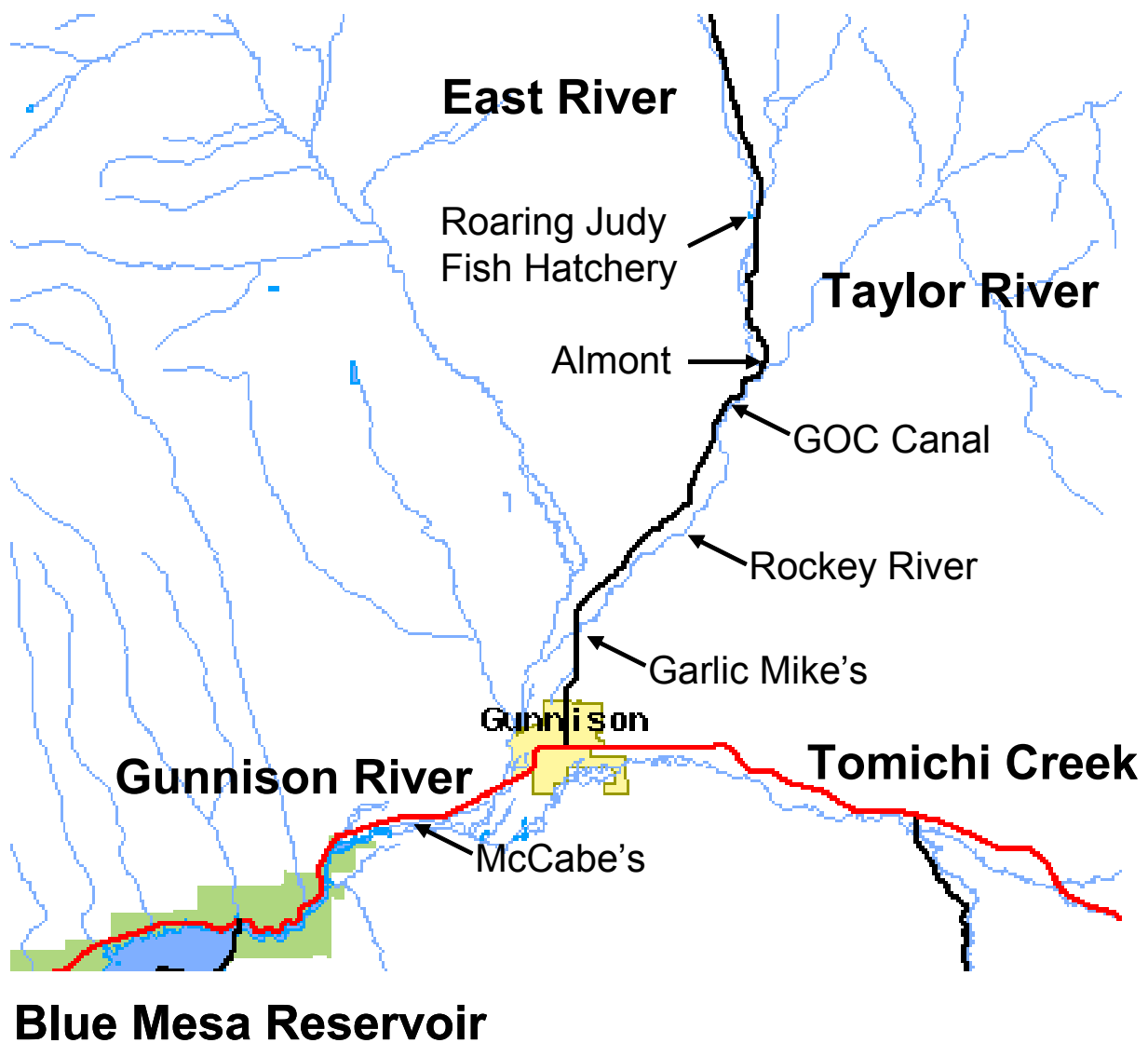


Figure 30. Five sites (Almont, GOC Canal, Rockey River, Garlic Mike's, and McCabe's) sampled along the riverine migration route of kokanee fry stocked from the Roaring Judy fish hatchery.

Analysis of Entrainment

We did not study losses of kokanee through the Blue Mesa Dam directly. We did evaluate the possibility that entrainment resulted in losses of kokanee by examining the relationship between kokanee survival and discharge. Although Wiltzius (1978) found large losses of kokanee through the dam in November and December in the early 1970s, the average discharge from BMR during winter was considerably lower after 1992 than during 1970-1992. Average monthly discharge was higher during May-July 1993-2003 than in previous years. Further, mean daily discharge was highly correlated ($r \approx 0.8$) among months. Therefore, we looked for correlations between kokanee survival and May discharge during 1993-2003.

We developed survival indices to compare to discharge volumes. Because Mueller and Hiebert (1997) and Wiltzius (1978) found that age-0 and age-1 were the predominant age classes in the sieve net below the BMR dam, our survival indices were compared to monthly discharge from BMR during the first and second years of life. The survival indices estimated the survival of each year-class and were based on the catch per unit effort (CPE) in the fishery divided by the number of kokanee stocked two and three years previously (Hansen et al. 1994), multiplied by a scaling factor. These indices assumed that 1) most entrainment occurs in the first or second year of life, 2) CPE was proportional to abundance, and 3) anglers captured primarily age-3 fish. The first assumption is consistent with results from previous studies at BMR. We found that CPE was positively correlated with pelagic fish abundance estimated from hydroacoustics surveys ($r = 0.64$), supporting our second assumption. Age and growth information showed that most of the kokanee in the harvest were indeed age-3 fish. We evaluated the risk of entrainment to age-0 kokanee from the depth distribution of small kokanee estimated from diel hydroacoustics surveys in spring and summer 2001 and 2002, and compared that to the findings of Wiltzius (1978) and Mueller and Hiebert (1997).

Gill Netting

Annual gill net surveys provided much of the data required for our fishery diet (Figure 31). We used both vertical and horizontal gill nets during the course of the project. Vertical gill nets measured 60 m long and 3 m wide (Figure A2) and were constructed with two mesh sizes each (standard CDOW coldwater net mesh sizes: 0.5 in, 0.75 in, 1.0 in, 1.25 in, 1.5 in, or 2.0 in) per net.

A gang of three nets was fished during nighttime hours at a midlake station. Nets floated on the surface and extended to within 1-2 m of the lake bottom. Sampling stations were standardized in 1994 and were used each year (Figure 6). In some years sampling occurred monthly during May-September; in several years we sampled a single month, coinciding with the time of whole reservoir hydroacoustics surveys. The depth at which each fish was caught was recorded, and each fish was measured (TL, mm) and weighed (g). Otoliths and stomachs were removed from a subsample of the catch. In 1997, 2001 and 2002, tissue samples were collected for stable isotope analysis.

Two configurations of horizontal gill nets were used to sample age-0 and age-1 kokanee in 2001 and 2002 (Johnson et al. 2001, 2002). Two nets consisted of 30 m x 1.5 m multifilament mesh (25 mm stretch measure) and three 15 m x 1.5 m "Swedish" nets (fine monofilament, stretch mesh sizes of 13 mm, 19 mm, and 25 mm). We set nets either on the bottom or floating on the surface (Johnson et al. 2001, 2002a). Nets were generally set at dusk and retrieved the following morning at about 0800 h. Horizontal gill nets were also used to capture lake trout for marking with cinch-up tags and sonic tags, and to recapture marked fish for population estimates (below).



Figure 31. Jason Stockwell, Shawndy Mawhorter, and Josh Hobgood (left to right) retrieve a horizontal gill net set to capture lake trout for diet and stable isotope analyses (photo: B. Johnson).

Midwater trawl

We used two midwater trawls to sample age-0 kokanee in the pelagic zone in 2001 and 2002 (Johnson et al. 2001, 2002a). These trawls were deployable from small boats without hydraulics (Figure 32); the design was obtained from Art Butts (EAGAR Corporation, Salt Lake City, UT). The first trawl was constructed of 6.4 mm mesh with a 2 m diameter opening (Figure A1). It was 6 m long and tapered to a detachable cod-end made of PVC. We also used a net with graduated mesh sizes (44 mm, 22, and 13 mm), similar in diameter and length to the original design.

In 2001 we made midwater tows at depths of 12 to 18 m, during nighttime hours. Hauls were made in June during two different weeks in Iola and Cebolla basins. The trawl was also fished during the day while a second boat tracked the trawl with a depth finder to determine approximate depths obtained while varying the tow line length and the speed of the boat. In 2002 we used a variety of towing techniques including surface trawling, zig-zag towing patterns with extended towlines, and a two boat towing method. Surface hauls were made during dusk hours up to 2 hrs after dusk. Midwater hauls were made primarily during night-time hours at depths of 10-18 m.



Figure 32. Midwater trawl being deployed and retrieved at BMR (photo: B. Johnson).

Hydroacoustics

All hydroacoustics work was performed with an HTI Model 243 split beam 200-kHz, 15-degree echosounder belonging to CDOW (Figure 33). The hydroacoustics equipment was calibrated monthly by collecting >1,000 echoes on a tungsten calibration sphere of known target strength suspended in an acoustically transparent monofilament net at >10 m depth. Calibration files were inspected *in situ* to ensure that the indicated target strength matched the expected value with <1 dB standard deviation, and that the sphere was accurately tracked as it moved through each quadrant in the X/Y plane.

Colorado Division of Wildlife conducted standardized hydroacoustics surveys of the entire reservoir annually, beginning in 1994 (Martinez 2004). Transects followed a “zig-zag” survey design previously established by the CDOW for Blue Mesa Reservoir (Martinez 1994).

In conjunction with the annual hydroacoustics surveys, we set vertical gill nets to estimate species composition. Six nets ranging in mesh size from 12.5 to 50.8 mm were set at mid-basin locations in Sapinero, Cebolla and Iola basins. Nets extended from the surface to within 5 m of the bottom, and were deployed in the same configuration as in

previous years. Nets were set at dusk, fished overnight, and lifted the following morning before 1000 h. Sampling was conducted for one night in each basin.

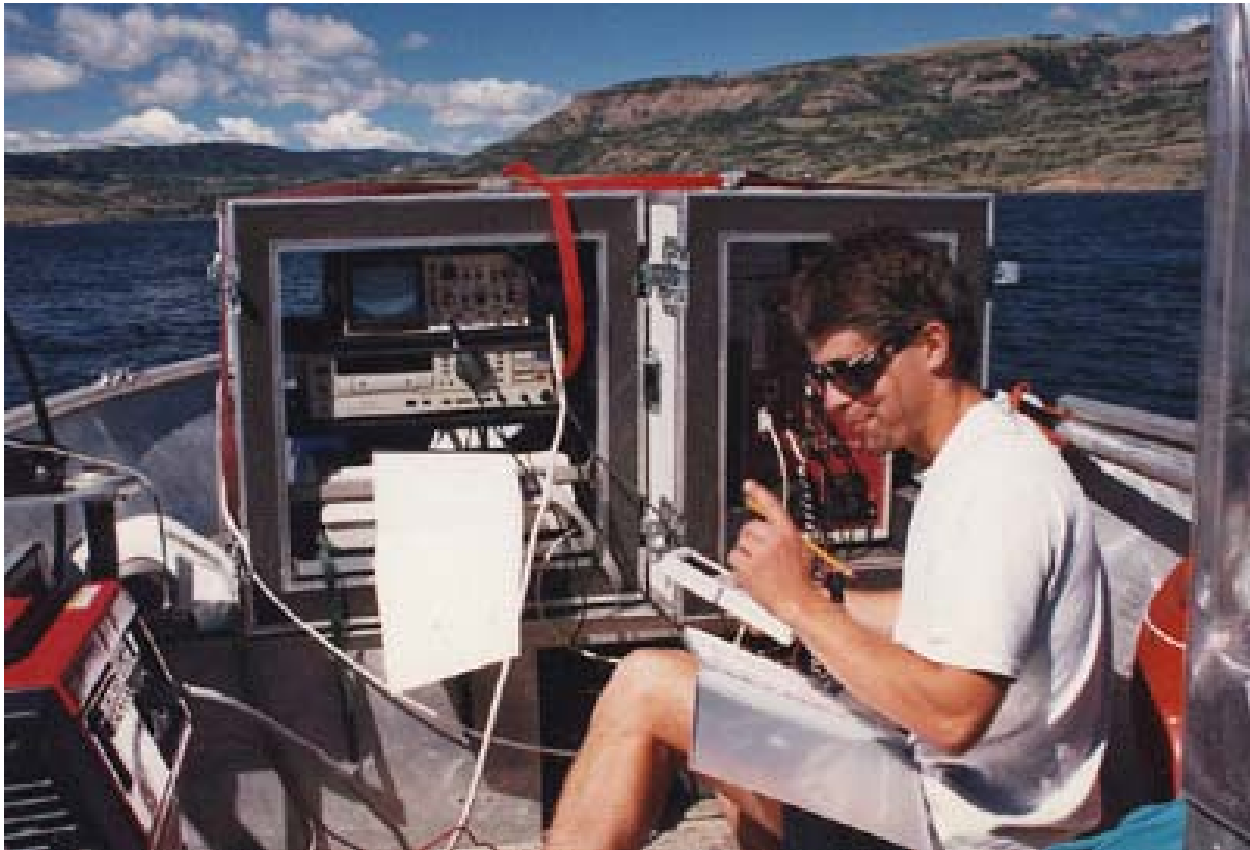


Figure 33. Jason Stockwell operating the split beam hydroacoustics system provided by Pat Martinez, CDOW.

In 2002, we conducted studies of the diel distribution of kokanee by repeatedly sampling a series of transects in Sapinero basin each month during the new moon (Hardiman 2003; Crockett 2004). Hydroacoustic sampling was performed continuously on a 1 km straight line transect at four time intervals during a 24 h cycle from May to August. Hydroacoustic transects were sampled for at least an hour before and after the sunrise (0400 – 0730 hours) and sunset (1830 – 2100 hours), and during mid-day (1130 – 1400 hours), and at night (2200 – 0030 hours). No surveys occurred during 0730 – 1100 hours when other sampling was being performed, or during 1400 – 1800 hours when afternoon winds made hydroacoustic surveys impossible.

Boat locations were recorded every five seconds using a global positioning system and were used to calculate transect lengths. Volumes sampled were determined from effective beam width acoustically sampled, bottom depth, and distance traveled at 5-s intervals summed over each transect. Transect volumes were parsed into 1-m depth strata to investigate fish vertical distribution. Fish densities were determined by counting the individual tracked fish in 1-m depth strata and dividing by the effective volume sampled per strata within each transect thus effectively weighting fish counts by volume sampled.

Fish echoes were discriminated from noise using a fish target-tracking algorithm in Echoscope™. Target selection criteria (Hardiman 2003) were recommended by the manufacturer to suit Blue Mesa Reservoir depths and target sizes of interest and had been used in previous hydroacoustic surveys of the reservoir (Johnson and Martinez 2000). We tested the sensitivity of the fish counts by varying the following target-tracking parameters: echo selection criteria, ping gap, velocity, change in range, and expansion area, and reprocessing the data. We found that the number of fish counted varied by less than 6% (coefficient of variation) and the standard deviation on fish counts by less than 2% (Hardiman 2003), increasing our confidence in the nominal parameter set.

Echoes from age-0 kokanee were classified on the basis of target strength (TS) estimated from observed growth and Love's (1971) equation (Hardiman 2003). Age-0 growth was determined from measurements ($n = 275$) of fish just prior to release from the hatchery and from catches in horizontal gillnets (stretch mesh sizes 1.3, 1.9, and 2.5 cm). Because behavioral changes in fish aspect can cause wide variations in TS (Gunderson 1993), a range of ± 3 dB was applied to the estimated TS of age-0 kokanee. This range corresponded to the average standard deviation of TS of individual tracked fish in our dataset and was consistent with values reported in the literature (MacLennan and Simmonds 1992; Ehrenberg and Torkelson 1996; Ransom et al. 1999).

Targets were classified as adult kokanee (ages 2, 3) in a similar fashion and for age 1 kokanee. When overlap occurred between the ranges (± 3 dB) for age 1 and adult kokanee the overlapping TS range was split equally and allocated to each age category. Age and growth data were not available for adult kokanee in 2002. However, length-frequency histograms of kokanee sampled in vertical gillnets in August 2002, closely matched those observed in 1997 when otolith-derived growth rates were available (Stockwell and Johnson 1999).

To describe temporal patterns in vertical distribution of kokanee we computed median, 25th and 75th percentiles, and the range of depths occupied by kokanee during each sampling interval. To investigate differences in distribution between age-0 and adult kokanee we computed the difference (adult – age-0) for each of the aforementioned statistics. We also tested whether median depths of age-0 kokanee differed from adults using the NPAR1WAY procedure in SAS 8.2, with Bonferroni correction for multiple comparisons.

Sonic Telemetry

Seventeen lake trout were surgically implanted with Sonotronics sonic tags and released on May 14-17, 2001 (Crockett 2004; Figure 34). Nine fish received location-only tags, 5 received depth-sensing tags and 3 received temperature-sensing tags. All implanted fish were sufficiently large to be piscivorous (>540 mm).



Figure 34. *Left:* Pat Martinez, CDOW, surgically implants a sonic tag into a lake trout at BMR. *Right:* Harry Crockett listens for sonic-tagged lake trout with an ultra-sonic hydrophone and receiver.

All the fish were released in Sapinero basin, primarily because during CDOW's spring gill netting the majority of piscivorous lake trout were captured there. All but one of the fish were released near the location where they were captured; the exception was captured in Cebolla basin but released in Sapinero with the others.

Fish were tracked with a Sonotronics USR-96 receiver and hydrophone. By experimenting with fixed tags at various depths and distances we developed the capability to pinpoint the location of fish to within ~100 ft based on qualities of the sonic signal. Fish were tracked using a search grid of fixed listening points at 0.8 km intervals, based on *in situ* testing with fixed tags indicating that this would be sufficient to detect all fish under typical daytime summer noise conditions (Figure 35).

In May-August 2002 we continued monthly tracking of seventeen lake trout tagged in 2001. Five of the tags were depth tags having a 14-month battery life and these batteries expired during the summer; hence, we were unable to track those fish through most of the season.

Mark-recapture

We assisted with a mark-recapture study led by Dan Brauch, CDOW, to estimate lake trout population size and demographic trends (Crockett 2004: Figure 36). In spring (May-June) of 2000, 2001, and 2002, CDOW sampled lake trout using 60 x 2 m, 4.5 cm stretch monofilament horizontal gill nets. The mesh size was chosen to target lake trout > 425 mm TL, the size corresponding to the onset of piscivory in BMR lake trout (Johnson and Martinez 2000).

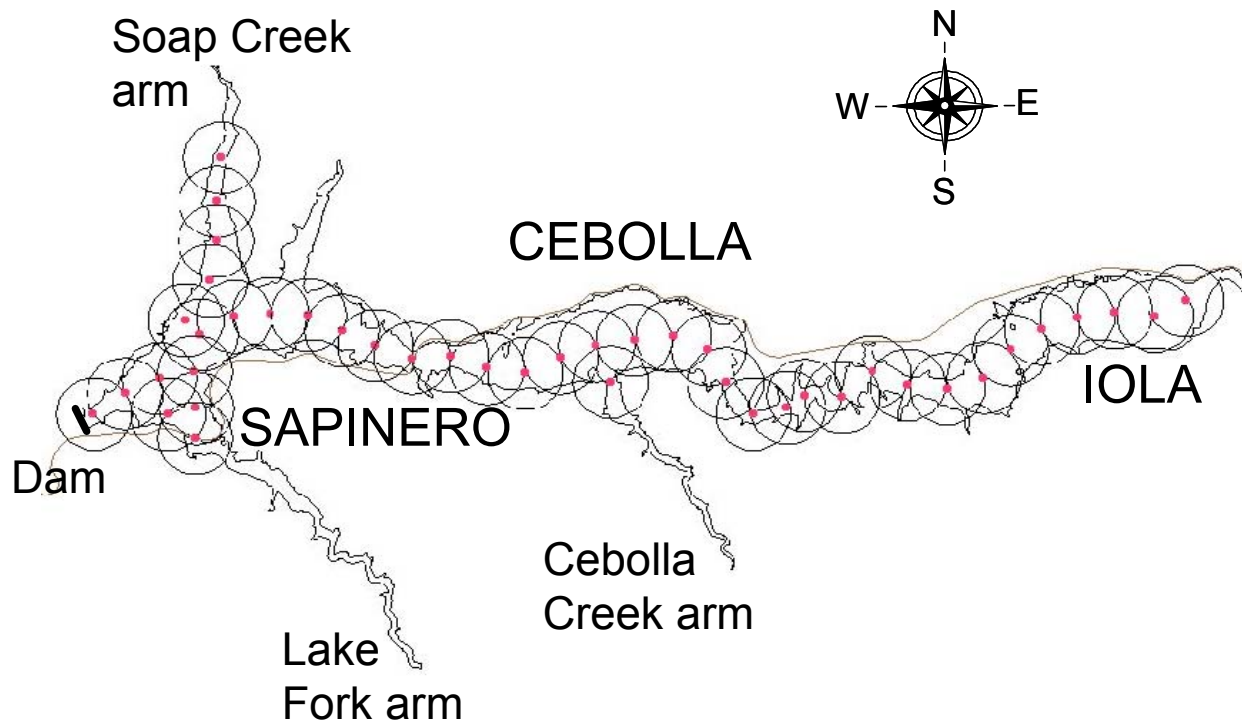


Figure 35. Listening stations (dots) used during the sonic telemetry study. The circles around each dot represent the 100% detection area under typical daytime, summer noise conditions at BMR, as determined by in situ tag testing in summer 2001. Other than the narrow arms, where noise conditions were considerably worse, the searched area included virtually the entire reservoir.

To reduce mortality, soak times were limited to 45 min, and nets were not set at depths greater than 36.5 m, with the majority set at 18 m or less. Captured lake trout were examined for marks, tagged with individually enumerated cinch-up tags, batch-marked as a means of estimating tag loss, and released. Length, weight, and additional relevant data were recorded for lake trout as well as for all by-catch.

Results of the mark-recapture study were used to develop Cormack-Jolly-Seber (CJS) models for model selection (Crockett 2004). The CJS structure is well-suited to open populations (Lebreton et al. 1992; Franklin et al. 2000) because it can be used to estimate abundance and survival. A candidate set of models was developed to include variables, such as fish size and time, that may be related to lake trout demographic parameters. Akaike's Information Criterion corrected for small sample bias (AICc) was used to select the most parsimonious models (Burnham and Anderson 2002). The computation-intensive processes required to select the most suitable model for estimating lake trout abundance was facilitated by the use of Program MARK (White and Burnham 1999). Population size ($\hat{N}$) was estimated by $n_i / \hat{p}_i$ where n_i = number of individuals captured on the i^{th} occasion and $\hat{p}_i$ = estimated capture probability;

“population” in this case denotes lake trout large enough to be at risk of capture, roughly those of piscivorous size, ≥ 425 mm.



Figure 36. Dan Brauch (CDOW) releases a lake trout that was tagged with a Floy cinch-up tag for the mark-recapture study.

Netting was conducted from ice-out until early summer, a season during which lake trout are often particularly mobile and found in shallower water than at most other times of year (Martin and Olver 1980; D. Brauch, CDOW, unpublished data). Sampling effort was distributed roughly equally across the reservoir's three basins.

Within each basin, the method of determining net locations was similar each spring. At least one net was set on every bar with a relatively flat bottom and depth < 25 m to reduce sampling mortality from air bladder distention. Subsequently, additional nets were set in “hot spots” that had yielded the highest catch per unit effort of lake trout on the first pass to maximize the number of fish marked.

An additional netting session was conducted in October-November 2001. At this time of year lake trout move into shallower water to spawn. Methods for the fall netting effort were the same as for the spring, except that net locations were randomized (Johnson et al. 2002a). We used a Geographic Information System (GIS) to grid each basin into 100

m² cells and identify all suitable cells, defined as having slope < 0.2 and depth < 25 m. A subset of these cells was then selected at random for netting.

Abundance estimates derived from the mark-recapture experiments were compared to estimates from hydroacoustics and methods to reduce the bias in those estimates were developed (Crockett 2004).

Age, Growth and Condition

Growth curves for age-0 kokanee were computed by fitting linear regressions to fish total lengths as a function of time. Measurements included fish measured in the hatchery before stocking, and fish sampled in the reservoir in 2001 and 2002. ANCOVA was performed to determine if growth differed by year. These growth regressions were used to estimate size cutoffs for age-0 kokanee in hydroacoustic surveys. The estimated length of age-0 kokanee on each survey date was converted to a target strength (TS) and that value was used to partition age-0 kokanee targets from other echoes in the hydroacoustic data. Love's equation (Love 1971) was used to determine TS in decibels given a length for each sample date. A power function was fit by regression to the length-weight sampling data for 2001 and 2002 in order to estimate growth in weight.

Otoliths were collected from kokanee, lake trout, rainbow trout, and brown trout, and were provided to Pat Martinez, CDOW, for analysis. We took scale samples from age-1 and older kokanee and rainbow trout sampled in vertical gill nets, and from a length-stratified sample of fish obtained from anglers. Scales were pressed onto acetate slides and examined in a microfiche reader at $\geq 36\times$. Each scale was read by two trained scale readers. Annuli were determined by the presence of cutting over and scales were measured to develop a scale-body length relationship. We transformed the scale/body length data and fit a Fraser-Lee function that we used in backcalculations (Everhart and Youngs 1981). Scale samples obtained by CDOW in 1989, and scales obtained by CSU in 1994 and 1996 were read by CSU undergraduate Dave Shuler. Historic data on kokanee backcalculated length at age were obtained from Wiltzius (1971, 1974).

A growth function for lake trout was computed by fitting a von Bertalanffy model to lengths at age determined from otoliths aged by Pat Martinez (CDOW):

$$L_t = 1154(1 - \exp(-0.1026(t + 0.7885))) \quad n = 134, r^2_{\text{adj}} = 0.721$$

where L_t is length at age t . Weight at age t was estimated using the von Bertalanffy model and the length-weight regression of Johnson and Martinez (2000).

Body condition of kokanee (Hyatt and Hubert (2000)), rainbow trout (Anderson and Neumann (1996)), brown trout (Hyatt and Hubert (2001)) and lake trout (Anderson and Neumann (1996)) was estimated from relative weight (W_r). Standard weight (W_s) was computed with the following formulae (value in parentheses is the minimum applicable size, TL):

$$\text{Kokanee} \quad \text{Log}(W_s) = 3.033 * \text{Log}(TL) - 5.062 \quad (120 \text{ mm})$$

Lentic rainbow trout	$\text{Log}(W_s) = 2.990 * \text{Log}(\text{TL}) - 4.898$	(120 mm)
Lentic brown trout	$\text{Log}(W_s) = 3.194 * \text{Log}(\text{TL}) - 5.422$	(140 mm)
Lake trout	$\text{Log}(W_s) = 3.246 * \text{Log}(\text{TL}) - 5.681$	(280 mm)

A length-weight relationship for lake trout was developed from data gathered in the 1990s, and 2000 pooled with state record fish caught since 1998. The relationship did not differ from the one presented in Johnson and Martinez (2000):

$$\text{Length} = (7.8906\text{E-}08) * \text{weight}^{3.7651} \quad n = 8, r^2 = 0.987$$

Overall, it appears that the length-weight relationship of lake trout in BMR has changed little since the mid 1990s. A more explicit analysis using ANCOVA to test for the effect of time on the relationship would be a reliable evaluation of this finding.

Diet Analysis

Stomachs were collected from age-0 kokanee obtained in midwater trawl hauls. Gut contents were removed and placed in a small, gridded Petri dish. Prey were sorted into major groups and the proportion of each group by volume and by number were determined. Stomach samples of age-1 and older kokanee were collected from vertical gill net catches during June, August, and October of 1994-1997, and by sampling the angler catch approximately biweekly (during weeks when routine zooplankton samples were taken) at cleaning stations at each lake basin. Stomachs were excised and preserved in 10% formalin. Kokanee samples were grouped into three size classes (<250 mm, 250-349 mm, or >349 mm); approximately five stomachs from fish of each size class from each date and sampling location were aggregated for analysis.

Proportions (by volume) of fish, macroinvertebrate, and zooplankton were visually estimated. The zooplankton contents were diluted to a density that would yield approximately 20-30 measurable zooplankters, and one aliquot was placed in a Sedgwick-Rafter cell. All identifiable organisms were counted. Copepods were counted but not identified to a lower taxonomic level because of their rarity in stomachs. Cladocerans of the genus *Ceriodaphnia*, *Bosmina*, and *Diaphanosoma* were lumped into a group. Daphnids were identified to species if possible. The first 10 specimens of each *Daphnia* species encountered were measured. When there was only one species of *Daphnia* present then the first 20 individuals of that species was measured. Only *Daphnia* with an intact carapace were measured.

Mean diet composition of lake trout was determined for five size classes: <200 mm, 200-425 mm, 425-600 mm, 601-900 mm, and >900 mm TL. These size classes correspond to important life stanzas in the trophic ontogeny of lake trout (Johnson and Martinez 2000). Small lake trout (size class I) were collected using small mesh, horizontal, gill nets set on the bottom from Cebolla basin during 11 July through 16 July, 2002. One 46 x 1.8 m swedish gill net with 1.3, 1.9, and 2.5 cm square mesh and two 30 x 1.8 m nylon gill nets with 2.5 cm square mesh were used. The nets were set at three sites at depths of 20 m each, a few hours prior to sunset (approximately 1830 h).

Nets were fished overnight and retrieved at approximately 800 h the following morning. Nine lake trout were captured by this method and collected for stomach analysis. Upon capture, fish were stored on dry ice in order to prevent further digestion and returned to the laboratory for analysis.

A shallow incision was made from the vent to the isthmus, the stomach (esophagus to pyloric sphincter) was removed and the contents placed in a Petri dish. Stomach contents were diluted with enough ethanol to distribute the material evenly around the Petri dish. Prey items too small to be weighed were counted. Zooplankton were counted but were not identified because of the advanced state of digestion of all the samples; otherwise we identified prey to the family or genus level. Total length of prey items were measured using an ocular micrometer on a stereoscope. Mass of each prey item was estimated from length:mass relationships from the literature (Wilhelm and Lasenby 1998; Burgherr & Meyer 1997). Diet overlap between small lake trout and kokanee was evaluated with an overlap index (Schoener 1971; Bowen 1996):

$$C_{xy} = 1 - 0.5 (\sum |p_{xi} - p_{yi}|) = \text{index value}$$

p_{xi} = proportion of food type i used by species x
 p_{yi} = proportion of food type i used by species y

Procedures differed for larger fish (Johnson et al. 2002a). Stomach samples were gathered from lake trout size classes II-V by gastric lavage in living fish or by stomach dissection from anglers' creels and fish inadvertently killed in gill nets. Samples were preserved in 10% formalin until they could be examined in the laboratory. We identified prey organisms to the lowest taxonomic level practical using external and internal morphological characters. Prey taxa included: kokanee, rainbow trout, unidentified salmonid, yellow perch, longnose sucker, white sucker, unidentified fish, chironomids, and crayfish.

Backbone lengths of prey fish were measured when possible. For lake trout sampled during April-October 1994-1997 we estimated the proportion of the stomach contents (by volume) consisting of fish and macroinvertebrates by eye and then counted all prey. Diet was computed on the basis of frequency of occurrence, excluding macroinvertebrates smaller than crayfish. It was assumed that diet composition on the basis of frequency of occurrence of large prey approximated diet expressed on a mass basis to facilitate comparisons with later samples. For samples collected from gill nets in 2001 we weighed the contents of each stomach and each prey item (fish and crayfish) and computed diet composition on a mass basis.

Stable Isotope Analysis

Zooplankton were sampled during May-October 1997 with a 500 μm simple plankton net from the top 10 m of the water column in summer. This net was highly selective for *Daphnia* > 1.0 mm (Stockwell et al. 1999), the size fraction preferred by planktivorous fish (O'Brien 1979). All invertebrate samples were frozen in the field and stored frozen until they could be dried and processed. No samples of terrestrial insects were available.

Tissue samples were taken opportunistically from fish captured in experimental vertical gill nets fished in Blue Mesa Reservoir during May through August, 1997 and May – October 2002. Additional samples were obtained from fish captured during electrofishing surveys conducted by Pat Martinez (CDOW) in 2002. Fishes were measured and weighed, and scales and/or otoliths were removed for aging. One cm³ dorsal muscle plugs were removed from each fish and placed on dry ice. A sample of hatchery pellets fed to kokanee and rainbow trout was also analyzed for stable isotopes.

Analysis methods generally followed those used by Johnson et al. (2002) and Martinez et al. (2001). We dried all samples at 60°C for 72 hours and then ground them with a mortar and pestle to a flour-like consistency. A 1-2 mg sample of each tissue was placed in tin cup and processed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in a VG Isochrom mass spectrometer with Carlo-Erba NA1500 elemental analyzer at the Colorado State University Natural Resources Ecology Laboratory. The quantity measured in stable isotope analysis, δ , is the relative difference between isotope ratios of the sample and a standard:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} * 10^3$$

where: δ (‰) is the per mil difference (parts per thousand), R_{sample} is the isotopic ratio of the sample, and R_{standard} is the isotopic ratio of the standard.

Standards employed were: Vienna Pee Dee Belemnite for $^{13}\text{C}/^{12}\text{C}$ and atmospheric N_2 for $^{15}\text{N}/^{14}\text{N}$ (Lajtha and Michener 1984). The mass spectrometer was calibrated at the start of each session and after every 10 samples using a glycine standard.

Consumption Demand

Consumption demand by lake trout in BMR was computed in 2000 (Johnson and Martinez (2000) and revised in 2003 (Johnson and Oplinger 2003) when new data became available. Revised estimates of size at age and diet were input to Fish Bioenergetics 3.0 (Hanson et al. 1997) to estimate per capita consumption of prey by lake trout. This bioenergetics model for lake trout was recently corroborated by Madenjian and O'Connor (1999). Simulations were performed for a single fish of a given size, for one year duration. Three diet compositions were used that corresponded to the following age/size groups: 1) age-5 and age-6 (425-600 mm TL size class), 2) ages 7-13 (601-900 mm TL) and 3) ages 14+ (> 900 mm TL). We used the same thermal experience as in Johnson and Martinez (2000), which assumed that lake trout behaviorally thermoregulated to 10°C when that temperature was available. These simulations also accounted for energy lost during spawning (6.8% for males and females, occurring on day 300). Revised diet, size at age, abundance and mortality data were input to the bioenergetics model to estimate consumption of prey by each lake trout cohort, age-5 and older.

Creel Survey

Creel surveys were sponsored and administered by CDOW and conducted by NPS personnel during spring and summer, 1993-2003. The survey was conducted according to standard CDOW protocols. The survey was of a stratified random design with weekdays and weekend/holidays as strata; separate estimates of creel parameters were computed by strata. Effort data were collected using the “bus route” method and instantaneous counts were made at pre-selected view points around the reservoir. Angler/boat counts times were randomized and all counts were completed during daylight hours. Catch and use information was gathered from angler interviews at access points (shore fishing locations and boat ramps). Effort estimates should be viewed as minimum estimates since there are locations in the reservoir that can't be observed by the creel clerks (e.g., arms and bays).

Methods-- Laboratory Experiments and Modeling

Models that link environmental characteristics with predator feeding rates are powerful tools for exploring the influence of food availability and foraging conditions on the behavior and growth of fishes. For kokanee and other visual feeders, including light level explicitly into the functional response is important because light modifies a predator's detection of prey, search time, and feeding rate, and because fish experience tremendous temporal and spatial variation in the light environment. With a bioenergetics-based foraging model (BBFM) that incorporates multiple environmental characteristics, we have a powerful predictive tool for forecasting how fish growth and behavior respond to environmental perturbations such as temperature and water clarity changes resulting from climate change or dam operations.

Between 1998 and 2000 we performed laboratory feeding experiments with age-0 kokanee foraging on zooplankton prey (Figure 37, 38) to calculate an improved feeding rate function (functional response) for a BBFM. Feeding rates were calculated as a function of both prey density and light level. After the bioenergetics model was enhanced with the new functional response and a user interface, it was used to determine whether or not there was a bioenergetic component to diel vertical migration (DVM) patterns exhibited by age-0 kokanee. The model was also employed to examine changes in daily growth and predation risk to age-0 kokanee as a result of both short-term climate effects (e.g., drought) and dam operations (i.e., the installation of a temperature control device, TCD).

Kokanee Foraging Behavior

Laboratory feeding trials with age-0 kokanee presented individual fish with a range of *Daphnia* densities at three different light intensities (Koski 2000; Koski and Johnson 2002). One hundred kokanee fingerlings (age 2 months, mean mass 3 g, 4.5 cm total length) were obtained from Roaring Judy state fish hatchery near Gunnison, Colorado three months prior to the start of experiments. *Daphnia pulex* and *D. galeata* ranged in size from 0.73 to 1.80 mm in length and were collected and reared in filtered river water in 38 L tanks at room temperature.



Figure 37. Marci Koski conducted feeding trials with age-0 kokanee for her M.S. thesis at CSU (Koski 2000). Here she counts zooplankton that remained in the arena after the completion of a feeding trial.

Experimental arenas were round plastic containers (bottom diameter = 48 cm, top diameter = 61 cm, height = 38 cm), painted a medium shade of gray inside. Arenas were filled with 35 L well water and was aerated during the acclimation period and feeding trials to aid in distribution of *Daphnia* in the arena. Light was manipulated by varying the number of screens in front of 91.5 cm fluorescent bulbs, which were suspended above the arenas so that light was reflected off the arena house ceiling into the arena (roughly 75 cm below). Three light levels were used in the feeding trials: 0.1, 15, and 30 lux.

A generalized linear models procedure (PROC GLM in SAS) was used to identify any covariates (fish mass, temperature, acclimation time, and *Daphnia* size) that were potentially important when data were classed by light level. Two data sets (low light and high light) were created by pooling sets of trials for which light level was not a significant factor (i.e., 15 and 30 lux light level feeding rates were not significantly different).



Figure 38. Tori Stecklein, CSU undergraduate, assisted with kokanee feeding trials by adding zooplankton into the arenas through the feeding tube. Experiments were monitored using a video camera and infrared light source (photo: M. Koski).

To fit functional response curves, linear and nonlinear analyses were performed for both the low light and high light data sets using PROC GLM and NLIN in SAS. Nonlinear curves were fit to the equation

$$(1) \quad N = \frac{(\beta_0 \cdot V)}{(\beta_1 + V)}$$

where N is consumption rate of the predator (*Daphnia*/min), V is prey density (*Daphnia*/L), β_0 is maximum consumption rate (*Daphnia*/min), and β_1 is the prey density (*Daphnia*/L) at which consumption rate reaches half its maximum (Real 1979). While trials were not conducted below 3 *Daphnia*/L, the intercepts for all functional response curves were forced through zero because kokanee do feed at extremely low prey densities (Hyatt 1980) and no suggestion of a negative intercept existed.

We calculated r^2 values for all functional response curves as the ratio of the explained sum of squares (ESS) over the corrected total sum of squares. Akaike's Information Criterion (AIC_c , AIC corrected for small sample size) was also used to help determine which functional response model (linear vs. nonlinear) was most appropriate for each data set. AIC/AIC_c is a powerful tool used for model selection and is applied on a relative scale where the most appropriate model is the one with the lowest AIC_c value

(Burnham and Anderson 2002). Holling's disc equation (1959; 1966; Houck and Strauss 1985) was also used to fit the type II functional response using PROC NLIN:

$$(2) \quad N = \frac{(a \cdot V)}{(1 + a \cdot T_h \cdot V)}$$

In this equation, T_h is handling time (min/prey) and a is rate of successful search, which is equal to the volume of foraging habitat a predator can search during a unit of time (volume/time, in L/min) (Madenjian and Carpenter 1991). Equations 1 and 2 can be linked by the following relationship (Gotelli 1998):

$$(3) \quad \beta_0 = \beta_1 \cdot a = \frac{1}{T_h}$$

Equation 1 was used to obtain values for β_0 and β_1 ; we then used PROC NLIN to calculate handling time and rate of successful search for the high light model with equation 3.

