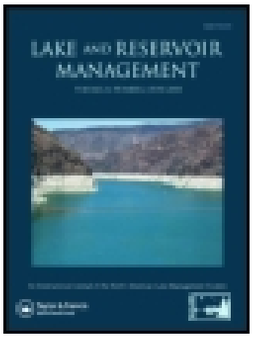

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Early trophic responses to nutrient addition in Dworshak Reservoir, Idaho

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ABSTRACT

Wilson SM, Brandt DH, Corsi MP, Dux AM. 2017. Early trophic responses to nutrient addition in Dworshak Reservoir, Idaho. Lake Reserv Manage. 00:00–00.

Dworshak Reservoir, Idaho, responded favorably across multiple trophic levels after 4 yr of nutrient (primarily ammonium nitrate) additions. Nitrogen (N) and phosphorus (P) concentrations in the epilimnion did not increase, suggesting rapid biological uptake. Secchi depth was not significantly lower during the treatment period and chlorophyll *a* concentrations were unchanged. At the lowest trophic level, densities of heterotrophic bacteria increased by 109% and pico-cyanobacteria increased by 60% for the treatment period. While we did not observe a significant increase in the mean biovolume of phytoplankton, the proportion of *Dolichospermum*, an inedible taxa, in the phytoplankton community declined by 74%, coupled with a 94% increase in the proportion of the phytoplankton biovolume that was edible to zooplankton. The mean density of *Daphnia* for the treatment period was 70% higher than the untreated period. In the fourth year of treatment, kokanee (*Oncorhynchus nerka*) biomass increased to 233% of the untreated mean and 143% of the highest untreated estimate. Our observations are consistent with reports from similar projects throughout British Columbia, Alaska, and Scandinavia, which suggests ammonium nitrate enrichment should be further explored as a management strategy for mitigating oligotrophication in N limited waters.

KEYWORDS
Daphnia; *dolichospermum*; kokanee; nutrient addition; reservoir

Nutrient additions have been used as a fishery management technique, especially in the sockeye salmon/kokanee (*Oncorhynchus nerka*) systems of western North America (Stockner and Shortreed 1985, Mazumder and Edmunson 2002, Hyatt et al. 2004). In most of these systems, oligotrophication resulted primarily from a decline in marine-derived nutrients concurrent with reductions in sockeye salmon escapement (Stockner and MacIsaac 1996). In kokanee systems, oligotrophication has occurred primarily from the construction and operation of hydroelectric impoundments (Ney 1996, Stockner et al. 2000, Schindler et al. 2014). Contributing factors include nutrient trapping (Ney 1996), increased sedimentation and nutrient export (Stockner et al. 2000), and loss of a functional littoral zone (Stockner et al. 2000), including reduced allochthonous inputs (Jansson et al. 2000, Carpenter et al. 2005). Nutrient addition programs seeking to increase production of planktivorous fishes assume that zooplankton is limited and can be influenced through bottom-up controls (Stockner and Shortreed 1985, Hyatt et al. 2004). The potential for these bottom-up responses of lake and reservoir food webs has been demonstrated across trophic levels in lakes and reservoirs in British Columbia, Alaska, and Scandinavia (Stockner and MacIsaac 1996, Ashley et al. 1999, Pieters et al. 2003, Hyatt et al. 2004, Perrin et al. 2006, Milbrink et al. 2008).

Fishery and lake managers have also used nutrient addition to manipulate N:P ratios in order to influence the species composition of the phytoplankton community, especially to decrease the prevalence of harmful algal blooms (Stockner and Shortreed 1988, Harris et al. 2014). Harmful algae in lacustrine systems have become increasingly common due to anthropogenic factors and can negatively influence recreational use and water quality (Paerl et al. 2001). A number of factors may have contributed to the increased prevalence of these algal blooms, including eutrophication (Downing et al. 2001, Paerl and Scott 2011) and climate (Paerl and Scott 2011). While there is evidence that these blooms may be the result of increased nutrient

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inputs (Downing et al. 2001, Paerl and Scott 2011), there is also evidence that they may be the result of low N:P ratios (Graham et al. 2004, Orihel et al. 2012, Harris et al. 2014), particularly blooms composed of N-fixing taxa (Stockner and Shortreed 1988, Schindler et al. 2008). In such situations, available N is rapidly depleted by the standing stock of algae and N-fixing cyanobacteria, such as *Dolichospermum* (formerly *Anabaena*), easily out-compete other taxa and become dominant (Schindler et al. 2008). While these taxa can be ingested by zooplankton, such as *Daphnia* (Work and Havens 2003), they have been found to be generally poor-quality food and often have a negative effect on population growth (Wilson et al. 2006), and are therefore considered to be generally inedible. A dominance of N-fixing cyanobacteria has the potential to reduce production of zooplankton, thereby reducing the potential for fish production (Stockner and MacIsaac 1996, Stockner et al. 2000).

