FISHERY RESEARCH

DWORSHAK RESERVOIR NUTRIENT RESTORATION RESEARCH, 2007-2015

Project Completion Report
March 1, 2007 – February 28, 2016

Prepared by:

Sean M. Wilson, Senior Fishery Research Biologist
and
Matthew P. Corsi, Principal Fishery Research Biologist
Idaho Department of Fish and Game

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By

Sean M. Wilson
and
Matthew P. Corsi
Idaho Department of Fish and Game
600 South Walnut Street
P.O. Box 25
Boise, ID 83707
USA

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ABSTRACT

The Idaho Department of Fish and Game and the U.S. Army Corps of Engineers cooperatively conducted a pilot project to test nutrient restoration as a means to restore the Dworshak Reservoir ecosystem, improve reservoir productivity, and promote recreational fisheries. Data were collected from 2004 through 2015, and nutrients (primarily nitrogen as ammonium nitrate) were added from 2007 through 2015, with an interruption in 2011. Water quality standards set by the Idaho Department of Environmental Quality and U.S. Environmental Protection Agency were not violated. The mean Secchi depth for the restoration period was similar to the mean for the non-restoration period. Mean concentrations of nitrogen (N) and phosphorus (P) in the reservoir did not increase following restoration, indicating rapid biological uptake of added nutrients. On average, heterotrophic bacteria densities were 71% higher during the restoration period and picocyanobacteria densities were 64% higher. The mean chlorophyll *a* concentration was slightly lower for restoration years. Although the mean biovolume of phytoplankton was similar for both periods, the mean biovolume of edible phytoplankton and the proportion of the phytoplankton community that was edible to zooplankton were substantially higher for the restoration period. The mean density of *Daphnia* large enough to be consumed by kokanee *Oncorhynchus nerka* was 103% higher for the restoration period as compared to non-restoration period. Kokanee grew faster at a given abundance as a result of increased food availability and there is evidence that the carrying capacity of the reservoir has increased as a result of nutrient restoration. As a result of improved growth and increased abundance, the biomass of kokanee, both in the reservoir and spawning in the watershed above, has increased by 50% and 40% respectively. An increase in the abundance of kokanee of the same size or slightly larger than pre-restoration is expected to improve catch rates in the recreational fishery and provide more forage for piscivorous fishes. Dworshak Reservoir appears to be responding to nutrient restoration as anticipated and greater improvements to the fishery are possible if results are sustained. Our results to date are consistent with those reported for nutrient restoration projects in Kootenay and Arrow lakes in British Columbia.

Authors:

Sean M. Wilson
Senior Fishery Research Biologist

Matthew P. Corsi
Principal Fishery Research Biologist

INTRODUCTION

Dworshak Reservoir is the most popular fishing destination in Clearwater County and the second most popular destination in the Clearwater region, based on total angler trips in 2011 (Thomas MacArthur, IDFG, unpublished data). It provides a multispecies fishery for naturally-reproducing kokanee *Oncorhynchus nerka*, Smallmouth Bass *Micropterus dolomieu,* and westslope cutthroat trout *Oncorhynchus clarkii lewisi*, as well as hatchery-stocked Rainbow Trout *Oncorhynchus mykiss*. The reservoir also provides important habitat for Bull Trout *Salvelinus confluentus*, which are listed as Threatened under the Endangered Species Act.

Kokanee were first stocked into Dworshak Reservoir in 1972 (Horton 1981). Although two stocks were originally introduced (early spawners from Anderson Ranch Reservoir, Idaho and late spawners from Lake Whatcom, Washington), the early-spawning variety quickly dominated (Horton 1981). Kokanee provide the most popular fishery on the reservoir, with annual effort levels that have exceeded 140,000 angler hours and annual harvest of over 200,000 fish (Mauser et al. 1989). The pelagic nature and planktivorous feeding habits of kokanee make them well-suited for an oligotrophic reservoir with fluctuating water levels, such as Dworshak Reservoir (Maiolie and Elam 1996).

Entrainment and oligotrophication have been identified as the primary factors limiting the kokanee population in Dworshak Reservoir (Stark and Stockner 2006). With the exception of high-runoff years, entrainment was reduced beginning in the early 1990s when drawdown began occurring primarily during the summer and early autumn to provide cool water for Chinook Salmon *Oncorhynchus tshawytscha* in the Snake River. During this time period, kokanee are distributed farther from the dam and are less vulnerable to entrainment than during winter (Maiolie and Elam 1997). Bennett (1997) found that discharge from January through March had the highest negative correlation with survival compared to other time periods examined. While entrainment remains a limiting factor for kokanee in some years, oligotrophication is more often the primary limiting factor. Bennett (1997) identified declining productivity as a critical factor limiting the kokanee fishery and recommended it be addressed before implementing intensive fisheries management practices.

Stockner and Brandt (2006) conducted a detailed assessment of the reservoir and gave recommendations for a nutrient restoration program. Based on phosphorous (P) loading and mean chlorophyll densities, they classified Dworshak Reservoir as borderline oligomesotrophic. However, they found that the phytoplankton communities and associated food web present during the spring were dominated by microbial (picoplankton) communities typical of ultraoligotrophic lakes and reservoirs. Dworshak Reservoir becomes nitrogen (N) limited by mid-summer, leading to a dominance of N fixing cyanobacteria (blue-green algae). Blue-green algae are typically abundant from mid-summer to early fall, and because they are inedible to zooplankton, represent a considerable carbon sink. Mid-summer N limitation and the subsequent reduction in zooplankton results in reduced fish production.

The Idaho Department of Fish and Game (IDFG) and the U.S. Army Corps of Engineers (USACE) initiated a five-year pilot project to evaluate nutrient restoration as a management strategy for restoring the Dworshak Reservoir ecosystem and improving the fishing opportunities it provides. The goal of the project was to provide a quality fishery by improving the flow of carbon (C) through all trophic levels to the kokanee. We intend to restore lost productivity by improving the N:P ratios in the reservoir, thereby promoting the growth of desirable phytoplankton (i.e., edible by zooplankton). Increased abundance of edible phytoplankton (including picoplankton) was expected to support increased abundance of zooplankton, and therefore an improved forage base for fish. Stockner and Brandt (2006) anticipated that a moderate N nutrient addition would benefit fish populations without degrading water quality.

The pilot project began in 2007, for which the USACE applied the nutrients and IDFG monitored the limnological and fisheries response. TG Eco-logics (later Advanced Eco-Solutions), a private consulting company, was contracted to assist in designing the monitoring program, interpret the results of the limnological data, and adjust the nutrient prescriptions as necessary. However, nutrient applications were suspended prematurely in late July of 2010 due to a legal challenge. At that time, the project was being conducted under the legal authority of a Consent Order issued by the Idaho Department of Environmental Quality (DEQ). The U.S. Environmental Protection Agency (EPA) then made a determination that a National Pollutant Discharge Elimination System (NPDES) permit would be required for nutrient applications to continue. An NPDES permit was not obtained until October of 2011, which did not allow for nutrient applications in the final year of the pilot study. In order to fully assess the effects of the project on longer lived organisms (i.e. kokanee), it was determined that a full five-year study was needed. Therefore, a second five-year pilot project was initiated in 2012.

The primary role of IDFG's monitoring program was to evaluate the effectiveness of the nutrient restoration program at improving the flow of carbon (C) to the kokanee population in Dworshak Reservoir without adversely affecting water quality. Thus, limnological surveys were conducted to meet three major requirements. The first requirement was to ensure that water quality standards, as stipulated by DEQ and EPA, were maintained. Second, limnological data were collected to make comparisons with non-restoration conditions to determine the biological effects of the project, including changes to the plankton communities. In restoration years, data were provided to the consultant to actively manage the nutrient applications. In addition to limnological monitoring, surveys were conducted to monitor the kokanee population. An effective nutrient restoration program is expected to increase the average size of kokanee at any given population density, which could result in larger kokanee at similar densities or kokanee of a similar size at a much higher density. Either outcome has the potential produce higher catch rates in the sport fishery (Rieman and Maiolie 1995).

This report summarizes data collected from 2004 through 2015, which includes both restoration and non-restoration years. These data were used to assess both the limnological and fishery responses to N restoration and evaluate whether nutrient restoration should be implemented in Dworshak Reservoir long-term.

OBJECTIVES

1. Maintain an annual median Secchi depth of ≥3.0 m and an annual median chlorophyll *a* concentration of ≤3.0 µg/L for treated areas of the reservoir, per IDEQ and EPA.

2. Increase densities of picoplankton by twofold in the first year of nutrient restoration.

3. Increase the mean total length of age-2 kokanee by 20 mm over that observed at a similar pretreatment kokanee density.

4. Maintain a kokanee population that can sustain a catch rate of 1.2 fish per hour with a minimum average size of 254 mm total length.

STUDY SITE

Dworshak Reservoir was impounded after the construction of Dworshak Dam in 1972 on the North Fork Clearwater River approximately 2.4 km from its confluence with the mainstem Clearwater River. The reservoir is narrow, steeply sloped, and primarily surrounded by coniferous forests. The North Fork Clearwater River and its tributaries drain nearly 632,000 ha, which is composed primarily of montane forests in steeply sloped terrain (Falter et al. 1977). The underlying geology is composed of Columbia River basalt and metamorphic sediments with granitic intrusions covered by shallow soils (Falter et al. 1977). Most of the North Fork Clearwater watershed above the reservoir lies within the Clearwater National Forest. The reservoir is immediately surrounded by land managed by the USACE, but much of the lower watershed is privately owned. Timber harvest is the primary commercial activity, although there is some agriculture in the lower watershed.

At full pool, Dworshak Reservoir is 86.3 km long with a surface area of 6,916 ha and a volume of 4.3 billion m^3 (Falter 1982). Typical annual drawdown lowers the pool elevation by 24 m and reduces the surface area by 27%. Peak pool elevation is typically reached by late June and drawdown begins after the first week of July, with typical minimum pool elevation reached by the second week of September. The mean hydraulic retention time is 10.2 months (Falter 1982) and the mean daily discharge from 2004-2015 was 151 m^3/s (http://www.cbr.washington.edu/dart/; accessed 1/12/16). Historically, Dworshak Reservoir begins to thermally stratify in April and stratification becomes pronounced from June through September. Destratification begins in the fall and occurs more rapidly at the upper end of the reservoir (Falter 1982).

METHODS

Environmental Conditions

Daily mean reservoir inflow, discharge, and pool elevation data provided by the USACE were acquired through the Columbia River Data Access in Real Time website (http://www.cbr.washington.edu/dart/; accessed 1/12/16).

Physical and Chemical Limnology

Sample Collection

We conducted limnological sampling at seven stations on the reservoir and one station on the North Fork Clearwater River (NFC) below Dworshak Dam (Figure 1). Five stations on the main reservoir were designated as RK-2, RK-31, RK-56, RK-66, and RK-72, corresponding with the approximate river kilometer (RKM). Two additional stations were located in untreated areas of the reservoir, RKM six of the Elk Creek arm (EC-6), and RKM three of the Little North Fork arm (LNF-3). Sampling at RK-66 was discontinued in 2012.

In 2004, we conducted limnological sampling once per month from May through November. In 2005, we sampled once per month from April through November. In 2006, we increased the sampling frequency to twice per month beginning in May. From 2007 through 2015, we sampled twice monthly from April through September and once monthly during March, October, and November. When all reservoir stations and the river station could not be sampled in one day, samples were collected over a two-day period.

Physical parameters measured included water depth, water clarity, water temperature, dissolved oxygen (DO), and photosynthetically active radiation (PAR). Chemical parameters included pH, total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN), nitrate plus nitrite nitrogen (N+N), total ammonia (TA), total dissolved solids (TDS), and dissolved organic carbon (DOC). Biological parameters included chlorophyll *a* (Chl *a*), picoplankton, phytoplankton, and zooplankton. Sampling for TN, TA (beginning in 2011), and DOC (beginning in 2007) was only conducted during the first event each month. Turbidity, measured using a Hach 2100Q Turbidimeter, along with all previously mentioned chemical parameters, was analyzed for NFC.

Water depth was measured using a Garmin™ Model GSD22 depth sounder in conjunction with a GPS MAP 4212 chart plotter. Water clarity was measured using a 20 cm Secchi disc, which was lowered from the shaded side of the boat until no longer visible, then raised until it reappeared. Water temperature and dissolved oxygen (DO) measurements were taken concurrently with a Yellow Springs Instruments® (YSI) model 58 or ProPlus meter with a 60 m cable and probe assembly with a high sensitivity membrane. The probe was calibrated at each site following the manufacturer's instructions. After recording air temperature, both water temperature and DO measurements were recorded at the surface, 1 m, 2 m, and every 2 m thereafter to 60 m or the reservoir bottom. The depth of the thermocline, defined as a one-degree change in temperature over a one-meter change in depth, was recorded.

The level of PAR was measured using a LI-COR® model LI-250A light meter and a 400-700 µm quantum sensor (model LI-192SA). The sensor was mounted on a frame and weighted with a lead weight. A 15-second average PAR reading was taken at the water surface and at one-meter intervals to 15 m or a reading of zero. A second meter and dry sensor were used to take air readings concurrently with the wet readings.

Water samples were collected from the epilimnion (EPI) and hypolimnion (HYPO) at each station using a 2.2-L Kemmerer bottle. EPI samples consisted of a composite of water from 1, 3, 5, and 7 m, regardless of the presence or depth of a thermocline. One liter of water from each depth was mixed in a splitter bucket. HYPO samples were collected at every station during each sampling event through 2008. In 2009, HYPO samples were collected from each station once per month, and from 2011 on, HYPO samples were collected only once per month and at RK-2. They consisted of a single 'grab' from 25 m, or 3 m above the bottom if the depth was <28 m. Two 250-mL polyethylene sample bottles were filled from each sample depth (EPI and HYPO). One bottle (unfiltered sample) was pretreated with sulfuric acid (H_2SO_4) by the contracting lab as a preservative. The other bottle (filtered sample) was filled with water filtered through a 47-mm filtering manifold and a 0.45-µm cellulose acetate filter. A vacuum of up to 38 cm of mercury (Hg) was applied using a hand operated pump. The DOC samples were collected by filling a 40-mL glass vial, leaving no headspace, with the EPI composite water. All bottles were labeled with station, date, time, depth (EPI or HYPO), and filtered or unfiltered. Sample bottles were stored on ice while in the field and transferred to a refrigerator until shipping. Samples were shipped via overnight carrier to the contracting lab within two days of collection. Chemical analyses were performed by AM Test Labs of Kirkland, Washington. Analytical methods used for each parameter can be found in Wilson et al. (2010). While collecting the EPI sample at each station, a 'grab' was collected from 1 m and the pH was measured using a pH10A meter from YSI.

A Chl *a* sample was collected by filtering 250 mL of the EPI composite water through a 0.45-µm glass fiber filter using a similar filtering manifold and hand pump, also taking care not to exceed a vacuum of 38 cm Hg. The filter was removed from the manifold and folded in half on a 15-cm^2 piece of aluminum foil. The foil was folded around the filter, placed in a Ziploc™ bag, and kept on ice until returning to the field office. After returning to the field office, Chl *a* samples were placed in a freezer until shipping.

Picoplankton samples were collected by filling a 60-mL amber polyethylene bottle with the EPI composite water and preserved with six drops of 50% glutaraldehyde. Phytoplankton samples were collected by filling a 125-mL amber polyethylene bottle with sample water and preserved with 15 drops of Lugol's solution. All sample bottles were labeled with station, date, time, and depth (EPI or HYPO).

Zooplankton were collected using a 50-cm diameter, 80-µm mesh Wisconsin style net fitted with an OceanTest Equipment flow meter. One vertical tow was performed at each station from 10 m to the surface. Tows were completed by lowering the net to depth and retrieving at a rate of 0.5 m/s. The number of revolutions on the flow meter was recorded on the datasheet and plankton were rinsed from the net into the collection bucket, then rinsed into a collection jar and preserved in 70% ethanol. Collection jars were labeled with station, date, and depth of tow. Prior to the field season, several tows were performed with no net and the number of revolutions recorded to serve as a reference point. All plankton and Chl *a* samples were sent to Advanced Eco-Solutions of Newman Lake, Washington for analysis. Analytical methods used for each parameter can be found in Wilson et al. (2010).

Analysis of Limnological Data

The compensation depth is the depth where light intensity is 1% of the light intensity at 0 m. Before calculating compensation depth, the light intensity at depth was adjusted according to the ratio of the concurrent air measurement divided by the air measurement concurrent with the surface reading. Compensation depths were then calculated from the adjusted light intensity profiles by transforming the data as follows:

$$x = Ln\left[100\left(\frac{l_D}{l_S}\right)\right]$$

Where: *Ln* = natural logarithm
I_D = light intensity at depth
I_S = light intensity at 0 m

A regression was then developed using the transformed data as the independent variable and the depth (m) at which the measurement was taken as the dependent variable. The resulting equation was solved for x = *Ln*(1) = 0 to determine the compensation depth.