Additionally, PROC GLM and PROC MIXED SAS procedures were used to detect significant differences in *Daphnia* size distributions before and after the feeding trials, and between light levels. To do this, the average difference in *Daphnia* lengths was first determined by comparing pre- and post-trial measurements for each feeding trial. Then, PROC GLM was used to compare the change in average *Daphnia* size across light levels. Finally, PROC MIXED was used to compare *Daphnia* lengths under different combinations of light level vs. pre-trial or after-trial *Daphnia* measurements.

Simulation Modeling

Forecasting the effects of changes in dam operations on fishes requires a comprehensive understanding of the factors that drive behavior and dictate growth and mortality. We configured a BBFM for kokanee (Koski 2004; Stockwell and Johnson 1997, 1999) to explain observed growth and behavior and to predict how these factors might change as their physicochemical environment changed. The BBFM was originally developed by Bevelhimer and Adams (1993). It operates on a 30-min timestep, and uses inputs of temperature and prey density profiles, and fish mass, to evaluate kokanee growth as a function of migration strategies, feeding durations, and prey handling times. The model is based on an energy budget and a functional response (Figure 39), and therefore can directly evaluate the interplay between energy intake and physiological costs in relation to diel vertical migration. An attraction of the modeling approach is that it could be readily applied to a range of systems exhibiting different thermal, resource, and predation conditions. Thus the model provides a framework for evaluating how kokanee respond to different spatial configurations of their environment.

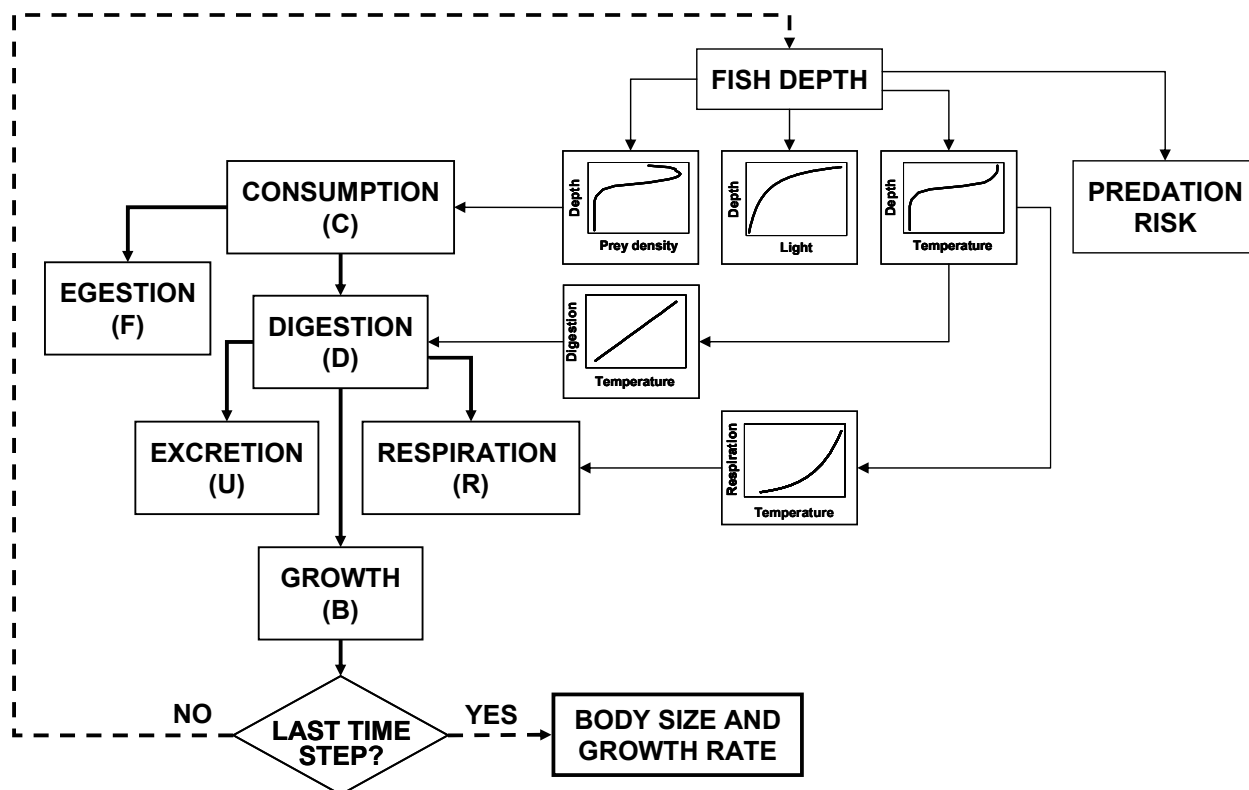


Figure 39. Model flowchart showing the computational steps in the bioenergetics-based foraging model developed by Stockwell and Johnson (1997) and enhanced by Koski (2004). Prey density, temperature and light intensity are depth-specific environmental factors that are determined by the depth at which the modeled fish is located and the physical characteristics of the reservoir input to the model.

Results from our laboratory feeding trials were used to enhance the BBFM's functional response, a critical link between food density and feeding rate of kokanee. When all data were grouped together and classed by light level in a generalized linear model, only light level ($p < 0.0001$) and *Daphnia* density ($p < 0.0001$) were significant factors in predicting feeding rate. Highest feeding rates were obtained with the intermediate light level, 15 lux, but were not significantly different from rates at 30 lux (least squares means test in SAS, $p = 0.28$) so these two sets of trials were combined to form the high light data set. Feeding rates obtained at the 0.1 lux light level (the low light data set) were significantly lower than in both the 15 and 30 lux light level trials (least squares means test, $p < 0.0001$).

We fit linear and nonlinear functional response curves to both of the data sets to obtain our two final models (Figure 40). We selected a different functional response shape for each based on AIC_c model selection. A linear, type I model with its intercept forced through zero was most appropriate for the low light model (Figure 40a). While the linear model predicts an infinitely high maximum consumption rate, we have no data that indicates what type of functional response would occur at extremely high prey densities; therefore, the type I functional response should be adequate to describe feeding rates

at low light over the range of *Daphnia* densities used in our feeding trials. A nonlinear type II functional response fit best for the high light data (Figure 40b). The AIC_c value for the nonlinear model was much lower than that of the linear model when intercepts were forced through zero and the R² value for the nonlinear model (0.58) was greater than that of the linear model (0.42).

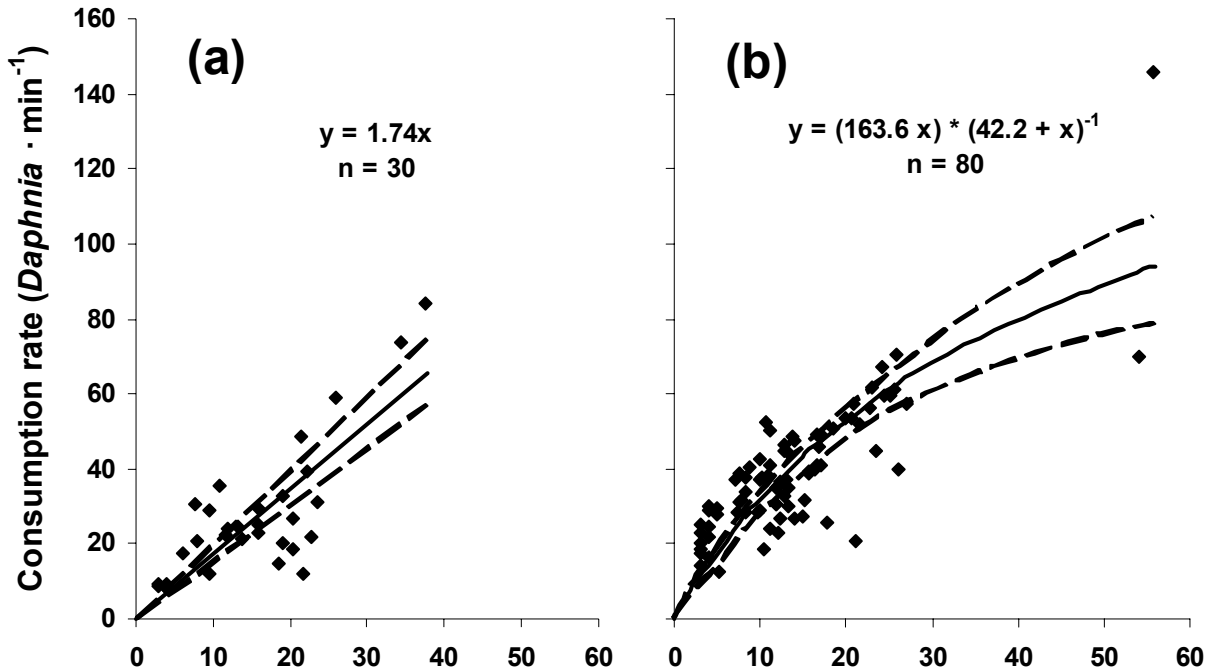


Figure 40. Functional response models for age-0 kokanee developed from laboratory feeding experiments. The low light (0.1 lux) model (a) was fit using a type I linear regression with an intercept forced through zero. The high light (15-30 lux) model (b) was fit using a type II nonlinear function. The dashed lines are 95% confidence intervals around the mean.

Using the type II functional response model obtained at the high light level and the relationships in **equation 3**, we calculated rate of successful search (a) and handling time (T_h) to be 3.86 L/min ($p < 0.0001$) and 0.36 seconds/*Daphnia* ($p < 0.0001$), respectively.

Changes in light level were associated with a shift in foraging mode (that is, fish utilized a different functional response as a result of light availability). Our 15 lux and 30 lux light levels (in the high light model), which are very similar to each other relative to the diel range of light intensities in nature, fall just above the lowest light level required to obtain maximum feeding rates (Ali 1959). Research in other ecosystems has shown that kokanee and juvenile sockeye feed mostly heavily during crepuscular periods (Eggers 1978; Bevelhimer and Adams 1993), and our 15 and 30 lx light levels correspond to light available in the epilimnion during these times of the day. The 0.1 lux level falls below the threshold for maximum feeding rates, but is still within the range for some visual feeding, as well as other means of prey detection (e.g., through the lateral line system or olfactory cues). Due to the linear relationship between density and

consumption rate, consumption rates might be more affected by chance encounters with *Daphnia* which happen to drift in front of the kokanee, a relationship that is very much a function of prey density. In our feeding trials we observed that at high light intensities (15 and 30 lux), fish actively pursued prey, but at the low light level, fish spent a greater proportion of their time remaining relatively still and striking at *Daphnia* that drifted in front of their snouts. Furthermore, at the high light levels, kokanee selectively fed on larger *Daphnia*; at the low light level, little selectivity occurred reinforcing the notion that prey consumption was largely based on random encounters.

There was no significant difference ($p = 0.13$) in average *Daphnia* length between light treatments before feeding trials began, confirming that *Daphnia* used in feeding trials at both light levels were of the same size distribution (the average length of *Daphnia* at the start of the 0.1 and 15 lux trials was 1.47 and 1.42 mm, respectively). After the feeding trials, the remaining *Daphnia* were significantly smaller than those at the start of the trial at both 0.1 and 15 lux (1.37 mm with $p = 0.0007$, and 1.05 mm with $p < 0.0001$, respectively), suggesting that larger *Daphnia* were eaten preferentially over smaller ones. This size selectivity was also clearly demonstrated from gut content analysis of fish sampled from BMR. In addition, the mean length of leftover *Daphnia* at 15 lux was significantly lower than that at 0.1 lux by 0.32 mm ($p < 0.0001$); that is, the difference between initial and final *Daphnia* lengths in trials was much greater at 15 lux (Figure 41).

Kokanee were particulate feeders that selectively chose larger *Daphnia* (Koski et al. 2003). We observed our fish striking at individual prey items, but no filter feeding was detected upon reviewing videotaped feeding trials. If age-0 kokanee were filter feeding, their smaller inter-gill raker spacing would also retain smaller prey items; but because smaller *Daphnia* remained after our feeding trials filter feeding probably did not occur. Furthermore, changing the foraging environment by varying light level caused changes in the degree of size-selectivity. This indicates that kokanee were distinguishing prey items by size; such behavior would not necessarily be expected to occur in planktivores that filter feed.

The Stockwell and Johnson (1997) model predicted the shift in functional response shape in relationship to light level (Figure 42). A fish's reaction distance (and therefore search volume) will increase with light level. When reaction distance was manipulated using their model, functional response shape gradually changed from a type II to a type I functional response as reaction distance decreased (which will happen as light decreases). Functional responses at low light levels then, close to the minimum feeding threshold, will resemble straight lines; as light level increases, curvature will appear because feeding rate is limited by search time at low prey densities and handling time at high prey densities instead of random encounters with prey.

Our functional response models should be suitable for application in oligotrophic, mesotrophic or well-mixed systems where kokanee experience zooplankton patch densities of less than 55 *Daphnia*/L. However, because wild kokanee probably seek patches of prey that can have an order of magnitude higher densities than the average

concentration measured by sampling gear (Pinel-Alloul 1995; Folt and Burns 1999), feeding trials at prey densities much higher than the 55/L we used may be necessary to accurately predict kokanee feeding rates at very high prey densities.

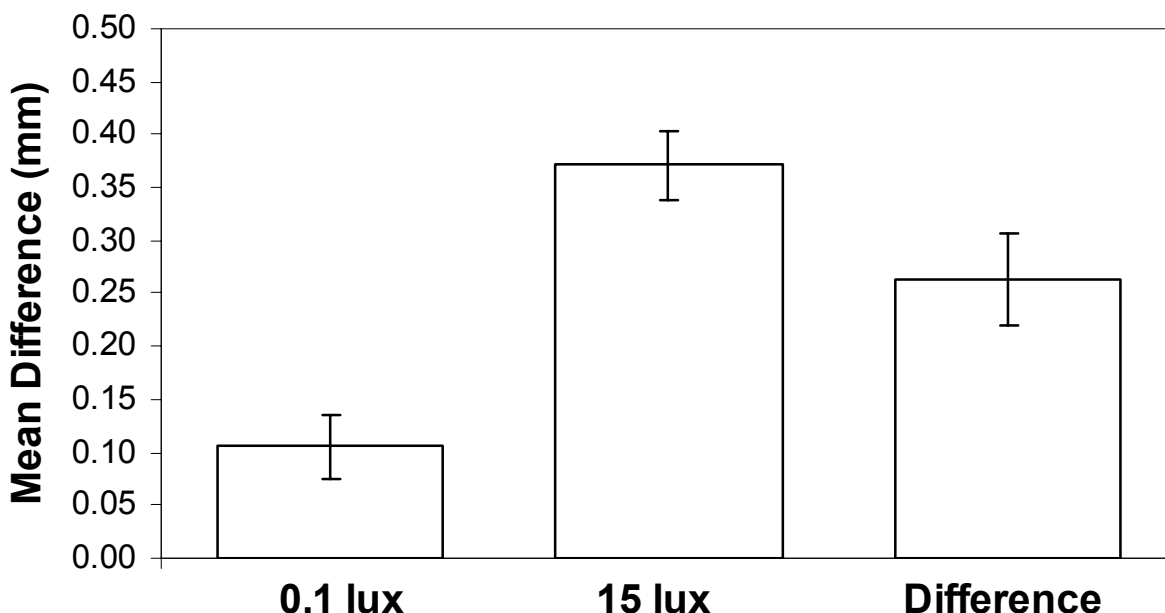


Figure 41. The mean difference ($\pm$ SE) in *Daphnia* lengths (mm) in feeding arenas measured before and after feeding trials conducted with age-0 kokanee at two light intensities, and the mean difference between 15 lux and 0.1 lux before-after differences. All differences were significant at $p < 0.001$.

The original versions of the BBFM were implemented in a Quattro Pro spreadsheet. Because of the complexity of the model and the large number of inputs and variables, using the model was extremely tedious and not suited to others unfamiliar with the intricate details of the model. Thus, we developed a user-friendly graphical user interface (Figure 43; Koski 2004) to facilitate use of the model by experts and by others interested in simulating kokanee growth and behavior.

Modeling Kokanee Diel Vertical Migrations

We used the BBFM to simulate daily growth of age-0 kokanee to evaluate the extent to which bioenergetic considerations drive their diel vertical migrations (Koski 2004). All simulations used data collected during June, July, and August 2002 by Hardiman et al. (2004; Table 4). Hydroacoustic surveys and gill nets were used to obtain information on DVM patterns and fish growth. We used the median monthly depth of age-0 kokanee determined by hydroacoustics to create generalized DVM patterns which were used for baseline simulations. To obtain estimates of kokanee growth rates we fit an exponential growth function to observed weights. We calculated W_t (fish mass at time zero for each day) and daily growth increment for June 5, July 10, and August 6 and

used these data to calibrate baseline simulations (through use of a zooplankton calibration factor).

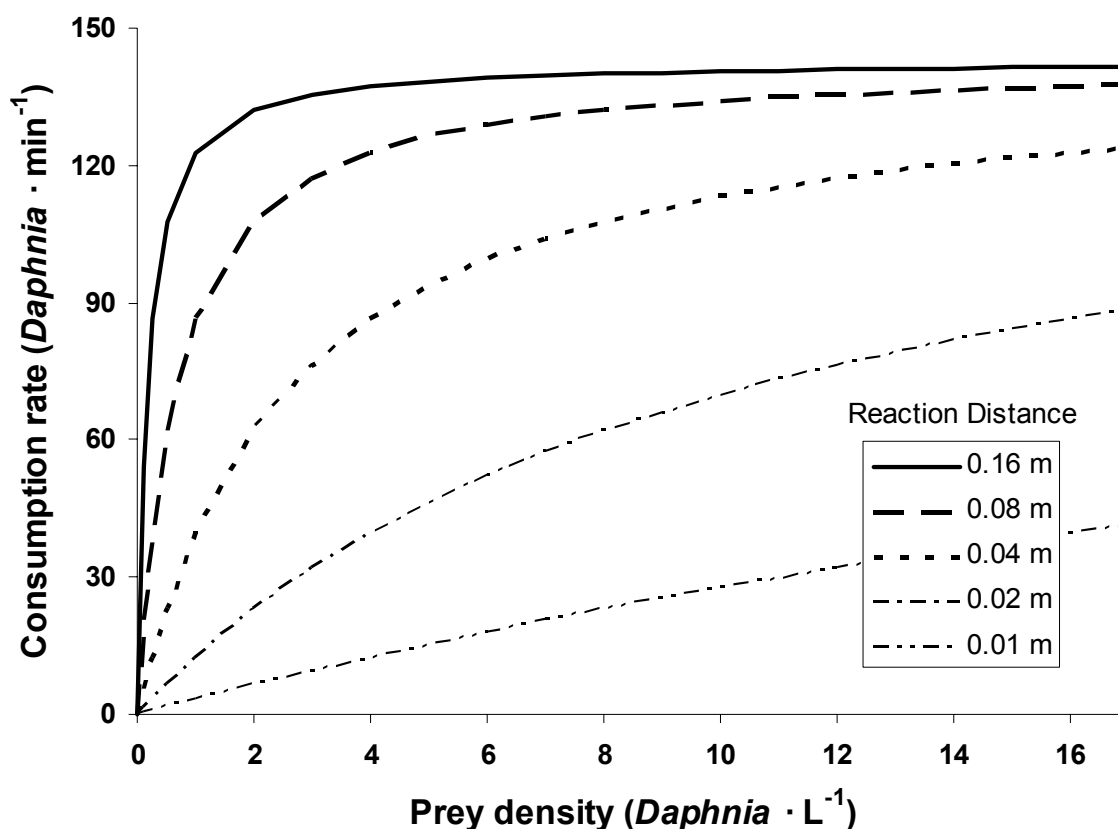


Figure 42. Functional response curves predicted with the Stockwell and Johnson (1997) model using a range of reaction distances and a 5 g kokanee feeding at 10 °C with a handling time of 0.36 seconds/*Daphnia*. As reaction distance increases (e.g., light level increases or turbidity decreases), a type II functional response is produced; with lower reaction distances the type II response shifts towards a type I functional response.

These three baseline simulations represent the observed movements of age-0 kokanee and their growth for each date; these are the simulations to which all other simulations were compared. Additional data collected for model inputs included secchi depths, temperature profiles, and zooplankton densities, which were collected in 0-5, 5-10, 10-15, and 15-30 m depth strata. Because zooplankton were not collected below 30 m, we used a negative exponential for each of June, July, and August to calculate *Daphnia* densities below 30 m using average monthly *Daphnia* densities collected from BMR in 1994-1997 and 2002.

New to this version of the model is the light-dependent functional response described in the previous section. In addition to the above information, the user must also provide a geographic location, time zone, and date so that a sub- model (Janiczek and DeYoung

1987) can calculate incident light levels. Using secchi depth, a light extinction coefficient (Idso and Gilbert 1974) is calculated (equation 4). This enables the model to calculate light level at any depth (equation 5), using the relationship described by Horne and Goldman (1994):

$$(4) \quad \eta = 1.7 / z_{sd}$$

$$(5) \quad I_z = I_0 / e^{-\eta z}$$

where η is the light extinction coefficient, z_{sd} is secchi depth in meters, I_0 is incident light level (lux), z is fish depth (m), and I_z is the light level at depth z . If light level experienced by the fish was below 0.001 lux we assumed it was too dark for the fish to feed (Ali 1959). If light level was between 0.001 and 3.4 lux the model selected the type I functional response for food consumption rate, and if light level was above 3.4 lux the fish utilized a type II functional response. The model then calculated feeding rate as a function of prey density at that depth.

The screenshot shows the 'KokanEat' application window with the 'Simulation' sub-window active. The 'Predator and Prey' tab is selected, displaying input fields for fish and prey parameters. Below these are settings for a migration strategy across five time periods.

	Start Period 1	Start Period 2	Start Period 3	Start Period 4	Start Period 5
Time	00:00	04:30	11:00	13:00	18:00
Depth	7.5	7.5	7.5	7.5	7.5
Feeding	☒ Yes/No	☒ Yes/No	☒ Yes/No	☒ Yes/No	☒ Yes/No

Figure 43. Screen shot showing one of the pages in the user-friendly version of the bioenergetics-based foraging model (Koski 2004) that was used to examine how physical conditions in the reservoir affected kokanee growth, behavior and risk of predation.

Table 4. Model inputs for each simulation date. Fish mass on each date was 4.31, 8.65, and 13.13 g, secchi depth was 5.1, 7.0, and 5.6 m, and the zooplankton calibration factor was 2.1, 2.4, and 12.5 in June, July, and August, respectively. Temperature and *Daphnia* densities (number/L) were averaged by 5 m depth intervals.

Depth	<u>June 5, 2002</u>		<u>July 10, 2002</u>		<u>August 6, 2002</u>	
	Temp. °C	<i>Daphnia</i> Density	Temp. °C	<i>Daphnia</i> Density	Temp. °C	<i>Daphnia</i> Density
2.5	13.9	13.3	19.6	11.2	19.4	6.7
7.5	12.2	6.2	18.1	8.4	19.1	7.4
12.5	10.0	11.1	14.2	2.7	18.1	1.8
17.5	9.0	2.4	10.8	0.66	14.7	0.21
22.5	7.9	2.4	8.1	0.66	10.9	0.21
27.5	6.8	2.4	7.2	0.66	8.3	0.21
32.5	6.3	0.57	6.7	0.52	7.2	0.06
37.5	6.0	0.46	6.3	0.42	6.7	0.04
42.5	5.7	0.38	5.9	0.34	6.3	0.03
47.5	5.5	0.32	5.6	0.29	6.0	0.03
52.5	5.4	0.27	5.6	0.24	5.9	0.02
57.5	5.1	0.23	5.5	0.21	5.8	0.01

We calibrated the new model with the light-dependent functional response to the conditions of BMR in 2002. Average *D. pulex* densities measured with a Clark-Bumpus sampler underestimated kokanee growth. This probably occurred because zooplankton are very patchily distributed in the environment (Pinel-Alloul 1995; Folt and Burns 1999), and kokanee likely seek patches of zooplankton in which to forage. Therefore, the average zooplankton density measured by a Clarke-Bumpus sampler is probably very different from the zooplankton density that is experienced by foraging kokanee. We corrected for patchiness by multiplying average *Daphnia* density by a calibration factor so that simulated kokanee growth in the three baseline simulations matched observed daily growth on each sampling date.

After calibrating the model using the three baseline simulations, we ran two suites of simulations that utilized varying DVM behaviors. For both suites of simulations on a given date, fish position was the only variable that changed among simulations. Fish depth was adjusted by 5 m increments down to 60 m so that fish could be positioned at depths of 0-5 m (or 2.5 m), 5-10 m (or 7.5 m), and so on down to 55-60 m (or 57.5 m).

For the first suite of simulations (the “Bioenergetic Efficiency” scenarios) we predicted fish growth as a function of food availability and temperatures at which the fish was feeding and digesting. Vertical migrations were triggered by stomach fullness, where fish initially located at a “feeding depth” stopped feeding when its stomach became full, moved to a deeper “non-feeding” depth during the day, and did not move up in the water column again to feed until its stomach was 90% empty. Brett (1971) suggested that appetite in young sockeye reached its maximum rate of change when the stomach had been 90% evacuated; therefore, we assumed that this change in appetite caused the fish to resume feeding. For the first of these scenarios, we started with a feeding depth of 2.5 m and let the fish feed until it reached stomach fullness. At this time the fish stopped feeding and we kept the fish at a 2.5 m non-feeding depth until the fish’s stomach was 90% emptied; we then let the fish feed again until $C_{\max}$ was reached. For the next eleven scenarios, while we kept the feeding depth at 2.5 m, the fish’s location for the non-feeding depth was moved downward (7.5 m to 57.5 m) for subsequent simulations. We then repeated this process but changed feeding depth so that we had a set of simulations where the feeding depth was 7.5 m, and the non-feeding depths were 7.5 m, 12.5 m, and so on down to 57.5 m. This pattern was repeated until we reached feeding depth / non-feeding depth combinations where the fish’s stomach didn’t completely fill, so that there was no trigger to initiate a downward migration.

One of the advantages of incorporating the light environment explicitly in the foraging model is the ability to evaluate how environmental cues affect behavior. While high light levels may enable kokanee to find and capture food at a high rate, light also exposes them to predators that forage visually. In this sense, light can be either a boon or a bane, potentially increasing growth and mortality rates at the same time. As the reservoir environment changes during the summer growing season (i.e., changes associated with thermal stratification and water clarity), kokanee behavior may change as well to balance both predation risk and bioenergetic demands. We performed a second suite of simulations, “Predator Avoidance” scenarios, where kokanee avoided depths that would put them in areas where light level exceeded 0.5 lux, making them more vulnerable to predators (Hardiman et al. 2004; Mazur and Beauchamp 2003). The general pattern for these simulations was the same for the Bioenergetic Efficiency scenarios; that is, kokanee stayed at a shallower depth during the night, early morning, and evening (the “safe upper depth”), but then retreated to greater depths during the day (the “midday hiding depth”).

For the first scenario in this suite, we positioned the fish at 2.5 m at midnight, and then waited until light level reached 0.5 lux, at which time the fish was moved down to its midday hiding depth, the shallowest depth at which light level was less than 0.5 lux at noon. When the light level at 2.5 m again dropped below 0.5 lux the fish was returned to its original position. For subsequent simulations, we kept the safe upper depth at 2.5 m, but moved the fish’s midday hiding depth further down by 5 m increments to a maximum depth of 57.5 m. We then repeated this process using a safe upper depth of 7.5 m, 12.5 m, and so on. For these scenarios, light level was used as the trigger for initiating a DVM instead of stomach fullness, which played little part in these simulations. Additionally, if the fish was initially located at a depth where light level

never exceeded 0.5 lux during the day, no DVM occurred. For these scenarios, there were no discrete feeding and non-feeding periods; if there was food and adequate light, fish could feed no matter the depth.

Modeling Effects of Climate and Dam Operations

We used the calibrated BBFM to predict how changes in physicochemical conditions in the reservoir would affect kokanee growth and their risk of predation (Figure 44). Growth and predation risk were compared under three scenarios: full-pool conditions, temperature control device (TCD) effects, and drought. Saito and Koski (in review) also examined the effects of spillway releases. Thermal stratification and maximum temperature change occurs during the summer so each of the three thermal scenarios were examined during June, July, and August. Temperature-depth profiles for full-pool conditions and TCD effects were predicted using CE-QUAL-W2 (A. Cutler, U.S. Bureau of Reclamation, unpublished data), a two-dimensional hydrodynamic and water quality model (Cole and Wells 2002) that provided thermal profiles in the middle of each month of summer. Full-pool and TCD temperature profiles were based on data collected during 1997, which was a full-pool year at BMR. Inputs used to model temperature-depth profiles included meteorological data (dew point temperature, air temperature, cloud cover, wind speed, and wind direction), inflow rates and temperatures from major tributaries to BMR, mass balance of the reservoir, observed temperature profiles in the reservoir, and reservoir elevation. We assumed that there would be no changes in water clarity with the implementation of a TCD. Field measurements collected at BMR in 2002, a drought year, were used as temperature inputs for drought scenarios.

Temperature-depth profiles generated by CE-QUAL-W2 for full-pool and TCD scenarios were compared to drought condition thermal profiles that were measured in 2002 (Figure 45). In June and July, drought profiles were similar to TCD profiles. In June and July, epilimnetic temperatures in the drought scenario were up to 2.5 °C warmer than the TCD scenario; in August however, the drought scenario was warmer than either of the 1997 scenarios by a maximum of approximately 6 °C at a depth of 12 m. In addition, the 10 °C isotherm in August was almost 20 m shallower in TCD and drought scenarios than in full-pool conditions. Water clarity was greatest during the drought year, peaking at 7 m in July 2002, and was lowest (1.75 m) in June 1997.

Predation risk was computed from light, water clarity, and observed depth distributions of lake trout for each month and thermal scenario. Incident light was calculated at BMR for June 6, July 10, and August 5 in 1997 and 2002 in 10 minute increments from midnight to midnight using a light model developed by Janiczek and DeYoung (1987). Secchi depths in 1997 and 2002 were used to calculate light at all depths using equations 4 and 5. Lake trout reaction distances were then calculated for each time/depth cell using equation 6 (Vogel and Beauchamp 1999):

$$(6) \quad RD = 26.84 + (2.81 \cdot I_z) - (6.09 \cdot \ln NTU) - (0.025 \cdot \ln NTU \cdot I_z)$$

where reaction distance (RD in cm) is calculated using light level (I_z , in lux) and turbidity (NTU in Nephelometric Turbidity Units). We used 2002 turbidity values for drought

simulations, but turbidity was not collected in the reservoir prior to 2001 so 2001 turbidity values were used for all 1997 simulations because Secchi depths were similar to those measured in 1997. Maximum lake trout reaction distances varied between 73.1 and 79.8 cm.

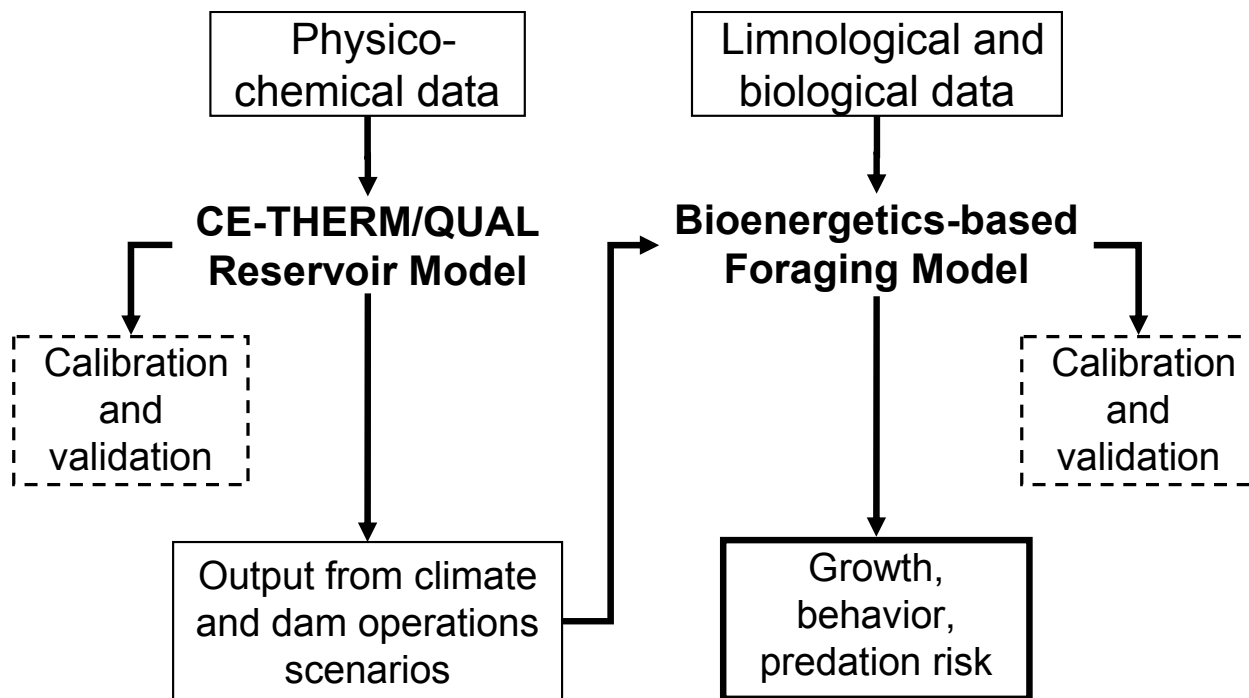


Figure 44. Conceptual framework of the linkage between the reservoir thermal model (CE-THERM or CE-QUAL) and the bioenergetics-based foraging model. A variety of dam operation and climate scenarios were simulated with the thermal model and the output from those simulations became inputs to the bioenergetics-based foraging model.

Depth (and hence temperature) distribution of lake trout in simulations was estimated from depths at which lake trout were captured in 3 m x 60 m vertical gill nets during June, July, and August 1994 – 2002. A total of 41 lake trout were caught in long vertical gill nets during June – August between the years of 1994 and 2002. Of the 41 lake trout netted, 51.2% were captured in temperatures ≤ 10 °C, 17.1% between 10.1-11 °C, 19.5% between 11.1-12 °C, 7.3% between 12.1-13 °C, and 4.9% were captured between 13.1-14 °C. No lake trout were observed at temperatures above 14 °C. Relative frequency of lake trout occurrence was calculated for each temperature above 10 °C in 1 °C intervals. Lake trout captured at or below 10 °C were combined to compute relative frequency of occurrence because these temperatures were within their thermal preference (Stewart et al. 1983; Madenjian and O'Connor 1999; Dillon et al. 2003).

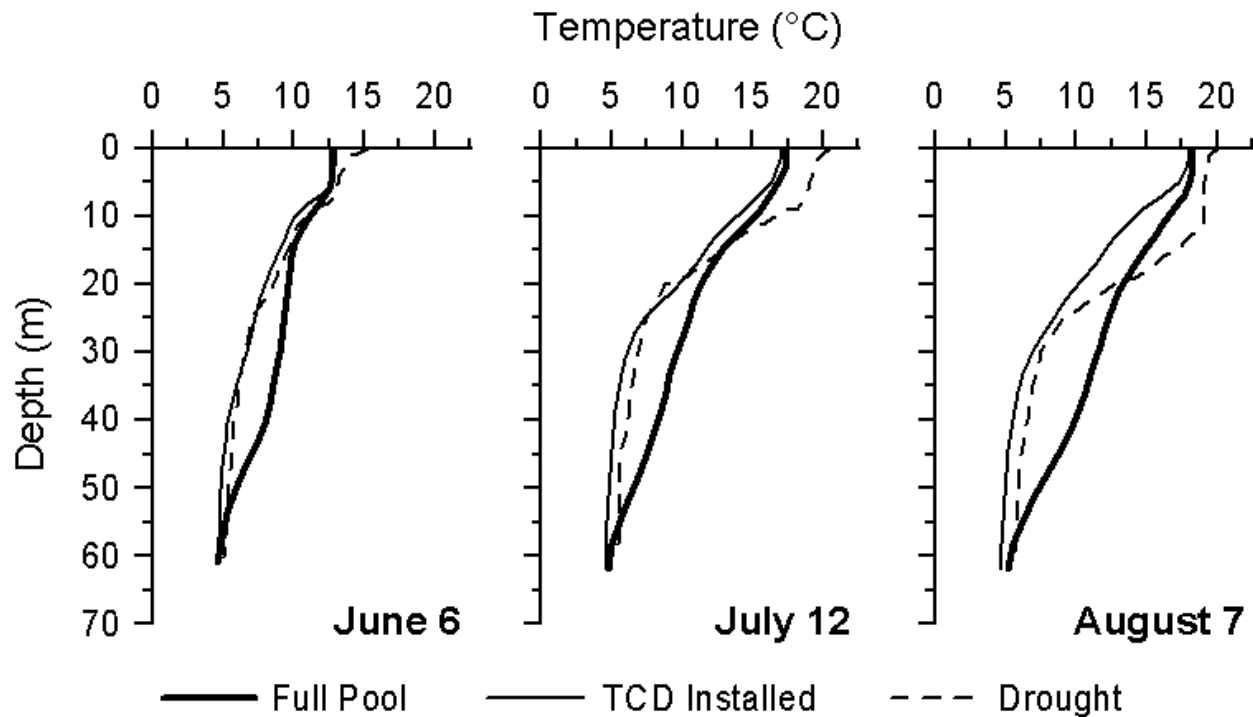


Figure 45. Temperature-depth profiles for June, July, and August in BMR. Bold lines are modeled temperatures for 1997 (a full-pool year), thin lines are modeled temperatures for 1997 after the installation of a temperature control device, and thin dashed lines are observed temperatures measured during 2002 (a drought year).

Predation risk (μ), a function of lake trout reaction distance (RD) and probability of lake trout occurrence (P) based on temperature, was calculated for each depth (z) and time (t):

$$(7) \quad \mu_{z,t} = RD_{z,t} \cdot P$$

The BBFM was used to predict potential foraging weight gain (g) of age-0 kokanee in June, July, and August under the three thermal scenarios. Aside from water clarity (Table 5) and temperature profiles, all inputs for the simulations in this study were the same as the inputs described in Table 4. We assumed that zooplankton densities would remain constant across the two 1997 thermal scenarios and the 2002 drought scenario because average zooplankton densities have been similar over the past decade, and the effects of drought and TCDs on zooplankton abundance have not been well studied. Thus, 2002 zooplankton densities and calibration factors were used for all thermal scenarios. Water clarity, however, varied over the past decade so 2002 Secchi depths were used for the drought scenario, and 1997 Secchi depths were used for full-pool and TCD scenarios.

Table 5. Water clarity input data for the three thermal scenarios in BMR. Secchi depths are listed in m, and turbidity values are in NTUs (*italicized*). The same Secchi depths and turbidity values from full-pool conditions were used in TCD scenarios.