Declining reservoir productivity has been identified as one of the primary factors limiting the popular kokanee fishery in Dworshak Reservoir (Bennett 1997, Stark and Stockner 2006). Stockner and Brandt (2006) conducted a detailed assessment of the reservoir and gave recommendations for a nutrient restoration program. Oligotrophication of Dworshak Reservoir is likely caused by multiple factors, including the loss of marine-derived nutrients (Stockner et al. 2000) because no upstream passage was provided for anadromous fish, and extreme water level fluctuations resulting in a nonfunctional littoral zone (Stockner et al. 2000, Milbrink et al. 2011). The reservoir becomes N limited by midsummer, leading to a dominance of *Dolichospermum* sp. (Stockner and Brandt 2006), which are typically abundant from midsummer to early fall. Stockner and Brandt (2006) hypothesized that midsummer N limitation and dominance of inedible forms of phytoplankton were limiting zooplankton production and subsequently fish production.

In 2007, the U.S. Army Corps of Engineers (USACE) and the Idaho Department of Fish and Game (IDFG) initiated a nutrient addition (hereafter, treatment) program to mitigate for oligotrophication and nuisance algal blooms. This study summarizes our evaluation of the effects of the first 4 yr of nutrient additions at multiple trophic levels. Specifically, we address the efficacy of the addition of N-based fertilizer as a management strategy for improving productivity at each trophic level while maintaining water quality standards through improved N:P ratios.

Study site

Dworshak Dam, completed in 1972, is located on the North Fork Clearwater River approximately 3.1 km from the confluence with the mainstem Clearwater River near Ahsahka, Idaho (Fig. 1). The resulting

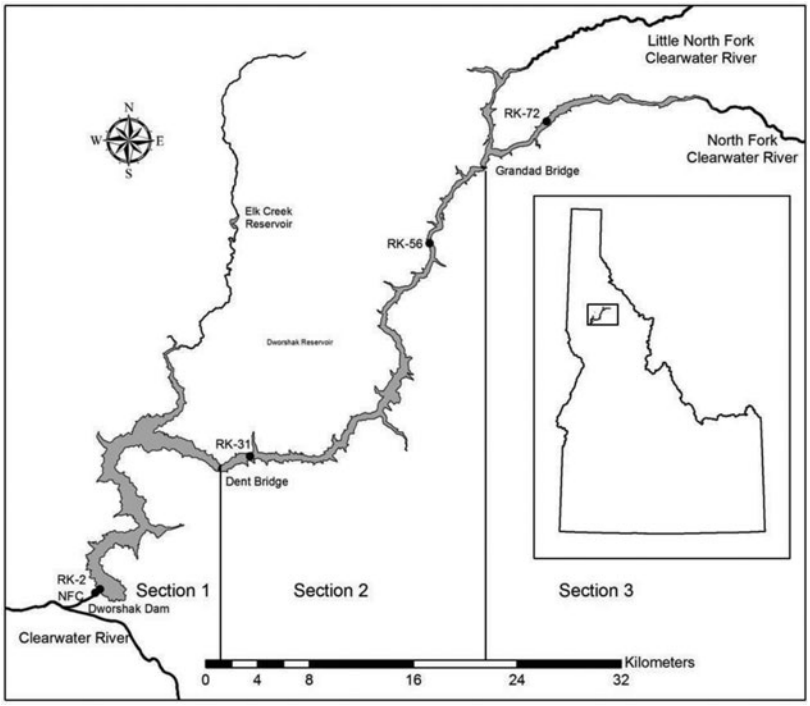

Figure 1. Map of Dworshak Reservoir depicting the locations of 4 limnological sampling stations on the reservoir and one on the North Fork Clearwater below Dworshak Dam. Boundaries of reservoir sections used in statistical stratification are also shown.

reservoir was narrow and steeply sloped (Falter et al. 1977). The land immediately surrounding the reservoir was managed by the USACE and maintained primarily as coniferous forest. The remainder of the watershed surrounding the reservoir was privately owned and primarily managed for timber production, with some agriculture around the southern end. The watershed above the reservoir drained nearly 632,000 ha, all contained within the Clearwater National Forest. The underlying geology was primarily basalts and granites covered by shallow soils that supported coniferous forest (Falter et al. 1977).

At the maximum pool elevation, Dworshak Reservoir was 86.3 km long, had a surface area of 6916 ha, and a volume of 4.3 billion m^3 (Falter et al. 1977). The reservoir typically reaches the maximum pool elevation in late June and is drafted 24 m by 15 September. The typical hydraulic retention time was 10.2 months (Falter et al. 1977). The reservoir was typically stratified from mid-May through late September, with shorter periods of stratification on the northern end (Fig. 1).