When summarizing the results of chemical analyses, numerous measurements were below the detection limit of a given assay. In order to calculate descriptive statistics, the detection limit for a given chemical analysis was used whenever the true value was below the detection limit.

Descriptive statistics were computed using package "plyr" in R 3.0.1. Means were reported for data that were normally distributed and medians were reported for data that were not normally distributed. In the case of normally distributed data for which a median value was stipulated in the Consent Order issued by IDEQ, both a mean and median value were reported.

Between year comparisons of limnological data were performed using a multiyear sampling frame, which consisted of months and stations that were sampled consistently for all years compared for the metric in question. This sampling frame included data from stations RK-2, RK-31, RK-56, and RK-72 from May through November, unless noted otherwise. When comparing chemical concentrations, in cases where the minimum detection limit was not consistent for all years compared, the minimum was artificially adjusted upward to match the year with the highest minimum level. That is, values in all years below the highest minimum level for any year were considered to be equal to that level for the purposes of calculating descriptive statistics.

Due to inconsistencies in these data, we chose to make comparisons between years using a graphical analysis of means and confidence intervals rather than attempting more rigorous statistical tests (Johnson 1999). Annual means were weighted by month to account for differences in sampling intensity throughout the year. Likewise, means for the restoration and non-restoration periods were weighted by year to account for interannual differences in sampling intensity. For data that was not normally distributed, we used a bootstrap technique to derive 95% confidence intervals (Chernick 1999; Efron and Tibshirani 1994). For this, the original data was resampled with replacement using the package “boot” in R 3.0.1. For each year, 1000 iterations were performed in which a bootstrap mean was calculated. Confidence intervals were derived using the percentile method, in which the lower confidence limit was equal to the 2.5 percentile of the bootstrap distribution and the upper confidence interval was equal to the 97.5 percentile (Chernick 1999).

Phytoplankton densities were recorded both in terms of natural counting units (NCU), which refers to colony numbers for some species and cells for others. Prior to 2008, cells/mL was not recorded for colonial species. Therefore, densities are reported as cells/mL whenever possible, except when making comparisons among years.

Inconsistencies also existed between years in zooplankton collection. To keep comparisons as consistent as possible, only data from collections with an 80 µm mesh net were used. Pre-restoration data were collected from a depth that was twice the Secchi depth to the surface. Since this depth was, on average, similar to the current depth strata, it was compared directly to the data collected from 2008 through 2011 taken from 10 m to the surface. Since data from 2007 was collected from 30 m to the surface, it was first adjusted by calculating the proportion of zooplankton collected in 2008 from 10 to 0 m to the total amount collected in the 10 to 0 m and 30 to 10 m tows (Wilson et al. 2013). The annual mean for this proportion was then applied to the 30 to 0 m data from 2007 to estimate the density of zooplankton from 10 to 0 m. A similar proportion was developed to adjust the estimated biomass of *Daphnia*. These estimates were used when comparing 2007 data to other years.

The forage base for kokanee was evaluated by examining changes in the density and biomass of *Daphnia*, since these are the preferred forage of kokanee and represent the bulk of their diet in most months (Stark and Stockner 2006). The weights of individual *Daphnia* were calculated using the following formula (McCauley 1984):

$$lnw = lna + b \times lnL$$

Where: lnw = natural log of weight in µg

lna = estimated intercept
b = estimated slope
lnL = natural log of length in mm

For these calculations, we used estimates from McCauley (1984) for *D. galeata* where:
lna = 2.64
b = 2.54

The density and biomass of consumable *Daphnia* were calculated for each tow. Kokanee in Dworshak Reservoir were found to primarily consume *Daphnia* that were 0.80 mm or longer TL (Wilson et al. 2013). The proportion of consumable *Daphnia*, as calculated from a sample of *Daphnia* from that tow, which were measured, was multiplied by the total density of *Daphnia* to determine the density of consumable *Daphnia*. The mean weight of consumable *Daphnia* was multiplied by the density of consumable *Daphnia* to estimate the biomass of available forage for kokanee.

In order to determine the effects of nutrient restoration on mean density of total zooplankton and biomass of consumable *Daphnia*, while controlling for top-down effects of grazing by kokanee, we fit the data to a series of linear models. These two sets of *a priori* models were used to estimate the importance of nutrient additions and kokanee abundance on either the mean density of total zooplankton or biomass of consumable *Daphnia*. The best model was determined by the lowest AIC_c value and the relative plausibility of each model was assessed using both the differences in AIC_c (ΔAIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). Models with $\Delta AIC_c < 2.0$ or $w_i \geq 0.1$ were considered to be relatively important. Individual factors were ranked by summing the w_i of each model with that factor. The higher the sum of w_i for a factor, the higher the importance of that factor (Burnham and Anderson 2002).

Quality Assurance

All equipment was rinsed in ethanol, followed by a triple rinse with distilled water, prior to each sampling event. The Kemmerer and splitter bucket were rinsed in surface water at each site prior to sample collection. Vacuum manifolds were rinsed in distilled water prior to installation of a new filter. For each sampling event, a station was randomly chosen to collect field duplicates, rinsates, and blanks. Field duplicates for chemical analysis were collected by filling additional sample bottles (one each for filtered and unfiltered) with EPI water. Rinsates were collected by transferring water provided by the analytical lab from the Kemmerer to the splitter bucket and the filtering manifold (filtered sample only) before filling additional sample bottles (one each for filtered and unfiltered). Blanks were obtained by filling additional sample bottles (one each for filtered and unfiltered) with water provided by the analytical lab. Additionally, a duplicate chlorophyll sample was obtained by filtering an additional aliquot of EPI water as previously described.

For each field duplicate that was collected, the relative percent difference (RPD) between the duplicate and original sample was calculated using the following formula:

$$RPD = \frac{|S_1 - S_2|}{(S_1 + S_2)/2} \times 100$$

Where: S_1 = Original sample
S_2 = Duplicate sample

Kokanee Population Monitoring

Abundance

As part of our sampling design, the reservoir was stratified into three sections (Figure 1). Section 1 extended from the dam to Dent Bridge at RKM 27.0, while Section 2 extended from Dent Bridge to Grandad Bridge at RKM 65.2. Section 3 encompassed the reservoir above Grandad Bridge.

A single hydroacoustic survey was conducted in July concurrent with a trawl survey. The survey was conducted using a Simrad model EK-60 echo sounder and a 120 kHz split beam transducer. The unit was calibrated prior to the survey using a -40.4 decibel (dB) calibration sphere. Kokanee abundance was estimated using a stratified systematic sampling design using the previously described strata. Transects of similar length were laid out in a zigzag pattern across the reservoir, with one transect beginning where the last one ended (Simmonds and MacLennan 2005). Boat speed during the survey averaged 2.0 m/s. The echo sounder was set to ping at 0.6 s intervals with a pulse width of 0.256 milliseconds.

The pelagic region of each echogram was analyzed using Echoview 4.0 software. For the analysis, a maximum beam compensation of 6.0 dB and a minimum and maximum normalized pulse length of 0.3 and 1.8 were used to distinguish fish from noise. Depths between 10 and 30 m were analyzed using an echo integration technique to calculate the nautical area scattering coefficient (NASC) and mean target strength (TS). Fish densities were calculated as:

$$\text{Density (fish/ha)} = (\text{NASC} / 4\pi 10^{TS/10})\ 0.00292$$

Frequency distributions were developed by binning the number of single targets in 1 dB intervals (adjusted target strength) for a given transect. Age breaks were then determined using length at age data from the trawl survey. For this, length at age breaks from trawl caught fish were converted into target strengths using Love's (1971) equation. The proportion of age-0 fish in a particular transect was then determined based on these age breaks and the target strength distribution from that transect. Fish above this age break (age-1 and older) were partitioned based on the proportion of each age class captured in the trawl.

The mean densities were multiplied by the area of kokanee habitat in each section to arrive at an estimate of age specific abundance for each section. This area was determined by first subtracting the mean depth for single targets in each section from the pool elevation at the time of the survey to determine the mean elevation of the kokanee layer. The reservoir area at this elevation was then looked up from a table based on data provided by the USACE (Sam Martin, USACE, personal communication). This table was created using USGS topographic data from pre-impoundment surveys from which the area was calculated at 12.2-m increments between 426.7 and 487.7 m. The areas in the table were then estimated for each 0.3-m increment of elevation using a second order polynomial regression.

During this study period, calculations used to produce population estimates have been refined. In order to ensure that estimates were comparable between years, we revised earlier estimates so that all estimates used the same methods and reservoir area data to the extent possible.

Age and Growth

Trawl surveys were based on methods described by Rieman (1992). An 8.5 m diesel powered boat was used to tow a fixed-frame midwater trawl. The net was 10.5 m long and attached to a 3.0-m high by 2.2-m wide steel frame. The body of the net consisted of four panels with bar mesh sizes of 32, 25, 19, and 13 mm. The cod end was composed of 6-mm delta mesh held open by a 0.8-m steel hoop.

Three trawl surveys were conducted during most years and occurred in April, July, and October. A November survey was conducted in lieu of an October survey in 2010 due to mechanical difficulties with the trawler. All surveys were conducted within five nights of the new moon to maximize capture efficiency (Bowler et al. 1979). For the July trawling, five randomly preselected transects were surveyed in each section. For the April and November trawling, 3-6 transects were conducted per section in Section 1 and 2. Trawling was not performed in Section 3 during spring or fall surveys due to low reservoir levels. All fish were measured to the nearest mm total length (TL) and a subsample was weighed to the nearest gram. Scales were collected from ten fish from every 1 cm length class from each section. Scales were later examined by two independent readers to determine age (Devries and Frie 1996).

The relative weight (W_r) was calculated for all fish greater than 119 mm TL. Standard weights (W_s) for kokanee of a given length were obtained from Hyatt and Hubert (2000). A W_r for each fish with a known TL and weight (W) was then calculated using the formula from Anderson and Neumann (1996).

We used an age-length key to estimate the age-specific abundance of kokanee in our trawl samples. For this, we first calculated the proportion of each age class represented in each 1-cm bin, as determined from scale analysis. These proportions were then applied to the remaining fish in the length bin, which were not aged, in order to estimate the number from each age class within each bin.

Descriptive statistics, including mean TL, weight, and W_r for each age class, were calculated in a similar manner. For these, we first calculated a mean for each length bin regardless of age. The means for each bin were then multiplied by the estimated number of fish from each age class in that bin, and the products were totaled for each age class to calculate an arithmetic mean. Standard deviations were calculated in a similar manner using the following formula from Zar (1999).

$$s = \sqrt{\frac{\sum X_i^2 - \frac{(\sum X_i)^2}{n}}{n-1}}$$

Where:
s = standard deviation of the population
X_i = i^{th} individual observation
n = sample size

To determine the effects of nutrient restoration on kokanee growth, we performed length back-calculations from scales collected from age-1 and older fish in the July trawl surveys between 2003 and 2013. These scales were imaged using a microscope and digital camera. The distance from the focus to each annulus and the margin were measured using either

FishBC 3.0.1 or ImageJ 1.46r software. Age-specific TL (mm) was estimated using the following formula (Carlander 1982):

$$TL_a = \left[\frac{(TL_C - 41)}{(D_M)} \times D_a\right] + 41$$

Where: TL_a = Total length-at-age *a*
TL_C = Total length at capture
DM = The distance from the focus to the margin
Da = The distance from the focus to annulus *a*
41 = The mean TL at scale formation

Annual growth was calculated as:

$$G_a = TL_{a+1} - TL_a$$

Where: G_a = Growth for age *a*

Since most fish spawned as age-2, the length at capture was used as $TL_{(a+1)}$ for age-2 fish.

Growth in terms of length is influenced by a numbers of factors, including environmental conditions present in a specific year and the length (and therefore age) of a fish at that time. Furthermore, since growth is also likely a result of the genetic makeup of an individual fish, the repeated measures from an individual are not likely to be independent. Therefore, back-calculated annual growth was first fit to a mixed effects model in order to separate year effects from those of age and individual fish, (Weisberg et al. 2010).

$$G_{cka} = t_a + y_{c+a-1} + f_{ck} + e_{cka}$$

Where: G_{cka} = The annual growth of fish *k*, of year class *c*, at age *a*
t_a = The annual growth of a fish at age *a*
y_{c+a-1} = The random annual growth effect
f_{ck} = The random effect for fish *k*
e_{cka} = Error term

The year effects estimated from these models were used as the response variable in subsequent linear regression models to determine which measure of fish abundance, total abundance or abundance of age-1 and older, was a better predictor of the growth. Finally, year effects were fit to linear models to estimate the importance of factors such as abundance, food availability, and nutrient addition on annual growth patterns (Quist and Spiegel 2012). Independent variables for these models included the best measure of abundance, the biomass of consumable *Daphnia*, and nutrient restoration. For this analysis, eight candidate models were chosen *a priori* based on our knowledge of kokanee ecology. The best model was determined by the lowest AIC_c value and the relative plausibility of each model was assessed using both the differences in AIC_c (ΔAIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). Models with ΔAIC_c <2.0 or $w_i \geq 0.1$ were considered to be relatively important.

A separate analysis was conducted by fitting mean age-specific annual growth to a suite of linear models (Isely and Grabowski 2007). As before, models were chosen *a priori* based on our knowledge of kokanee ecology. Predictor variables included the abundance of that age class corresponding to that growth estimate, the biomass of consumable *Daphnia*, whether or not nutrients were added, and interactions of interest.

Production

Production refers to the overall gain in biomass of a fish stock over a specific period, regardless of the fates of the individual fish that make up the stock (Ricker 1975). To estimate kokanee production between years for which a July trawl survey was performed, we adapted a summation method described by Hayes et al. (2007). For this, we first calculated the mean abundance of each cohort using acoustic estimates for each year. We then calculated the mean weight gain for an individual in each cohort based on data from trawling surveys conducted at the same time. The mean weight gain was multiplied by the mean abundance to obtain an estimate of production, assuming linear rates of growth and mortality.

Spawner Counts

Peak spawner counts were conducted on all four index streams on the lower North Fork Clearwater River above the reservoir within three days of the historical peak, September 25 (Horton 1980; Stark and Maiolie 2004). Each of the index streams were walked from the mouth to the uppermost extent of kokanee spawning activity. All spawning kokanee were individually counted when possible or estimated in the case of a deep pool with a large group of fish.

Creel Surveys

Creel surveys were conducted from March 11 to October 18, 2015. For these surveys, we used an access-access design (Pollock et al. 1994). The survey was stratified by month and day type (weekday or weekend/holiday). Sampling days, locations, and shifts (am or pm) were chosen at random. Each day within a strata and each shift within a day were given equal selection probabilities. Selection probabilities for locations were determined by assessing use from previous years, recent use during the current year, and whether or not a ramp was usable at the time (ramp availability changed with pool elevation).

Creel clerks were instructed to make every effort to interview every party returning to the access site by boat, or departing from the access site by vehicle in the case of shore anglers. In the event that an interview could not be obtained, clerks recorded the party as unknown and noted the time of return.

Daily effort ($\hat{e}_d$), measured in angler hours, was estimated in the following manner:

$$\hat{e}_d = \frac{e_{rsd}}{(\pi_r \times \pi_s \times \pi_b)}$$

Where: $\hat{e}_d$ = Estimated total fishing effort for day *d*.
e_{rsd} = Fishing effort sampled at site *r*, during shift *s*, on day *d*.
π_r = Selection probability of access site *r*.
π_s = Selection probability of shift *s*.
π_b = Probability of sampling a given boat during that shift.

The probability of sampling a given boat during a particular shift was simply calculated as the ratio of the number of boats sampled during that shift (including those that were not fishing) over the number returning (including those that were not sampled). Effort in terms of fishing trips was calculated in a like manner, substituting the number of trips for angler hours in the preceding equations.

Total effort for a given strata was calculated by multiplying the mean daily effort for that strata by the number of days in the strata. Monthly effort was calculated by summing the effort of the strata within each month, and annual effort was calculated by summing the monthly effort.

Total catch and total harvest were estimated in the same manner as effort, substituting each into the above formulas. Formulas used to calculate standard errors for catch and effort can be found on pages 234-236 of Pollock et al. (1994). Catch rates were calculated by dividing total catch for the respective period by total effort. In addition, we calculated these metrics for anglers that specifically targeted kokanee or bass. Confidence intervals for catch rates were calculated using a bootstrap method. For this, mean daily catch and effort were resampled with replacement 1,000 times for each strata. Confidence intervals were then calculated in the same manner as described for limnology metrics.