Thermal Scenario	<u>June 5</u>		<u>July 10</u>		<u>August 6</u>	
	Secchi Depth	Turbidity	Secchi Depth	Turbidity	Secchi Depth	Turbidity
Full-pool Conditions (1997)	1.75	<i>1.8</i>	4.5	<i>0.65</i>	4.0	<i>0.75</i>
Drought (2002)	5.06	<i>0.9</i>	7.0	<i>0.8</i>	5.6	<i>0.95</i>

We first used the model to predict daily kokanee growth for each of the three thermal scenarios in June, July, and August using the observed generalized DVMs from 2002. Predation risk was averaged over all 48 thirty-minute time steps to obtain an average predation risk value for that day. Then, μ/g was calculated for each simulation by dividing average daily predation risk by daily growth increment (g/d).

Because predation risk profiles indicated that drought conditions posed the most predation risk to kokanee, we assumed that fish in the other two thermal conditions would change their DVMs to increase bioenergetic efficiency. Both predicted growth and predation risk were compared among thermal scenarios for different months by conducting a series of simulations based on alternative DVMs that would enhance bioenergetic efficiency.

For each thermal scenario during each month, two fish depths were designated: a feeding depth and a non-feeding depth. The fish initially stayed at the feeding depth until its stomach became full, at which time it moved to a deeper non-feeding depth. The fish remained at the non-feeding depth until its stomach became 90% empty. The fish was then returned to its original feeding depth to consume food. All possible combinations of feeding / non-feeding depths were simulated from 2.5 – 57.5 m, until the fish could either not fill its stomach or reach C_{max} during the day, or if it didn't have time to evacuate its stomach by 90% by the end of the 24 hour simulation period. For all simulations, fish depth was the only variable; temperature profiles, zooplankton densities, and water clarity remained consistent within each month/thermal scenario combination. Simulations within each month/thermal scenario set were then compared to determine which DVMs would yield lowest μ/g values and predict how kokanee might respond to conditions with varying degrees of predation risk.



Figure 46. Iola basin of BMR during drought conditions. Perspective is looking down reservoir to the west-southwest from the north side of the reservoir near the Highway 149 bridge (photo: B. Johnson).

4.3 Results and Discussion

The Sport Fishery

Kokanee was the predominant species caught in the open water fishery at BMR during 1993-2003, comprising an average 68% of the catch (Dan Brauch, CDOW, unpublished data). The average annual harvest of kokanee during summer 2003 was about 103,000 fish (range: 50,000-227,000), comprising more than 80% of the total fish harvest from BMR (Table 6). Rainbow trout made up on average about 24% of the catch, and mean number harvested each summer was about 28,000 fish (range: 1,353-56,000) during that period. Brown trout made up about 6% of the catch and lake trout <3%. The summer harvest of lake trout since 1996 has been primarily fish <500 mm TL; the harvest of lake trout >750 mm TL has been highly variable. A few yellow perch (*Perca flavescens*) have been caught and kept each year since 2001 but their mean size (<180 mm) has not increased since 2001.

The fishery at BMR has attracted anglers from 49 states, and although most anglers are Colorado residents about 75% drove more than one hour from home to fish at BMR. Most of the resident anglers come from the Front Range. It appears that fishing effort at BMR is driven partly by the catch rate anglers enjoy during summer; this phenomenon has been documented in other fisheries (Johnson and Carpenter 1994; Carpenter et al.

1994). In years when the catch rate is high, fishing effort also tends to be high (Figure 48).



Figure 47. Male kokanee in spawning condition (photo: K. Rogers).

During 1993-2000 effort appeared to be particularly responsive to kokanee catch rate (Figure 48). After 2000 angler response to increasing catch rate was much reduced suggesting that other factors, for example the multi-year drought, may have dictated fishing effort in those years. The importance of high quality kokanee fishing in BMR is highlighted by the 50% increase in fishing effort (~100,000 angler-hours) during years when catch rate was high. Using an approximate economic multiplier of \$102 per day (computed from data provided by Pickton 2002) this increase would translate into over \$1,000,000 of additional economic activity, with implications for the economy of the Gunnison area.

Based on the mean size in the creel, harvest of kokanee occurs primarily on age-2 and age-3 fish; very few kokanee were caught and released (~8%). Summer exploitation rate of kokanee, the number of kokanee harvested divided by hydroacoustics-derived abundance of kokanee 15-45 cm TL, averaged 27% (range: 13-49%) since 1998. It is likely that the abundance estimate of kokanee >150 mm TL is biased high due to variation in estimated size of kokanee <150 mm that would result in the inclusion of

some of this most abundant size class in the estimate of fish >150mm. Therefore, true exploitation rate of kokanee could be higher than estimated, and this value does not include winter harvest. Despite these caveats, the exploitation rate of kokanee in BMR is probably reasonable for a put-grow-take fishery, as long as the egg take can be maintained.

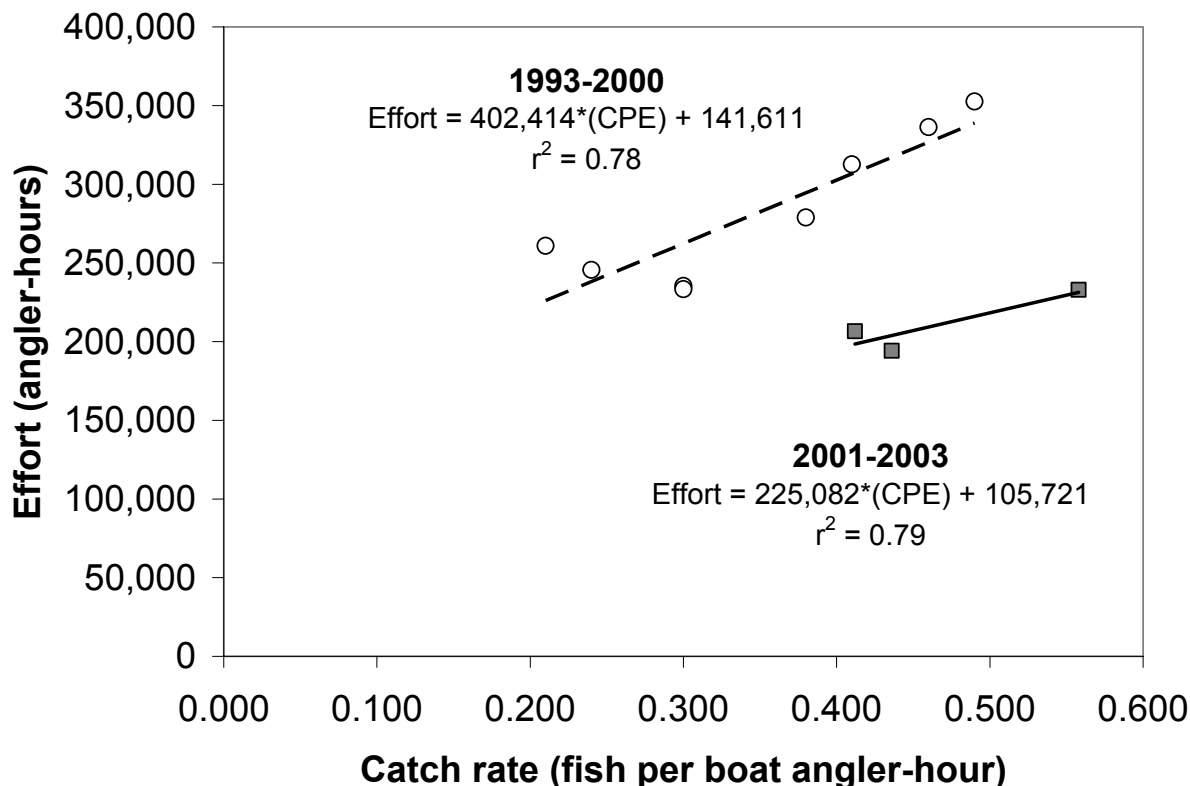


Figure 48. Relationship between fishing effort during May-October (angler-hours, fishing from boats only) and the catch rate of kokanee during summer 1993-2000 (circles) and 2001-2004 (squares).

“Stringer table” analysis (Dan Brauch, CDOW, personal communication) showed that reductions to daily bag limits would not be particularly effective at increasing the abundance of adult kokanee or the egg take from this population unless the bag limit was reduced by at least 50%. Reducing intensity of mortality on younger age-classes of kokanee would have a much larger effect than bag limits on overall kokanee abundance and egg take, while at the same time improving sport fishing opportunity.

Table 6. Creel survey estimates of fishing effort (angler-hours), catch rate (fish per angler-hour), harvest, and mean length of kokanee and rainbow trout by anglers fishing from boats at BMR during May-October 1993-2003 (Dan Brauch, CDOW, unpublished data).

Year	<u>Angler-hours</u>			Catch rate	<u>Kokanee</u>		<u>Rainbow trout</u>		
	Bank	Boat	Total		Harvest	Length (mm)	Catch rate	Harvest	Length (mm)
1993	66,913	285,707	352,620	0.49	149,220	319	0.15	47,847	289
1994	58,817	277,511	336,328	0.46	148,116	344	0.09	28,331	272
1995	43,320	235,632	278,952	0.38	99,617	348	0.13	33,192	317
1996	29,134	206,290	235,424	0.30	69,535	345	0.03	18,382	297
1997	28,494	204,751	233,245	0.30	65,676	362	0.18	29,166	286
1998	46,878	198,695	245,573	0.24	56,207	355	0.30	56,062	317
1999	58,476	202,435	260,911	0.21	50,009	368	0.20	38,665	348
2000	54,919	257,648	312,567	0.41	114,025	358	0.12	31,021	347
2001	28,410	165,766	194,176	0.44	73,631	342	0.08	11,186	346
2002	26,122	206,786	232,908	0.56	122,072	355	0.02	3,433	350
2003	18,051	188,493	206,544	0.41	80,092	387	0.02	1,353	312

Spatial Distribution

An understanding of the spatial distributions of fish populations on diel, seasonal and inter-annual time scales is essential to interpreting changes in growth, recruitment, emigration and survival that may be linked to dam operations or other factors. Kokanee differ from the other fishes in BMR in that they perform diel vertical migrations (DVMs), moving up and down in the water column one or more times each day. This behavior has implications for their growth, and their exposure to risk from entrainment and from their predators.

Age-0 Kokanee

The migratory behavior of age-0 kokanee changed over the summer. Hydroacoustics surveys in 2001 and 2002 documented a behavioral change from a single, large DVM and deeper median depth distribution observed on May 11 and 12 to multiple, smaller amplitude migrations and shallower median daytime depths on August 6 and 7 (Figure 50). Age-0 kokanee occupied average daytime median depths of 67 m in May, 74 m in June, 29 m in July, and 19 m in August. During sampling in each month fish were least dispersed vertically at night and the median nighttime depth occupied varied from 21 m in May, 14 m in June, 21 m in July, to 23 m in August. Fish were never schooled to a degree that individual target tracking was not possible.



Figure 49. Jill Hardiman, CSU graduate student, leads a crew retrieving vertical gill nets at BMR (photo: B. Johnson).

Depths of age-0 kokanee were greater during May and they performed larger DVM than later in the summer (Figure 50). The median depths of the cohort were always located where light was less than the 0.001 lx threshold for kokanee visual feeding (Figure 51). We also observed fish more dispersed throughout the water column at the period of sampling in May during non-night hours. Fish descended at around 0500 hours, spent the day at great depths (~67 m), and ascended to about 25 m after nightfall, performing a single, normal migration per day.

In June, the age-0 kokanee depths continued to be distributed in deeper water during the day, with some bimodality observed near 15 m. Fish were also observed scattered throughout the water column during the crepuscular hours, similar to May. During June, age-0 kokanee descended later in the morning (0600 hours) and ascended earlier in the evening (1900 hours) than during May observations. The fish appeared to perform a single DVM, as observed in May.

By July the cohort was much less dispersed in the water column during the crepuscular periods than in May and June with the median depths occurring between 15 and 20 m. Many fish still occupied the deeper depths during the day; however, median daytime depths were shallower than those observed in May and June sampling. There appeared to be two diel vertical migrations of lower amplitude in July. Fish were observed ascending for an extended period in the morning, descending at midday, then ascending again to near the surface until about 2100 hours, and lastly descending to a nighttime depth of 20 m. In August, fish showed the shallowest median diel distribution. Fish were observed ascending near 0500 hours and occupied the upper 20 m throughout the day with very few fish observed in the deeper depths throughout the diel cycle. The distribution pattern suggested multiple diel migrations per day of smaller amplitude in the upper water column. Fish were aggregated near the thermocline during the night.

Our simulation modeling indicated that neither predator avoidance nor bioenergetic optimization alone can explain observed behavior of age-0 kokanee in BMR. On average, the Bioenergetic Efficiency simulations overestimated growth by 0.10 g in June and July, and 0.06 g in August; and the Predator Avoidance simulations underestimated growth by 0.03 g, 0.14 g, and 0.26 g in June, July and August (Figure 52). This suggests that observed DVMs are a result of a combination of both predator avoidance and bioenergetic considerations. Further, the relative strengths of behavioral influences appeared to change during the summer of 2002. Avoiding predators early in the summer may outweigh the benefits of growing quickly and spending more time in high-light, high-exposure environments. However, the strategy appears to change in July and August, when observed growth was achieved in only two of the July Predator Avoidance simulations. By August, observed growth more closely resembled the results of the Bioenergetic Efficiency simulations. Thus, in August, kokanee had to assume more light-dependent risk than in other months in order to obtain the amount of food necessary to grow the observed amount. The presence of a thermal refuge in the epilimnion may reduce actual risk from predators like cold-water lake trout. In BMR, lake trout have rarely been observed at temperatures above 10 °C, which occurs at a depth of approximately 25 m in August (Hardiman et al. 2004). In the observed DVM the average kokanee remained just above this depth in the metalimnion during most of the day.

The lateral distribution of age-0 kokanee also changed seasonally. Whole reservoir and diel hydroacoustics surveys of age-0 kokanee spatial distribution in 2001 and 2002 showed that young kokanee got closer to the dam as the summer progressed (Figure 53). In both years, the relative density of small kokanee was greatest in Iola basin in

May and the fish appeared to move downstream thereafter. By August, the abundance of kokanee in each basin was not different (Hardiman 2003).

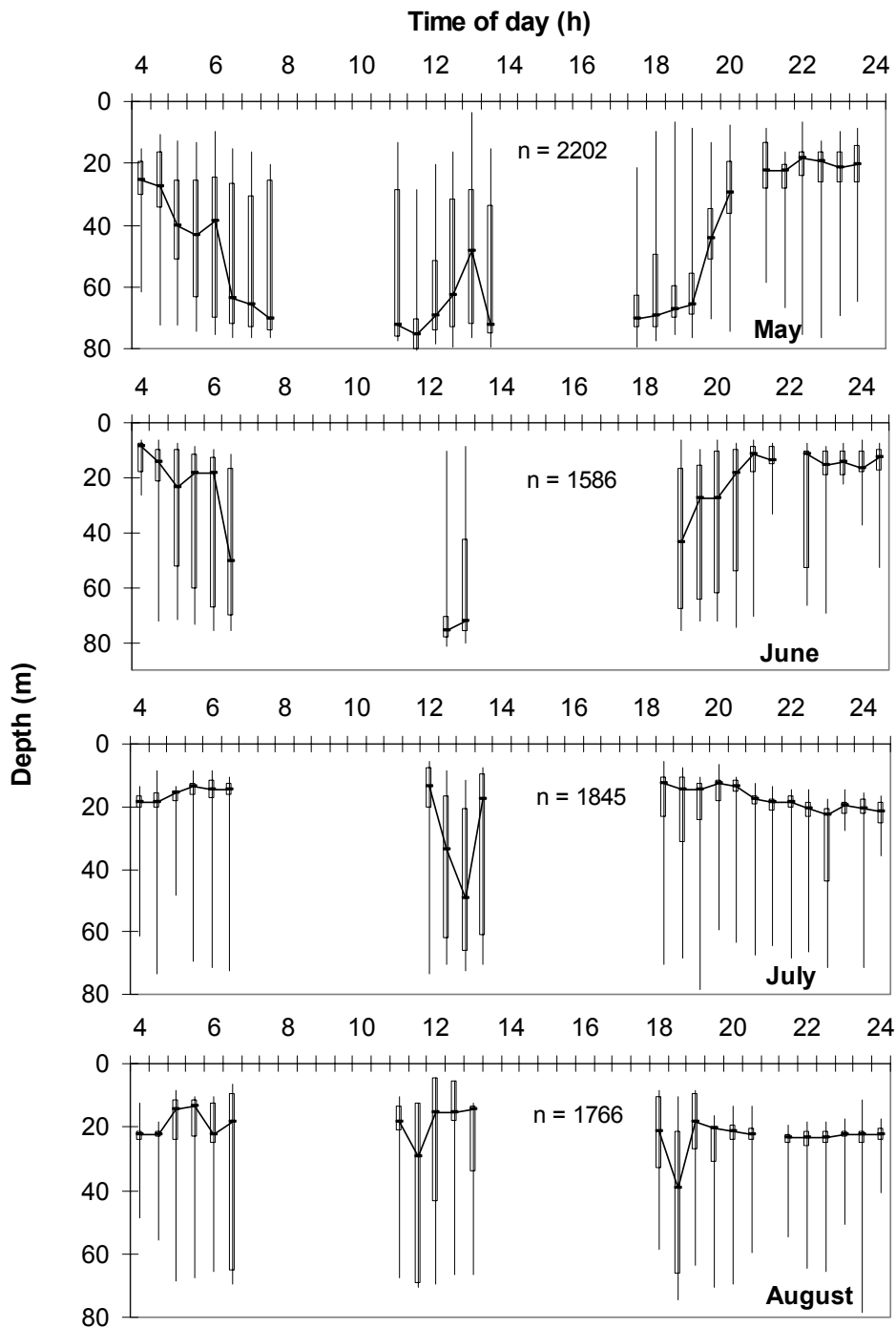


Figure 50. Diel vertical distribution of age-0 kokanee targets in BMR in May, June, July, and August, 2002, shown as median (dashes), 25th and 75th percentiles (boxes), and range (vertical lines) of depths for hydroacoustic sampling performed during the new moon each month. The n value indicates the number of fish observed, uncorrected for differential sampling volumes by depth.

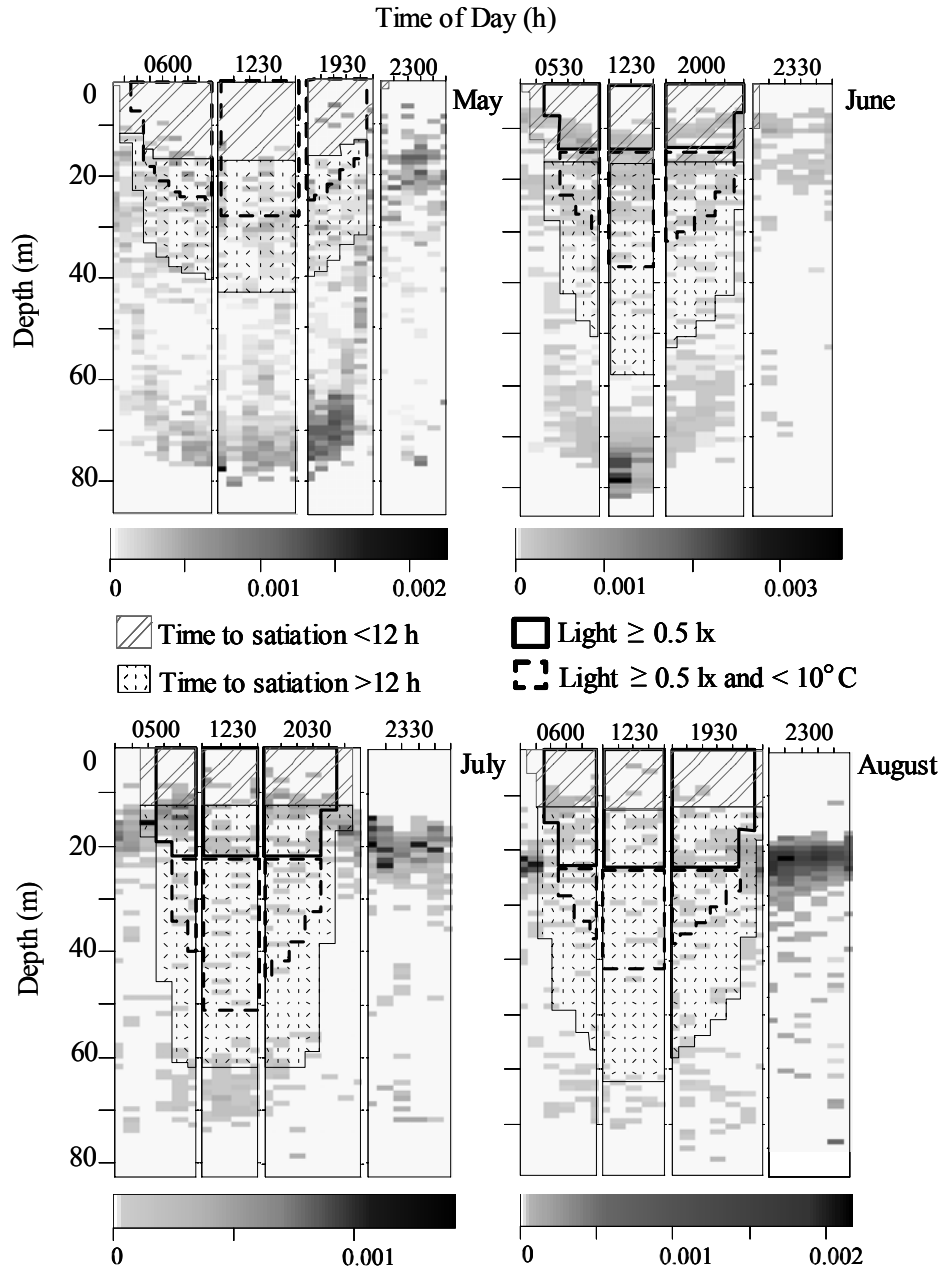


Figure 51. Diel vertical distribution of age-0 kokanee target densities from hydroacoustic transects showing regions where time to satiation < 12 h and time to satiation > 12 h, estimated from kokanee size, *Daphnia pulex* densities, water clarity, and a light dependent functional response. Predation risk areas are indicated by regions where temperature $< 10^\circ\text{C}$ and light ≥ 0.5 lx (dashed outline) and areas available for lake trout feeding where light ≥ 0.5 lx (solid dark outline) from May, June, July, and August, 2002, at BMR, Colorado. Bar scales beneath panels are kokanee/m³ densities within 1 m stratum and are scaled for each month. Time of day is the median transect time for a series of transects from approximately one hour before and after the sunrise (0400 – 0730 hours) and sunset (1830 – 2100 hours), and during mid-day (1130 – 1400 hours), and at night (2200 – 0030 hours) for each month.

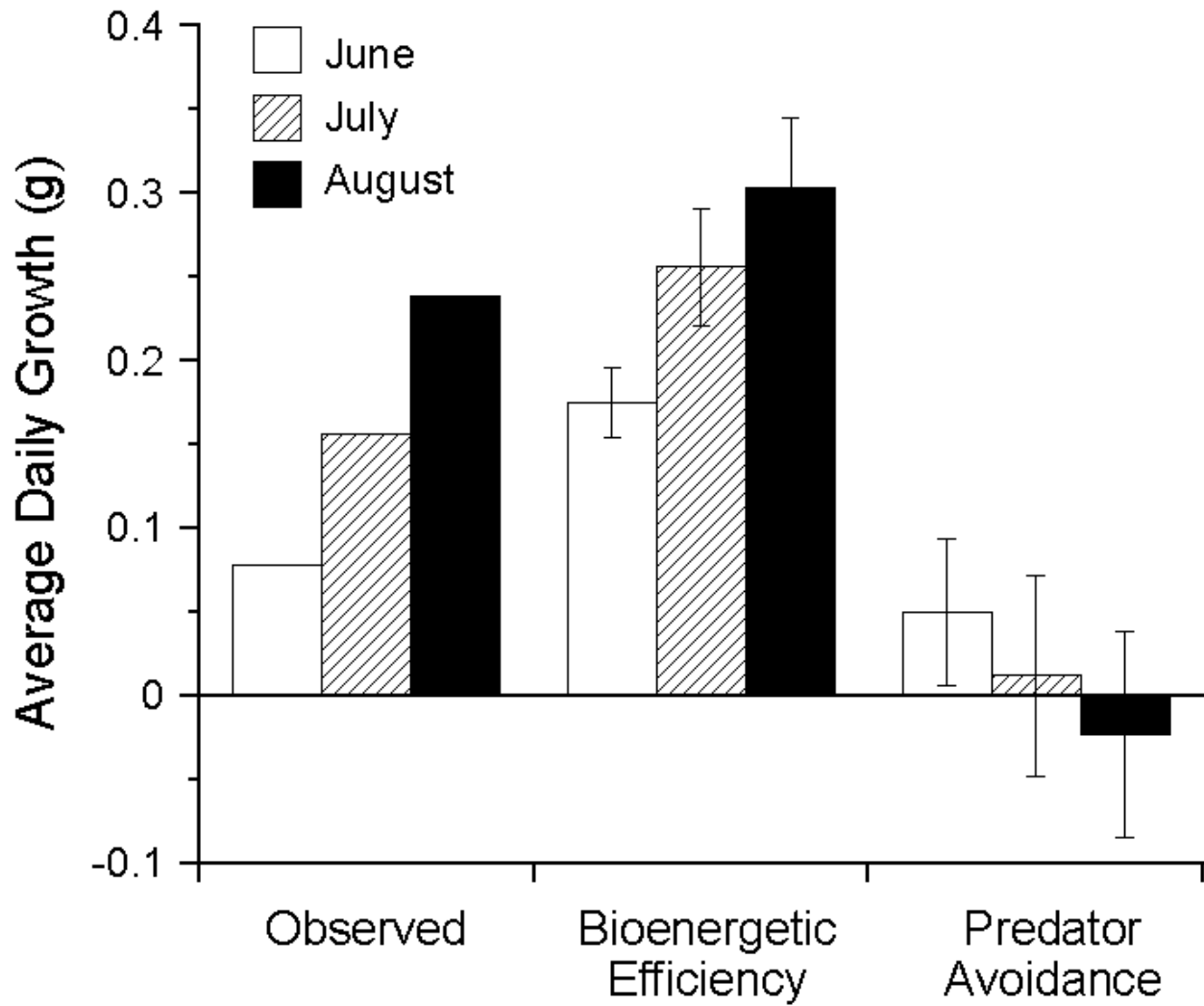


Figure 52. Comparisons of the observed daily growth of age-0 kokanee in BMR to averaged Bioenergetic Efficiency and Predator Avoidance simulations for June, July, and August 2002. Vertical lines indicate $\pm$ one standard deviation.

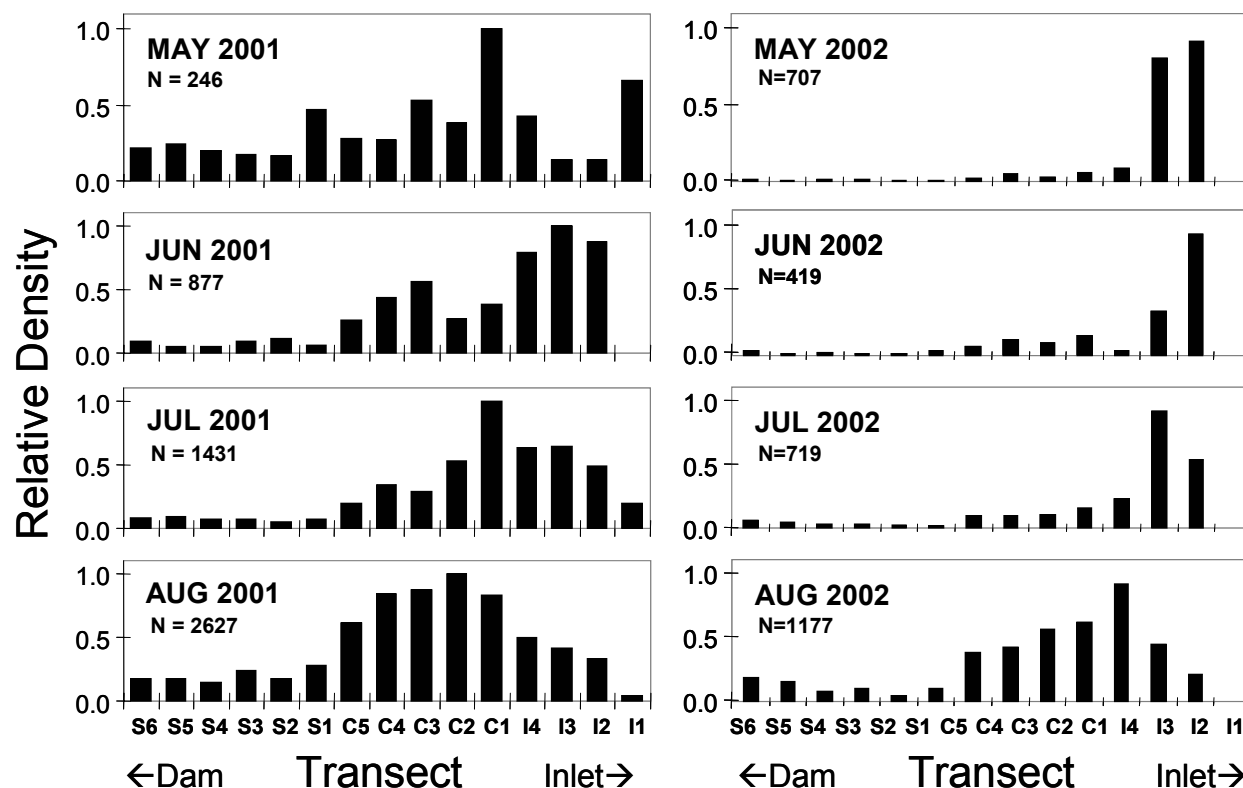


Figure 53. Relative density of age-0 kokanee in 15 hydroacoustics transects sampled during May-August, 2001 and 2002. The sample size (N) is the number of tracked age-0 sized targets observed in each month. Transects are listed in order of geographic location from the dam to the inlet; “S” indicates transects in Sapinero basin, “C” in Cebolla, and “I” in Iola. NA indicates that a transect was not sampled during that month.

Distribution of Age-1 and Older Fishes

Based on hydroacoustics surveys in 2002, older kokanee did not display the large vertical migrations that were observed in age-0 kokanee (Figure 54). Vertical migrations appeared to be of very small amplitude (~10 – 20 m) throughout the summer of 2002. In May adult median depths were at approximately 15 m during hours of darkness with a small ascent to shallower waters during the crepuscular time periods; daytime depths were closer to 30 m. Daytime medians from June to July were from 6 to 15 m and fish were more aggregated about the thermocline in August from 14 to 30 m. Kokanee were typically located between 10 and 22 m during hours of darkness in May, 2002. In August they were located a little deeper at 20 - 25 m. Diel distribution patterns observed in 1997 (Stockwell and Johnson 1999) were qualitatively similar, but differences in limnological conditions across the two years likely make inter-annual comparisons less informative.

It is difficult to compare fish distributions seen in overnight vertical gill nets with those observed in diel hydroacoustics surveys because gill net catches represent an integration of fish distribution over the nighttime but also the twilight periods around

dawn and dusk. However, it appears that adult kokanee orient themselves at or just below the thermocline during hours of darkness, typically in temperatures of 11 to 16°C (Figure 55). That finding is consistent among hydroacoustics surveys in 1997 and in 2002, and in gill net catches in 1994-1996 and 2002.

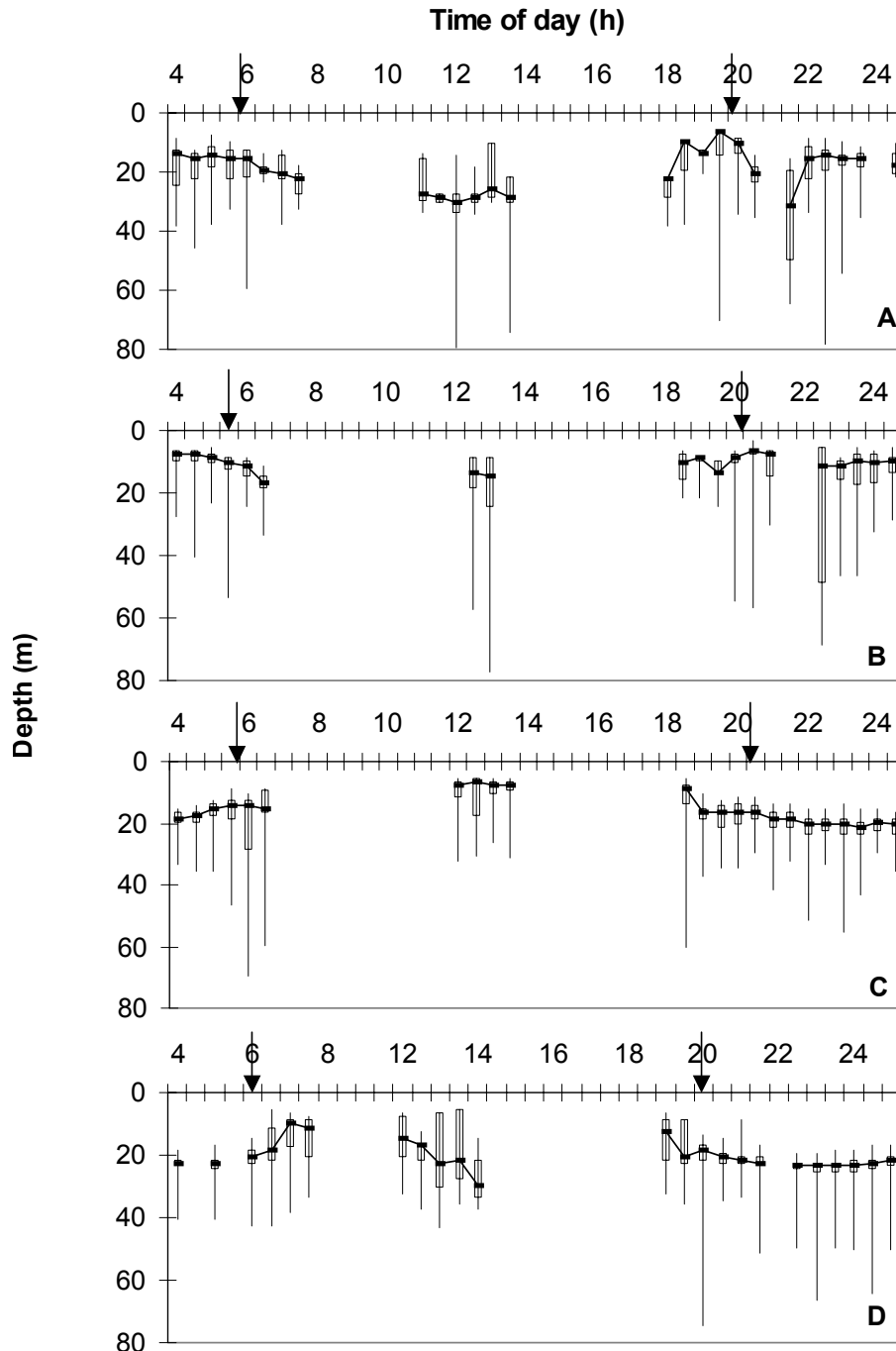


Figure 54. Diel vertical distribution of adult kokanee targets in BMR in early A) May, B) June, C) July, and D) August 2002 shown as median (dashes), 25th and 75th percentiles (boxes), and range (vertical lines) of depths. Arrows indicate time of sunrise and sunset.

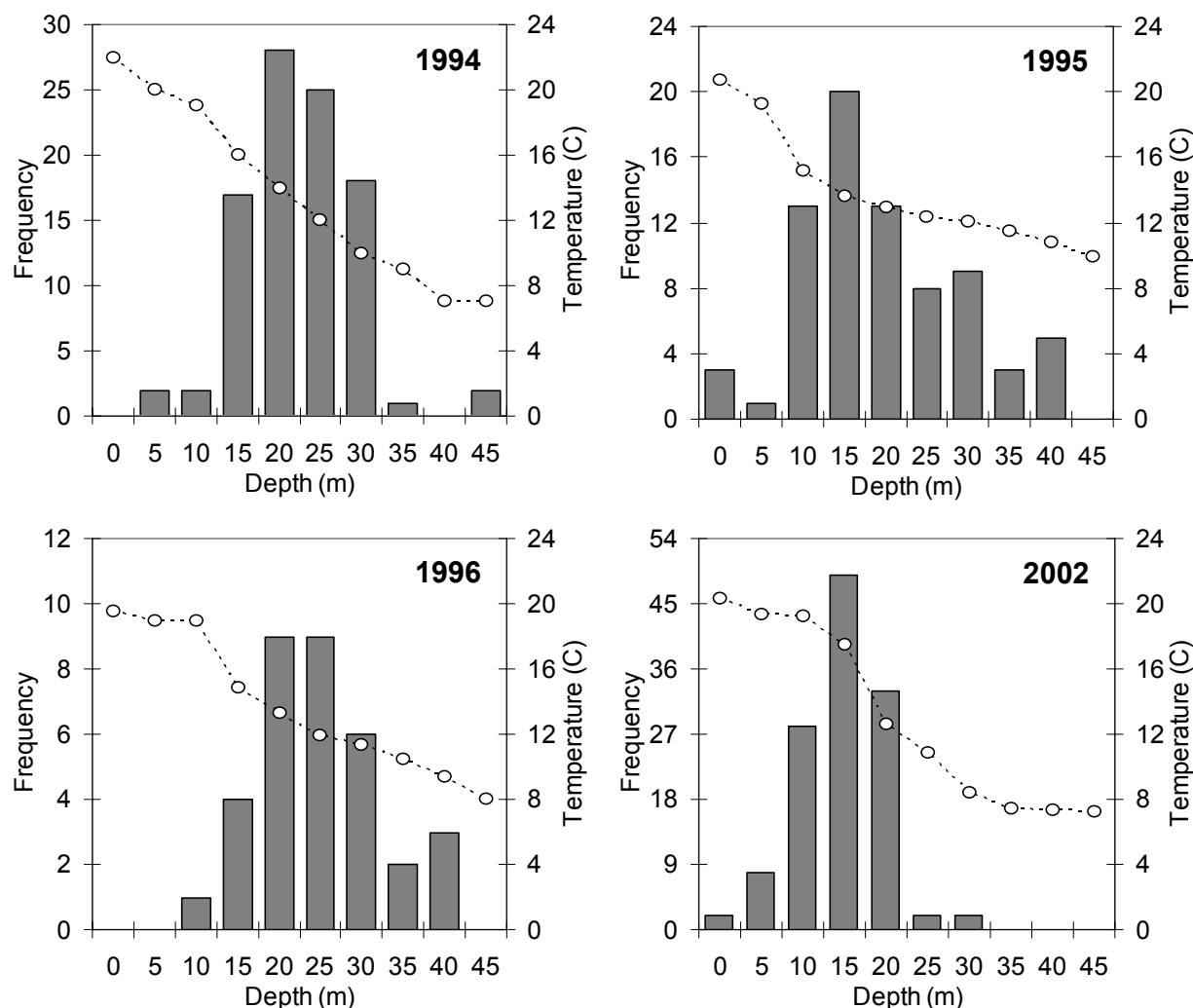


Figure 55. Depth distribution of kokanee (mainly age-2 and older; bars) captured in overnight vertical gill net sets and water temperature (dashed line) on the day of sampling during four years in August. Data are from Sapinero and Cebolla basins of BMR.

Rainbow trout inhabited shallower water than other salmonids in the reservoir. Only 25 rainbow trout were captured during 1994-1996, and 2002 (Figure 56); however, all were captured at depths < 18 m, 95% < 13 m, and 59% < 8 m of depth. The mean depth at which brown trout were captured was 16 m, with most fish caught in 5-20 m. Summertime depth distributions of these two species do not appear to have changed since shortly after the reservoir filled. During summer 1968-1970, at least 70% of the rainbow trout were captured in water shallower than 10 m (Wiltzius 1974). About 90% of brown trout sampled by Wiltzius (1974) were also captured in depths of 5-20 m, with a mean of 11 m.