Dworshak Reservoir has been used for aquatic recreation, including boating, water skiing, and swimming. It also supported a popular fishery for kokanee, the dominant pelagic species (Stark and Stockner 2006). It further supported a popular fishery for smallmouth bass (*Micropterus dolomieu*), and limited catches of rainbow trout (*O. mykiss*). In addition, the reservoir provided overwintering habitat for bull trout (*Salvelinus confluentus*), which were protected under the Endangered Species Act (ESA), and westslope cutthroat trout (*O. clarkii lewisi*).

Methods

Nutrient applications

The USACE applied nutrients using a 10,600 L tank mounted on a truck and loaded onto an 18 m barge. Nutrients were metered into the prop wash of the barge using a SprayMate II automatic rate controller (Micro-Trak Systems, Eagle Lake, MN, USA). Applications were conducted weekly, typically from May through September, but occasionally started as early as April and lasted as late as October. Nutrients were applied along the center of the reservoir from approximately river kilometer 9 on the south end to between river kilometers 70–76 on the north end, depending on pool elevation. Nutrients consisted primary of liquid urea-ammonium nitrate (32–0-0), ranging from 21 MT in 2010 (due to early suspension of the applications) to approximately 73 MT in 2008 and 2009 (Table 1). A total of 2.8 MT of ammonium phosphate (10–34-0) was applied during the first year (2007), reduced to 1.4 MT during the second year (2008), and terminated by the third year (2009). The N:P ratio of applied nutrients was 15:1 in 2007 and increased to 55:1 in 2008. Weekly applications were determined using current and historical nutrient concentrations, chlorophyll *a* (Chl-*a*) concentrations, standing stock of phytoplankton and zooplankton, volume of the epilimnion, and depth of the photic zone. Applications were lowest in the spring, when natural nutrient concentrations were highest, and highest in the summer, as available nutrients were depleted (see Table S1 for weekly loading).

Table 1. Volume (L) of ammonium nitrate (32–0-0) and ammonium phosphate (10–34-0) and resulting metric tons of elemental nitrogen (N) and phosphorus (P) added to Dworshak Reservoir by year.

Year	32–0-0	10–34-0	N	P
2007	87,083	6295	39.9	2.8
2008	162,144	3149	73.1	1.4
2009	162,114	0	72.7	0
2010	46,844	0	21.0	0

Environmental data

We acquired data for mean daily air temperature (C), mean daily solar radiation (Langleys), and cumulative annual precipitation (cm) by water year (beginning on 1 Oct of the previous calendar year) from an AgriMet weather station on the reservoir at river kilometer 26 (https://www.usbr.gov/pn/agrimet/webarcread.html, accessed Jan 2016). We also acquired data for cumulative annual precipitation (cm) by water year (beginning on 1 Oct of the previous calendar year) from 3 Snow Telemetry (SNOTEL) sites located at Cool Creel, Crater Meadows, and Elk Butte Mean from the Natural Resources Conservation Service (https://www.wcc.nrcs.usda.gov/snow/snotel-precip-data.html accessed March 2017). We acquired data for mean annual inflow (m^3/s) from the Columbia Basin Research DART (data access in real time, http://www.cbr.washington.edu/dart, accessed Jan 2016).

Sample collection

For consistency, we used data collected at 4 stations on the reservoir that were sampled consistently

throughout the study period, designated as RK-2, RK-31, RK-56, and RK-72 (Fig. 1), corresponding with the approximate distance from the southern end of the reservoir along the original river channel. We also limited comparisons to data that were collected during a consistent timeframe. For most metrics, we used data from May through November. For picoplankton, we used May through October data, and for zooplankton, we used April through November. To avoid influence of colloidal particles from spring runoff, we used Secchi data from June through November. Sampling typically occurred twice per month from April through September and monthly thereafter.

We measured water temperature at the surface, 1 m, 2 m, and every even meter thereafter to 60 m or the bottom using a YSI model 58 dissolved oxygen meter. The presence of a thermocline, defined as a change in temperature of 1 C over 1 m in depth (Wetzel 2001), was also noted. We measured water clarity using a 20 cm Secchi disk.

Water samples were collected from the epilimnion and hypolimnion. Epilimnetic samples consisted of a composite of water, typically from 1, 3, 5, and 7 m. Hypolimnetic samples consisted of a single grab from 25 m, or 3 m above the bottom when depth was less than 28 m. For chemical analysis, we shipped samples to the Cooperative Chemical Analysis Laboratory at Oregon State University (2005) or AmTest Labs in Kirkland, Washington (2006–2011), for measurement of total phosphorus (TP) using EPA 365.2, total dissolved phosphorus (TDP) using EPA 365.2, and nitrate plus nitrite nitrogen (N+N) using EPA 300.0. The MDL for TP was 0.01 mg/L in 2005, 0.05 mg/L in 2006, and 0.001 mg/L thereafter. The MDL for N+N was 0.01 mg/L in 2006 and 2007, and 0.001 mg/L in all other years. The MDL for TDP was 0.001 mg/L. For chemical analysis, field duplicates, field blanks, and equipment blanks (rinsates) were collected at a randomly chosen station during each sampling event. In addition, we analyzed epilimnetic samples for Chl-*a*, picoplankton, and phytoplankton.