RESULTS

Environmental Conditions

From 2004 through 2015, inflow to Dworshak Reservoir averaged 151 m^3/s. The highest annual mean (mean = 221 m^3/s) occurred in 2011 and the lowest (mean = 113 m^3/s) occurred in 2010. Mean inflow was higher during the non-restoration period (mean = 164 m^3/s) than the restoration period (mean = 146 m^3/s). Reservoir elevation typically reached full pool at 488 m above mean sea level in late June to early July from spring runoff. In early July, hypolimnetic water was evacuated from the reservoir. A typical low pool elevation of 463 m was reached by mid-September and maintained until the following spring. In years of heavy snowpack, additional water was released in the spring in order to capture a larger volume of runoff. The pool elevation was dropped below 460 m in three years during the study period. Low pool elevations were reached on May 4, 2008 (449 m), May 2, 2011 (441 m) and April 18-19, 2014 (453 m).

Physical and Chemical Limnology

Temperature

Water temperatures at 1 m were compared between years using the multiyear sampling frame. Mean temperatures ranged from 16.6 to 19.8°C. The mean for the restoration period (mean = 18.3°C) was warmer than that for the non-restoration period (mean = 17.9°C).

A thermocline first developed as early as April in some years and not until June in others. Thermal stratification typically lasted through September on the upper end of the reservoir and through November on the lower end. The mean length of stratification was longer for the restoration period (mean = 145 days) than the non-restoration period (mean = 130) period.

Dissolved Oxygen

In all years, DO concentrations remained near saturation for most of the season. However, concentrations less than 5 ppm were frequently observed in the metalimnion and hypolimnion late in the season for all years. Low DO readings (≤5 ppm) were typically observed at stations on the upper end of the reservoir. The proportion of sites with a low DO reading ranged from 0 to 20% during the non-restoration period and from 2 to 23% during the restoration period. The proportion for the restoration period was higher (14%) than the non-restoration period (10%). The proportion of low DO readings in a given year was weakly correlated with both length of stratification ($r^2 = 0.14$) and whether or not nutrients were added to the reservoir ($r^2 = 0.13$).

Water Clarity

Annual mean Secchi depths for the modified multiyear sampling frame (Jun – Nov) were variable, but without an obvious temporal trend (Figure 2). Mean Secchi depth was similar for the restoration (mean = 4.1 m) and non-restoration (mean = 4.2 m) periods. Bootstrap confidence intervals for this difference include zero.

Compensation depths were calculated beginning in 2007, the year that nutrient restoration was initiated. Annual means for the modified multiyear sampling frame tended to increase during this period. Because this dataset includes only one non-restoration year, no comparison was made between periods. Water clarity data is summarized in Appendix A.

Nutrients

Mean TP concentrations for the epilimnion trended downward during the study period (Figure 3). Mean TP concentrations tended to be higher for non-restoration years than for restoration years. However, non-restoration years occurred earlier in the time series, with the exception of 2011, for which the mean TP was similar to restoration years. Mean TP concentrations for the hypolimnion and the river were similar to those for the epilimnion and exhibited similar trends.

Mean TDP concentrations in the epilimnion trended downward during the study period (Figure 3). In contrast, mean TDP in the hypolimnion initially trended downward, but has trended back up in the final three years (Figure 3). Mean TDP in both depth strata also tended to be higher during non-restoration years than for restoration years, although 2011 was both a non-restoration year and among the lowest means for both reservoir strata. Mean TDP for the river was fairly constant over the study period.

Mean concentrations for N+N in the epilimnion were variability, but no temporal trend was evident (Figure 3). Mean N+N concentrations for the epilimnion were similar for restoration and non-restoration years. Mean N+N concentrations for the hypolimnion, on the other hand, declined during the study period. Mean N+N for the hypolimnion tended to be higher for non-restoration years than for restoration years. However, non-restoration years occurred earlier in the time series, with the exception of 2011, for which the annual mean was similar to restoration years. As with the epilimnion, mean N+N levels for the river were highly variable and did not exhibit a temporal trend. Mean N+N levels tended to by highest in the river and lowest in the epilimnion.

Data for TN were only available for 2011. Mean TN concentrations were highest in 2011, the only non-restoration year in the series, but did not exhibit a temporal trend afterwards. Mean concentrations also tended to be higher for the epilimnion and the river than for the hypolimnion. Monthly TN concentrations tended to be highest during the spring and summer, and decreased beginning in September.

Data for TIN were also only available for 2011. Mean annual TIN for the multiyear sampling frame was variable with no apparent temporal trend. The mean for 2011, the only non-restoration year, was similar to restoration years. Mean TIN tended to be similar for the epilimnion and hypolimnion, but higher for the river. Monthly TIN was typically highest in May and June, lowest in July and August, and increase again in October and November. Nutrient data is summarized in Appendix B.

Total Dissolved Solids

Data for TDS were only available since 2007, the same year that nutrient restoration was initiated. Mean TDS concentrations were similar for treated and untreated areas of the reservoir and traditional confidence intervals overlapped for all years. Means for the river were lower than means for the reservoir in every year, but confidence intervals overlapped in most years. The mean TDS concentrations for both the reservoir and river exhibited a similar trend, with means decreasing from 2007 through 2012 and then increasing through 2015, though remaining less than 2007.

Dissolved Organic Carbon

Data for DOC were available since 2007, the same year that nutrient restoration was initiated. Mean DOC concentrations trended upwards during the first pilot period, peaking in 2010 (mean = 4.9 mg/L). Beginning with 2011, mean DOC then decreased through the third year of the second pilot phase. Then in the fourth year of the second pilot phase, mean DOC increased to a new high, although confidence intervals overlap considerably for 2010 and 2015.

Biological Indicators

Chlorophyll *a*

Mean epilimnetic Chl *a* for the multiyear sampling frame tended to decrease over the course of the study period (Figure 4). The mean for the restoration period (mean = 1.95 µg/L) was less than the non-restoration period (mean = 2.28 µg/L) and 95% of the bootstrap iterations had a difference of 0.12 µg/L or more.

Data from the river were available since 2007, the year that nutrient restoration was initiated. Annual means for the river were variable and tended to trend downward during the study period. Annual means for the river were substantially lower than means for the epilimnion and confidence intervals did not overlap (Figure 4).

Picoplankton

Data for picoplankton were available since 2006, one year before nutrient restoration was initiated. The mean density of heterotrophic bacteria for the modified multiyear sampling frame (May – Oct) was higher for the restoration period (mean = 975,000 cells/mL) than for the non-restoration period (mean = 571,000 cells/mL). This represents a 71% increase, with a bootstrap confidence interval from 55 to 88%. The mean density was much lower in 2006 (mean = 273,000 cells/mL) than all other years and has trended downward since 2007. The mean for 2011 (mean = 870,000 cells/mL) was only slightly less than the mean for the restoration period (Figure 5).

The mean density of picocyanobacteria for the modified multiyear sampling frame was higher for the restoration period (mean = 138,000 cells/mL) than for the non-restoration period (mean = 84,000 cells/mL). This represents a 64% increase, with a bootstrap confidence interval from 35 to 99%. The mean density was much lower in 2006 (mean = 43,000 cells/mL) than all other years. Since 2006, means have been variable with no apparent temporal trend. The mean for 2011 (mean = 125,000 cells/mL) was only slightly less than the mean for the restoration period (Figure 5).

Phytoplankton

Mean annual biovolumes of total phytoplankton for the multiyear sampling frame were variable and tended to be higher during the first half of the study period (Figure 6). The mean for the restoration period (mean = 0.410 mm^3/L) was 9% lower than for the non-restoration period (mean = 0.449 mm^3/L), but the bootstrap confidence interval for this decrease includes zero (95% CI = -23 to 7%).

Mean biovolumes of edible phytoplankton exhibited a similar trend to that of total phytoplankton. The mean biovolume for the restoration period (mean = 0.231 mm^3/L) was 22% higher than for the non-restoration period (mean = 0.190 mm^3/L) and the bootstrap confidence interval for this increase ranged from 1 to 63%.

The proportion of the phytoplankton community that is known to be edible was higher in every restoration year than for every non-restoration year, except for 2015, which had the lowest edibility of the study period (Figure 6). The mean proportion of edible phytoplankton for the restoration period (mean = 55%) was higher than for the non-restoration period (mean = 40%) and the bootstrap confidence intervals did not overlap.

The dominant taxa of toxigenic cyanobacteria (i.e., blue-green algae) in Dworshak Reservoir has historically been *Anabaena*. The mean biovolume of *Anabaena* was lower for the restoration period (mean = 0.03 mm^3/L) than the non-restoration period (mean = 0.11 mm^3/L). The proportion of the total phytoplankton biovolume that was composed of *Anabaena* for the restoration period (mean = 6%) was lower than that of the non-restoration period (mean = 22%) and the bootstrap confidence intervals did not overlap (Figure 6).

The mean biovolume of *Microcystis*, another toxigenic taxa, was also lower for the restoration (mean = 0.006 mm^3/L) than the non-restoration period (mean = 0.013 mm^3/L). Likewise, the mean proportion of *Microcystis* was lower for the restoration (1%) than the non-restoration period (3%). For 1,000 bootstrap iterations, 988 showed a decrease in the proportion of *Microcystis* in our samples, and none showed an increase. Based on biovolume, the proportion of times the World Health Organization (WHO) threshold for a low health risk for recreational contact was exceeded during the multiyear sampling frame was lower for the restoration period (mean = 3%) than for the non-restoration period (mean = 14%).

Zooplankton

The mean density of all zooplankters for the modified multiyear sampling frame (April – November) were lowest in 2004 (mean = 13.5 individuals/L) and 2006 (mean = 9.6 individuals/L) and highest in 2010 (mean = 50.9 individuals/L). Means for all other years were similar, with overlapping bootstrap confidence intervals (Figure 7). The mean density for the restoration period (mean = 30.1 individuals/L) was 79% higher than the mean for the non-restoration period (mean = 17.5 individuals/L) and bootstrap confidence intervals for this increase ranged from 51 to 114%.

The mean densities of *Daphnia* that were large enough for kokanee to consume (≥0.80 mm TL) were lowest in 2005 (mean = 1.8 individuals/L) and 2006 (mean = 1.3 individuals/L) and highest in 2012 (mean = 6.4 individuals/L, Figure 7). The mean for the restoration period (mean = 4.3 individuals/L) was 88% higher than that of the non-restoration period (mean = 2.3 individuals/L) and the bootstrap confidence interval for this increase ranged from 52 to 137%. This increase was 50% or more in 98.3% of the bootstrap iterations.

The mean biomass of *Daphnia* that were large enough for kokanee to consume was lowest in 2005 (mean = 34 µg/L) and 2006 (mean = 29 µg/L), and highest in 2012 (mean = 160 µg/L, Figure 7). The mean for the restoration period (mean = 100 µg/L) was 103% higher than the non-restoration period (mean = 49 µg/L) and the bootstrap confidence interval for this increase ranged from 65 to 158%. This increase was 50% or more in 99.6% of the bootstrap iterations.

A set of *a priori* models were used to determine the effects of nutrient restoration and the abundance of age-1 kokanee on the biomass of consumable *Daphnia* and density of total zooplankton. The best competing model for explaining differences in *Daphnia* biomass included both factors without an interaction term ($\Delta AIC_c = 0$, $w_i = 0.74$, Table 1). This model predicts that *Daphnia* biomass declines as kokanee abundance increases, but that *Daphnia* biomass is higher at any level of kokanee abundance during nutrient restoration (Figure 8). The model using nutrients alone to explain *Daphnia* biomass also warrants consideration based on Akaike's weight ($w_i = 0.21$, Table 1). Based on the sum of Akaike's weights from models incorporating each factor, nutrient restoration had the most influence on the biomass of consumable *Daphnia* ($\sum w_i = 0.98$), followed by kokanee abundance ($\sum w_i = 0.79$).

The best competing model for total zooplankton density used nutrient restoration alone as an explanatory variable ($\Delta AIC_c = 0$, $w_i = 0.42$). However, there was also strong evidence in support of the model containing nutrient restoration, kokanee abundance, and an interaction ($\Delta AIC_c = 0.2$, $w_i = 0.37$, Table 1). This model predicts that zooplankton density decreases with increasing kokanee abundance during the non-restoration period, but increases with increasing kokanee abundance when nutrients are added (Figure 8). However, the model containing nutrient restoration and kokanee abundance, but no interaction term merits some consideration based on Akaike's weight ($w_i = 0.14$). Based on the sum of Akaike's weights from models incorporating each factor, nutrient restoration had the most influence on zooplankton density ($\sum w_i = 0.93$), followed by kokanee abundance ($\sum w_i = 0.58$) and the interaction term ($\sum w_i = 0.37$).

Kokanee Population and Fishery

Abundance and Density

Kokanee abundance from 2003 through 2015 ranged from 769,000 in 2004 to 4.6 million in 2006, with a mean of 2.5 million and a median of 2.3 million. The abundance of age-1 and older kokanee ranged from 304,000 in 2008 to 2.6 million in 2006 and 2014, with a mean of 1.2 million and median of 702,000. The mean abundance of age-1 and older fish was higher for restoration years (mean = 1.3 million) than for non-restoration years (mean = 1.0 million) for which trawl surveys were performed.

Adult (age-2 and older) density ranged from 14 fish/ha in 2004 to 348 fish/ha in 2015, with a mean of 87 fish/ha and a median of 35 fish/ha. The mean adult density was higher for restoration (mean = 92 fish/ha) than for non-restoration years (mean = 79 fish/ha) for which trawl surveys were performed. Revised abundance and density estimates for kokanee are presented in Appendix C.

Size at Age

The mean TL of age-1 kokanee was similar for the restoration and non-restoration periods, but age-1 fish were slightly heavier during the restoration period (Table 2). The mean TL of age-2 fish was 18 mm longer for the restoration period, the mean weight was 41 g heavier, and fish were heavier for a given length (Table 2).

Growth Comparisons

Mean age-specific annual growth increments, as calculated from back-calculated length-at-age, were similar to those calculated from mean age-specific length of trawl caught fish for years in which both estimates were available. Based on back-calculated lengths, the mean growth was higher for restoration years than for non-restoration years (Table 3). The mean growth advantage during the restoration period was summed over all age classes, resulting in an age-2 kokanee that is on average 26 mm TL longer in July.

Back-calculated growth was further analyzed using a combination of a mixed effects linear model to estimate annual effects, and fixed effects linear models to evaluate influence of other factors on the annual growth effect. The mixed effects model provided a reasonable fit to the data ($R^2_{adj} = 0.68$) and year effects estimated from this model are shown in Table 4.

Year effects, as estimated from the mixed effects model, were negatively correlated with kokanee abundance, positively correlated with consumable *Daphnia* biomass, negatively correlated with total zooplankton density and higher for restoration years. Of the models we considered *a priori*, the model using only consumable *Daphnia* biomass as an explanatory variable was the best fitting model ($r^2_{adj} = 0.51$, $\Delta\ AIC_c = 0$, $w_i = 0.76$, Table 5). Based on Akaike's weights, the models using both kokanee abundance and Daphnia ($w_i = 0.13$) and kokanee abundance ($w_i = 0.10$) alone warranted some consideration. Based on the sum of Akaike's weights from models incorporating each factor, the biomass of consumable *Daphnia* had the most influence on growth ($\sum w_i = 0.90$), followed by kokanee abundance ($\sum w_i = 0.24$). Nutrient restoration and total zooplankton densities were not important in predicting growth in these models.

Using a different approach, we also modeled the effects of kokanee abundance, food availability, and nutrient restoration on the mean age-specific annual growth, as estimated via back-calculation. Initially, we investigated the abundance of age-1 and older kokanee and the corresponding abundance of the age class for each growth increment. While there was strong support for both measures of abundance, we chose to use age-1 and older abundance (r^2_{adj} = 0.84, Δ AIC_c = 0, w_i = 0.70) over the abundance of the corresponding age class (r^2_{adj} = 0.84, Δ AIC_c = 1.8, w_i = 0.29) based on the relative strength of support.

All of the *a priori* models that were tested used age as an explanatory variable to control for differences in growth among age classes. The best competing model, and only model with strong support, also included the biomass of consumable *Daphnia*, the abundance of age-1 and older kokanee, and an interaction between age and kokanee abundance (r^2_{adj} = 0.91, Δ AIC_c = 0, w_i = 0.58, Table 6). Based on Akaike's weights, the model using *Daphnia*, kokanee abundance and an interaction between age and *Daphnia* (w_i = 0.20) and the model using *Daphnia* and an age by *Daphnia* interaction (w_i = 0.13) warranted some consideration. All other models had considerably less to essentially no support. Based on the sum of Akaike's weights from models incorporating each factor, the biomass of consumable *Daphnia* had the most influence on growth ($\sum w_i$ = 0.97), followed by kokanee abundance ($\sum w_i$ = 0.86), an age by kokanee abundance interaction ($\sum w_i$ = 0.65) and an age by *Daphnia* interaction ($\sum w_i$ = 0.36).