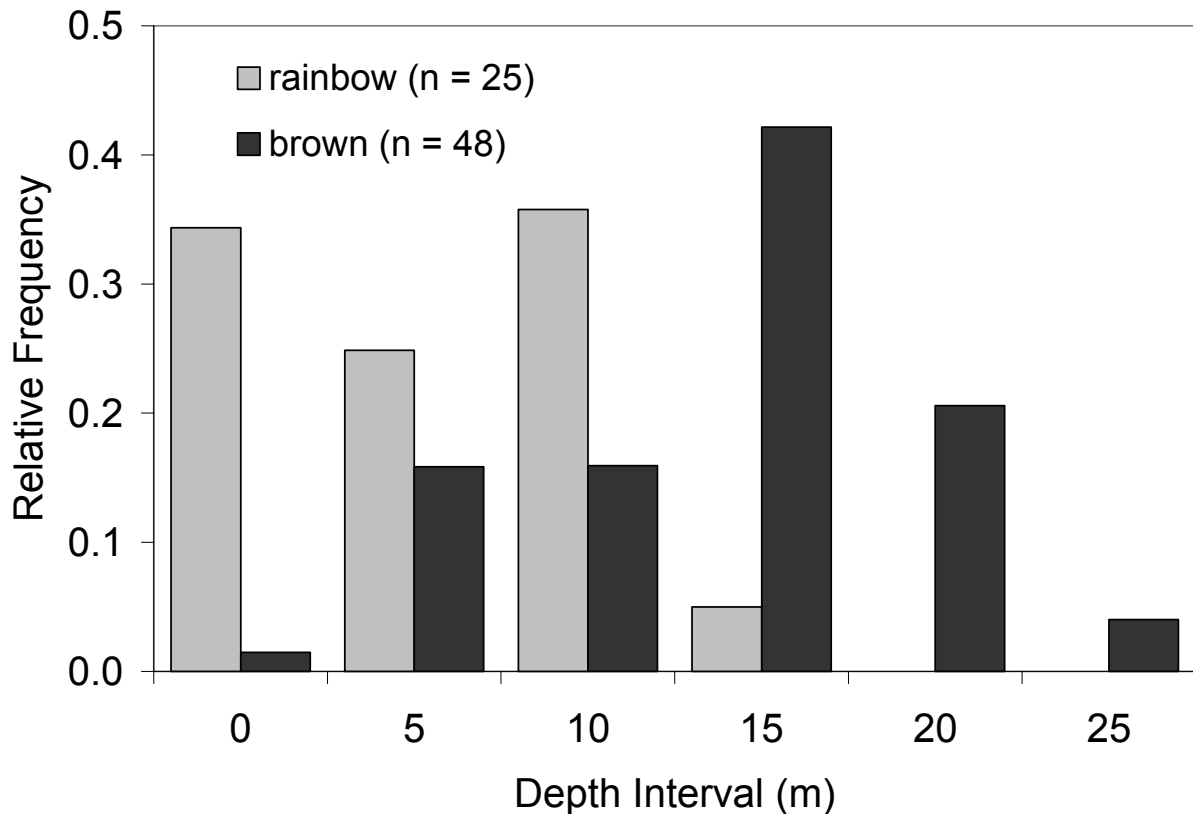


Figure 56. Depth distribution of rainbow trout and brown trout captured in overnight vertical gill nets during all months in 1994-1996, 2001, and 2002. Rainbow trout catch data were included all basins of BMR because they were never found at depths greater than about 15 m. Brown trout catches were limited to Sapinero and Cebolla basins because the maximum depth in Iola basin was less than the maximum depth that brown trout were observed elsewhere in the reservoir. Note that the months sampled differed among years, but were always within May-October.

Lake trout: vertical distribution

Relatively few lake trout were observed in hydroacoustics surveys in May, substantiating the assumption that most lake trout were inshore. No potential thermal refuge exists for kokanee in May, and the kokanee distribution largely coincides with optimal light levels for lake trout foraging. However, the relatively few lake trout detected were roughly evenly distributed between the optimal foraging zone and much greater depths. Many more lake trout were detected in June, at depths near or below the 10 °C isotherm. In many cases the same density was observed at a given depth for two or three consecutive transects; this is likely the result of detecting the same fish multiple times. Lake trout were not observed at depths below the 0.5 lux light penetration zone at midday, but were otherwise widely distributed in the water column. For most of the diel period, kokanee were largely concentrated above the 10 °C isotherm, potentially reducing opportunity for predator-prey encounters.

In July and August relatively fewer lake trout were observed at light levels <0.5 lux. Lake trout appeared to be more concentrated in zones where both temperature and foraging light level preferences were met. Additionally, a brief period of high predator concentration above the 10°C isotherm occurred at dusk in both months (Figure 57). Crockett (2004) speculated that lake trout were moving out of their physiologically optimal zone for short intervals in order to capitalize on higher kokanee densities above the isotherm. Snucins and Gunn (1995) found that body temperature of a 1,100 g lake trout required nearly an hour to equilibrate to a 5°C water temperature increase, with equilibration times increasing for larger fish. All lake trout observed in the current study were substantially larger (the minimum being approximately 2,000 g) because the TS model only enabled us to identify fish of this size as lake trout. Based on the timing of the repeated transect surveys, the heavy concentration of piscivores above the 10°C isotherm appeared to be limited to <45 min in each month. A large lake trout could therefore make such a foray at little bioenergetic cost. Dusk may be the optimum time to do so, when light levels are dropping rapidly, potentially giving lake trout the greatest visual advantage over their prey. We can suggest no other hypothesis as to why these forays would not also occur at other times, particularly at dawn when light levels undergo a comparably fast transition. Kokanee densities above the 10°C isotherm at dusk are no higher than at other times throughout the day; thus there is no apparent benefit from having prey more concentrated at that time.

Vertical gill net catches (Figure 58) qualitatively agree with results seen in the hydroacoustics surveys; however, the temporal resolution in overnight net sets is poor, and lake trout may have been able to avoid gill nets during twilight periods when the hydroacoustics surveys suggested that some lake trout may make forays into water above the 10°C thermal preference for the species. Still, some 40% of the lake trout captured in vertical gill nets were found in water $>10^{\circ}\text{C}$. The maximum temperature at which a lake trout was captured was 14°C .

Lake trout: horizontal distribution

Most of the tagged lake trout were located nearly every month of tracking (Crockett 2004). Twelve of 17 tags (70.5%) were still detected in July 2002, 14 months after tagging, while 9 of 12 (excluding five expired depth transmitters) were detected in August 2002. These relatively high detection rates corroborate the high survival rates for piscivorous lake trout estimated in the mark-recapture study. Tagged lake trout showed considerable fidelity to specific locations (Figure 59). The mean change in fish position from one tracking occasion to the next was 372 m. This value varied widely among fish however, from under 100 m to over 2,100 m. Of course, "position change" merely indicates how far apart a fish was found on two successive tracking occasions; it is in no way a measure of the fish's level of activity in the interim (Rogers and White, in press). Vastly more intensive tracking effort would be required to fully capture the dynamism of fish movement. Nevertheless, the clear tendency of these lake trout to be found repeatedly in the same general area suggests that they may establish and hold specific territories, perhaps because the forage supply is so abundant that they have little need to cruise long distances in search of food. In a few cases, putative site fidelity

may have been an artifact of tracking transmitters that were no longer in fish, due to mortality or tag expulsion. We considered it most likely that these tags were expelled. Some or all of the fish may have died, but the longevity of lake trout, their high estimated survival rate in BMR, the excellent condition of all fish when tagged, and the fact that they manifestly survived for some months after tagging, all argue against wholesale mortality.

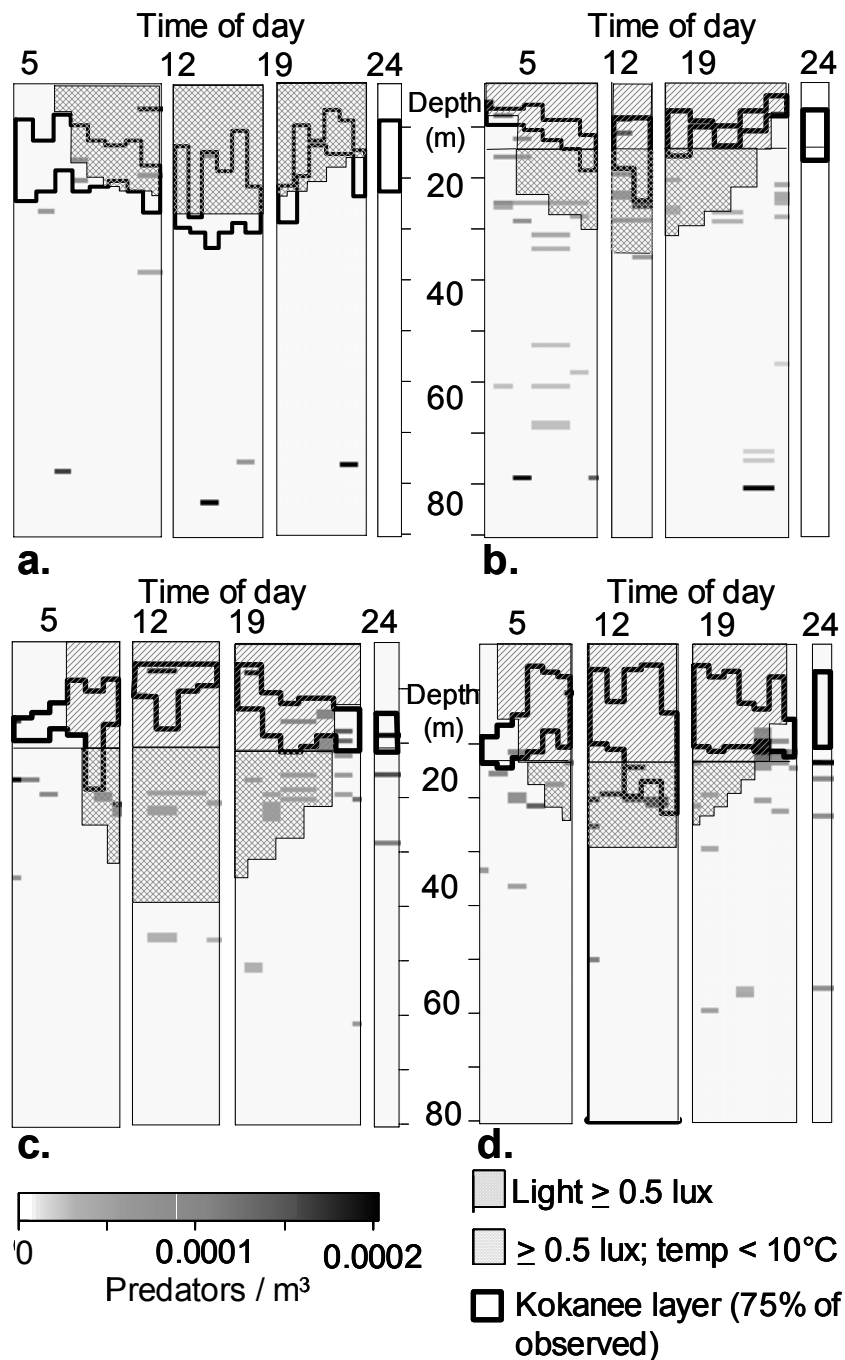


Figure 57. Diel vertical distribution of lake trout and age 2-3 kokanee in BMR in early a) May, b) June, c) July, and d) August, 2002. Depth of the 10°C isotherm is shown by a solid horizontal line except in May, when the entire reservoir was $< 10^\circ\text{C}$.

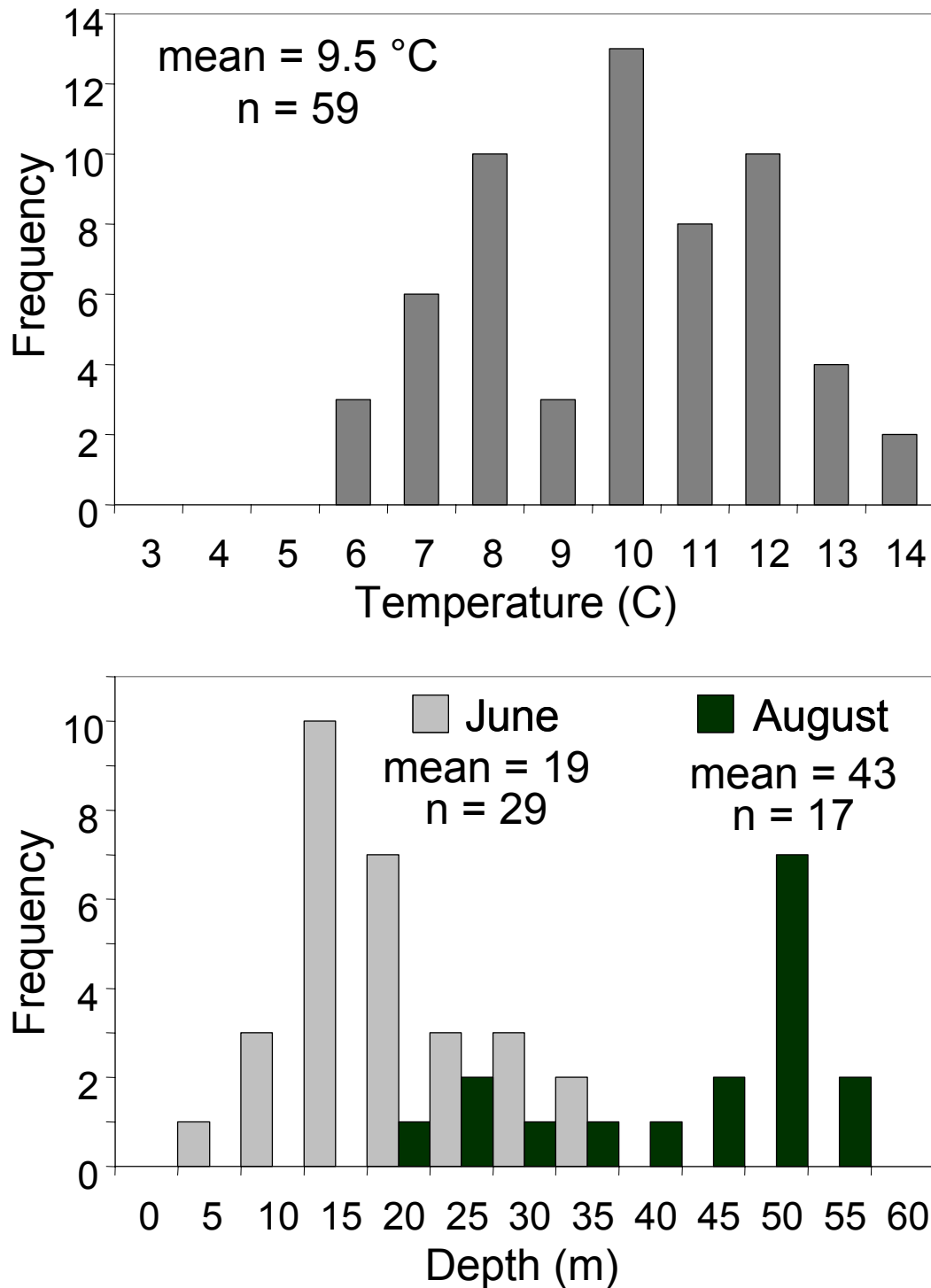


Figure 58. Distribution of temperatures (upper panel) and depths (lower panel) at which lake trout were captured in overnight vertical gill nets during all months in 1994-1996, and 2002. Nets were usually set at dusk and retrieved after approximately 0700 hours the following morning. Data include catches in Cebolla and Sapinero basins of BMR.

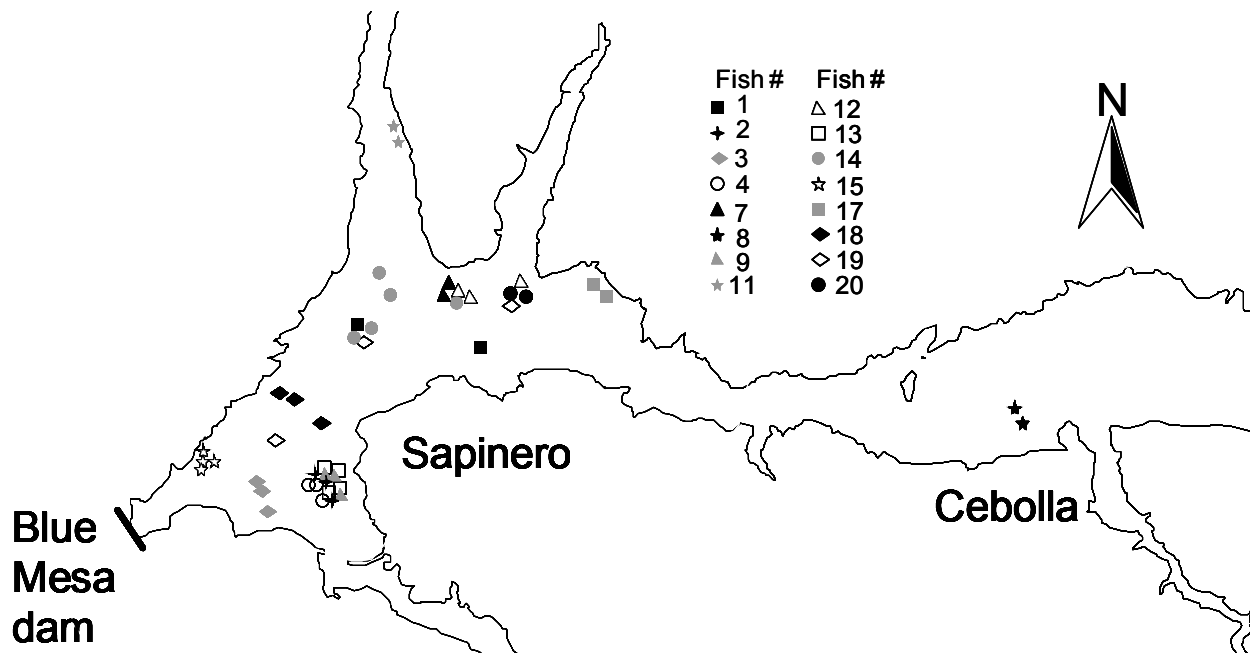


Figure 59. Locations of sonic tagged lake trout in BMR, 2001-2002. Each symbol represents an individual tagged fish.

Growth, Body Condition and Diet

To evaluate possible changes to food availability for sport fishes from new dam operations we examined growth rate of kokanee and rainbow trout before and after new operations began. Laboratory experiments and simulation modeling were used to study kokanee foraging behavior and to uncover the likely mechanisms driving diel vertical migrations in kokanee. Models were also used to predict how kokanee growth would respond to changes in the thermal environment induced by a variety of dam operation scenarios and by hydrometeorological variables. Body condition indices were computed for kokanee, rainbow trout and brown trout to examine inter-annual variation in fish condition during 1994-2002. Diet and stable isotope studies were performed to understand the food base supporting kokanee and trout production, and to assess the degree of diet overlap among various fish species. Analysis of lake trout diet was necessary to determine the predation pressure exerted by this species on other fishes.

Kokanee

Hardiman (2003) found that age-0 kokanee grew from 68 mm on May 7 to 86 mm on June 1, 107 mm on July 9, and 122 mm on August 5 (Figure 60). There was excellent agreement between our age estimates from scales, otoliths and length-frequency analysis (Table 7). Mean length at age-1, 2 and 3 was consistent among years during the 1990s. The vast majority of the kokanee in BMR appeared to be < 4 years old (Figure 61) and very few age-4 fish remained in the reservoir until August. Growth of kokanee in BMR is among the fastest reported in the literature. We summarized age-length information from 19 lakes and reservoirs representing six western states. After

accounting for the time of year that sampling occurred no system had consistently greater lengths at age than BMR.

Backcalculation suggested that growth of age-1 and older kokanee changed very little during 1966-1996 (Figure 62). The overall mean lengths at age were 171 mm, 264 mm, and 331 mm. Standard deviation of these means was between 3 and 9 % of the mean length, suggesting that inter-annual variation in growth was minimal. There is no evidence at this time to suggest that new dam operations had a major effect on growth of age-1 and older kokanee in BMR.

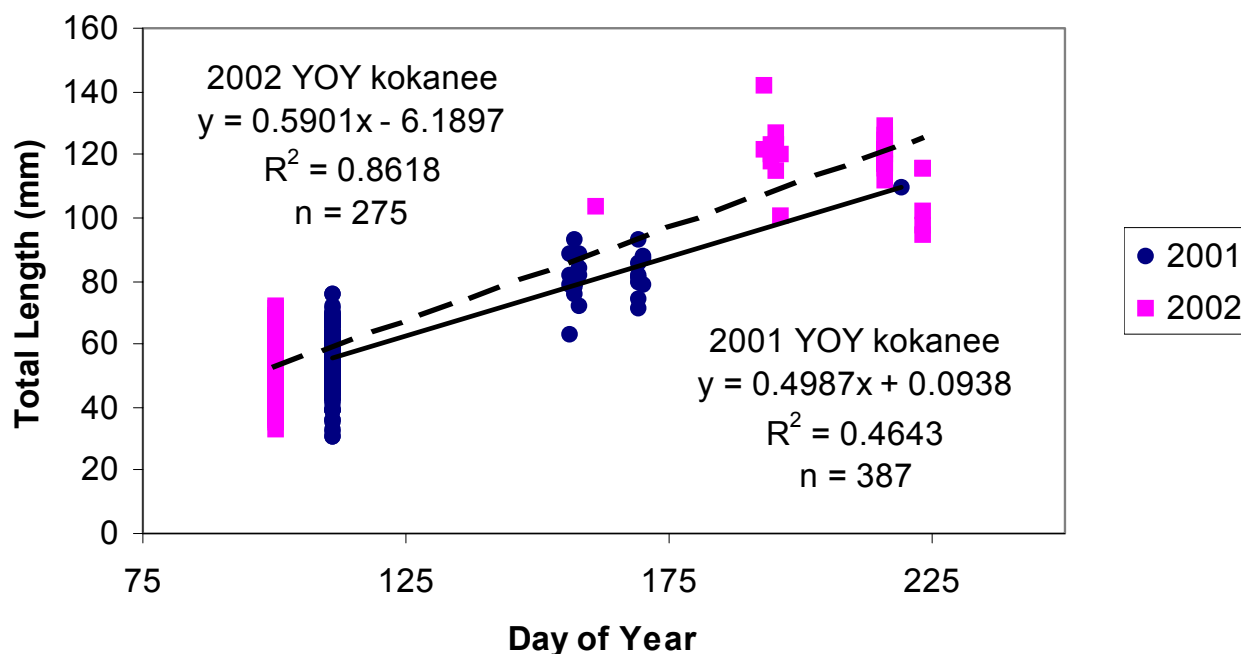


Figure 60. Growth of age-0 kokanee in 2001 and 2002 at BMR. Fish were sampled with gill nets and mid-water trawl or at the Roaring Judy Hatchery prior to release. Linear regressions were fit to predict growth over time. The dashed line represents the fit to the 2002 data and the solid line is the fit to the 2001 data.

Growth of Other Fish

Length-frequency histograms (Figure 63) of rainbow trout sampled during June 1994-1997 suggest the presence of four cohorts with approximate modal lengths of 230 mm, 300 mm, 340 mm and ≥ 390 mm TL. After allowing for spring growth, these modes correspond well with mean lengths at age-1 through age-4 determined from backcalculation. Wiltzius (1971) rarely sampled any rainbow trout older than age-4 in BMR, speculating that 4 years was their lifespan in this system. We did not age brown trout from scales or otoliths but there appeared to be three modes in the length-frequency distribution (Figure 63): 320 mm, 420 mm and 470 mm TL. Backcalculated lengths at age reported by Wiltzius (1971) suggest that ages 3-7 were present in our samples, so the length distributions of cohorts must have overlapped. Younger age classes were also absent from Wiltzius' samples and he speculated that the brown trout

reproduced in tributaries and the young did not move into the reservoir until after their first or second year.

Table 7. Correspondence between mean lengths (TL, mm) at age of kokanee sampled from BMR during June of several years and aged by various methods and investigators.

Ageing Method	Years	Age-0+	Age-1+	Age-2+	Age-3+	Age-4+	Source
June							
Petersen I-f method ¹	1994-1997	--	180	290	370	435	3
Otoliths	1992-2001	--	211	336	348	468	4
Otoliths	1997	--	182	288	388	--	5
Backcalculation-scales ²	1966-1969, 1980, 1989, 1994-1996	--	171	264	331	--	6
Petersen I-f method	2001-2002		--	--	--	--	7
August							
Petersen I-f method	1994-2002	135	227	320	400	--	3
Otoliths	1992-2001	--	230	326	372	432	4
Otoliths	1997	--	227	318	406	--	5
Petersen I-f method	2001-2002	122	--	--	--	--	7

¹Petersen length-frequency method is explained in Murphy and Willis (1996).

²Backcalculations refer to length at the start of the growing season and thus should be expected to be less than other methods that refer to ages in June.

³Present study

⁴Martinez (CDOW, unpublished)

⁵Stockwell and Johnson (1999)

⁶Johnson et al. (1996)

⁷Hardiman (2003)

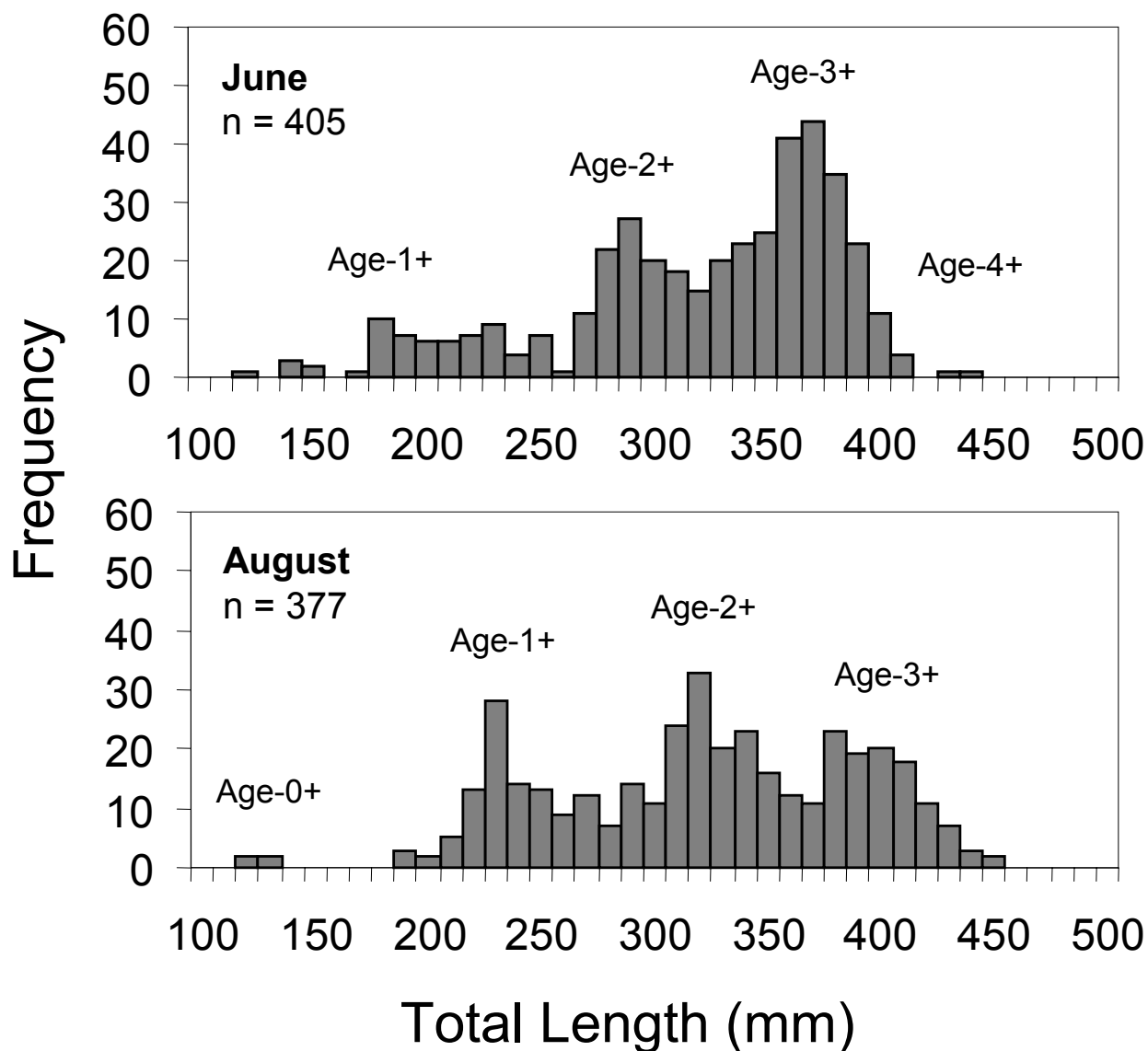


Figure 61. Length-frequency histograms of all kokanee captured in vertical gill net sets in June 1994-1997 (upper panel) and August 1994-2002 (lower panel). Age classes were identified from modes in the histograms and were corroborated with lengths at age from two otolith studies and from scale back calculations (Table 7).

Unlike kokanee, the mean length at age of rainbow trout declined between 1967 and 1996 (Figure 62). The decline began well before dam operations changed suggesting that some other factor was responsible for the lower growth rate of rainbow trout.

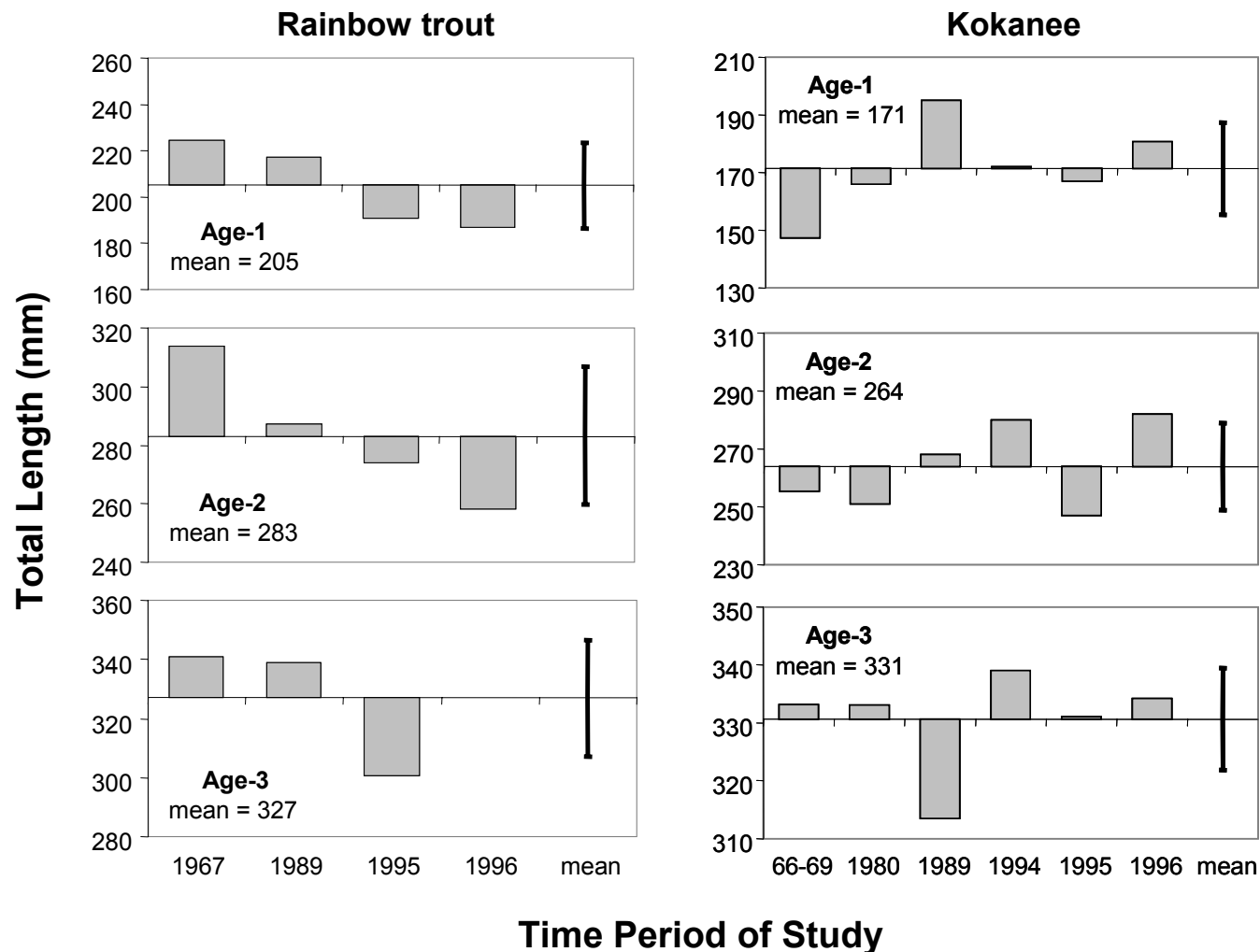


Figure 62. *Left:* Mean length at age of three age classes of rainbow trout sampled from BMR during two periods before dam operations changed (1967, 1989) and during two years after the change (1995, 1996). *Right:* Mean length at age of three age classes of kokanee sampled from BMR during three periods before dam operations changed (1966-1969, 1980, and 1989) and three periods after the change (1994-1996). The overall mean for each species and age class is shown (horizontal line) with its standard deviation (error bar).

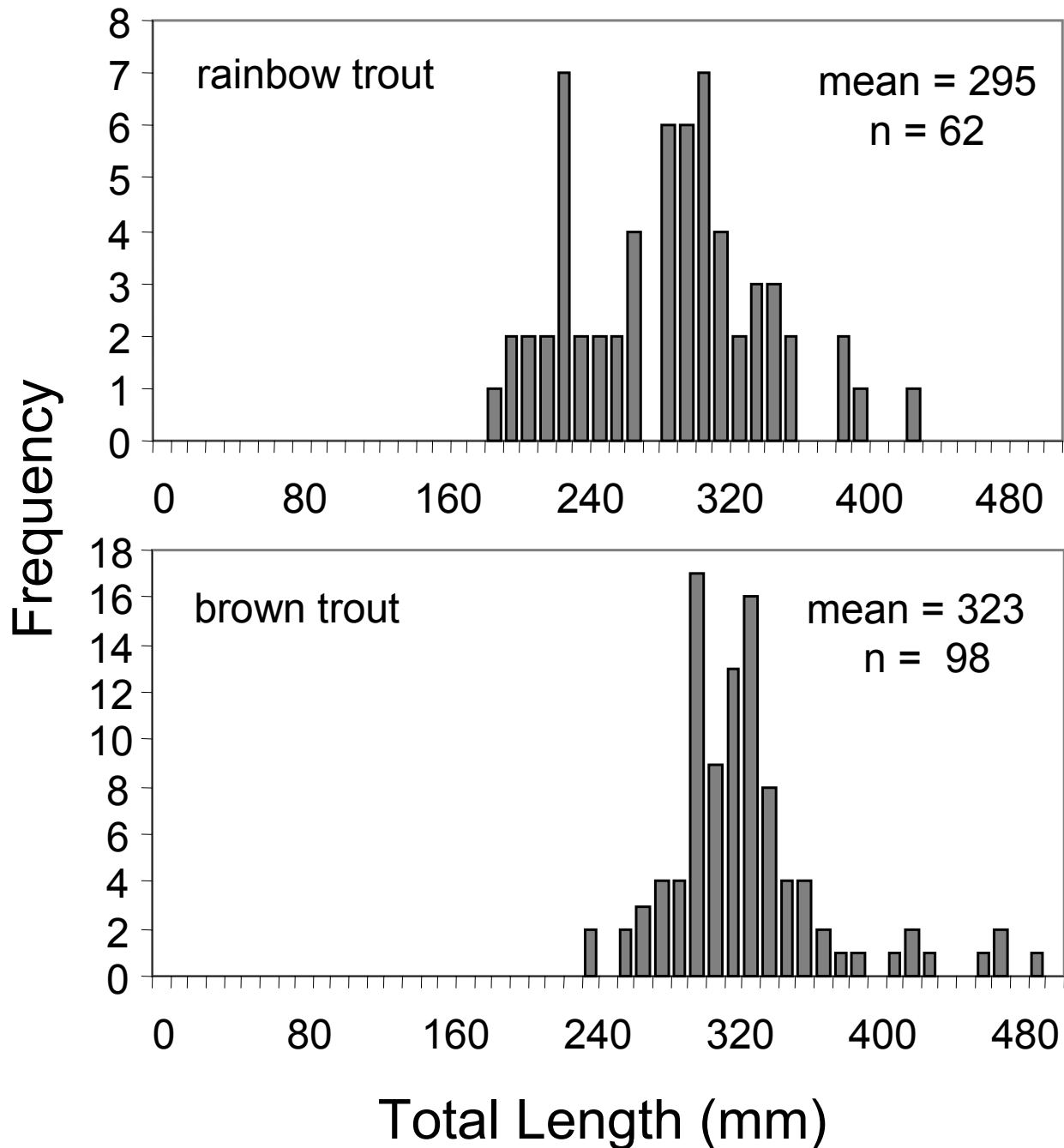


Figure 63. Length-frequency histogram of all rainbow trout and brown trout captured in experimental vertical gill net sets during June 1994-1997. In 1997 sampling occurred during short intervals over a 24 h period with mesh sizes 13, 25, and 32 mm, instead of the overnight sets with meshes 13-50 mm used in other years.

Growth of lake trout in BMR was above average for the species (Figure 64). We revised our estimate of growth rate from what was presented by Johnson and Martinez (2000) when new data from a very large fish became available but growth rate remained

very good. Lake trout are known to live for over 40 years (Power 1978; Schram and Fabrizio 1998). The oldest lake trout aged from BMR was 24 years old (Johnson and Oplinger 2003) and the von Bertalanffy growth trajectory fit to all the available data suggest that BMR lake trout are not yet approaching W_{∞} . Therefore, older and heavier fish can be expected to be found in the future. Several state record lake trout have already been taken from BMR since 1998 but age and growth data suggest that more record fish will be captured in the lake.