Picoplankton samples were obtained from the composite of epilimnetic water and preserved with glutaraldehyde. We determined picoplankton density and biovolume by filtering a known quantity of preserved sample onto black 0.2 micron polycarbonate filters and made counts using epifluorescence (MacIsaac and Stockner 1993). We calculated biovolume using biovolume standards for an individual cell for both pico-cyano bacteria and heterotrophic bacteria and multiplying by the previously determined cell density.

Phytoplankton samples were also obtained from the composite of epilimnetic water, but preserved with Lugol's solution. We made quantitative counts of phytoplankton samples using an Utermöhl chamber under 900X magnification (Utermöhl 1958) following the guidelines of McQuaker (1994). The compendia of Prescott (1978), Canter-Lund and Lund (1995), and Wehr and Sheath (2003) were used as taxonomic references. Biovolume calculations were based off of approximate geometric shapes (Hillebrand et al. 1999). Edibility was determined based on cell size, structure and growth form (i.e., colonies or individual cells; Litchman and Klausmeier 2008).

To collect zooplankton we performed vertical tows with a 50 cm diameter, 80 µm mesh, Wisconsin-style net and plankton were preserved in 70% ethanol. From 2005 to 2006, tows were performed from a depth of twice the Secchi reading to the surface. The depth of these tows averaged 9.3 m in 2005 and 7.0 m in 2006. In 2007, tows were performed from 30 m to the surface and therefore not used in our comparisons. From 2008 to 2011, tows were performed from 10 m to the surface and compared directly with the 2005–2006 data. Zooplankton counts were performed following method B-2501–85 from Britton and Greeson (1987).

Kokanee sampling

We used a stratified approach for kokanee surveys, wherein the reservoir was divided into 3 sections. Section 1 included the area from Dworshak Dam to Dent Bridge at RKM 27.0. Section 2 ranged from Dent Bridge to Grandad Bridge at RKM 65.2. Section 3 comprised the reservoir above Grandad Bridge (Fig. 1).

Abundance was estimated from hydroacoustic surveys conducted in July of each year using either a BioSonics DT-E, a Simrad model EK-500, or a Simrad model EK-60 echo sounder and split beam transducer. Transects were performed in a zigzag pattern during hours of darkness. Echograms were analyzed using the current version of either Visual Analyzer from BioSonics or Echoview from Myriax. Echo integration was used to determine fish densities within the kokanee layer (depths kokanee occupy during hours of darkness). The density of age-0 fish was partitioned out by target strength, after which the densities of age-1 and older fish were partitioned using age proportions from

the mid-water trawl catch in that strata of the reservoir. Targets considered too small or too large to be kokanee were partitioned out by target strength using Love's equation (1971). Other fish species, such as rainbow trout, that were within the range of target strengths returned by kokanee were partitioned out based on their numbers relative to kokanee in mid-water trawl catches. Kokanee abundance was estimated by multiplying the mean density (fish/ha) for that strata by the area (ha) with sufficient depth for kokanee to occupy.

Size at age data were obtained from mid-water trawl surveys that were conducted during hours of darkness within one week of the acoustic surveys and within five days of the new moon. Trawls were performed using a 3.0 × 2.2 m fixed frame net with panels of decreasing mesh size ranging from 32 to 13 mm. Anywhere from 4 to 6 transects were performed at randomly chosen points in each reservoir section. Captured fish were measured to the nearest mm in total length (TL) and weighed to the nearest g. Scales were collected from up to 10 fish from each 1 cm size bin per reservoir section from fish that were too large to be age-0. Scales were aged by 2 independent readers (Devries and Frie 1996).

Data analysis

For assessing the effect of environmental variables on trends in limnological data, we calculated mean air temperature (C), mean water temperature at 1 m (C), and solar radiation (Langleys) from April through November of each year. We calculated mean cumulative precipitation for the water year using the 3 SNOTEL sites. We calculated mean annual reservoir inflow for the calendar year. These metrics, along with cumulative precipitation at the AgriMet site, were compared between treated and untreated periods, and visually assessed for explanatory trends.

To calculate descriptive statistics, we used the minimum detection limit (MDL) of a given assay whenever the true value was below the MDL. However, the MDLs for TP and N+N were not the same for all years in our comparison. Since a higher MDL would result in higher calculated mean, the MDL for these analytes was artificially adjusted upward to 0.010 mg/L, the highest MDL for the study period, for all years. That is, all values below 0.010 mg/L were changed to 0.010 mg/L for the purposes of calculating descriptive statistics. Furthermore, medians were calculated in lieu of means due to non-normal distributions. Nutrient concentrations were reported as elemental N or P. Due to the low range of observed values, we chose to report the mean standard deviation of field duplicates with consistent detections (Mueller et al. 2015). For blanks, we reported the percentage of detections (i.e., contamination), the mean concentration for all blanks, assuming zero for non-detections, and the maximum observation.