Biomass and Production

Kokanee production could only be estimated from one time period that did not coincide with nutrient restoration, which was 2003-2004. Production estimates for the time periods that occurred during nutrient restoration were all higher (Table 7), and production for the restoration period averaged about twice that of the 2003-2004 period. Time periods ending in July of 2008 and 2013 were most similar to 2004 in terms of both fish size and abundance. These two time periods were almost identical in terms of production, and 75% greater than that of the 2003-2004 period.

Estimates of kokanee biomass for the first three years of both pilot periods were similar to those for non-restoration years. Biomass then increased to record highs by the fourth year in both cases. The mean biomass for the restoration period was 37% higher than that of the non-restoration period and the highest biomass observations during the restoration period were approximately 50% higher than the highest observed during the non-restoration period (Table 7, Figure 9).

As with total biomass, the mean biomass of mature kokanee for the first three years of each pilot phase was similar to the non-restoration period. However, in both cases the biomass of mature fish peaked in the fourth year at over 90 t. This represents an increase of 75% over the highest observation from the non-restoration period. The mean biomass of mature kokanee for the restoration period (mean = 44 t) was 40% higher than the non-restoration period (mean = 31 t).

Spawner Counts

Peak counts of spawning kokanee observed during the study period were quite variable and counts for the first three years of both pilot phases of nutrient restoration were similar to those for non-restoration years. However, counts peaked in the fourth year of both periods, with the highest count on record occurring in 2010. On average, spawner counts were 23% higher and spawning kokanee were 9% longer for restoration years. Historical spawner count data are shown in Appendix D.

Creel Surveys

A total of 223 shifts were completed from March-October of 2015, during which 1,638 interviews were conducted. From this, we estimated a total of 17,660 fishing trips and 135,869 angler hours (SE = 33,188, Table 8). Effort peaked in June at 4,681 trips and 33,651 angler hours. Effort was lowest in March (750 trips and 6,993 angler hours) and October (901 trips and 5,431 angler hours). The mean party size for fishing trips was 2.3 anglers (range = 1 – 10 anglers). The mean duration of single day fishing trips was 5.7 hours (range = 0.5 – 13 hours). We estimated that anglers caught 54,780 kokanee (SE = 15,863) and harvested 51,922 (SE = 15,456). In addition, we estimate that anglers caught 147,972 Smallmouth Bass (SE = 57,709) and harvested 17,612 (SE = 4,223). The catch of all other fish was estimated at 7,928 caught and 2,465 kept. Other species that were caught included Rainbow Trout, Westslope Cutthroat Trout, Bull Trout, Black Crappie *Proximus nigromaculatus*, and various sunfish *Lepomis sp.*, in order of prevalence.

For anglers that were strictly fishing for kokanee, we estimated 42,827 angler hours (SE = 11,388, Table 8). Effort for kokanee peaked in June (1,475 trips and 12,972 angler hours) and July (1,389 trips and 13,182 angler hours) and very few anglers fished for kokanee during September (33 trips and 406 angler hours). Kokanee anglers caught 50,727 kokanee (SE = 15,439) and 8,557 fish other than kokanee. Kokanee anglers harvested 49,807 kokanee (SE = 15,313) and 2,597 fish other than kokanee. Harvested kokanee had a mean TL of 207 mm. Because anglers reported releasing only a small percentage of the kokanee they caught, catch and harvest rates were essentially the same. We estimated a catch rate of 1.2 kokanee/hour (95% CI = 0.8 – 1.7 kokanee/hour) for the duration of the survey. Catch rates for kokanee were low in March (0.2 kokanee/hour) and April (0.1 kokanee/hour) and highest in June (1.6 kokanee/hour) and July (1.7 kokanee/hour, Table 8).

For 78% of the kokanee trips that we contacted, at least one angler in the group reported catching a kokanee. This proportion ranged from 29% in April to 92% in July. We documented harvest in 72% of the kokanee trips we contacted. This proportion ranged from 21% in April to 91% in July. Overall, 7% of the anglers we interviewed harvested a limit of 25 kokanee. This proportion ranged from none in March and April to 11% in July.

For anglers who were strictly fishing for bass, we estimated 85,598 angler hours (SE = 27,474, Table 8). Effort for bass was lowest in March (332 trips and 2,568 angler hours) and highest in June (2,282 trips and 19,390 angler hours). Bass anglers caught 136,774 bass (SE = 57,321) and 7,206 fish other than bass, for a catch rate of 1.6 bass/hour (95% CI = 1.1 – 2.4 bass/hour). Catch rates for bass were lowest in April (0.5 bass/hour) and highest in June (2.0 bass/hour), September (1.9 bass/hour), October (2.1 bass/hour). Bass anglers harvested 14,748 bass (SE = 4,072) with a mean TL of 307 mm.

For 84% of the bass trips that we contacted, at least one angler in the group reported catching a bass. This proportion ranged from 72% in April to 100% in October. We documented harvest in 34% of the bass trips we contacted. This proportion ranged from 22% in March to 42% in August. Overall, 4% of the anglers we interviewed harvested a limit of six bass. Limits of bass were documented during every month we surveyed. The proportion of anglers with limits ranged from 2% in June to 11% in August. Twenty-two percent of the bass anglers we interviewed reported catching six or more bass, although most did not harvest a limit.

Estimates of total fishing effort during 2015 were similar to most estimates for previous years, but substantially less than 2003 and 2004 (Table 9). However, the amount of effort directed strictly at kokanee during 2015 was lower than any other year for which we have data. The catch rate estimated for all fishermen during 2015 was higher than any other year, even those with higher estimated fishing effort. The catch rate estimated for anglers targeting kokanee during 2015 was similar to catch rates estimated for kokanee anglers during 1988 and 1989 (Table 9).

DISCUSSION

We observed positive responses to nutrient restoration in Dworshak Reservoir across most trophic levels, including increases in edible phytoplankton (Figure 6), *Daphnia* large enough for kokanee consumption (Figure 7), kokanee abundance, and kokanee biomass (Table 7, Figure 9). We also observed a positive kokanee growth response, which is proximally attributable to *Daphnia* biomass increases and ultimately attributable to nutrient restoration. We did observe some counterintuitive results, including lack of evidence (using typical measures) that productivity increased in the reservoir, which we attribute to complex food web interactions. In the discussion below, we interpret the results in detail at each trophic level to further elucidate these complexities.

Water Quality

While the intent of the nutrient restoration project is to restore lost productivity to the reservoir, it is imperative to do so without degrading overall water quality. DO is an important water quality parameter that could be negatively affected by the project. Dworshak Reservoir typically experiences low DO levels during late summer and early fall. These minima are presumed to be caused by phytoplankton that senesce, settle out of the epilimnion, and collect in the metalimnion where they begin to decay (TG Eco-Logic 2008). Although these metalimnetic DO minima occurred prior to the nutrient enhancement project, it is possible that the addition of nutrients and the increased productivity of the system could intensify this phenomenon (TG Eco-Logic 2008). While we observed a higher incidence of low DO measurements during the restoration period, thermal stratification also tended to last longer. Longer periods of thermal stratification result in lengthening the period of time that the hypolimnion cannot exchange atmospheric gasses, such as oxygen, therefore making it more likely for DO to be depleted. The incidence of low DO is similarly, but only weakly correlated to both the length of thermal stratification and nutrient addition. Since stratification tended to be longer during restoration years, it is likely that the increased incidence of low DO is due to longer stratification. Therefore we find no evidence that nutrient restoration is resulting in increased incidence of low DO, but this should be closely monitored in the future.

Water clarity is another common metric for water quality. Both EPA and IDEQ stipulated that the median Secchi depth not fall below 3 m due to nutrient restoration. Secchi depth is influenced by a variety of factors. Two of the most important of these are suspended solids from spring runoff and chlorophyll concentration due to summer algal blooms. In order to examine the effects of algal production on water clarity, we concentrated on data from June through November, when the effect of runoff should be minimal. We observed very little difference in the mean Secchi depth between the restoration and non-restoration periods, suggesting that nutrient addition has not had a noticeable effect on water clarity (Figure 2).

Although Secchi depth has been long established as the standard measurement of water clarity, it is not without drawbacks. Preisendorfer (1986) identified numerous factors that affect Secchi readings. Many of these, such as wind speed, time of day, and ambient light conditions are not accounted for in our surveys yet have the potential to influence the results. However, we have been taking PAR readings since 2007. These reading are measured by an instrument, so they are not susceptible to observer bias. Although measurements are certainly affected by many of the same factors that influence Secchi measurements, PAR data is used to calculate CD, which is based on the percentage of light that is attenuated in the water column, not an absolute measure at a given depth. Therefore, it would be more reliable to base continued trends in water clarity and permitting compliance on CD rather than Secchi depth.

While nutrients are essential to sustaining aquatic life, it is important not to introduce excessive amounts of nutrients into surface waters. Eutrophication is a common problem in surface waters that results from excessive nutrients (Smith et al. 2006). Mean concentrations of N and P as measured in Dworshak Reservoir have not increased despite restoration. It is not surprising that the addition of N has not resulted in a detectable increase. Dworshak Reservoir was found to be N limited (Stockner and Brandt 2006) and N in the form of ammonia is absorbed rapidly by the phytoplankton community, usually in 24 hours or less (Stockner 1995). The theoretical concentration of N applied to the reservoir, once fully mixed into the epilimnion, was only 8 µg/L during the heaviest applications. Therefore, there is no evidence that the amount of N being added to the reservoir is excessive.

Since P has not been added to the reservoir since 2008, and then only in very small amounts, the project is not expected to have an effect on P concentrations. However, mean concentrations of P in the epilimnion have declined since the beginning of restoration. This could be due to more efficient uptake of P as a result of more balanced N:P ratios, a reduction in P inputs to the reservoir, or improved analytical procedures.

While P concentrations have tended to decline over the study period, the concentration of TDP in the hypolimnion increased slightly but steadily during the last three years of the project. While this increase was not great, nor did it increase above earlier levels, this trend should be monitored in the future.

There have been concerns that nutrients added to the reservoir would be discharged through the dam into the North Fork Clearwater River, causing nuisance algal growth and adversely affecting water quality for anadromous fish hatcheries. The lower reservoir is typically thermally stratified by the time nutrient restoration is implemented in the spring. N is added to the epilimnion, while dam discharge occurs primarily from the hypolimnion. Furthermore, with the exception of the first year, N additions have not occurred within 8 km of the dam. Therefore, it is unlikely for supplemented N to be discharged directly into the river. Any increase in the nutrient loading to the river would likely be as a result of increased nutrient cycling to the hypolimnion. Nutrient levels in the North Fork Clearwater River below the dam were not measured until 2007, the first year of nutrient restoration. Since that time, there has been no observable increase in N or P concentrations in the river. While measurements from the river were not taken prior to restoration, nutrient levels in the reservoir hypolimnion have not increased. Since this is the source for the river, it is unlikely that nutrient loading to the river has increased.

Nutrient restoration has generated public concerns about whether or not toxigenic cyanobacteria (blue-green algae) have become more prevalent in the reservoir. *Anabaena* and *Microcystis* are the two predominant taxa that have been documented in the reservoir. These taxa typically become prevalent in late summer and fall after available N has been exhausted. Prior to 2008, densities of these taxa were counted in terms of colonies. Beginning in 2008, the counting methodology was changed to cell counts for as many taxa as possible, including *Anabaena* and *Microcystis*. Since then, densities of *Microcystis* in excess of the threshold that the WHO determined was a mild health concern (20,000 cells/mL; Falconer et al. 1999) have been observed on several occasions. Since this was not monitored closely prior to nutrient restoration, there has been a perception that the project has resulted in an increase of toxigenic taxa that were previously absent or present only at very low levels. However, the mean biovolume of *Microcystis* and the percentage of the total biovolume accounted for by *Microcystis* where both lower for the restoration period. Furthermore, we were nearly five times more likely to observe a biovolume exceeding that corresponding with the WHO threshold (0.04 mm^3/L) in non-restoration years than in restoration years. Therefore, there is no evidence that *Microcystis* has become more prevalent due to nutrient restoration.

Anabaena have historically been the dominant form of potentially toxic cyanobacteria in Dworshak Reservoir. Unlike *Microcystis*, *Anabaena* are known to fix N and believed to have a competitive advantage when fixed N is no longer available (Darren Brandt, Advanced Eco-Solutions, personal communication). Therefore, it was anticipated that N restoration would reduce the prevalence of *Anabaena* (Stockner and Brandt 2006). While *Anabaena* blooms have been observed during restoration years, both the mean biovolume and the percent contribution of *Anabaena* in samples taken at consistent times and locations was over three times lower for the restoration period than the non-restoration period (Figure 6). Similar observations have been made in other North American lakes (Harris et al. 2014; Schindler et al. 2008; Stockner and Shortreed 1988). These observations, along with our understanding of the ecology of these organisms, strongly support the idea that N restoration has reduced the prevalence of *Anabaena* in the reservoir.

Relationships between cyanobacteria and nutrient concentrations are not always straightforward. While many investigators have reported that cyanobacteria tend to decrease as N:P ratios increase (Harris et al. 2014; Schindler et al. 2008; Graham et al. 2004; Smith 1983), Downing et al. (2001) found that increasing TN or TP concentration were better predictors of cyanobacteria dominance than N:P ratio. However, the authors also note a strong negative correlation with N:P ratios and nutrient concentrations, which confounds analyses of this type. Furthermore, most cyanobacteria are not N-fixers, and therefore do not necessarily have a competitive advantage at low N:P ratios. Paerl and Scott (2010) reported a worldwide increase in cyanobacteria dominance concurrent with increased eutrophication despite efforts to limit P inputs. In some cases, the authors noted a shift in dominance from N-fixing taxa, such as *Anabaena*, to non-N-fixing taxa, such as *Microcystis*. Two major examples cited by the authors were extremely shallow eutrophic lakes which became dominated by *Microcystis*, which could sequester P from nutrient rich sediments and rise into the water column to form blooms (Paerl and Scott 2010). The role of nutrients and stoichiometry in determining cyanobacteria dominance is likely to depend on other characteristics of individual lakes and their respective watersheds. The response to N additions we observed for Dworshak, a cold, deep oligotrophic reservoir, may be different from the response for a warm, shallow, eutrophic lake.

Reservoir Productivity

Chl *a* is often used as an indicator of productivity in lakes and reservoirs (Carlson 1977). Mean Chl *a* has not increased in response to N restoration, suggesting that productivity has not increased (Figure 4). However, the relationship between Chl *a* and phytoplankton biovolume is dependent on many variables, including species composition (Felip and Catalan 2000).

Furthermore, if the composition of the phytoplankton community has shifted to more edible species, those species may be grazed off by zooplankton at a higher rate, thus masking the increase in productivity (Scofield et al. 2010). Since the intent of this project is to increase the amount of carbon (C) that is passed up to higher trophic levels (i.e. fish), rather than the accumulation of C at lower levels (i.e. algae) an increase in Chl *a* should not be viewed as a prerequisite for success.

Densities of picoplankton were substantially higher for the restoration period than the non-restoration period. The initial picoplankton response in Dworshak Reservoir was similar in magnitude to that observed during the first years of nutrient restoration in BC lakes and reservoirs (Pieters et al. 2003; Stockner and MacIsaac 1996; Stockner and Shortreed 1994). However, picoplankton densities did not drop off to 2006 levels following the suspension of nutrient application in 2011 (Figure 5). The reason that picoplankton did not return to 2006 levels following the suspension of N restoration is unclear. It is possible that 2006 was an anomalously low year, or that reservoir productivity did not decline as fast as anticipated.

There is no evidence that the standing crop of phytoplankton has increased due to nutrient restoration (Figure 6). However, as previously noted, an increase in phytoplankton is not a prerequisite for success. The most notable response has been shifts in the species composition of the phytoplankton community. While the total biovolume of phytoplankton was actually lower for the restoration period, the biovolume of edible species did increase. This, coupled with a decline in inedible species (*i.e. Anabaena*), has resulted in increased edibility within the phytoplankton community during nutrient restoration (Figure 6). These results suggest that the additional productivity from nutrient additions is being channeled into edible phytoplankton species, which are in turn being grazed off efficiently by the zooplankton community. Furthermore, Cole et al. (2002) found that food quality, rather than food quantity or water temperature, was the most important factor controlling *Daphnia* production in oligotrophic lakes. Therefore, shifts in phytoplankton composition, not just increased primary production, could drive increases in secondary production.

This idea is further supported by observed responses in the zooplankton community. Zooplankton densities have increased substantially (Figure 7), presumably due to the increase in edible phytoplankton, and our analysis provides strong evidence that nutrient restoration is the most important factor in this increase. Interestingly, there is little evidence that grazing pressure from kokanee limit the combined density of zooplankton, at least when nutrients are added (Figure 8). The most parsimonious model included only nutrient addition as an independent variable (Table 1). The other model with strong support predicts that zooplankton densities actually increase with increasing kokanee abundance with nutrient additions but decline without them (Figure 8). However, caution should be used in interpreting this result, as there is only one data point for zooplankton density at high kokanee abundance prior to nutrient additions. In either case, there is no evidence that grazing from kokanee is controlling the zooplankton population.