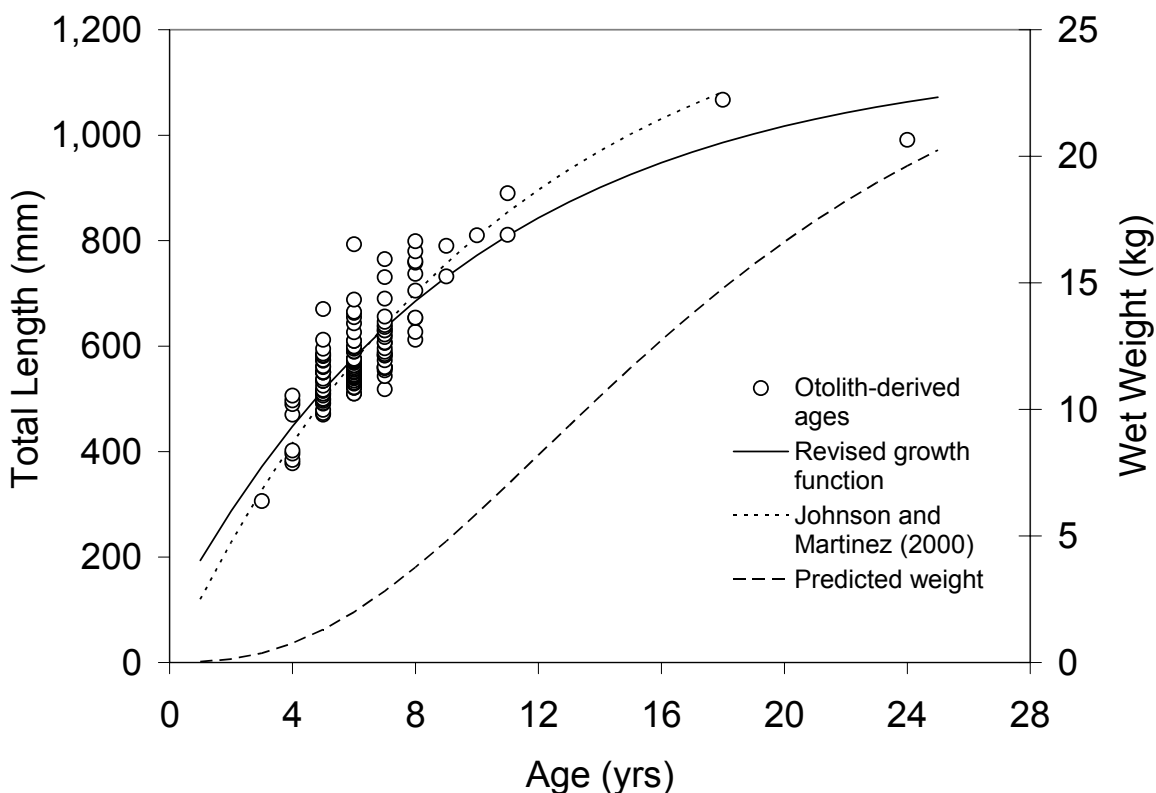


Figure 64. Length at age of BMR lake trout estimated from otoliths (circles), a von Bertalanffy (VB) growth function fit to those ages (solid line), the von Bertalanffy fit reported previously (Johnson and Martinez 2000; dotted line), and the growth in weight estimated from the new VB fit (dashed line).

Body Condition

There was no evidence that new dam operations affected body condition of kokanee and rainbow trout. Body condition of kokanee in BMR (Table 8) was normal for the species. The mean relative weight (W_r) over the course of the present study was 99, with 100 being “normal”. There was no indication of any inter-annual variations in condition since 1993 and relative weight was nearly the same in 1966-1970 ($W_r = 97$; Wiltzius 1971). The extremely low water during the 2002 drought did not appear to have any short term effects on body condition of kokanee. We compared Fulton’s condition factor, a sensitive body condition index, from 2002 with 1995 because these years represent the biggest contrast in dry vs. wet conditions in our dataset. Mean condition factor (k) of all kokanee in sampled in vertical gill nets in August 2002 ($n =$

124; $\bar{k} = 0.102$) was not different (t-test, $p = 0.40$) from the mean from July 28, 1995 ($n = 41$; $\bar{k} = 0.103$). Samples consisted primarily of age-1 and older kokanee. Catches of other fish species were too low to test for differences in condition. There was no evidence in body condition datasets to suggest that the physical conditions in the reservoir resulted in poorer opportunities for growth in 2002 but growth data from 2003 would have been required for a more definitive conclusion. It is possible that the ability of kokanee to undergo diel vertical migration allows them to cope with a warmer epilimnion without great losses in growth potential, as was shown in simulation modeling by Koski (2004).

Body condition (Table 8) of rainbow trout was slightly below normal ($W_r = 87$), with very little inter-annual variation during 1993-2002. During 1966-1970, the body condition of rainbow trout (198-358 mm TL) was nearly the same ($W_r = 86$; Wiltzius 1971). Body condition of brown trout was moderately poor ($W_r = 75$) and was lower than that measured by Wiltzius (1971) during 1966-1970 ($W_r = 86$). Reasons for the decline in body condition of brown trout since 1970 are unknown.

Length-weight relationships were developed from sizes of fish captured over the course of the study (Table 9). The fit of each regression was excellent ($r^2 \geq 0.94$). These relationships provide an alternative means of studying changes in body condition and can be used in biomass calculations for evaluating trophic interactions.

Body condition of lake trout changed with size; mean W_r was approximately 90 for lake trout < 700 mm TL and > 110 for lake trout > 700 mm TL (Johnson and Martinez 2000).

Diet Composition

In 2001 about 90% of the diet of age-0 kokanee was *Daphnia*, the remainder was chironomid larvae and pupae (Table 10). In 2002, composition of the diet was not quantified but all stomachs from age-0 kokanee contained at least some zooplankton; 27% of the stomachs contained chironomid larvae or pupae (Johnson et al. 2002a). There was overlap in the diet of age-0 kokanee with rainbow trout (Table 11) and with small (< 200 mm TL) lake trout (Figure 65a), all of which consumed a significant fraction of chironomids and zooplankton. Subsequent studies (Johnson et al. 2004) have found that yellow perch sampled from nearshore areas also consumed a high fraction of chironomids. Future studies should examine diet overlap between age-0 kokanee with rainbow trout and yellow perch to determine if competition for food is possible. We did not examine diet of brown trout.

Age-1 and older kokanee fed almost exclusively on zooplankton (99%) during summers of 1994-1997 and 90% of the diet was *Daphnia pulex* (90%) (Table 10; Stockwell et al. 1999). Wiltzius (1974) studied diets of kokanee, rainbow trout and brown trout during 1966-1970. He stated that kokanee guts contained only cladocerans during summer.

The *Daphnia* in kokanee guts was always larger than that seen in the reservoir (Table 12; Johnson et al. 1995). The extreme selectivity of age-1 and older kokanee for large

Daphnia suggests that food availability for kokanee was far from limiting for these fish during the summer. Stockwell et al. (1999) showed that kokanee reduced the water content of the *Daphnia* they consumed by about half; thus, they were capable of consuming a greater number of prey in a given stomach volume. Consequently, the energy content of a stomach full of *Daphnia* was about double what it would be without water reduction, and the maximum ration (by mass) had about twice the energetic value compared to an equivalent mass of *Daphnia* in the reservoir.

About half of the diet of all sizes of rainbow trout was terrestrial insects indicative of their distribution near the surface of the reservoir. Terrestrial insects were not found in any other species. Wiltzius (1974) also found that terrestrial insects were common in rainbow trout guts, mainly in fish > 250 mm TL. He found that small rainbows (<200 mm TL) ate mainly *Daphnia*. We did not sample fish for gut content analysis during spring when fingerling kokanee arrived in the reservoir but Wiltzius (1974) found fish remains in rainbow trout and brown trout >250 mm TL sampled from areas where rainbow and kokanee fingerlings were stocked. Fish were very rare in guts of rainbow and brown trout sampled elsewhere.

The diet of lake trout < 200 mm TL was composed entirely of invertebrates, mainly chironomid larvae and pupae (Figure 65). Crayfish were an important diet item for lake trout 200-400 mm. Lake trout diet included more fish (primarily salmonids) as lake trout size increased. The diet of all lake trout greater than approximately 400 mm was similar in 1994-1997 and in 2001 (about 70% salmonids, 20% crayfish, and 10% other fish).

In 2001, diet of lake trout ≥600 mm was 96% fish, of which 90% were kokanee and rainbow trout. The average diet composition of lake trout ≥600 mm during 2001 (Figure 65) included 88% salmonids and 12% invertebrates. Lake trout over 700 mm ate almost exclusively fish.

Food Web Configuration

Diet studies and stable isotope analyses lent insights into food web structure at BMR. In general, carbon signatures of BMR fishes were in accord with diet information suggesting that the short-term information in diet samples reflects longer term diet composition. The isotopic signature of kokanee was consistent with a pelagic-based production pathway, while carbon signatures of rainbow trout and catostomids suggested a diet primarily composed of prey of benthic or terrestrial origin (Figure 67, 68). Diet data have shown that kokanee consumed almost exclusively cladocerans, and that rainbow trout diet is composed of about half zooplankton and half insects. Lake trout carbon values confirmed that kokanee were important prey for lake trout in BMR. Diet analysis showed that juvenile lake trout fed mainly on insects and decapods with some fish in BMR; lake trout diet switched to an increasing fraction of fish as they grew (Figure 67).

A study conducted after ours (Johnson et al. 2004) found that yellow perch sampled from the littoral zone at BMR fed mainly on chironomid larvae and pupae. Zooplankton were not an important diet component in those samples but we believe the contribution

Table 8. Mean relative weight (W_r) of all kokanee, rainbow trout, and brown trout captured in vertical gill net sets in BMR during 1994-2002 and by Wiltzius (1971) in 1966-1970. There was no trend in W_r with TL for any species; thus, a mean W_r was computed each year, without regard to the size of fish sampled. "Range" shows the range in TL of fish included in the computations. Standard deviation of the mean is shown as SD (not available for 1966-1970); sample size is n.

Year	<u>Kokanee</u>				<u>Rainbow trout</u>				<u>Brown trout</u>			
	Range (mm)	W_r	SD	n	Range (mm)	W_r	SD	N	Range (mm)	W_r	SD	n
1966-1970	201-356	97	--	10	201-356	87	--	20	201-353	86	--	15
1994	120-322	95	10	332	200-322	88	8.8	13	238-468	69	8.3	23
1995	120-438	99	9.4	222	221-387	86	7.9	6	239-424	73	6.4	36
1996	182-447	100	7.6	88	189-421	85	9.7	5	239-322	85	3.8	3
1997	131-445	98	8.0	363	198-383	88	8.1	36	232-489	72	7.2	57
2001	230-412	103	10	17	--	--	--	--	285-312	76	6.2	4
2002	125-437	97	7.4	125	400	88	0.0	1	266-431	75	15.3	4
1994-2002	120-447	99	2.7	6	189-421	87	6.9	5	266-489	75	7.9	6

Table 9. Length-weight relationships for kokanee, rainbow trout, brown trout and lake trout sampled from BMR during summer, 1994-2002. Log is $\log_{10}$ and Ln is $\log_e$. Age-0 kokanee were only captured in 2001, 2002. ANCOVA did not detect year effects ($p = 0.98$) so length and weight data from age-0 kokanee sampled in 2001 and 2002 were combined (Hardiman 2003).

Species	Age or size (mm)	Equation (mm, g)	r^2	n
Kokanee	Age-0	$\text{Ln}(W) = 3.068 \cdot \text{Ln}(TL) - 12.108$	0.96	--
	109-447	$\text{Log}(W) = 3.024 \cdot \text{Log}(TL) - 5.046$	0.98	1,162
Rainbow trout	189-421	$\text{Log}(W) = 2.781 \cdot \text{Log}(TL) - 4.398$	0.98	61
Brown trout	232-489	$\text{Log}(W) = 2.956 \cdot \text{Log}(TL) - 5.000$	0.94	127
Lake trout	306-890	$\text{Log}(W) = 3.765 \cdot \text{Log}(TL) - 7.103$	0.99	8

Table 10. The mean percentage (by volume) of *Daphnia pulex*, other zooplankton and macroinvertebrates found in diet samples collected from kokanee sampled with vertical gill nets and from angler catch at BMR in 1994-1996, and in a midwater trawl in 2001. Stomach contents from up to 10 fish were pooled prior to analysis; n is the number of pooled samples examined. Size class 1 contained fish 109-249 mm TL (mostly age-1 and older), size class 2: 250-349 mm TL, and size class 3: ≥ 350 mm. Size class 2.5 contains fish from size classes 2 and 3. In 2001, only age-0 fish were sampled and stomach contents were not pooled across fish.

Year	Age or Size class	n	<i>Daphnia pulex</i>	Mean (%) Other zooplankton	Macro- invertebrates
1994	1	5	95.8	4.0	0.2
	2	14	94.1	1.9	4.0
	3	23	96.8	2.0	1.2
1995	1	27	100.0	0.0	0.0
	2	25	98.5	1.0	0.5
	2.5	35	99.0	1.0	0.0
	3	37	97.5	2.0	0.5
1996	1	1	100.0	0.0	0.0
	2	3	99.7	0.0	0.3
	3	4	95.8	4.0	0.2
Mean	Age 1-3	10	97.7	1.6	0.7
2001	Age-0	27	89.9	0.0	10.1

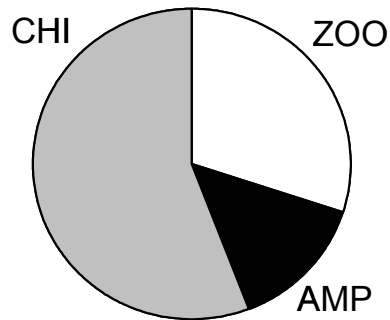
Table 11. Mean composition (%) of the diet of two size classes of rainbow trout sampled from vertical gill nets and angler catch at BMR in 1995, 1996 and 1997. The number of stomachs examined is n. Aquatic insects were primarily chironomid larvae and pupae. Terrestrial insects included Hymenoptera, Coleoptera, Hemiptera, and Tricoptera (adults).

Size class (mm)	n	Taxon	Mean (%)	SD	CV (%)
<300	23	Terrestrial insects	28	33	127
		Aquatic insects	19	36	196
		Crayfish	3	17	480
		Fish	4	18	480
		Cladocerans	46	41	94
>300	22	Terrestrial insects	67	41	62
		Aquatic insects	2	11	459
		Crayfish	0	0	0
		Fish	0	0	0
		Cladocerans	31	42	135
All	45	Terrestrial insects	47	42	92
		Aquatic insects	11	28	263
		Crayfish	2	12	671
		Fish	2	13	671
		Cladocerans	38	42	111

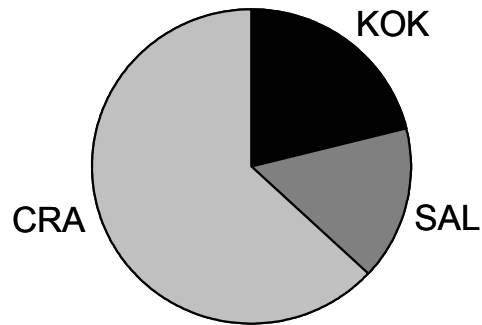
Table 12. The mean length of *Daphnia pulex* found in the stomachs of all sizes of kokanee captured in gill nets and sampled from angler catch at BMR, 1994-1996.

Year	Month	n	Mean (mm)	SD	SE
1994	June	317	1.6	0.22	0.01
	July	333	1.72	0.18	0.01
	August	105	1.53	0.22	0.02
	October	107	1.44	0.18	0.02
1995	May	21	1.61	0.2	0.04
	June	227	1.61	0.22	0.01
	July	131	1.72	0.22	0.02
	August	109	1.72	0.28	0.03
	September	46	1.78	0.19	0.03
1996	June	53	1.66	0.19	0.03
	July	59	1.88	0.24	0.03
Summary		11	1.67	0.12	0.04

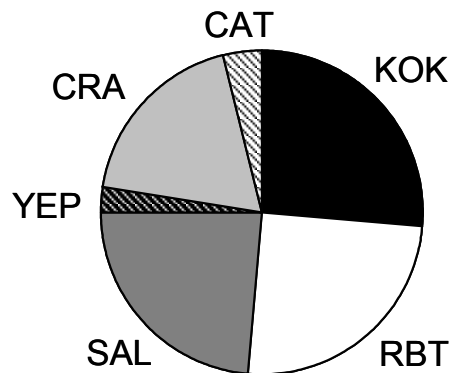
(a) <200 mm (n = 9)



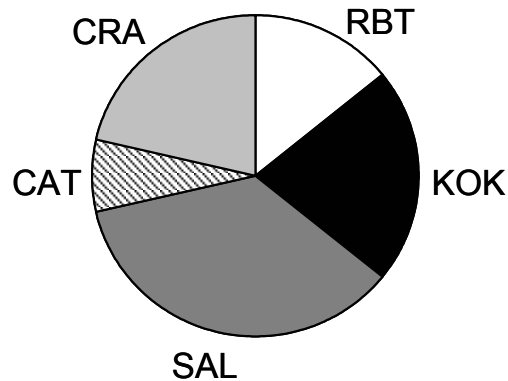
(b) 234-440 mm (n =49)



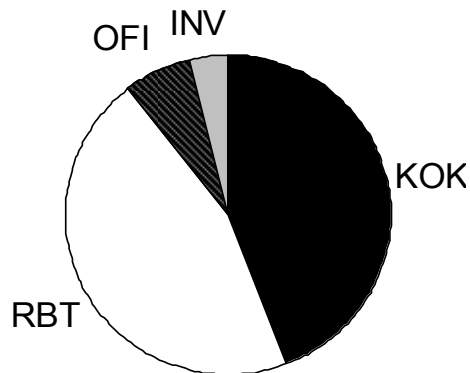
(c) 442-827 (n = 101)



(d) 450-965 (n = 28)



(e) 606-827 mm (n =19)



Taxonomic codes

AMP	amphipod
CAT	catostomid
CHI	chironomid
CRA	crayfish
INV	invertebrate
KOK	kokanee
RBT	rainbow trout
SAL	salmonid
YEP	yellow perch
ZOO	zooplankton

Figure 65. Diet composition of five groups of lake trout from BMR. Fish were sampled during (a) July 2002; (b) summer, 1994-1997; (c) April-May and November 2001; and (d) summer, 1994-1997, and (e) April-May and November 2001; n is the number of non-empty stomachs examined. Fish prey included only those that could be identified to family.



Figure 66. Undergraduate Alissa Gigliotti holds an age-0 kokanee sampled with a small mesh gill net used to study vertical distribution of young kokanee.

of zooplankton to the diet may have been underestimated due to the habitat where the samples were collected. More detailed study of the trophic ecology of yellow perch in BMR is needed. More samples of yellow perch for diet and stable isotope analyses should be gathered from BMR, with fish from different seasons and across a range of sizes.

Because diet and isotopic data were not available for brown trout or northern pike (*Esox lucius*), it was not possible to confirm their roles in the food web. Most fishes undergo a trophic ontogeny, changing their diet as they grow (Mittelbach and Persson 1998) and

brown trout and northern pike are known to be piscivorous, at least as adults. We presume that young brown trout fed mainly on invertebrates, including benthic organisms and to a lesser degree, zooplankton. Wiltzius (1971) found that brown trout began eating fish at about 250 mm TL. No information exists regarding the food habits of northern pike at BMR. Diet samples of brown trout and northern pike are required to assess their trophic impact. Particularly, it is important to obtain samples over a broad size range, during each season of the year, and from both littoral and pelagic habitats.

The importance of piscivory by lake trout to kokanee survival has been well documented by this study and others (Johnson and Martinez 2000). However, consumption by lake trout should be considered a minimum estimate of the intensity of piscivory faced by kokanee until more detailed information on yellow perch, brown trout and northern pike diets are available.

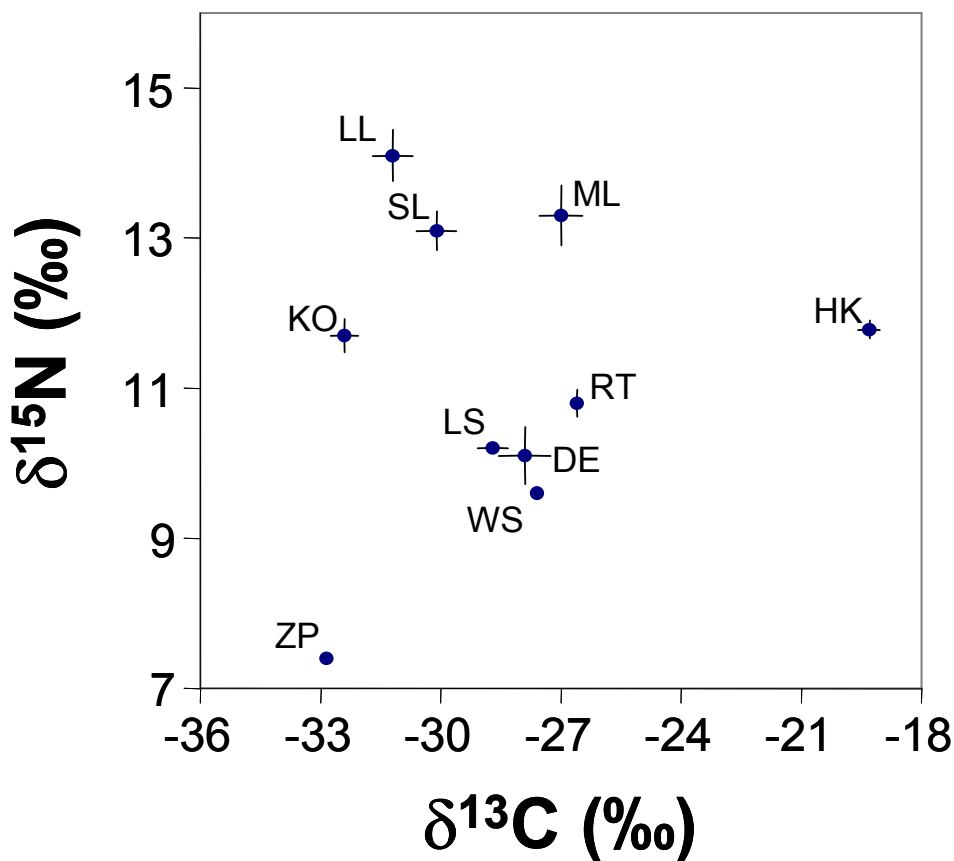


Figure 67. Least squares mean (with error bars, +/-SE) or simple mean (without error bars) carbon and nitrogen isotope ratios of biota sampled from BMR in 1997 (Johnson et al. 2002b). ZP=zooplankton, KO=kokanee, MR= *Mysis relicta*, DE=decapods, LS=longnose sucker, WS=white sucker, RT=rainbow trout, SL=lake trout <426 mm, ML=lake trout 426-600 mm, and LL=lake trout >600 mm.

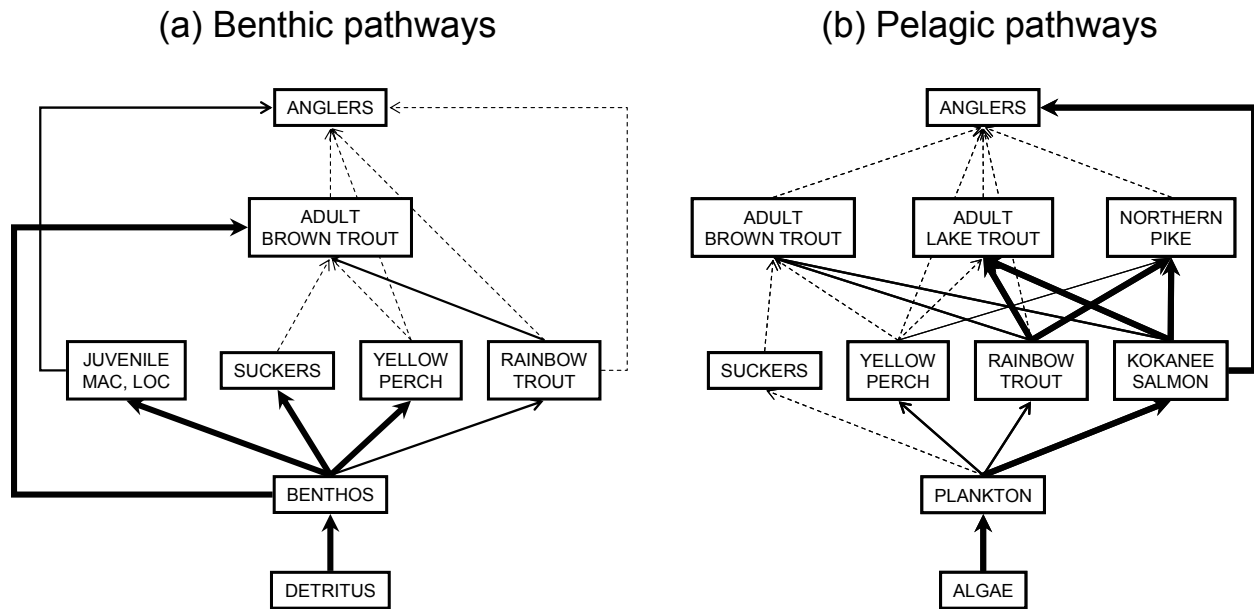


Figure 68. Primary linkages in the (a) benthic, and (b) pelagic food web of BMR. In most cases linkages were determined from diet, stable isotope analysis, and creel survey data. Thickness of the arrows represents presumed strength of the interaction. Note that northern pike and yellow perch invaded the reservoir late in the present study and their role in the food web is not well known.

Recruitment and Survival

Recruitment and survival are linked because the survival of a cohort dictates its recruitment to later life stages. We evaluated several potential factors that could have contributed to trends in recruitment and survival, primarily of kokanee, in BMR: stocking rates, survival during the river transit stage immediately post-stocking, entrainment, predation, and harvest in the sport fishery. We also considered how dam operations and climate might affect risk of predation by lake trout.

Natural Reproduction

There is some evidence of natural reproduction of BMR kokanee. We captured two cohorts of age-0 kokanee during midwater trawl sampling in 2001 (Figure 69). The smaller cohort was approximately the same size as the fry that had been stocked in April (mean ≈ 50 mm TL). Stable isotope analysis showed that those fish possessed a reservoir rather than a hatchery ^{13}C signature (Johnson and Oplinger 2003). If this cohort was actually hatchery fish that did not grow since April then they would likely have shown an isotopic signature that was some combination of hatchery and reservoir signatures. However, this was not the case, strongly suggesting that these fish hatched in the wild. Mueller and Hiebert (1997) also sampled age-0 kokanee < 50 mm TL in August and September 1995 and kokanee ≤ 40 mm TL in June and July 1995, 1996. We suspect that these fish were also the result of natural reproduction but stable isotope signatures were not available. While definitive data are lacking, the very small size of the purported wild fish suggests they would not recruit to the adult population.

because they would be more subject to size-selective predation and overwinter mortality. We assume that the kokanee population in BMR is composed almost entirely of stocked fish.

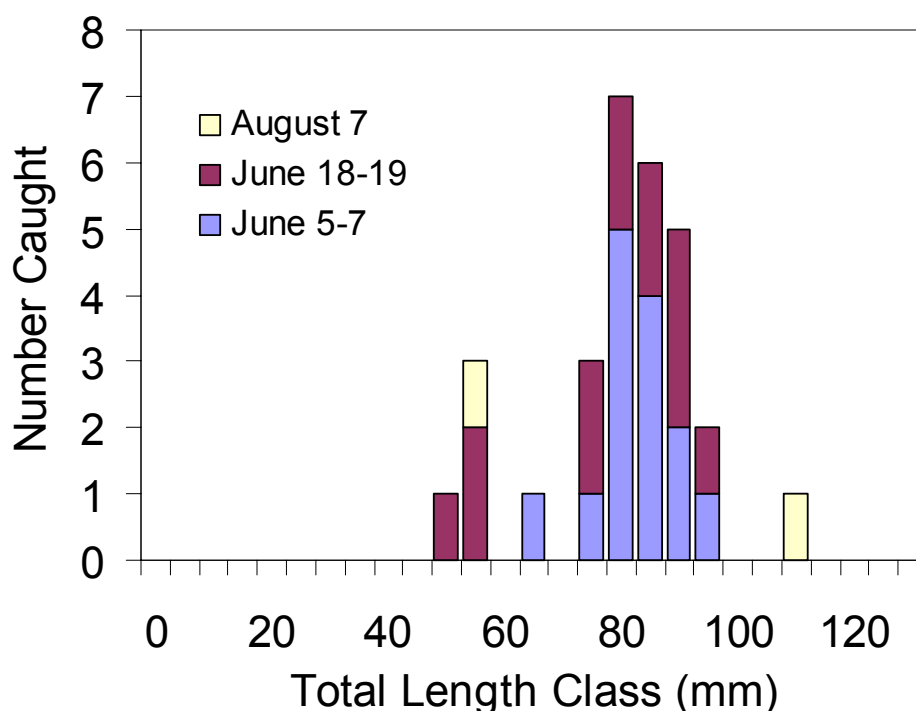


Figure 69. Length-frequency histogram of all age-0 kokanee captured in a midwater trawl during three periods in summer, 2001.

Natural reproduction of rainbow trout was documented by Wiltzius (1971). He observed spawning activity in West Elk, Willow and Coal creeks, and age-0 rainbow trout were found in Coal Creek. We observed spawning aggregations of rainbow trout in West Elk Creek but we did not sample for young. Wiltzius deemed natural reproduction of rainbow trout insufficient to sustain a reservoir population, necessitating regular stocking of this species. Brown and lake trout are self-sustaining in BMR. Blue Mesa Reservoir brown trout reproduce in the Gunnison River, Lake Fork of the Gunnison and Cebolla Creek (Wiltzius 1971). Age and growth information suggested that recruitment was fairly consistent with ages 3-7 present in our gill net samples from the reservoir. Fourteen age-classes of lake trout (ages 5-17 and age-19) were found in gill net samples in 2001 suggesting that recruitment occurs virtually annually at BMR. One 24 year old fish was documented in 1998 but sample size of old fish was insufficient to judge consistency of recruitment before 1982.

Stocking and Abundance

Stocking of kokanee fry into BMR has generally increased since the reservoir was constructed, with rapidly increasing stocking rates during the term of the present study

(Figure 70). Hydroacoustics surveys and angler catch rate suggested that the abundance, and therefore recruitment and survival of kokanee varied greatly during 1993-2003. Overall, survival, adult abundance, and the proportion of stocked kokanee that were harvested by anglers (Figure 71) showed a decreasing trend since 1993.

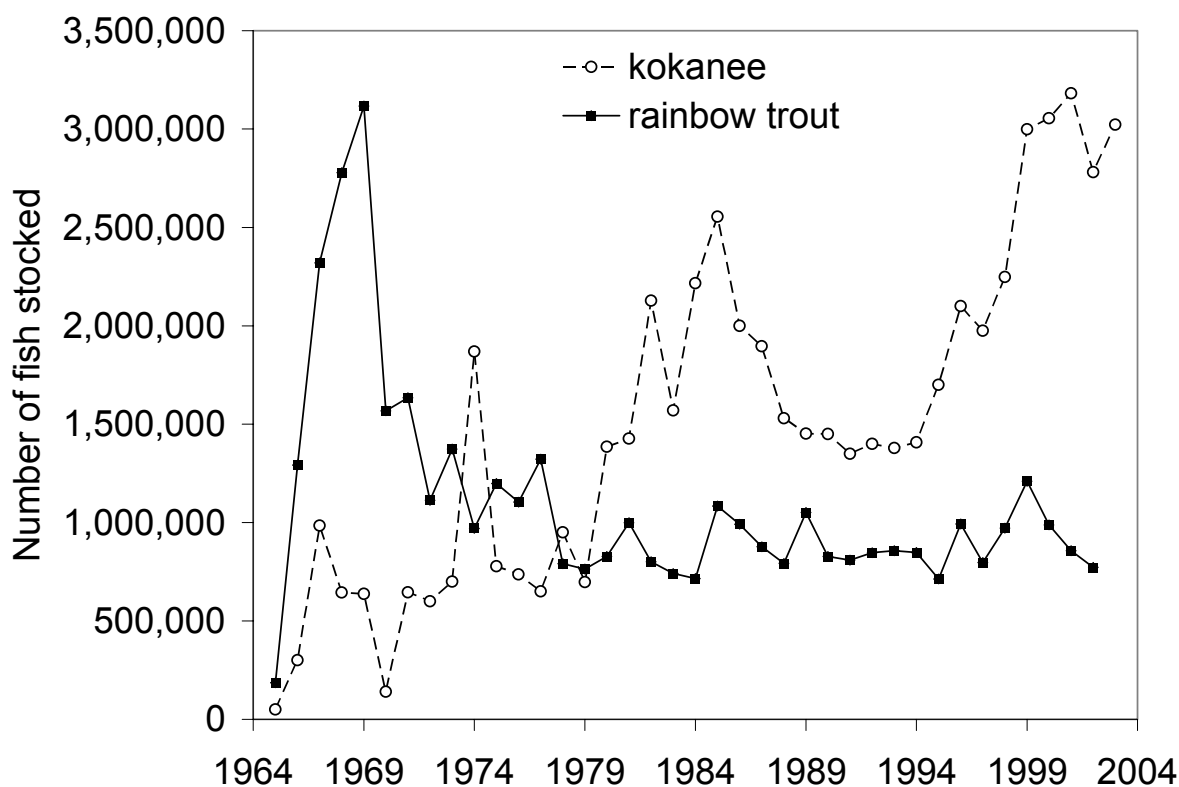


Figure 70. Number of kokanee and rainbow trout stocked into BMR during 1965-2004 (Dan Brauch, CDOW)

An evaluation of the importance of four mortality sources for the BMR kokanee population (short term losses of stocked fry as they migrated to the reservoir, entrainment of fish in the dam outflow, predation by lake trout, and angler harvest) suggested that multiple factors are responsible for these variations.

Sonar estimates of pelagic fish abundance (all sizes and all species) from surveys conducted in August each year generally tracked the number of kokanee stocked (Figure 72). This was not surprising because gill net sampling and the creel survey suggest that the vast majority of the fish in BMR are kokanee, particularly in the pelagic zone. However, the survival of kokanee and abundance of larger kokanee (15-45 cm) appears to have been on a declining trend. Hydroacoustics estimates of adult kokanee indicated that adult abundance decreased during 2001-2003. Catch rate of kokanee (fish/angler-hour) suggested that adult kokanee density declined during 1993-1999 despite increasing stocking during that period. Catch rate of kokanee began to increase

after 1999, but dipped again in 2003. Catch rate in 2002 (0.56 kokanee per angler-hour) was the highest it had been since 1993. The high catch rate may be explained by greater catchability of the kokanee stock due to the smaller reservoir volume that year. Catch rate can also be a misleading indicator of kokanee abundance because kokanee appear to become more catchable as their size increases (P. J. Martinez, CDOW, personal communication). Unfortunately, a larger mean size of kokanee is usually associated with lower population abundance.

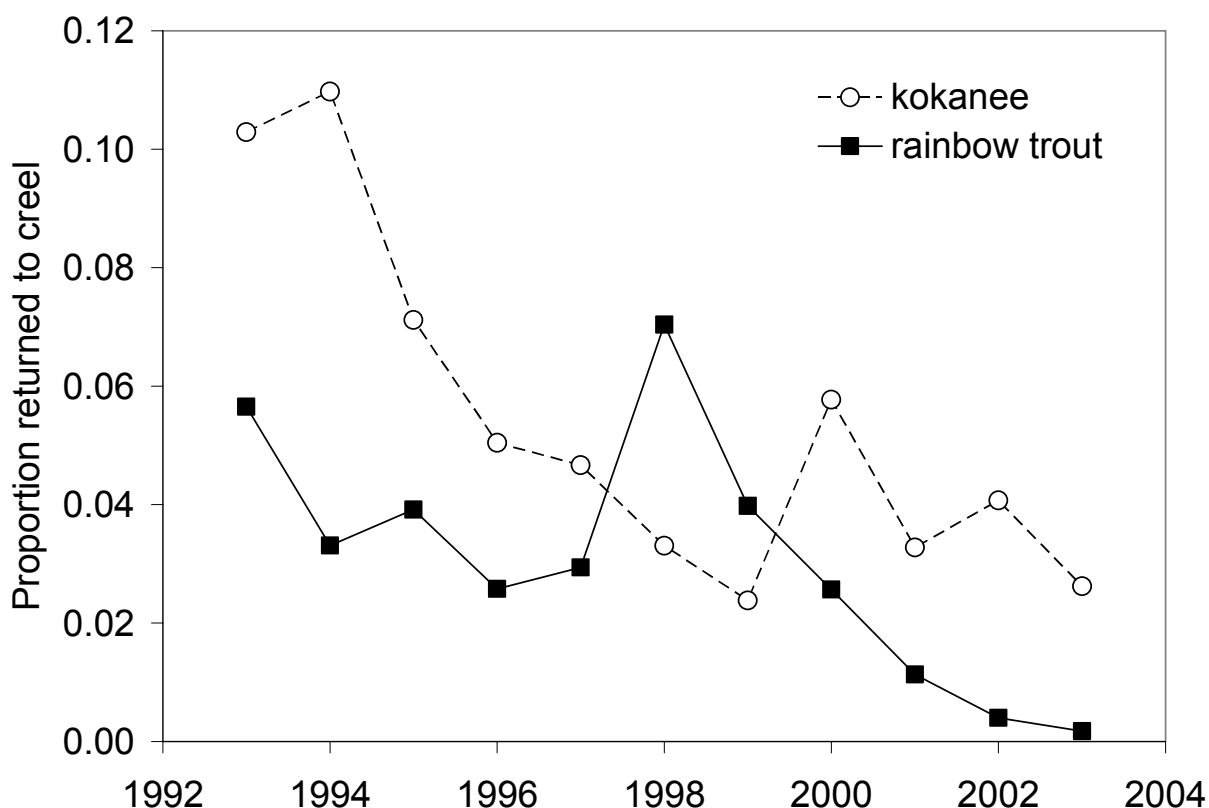


Figure 71. Proportion of the fish stocked that were harvested by anglers, assuming that rainbow trout are caught in the year following stocking and kokanee are caught three years after stocking.

We believe catch rate is a better indicator of abundance of rainbow trout because there is no indication that catchability is size-related, within the size range seen at BMR. Judging from Figure 73 it appears that rainbow trout abundance was low during 1993-1996 and 2000-2003. Catchable rainbow trout were only stocked during 1997-1998, which likely explains the catch rate in those years. It is unclear why subcatchable rainbow trout do not appear to survive well in BMR, given the large supply of zooplankton prey. If survival of rainbow trout is indeed size-dependent then catch rate and harvest of rainbow trout could improve if CDOW returned to stocking catchable rainbow trout in BMR.

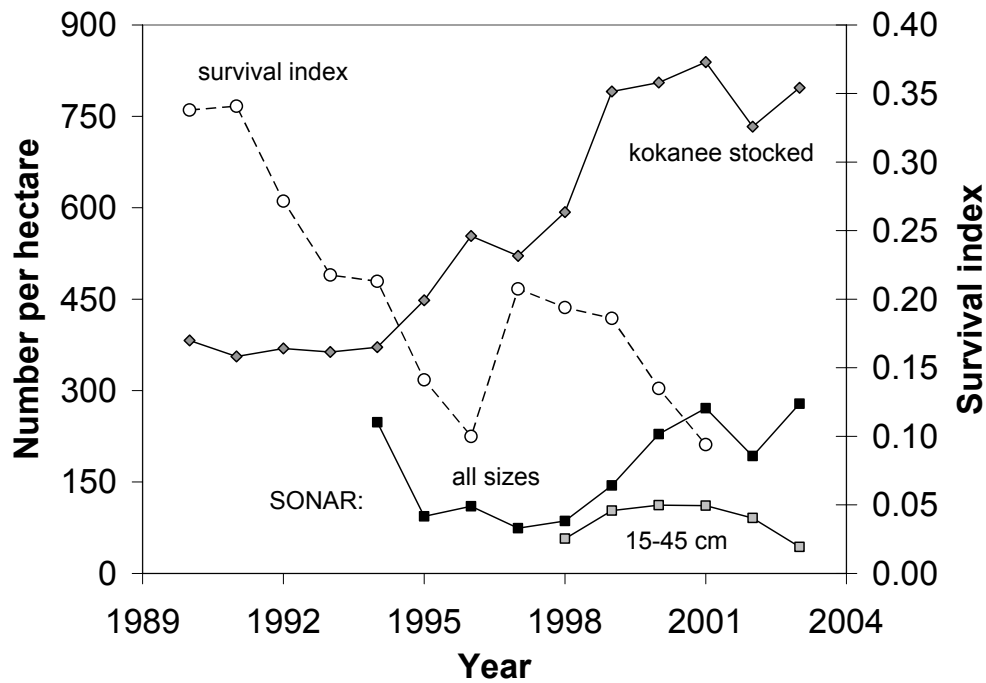


Figure 72. An index of kokanee survival by year-class, number (per ha) of kokanee fry stocked and the estimated abundance of pelagic fish from SONAR surveys performed during August, 1993-2003 (all sizes: black squares, and 15-45 cm fish: gray squares).