We estimated individual weights for *Daphnia* sp. using the following formula from 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
We used estimates of lna and b for *D. galeata* from McCauley (1984) where:
$lna = 2.64$
$b = 2.54$

When calculating annual means, months were given equal weight to account for differences in sampling intensity throughout the year. Likewise, when calculating means for the treated and untreated periods, we gave each year equal weight. For non-normal data, we calculated 95% confidence intervals using a bootstrap technique (Efron and Tibshirani 1994, Chernick 1999). For this analysis, we resampled the original data with replacement using R 3.0.1, performing 1000 iterations for each year. We used the percentile method to calculate confidence intervals, where the lower and upper confidence limits were equal to the 2.5th and 97.5th percentiles, respectively (Chernick 1999).

Due to the nature of this study, classical statistical hypothesis testing was deemed inappropriate (Johnson 1999). Following the recommendations of Johnson (1999) we instead estimated the magnitude of the difference between treated and untreated periods and associated confidence intervals for metrics of interest. To calculate confidence intervals, we employed a bootstrapping technique wherein bootstrap means were calculated for the untreated and treated periods for each metric, in the same manner as confidence intervals were obtained for annual means. We then calculated

the percent change for the treated period for each iteration and used the percentile method to obtain confidence limits for the percent change. Confidence intervals that did not include zero were considered statistically significant.

When trawl catches were large enough that not all fish were aged using scales, we developed an age–length key using fish that were aged. For length bins where not all fish were aged, we estimated the number of fish of each age using proportions from the key (Devries and Frie 1996). The mean length and weight of a specific age class was then calculated using the mean length or weight for that bin and the estimated number of fish caught for that bin.

Kokanee biomass was calculated by multiplying the estimated abundance of each age class by the mean weight of that age class to obtain age-specific estimates of biomass. These estimates were summed to produce an estimate of total biomass. Confidence intervals were obtained using the percentile method along with bootstrap means for both age-specific abundance and weight.

Results

Mean air temperature (treated = 13.7 C, untreated = 13.9 C) and solar radiation (treated = 410.9, untreated = 409.4) were both similar for treated and untreated periods (Table 2). Cumulative precipitation was slightly higher for untreated years (AgriMet = 71 cm, SNOTEL = 171 cm) than treated years (AgriMet = 67 cm, SNOTEL = 165 cm). Water temperature at 1 m (Fig. S1) was also slightly higher for untreated years (9.8 C) than treated years (9.3 C). Reservoir inflow was higher for untreated years (162 m^3/s) than for treated years (138 m^3/s), primarily due to high inflow (221 m^3/s) observed in 2011.

Concentrations of TP and TDP for the epilimnion tended to be higher during the earlier years of the study (Fig. 2). Medians for both tended to be higher for untreated years than for treated years. However, untreated years, with the exception of 2011, occurred earlier in the time series. The percentage of non-detections of TP increased in a linear fashion from a low of 0% in 2006 to a high of 87% in 2011 (Fig. 2). The percentage of non-detections of TDP increased in a similar fashion from a low of 0% in 2005 to a high of 58% in 2011. Median TP and TDP concentrations for the hypolimnion exhibited similar trends to those for the epilimnion (Fig. 2). The mean SD of duplicate samples was 0.0019 for TP and 0.0014 for TDP, which were within the acceptable limits set in consultation with the Idaho Department of Environmental Quality (IDEQ). No contamination was detected in blanks for TP. For TDP, contamination was detected in 25% of blanks, nearly half of which occurred in 2009. Blanks had a mean concentration of 0.001 mg/L and a maximum of 0.009 mg/L.

Concentrations of N+N for the epilimnion varied from year to year with no obvious temporal trend (Fig. 2). Median values for the epilimnion were similar for treated and untreated years. The

Table 2. Mean air temperature (C) and solar radiation (Langleys) from April through November, and cumulative precipitation (cm) for the water year (starting on 1 Oct), measured at the Dent Acres AgriMet station (https://www.usbr.gov/pn/agrimet/webarcread.html, accessed Jan 2016). Mean cumulative precipitation (cm) for the water year from SNOTEL sites at Cool Creel, Crater Meadows, and Elk Butte (https://www.wcc.nrcs.usda.gov/snow/snotel-precip-data.html accessed Mar 2017). Mean water temperature (C) at 1 m from April through November measured during limnological surveys. Mean annual reservoir inflow and outflow (m^3/s) acquired from the Columbia Basin Research DART (data access in real time, http://www.cbr.washington.edu/dart, accessed Jan 2016). Shading indicates years of nutrient additions.