Along with this increase in the overall density of zooplankton, we have also observed an increase in both the density and biomass *Daphnia* (Figure 7), the preferred forage of kokanee (Stark and Stockner 2006). The biomass of consumable *Daphnia* is at least double when nutrients are added (Figure 7). While our analysis indicates that nutrient restoration is the most important factor behind this increase, there is also strong evidence that grazing pressure from kokanee limits the biomass of consumable *Daphnia* (Table 1). However, our observations are consistent with a substantially higher biomass of consumable *Daphnia* at any level of kokanee abundance due to nutrient restoration (Figure 8).

This increase in *Daphnia* is similar to the response for BC lakes reported by Stockner (1995). However, changes in zooplankton production do not always translate into increases in standing biomass. The mean biomass of *Daphnia* in Upper Arrow Lake increased by only 45% over the first four years of fertilization and the mean for the first eight years dropped to be nearly identical to the pre-restoration mean. Despite the lack of a measurable increase in *Daphnia* biomass over the first eight years, average biomass of kokanee increased by three fold during nutrient restoration (Schindler et al. 2009). The response observed in Dworshak thus far is encouraging. However, a return of *Daphnia* biomass to non-restoration levels should not be a cause for alarm if kokanee biomass is sustained at a higher level.

Kokanee Population Monitoring

Improved kokanee growth is a key indicator of whether or not nutrient restoration is having desirable effects. Since kokanee typically exhibit density dependent growth (Rieman and Meyers 1992), it is important to consider densities when evaluating growth. To account for the effects of density on fish growth, we instead used age specific abundance, because density changes with available habitat. The current regime of summer reservoir drawdowns leads to rapid changes in available habitat and therefore fish density. Thus, measured fish density can be affected by the timing of the survey more so than abundance. However, since summer drawdowns are very consistent from year to year due to court mandates, density changes are expected to be consistent for any level of abundance. Furthermore, we only considered the abundance of age-1 and older fish, as age-0 fish represent a small proportion of the overall biomass and abundance estimates for age-0 fish are less certain.

During both pilot phases, kokanee abundance was relatively low during the first two years and age-2 kokanee achieved greater size, both in terms of length and weight, than at similar densities during non-restoration years. However, in both cases, kokanee abundance increased to near record levels by the fourth year. In response, the size of age-2 kokanee dropped precipitously, but fish were still larger than those observed in 2006, the non-restoration year with similar abundance. Overall, statistics on mean length and weight at age show that kokanee were only slightly longer and a bit heavier during the restoration period (although relative weight was always higher, Table 2). However, abundance tended to be higher during the restoration period. Therefore, if nutrient restoration did not result in improved growth, age specific sizes should have decreased accordingly. These results are similar to both Kootenay and Arrow lakes in British Columbia, where kokanee lengths increased initially, but declined as fish densities increased (Schindler et al. 2014; Schindler et al. 2009). Long-term, kokanee in these lakes appear to be only slightly longer on average, but at a much higher abundance. Moreover, mean weights were on average 30-40% higher when nutrients were added (Schindler et al. 2014, Schindler et al. 2009).

The results of our modeling suggest that the biomass of *Daphnia* is the proximate (direct) driver of kokanee growth increases, while nutrient restoration is likely an ultimate driver of these increases. These results are consistent with those of Teuscher and Luecke (1996) and Johnson and Martinez (2012), both of whom reported *Daphnia* density to exert the most influence on kokanee growth of the factors they examined. This makes sense, as added nutrients act directly on primary production, not fish production. However, changes in phytoplankton composition, which was driven by nutrient additions, likely led to the increase in *Daphnia* (Cole et al. 2002). Therefore, while nutrient restoration did not have a direct effect on kokanee growth, it acted indirectly to influence food quality, and was the engine behind the driver of kokanee growth. As kokanee abundance has risen in response to the increasing food supply, competition for this food has increased, and growth has begun to decline toward levels seen pre-restoration, albeit at much higher levels of abundance. As we have more years of data, and more years for which kokanee abundance was higher during nutrient restoration, the observed growth advantage has diminished. However, growth was still greater at a given level of kokanee abundance when nutrients were added, and when abundance is not taken into account, the growth advantage can be masked.

Another way to assess benefits to the kokanee population is to assess production. The growth of an individual fish is related to the quantity and quality of forage as well as the number of fish competing for the available forage. Production, on the other hand, is a measure of how the biomass of the population increased over time, irrespective of the fates of individual fish. Since production is dependent on all dynamic rate functions of a population, it may be a better indicator of how the population responds to increased forage. It should be noted that the method we have used provides an estimate of production from July of the first year to July of the second. Since trawl surveys were not performed every year prior to nutrient restoration, there is only one period that we could estimate production for that did not overlap with a restoration period (2003-2004), while there are six estimates that incorporate a set of restoration years. These estimates were all higher than the non-restoration estimate, with the lowest almost 40% higher (Table 7). However, our production estimates were also positively correlated ($r^2 = 0.93$) to the abundance of age-1 and older fish at the beginning of the period for which the estimate was calculated. Downing and Plante (1993) also found that production in the lakes they examined was strongly correlated to biomass. Therefore, while caution should be used in interpreting our production results, the observed increase in kokanee biomass is an indication that production has also increased.

The most significant effect of N restoration on the kokanee population appears to be an increase in biomass (Table 7, Figure 9). As a result of faster growth at a higher fish density, by the fourth year of each pilot phase kokanee biomass had reached record highs, at more than double the mean for the non-restoration period. In Kootenay Lake, BC, kokanee biomass did not increase above pre-fertilization levels until the third year of treatments. Kokanee biomass peaked at over five times the pre-fertilization biomass in the seventh year of treatments, and average biomass during fertilization was three times that of pre-fertilization (Schindler et al. 2014). Observations for Dworshak Reservoir are consistent with those from Kootenay Lake, although magnitude of the increase in biomass is yet to be determined. Another uncertainty unique to Dworshak is how kokanee entrainment loss will affect biomass trends under N restoration. Unusually heavy snowpack and high runoff in the spring of 2011 coincided with a decline in the kokanee population of around 80% (all sources of mortality combined), and entrainment is believed to be the primary source of this mortality. Regular entrainment losses of this magnitude could result in period drops in kokanee biomass to pre-restoration levels.

Barring significant entrainment events, the current trend of increasing kokanee abundance and declining size at age suggests that Dworshak Reservoir will sustain higher densities of kokanee at about the same size or slightly larger than pre-restoration. This pattern is consistent with what has been observed as a result of nutrient restoration on Kootenay Lake, BC. Furthermore, our analysis of the effects of nutrient restoration and kokanee abundance on *Daphnia* biomass suggests that the carrying capacity of the reservoir has been increased, as it should now take a much higher abundance of kokanee to drive biomass to zero.

Fishery Performance

For IDFG, an ultimate objective of nutrient restoration is to improve recreational fishing in the reservoir. Catch rates for the kokanee fishery have met or exceeded objectives in recent years, although size was lacking, particularly in 2015. It should also be noted that catch rates in early 2015 were very low (Table 8), due to the size of the fish, most of which were not quite big enough to recruit into the fishery. However, by June almost all the age-2 kokanee had fully recruited into the fishery and catch rates were relatively high (Table 8), although size was still below average. More fish than normal appear to have carried over to spawn at age-3, which was expected to produce substantially better fishing in 2016.

In the long run, sustaining populations of slightly larger kokanee at a much higher abundance should ultimately improve catch rates. However, caution must also be taken when comparing the results of previous creel surveys to current ones. Over the years, several different survey designs have been employed. Each of these designs has different biases. Furthermore, the results reported for some of these surveys included only kokanee anglers, while others report summaries for all anglers, regardless of the target species. Further still, the time periods that these surveys encompass are typically different. Since we have yet to observe the long-term effect of nutrient restoration on the kokanee population, we also have yet to observe the full effect on the fishery.

In addition to kokanee fishing, increased abundance and biomass of kokanee in the reservoir should benefit piscivorous fishes that reside in the reservoir. The reservoir is considered to be critical habitat for Bull Trout in the North Fork Clearwater core area, and kokanee are thought to be an important food source (USFWS 2015). Kokanee are also thought to be an important food source for larger Smallmouth Bass. Bass also provide a popular fishery on the reservoir, and when kokanee fishing was poor in early 2015, many anglers switched to bass fishing. This was the first year for which a creel survey was performed that anglers spent more effort fishing for bass than kokanee.

In addition to increased biomass of kokanee in the reservoir, the biomass of mature kokanee has also increased substantially. This could have further ecological implications to the watershed above the reservoir, as it would result in increased upstream transfer of nutrients. These recycled nutrients are expected to benefit resident fish communities (Grant et al. 1998; Wipfli et al. 1998; Richardson 1993; Wilzbach 1985).

CONCLUSIONS

Nutrient restoration in Dworshak Reservoir has shown continued signs of success and similar responses to those observed in several BC lakes and reservoirs following nutrient addition. Water clarity was not impaired and harmful algal blooms were reduced. The effects of N restoration were observed at all trophic levels. We observed increases in picoplankton, which represent the lowest trophic level, beginning with the first year of nutrient additions. Observed increases in the proportion of edible phytoplankton have resulted in increased zooplankton density and biomass. The increased biomass of consumable *Daphnia* was likely responsible for increased kokanee growth, which in turn has led to increased biomass. Evidence suggests that the carrying capacity of the reservoir was increased and the trend of slightly larger kokanee at an increased level of abundance should produce increased catch rates in the recreational fishery. The increase in kokanee biomass is also expected to benefit piscivorous fishes, including Bull Trout and Smallmouth Bass. Furthermore, the increased abundance and biomass of spawning kokanee in the North Fork Clearwater subbasin should benefit resident fish and wildlife well beyond the reservoir itself. While it will take additional years of data to realize the full effect on the kokanee population and fishery, nutrient restoration appeared to have a beneficial effect on the ecology of the reservoir and should be continued.

RECOMMENDATIONS

1. Work with the USACE to pursue implementation of nutrient restoration as a long-term management strategy for Dworshak Reservoir.

2. Conduct controlled and replicated mesocosm experiments to separate environmental effects from N restoration, determine causation, and fine tune application rates.

3. Continue to monitor the kokanee population and fishery to assess the long-term effects of nutrient restoration.

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Table 1. Comparison of linear models used to determine the effects of several factors on the biomass of *Daphnia* large enough to be consumed by kokanee and the density of total zooplankton. Independent variables included whether nutrients were added to the reservoir in a given year (Nutr), the abundance of age-1 and older kokanee (Kok) and an interaction term (int). Fit statistics, including the adjusted coefficient of determination (R^2_{adj}), maximized log-likelihood (Log$L$), number of parameters (K), Akaike's Information Criterion corrected for sample size (AIC$_c$), simple differences (ΔAIC$_c$) and Akaike's weight (w_i) are given. Shading indicates models with the strongest support.

Biomass of Consumable *Daphnia*								
Independent variables			R^2_{adj}	**Log*L***	***K***	**AIC$_c$**	**ΔAIC$_c$**	w_i
Nutr	Kok		0.63	-56.94	2	117.9	0.0	0.74
Nutr			0.39	-59.67	1	121.3	2.5	0.21
Nutr	Kok	int	0.60	-58.08	3	122.2	5.9	0.04
Kok			0.10	-62.28	1	126.6	7.7	0.02
Total Zooplankton Density								
Independent variables			R^2_{adj}	**Log*L***	***K***	**AIC$_c$**	**ΔAIC$_c$**	w_i
Nutr			0.33	-45.56	1	93.5	0.0	0.42
Nutr	Kok	int	0.66	-42.37	3	93.7	0.2	0.37
Nutr	Kok		0.39	-45.17	2	95.7	2.2	0.14
Kok			0.08	-47.40	1	97.2	3.7	0.07

Table 2. Summary statistics for total length (TL), weight and relative weight (W_r) for two age classes of kokanee captured during July trawl surveys on Dworshak Reservoir. Data are presented for four non-restoration years and eight years of N restoration (shaded), including summary statistics for both periods. Statistics include the mean and standard error (SE).

Age-1 Kokanee

	TL (mm)		Weight (g)		W_r	
Year	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
2003	204	2.4	71.3	3.0	81	1.0
2004	202	1.6	72.3	1.8	83	0.6
2006	145	2.0	23.9	1.0	76	0.7
2007	198	2.5	66.9	2.3	81	0.6
2008	209	2.2	81.0	3.3	86	1.2
2009	169	0.7	43.0	0.6	86	0.6
2010	172	0.4	45.2	0.3	87	0.3
2011	170	1.1	45.6	1.0	89	1.1
2012	206	2.7	88.8	3.8	95	0.8
2013	201	1.8	74.2	2.1	87	0.6
2014	145	0.4	25.9	0.3	82	0.4
2015	163	2.7	40.3	2.0	86	0.5
Non-restoration	180	1.6	53.3	1.7	82	0.8
Restoration	183	1.2	58.2	1.4	86	0.5

Age-2 Kokanee

	TL (mm)		Weight (g)		W_r	
Year	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
2003	262	1.8	159.1	4.3	85	1.1
2004	293	2.7	226.4	6.5	85	0.8
2006	196	2.1	59.6	2.4	76	1.3
2007	241	1.2	125.2	2.0	86	0.5
2008	303	1.4	262.5	4.7	89	0.8
2009	272	2.4	178.1	5.4	85	0.9
2010	219	0.9	94.2	1.4	86	0.4
2011	220	1.2	98.1	1.8	89	0.6
2012	308	2.2	297.3	5.6	97	0.9
2013	296	2.6	242.4	6.3	89	1.4
2014	248	2.8	131.6	5.1	82	2.2
2015	202	1.4	80.4	1.6	93	0.1
Non-restoration	243	1.8	135.8	3.9	84	0.9
Restoration	261	1.2	176.4	3.3	86	0.8

Table 3. Annual growth, given as the change in total length (mm) from April of one year to the next for age-0 and age-1 kokanee. Growth of age-2 kokanee is from April to July of the same year. Growth was independently estimated from back-calculation using scales and as the differences in mean length of trawl caught fish at the beginning of each year. Mean growth is reported for each year that data is available, and means are reported for periods of nutrient restoration (Rest, shaded rows) or no nutrient additions (Non).

Year		**Back-calculation**			**Trawl**		
		0	**1**	**2**	**0**	**1**	**2**
2001	Non	101					
2002	Non	112	118				
2003	Non	96	136	40			
2004	Non	113		48			
2005	Non	98	71				
2006	Non	120	91	14	113		
2007	Rest	118	132	47	110	133	46
2008	Rest	109	135	46	107	138	57
2009	Rest	119	89	22	117	91	25
2010	Rest	113	83	28	105	83	21
2011	Non	115	130	16	114	128	20
2012	Rest	115	134	67	117	132	75
2013	Rest	101	111	39	107	118	50
2014	Rest	99	69	21	113	66	13
2015	Rest			29			29
	Means	109	108	35	111	111	37

Summary statistics for years with trawl data

	Back-calculation			**Trawl**		
	0	**1**	**2**	**0**	**1**	**2**
Non	118	130	16	113	128	20
Rest	111	108	38	111	109	39

Summary statistics for all years with back-calculation data

	0	**1**	**2**
Non	108	109	29
Rest	111	108	38

Table 4. Annual growth effects for kokanee from Dworshak Reservoir estimated from a mixed effects model. For each year, the best linear unbiased predictor (BLUP), standard error (SE), t statistic (t), and p-value (p) are given.

Year	BLUP	SE	t	p
2004	116.07	3.72	28.74	<.0001
2005	92.17	2.34	40.44	<.0001
2006	106.54	2.20	54.35	<.0001
2007	123.44	1.97	65.49	<.0001
2008	117.33	2.05	60.12	<.0001
2009	103.05	2.01	54.06	<.0001
2010	105.01	1.97	54.31	<.0001
2011	118.35	2.19	59.11	<.0001
2012	132.23	2.13	67.38	<.0001
2013	110.56	2.53	46.51	<.0001
2014	96.53	4.17	21.63	<.0001

Table 5. Comparison of linear models used to determine the effect of several factors on annual growth patterns of kokanee from Dworshak Reservoir. The dependent variable was the annual effect previously estimated from a mixed effects model. Models assessed the effects of consumable *Daphnia* biomass (Daph), total zooplankton density (Zoop), abundance of age-1 and older kokanee (Kok), and nutrient addition (Nutr) on annual growth using a set of a *priori* models. Fit statistics, including the adjusted coefficient of determination (R^2_{adj}), maximized log-likelihood (Log$L$), number of parameters (K), Akaike's Information Criterion corrected for sample size (AIC_c), simple differences (ΔAIC_c), and Akaike's weight (w_i) are given. Best approximating models are shaded in gray.