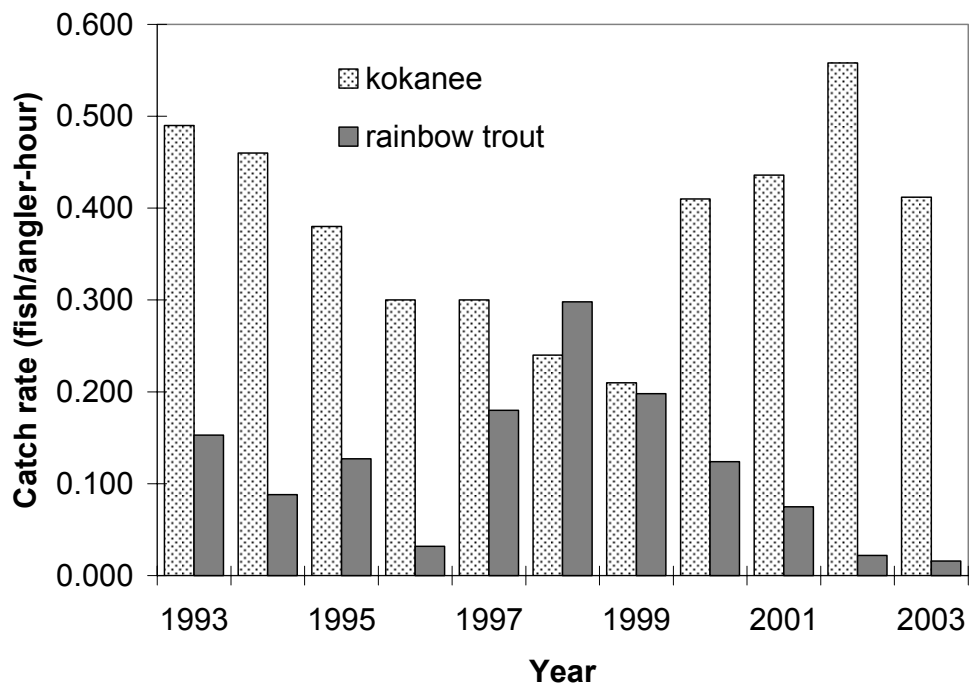


Figure 73. Catch rate of kokanee and rainbow trout in BMR estimated from creel surveys during 1993-2003.

Lake trout were stocked in BMR in six years, initially in 1968 (Table 13). The oldest lake trout aged from BMR was estimated to be 24 years (from otoliths aged by noted expert) in 1998. This suggests that the initial plant may not have been successful and that subsequent plants made in the 1970's resulted in the establishment of the BMR lake trout population. Age structure of the lake trout population estimated from length-frequency data and aging of otoliths from fish sampled in 1998-2001 indicate that lake trout have reproduced successfully in every year since 1992; because few large fish died during sampling data from older fish are too sparse to assess recruitment prior to this period. Crockett (2004) estimated that there were approximately 5,000 lake trout of piscivorous size (425 mm TL, Johnson and Martinez 2000) in 2001 and about 2,000 of those fish were > 592 mm TL.

Table 13. Summary of lake trout stocking at BMR during 1968-1992. The initial plant (1968) was accidental; the airplane that was to stock the fish in Morrow Point Reservoir was unable to do so and the fish were stocked into BMR without authorization. No lake trout have been stocked since 1992 (source: Dan Brauch, CDOW, unpublished data).

Date	Number stocked	Size (mm)	Number per kg	Total weight (kg)
May-68	28,000	25	--	--
Jun-72	35,200	25	--	--
Jun-73	24,960	64	73	71
Jun-74	18,060	66	67	56
Sep-88	10,000	117	18	114
Oct-92	24,709	130	13	398

River Transit Stage

This study provided some significant insights about the early life history of BMR kokanee immediately after stocking. First, we found that there was no substantial size-selective mortality during the transit of the fish from the hatchery to the reservoir. There appeared to be no trend in the size of kokanee passing each of the sampling sites (Hardiman and Johnson 2001). Mean total length ranged 54-65 mm across sites and did not differ through time or across sites.

Second, stocked fish migrated from the hatchery to the reservoir relatively quickly. Catch per unit effort (CPE) of kokanee captured in the seines declined rapidly after stocking. Peak CPE in the most downstream site occurred about 8.5 hours after stocked fish first entered the East River at Roaring Judy Hatchery, suggesting that the fish migrated at an average rate of approximately 3.8 km/h. Overall, trends in CPE vs. sampling location suggest that the fish traversed the distance from the hatchery to the reservoir in <12 hours. However, the stocked fish still arrived at the reservoir during

daylight hours. The kokanee may also have been somewhat disoriented and naïve about predators, making them vulnerable to attack from in-reservoir piscivores such as brown trout and lake trout. This mortality component could not be evaluated in our study.

Third, we discovered extremely high losses of stocked kokanee in one of the irrigation diversion sites (833 fish per minute or about 50,000 fish per hour) in 2001 (Figure 74). This value is probably an underestimate of the entrainment losses at the site because of incomplete sampling of the flow leaving the river and entering the ditch. Dan Brauch (CDOW, personal communication) estimated that in 2001 about one third of the kokanee stocked from the Roaring Judy Hatchery were lost to irrigation ditches. Based on minimum hatchery production cost estimates, the cost to produce kokanee fry in 1996 (Martinez 1996, Johnson and Martinez 2000) losses to irrigation diversions would have cost upwards of \$150,000 in that year. Of course, stocked kokanee have a much higher value if they survive to enter the fishery.

Wiltzius (1978) estimated that in 1974 about 60% of the 1,000,000 kokanee fry stocked from Roaring Judy Hatchery did not make it to the reservoir, citing predation and losses to irrigation ditches as the causes. Given the lack of any changes in the size distribution of the cohort and the short period of the downstream migration in 2001, we assume that irrigation ditches represent the most significant and preventable mortality factor related to the success of fry stocking.

Whether or not irrigation diversions are open when the kokanee are stocked varies from year to year, but they are more likely to be open in dry years when ranchers are concerned about drawing off enough water for their fields (Dan Brauch, CDOW, personal communication). Inflow to BMR showed a declining trend since 1993 and we speculate that the irrigation diversions may be partly responsible for the downward trend in kokanee fry survival over the same period. Closing or blocking irrigation diversions with nets for just a few hours on the night of the kokanee fry stocking could minimize this mortality source and result in significantly more kokanee successfully traversing the river to Blue Mesa and entering the fishery. The CDOW began blocking off diversions as a result of this study.

A useful byproduct of this study was the thermal marking procedure we developed (Figure 75). The technique was highly effective and will provide an efficient method of uniquely marking different lots of hatchery fish for future studies of kokanee stocking procedures and recruitment in Colorado reservoirs (Hardiman and Johnson 2001).

Entrainment Losses

Entrainment of sport fish is a direct effect of dam operations on reservoir fisheries, and kokanee are particularly susceptible to entrainment (Maiolie et al. 1992). There is conflicting evidence about the intensity of fish entrainment at BMR. Wiltzius (1978) reported that beginning in 1971 there was evidence of entrainment of kokanee and rainbow trout through Blue Mesa Dam. He initiated a study of entrainment in 1973 by marking several million small rainbow trout and kokanee with either fluorescent



Figure 74. Screen set up by CDOW to divert stocked kokanee away from an irrigation ditch on the Gunnison River above BMR.

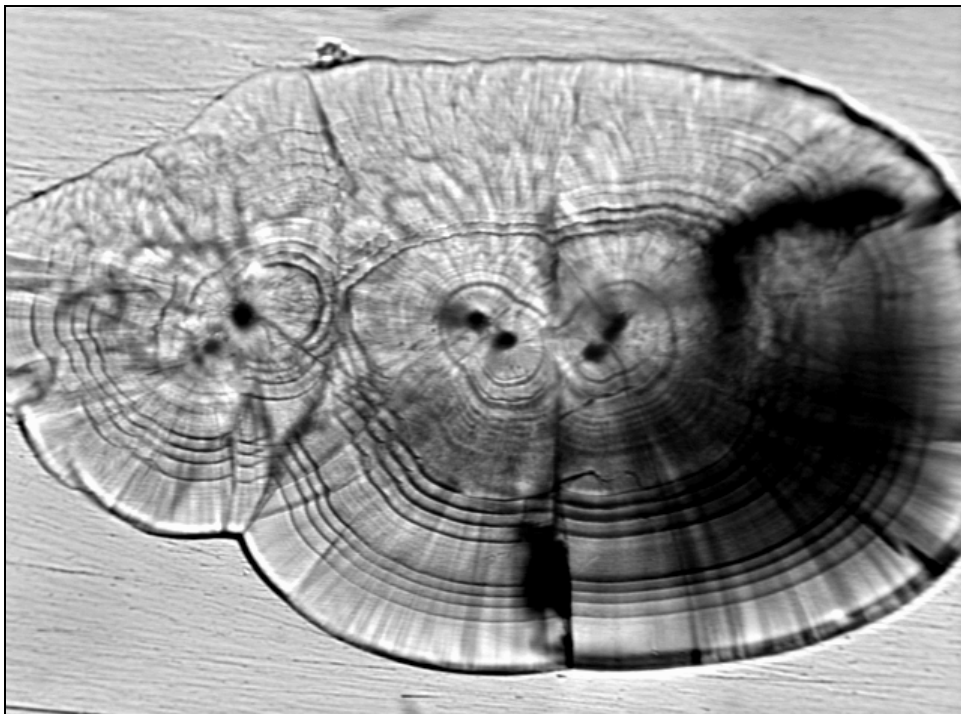


Figure 75. Otolith from a young kokanee showing thermal marks (two series of dark bands) imparted to the otolith by varying water temperature in the hatchery.

pigments or tetracycline prior to stocking and looking for marked fish in the river and reservoirs below BMR. No spills occurred at BMR during the period of his study so presumably emigration occurred through the penstock.

Surveys at Morrow Point Reservoir in 1977 showed that nearly the entire kokanee population was composed of marked fish that had passed through the turbines of Blue Mesa Dam. It was determined that these fish were entrained as age-0 and age-1 fish during November and December of 1974 and 1975, respectively.

It appears that in some years, losses of kokanee through Blue Mesa Dam can be high. Significant entrainment losses have been observed in many other kokanee populations in western reservoirs (Skaar et al. 1996; Maiolie et al. 1992; Stober et al. 1979). Maiolie and Elam (1996) determined that about 90% ($>1.5 \times 10^6$) of the kokanee population in Dworshak Reservoir, Idaho, passed through the dam during winter of one year, but entrainment was low during summer. Longitudinal position of the fish in the reservoir appeared to explain the variation in entrainment rates; in summer the bulk of the population was not located near the dam.



Figure 76. Blue Mesa dam releasing water through its jet tubes used during periods of large releases (photo: Reclamation).

Estimates of fish entrained in the outflow from BMR during the present study were derived from work conducted by BR (Hiebert and Mueller 1997). Entrainment was measured with a sieve net placed in the outflow from one of the dam's turbine outlets (Figure 77). The sieve netting occurred during August-November 1994, April-September 1995, and June-August 1996. No sampling occurred during winter months due to excessive ice buildup on the gear.



Figure 77. Sieve net used by Mueller and Hiebert (1997) to sample the outflow from one of the turbines below BMR dam.

Mueller and Hiebert (1997) found that in 1995, a year of high discharge, entrainment was positively correlated with discharge on a daily basis. Maximum entrainment occurred during July 1995. During April to mid-May, most of the fish sampled below the dam were age-1 kokanee (110-150 mm TL). Starting in mid-May the mean size of

kokanee sampled dropped to 65-70 mm and the mean size of entrained fish closely followed the growth trajectory of age-0 kokanee for the remainder of the growing season. It appears that at least some of the stocked kokanee find their way to the dam shortly after stocking, by sometime in May, and that most of the entrainment during summer is comprised of age-0 fish. They found no consistent temporal patterns (diel, monthly or annual) and suggested the factors driving entrainment were a complex interaction of fish behavior, reservoir elevation, season and discharge. The investigators estimated that about 61,000 kokanee were lost from BMR during June-August 1995, and they concluded that entrainment was not responsible for the population declines seen during 1993-1996. However, without knowledge of the longitudinal distribution of kokanee during the winter, when no sieve netting was conducted, we cannot assess the possibility that significant entrainment was occurring during that season, as was reported by Wiltzius (1978) and as was seen in Dworshak Reservoir (Maiolie and Elam 1996).

Although direct evidence of entrainment via sampling in the outflow is more compelling, we were able to examine a longer time series than Mueller and Hiebert (1997) by comparing survival indices with discharge during 1990-2001. There did not appear to be any pattern between the age-1 survival index and discharge. It appears that survival of age-0 kokanee has been on downward trend since 1991 (Figure 78). Overall, during 1990-2001 there was a very weak negative correlation ($r = -0.36$) between age-0 kokanee survival and discharge in May. However, it appears that prior to 1997 there was a relatively strong negative correlation ($r = -0.77$, $n = 7$) between survival and discharge (Figure 78). During 1997-2001, a relatively strong positive correlation was detected despite declining survival during the entire period of study. This pattern does not support the hypothesis that discharge-related entrainment is a driver of survival in all years. Of course it is still possible that significant entrainment has occurred in some years but that the losses were not proportional to discharge rates. It is very important to note that inflow and discharge at BMR were below average and declining during most of the years of the present study.

Factors unrelated to discharge may control distribution of kokanee across the reservoir, and hence the potential for entrainment. Hardiman (2003) found that the density of age-0 kokanee was low in Sapinero basin during May-July. If the low density of fish near the dam during summer is a repeatable pattern, then this may explain the low entrainment rates observed by Mueller and Hiebert (1997) in their summer sampling. However, our work in 2002 indicated that any kokanee in the vicinity of the dam would be at risk of entrainment because their vertical migrations took them to a depth of 60 m in the daytime during May. Even when the reservoir is full, these migrations would take the fish past the penstock (50 m below the surface). In drier years the risk of entrainment may be greater because more fish reach penstock elevation or below throughout the diel cycle during the entire summer. For example, in 2002 the penstock was as shallow as 26 m below the surface. Entrainment of rainbow and brown trout would not be expected, even in dry years such as 2002 because these species rarely were found below 20 m depth.

The distribution of small kokanee during fall-spring was unknown. Although winter weather conditions are extremely challenging at BMR, a thorough evaluation of kokanee entrainment can only be accomplished by either sieve netting below the dam and/or hydroacoustics surveys above the dam during this season.

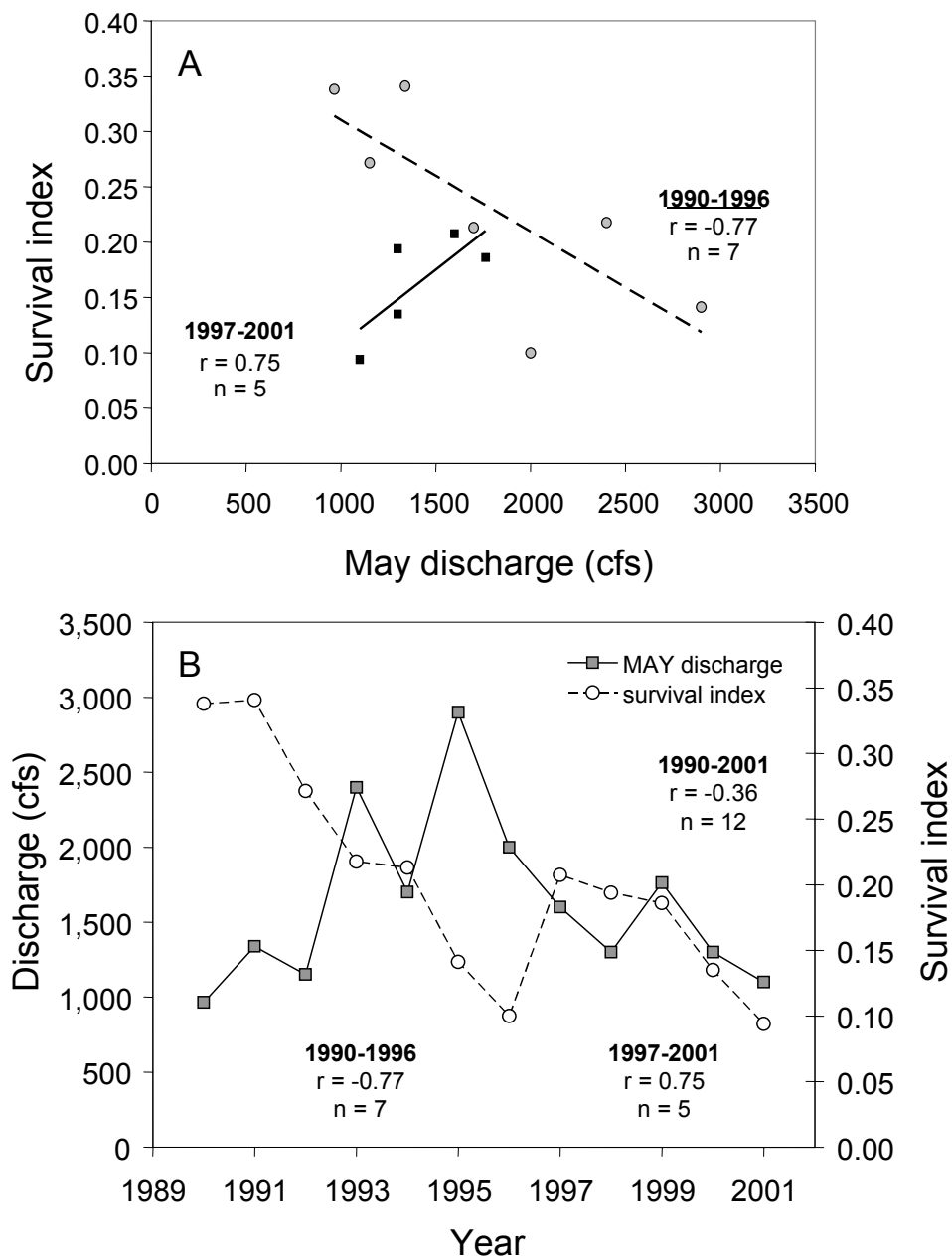


Figure 78. Relationships between mean daily discharge during May and an index of kokanee year-class survival. Panel A shows the correlation between the survival index and May discharge during two groups of years. Panel B shows the annual data for discharge and survival as well as the correlation between these two variables for three sets of years.

Predation

Fish constitute an increasingly important fraction of brown trout diets as they grow (L'Abée-Lund et al. 2002; Jonsson et al. 1999; Scott and Crossman 1973). The average size of brown trout sampled during 1993-2003 was 317 mm ($n = 127$, $SD = 31$). Assuming a maximum prey:predator length of 50% (Mittelbach and Persson 1998), the size structure of the brown trout population in BMR suggests that this species would only be capable of preying on subcatchable rainbow trout and age-0 and age-1 kokanee. The average prey:predator ratio for brown trout is 25% of TL (Mittelbach and Persson 1998) suggesting that brown trout would only constitute a threat to age-0 rainbow trout and kokanee.

Preliminary estimates of consumption demand of lake trout were presented by Johnson and Martinez (2000). A great deal of new information on lake trout abundance, growth, diet and mortality was collected. New estimates of consumption by lake trout using this information are presented here.

Lake trout predation appears to remain a significant mortality source for rainbow trout and kokanee in BMR. Piscivorous cohorts (age-4 and older) of lake trout consumed about 17,000 kg of kokanee per year (Figure 80); lake trout consumed slightly less rainbow trout (about 14,000 kg per year). Lake trout consumed much smaller amounts of other fish. Biomass of rainbow trout consumed is greater than the annual biomass of subcatchables stocked (assuming average size of stocked rainbows was 125 mm; D. Brauch, CDOW, personal communication) and many times higher than the biomass harvested by anglers (Figure 80). The costs of feeding piscivores hatchery trout are well established and they are high (Johnson and Martinez 2000). Managers should evaluate whether or not continued stocking of rainbow trout is justified without reductions in piscivore consumption demand. Stocking catchable sized rainbow trout could reduce their vulnerability to lake trout.

Consumption of kokanee by lake trout is a significant fraction of the estimated annual production of kokanee and approximately equal to the biomass harvested by anglers in 2003 (Figure 80). Because lake trout consume kokanee that are smaller on average than those in the harvest, the number of kokanee consumed by lake trout is much higher than the number harvested by anglers. If one assumes that lake trout consume kokanee that are 33% or 20% of lake trout total length, then the number of kokanee consumed by age-4 and older lake trout would be 183,000-832,000 kokanee per year, compared to 58,000 kokanee harvested by anglers in 2003.

It is possible that we underestimated consumption of kokanee and rainbow trout because 1) there is considerable uncertainty around our estimate of lake trout abundance and 2) our new diet data came from spring and fall only. It would be prudent to consider what consumption demand would be if the true number of lake trout was closer to the upper end of the 95% confidence interval on abundance. Under this assumption, consumption demand would be about 76% higher than the nominal estimate. One might expect kokanee to be more important in lake trout diet in summer. Blue Mesa Reservoir is the state's last reliable kokanee egg source and

kokanee are the cornerstone to Colorado's quality reservoir fisheries for piscivores and non-piscivores alike. Given the tragic consequences in store for reservoir sport fisheries statewide in the event of a kokanee crash at BMR it seems prudent to prioritize maintaining a strong kokanee population there. Threats to kokanee from competition with introduced yellow perch and the additional predation posed by invading northern pike should make managers especially cautious about management actions that could increase consumption demand of piscivores and jeopardize sustainable populations of kokanee.



Figure 79. Dr. Chris Myrick, CSU, showing a kokanee that was consumed by a lake trout he caught while ice fishing at BMR (photo: B. Johnson).

Lake trout predation alone can account for the decline in rainbow trout survival since 1993. However, despite the large number of kokanee consumed by lake trout during the course of the present study, there was still a considerable amount of kokanee mortality unaccounted for and hence, other factors must have contributed to the decline in adult kokanee abundance since new operations began. We showed that up to a third of stocked kokanee fry could be lost to irrigation diversions. The total number of kokanee lost each year to irrigation diversions, consumption by lake trout, and angler harvest was estimated to be about 1.9×10^6 fish compared to the approximately 3.0×10^6 fish stocked per year during 2000-2003. Disease, other post-stocking mortality,

predation by brown trout and small lake trout, and entrainment of kokanee remain as possible factors that could not be evaluated in this study.

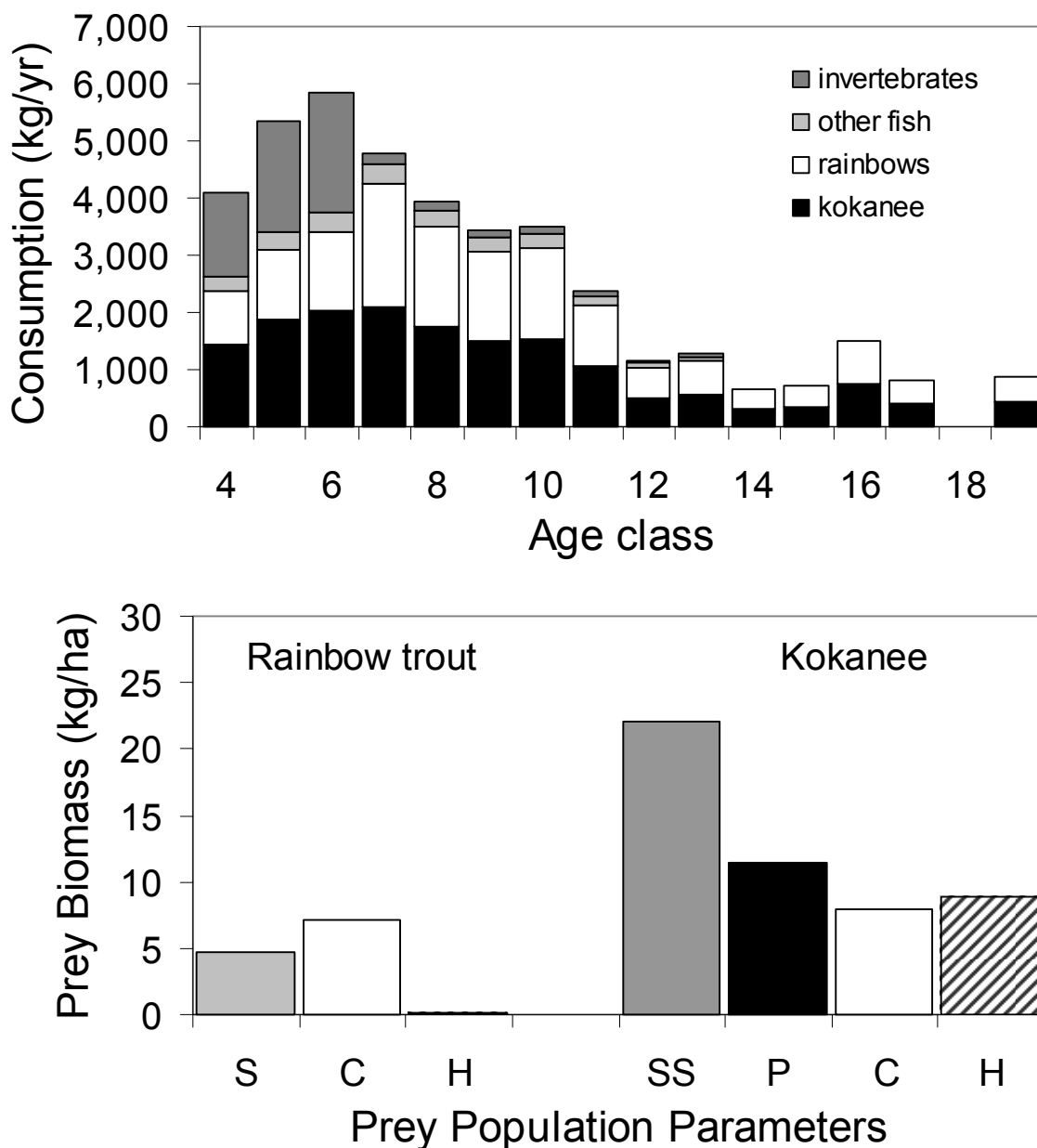


Figure 80. *Upper panel:* Annual consumption of four prey types by age-4 and older lake trout in BMR. The category “other fish” includes yellow perch and catostomids and “invertebrates” includes chironomids and crayfish. *Lower panel:* Biomass (kg/ha) of rainbow trout (left) and kokanee (right) consumed (C) by age-4 and older lake trout in one year at BMR (white bars) compared with biomass of rainbow trout stocked (S), harvest by fishery in 2003 (H), and the standing stock (SS) and production (P), and harvest of kokanee in 2003 (H).

Concerns About Invading Species

Recently there have been discoveries of apparent illicit introductions of two nonnative species, yellow perch (Figure 81) and northern pike (Figure 82), into BMR. These species pose competitive and predatory threats to the kokanee and rainbow trout fisheries of the reservoir.

Apparently, yellow perch were illegally introduced into BMR sometime after 1997 and they became established. Yellow perch first showed up in BMR in creel surveys in 2000. Expansion of the yellow perch population in Blue Mesa is a concern for several reasons.



Figure 81. The yellow perch (*Perca flavescens*) is a coolwater species native to the northern United States east of the Dakotas and Canada (Colorado Division of Wildlife photo).

Yellow perch will compete for food with kokanee and rainbow trout. Yellow perch are very capable planktivores, preferring the very same *Daphnia* species (*D. pulicaria*) (Galbraith 1967) that form 99% of the kokanee diet and about 50% of the rainbow trout diet at BMR (Johnson et al. 2002b). While rainbow trout have the ability to exploit alternative prey (e.g., terrestrial insects), both perch and kokanee are more planktivorous in BMR and thus have the greatest diet overlap and potential for negative competitive interactions. In other systems, yellow perch are capable of stripping lakes of large zooplankton, shifting the species composition and size structure to smaller forms (Shrader 2000, Johnson and Kitchell 1996). Consumption by perch results in reduced food resources for other planktivorous fishes such as kokanee. Competitive interactions among planktivorous fishes could become intense if exotic, predation-resistant zooplankters such as *Bythotrephes cederstroemi*, *Cercopagis pengoi*, and *Daphnia lumholtzi* invade the system. These zooplankton have already become established across a wide range of the nation,

reconfiguring zooplankton community structure with negative impacts to many species of fish and many sport fisheries (New York Sea Grant 2001).

Yellow perch are opportunistic feeders but they are also known to be piscivorous. They typically begin to feed on fish at a total length of 100-170 mm (about age-4 or age-5; Mittelbach and Persson 1998). The yellow perch sampled in BMR in 2002 were too small (mean TL = 105, n = 13, range: 82-142) to prey on anything but small age-0 kokanee, but fish up to 250 mm TL were sampled in 2004. Thus, yellow perch pose a serious threat to kokanee recruitment if they become abundant. It is possible that given the yellow perch's temperature preference ($T_{opt} = 23^{\circ}\text{C}$; Hanson et al. 1997) they will be most numerous in the upper end of the reservoir where age-0 kokanee are concentrated. The relatively high thermal preference of yellow perch also suggests that they will not provide a very suitable forage base for lake trout. Because of the radically different thermal preference of lake trout (10°C ; Stewart et al. 1983) and lower energy density of yellow perch compared to kokanee (Hanson et al. 1997), it is unlikely that lake trout will benefit from or control an expanding perch population. Thus, an increasing yellow perch population will not result in reduced predation rates on kokanee during the summer months when lake trout consumption demand is maximal.

Yellow perch have a propensity to reproduce very rapidly, resulting in overexploitation of their food resources and reduced perch growth and body condition ("stunting"; Scott and Crossman 1973), especially in the absence of predators. Electrofishing surveys and creel survey data during 2001 to 2003 (Dan Brauch, CDOW, personal communication) suggest that yellow perch abundance is increasing rapidly but that the fish were not reaching a size that is attractive to anglers. Thus, yellow perch will probably not supplement the sport fishery at BMR. An unfortunate consequence of the perch introduction is that anglers may perceive a need for a new predator to control yellow perch, setting the stage for additional illegal introductions of exotic predators that will further threaten the BMR fishery, and native and sport fish populations downstream.



Figure 82. The northern pike (*Esox lucius*) is a voracious predator native to the Great Lakes states and Canada (photo: Konrad Schmidt).

Northern pike were recently discovered in BMR and very little is known about their status. Northern pike are coolwater piscivores native to the Great Lakes states and most of Canada. They have been introduced into several waters across the west slope of Colorado. Critical information needs at BMR include: abundance, reproduction rate, distribution, and diet. Northern pike are a growing menace on the west slope with a rapidly developing angler clientele that may make management of the threat difficult. Northern pike grow large quickly on a stocked salmonid prey base thereby providing trophy gamefishing opportunity that previously was scarce in the region. However, this opportunity likely comes at considerable economic and ecological cost that should be quantified. At BMR northern pike likely pose a significant threat to the stocked rainbow trout and kokanee fisheries, and the reservoir serves as yet another stepping stone for a nonnative fish's expansion to new waters in the region.

Effects of Dam Operations and Climate on Growth and Predation Risk

While effects of increased spring releases from the hypolimnetic outlet on kokanee growth were not detected in the field during 1993-2003, modeling suggested that the behavior of kokanee in BMR is driven by the need to balance bioenergetic efficiency with predation risk. Alternative release regimes, such as a TCD and spillway releases, could alter the ability of kokanee to cope with these constraints. Other factors, such as climate and eutrophication, may also have important implications for kokanee growth and survival in the future.

Whether driven by climate change or reservoir management, fishes must respond to changing physical conditions in their environment to both maintain energy acquisition and avoid predation. Modeling performed in associated studies suggested that both spillway releases (Saito and Koski in review) and installation of a TCD to increase release temperatures (Amy Cutler, Reclamation, personal communication) would result in cooler epilimnetic temperatures in the reservoir.

In simulations where kokanee altered their DVM to optimize bioenergetic efficiency, growth was not very different between full-pool, TCD, or drought conditions (Figure 83). Most differences in growth occurred with non-feeding depths that were in the metalimnion, owing to differences in temperatures and rates that energy was assimilated. While a TCD did not directly affect growth in our simulations, kokanee growth may be affected by other dam operations. In a study examining the effects of spillway release on kokanee growth in BMR, Saito and Koski (in review) found that when some water was released over the spillway instead of the hypolimnetic outlet, the epilimnion became thinner and metalimnetic temperatures decreased. This resulted in almost a 9% decrease in daily growth rate for juvenile kokanee when compared to growth in traditional release scenarios. In this case, growth rates were inhibited by both cooler temperatures and decreased zooplankton productivity.

Dam operations and climatic conditions that resulted in changes in temperature and water clarity affected predation risk, impacting not only the magnitude of predation risk, but times and depths in the reservoir where predation risk was highest. In all months,

predation risk was lowest during full-pool conditions and greatest during drought conditions. In general, the amount of time and locations that were characterized by high predation risk increased with warmer months, and shifted to deeper depths.

The tradeoffs between energetic gain and predation risk in different habitats can be evaluated by calculating μ/g , and the ideal habitat (or combination of habitats) is one where this ratio is minimized (Giske et al. 1998). Unlike growth, there were notable changes in μ/g among TCD, full pool and drought scenarios (Figure 83). First, μ/g was generally highest for all three scenarios in June. This was because thermal stratification was not strong and temperatures were lower throughout the water column; lake trout had a higher probability of occurring anywhere in the reservoir. Also, kokanee were small at this time (4.3 g) and were limited in energy acquisition by their stomach size and C_{max} in how much food they could consume and subsequently, how much they could grow. Later in the season, larger kokanee could consume more food and growth was higher relative to predation risk. Among the three scenarios, μ/g was highest for drought conditions in the reservoir foraging environment. This was because water clarity was higher during the drought year, allowing for greater light penetration and increased lake trout reaction distances at greater depths. In addition, both drought and TCD scenarios yielded cooler temperatures between 5 – 60 m. In August, the 10 °C isotherm was almost 20 m shallower in both TCD and drought scenarios compared to full-pool conditions, which could allow lake trout to exploit more of the water column under these thermal scenarios. Under full-pool conditions, warmer epilimnetic temperatures in July and August can create a thermal barrier to lake trout preying on kokanee. As temperatures warm over the summer, DVMs are driven more by bioenergetic efficiency, presumably because of reduced risk in the epi- and metalimnions from coldwater piscivores. However, under TCD and drought conditions, the depth of this thermal barrier was shallower and predation risk increased over a greater volume of the reservoir because light penetration remained high in combination with lower temperatures.

In addition to short-term climate effects (e.g., drought) on kokanee, we also examined the potential consequences of larger-scale environmental change, specifically climate warming and eutrophication (Koski 2004). We assumed that climate warming would affect kokanee directly through bioenergetic mechanisms and indirectly through zooplankton reproductive rate changes. While higher temperatures (with a maximum increase of 6°C in surface waters) increased bioenergetic demands, increased zooplankton productivity was able to meet the kokanee's energetic needs. In eutrophication scenarios we assumed that zooplankton productivity would also increase. However, water clarity was greatly reduced, limiting the ability of kokanee to find and consume their prey. Neither the climate warming nor eutrophication scenarios resulted in significantly different growth rates for age-0 kokanee during the summer growing season alone. However, the interactive effects of climate warming resulted in greatly decreased growth rates, up to 3% body weight loss per day in July and August. This was because kokanee, in order to have enough light to find prey, had to move up to shallower waters that were much warmer than the metalimnion (up to 24 °C, which approaches the lethal temperature range for kokanee). Regardless of the abundant

zooplankton prey, food consumption was unable to match energetic demands in this warmer environment.

Overall, simulation modeling suggests that changes to reservoir thermal structure caused by climatic events such as drought and climate warming, and by new operational modes such as surface spills and use of a TCD, affect the kokanee's opportunity for growth and their risk of predation from lake trout. However, when coupled with increased nutrient loading from the watershed, effects of changes to the thermal environment are compounded by reduced water clarity. If such conditions come to pass at BMR then fishery managers should expect the kokanee population and fishery to become jeopardized. Because climatic events are beyond control, and because drought and warming are likely events in the future, efforts to protect water clarity, e.g., land use controls in the watershed, and reducing piscivore density are recommended to sustain long term viability of kokanee in BMR.

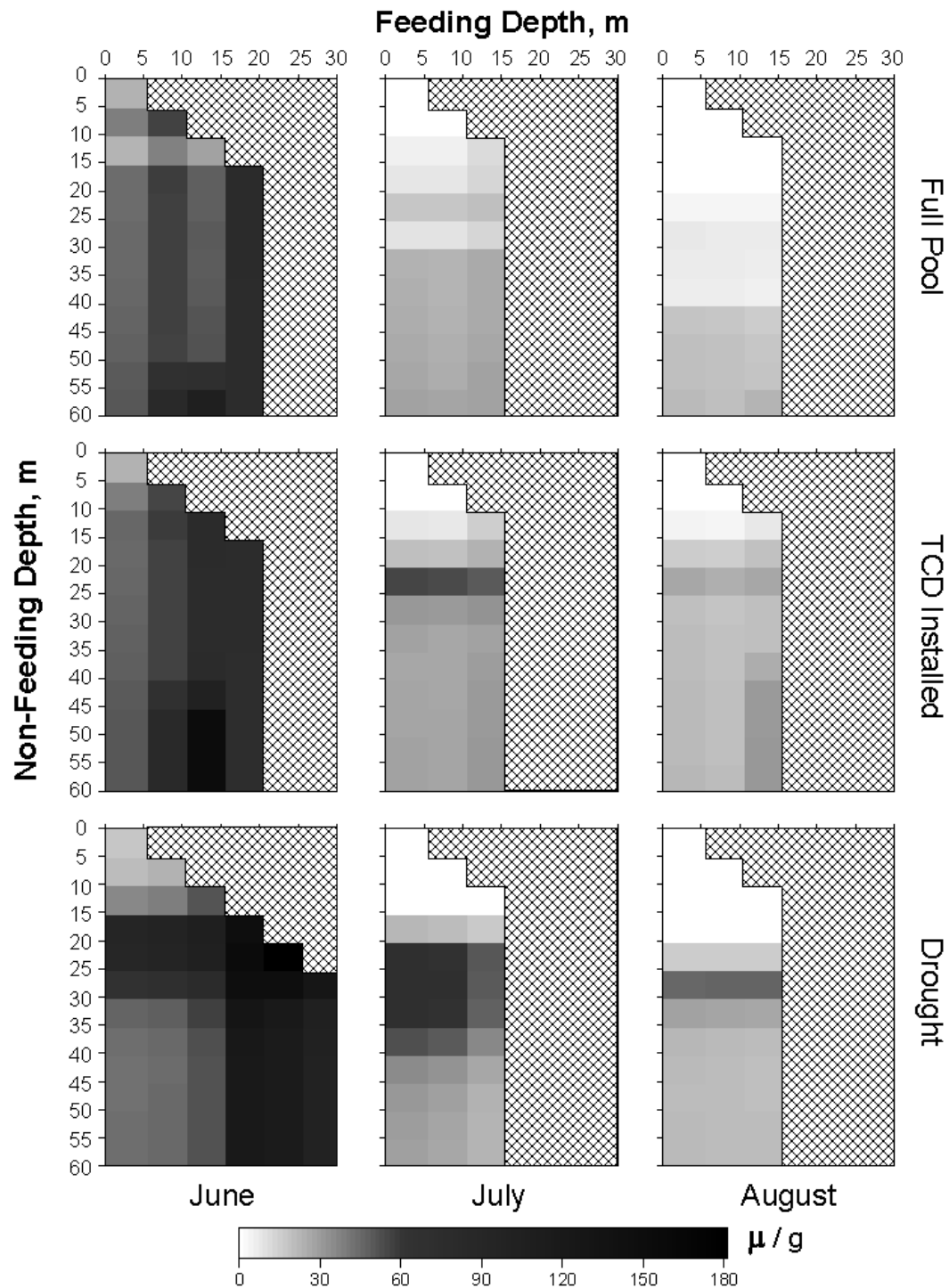


Figure 83. Predation risk:foraging gain ratios for simulations executed over a range of age-0 kokanee diel vertical migration patterns (DVM) and thermal conditions in BMR. Crosshatched areas represent depth combinations that did not meet criteria for simulations. Lighter areas indicate favorable feeding/non-feeding depth combinations for DVM patterns (i.e., those that minimize μ/g); darker areas have greater μ/g values.