Year	Air temp	Solar radiation	AgriMet precip	SNOTEL precip	Water temp	Inflow
2003	14.2	419.6	68	159		154.9
2004	14.1	405.0	75	190	10.5	154.9
2005	13.7	403.0	43	128	9.9	113.9
2006	14.2	421.0	82	174	10.0	166.8
2007	14.3	411.8	60	158	9.5	122.3
2008	13.3	409.7	73	199	9.0	174.3
2009	14.0	424.8	69	160	9.4	144.0
2010	13.4	397.5	65	143	9.6	113.1
2011	13.2	398.5	86	206	9.1	220.8
Mean	13.8	410.1	69	169	9.6	154.9
Untreated	13.9	409.4	71	171	9.8	162.3
Treated	13.7	410.9	67	165	9.3	138.4

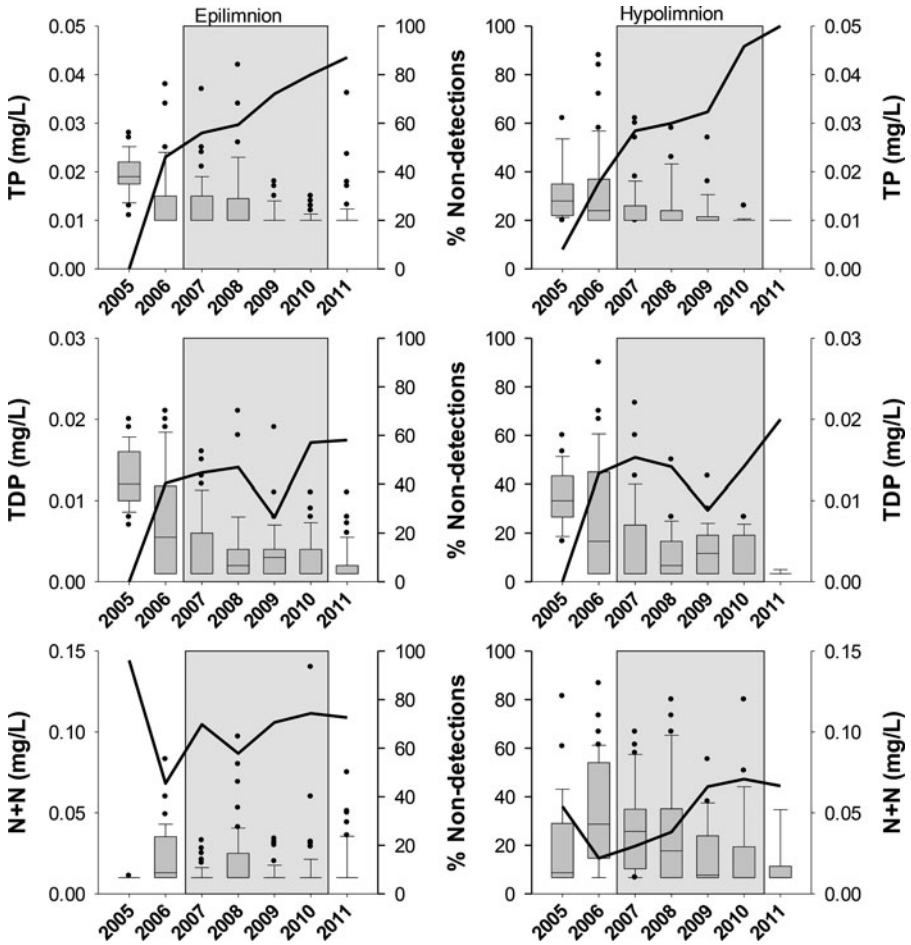

Figure 2. Concentrations of total phosphorus (TP), total dissolved phosphorus (TDP), and nitrite plus nitrate nitrogen (N+N) measured from 2 depths at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. In the box plots, the boxes represent measurements from the 25th to 75th percentiles with the median represented by the black line in the middle. Whiskers represent the 10th and 90th percentiles, and dots represent outliers. The line graph represents the percentage of measurements each year that were below the detection level. Because detection limits for N+N and TP differed between years, values for these nutrients were adjusted to reflect the highest detection limit.

percentage of non-detections ranged from 45% in 2006 to 96% in 2005 with no detectable trend. Conversely, median N+N values for the hypolimnion declined during the study period. N+N concentrations tended to be higher for untreated years than for treated years. However, untreated years, with the exception of 2011, also occurred earlier in the time series. Median N+N levels tended to be higher in the hypolimnion than the epilimnion. The mean SD of duplicate samples was 0.0029 for N+N, which was within the acceptable limits set in consultation with IDEQ. Contamination was detected in 3% of all blanks which had a mean concentration of 0.001 mg/L and a maximum of 0.036 mg/L.