Independent variables			**R^2_{adj}**	**Log$L$**	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Daph			0.51	-41.26	1	85.0	0.0	0.76
Kok	*Daph*		0.53	-41.50	2	88.5	3.5	0.13
Kok			0.29	-43.30	1	89.1	4.1	0.10
Kok	*Daph*	int	0.60	-41.64	3	92.7	7.7	0.02
Zoop			-0.04	-45.66	1	99.6	14.6	0.00
Nutr			-0.07	-45.82	1	100.3	15.3	0.00
Kok	Nutr		0.25	-44.79	2	102.3	17.4	0.00
Kok	Nutr	int	0.28	-46.56	3	104.0	19.0	0.00

Table 6. Comparison of linear models used to determine the effect of several factors on annual growth patterns of kokanee from Dworshak Reservoir. The dependent variable was the mean annual growth for each age class in a given year. Growth was estimated by back-calculation. Independent variables included consumable *Daphnia* biomass, abundance of the corresponding age class in that year, and nutrient addition. Models were selected *a priori* based on existing knowledge. Fit statistics, including the coefficient of determination (R^2), maximized log-likelihood (Log$L$), number of parameters (K), Akaike's Information Criterion corrected for sample size (AIC$_c$), simple differences (ΔAIC$_c$) and Akaike's weight (w_i) are given. Plausible models, defined as those with an ΔAIC$_c \leq 2$ or $w_i \geq 1$, are shaded in gray.

Independent variables					R^2	**Log$L$**	K	**AIC$_c$**	**ΔAIC$_c$**	w_i
Age	Daph	1+	Age:1+		0.91	-127.77	4	265.0	0.0	0.58
Age	Daph	1+	Age:Daph		0.90	-128.81	4	267.1	2.1	0.20
Age	Daph	Age:Daph			0.89	-130.70	3	268.3	3.2	0.12
Age	Daph	1+	Age:Daph	Age:1+	0.91	-128.97	5	270.3	5.2	0.04
Age	Daph				0.86	-133.37	2	271.1	6.1	0.03
Age	1+	Age:1+			0.88	-132.31	3	271.5	6.5	0.02
Age	1+				0.84	-134.14	3	275.1	10.1	0.00
Age	Fert	1+			0.85	-135.01	3	276.9	11.9	0.00
Age	Fert	1+	Age:1+		0.85	-133.94	4	277.4	12.4	0.00
Age	Fert	1+	Age:Fert		0.84	-136.63	4	282.7	17.7	0.00
Age					0.79	-140.81	1	283.8	18.7	0.00
Age	Fert				0.78	-140.62	2	285.7	20.6	0.00
Age	Zoop				0.78	-140.66	2	285.7	20.7	0.00

Table 7. Estimates of production and biomass of kokanee in Dworshak Reservoir. Production estimates span the period from July of the first year to July of the second year. Both estimates are based on July acoustic and midwater trawl surveys. Production estimates could only be obtained when trawl surveys were performed in subsequent years and biomass estimates were obtained for every year that a trawl survey was performed.

	Production (metric tonnes)			
Period	**Age 0-1**	**Age 1-2**	**Age 2-3**	**Total**
2014-15	45.7	115.4	1.3	162.4
2013-14	81.5	18.5	0.0	100.0
2012-13	50.3	37.1	0.0	87.4
2011-12	36.9	56.2	26.4	119.5
2010-11	60.6	37.6	0.0	98.1
2009-10	48.9	54.8	0.0	103.7
2008-09	52.3	16.4	0.0	68.7
2007-08	32.2	21.3	32.7	86.2
2006-07	71.2	99.6	0.0	170.8
2005-06				NA
2004-05				NA
2003-04	23.5	26.2	0.0	49.7

	Biomass (metric tonnes)				
Year	**Age-0**	**Age-1**	**Age-2**	**Age-3**	**Total**
2015	0.9	28.2	139.3	0.5	168.9
2014	0.7	64.9	12.1	0.6	78.3
2013	3.0	41.0	34.6		78.7
2012	0.7	30.3	25.3	2.0	58.3
2011	0.2	16.5	22.8		39.4
2010	1.4	53.2	97.1	0.3	152.0
2009	0.7	47.7	21.1		69.6
2008	0.9	19.8	18.6	5.8	45.1
2007	0.3	9.9	57.4		67.5
2006	1.0	40.7	64.5		106.1
2005					NA
2004	0.3	20.1	10.9	7.4	38.7
2003	0.3	20.1	56.7		77.1

Table 8. Estimates of angler effort, in terms of trips and angler hours, and catch. Estimates were derived from access-access creel surveys conducted from March 11 through October 18. Estimates are given for all anglers, those only targeting kokanee, and those only targeting bass.

All anglers

	Angler		Kokanee		Bass		Other	
	Trips	**Hours**	**Caught**	**Kept**	**Caught**	**Kept**	**Caught**	**Kept**
March	775	6,993	469	360	3,915	1,035	2,446	619
April	1,940	12,127	715	115	8,179	1,456	538	155
May	2,668	23,262	3,584	3,204	26,291	4,663	1,390	494
June	4,681	33,651	22,560	21,316	41,620	2,793	2,258	621
July	3,389	31,175	23,276	22,750	27,015	2,715	968	409
August	1,794	14,533	4,177	4,177	14,932	2,577	163	33
September	1,512	8,698	0	0	15,362	1,404	67	67
October	901	5,431	0	0	10,658	970	98	67
Total	17,660	136,033	54,391	51,887	147,972	17,612	7,928	2,465

Anglers targeting kokanee only

	Angler		Kokanee			Other	
	Trips	**Hours**	**Caught**	**Rate (Fish/hr)**	**Kept**	**Caught**	**Kept**
March	325	2,568	469	0.2	360	1,539	677
April	347	1,933	147	0.1	67	90	79
May	703	5,687	3,400	0.6	3,124	2,181	726
June	1,475	12,972	20,332	1.6	19,860	1,773	418
July	1,389	13,182	22,530	1.7	22,506	2,098	284
August	556	6,072	3,848	0.6	3,848	876	414
September	33	406	0	0.0	0	0	0
October	0	0	0	NA	0	0	0
Total	4,829	42,827	50,727	1.2	49,807	8,557	2,597

Anglers targeting bass only

	Angler		Bass			Other	
	Trips	**Hours**	**Caught**	**Rate (Fish/hr)**	**Kept**	**Caught**	**Kept**
March	332	3,144	2,702	0.9	497	616	141
April	1,504	9,491	8,023	0.8	1,361	1,054	114
May	1,677	16,818	24,036	1.4	4,050	1,257	320
June	2,282	19,390	39,226	2.0	2,411	3,106	1,697
July	1,631	16,592	24,848	1.5	2,500	1,050	574
August	1,074	7,286	12,317	1.7	1,642	33	33
September	1,355	8,045	15,268	1.9	1,404	67	67
October	782	4,832	10,354	2.1	885	22	22
Total	10,637	85,598	136,774	1.6	14,748	7,206	2,970

Table 9. Summary of historical creel survey data from Dworshak Reservoir, including the year and time period of the survey, estimated effort (angler hours), and number of fish caught and harvested, catch rates (fish/hr), and type of survey. Surveys were conducted using an access-access (A-A), Malvestuto (Mal), or roving-access (RA) design. Surveys estimated catch and effort for all angler (All) or kokanee anglers only (Kok).

			All Fish				**Kokanee**					
Year	**Time frame**	**angler hours**	**caught**	**fish/hr**	**harvest**	**fish/hr**	**caught**	**fish/hr**	**harvest**	**fish/hr**	**Survey type**	
1980	Jun-Sep	104,014			71,541	0.69			44,627	0.43	A-A	All
1988	Jan-Dec	140,416							206,976	1.47	Mal	Kok
1989	Jan-Dec	128,703							161,175	1.25	Mal	Kok
1990	Jan-Dec	149,592							94,757	0.63	Mal	All
2003	Apr-Sep	188,305	214,631	1.14	167,995	0.89			161,501	0.86	R-A	All
2004	Apr-Aug	273,531	248,069	0.91	206,308	0.75			190,185	0.70	R-A	All
2014	Apr-Jul	82,852	108,899	1.31	84,230	1.02	81,692	0.99	79,746	0.96	A-A	All
2014	Apr-Jul	56,134	80,486	1.43	78,184	1.39	79,763	1.42	77,891	1.39	A-A	Kok
2015	Mar-Oct	136,033	352,574	2.59	88,485	0.65	54,391	0.40	51,887	0.38	A-A	All
2015	Mar-Oct	41,580	59,172	1.42	52,306	1.26	50,672	1.22	49,765	1.20	A-A	Kok

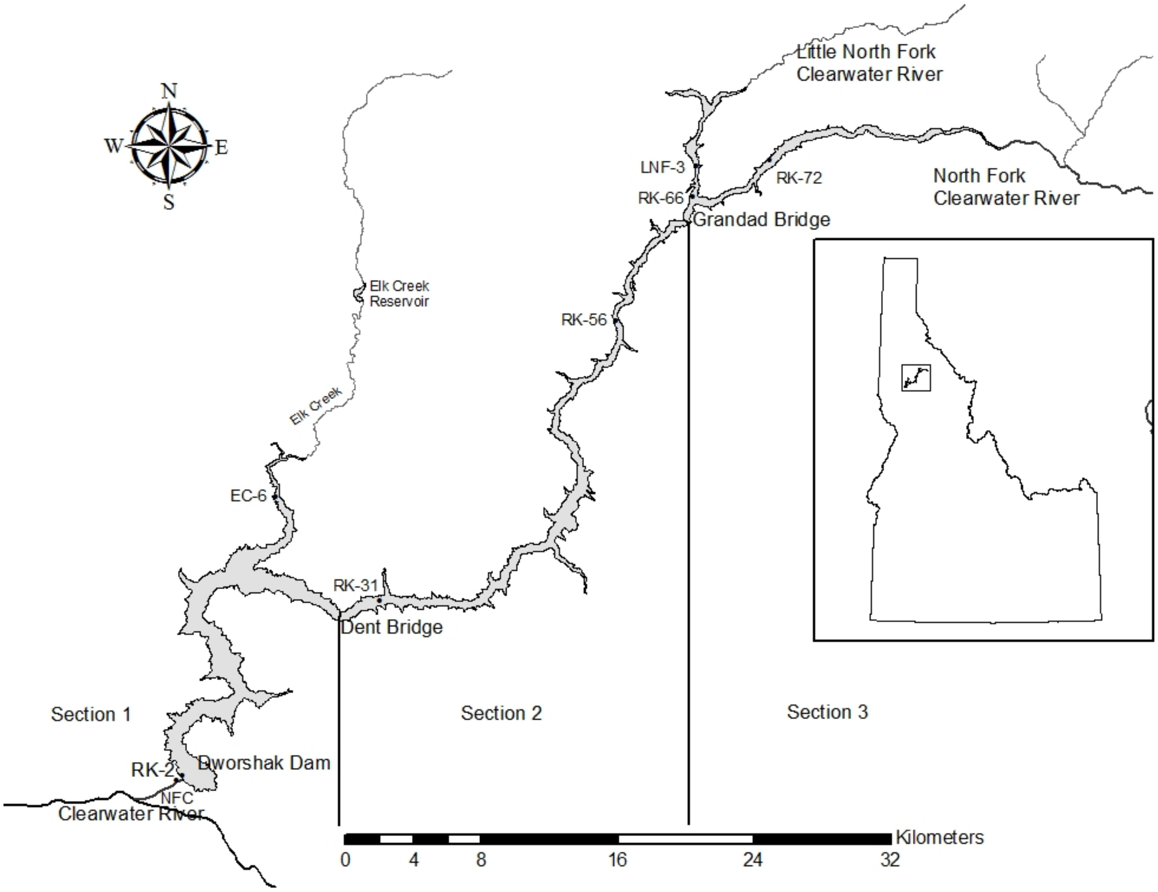

Figure 1. Map of Dworshak Reservoir depicting the locations of seven limnological sampling stations on the reservoir and one on the North Fork Clearwater below Dworshak Dam. Boundaries of reservoir sections used in statistical stratification are also shown.

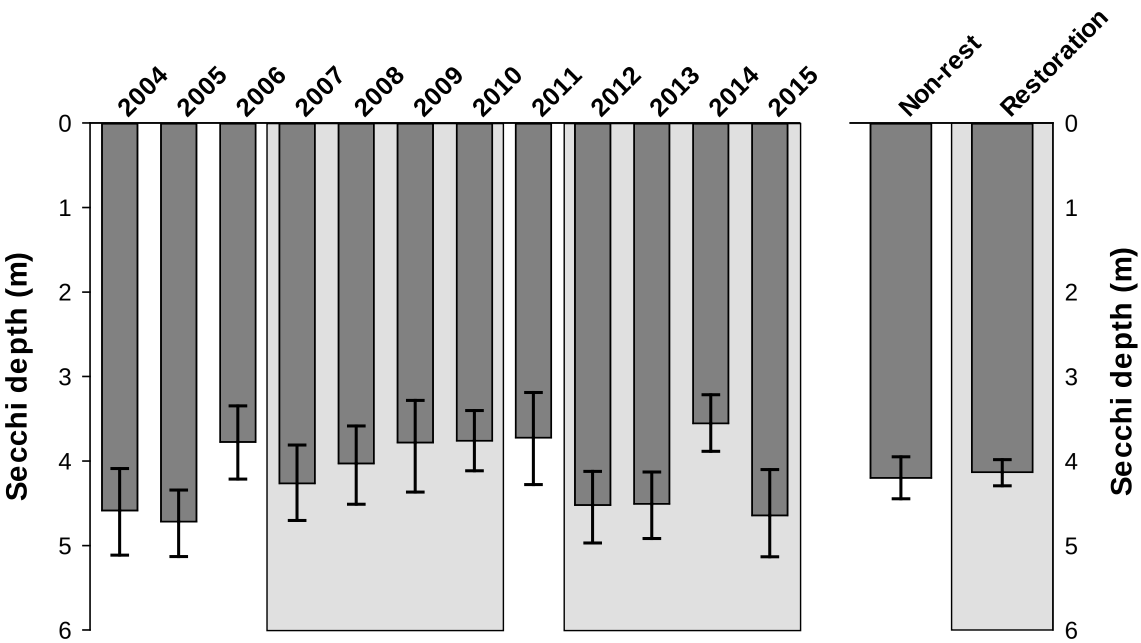

Figure 2. Mean Secchi depth measured at four sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from June through November. Error bars represent 95% confidence intervals derived by classical methods. Shading indicates the periods that nutrients were added to the reservoir.

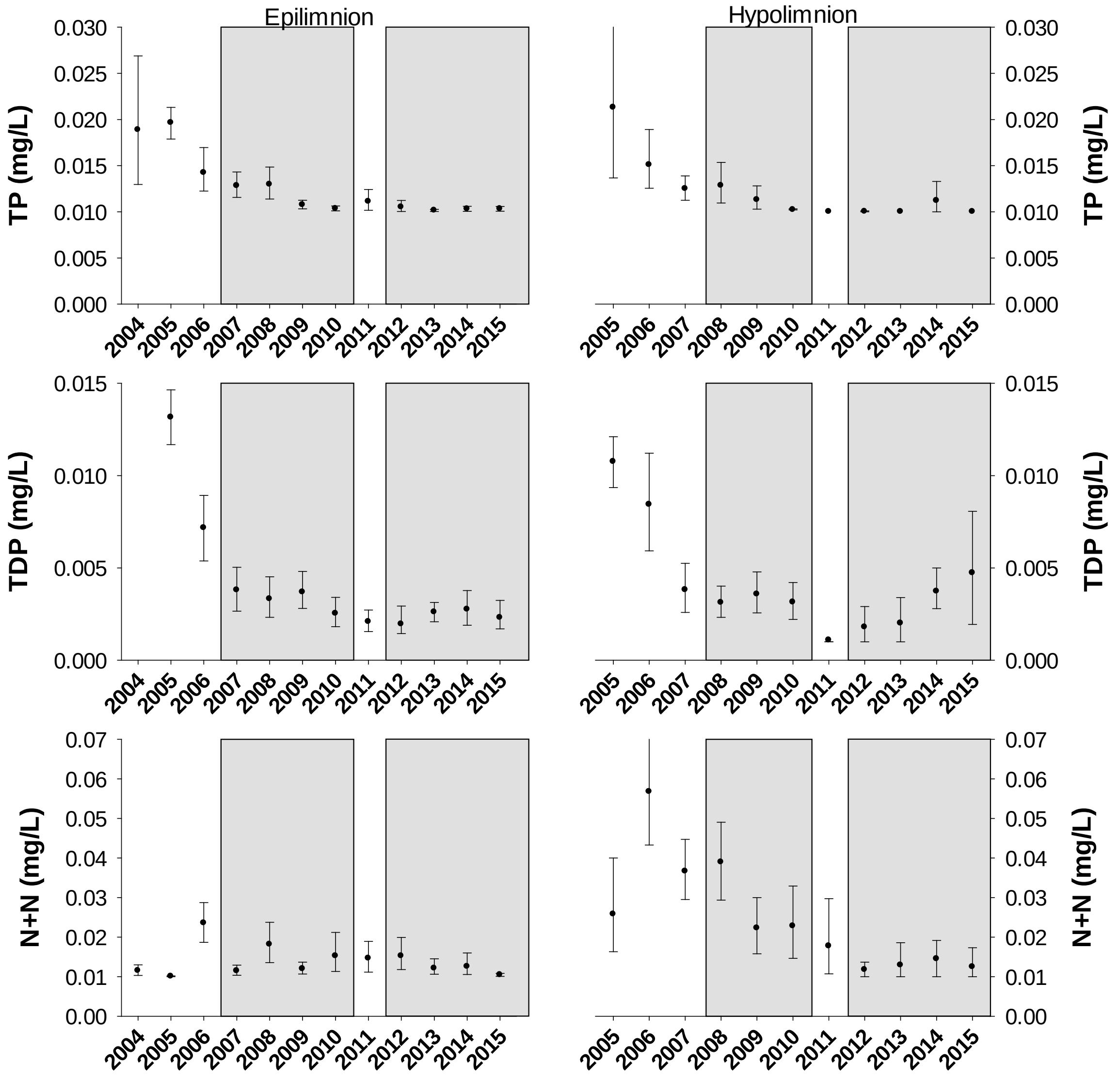

Figure 3. Mean concentration of nutrients measured from two depths at four sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. Nutrients include total phosphate (TP), total dissolved phosphate (TDP), and nitrite plus nitrate nitrogen (N+N). Because detection limits for TP and N+N differed between years, means were calculated from concentrations that were adjusted to reflect the highest detection limit. Hypolimnetic samples were only taken at RK-2 beginning in 2011. Error bars represent 95% confidence intervals derived by bootstrapping. Shading indicates the periods that nutrients were added.