4.4 Summary

The Sport Fishery

- Both the catch and harvest of fishes in the BMR fishery are dominated by kokanee (68% and 80%, respectively). Rainbow trout made up on average about 24% of the catch, brown trout made up about 6% and lake trout <3%.
- The fishery at BMR has attracted anglers from 49 states, and although most anglers are Colorado residents about 75% drove more than one hour from home to fish at BMR. Most of the resident anglers come from the Front Range. It appears that fishing effort at BMR is driven partly by the catch rate that kokanee anglers enjoy during summer
- The importance of high quality kokanee fishing at BMR is highlighted by the 50% higher fishing effort (~100,000 angler-hours) during years when catch rate was high. Using an approximate economic multiplier this difference would translate into > \$1,000,000 of economic activity in the regional economy.

Spatial Distribution of Fishes

- Rainbow trout inhabited shallower water than other salmonids, with 95% of the fish we sampled captured in water < 18 m deep. The mean depth that brown trout were captured during summer was 16 m, with most fish sampled at 5-20 m.
- Lake trout were distributed in the deepest water, at about 15-20 m in June and closer to 50 m in August. Most of the adult population was located inshore in May. Thereafter, lake trout were widely distributed in the water column at depths near or below the 10°C isotherm, but during crepuscular periods they appeared to aggregate above that depth, in close association with kokanee.
- During summer, lake trout appeared to maintain small home ranges. More intensive study would be required to fully capture the dynamism of lake trout movement.
- Both age-0 and age-1 and older kokanee exhibited diel vertical migrations (DVM) and their migratory behavior changed over the summer.
- Age-0 kokanee minimized near surface foraging in May, perhaps to avoid predation by visual predators such as lake trout in the well lit surface waters.
- In early summer, when the entire water column was less than 10°C there was a high degree of spatial overlap between lake trout preferred habitat and age-0 kokanee distribution. Age-0 kokanee descended to about 60 m during the day at this time of year.
- In August young-of-year were located in the shallower, warmer waters that were unavailable to lake trout during daylight and descended to about 25 m during nighttime and crepuscular periods.

- These results suggest a seasonal ontogenetic shift in diel vertical migration (DVM) of young kokanee as predation risk and foraging opportunities changed and that age-0 kokanee are attempting to balance energetic demands with predation risk.
- The DVM pattern of age-0 kokanee was similar to that exhibited by older fish by August, and the entire population was aggregated near the thermocline during the night. As the summer progressed kokanee migrated to deeper water at night.
- The lateral distribution of age-0 kokanee also changed seasonally. Once stocked kokanee reached the reservoir their downstream dispersal toward the dam was slow. Most of the cohort concentrated in Iola and Cebolla basins until August when the abundance of age-0 kokanee in each basin was not different.
- Our findings with respect to age-0 kokanee behavior and distribution came from work in 2002, an atypical year due to a severe drought. Studies in a normal water years should be conducted before generalizations can be made about age-0 kokanee in BMR.

Growth, Body Condition and Diet

- Mean lengths at age of rainbow trout were: age-1: 205 mm, age-2: 283 mm, age-3: 327 mm, age-4: 353 mm TL. It appeared that growth of rainbow trout declined from 1966-1996. Lifespan of rainbow trout in this system is about four years.
- Body condition of rainbow trout was slightly below normal ($W_r = 87$), with very little inter-annual variation during 1993-2002. During 1966-1970, the body condition of rainbow trout was nearly the same.
- We did not age brown trout from scales or otoliths. Wiltzius (1971) found that age classes 3-7 were present in the reservoir. Younger age classes are thought to remain in tributaries before migrating to the reservoir at around age-3.
- Body condition of brown trout was moderately poor ($W_r = 75$); the reasons for the poor condition of brown trout are unknown
- Growth of lake trout in BMR was well above average for the species. A von Bertalanffy growth trajectory fit to all the available growth data suggested that lake trout will maintain rapid growth rates as they age. Managers and anglers should expect more record sized lake trout to be captured in the future.
- Body condition of lake trout changed with size; mean W_r was approximately 90 for lake trout < 700 mm TL and > 110 for lake trout > 700 mm TL.
- Juvenile kokanee did not filter feed in our laboratory trials, but rather they were particulate-feeders that selectively chose larger zooplankton when available. The degree to which they were size-selective was affected by light availability.

- At higher light levels (above 3.4 lux) kokanee utilized a type II functional response, but at lower light levels (between 0.001 and 3.4 lux) kokanee exhibited a type I functional response. Kokanee did not feed when light level was below 0.001 lux.
- Growth of kokanee in BMR is among the fastest reported in the literature. Lengths at age were: age-1: 171 mm, age-2: 264 mm, age-3: 331 mm TL. Growth of age-1 and older kokanee changed very little during 1966-1996.
- The severe drought in 2001-2002 did not appear to have any short term effects on body condition of kokanee. It is possible that the ability of kokanee to undergo diel vertical migration allows them to cope with a warmer epilimnion without great losses in growth potential, as was shown in simulation modeling by Koski (2004).
- Modeling suggested that climate warming (up to a 6 °C increase in air temperature) would not greatly affect juvenile kokanee growth because increased zooplankton productivity compensates for increased energetic demands with warmer water temperatures.
- About half of the diet of all sizes of rainbow trout during the 1960s and during the present study was terrestrial insects, indicative of their distribution near the surface of the reservoir. No diet data for brown trout were collected.
- Kokanee in BMR were nearly entirely planktivorous feeding almost exclusively on the largest *Daphnia* individuals; their diet had not changed since the 1960s. The extreme selectivity of kokanee for large *Daphnia* suggests that food availability for kokanee was far from limiting for these fish during the summer.
- Lake trout exhibited a classic trophic ontogeny. The diet of lake trout changed as they grew, transitioning from mainly small macroinvertebrates to some crayfish and then to an increasing fraction of fish. Diet of large lake trout (≥ 600 mm TL) was almost exclusively fish, primarily kokanee and rainbow trout.
- Diet and stable isotope analysis suggested that both pelagic and benthic pathways were important to fish production. Energy produced in the pelagic zone supported kokanee, rainbow trout and juvenile lake trout to varying degrees. Benthic production supported rainbow trout and small lake trout, and larger lake trout relied on fish biomass originating from both pelagic and benthic pathways.

Recruitment and Survival

- Natural reproduction of rainbow trout has been documented in tributaries to BMR but is insufficient to sustain a reservoir population, necessitating regular stocking of this species. Stocking of rainbow trout decreased shortly after impoundment but stabilized at about 1,000,000 fish per year in the 1970s. Survival of stocked rainbow trout was poor in 1993-1996 and 2000-2003, and this was attributed partly to size at stocking and timing of stocking in those years.
- Brown trout are self-sustaining in BMR. Brown trout have been shown to reproduce in the Gunnison River, Lake Fork of the Gunnison and Cebolla Creek, and recruits migrated to the reservoir after their second year.

- Entrainment of rainbow and brown trout through the penstocks would not be expected, even in dry years such as 2002, because these species are rarely found below 20 m depth.
- Lake trout were originally introduced by accident in 1968 and they were stocked intermittently up until 1992 when all stocking of lake trout ceased. In recent years it appears that recruitment of lake trout via natural reproduction occurs virtually annually.
- Natural reproduction of kokanee appeared to be negligible and the kokanee population was composed almost entirely of stocked fish. Stocking of kokanee fry into BMR has generally increased since the reservoir was constructed, with rapidly increasing stocking rates to about 3,000,000 fry per year during the term of the present study.
- Overall, kokanee and rainbow trout survival, adult abundance, and the proportion of stocked fish that were harvested by anglers were on a decreasing trend since dam operations changed.
- Diet, growth and body condition do not suggest that the declines in abundance were the result of changes in reservoir productivity or thermal conditions. Rather, it was most likely due to three factors: short-term post-stocking losses, losses to entrainment, and predation.
- Kokanee stocked from the Roaring Judy Hatchery traverse the distance to the reservoir in less than 12 hours, minimizing the opportunity for predation by riverine piscivores. However, loss of fry to irrigation diversions along the river migration route was estimated to be about 30% in 2001 and 60% in 1974.
- Because it is believed that losses of kokanee fry to irrigation diversions are highest in dry years, and inflow to BMR showed a declining trend since 1993, we speculate that irrigation diversions may be partly responsible for the downward trend in kokanee fry survival observed during the present study.
- Kokanee lost through the BMR dam were primarily age-0 and age-1 fish but there is conflicting evidence about the intensity of fish entrainment at BMR. Studies at BMR in the 1970s concluded that entrainment was high in late fall and winter. In the 1990s entrainment was only studied during spring and summer and was found to be low, but kokanee were not located in the vicinity of the dam during their first summer.
- Lake trout predation alone can account for the decline in rainbow trout survival since 1993. Biomass of rainbow trout consumed was greater than the annual biomass of subcatchables stocked and many times higher than the biomass harvested by anglers. The costs of sustaining lake trout fisheries with hatchery trout are well established and they are very high.
- Consumption of kokanee by lake trout was a significant fraction of the estimated annual production of kokanee and similar to the biomass harvested by anglers. Because lake trout consume kokanee that are smaller on average than those in the harvest, the number of kokanee consumed by lake trout is much higher than the number harvested by anglers.

- Despite the large number of kokanee consumed by lake trout, other factors must have contributed to the decline in adult kokanee abundance since new operations began. Disease, other post-stocking mortality, predation by brown trout and small lake trout, and entrainment of kokanee remain as possible factors that could not be evaluated in this study.
- Recent illicit introductions of yellow perch and northern pike pose competitive and predatory threats to the kokanee and rainbow trout fisheries of the reservoir.
- Yellow perch may compete for food with kokanee and rainbow trout. Competitive interactions among planktivorous fishes could become intense if exotic, predation-resistant zooplankters such as *Bythotrephes cederstroemi*, *Cercopagis pengoi*, and *Daphnia lumholtzi* invade the system. Yellow perch are known to be piscivorous and they would pose a serious threat to kokanee recruitment if they become abundant.
- Yellow perch will not provide a very suitable forage base for lake trout during summer because of radically different thermal preferences and the lower energy density of yellow perch compared to kokanee. Thus, an increasing yellow perch population will not result in reduced predation rates on kokanee during the summer months when lake trout consumption demand is maximal.
- Because of their propensity for stunting, yellow perch will probably not supplement the sport fishery at BMR. Anglers will perceive a need for a new predator to control yellow perch, setting the stage for additional illegal introductions of exotic predators that will further threaten the BMR fishery, and native and sport fish populations downstream.
- Little is known about the status of northern pike in BMR. Northern pike grow large quickly on a stocked salmonid prey base but at considerable economic and ecological cost that should be quantified. At BMR northern pike likely pose a significant threat to the stocked rainbow trout and kokanee fisheries, and the reservoir serves as yet another stepping stone for a nonnative fish's expansion to new waters in the region.
- Changes to reservoir thermal structure caused by climatic events such as drought and climate warming, and by new operational modes such as surface spills and use of a TCD, affect the kokanee's opportunity for growth and their risk of predation from lake trout.
- In early summer when thermal stratification is weak and temperatures in the reservoir are cooler, kokanee DVMs are driven primarily by predator avoidance. Predation risk is especially high during this time because lake trout can exploit more habitat in which there is sufficient light to find prey.
- In later summer months, thermal stratification is stronger and a "thermal refuge" may offer some protection from lake trout predation. Kokanee are able to assume more risk by foraging in well-illuminated epi- and metalimnetic waters, which may be too warm for lake trout to forage in for extended periods of time.
- Increased water clarity and changes to thermal stratification during droughts increase predation risk to kokanee. With increased water clarity and a shallower

depth of the 10 °C isotherm, suitable lake trout habitat is greatly increased in the reservoir. Kokanee behavior must be flexible in order to balance increased predation risk with energetic needs.

- Climate warming interacted strongly with reduced water clarity arising from eutrophication to decrease kokanee growth. Kokanee lost up to 3% body mass per day with climate warming in conjunction with eutrophication. Weight loss occurred because the only habitat sufficiently illuminated to find prey was located in the epilimnion, where water temperatures often approached lethal temperatures for kokanee.
- Reduced water clarity arising from increased nutrient loading from the watershed would compound effects of changes to the thermal environment on kokanee growth. If such conditions come to pass at BMR then fishery managers should expect the kokanee population and fishery to become jeopardized. Because climatic events are beyond control, and because drought and warming are likely events in the future, efforts to protect water clarity, e.g., land use controls in the watershed, reducing piscivore density, and protecting the system from invasive species are recommended to sustain long term viability of kokanee in BMR.



Photo: M. Koski

4.5 Fishery Management Recommendations

Intensive field studies examining potential effects of dam operations afforded the opportunity to evaluate the status of BMR fish populations and a number of fishery management recommendations derive from these analyses.

- Rainbow trout must be stocked to sustain the reservoir fishery but stocking of subcatchables appears to be ineffective. The sport fishery for rainbow trout would be maximized by stocking catchable rainbow trout.
- Kokanee fry stocking must be continued to sustain the population but the fishery, the egg take, and indeed kokanee management statewide, is jeopardized unless recent increases in kokanee mortality can be controlled.
- Continued stocking of kokanee as early in the night as possible is recommended to maximize the number of hours of darkness during the downstream migration and thereby minimize piscivory by riverine predators.
- Blocking irrigation diversions along the migration route during a portion of the night when stocking occurs should greatly reduce short term mortality of stocked kokanee. A program implemented by CDOW to block irrigation diversions should be sustained.
- Studies at BMR in the 1970s, and more recently elsewhere, suggest that entrainment of young kokanee is most severe in fall and winter. Although winter weather conditions are extremely challenging at BMR, a thorough evaluation of kokanee entrainment can only be accomplished by either sieve netting below the dam and/or hydroacoustics surveys above the dam during this season.
- Reductions to daily bag limits on kokanee would not be particularly effective at increasing the abundance of adult kokanee and or the egg take from this population unless the bag limit was reduced by at least 50%. Reducing intensity of mortality on younger age-classes of kokanee would have a much larger effect than bag limits on overall kokanee abundance and egg take, while at the same time improving sport fishing for the species.
- Because piscivory accounts for a significant fraction of kokanee mortality, close monitoring of consumption demand by the lake trout population and their effects on prey biomass should be continued.
- Given the disproportionately great impact of large lake trout on kokanee and rainbow trout, changes to harvest regulations that limit the number of large fish bagged (“one over X inches”) would be 1) contrary to management goals of protecting kokanee egg take, maintaining kokanee and rainbow trout fisheries, and providing a sustainable prey supply for lake trout, and 2) ineffective at protecting large fish if few anglers interested in harvesting lake trout have the opportunity to do so. Further, such regulations promote a fallacious mindset among anglers that maximizing trophy lake trout is a management priority at BMR.

- Recently introduced yellow perch and northern pike pose new competitive and predatory threats to BMR's kokanee population. Estimates of the consumption of kokanee and rainbow trout by lake trout should be considered minimum estimates and consumption by yellow perch and northern pike needs to be quantified. The potential for competitive interactions between salmonids and yellow perch should also be investigated. More detailed studies of the trophic ecology of yellow perch and northern pike in BMR are needed.
- Illicit introductions confound the best efforts of fishery managers to provide cost-effective, ecologically sound and sustainable fisheries. Preventing illicit introductions is far more likely to be successful than efforts to eradicate invading species once they are established. A harsh condemnation of illicit introductions and a public education campaign are recommended.
- Blue Mesa Reservoir is a keystone to the state's egg supply and therefore kokanee management program. Given the tragic consequences in store for reservoir sport fisheries statewide in the event of a kokanee crash at BMR it seems prudent to prioritize maintaining a strong kokanee population there.
- Because recent introductions of piscivorous fishes (yellow perch, northern pike) will compound the predation pressure exerted by lake trout on kokanee, managers should encourage harvest of all piscivores at BMR if they intend to maintain BMR's kokanee population.
- Reduced water clarity arising from increased nutrient loading from the watershed would compound effects of changes to the thermal environment. If such conditions come to pass at BMR then fishery managers should expect the kokanee population and fishery to become jeopardized. Because climatic events are beyond control, and because drought and climate warming are likely events in the future, efforts to protect water clarity, e.g., land use controls in the watershed, reducing piscivore density, and protecting the system from invasive species are recommended to sustain long term viability of kokanee in BMR.

5 CONCLUSIONS

5.1 Hydrologic Conditions

- Causal inference about the impact of new dam operations at BMR would have been strengthened by an experimental approach, but the lack of adequate controls or replication necessitated an observational study.
- The high degree of variation in hydrologic conditions observed during 1993-2002, and the strong influence of hydrology on reservoir physicochemical conditions confounds comparisons of limnological variables before and after the change in dam operations, to some degree.
- Because of the unusually dry conditions that occurred during the course of our study, CE-THERM proved to be a useful tool for evaluating effects of alternative dam operation regimes on reservoir thermal conditions, while controlling for potentially confounding hydro-meteorological variables.
- The overall results indicate that reservoir thermal regime was extremely insensitive to changes in the hypolimnetic release pattern under “normal” climatic and hydrologic conditions. Changes in weather or hydrologic variables such as inflows, starting elevations, and air temperatures had a much larger effect on reservoir thermal patterns.
- The model predicted that hypolimnetic release patterns that approximated the new dam operations regime implemented starting in 1993 would have virtually no effect on reservoir thermal structure under normal hydro-meteorological conditions, compared to the historic operating pattern. Even an extreme operations scenario, with a run-of-the-river hypolimnetic release pattern, produced small changes in predicted thermal regime of the reservoir relative to those induced by climatic and hydrologic variables.
- It appears that water managers at Blue Mesa Reservoir have considerable latitude for changing hypolimnetic release patterns without negative thermal consequences for the reservoir.
- Other work showed that releases over the spillway to supplement hypolimnetic releases, or the installation of a TCD to increase downstream temperatures would produce ecologically important changes to the reservoir’s thermal regime, creating a shallower and cooler epilimnion.

5.2 Limnology

- Some limnological characteristics differed before and after dam operations changed; however, attributing the change to dam operations is confounded by the drought that persisted during the term of our study.
- Chlorophyll-a concentration was on average lower and Secchi depth was higher during the period after new dam operations began than before and TSI declined during the study. It appears that nutrient availability and algal biomass may be declining but the reservoir remained in a mesotrophic condition.
- Because CE-THERM simulations showed that altering the pattern of withdrawals from the hypolimnetic outlet would have very limited effects on reservoir temperatures, increased spring releases should not alter *Daphnia* production via temperature effects.
- Entrainment of *Daphnia* through the dam during summer was not significant relative to the standing stock in the reservoir.
- Factors that lower epilimnetic temperatures, for example, a TCD, can be expected to negatively impact *Daphnia* production by increasing egg development time and thereby depressing reproductive rates.
- Invasion of the reservoir by non-native species poses a far more significant threat to the stability of the food web and sustainability of the sport fishery in BMR than does the change in dam operations.
 - *Mysis relicta* are capable of decimating cladoceran zooplankton populations, resulting in reduced growth rates of kokanee.
 - Other crustaceans also have the potential to seriously disrupt the zooplankton assemblage and thus pose a significant threat to the system's kokanee population. *Bythotrephes*, *Cercopagis pengoi*, and *Daphnia lumholtzi* are exotic zooplankters that either prey on other cladocerans or eliminate them by competition, and they are not fed on by fish.
 - Recently introduced yellow perch may compete with kokanee for food; zooplankton prey may become very scarce if predaceous crustaceans invade the system resulting in poor growth rates and survival of planktivorous fishes.

5.3 The Fishes and Fishery

- New dam operations did not appear to affect food availability, growth or body condition of age-1 and older kokanee in BMR. This finding was supported by the fact that kokanee fed extremely selectively on large *Daphnia*, both before and after dam operations changed.
- There was no evidence to suggest that new dam operations affected growth of rainbow trout. Although rainbow trout growth showed a declining trend since BMR was formed, this decline began before 1993. Body condition of rainbow trout was below average, but there were no trends in body condition since 1966.
- Kokanee and rainbow trout survival declined steadily after dam operations changed at BMR.
- Factors unrelated to dam operations could account for significant mortality of both rainbow trout and kokanee. Lake trout predation alone was sufficient to account for the decline in rainbow trout survival, but predation, losses to irrigation ditches, and harvest could not entirely explain kokanee declines.
- Other factors must have contributed to the decline in kokanee abundance since new operations began. Changes in the incidence of disease, the intensity of post-stocking mortality, predation by brown trout and small lake trout, and entrainment of kokanee remain as possible factors that could not be evaluated in this study.
- We did not measure entrainment but past studies provide conflicting evidence about the degree of entrainment of kokanee at BMR. Studies in the 1970s concluded that entrainment was high in late fall and winter. In the 1990s entrainment was only studied during spring and summer and was found to be low, but kokanee were not located in the vicinity of the dam during their first summer.
- We found no strong relationship between kokanee survival and discharge volumes during summer 1993-2001. It is not known if the amount of entrainment that occurs is proportional to discharge, but since 1993 discharge during winter was below the long-term average.
- Thermal effects of the new dam operations implemented at BMR on fish energy budgets and growth were not expected because modeling showed that high spring releases from a hypolimnetic outlet do not have a significant effect on the reservoir's thermal regime.
- Because vertical distribution and behavior of kokanee is driven by energetic considerations and predator avoidance, dam operations that do affect the physical environment can be expected to alter kokanee behavior, with implications for their growth and survival.
- Dam operating regimes that promote lower turbidity (e.g., by reducing nutrient availability for phytoplankton) provide better foraging conditions for kokanee but also for their predators.

- Operational regimes that increase turbidity (from suspended sediments or phytoplankton blooms) diminish the ability of kokanee to find their food. Under these conditions kokanee may avoid predators but they could be forced into warmer , more well-lit waters where they may be unable to meet energetic demands.
- Thermal stratification resulting in a deep 10 °C isotherm may protect kokanee from lake trout predation; when reservoir temperatures are cooler (or if thermal stratification is weak) kokanee may experience higher predation risk from lake trout.
- If water was released via the spillway instead of the hypolimnetic outlet, modeling predicted that the epilimnion would become thinner and metalimnetic temperatures would decrease. Modeling predicted a 9% decrease in daily growth rate for juvenile kokanee when compared to traditional release scenarios. Spillway releases inhibited kokanee growth by causing cooler conditions and decreased zooplankton productivity.
- Modeling showed a TCD would result in a shallower 10 °C isotherm in August (approximately 20 m) than without a TCD (approximately 40 m). While there was no predicted change in kokanee growth, predation risk to kokanee from lake trout would be higher if a TCD were installed.

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APPENDICES

Table A1. UTM coordinates of standardized sampling stations used in limnological and fisheries surveys at BMR. Map datum: NAD 27 CONUS.

Station ID	Station Description	UTM Coordinates
<u>Iola Basin</u>		
IOLVGN	vertical gill net station	13 S 317429 4260776
IOLZP	plankton and limnology station	13 S 317242 4260731
BMMY1	limnology station	13 S 320124 4261464
BMMY2	limnology station	13 S 319076 4261192
BMMY3	limnology station	13 S 317927 4260913
BMMY4	limnology station	13 S 316769 4260376
BMMY5	limnology station	13 S 314563 4259034
<u>Cebolla Basin</u>		
CEBVGN	vertical gill net station	13 S 308379 4260824
CEBZP	plankton and limnology station	13 S 308360 4260915
BMMY6	limnology station	13 S 312978 4259589
BMMY7	limnology station	13 S 311534 4258938
BMMY8	limnology station	13 S 310084 4259099
BMMY9	limnology station	13 S 309041 4261028
BMMY10	limnology station	13 S 307372 4259630
BMMY11	limnology station	13 S 304886 4260196
<u>Sapinero Basin</u>		
SAPVGN	vertical gill net station	13 S 297824 4259365
SAPZP	plankton and limnology station	13 S 298127 4259702
SONAR1	limnology station	13 S 298390 4259821
SONAR2	limnology station	13 S 300079 4260794
BMMY12	limnology station	13 S 301084 4262378
BMMY13	limnology station	13 S 299121 4263299
BMMY14	limnology station	13 S 298299 4260129
BMMY15	limnology station	13 S 298772 4257967

Table A2. Temperature profiles (°C) measured with a YSI model 58 meter at Sapinero basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1993			1994							1995					
	07/20	09/16	05/24	06/09	06/22	07/07	07/21	08/01	08/18	09/16	05/21	05/31	06/16	06/24	06/30	07/07
0	20.4	16.6	.	14.1	16.5	16.9	17.8	19.1	19.8	17.3	8.9	10.4	13.6	15.8	15.3	17.0
1	19.2	16.5	12.6	14.2	16.1	17.0	17.8	19.4	19.8	17.3	8.8	9.9	13.5	14.7	15.5	16.7
2	18.8	16.2	12.0	14.2	15.8	17.0	17.8	19.4	19.8	17.3	8.8	9.8	13.5	14.0	15.5	16.1
3	18.5	16.1	11.7	14.2	15.7	17.0	17.8	19.4	19.8	17.2	8.7	9.7	13.5	13.6	15.5	15.9
4	18.4	16.1	11.7	14.1	15.7	16.9	17.8	19.4	19.7	17.2	8.7	9.6	13.4	13.3	15.5	14.8
5	18.2	16.1	11.6	14.0	15.7	16.8	17.8	19.4	19.7	17.2	8.6	9.6	13.3	13.1	15.4	14.6
6	18.1	16.0	11.5	13.4	15.1	16.8	17.7	19.4	19.7	17.2	8.8	9.5	13.3	12.8	15.0	14.5
7	17.8	16.0	10.8	12.5	14.8	16.8	17.6	19.3	19.6	17.2	8.3	9.5	13.2	12.2	14.7	14.0
8	17.7	16.0	10.1	12.3	14.5	16.6	17.5	19.1	19.5	17.2	8.2	9.4	13.2	11.9	13.0	13.3
9	16.6	16.0	10.0	11.8	14.3	15.5	17.2	18.9	19.1	17.1	8.1	9.4	13.1	11.8	12.7	12.8
10	16.5	16.0	9.8	11.3	14.3	14.9	17.1	18.7	18.8	17.1	8.0	9.4	13.0	11.7	12.6	12.7
11	16.2	16.0	9.6	11.0	14.2	14.8	16.7	18.2	18.5	17.1	7.7	9.3	12.4	11.5	12.3	12.2
12	16.0	15.9	9.4	10.8	13.7	14.1	16.3	17.0	17.4	17.1	7.6	9.3	12.1	11.3	12.1	12.0
13	15.7	15.9	9.2	10.5	13.1	13.5	15.5	16.2	16.6	17.1	7.6	9.1	12.0	11.0	11.9	11.9
14	15.5	15.9	8.7	10.0	12.7	13.3	14.7	15.5	16.3	17.1	7.5	8.9	11.8	11.0	11.7	11.8
15	15.4	15.9	8.3	9.8	12.2	13.1	14.1	14.9	15.9	17.1	7.4	8.7	11.4	10.9	11.6	11.6
16	15.2	15.9	8.1	9.5	12.1	13.0	13.8	14.6	15.4	17.1	7.2	8.6	11.2	10.7	11.5	11.5
17	15.0	15.9	7.5	9.2	11.5	12.4	13.5	14.3	15.0	16.2	7.0	8.5	11.0	10.7	11.1	11.3
18	14.5	15.5	7.1	8.9	11.2	11.8	13.0	14.0	14.4	15.8	7.0	8.0	10.7	10.5	11.0	11.2
19	14.2	15.0	6.9	8.8	10.8	11.4	12.5	12.9	14.1	15.5	6.9	7.6	10.4	10.4	10.8	11.0
20	13.9	14.9	6.6	8.5	10.3	11.0	12.2	12.4	13.5	15.2	6.7	7.5	10.1	10.2	10.7	11.0
25	12.6	14.2	5.7	7.3	7.8	9.6	9.7	10.7	11.8	13.3	6.0	6.8	9.0	9.6	9.9	10.4
30	12.0	13.5	5.2	6.2	6.7	8.0	8.4	9.4	10.1	11.5	5.7	6.2	7.7	9.2	9.4	10.0
35	11.4	12.6	4.9	5.8	6.2	6.9	7.5	8.1	8.7	9.6	5.4	5.8	6.8	9.1	9.1	6.7
40	10.3	11.9	4.7	5.3	5.7	6.3	6.5	7.0	7.1	7.7	5.2	5.6	6.0	8.9	8.8	9.3
45	8.9	10.4	4.6	5.1	5.4	5.9	5.9	6.3	6.3	6.7	5.1	5.5	5.7	8.9	7.8	8.5
50	7.6	8.2	4.4	5.0	5.1	5.6	5.7	5.9	5.9	6.1	5.1	5.4		8.9	7.0	7.3
55	6.9	6.8	4.3	4.9	5.0	5.4	5.4	5.6	5.6	5.7	5.0	5.3		8.9	6.5	6.6
58	6.7		4.3	4.8	4.9	5.3	5.2	5.5	5.4	5.6	5.0				6.2	

Table A2. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Sapinero basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1995							1996				1997		1998	1999	
	7/14	7/21	7/28	8/08	8/17	9/11	6/03	7/23	8/10	9/13	5/31	7/08	8/04	7/30	7/14	8/04
0	16.9	18.0	20.8	19.1	20.4	19.0	13.0	19.1	18.0	17.3	12.7	16.3	19.5	20.0	19.0	19.6
1	16.9	17.4	19.3	19.0	19.8	18.6	12.0	19.2	18.5	17.4	12.3	16.3	19.5	20.0	19.0	19.8
2	16.8	17.2	18.3	19.0	19.3	18.5	11.3	19.2	18.4	17.4	12.2	16.3	19.5	20.0	19.0	19.8
3	16.5	17.1	18.0	18.9	18.9	18.4	11.1	19.0	18.4	17.4	12.1	16.3	19.5	20.0	18.5	19.8
4	15.8	16.6	17.7	18.9	18.7	18.2	11.1	19.0	18.4	17.4	11.9	16.3	19.4	20.0	18.0	19.9
5	15.2	16.0	17.5	18.7	18.6	18.1	11.1	18.9	18.4	17.4	11.6	16.3	19.1	20.0	18.0	19.9
6	14.4	15.1	16.7	18.6	17.7	18.1	11.0	18.9	18.4	17.4	11.4	16.3	18.7	20.0	18.0	19.9
7	14.2	14.6	15.5	18.0	17.1	18.0	10.8	17.6	18.4	17.4	11.2	16.3	18.5	18.0	17.5	19.9
8	14.0	14.2	14.5	16.7	16.6	18.0	10.6	16.8	18.4	17.4	10.6	16.3	17.8	17.0	17.0	19.8
9	13.7	13.9	14.0	15.8	16.0	17.5	10.4	16.0	18.4	17.4	10.2	16.0	17.1	17.0	16.5	19.2
10	13.4	13.6	13.7	15.4	15.1	16.5	10.2	15.5	17.3	17.4	9.8	14.8	16.5	16.0	16.0	19.0
11	13.1	13.1	13.5	14.9	14.8	15.8	10.1	15.0	16.5	17.4	9.8	14.5	16.0	15.0	15.5	16.4
12	12.7	13.0	13.4	14.5	14.5	15.2	10.0	14.8	15.5	17.3	9.7	13.9	15.5	15.0	15.0	15.9
13	12.5	12.8	13.2	14.0	14.2	14.7	10.0	14.7	15.0	17.2	9.4	13.0	15.2	15.0	14.5	15.5
14	12.1	12.7	13.1	13.6	14.0	14.5	9.9	14.3	14.4	16.8	9.4	12.9	14.5	14.0	14.0	15.2
15	12.1	12.6	12.8	13.3	13.7	14.4	9.5	13.9	14.3	15.9	9.3	12.5	13.9	14.0	13.0	15.0
16	12.0	12.4	12.8	13.1	13.6	14.3	9.5	13.7	14.7	15.3	9.2	12.4	13.5	14.0	12.5	14.5
17	12.0	12.4	12.6	13.0	13.6	13.9	9.5	13.3	13.9	15.0	9.1	12.2	13.3	14.0	12.0	14.0
18	12.0	12.3	12.6	12.9	13.2	13.8	9.5	12.7	13.6	14.8	8.8	11.8	13.0	14.0	12.0	14.0
19	11.8	11.9	12.4	12.7	13.0	13.4	9.0	12.3	13.3	14.6	8.7	11.5	12.9	13.0	11.0	13.5
20	11.6	11.7	12.4	12.6	12.9	12.9	9.0	11.9	13.0	14.1	8.5	11.3	12.7	13.0	11.0	12.9
25	11.0	11.6	11.9	12.3	12.5	12.5	8.0	11.3	11.8	12.7	7.8	10.8	11.8	12.0	10.0	11.0
30	10.7	11.1	11.5	12.0	12.1	12.2	8.5	10.7	11.2	12.0	6.5	10.4	11.2	11.0	9.0	10.2
35	10.4	10.9	10.9	11.5	11.6	11.8	6.7	10.2	10.6	11.3	5.8	10.0	10.6	10.0	8.0	9.5
40	9.7	10.5	10.5	10.9	10.9	10.7	6.2	9.3	9.7	9.9	5.3	9.1	10.1	8.0	7.0	8.5
45	8.6	9.8	10.0	10.1	10.2	9.7	5.9	8.1	8.5	8.2	5.0	7.2	8.8	7.0	7.0	7.8
50	8.0	8.4	8.8	9.0	9.1	7.8	5.5	7.1	6.9	7.0	4.8	6.4	6.9	6.0		7.0
55	7.3	7.4	7.4	7.4	7.7	7.1	5.2	6.5	6.5	7.1	4.7	5.9	6.0	6.0		6.8
58	7.0	7.1	6.9	6.8	7.2									6.0		6.3

Table A2. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Sapinero basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1999			2000			2001						2002				
	9/22	5/19	7/11	7/16	8/02	9/12	5/23	6/19	7/16	8/24	5/15	6/06	6/25	7/12	7/31	8/07	9/25
0	15.8	8.7	18.0	14.1	20.0	18.0	10.1	15.1	18.7	20.3	9.5	15.2	.	20.5	.	20.0	.
1	15.9	8.7	18.0	14.0	20.1	17.8	10.0	15.1	18.7	19.3	9.0	14.3	17.7	19.9	19.8	19.4	15.7
2	15.9	8.5	18.0	14.0	20.1	17.8	9.9	15.1	18.7	19.0	8.7	13.8	17.3	19.6	19.7	19.4	15.7
3	15.9	8.5	18.0	14.0	20.1	17.8	9.8	15.1	18.7	18.8	8.5	13.6	17.2	19.4	19.4	19.3	15.7
4	15.9	8.5	18.0	14.0	20.1	17.8	9.8	15.0	18.7	18.6	8.3	13.3	16.9	19.3	19.3	19.2	15.6
5	15.9	8.5	18.0	13.8	20.1	17.8	9.7	14.1	18.7	18.5	8.2	13.2	16.8	19.1	19.3	19.1	15.6
6	15.9	8.2	18.0	13.5	20.1	17.8	9.7	13.9	18.7	18.4	8.2	13.0	16.7	18.9	19.2	19.1	15.6
7	15.9	8.1	18.0	12.3	20.1	17.7	9.7	13.8	18.7	18.3	8.1	12.9	16.5	18.7	19.2	19.1	15.6
8	15.9	8.1	17.7	12.0	20.0	17.7	9.7	13.5	17.0	18.3	8.0	12.4	15.4	18.6	19.1	19.1	15.6
9	15.9	8.1	16.9	11.5	19.5	17.5	9.6	13.3	16.2	18.3	7.7	11.6	15.0	18.1	19.0	19.1	15.6
10	15.9	8.0	16.4	11.1	18.1	17.5	9.5	13.1	15.5	18.1	7.5	11.0	15.0	17.4	18.8	19.1	15.6
11	15.9	8.0	16.1	10.8	17.3	17.4	9.4	13.0	15.2	17.7	7.4	10.4	14.7	16.6	18.4	19.1	15.6
12	15.9	7.9	15.5	10.5	16.8	17.0	8.6	12.7	14.6	16.7	7.4	10.2	14.2	15.9	17.4	18.9	15.6
13	15.9	7.9	14.8	10.2	16.0	17.0	8.1	12.2	13.9	16.4	7.3	10.1	13.8	14.8	17.1	18.0	15.6
14	15.9	7.8	14.2	10.0	15.5	16.5	8.0	11.9	13.6	16.2	7.3	9.9	12.5	14.0	16.2	17.6	15.6
15	15.9	7.7	13.9	9.9	15.0	16.3	7.9	11.3	13.3	15.8	7.2	9.6	11.6	13.5	15.2	17.0	15.6
16	15.5	7.5	13.5	9.5	14.5	16.0	7.7	11.1	13.2	15.2	7.0	9.4	11.0	13.0	14.5	16.2	15.6
17	15.5	7.2	13.0	9.0	14.1	15.8	7.6	10.6	12.8	14.9	6.9	9.1	10.4	12.3	13.9	15.5	15.6
18	15.5	7.1	12.4	9.0	13.8	15.3	7.5	10.4	12.4	14.6	6.7	8.9	9.7	11.6	13.3	15.0	15.6
19	15.2	7.0	11.5	9.0	13.3	15.0	7.3	10.3	12.2	14.1	6.6	8.8	9.4	10.8	12.4	14.2	15.5
20	15.0	7.0	11.1	8.7	12.9	14.9	7.0	9.9	11.7	13.6	6.5	8.6	9.0	10.3	11.6	12.7	15.5
25	14.0	6.2	9.6	8.0	10.7	13.3	6.6	8.4	10.3	12.5	6.2	7.1	8.7	8.8	8.4	9.1	9.5
30	13.8	6.0	8.2	7.7	9.1	11.0	6.4	7.1	9.0	11.2	5.9	6.5	7.6	7.4	7.0	7.5	7.2
35	12.5	5.9	7.5	7.0	8.1	9.0	5.8	6.4	7.5	9.3	5.5	6.1	6.6	6.9	6.4	6.9	6.7
40	11.0	5.8	6.8	6.2	7.0	7.5	5.4	6.0	6.6	.	5.3	5.8	6.2	6.4	6.1	6.5	6.4
45	8.5	5.2	6.2	6.0	6.5	7.0	4.9	5.8	6.1	.	5.1	5.6	5.8	6.2	5.7	6.1	5.9
50	7.1	5.0	6.0	5.8	6.0	6.4	4.7	5.5	5.7	.	5.0	5.4	5.6	5.7	5.5	5.9	5.7
55	6.8	5.0		5.5			4.6	5.3	5.5	.	4.9	5.3	5.3	5.6	5.3	5.8	5.5
58	6.5	5.0		5.4			.	5.2	5.3	.	.	.	5.1	.	5.3	5.6	5.4