Mean Secchi depths were highest in 2004 and 2005, and were similar from 2006 to 2011, with the lowest observed mean depth occurring in 2011 (Fig. 3). Mean

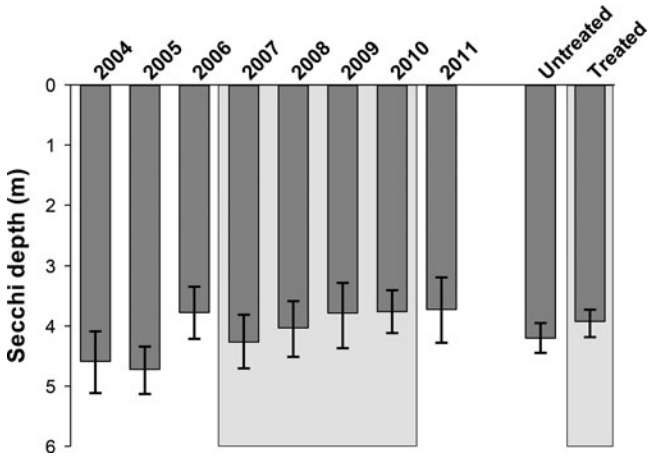

Figure 3. Mean annual Secchi depth measured at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from June through November. Error bars represent 95% confidence intervals obtained by bootstrapping. The period that nutrients were added to the reservoir is indicated by shaded boxes.

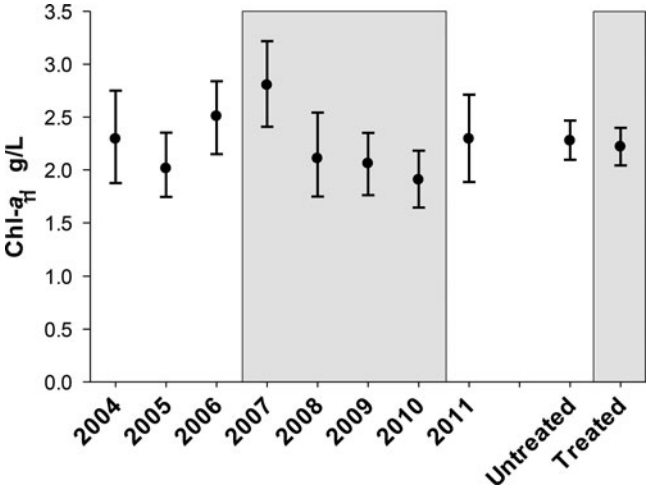

Figure 4. Mean concentration of chlorophyll *a* (Chl-*a*) measured at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. Error bars represent 95% confidence intervals obtained by bootstrapping. The period that nutrients were added to the reservoir is indicated by shaded boxes.

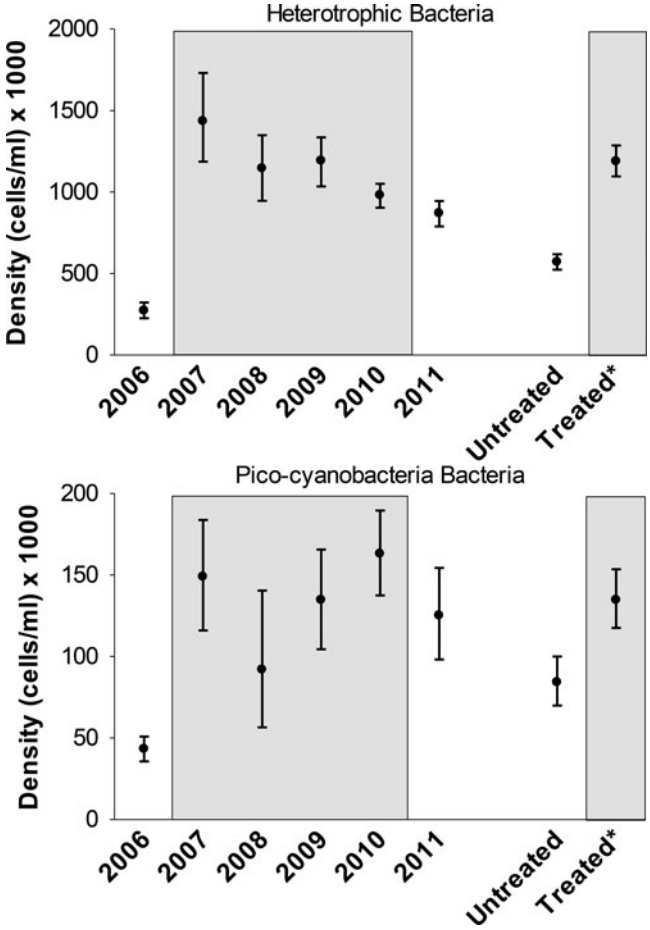

Figure 5. Mean annual density of heterotrophic bacteria and pico-cyanobacteria measured at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. Error bars represent 95% confidence intervals obtained by bootstrapping. The period that nutrients were added to the reservoir is indicated by shaded boxes. An asterisk indicates that confidence intervals for the observed increase or decrease for the treatment period did not include zero.