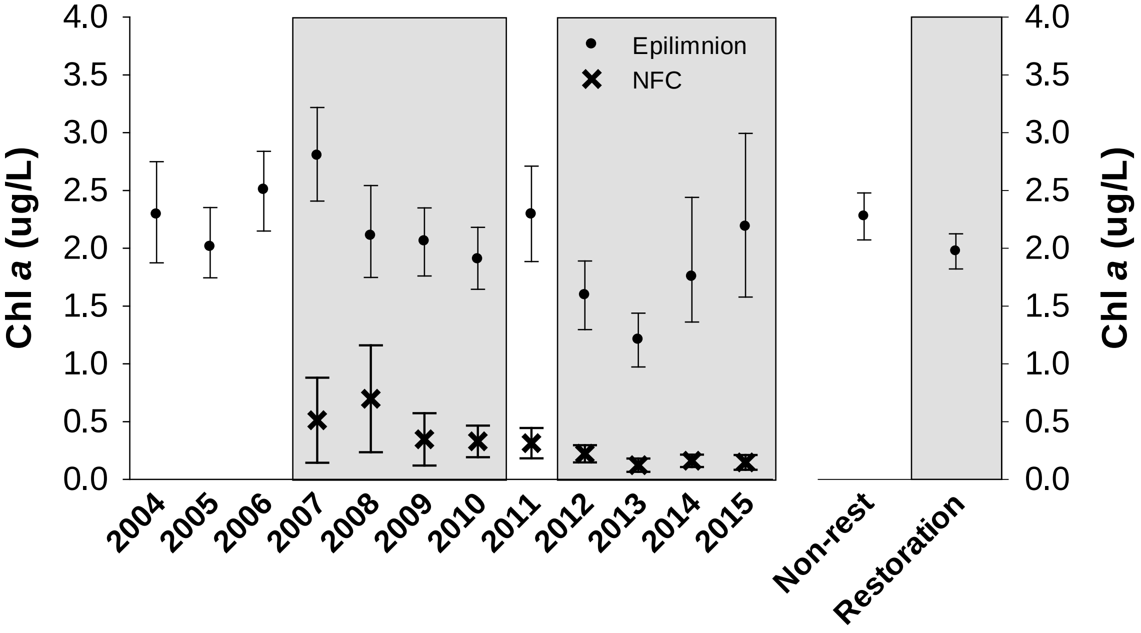

Figure 4. Mean concentration of chlorophyll *a* (Chl *a*) measured at four sampling stations (RK-2, RK-31, RK-56, and RK-72) from May through November of 2004–2015 and NFC, the station below Dworshak Dam, for 2007-2015. Error bars represent 95% confidence intervals derived by bootstrapping. Shading indicates the periods that nutrients were added.

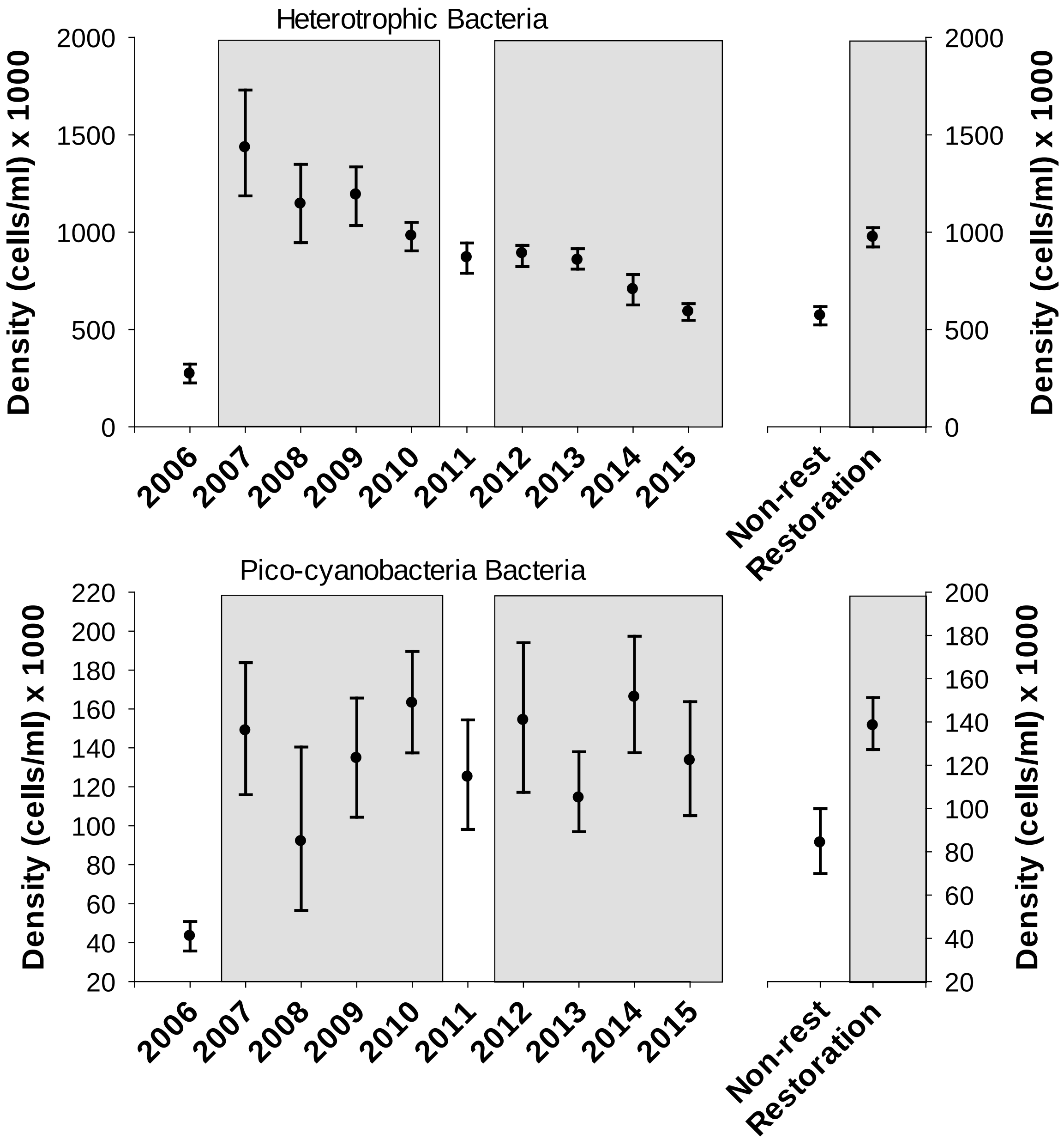

Figure 5. Mean density of picoplankton measured at four sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. Error bars represent 95% confidence intervals derived by bootstrapping. Shading indicates the period that nutrients were added.

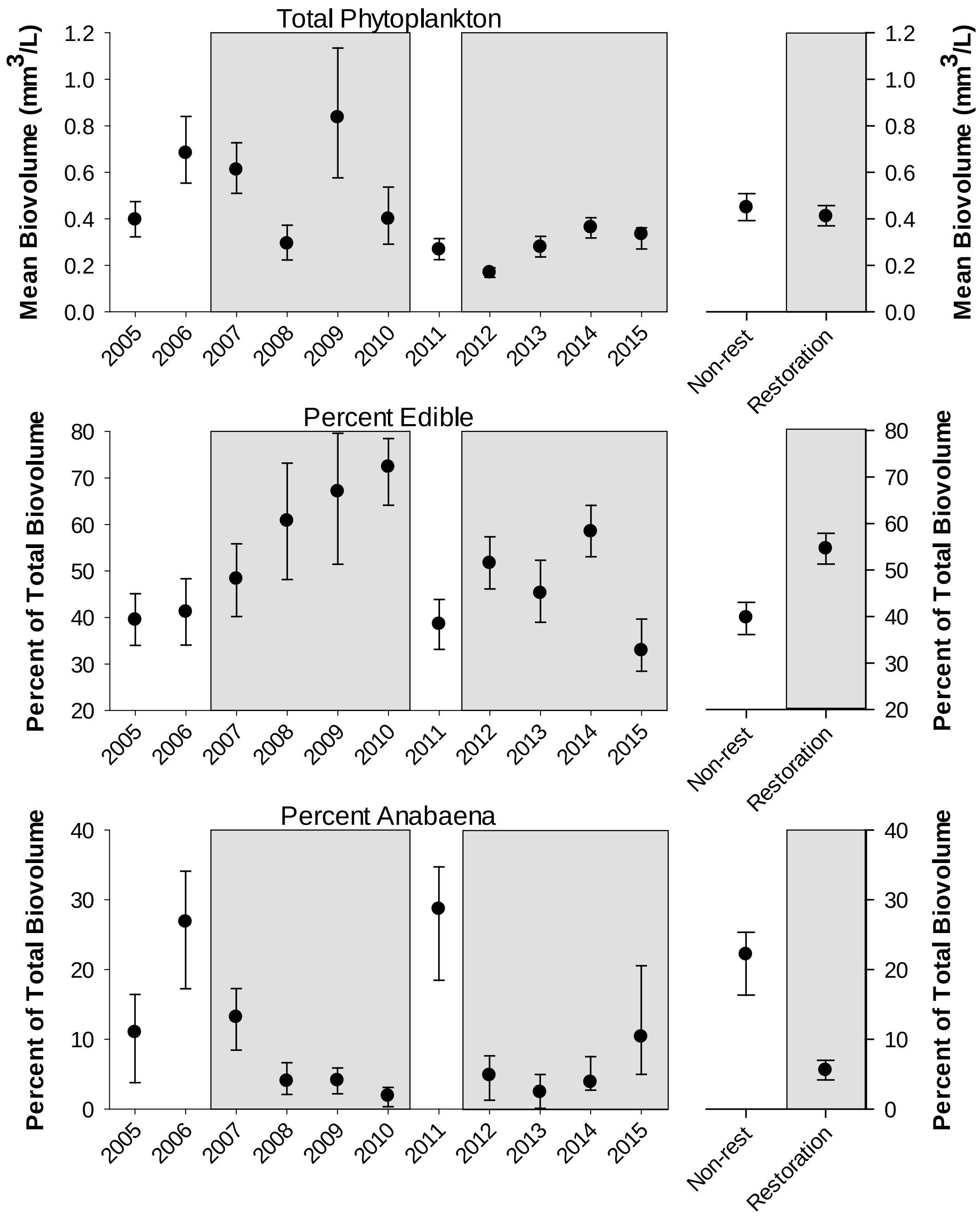

Figure 6. Mean biovolume (mm^3/L) of phytoplankton measured at four sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November, along with the proportion of the total biovolume that was edible and the proportion that was *Anabaena*. Error bars represent 95% confidence intervals obtained by bootstrapping. Shading indicates the period that nutrients were added.

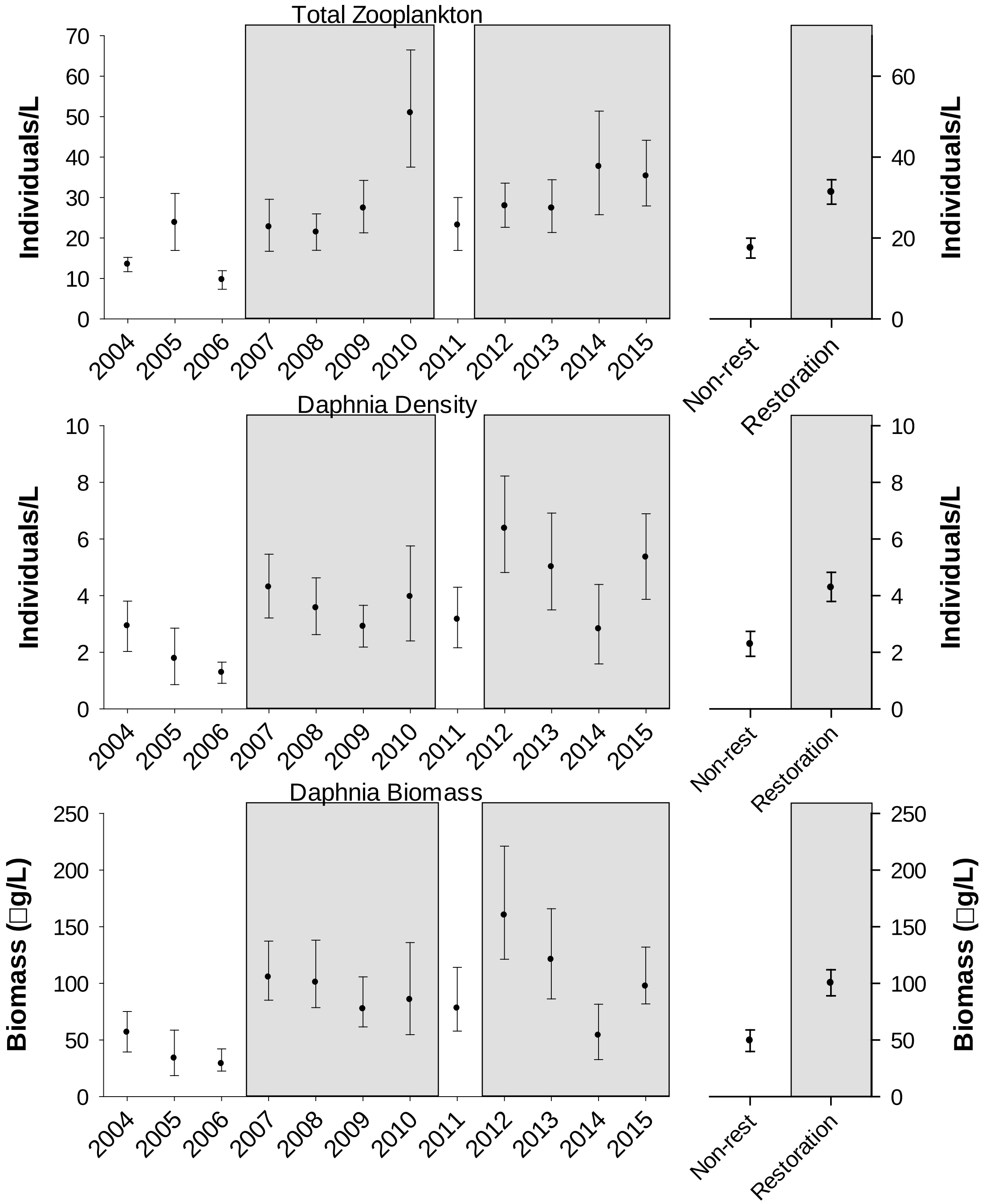

Figure 7. Mean density of zooplankton collected at four sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from April through November. Densities (individuals/L) are presented for total zooplankton and *Daphnia* that were large enough to be consumed by kokanee. Biomass (µg/L) is also presented for consumable *Daphnia*. Error bars represent 95% confidence intervals obtained by bootstrapping. Shading indicates the period that nutrients were added.