Table A3. Temperature profiles (°C) measured with a YSI model 58 meter at Cebolla basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1993						1994						1995					
	6/08	7/19	9/15	5/23	6/06	6/23	7/05	7/18	7/30	8/14	9/17	5/21	6/06	6/19	7/12	8/02	8/15	
0	12.0	18.7	17.0	12.0	16.0	17.0	19.0	18.0	19.0	22.0	17.0	10.0	13.1	17.4	21.0	19.5	20.7	
1	11.9	18.7	16.8	12.0	16.0	17.0	19.0	18.0	20.0	21.0	17.0	10.3	13.0	15.2	20.0	19.1	20.0	
2	11.8	18.8	16.7	12.0	16.0	17.0	19.0	18.0	20.0	21.0	17.0	10.2	12.7	14.5	19.6	18.9	19.7	
3	11.7	18.8	16.6	12.0	15.0	17.0	19.0	18.0	20.0	20.0	17.0	10.2	12.5	13.9	17.6	18.8	19.4	
4	11.7	18.8	16.5	11.0	15.0	17.0	19.0	18.0	20.0	20.0	17.0	10.2	12.4	13.7	16.0	18.7	19.3	
5	11.7	18.7	16.5	11.0	15.0	17.0	19.0	19.0	20.0	20.0	17.0	10.2	12.3	13.3	15.3	18.5	19.3	
6	11.6	18.7	16.5	11.0	15.0	17.0	19.0	18.0	20.0	20.0	17.0	10.1	12.1	12.8	14.9	18.3	19.2	
7	11.5	18.5	16.5	11.0	14.0	17.0	19.0	18.0	20.0	20.0	17.0	10.1	11.7	12.3	14.5	18.2	19.2	
8	11.7	18.2	16.5	11.0	13.0	17.0	19.0	18.0	20.0	20.0	17.0	10.0	11.6	12.1	14.0	17.2	17.5	
9	11.5	17.9	16.5	10.0	13.0	17.0	19.0	18.0	18.0	19.0	17.0	9.7	11.4	12.1	13.3	14.3	16.2	
10	11.5	17.2	16.5	10.0	13.0	15.0	18.0	18.0	18.0	19.0	17.0	9.4	10.9	11.5	12.8	14.0	15.2	
11	11.4	16.3	16.5	10.0	12.0	15.0	17.0	17.0	18.0	19.0	17.0	9.2	10.8	11.4	12.6	13.8	14.9	
12	11.4	15.9	16.5	10.0	11.0	15.0	16.0	16.0	17.0	18.0	17.0	9.0	10.7	11.3	12.5	13.7	14.3	
13	11.3	15.1	16.4	9.0	11.0	13.0	15.0	16.0	16.0	17.0	17.0	8.6	10.1	11.0	12.4	13.3	14.1	
14	11.2	15.0	16.5	9.0	10.0	13.0	14.0	15.0	16.0	17.0	17.0	8.3	9.8	10.8	12.2	13.1	13.7	
15	11.5	14.8	16.4	8.0	10.0	13.0	14.0	15.0	15.0	16.0	17.0	8.1	9.7	10.7	12.1	13.0	13.6	
16	11.2	14.4	16.4	8.0	9.0	12.0	13.0	14.0	15.0	16.0	17.0	8.0	9.6	10.7	11.7	13.0	13.4	
17	11.1	14.2	16.3	7.0	9.0	11.0	13.0	14.0	14.0	15.0	17.0	7.9	9.4	10.6	11.6	12.8	13.2	
18	11.1	13.9	16.3	7.0	9.0	10.0	12.0	13.0	14.0	15.0	16.0	7.7	9.1	10.5	11.4	12.7	13.2	
19	11.0	13.8	15.6	7.0	8.0	10.0	12.0	13.0	13.0	15.0	16.0	7.7	8.9	10.5	11.4	12.5	13.1	
20	11.0	13.5	15.3	7.0	8.0	10.0	12.0	12.0	13.0	14.0	16.0	7.6	8.8	10.1	11.3	12.5	12.9	
25	9.0	12.3	14.3	6.0	7.0	9.0	9.0	10.0	11.0	12.0	14.0	7.4	8.4	9.7	10.9	12.0	12.3	
30	7.1	11.8	13.7	6.0	6.0	7.0	8.0	9.0	9.0	10.0	12.0	6.9	7.5	8.9	10.5	11.6	12.0	
35		11.8	12.8	5.0	6.0	7.0	7.0	8.0	8.0	9.0	10.0	6.6	6.7	7.9	10.2	11.2	11.5	
40		10.1	11.9	5.0	5.0	6.0	6.0	7.0	7.0	7.0	8.0		6.5	7.2	9.7	10.7	10.8	
45		8.5	10.4	5.0	5.0	6.0	6.0	6.0	6.0	7.0	7.0			6.7	8.8	10.2	10.0	
50		7.5	8.3		5.0	6.0	6.0	6.0	6.0	6.0				6.6	7.9	9.7	8.7	
55					5.0		6.0	6.0		6.0	55				7.4	9.3	7.5	
58							6.0											

Table A3. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Cebolla basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1995		1996			1998		1999			2000			2001		
	9/10	6/03	7/22	8/10	9/12	7/30	7/14	8/04	9/22	5/19	7/11	7/16	8/02	9/12	5/09	5/22
0	19.8	12.1	20.7	19.5	18.0	21.0	19.0	19.9	16.2	10.0	19.2	15.5	20.3	17.5	9.9	11.8
1	19.3	12.1	20.6	19.1	17.9	21.0	19.0	19.9	16.2	10.0	19.0	15.5	20.3	17.5	9.7	11.8
2	19.2	12.1	20.6	19.0	17.8	21.0	19.0	19.9	16.2	10.0	18.9	15.5	20.3	17.5	9.7	11.8
3	19.2	12.1	20.5	19.0	17.8	21.0	19.0	19.8	16.2	10.0	18.8	15.3	20.3	17.5	9.6	11.8
4	19.2	12.1	20.5	19.0	17.8	21.0	19.0	19.8	16.2	10.0	18.8	15.3	20.3	17.6	9.0	11.7
5	19.1	12.0	20.4	18.9	17.8	20.0	19.0	19.9	16.2	10.0	18.8	15.3	20.3	17.6	8.6	11.7
6	19.1	12.0	20.2	18.9	17.8	20.0	19.0	19.9	16.2	9.9	18.8	15.1	20.2	17.6	8.4	11.7
7	19.1	12.0	19.8	18.9	17.8	20.0	19.0	19.9	16.2	9.9	18.8	15.1	19.9	17.6	8.3	11.7
8	19.0	12.0	18.7	18.9	17.8	19.0	19.0	17.8	16.2	9.9	18.8	15.1	19.2	17.6	8.0	11.7
9	17.9	11.8	16.3	18.9	17.8	18.0	17.0	17.0	16.2	9.5	18.8	15.1	18.5	17.6	7.7	11.7
10	17.4	11.8	15.7	18.9	17.6	17.0	16.5	16.5	16.2	9.5	17.6	15.0	17.4	17.6	7.6	11.7
11	17.0	11.6	15.3	18.8	17.4	16.0	15.0	16.3	16.2	9.1	16.5	15.0	17.0	17.9	7.5	11.6
12	16.6	11.5	14.8	16.6	17.4	15.0	14.5	16.1	16.2	9.0	15.4	15.0	16.4	17.9	7.4	11.5
13	16.1	11.5	14.5	15.6	17.1	15.0	14.0	16.0	16.1	9.0	14.9	14.9	15.9	17.9	7.3	11.1
14	15.7	11.4	14.2	15.0	16.7	15.0	14.0	15.8	16.1	8.9	14.5	14.8	15.6	17.8	7.2	11.0
15	15.2	11.3	13.8	14.8	15.7	14.0	13.0	15.3	16.1	8.9	14.0	14.2	15.1	17.8	7.2	10.8
16	14.8	11.1	13.6	14.4	15.3	14.0	13.0	15.0	16.0	8.6	13.3	13.0	14.9	17.8	7.2	10.4
17	14.5	11.0	13.3	14.2	14.9	14.0	12.5	14.8	16.0	8.4	13.0	11.0	14.2	16.9	7.1	10.0
18	14.2	10.0	13.1	13.9	14.6	14.0	12.0	14.5	15.5	8.1	12.4	10.4	13.6	16.3	7.0	9.9
19	14.1	9.9	12.9	13.5	14.4	13.0	11.5	13.9	15.0	8.0	11.9	10.0	13.1	16.1	6.9	9.7
20	14.0	9.8	12.6	13.3	13.9	13.0	11.0	13.2	15.0	7.8	11.0	10.0	12.6	15.9	6.8	9.1
25	13.0	8.2	11.5	11.9	13.2	12.0	10.0	11.3	14.5	7.0	10.2	8.1	10.5	13.9	6.5	6.8
30	12.4	7.2	10.9	11.3	12.6	11.0	9.0	10.5	14.0	6.5		7.7	9.1	11.5	6.3	6.3
35	12.0	6.9	10.0	10.4	11.3	9.0	8.0	9.8	13.0	6.0		7.1	7.9	9.2	6.2	5.7
40	11.5	6.2	9.0	9.4	10.1	7.0	7.0	8.3	11.5	6.0		6.5	7.2	7.9	6.1	.
45	10.4	6.0	7.8	8.0	8.4	7.0		7.5	9.5	5.9		6.0	6.8	7.1	.	5.4
50	9.1	6.0	7.0	7.3	7.3	6.0			7.8				6.0			
55		6.0		7.0		6.0			7.1						.	5.4
58															.	5.4

Table A3. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Cebolla basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	<u>2001</u>				<u>2002</u>		
	6/19	7/16	8/24	5/12	6/06	7/12	8/08
0	16.3	19.6	20.1	8.6	14.6	19.6	20.3
1	16.3	19.5	19.5	8.7	14.5	19.4	19.7
2	16.2	19.4	19.2	8.6	14.4	19.3	19.5
3	16.2	19.3	19.0	8.6	14.4	19.1	19.4
4	16.1	19.3	18.9	8.6	14.4	19.0	19.3
5	16.0	19.3	18.8	8.6	14.3	18.9	19.3
6	15.9	19.2	18.7	8.5	14.2	18.8	19.7
7	15.7	19.2	18.7	8.4	14.2	18.8	19.2
8	15.6	19.2	18.7	8.3	13.5	18.7	19.2
9	15.4	17.5	18.7	8.2	13.2	18.3	19.2
10	15.1	16.5	18.7	8.2	12.8	17.6	19.2
11	14.7	15.6	18.6	8.2	12.4	17.2	18.9
12	14.3	15.3	18.5	8.1	11.9	16.1	18.9
13	13.9	14.7	17.2	8.0	10.9	15.3	18.5
14	12.4	14.1	16.7	8.0	10.4	14.6	18.0
15	12.0	13.7	16.2	7.9	9.7	13.7	17.5
16	11.6	13.4	15.8	7.8	9.1	13.2	16.7
17	11.2	12.9	15.5	7.7	8.7	12.7	16.2
18	10.7	12.6	15.4	7.5	8.3	11.9	15.4
19	10.4	12.4	14.9	7.4	8.2	11.4	14.2
20	10.2	11.9	14.5	7.3	7.9	10.2	12.6
25	8.5	10.7	12.9	7.1	7.1	8.5	10.8
30	7.0	8.8	.	6.8	6.5	7.2	8.4
35	6.5	7.3	.	6.5	6.3	6.7	7.4
40	.	.	.	6.5	.	.	.
45	6.1	6.5	.	6.5	.	.	.
50		6.4		6.3	6.1	6.6	7.0
55	5.9	.	.	.	6.0	6.5	
58	.	.	.	.	.	.	.

Table A4. Temperature profiles (°C) measured with a YSI model 58 meter at Iola basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	1993					1994					1995					
	7/19	9/14	5/23	6/05	6/24	7/06	7/20	7/31	8/17	9/17	5/31	6/21	7/12	8/2	8/15	9/12
0	19.9	16.6	13.0	15.0	18.0	19.0	18.0	19.0	20.0	18.0	9.6	15.4	20.8	19.6	19.0	18.3
1	19.5	16.8	12.0	15.0	18.0	19.0	19.0	19.0	20.0	18.0	9.9	14.7	19.3	18.5	19.0	18.3
2	19.4	16.8	12.0	15.0	18.0	19.0	19.0	19.0	20.0	18.0	9.8	14.5	18.2	18.1	19.0	18.3
3	19.0	16.8	12.0	15.0	18.0	19.0	19.0	19.0	20.0	18.0	9.7	14.3	15.8	18.0	18.9	18.3
4	18.9	16.8	11.0	15.0	18.0	19.0	19.0	19.0	20.0	18.0	9.7	14.1	14.8	17.9	18.8	18.2
5	18.8	16.8	11.0	15.0	18.0	19.0	19.0	19.0	20.0	18.0	9.7	13.6	14.1	17.8	18.8	18.2
6	18.8	16.8	11.0	15.0	18.0	19.0	19.0	19.0	20.0	17.0	9.6	13.3	14.1	17.6	18.8	18.2
7	18.5	16.8	11.0	14.0	17.0	18.0	19.0	19.0	20.0	17.0	9.4	13.1	14.0	17.5	18.8	18.2
8	18.4	16.8	11.0	14.0	17.0	18.0	18.0	19.0	20.0	17.0	9.3	12.8	13.9	17.3	18.4	18.2
9	18.4	16.8	11.0	14.0	17.0	18.0	18.0	19.0	20.0	17.0	9.3	12.5	13.7	16.3	17.1	18.2
10	18.3	16.8	10.0	14.0	16.0	18.0	18.0	18.0	19.0	17.0	9.1	12.0	13.6	15.6	16.0	18.2
11	18.0	16.8	10.0	14.0	15.0	18.0	18.0	17.0	19.0	17.0	8.5	11.8	13.5	15.1	15.4	18.2
12	16.9	16.8	10.0	14.0	15.0	17.0	17.0	17.0	18.0	17.0	8.2	11.7	13.2	14.6	15.1	18.2
13	16.1	16.8	10.0	14.0	14.0	15.0	16.0	16.0	17.0	17.0		11.6	13.0	14.3	15.0	17.0
14	15.9	16.8	9.0	12.0	14.0	15.0	15.0	15.0	17.0	17.0		11.1	12.9	14.1	14.7	16.2
15	15.7	16.8	8.0	11.0	13.0	14.0	15.0	15.0	17.0	17.0		10.8	12.6	13.8	14.0	15.5
16	15.5	16.8	8.0	11.0	13.0	14.0	14.0	14.0	16.0	17.0		10.7	12.4	13.6	13.7	15.2
17	15.0	16.7	8.0	11.0	13.0	13.0	14.0	14.0	16.0	17.0		10.6	12.3	13.3	13.5	15.0
18	15.0	16.5	8.0	11.0	12.0	12.0	13.0	14.0	16.0	16.0		10.5	12.1	13.2	13.5	14.8
19	14.9	16.2		10.0	12.0	12.0	13.0	14.0	15.0			10.3	11.7	13.1	13.4	14.6
20	14.6	15.9		9.0	11.0	12.0	13.0	13.0	15.0			10.2	11.5	13.1	13.1	14.5
25	13.0	14.7			10.0	11.0								12.1	12.3	13.3

Table A4. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Iola basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	<u>1996</u>				<u>1998</u>		<u>1999</u>			<u>2000</u>				<u>2001</u>			
	6/3	7/23	8/10	9/13	7/30	7/14	8/4	9/22	5/19	7/11	7/16	8/2	9/12	4/20	5/9	5/24	6/19
0	12.3	19.8	20.1	17.7	23.0	20.0	19.5	16.0	11.0	18.8	16.2	19.5	17.5	6.9	11.8	13.0	17.0
1	12.0	19.8	19.3	17.6	21.0	20.0	19.5	16.0	10.9	18.8	16.1	19.5	17.5	6.9	11.2	13.0	16.8
2	12.0	19.9	19.0	17.6	21.0	19.0	19.5	16.0	10.8	18.8	16.1	19.5	17.5	6.9	10.8	13.0	16.5
3	12.0	19.9	19.0	17.6	21.0	19.0	19.5	16.0	10.8	18.8	16.0	19.5	17.5	6.9	10.5	13.0	16.4
4	12.0	19.9	19.0	17.6	21.0	19.0	19.3	16.0	10.8	18.8	16.0	19.5	17.5	6.9	10.2	12.9	16.3
5	12.0	19.9	18.9	17.6	21.0	19.0	19.5	16.0	10.8	18.8	16.0	19.5	17.5	6.8	9.5	12.9	16.2
6	12.0	19.9	18.9	17.6	20.0	19.0	19.5	16.0	10.8	18.8	16.0	19.5	17.5	6.1	9.4	12.9	16.1
7	12.0	19.9	18.8	17.6	20.0	19.0	18.0	16.0	10.8	18.7	15.9	19.5	17.5	5.8	9.3	12.9	16.0
8	12.0	19.9	18.8	17.6	20.0	19.0	17.2	16.0	10.8	18.2	15.9	19.0	17.5	5.7	9.2	12.8	16.0
9	12.0	19.9	18.8	17.6	19.0	18.0	17.0	16.0	10.5	18.1	15.8	17.9	17.5	5.6	9.2	12.8	15.9
10	12.0	19.1	18.6	17.5	17.0	17.0	16.5	16.0	10.2	16.5	15.8	17.4	17.5	5.5	9.0	12.8	15.9
11	12.0	16.6	18.3	17.5	17.0	16.0	16.0	16.0	10.1	16.1	15.8	17.1	17.5	5.4	8.9	12.8	15.8
12	11.9	15.9	17.5	17.5	16.0	15.5	15.9	16.0	10.1	15.7	15.5	16.8	17.5	5.4	8.8	12.7	15.4
13	11.9	15.5	16.3	17.4	16.0	15.0	15.5	16.0	10.1	15.0	15.5	16.5	17.4	.	.	12.3	13.9
14	11.8	15.1	15.7	17.3	16.0	15.0	15.3	16.0	10.0	14.6	15.5	16.0	17.4	.	.	11.2	13.3
15	11.7	14.6	15.2	17.2	15.0	14.0	15.1	16.0	9.6	14.0	15.5	15.9	17.4	.	.	11.1	12.9
16	11.4	14.3	14.9	16.4	15.0	13.5	15.0	16.0	9.5	13.5	15.5	15.3	17.3	.	.	.	12.8
17	11.2	13.8	14.6	15.8	15.0	13.0	14.3	16.0	9.4	12.3	15.0	14.9	16.9	.	.	.	12.4
18	11.0	13.4	14.4	15.2	15.0	12.5	14.1	15.5	9.2	11.9	14.5	14.5	.	.	.	.	11.7
19	10.8	13.0	14.2	14.7	14.0	12.0	14.8	15.0	8.8	11.7	13.5	13.5	.	.	.	.	11.4
20	10.5	13.0	14.1	14.3	14.0	11.5	13.5	14.5	.	11.2	12.0	12.6	.	.	.	.	10.9
25	.	.	.	.	.	.	12.5	13.8	.	9.3	.	.	.	.	.	.	.

Table A4. Continued. Temperature profiles (°C) measured with a YSI model 58 meter at Iola basin in BMR during 1994-2002. Some data contributed by Pat Martinez, Colorado Division of Wildlife, and Matt Malick, National Park Service.

Depth (m)	<u>2001</u>		<u>2002</u>				
	7/16	8/23	4/13	5/12	6/6	7/12	8/8
0	20.0	18.7	6.6	10.7	15.1	18.9	18.9
1	20.0	18.7	5.9	10.7	15.1	18.9	19.0
2	19.8	18.7	5.6	10.6	15.2	18.9	19.0
3	19.6	18.6	5.5	10.6	15.2	18.9	19.0
4	19.3	18.6	5.4	10.6	15.2	18.9	19.0
5	19.3	18.6	5.3	10.5	15.2	18.9	19.1
6	19.3	18.6	5.1	10.5	15.2	18.9	19.1
7	19.2	18.6	4.7	10.5	15.2	18.7	19.0
8	19.2	18.6	4.6	10.5	15.1	18.0	19.0
9	18.9	18.6	4.5	10.3	14.7	17.4	19.0
10	18.1	18.6	4.5	9.9	14.1	16.5	18.8
11	16.6	18.6	4.5	9.6	13.1	15.9	18.7
12	16.0	18.6	4.4	9.4	11.8	15.3	18.7
13	15.5	17.7	4.2	9.3	10.8	14.6	18.3
14	14.9	16.9	4.2	.	.	.	18.1
15	14.5	16.2	4.3	.	.	.	17.8
16	14.4	15.7	4.3	.	.	.	16.4
17	.	15.3	4.3	.	.	.	14.6
18	.	15.0	4.3	.	.	.	.
19	.	14.7	4.3	.	.	.	.
20	.	.	4.3	.	.	.	.
25	.	.	.	.	.	.	.

Table A5. Standardized transects used during hydroacoustics surveys at BMR during spring and summer 2002. Waypoint names were changed in 2001 to follow CDOW naming convention. SONAR1 and SONAR2 are start and end points for the diel survey conducted in June 2002. Approx. time is the estimated time to complete the transect at normal surveying speed. Map datum = NAD 27 CONUS.

Basin	Waypoint Name	UTM Zone	UTM Easting	UTM Northing	Transect Length (m)	Approx. time (min.)
Iola	BMIT0	13 S	0319334	4261446	Start	0
	BMIT1	13 S	0318384	4260487	1349.88	14
	BMIT2	13 S	0317105	4261126	1429.74	17
	BMIT3	13 S	0316179	4259915	1524.47	16
	BMIT4	13 S	0314781	4259150	1593.62	27
Cebolla	BMCT0	13 S	0310077	4259131	Start	0
	BMCT1	13 S	0309339	4260512	1565.82	17
	BMCT2	13 S	0307918	4261238	1595.72	18
	BMCT3	13 S	0307456	4259614	1688.44	18
	BMCT4	13 S	0306273	4260667	1583.76	16
	BMCT5	13 S	0305394	4259393	1547.81	20
Sapinero	BMST0	13 S	0298750	4258321	Start	0
	BMST1	13 S	0297398	4259367	1709.39	19
	BMST2	13 S	0299027	4260487	1976.88	18
	BMST3	13 S	0299356	4262031	1578.66	26
	BMST4	13 S	0300143	4260409	1802.85	17
	BMST5	13 S	0301586	4261293	1692.25	21
	BMST6	13 S	0302498	4260081	1516.80	19
	SONAR1	13 S	0298390	4259821	Start	
	SONAR2	13 S	0300079	4260794		

Table A6. Mean total length (TL, mm) of all kokanee, rainbow trout and brown trout captured in experimental vertical gill net sets during 1994-2002. In 1997 sampling occurred during short intervals over a 24 h period with mesh sizes 13, 25, and 32 mm, instead of overnight sets with meshes 13-50 mm, in other years. Note that the mean would have been affected by the months sampled each year. Standard deviation of the mean is shown as SD; n is sample size.

Year	Months	<u>Kokanee</u>			<u>Rainbow trout</u>			<u>Brown trout</u>		
		TL	SD	n	TL	SD	n	TL	SD	n
1994	Jun, Aug, Oct	310	64.2	335	256	48.6	13	334	58.7	23
1995	Jun, Jul, Sep	284	70.5	225	317	55.2	6	313	29.4	36
1996	Aug, Sep	329	52.9	88	315	89.2	5	274	42.9	3
1997	Jun, Jul, Aug	318	59.3	363	284	43.0	36	318	44.5	57
2001	Jul	329	66.3	17	--	--	--	296	11.4	4
2002	Aug	327	68.3	125	400	0.0	1	364	73.9	4
Mean		316	6.5	6	314	54.2	5	317	31.0	6

Table A7. Linear regressions models relating total length (mm) as a function of head length (mm) derived from fish sampled in vertical gill nets in 1995. These relationships were developed to help determine sizes of fish from body parts sampled below the dam. Models are of the form: $TL = a + b \cdot HL$ or $TL = a + b \cdot \ln(HL)$. “Max” and “Min” show the maximum and minimum values for head lengths that were used in the regressions.

Species	Predictor	a	b	n	r ²	Max	Min
Brown trout	Ln(HL)	-157	123	30	0.54	78	30
Kokanee	Ln(HL)	-541	236	189	0.91	68	13
Lake trout	HL	17.0	6.77	21	0.93	131	21
Rainbow trout	HL	77.0	6.10	4	0.91	46	23

A. Methodological Recommendations

The intensive field sampling that occurred over the course of this study gave us the opportunity to evaluate a number of sampling techniques. This information should be useful in future studies at BMR and at other large, coldwater reservoirs.

Methods for Sampling Age-0 Kokanee

Of all the sampling methods we tried we caught the most age-0 kokanee in horizontal gill nets set on the bottom in about 20 m depth in Cebolla basin (Hardiman 2003). The multifilament nets appeared to be more productive than monofilament nets. We caught 36 age-0 kokanee, 10 juvenile lake trout, and 2 yellow perch in gill nets from June to August. We also captured a few white suckers, brown trout and some adult kokanee and lake trout. However, the nets were very size selective for juveniles so by-catch of adult fishes was never a problem. The floating “Swedish” gill nets were used in May and June mostly in Iola basin. These floating sets caught 5 age-0 kokanee in overnight sets. Only 3 age-0 kokanee were caught later in the summer in the Swedish gill nets set on the bottom. This could be an effect of slightly smaller mesh sizes and smaller nets in general (50 ft vs. 100 ft) compared to the multifilament nets or the material itself being less effective for age-0 kokanee. The monofilament, being a stiffer material may allow fish to bounce off of the net material instead of being entangled.

The mid-water trawl was not very effective for catching age-0 kokanee in 2002. We caught two age-0 kokanee in July that were assumed to be from natural reproduction as they were significantly smaller (39 and 40 mm total lengths) than fish released in April from the hatchery (average of 52.4 mm). Further, stable isotope signatures from similar sized kokanee captured in 2001 were very different from those of fish taken from the Roaring Judy Hatchery or CSU’s Aquatic Research Lab but similar to signatures of larger age-0 sampled in the trawl. Thus, it appears unlikely that these fish are simply hatchery fish that failed to grow in the reservoir prior to capture since one would expect them to retain strong hatchery-based signatures in the absence of growth on within-reservoir food supplies. A more likely explanation is that these fish were actually hatched within the reservoir. While we are unsure if our midwater trawl was selective for smaller fish, having such a large fraction of the total age-0 sampled that may be naturally reproduced fish suggests that it is size-selective. Previous assumptions have been that natural reproduction in Blue Mesa is negligible. It is unknown whether or not the small age-0 are naturally produced and whether or not these fish would be large enough to survive and recruit to the fishery but the finding suggests that there is more to learn about kokanee biology in Blue Mesa.

The midwater trawl is likely to be most effective early in the summer when the fish are smaller. As the fish grow they are more able to evade the net. Furthermore, we believe the single mesh trawl was less effective due to lower water sieving efficiency. This could either push fish out of the opening of the net or allow them to detect the net and move to the side. Although we only had time to test it twice, we believe the modified, graduated mesh net, would be a more effective sampling tool. However, the depths it could fish would need to be determined by working with another boat and verifying depths reached with appropriate boat speed, towline, and weight combinations. We

caught two fish with this net in August. One was an age-0 kokanee and the other estimated to be a 2+ year old kokanee, indicating that older, larger fish were not as likely to evade this net. This net was not tested further due to a break down in our hauling winch and a conflict with boat needs with another crew. More testing in the future would be useful to determine the modified design's overall effectiveness for monitoring age-0 kokanee populations in large reservoirs.

Only one kokanee < 150 mm TL was captured in standardized gill net sets used in all three basins in August 2002 (Hardiman 2003), and none were caught in 2001. However, none were expected given the large size of the smallest mesh in this gear type. Age-1 and older kokanee comprised the vast majority of fish sampled in these net sets. These data are required for partitioning pelagic hydroacoustics targets into species.

Midwater Trawl Configuration

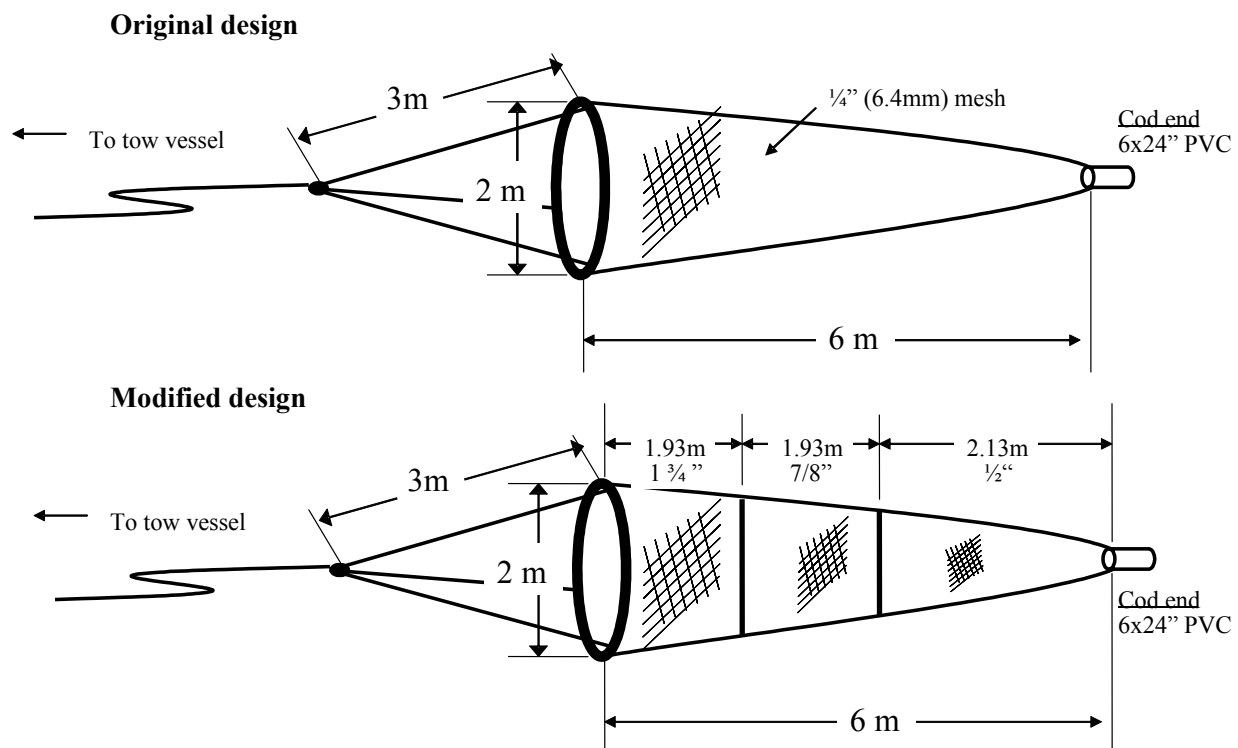


Figure A1. Original configuration of the midwater trawl employed in 2001-2002 and modified design, used in late summer 2002.

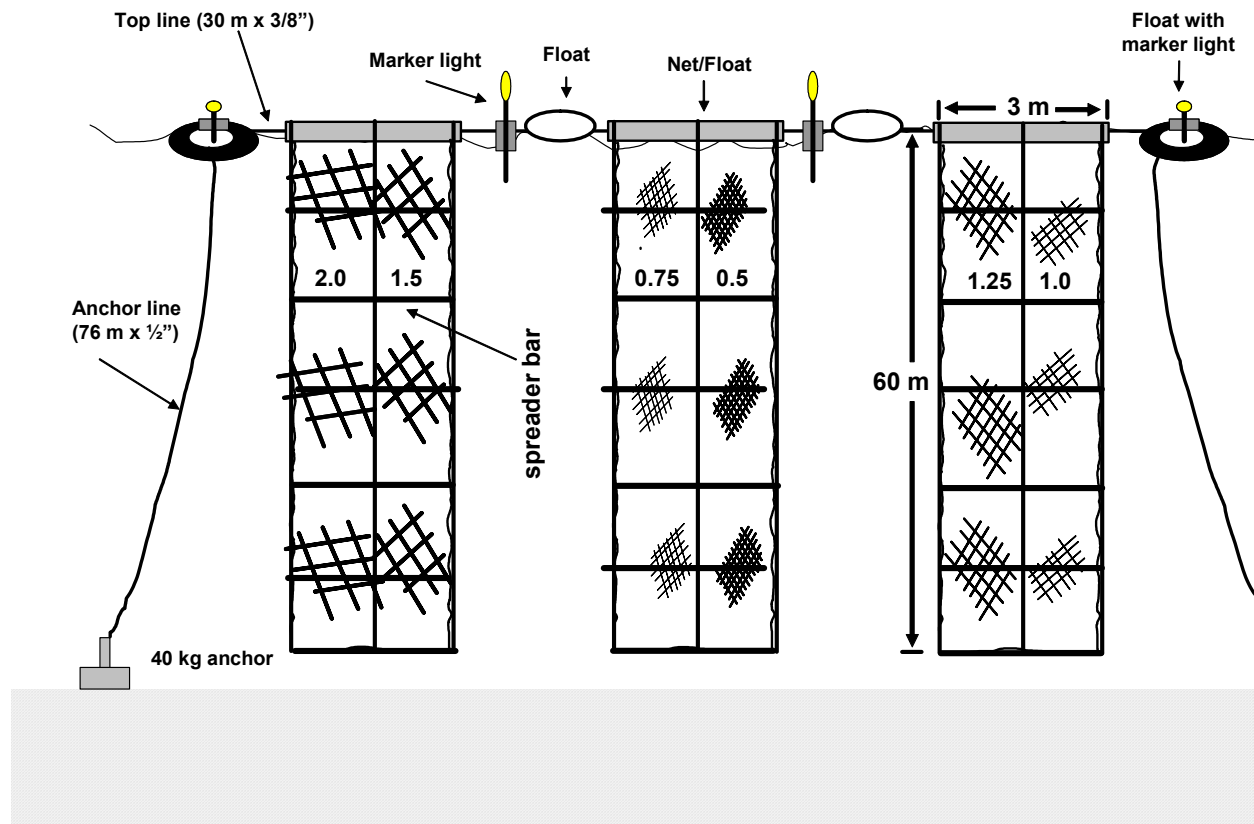


Figure A2. Configuration of vertical gill nets used in standardized surveys at mid-basin stations in BMR during 1994-2002. Mesh size (inches) is shown on each panel of each net.

Sonic Tracking of Lake Trout

The primary methodological shortcoming was that we undertook the study without sufficient consideration of the resources required. To accomplish the goal of assessing whether lake trout movement and habitat use facilitate predation on kokanee would have required much more frequent tracking at all times of day and night, as well as a more thorough analysis plan formulated in advance (Rogers and White, in press). As a consequence, the data yield some interesting trends, particularly with regard to site fidelity, but no firm conclusions.

Given the time and logistical obstacles to systematically tracking mobile fish in a large reservoir, we believe future telemetry studies at BMR should entail either very targeted evaluation of specific hypotheses, or remote data collection. For example, diel hydroacoustic surveys suggest that lake trout may foray into warmer water only around dusk; depth tagged fish could be located in advance and then tracked continuously throughout this brief period of rapidly changing light levels, resulting in a much more efficient collection of the data necessary to evaluate that hypothesis.

Regarding remote data collection, we contemplated building a remote system using a Sonotronics DL-01 data logger attached to a receiver, but did not pursue that effort because given the receivers' range (wide- or narrow-band), it would require a number of such systems at >\$1,000 each to cover the reservoir. (Additionally, it must be noted that the DL-01 employs an outdated operating system and the unit we used had untrustworthy RS232 connections.)

More potential lies in data archiving tags. The CSU Fisheries Ecology Lab tested a very impressive archiving tag manufactured by Star-Oddi (Star-Oddi 2004); had these tags been available at the outset of the project we would have advocated using them, although we would have then faced the daunting problem of retrieving the tags at the end of the study. Additional desirable features of a transmitter/receiver system include a signal strength indicator, a mortality signal, and better consistency on pulse interval calculation/display. Depth and temperature data are encoded in the pulse interval, with each tag having its own conversion chart, but in practice the pulse interval was often too variable to yield a reliable depth estimate.

Regarding study design and sample size, the number of tagged fish would have been adequate or nearly so, had it been practical to collect more data from each individual. However, it would have been far better to have captured, tagged and released fish in each basin. As temperature and dissolved oxygen levels in lola and Cebolla become increasingly unsuitable in late summer, lake trout in those basins presumably must move about in search of better habitat, perhaps leaving lola basin entirely. Yet in October and November 2001 substantial numbers of lake trout were netted in both basins. Is there a sub-population of lake trout that moves seasonally around the reservoir, while a second sub-population remains in Sapinero year-round? It would be interesting to know, particularly as this question has important implications for population size estimation.

The secondary objective, that of learning as much as possible about the technique so as to improve future telemetry studies, was more fully accomplished than the first. Quantifying signal characteristics in advance with a fixed transmitter, establishing a search grid, and the tracking routine and minimum movement analyses described above are all techniques that would be applicable with any transmitter / receiver system, as even archival tags must eventually be tracked for retrieval. Any future telemetry study at BMR will be greatly facilitated by having this advance work already accomplished, and the method would be equally applicable in other reservoirs. Additionally, the insights about survival rate and site fidelity are worthwhile in themselves.

In a minority of cases, putative site fidelity may have been an artifact of tracking transmitters that were no longer in fish, due to mortality or tag expulsion. The 2002 drought conditions indirectly alerted us to this possibility: as the reservoir dropped and epilimnetic temperatures rose, four tags continued to be found in locations that by August 2002 were shallow enough that water temperatures approached 18° C all the way to the bottom. Although one of the study objectives was to explore whether lake trout venture into warmer water to prey on kokanee, we expected that if such forays occurred they would be brief and unusual. It seems quite unlikely that lake trout would repeatedly be found in the same increasingly untenable location with colder water only meters away.

To assess whether relatively small changes in position might result from tracking error on an immobile transmitter, we computed position change for each successive pair of locations per fish. In a worst-case scenario, ~30 m of tracking error would be compounded by 13 m GPS error due to atmospheric fluctuations and other systemic error sources (U.S. Department of Defense 2001), with the resulting 43 m error doubled if the second tracking occasion erred by an equal amount in the opposite direction. Thus, any position change of ~90 m or less might be attributable to error rather than transmitter movement (although in practice this coincidence of worst-cases would be quite unlikely). Obviously, if a small position change is followed at a later time by a change of several hundred meters, the transmitter is still aboard a live fish. If, however, a once-mobile fish changes position by less than 90 m for several months running, and that pattern is not subsequently reversed, the transmitter must be suspected of being stationary, particularly if the habitat it occupies becomes less suitable as described above. Four fish (numbers 2, 3, 4, and 9) met this description; unfortunately, all had standard transmitters, so no depth or temperature data could be collected.

We consider it most likely that these tags were expelled. Some or all of the fish may have died, but the longevity of lake trout, their high estimated survival rate in BMR, the excellent condition of all fish when tagged, and the fact that they manifestly survived for some months after tagging, all argue against wholesale mortality. The remaining possibility, that the fish in fact regularly occupied such shallow warm water, is the least likely. We are aware of no studies specifically documenting tag expulsion by lake trout although low rates of tag expulsion have been found in other salmonids (Helm & Tyus, 1992). It may be noteworthy that the four fish suspected of having lost their transmitters

were among the five smallest fish tagged, by weight. Although all were well within tag:body weight guidelines, it seems plausible that a smaller fish might be more likely to experience an implanted tag as an irritant and encapsulate and expel it as a result. Winter (1996) reported that large transmitters are more likely to be expelled. If this is in fact what happened, a tag loss rate of 23.5% certainly warrants effort to lower it if future telemetry studies are undertaken.

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