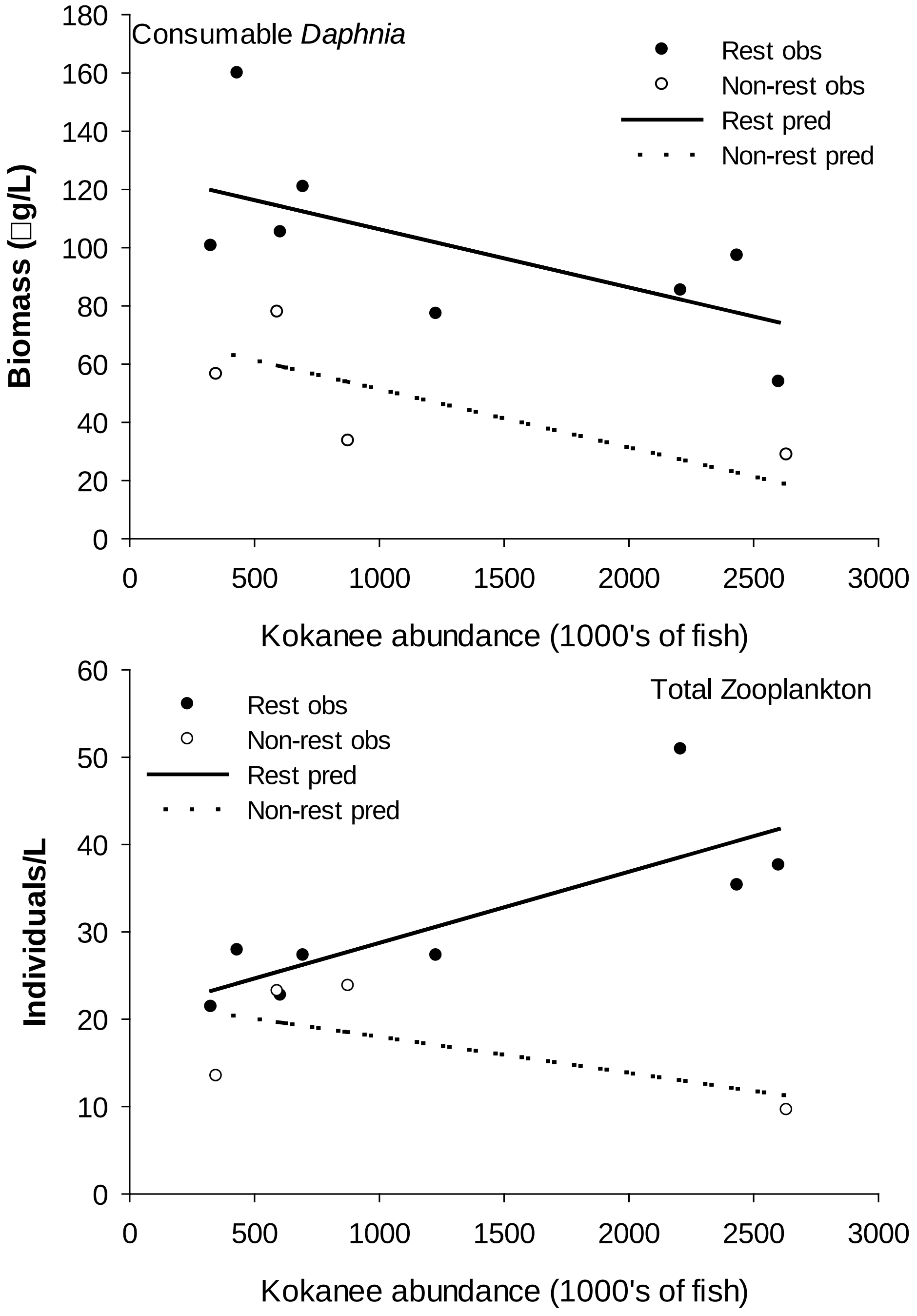

Figure 8. Best competing models explaining the relationship between nutrient restoration, the abundance of age-1 and older kokanee, and either consumable *Daphnia* biomass or total zooplankton density. Restoration years (Rest) are indicated by solid circles and lines, whereas non-restoration years (Non-rest) are indicated by open circles and solid lines. Circles represent observed data (obs) and lines represent model predictions (pred).

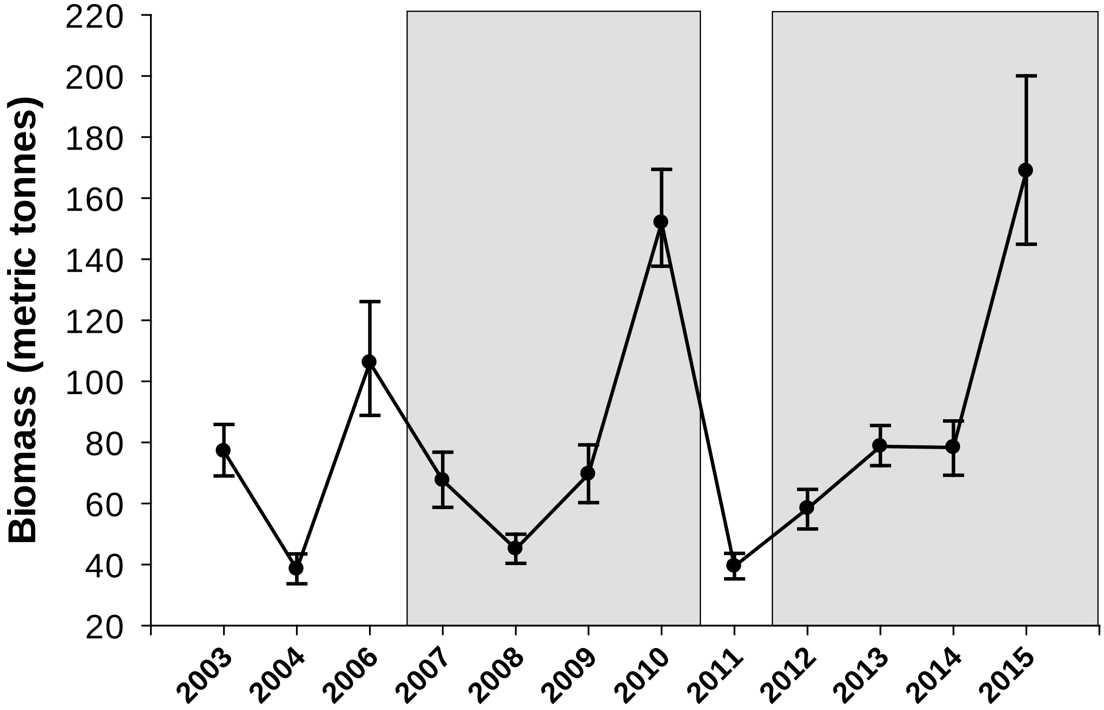

Figure 9. Estimated biomass of kokanee in Dworshak Reservoir derived from July acoustic and trawl surveys. Error bars represent 95% confidence intervals obtained by bootstrapping. Shading indicates the periods that nutrients were added.

APPENDICES

Appendix A. Summary of water transparency measures from Dworshak Reservoir, including 95% lower (LCL) and upper (UCL) confidence limits for mean Secchi depth, and standard error (SE) for the mean compensation depth. The restoration period (Rest) is indicated by shading and the non-restoration period (Non) is unshaded.

	Secchi Depth			**Compensation Depth**	
Year	**mean**	**LCL**	**UCL**	**mean**	**SE**
2004	4.6	4.2	5.0		
2005	4.7	4.6	4.9		
2006	3.8	3.6	4.0		
2007	4.3	3.9	4.6	9.8	0.19
2008	4.0	3.9	4.2	10.2	0.26
2009	3.8	3.4	4.1	9.6	0.24
2010	3.8	3.6	3.9	9.8	0.25
2011	3.7	3.6	3.9	9.7	0.28
2012	4.5	4.1	5.0	10.7	0.23
2013	4.5	4.1	4.9	11.1	0.20
2014	3.6	3.2	3.9	10.3	0.21
2015	4.6	4.1	5.1	10.9	0.29
Non	4.2	3.9	4.4		
Rest	4.1	4.0	4.3		

Appendix B. Summary of nutrient concentrations from two depth strata in Dworshak Reservoir and the North Fork Clearwater River below Dworshak Dam. Statistics are calculated for the same times (May – November) and locations (RK-2, RK-31, RK-56, and RK-72). Concentrations below the detection limit were treated as if they were at the detection limit for calculations. Because detection for TP and N+N were different among years, they were artificially adjusted upward to 0.01 mg/L, the highest detection limit used during the study period. Beginning in 2011, hypolimnion samples were taken at RK-2 only. Years in which nutrients were added to the epilimnion of the reservoir are shaded.

Epilimnion

	TP		**TDP**		**TN**		**N+N**		**TAN**		**TIN**	
Year	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**
2004	0.019	0.010					0.011	0.010				
2005	0.020	0.019	0.013	0.012			0.010	0.010				
2006	0.014	0.010	0.007	0.006			0.024	0.013				
2007	0.013	0.010	0.004	0.001			0.011	0.010				
2008	0.013	0.010	0.003	0.002			0.018	0.010				
2009	0.011	0.010	0.004	0.003			0.012	0.010				
2010	0.010	0.010	0.003	0.001			0.015	0.010				
2011	0.011	0.010	0.002	0.001	0.109	0.110	0.015	0.010	0.019	0.005	0.026	0.006
2012	0.011	0.010	0.002	0.001	0.042	0.030	0.015	0.010	0.023	0.005	0.034	0.008
2013	0.010	0.010	0.003	0.002	0.043	0.010	0.012	0.010	0.006	0.005	0.011	0.010
2014	0.010	0.010	0.003	0.001	0.069	0.055	0.013	0.010	0.021	0.019	0.026	0.024
2015	0.010	0.010	0.002	0.002	0.055	0.040	0.010	0.010	0.014	0.009	0.016	0.012

Appendix B. Continued.

Hypolimnion

	TP		TDP		TN		N+N		TAN		TIN	
Year	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**
2005	0.021	0.014	0.011	0.010			0.026	0.013				
2006	0.015	0.012	0.008	0.005			0.057	0.043				
2007	0.012	0.010	0.004	0.001			0.037	0.039				
2008	0.013	0.010	0.003	0.002			0.039	0.027				
2009	0.011	0.010	0.004	0.004			0.022	0.012				
2010	0.010	0.010	0.003	0.001			0.023	0.010				
2011	0.010	0.010	0.001	0.001	0.081	0.070	0.018	0.010	0.014	0.005	0.028	0.014
2012	0.010	0.010	0.002	0.001	0.019	0.010	0.012	0.010	0.043	0.005	0.048	0.007
2013	0.010	0.010	0.002	0.001	0.016	0.010	0.013	0.010	0.007	0.005	0.014	0.007
2014	0.011	0.010	0.004	0.004	0.070	0.050	0.014	0.010	0.019	0.010	0.028	0.019
2015	0.010	0.010	0.005	0.003	0.036	0.030	0.012	0.010	0.009	0.010	0.015	0.015

River

	TP		TDP		TN		N+N		TAN		TIN	
Year	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**	**mean**	**median**
2007	0.013	0.010	0.003	0.002			0.036	0.039				
2008	0.013	0.010	0.003	0.001			0.053	0.052				
2009	0.011	0.010	0.004	0.003			0.029	0.024				
2010	0.018	0.010	0.003	0.001			0.043	0.038				
2011	0.011	0.010	0.003	0.002	0.126	0.110	0.037	0.038	0.008	0.005	0.044	0.044
2012	0.011	0.010	0.003	0.001	0.037	0.020	0.029	0.031	0.005	0.005	0.033	0.034
2013	0.010	0.010	0.003	0.003	0.056	0.060	0.047	0.047	0.008	0.005	0.056	0.052
2014	0.010	0.010	0.003	0.002	0.063	0.040	0.025	0.023	0.016	0.010	0.032	0.029
2015	0.010	0.010	0.002	0.002	0.060	0.050	0.028	0.025	0.006	0.005	0.037	0.031

Appendix C. Estimates of kokanee abundance by age class and adult (age-2 and older) densities for Dworshak Reservoir. Estimates from 2003 to present have been revised using estimates of available kokanee habitat from data provided by Sam Martin of the USACE.

		Kokanee Abundance					**Adult**
Year	**Sampling Method**	**Age-0**	**Age-1**	**Age-2**	**Age-3**	**Total**	**Density (fish/ha)**
2015	Hydroacoustic	1,608,968	699,689	1,732,890	2,905	4,041,546	348
2014	Hydroacoustic	1,594,460	2,505,608	92,027	3,574	4,198,439	19
2013	Hydroacoustic	3,974,504	553,133	142,806	0	4,670,443	29
2012	Hydroacoustic	819,012	340,809	85,023	6,343	1,246,327	17
2011	Hydroacoustic	494,073	361,416	230,670	972	1,087,132	43
2010	Hydroacoustic	2,331,120	1,177,439	1,030,226	1,483	4,538,785	190
2009	Hydroacoustic	1,022,086	1,109,492	118,753	0	2,250,331	15
2008	Hydroacoustic	1,359,430	233,123	71,024	21,986	1,685,563	18
2007	Hydroacoustic	531,703	147,300	457,245	0	1,136,248	93
2006	Hydroacoustic	1,996,987	1,550,134	1,082,431	0	4,629,552	242
2005	Hydroacoustic	2,339,695	696,738	179,734	0	3,216,167	35
2004	Hydroacoustic	448,833	272,802	74,419	0	796,054	14
2003	Hydroacoustic	372,664	281,254	356,434	0	1,010,353	69
2002	Hydroacoustic	1,246,959	1,101,232	127,933	0	2,476,124	24
2001	Hydroacoustic	1,962,000	781,000	405,000	0	3,150,000	75
2000	Hydroacoustic	1,894,857	303,680	199,155	0	2,397,691	37
1999	Hydroacoustic	1,143,634	363,250	38,464	0	1,545,347	7
1998	Hydroacoustic	537,000	73,000	39,000	0	649,000	7
1997	Trawling	65,000	0	0	0	65,000	0
1996	Hydroacoustic	231,000	43,000	29,000	0	303,000	5
1995[a]	Hydroacoustic	1,630,000	1,300,000	595,000	0	3,539,000	110
1994	Hydroacoustic	156,000	984,000	304,000	9,000	1,457,000	69
1993	Trawling	453,000	556,000	148,000	6,000	1,163,000	33
1992	Trawling	1,040,000	254,000	98,000	0	1,043,000	22
1991	Trawling	132,000	208,000	19,000	6,000	365,000	5
1990[a]	Trawling	978,000	161,000	11,000	3,000	1,153,000	3
1989[b]	Trawling	148,000	148,000	175,000	0	471,000	32
1988	Trawling	553,000	501,000	144,000	12,000	1,210,000	29

[a] June sampling likely resulted in an underestimate of age-0 kokanee.

[b] September sampling likely resulted in an underestimate of mature kokanee.

Appendix D. Number of kokanee spawners counted in index tributaries to the North Fork Clearwater River above Dworshak Reservoir, Idaho during September 1988-2015. Counts were performed on or near September 25, the historical peak of spawning activity.

Year	**Isabella Creek**	**Skull Creek**	**Quartz Creek**	**Dog Creek**	**Total**	**Mean TL (mm)**
2015	19,091	9,204	3,121	1,827	33,243	225
2014	10,601	5,292	1,609	1,775	19,277	274
2013	7,535	3,507	758	409	12,209	309
2012	1,447	1,676	574	658	4,355	327
2011	3,598	2,846	773	1,396	8,613	244
2010	26,529	24,212	5,283	3,385	59,409	249
2009	5,366	4,343	918	626	11,253	285
2008	3,738	2,160	462	1,073	7,433	306
2007	11,342	10,913	1,268	1,771	25,294	264
2006	12,604	12,077	2,717	2,345	29,743	210
2005	6,890	3,715	2,137	617	13,359	243
2004	6,922	2,094	450	1,474	10,940	308
2003	12,091	10,225	1,296	1,083	24,695	278
2002	15,933	7,065	2,016	1,367	26,381	267
2001	3,751	1,305	722	301	6,079	305
2000	3,939	402	124	565	5,030	314
1999	10,132	361	827	2,207	13,527	
1998	627	20	13	18	678	
1997	144	0	0	0	144	
1996	2,552	4	13	82	2,651	
1995	12,850		2,780	1,160	16,790	
1994	14,613	12,310	4,501	1,878	33,302	
1993	29,171	7,574	2,476	6,780	46,001	
1992	7,085	4,299	1,808	1,120	14,312	
1991	4,053	1,249	693	590	6,585	
1990	10,535	3,219	1,702	1,875	17,331	
1989	11,830	5,185	2,970	1,720	21,705	290
1988	10,960	5,780	5,080	1,720	23,540	280

Prepared by:	**Approved by:**
	IDAHO DEPARTMENT OF FISH AND GAME
Sean M. Wilson Senior Fishery Research Biologist Idaho Department of Fish and Game	Daniel J. Schill Fisheries Research Manager
Matthew P. Corsi Principal Fishery Research Biologist Idaho Department of Fish and Game	James P. Fredericks, Chief Bureau of Fisheries