Secchi depth was 0.3 m lower for the treated period (mean = 3.9 m) than the untreated period (mean = 4.2 m). Confidence intervals for this difference ranged from 0.1 to −0.6 m, indicating a lack of statistical significance. Mean Secchi depths observed during treated years were all within the range observed for untreated years.

Means for Chl-*a* concentrations in the epilimnion exhibited some annual variability, but there was no obvious temporal trend (Fig. 4). The means for the untreated period (mean = 2.22 μg/L) and the treated period (mean = 2.28 μg/L) were nearly identical.

Picoplankton densities were higher for the treated period (Fig. 5). The mean density of heterotrophic bacteria was 109% higher for the treated period (mean = 1,191,000 cells/mL) than the untreated period (mean = 567,000 cells/mL) and the confidence interval ranged from 94 to 125%. The mean density in 2006 was significantly lower than all other years, but densities did not drop significantly in 2011 after nutrient additions were suspended (Fig. 5). The mean density of pico-cyanobacteria was 60% higher for the treated period (mean = 135,000 cells/mL) than the untreated period (mean = 84,000 cells/mL) and the confidence interval ranged from 32 to 85%. The mean density of pico-cyanobacteria in 2006 was also much lower than all other years, whereas the density in 2011 was within the range observed for treated years (Fig. 5).

Mean biovolumes of total phytoplankton in the epilimnion exhibited some annual variability, but there was no obvious temporal trend (Fig. 6). The mean biovolume of total phytoplankton was 19% higher for the treated period (mean = 0.535 mm^3/L) than for the untreated period (mean = 0.449 mm^3/L). However, the confidence interval for this increase (−3 to 45%) included zero, indicating a lack of statistical significance. Mean biovolume of edible phytoplankton exhibited a similar trend to that of total phytoplankton, but the mean was 160% higher for the treated period (mean = 0.27 mm^3/L) than for the untreated period (mean = 0.10 mm^3/L) and the confidence interval for this increase ranged from 99 to 237%, indicating a high degree of statistical significance.

The mean proportion of edible phytoplankton was 94% higher for the treated period (mean = 50%) than for the untreated period (mean = 26%; Fig. 6)

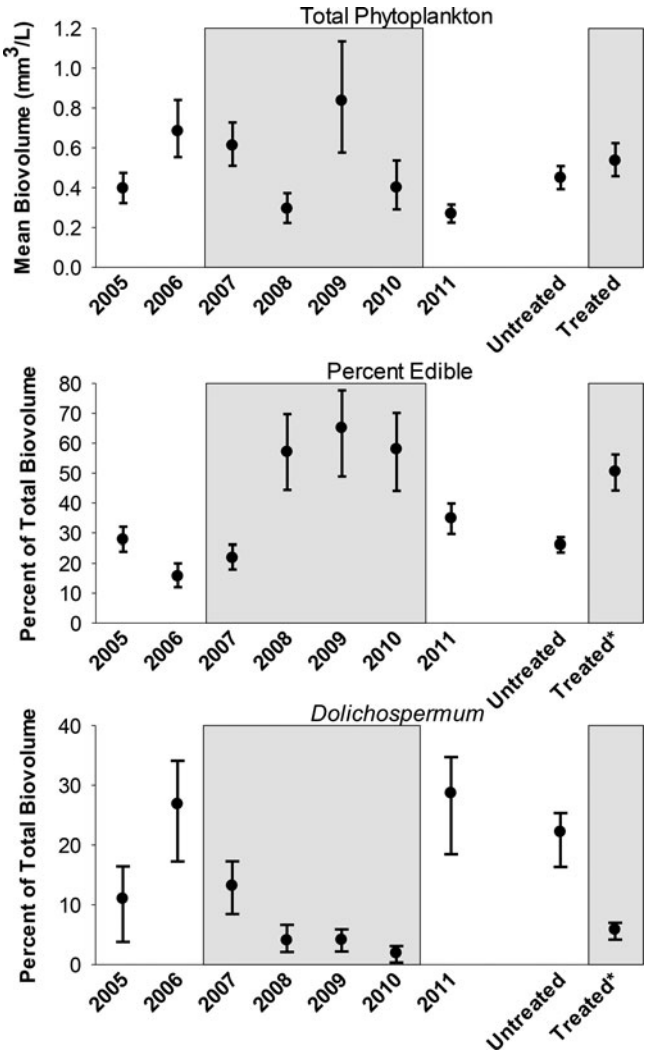

Figure 6. Mean biovolume (mm^3/L) of phytoplankton measured at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from May through November. The proportion of the total biovolume that was composed of edible taxa and the proportion that was *Dolichospermum* sp. are also shown. The treatment period is indicated by shaded boxes. Error bars represent 95% confidence intervals obtained by bootstrapping. An asterisk indicates that confidence intervals for the observed increase or decrease for the treatment period did not include zero.

and the bootstrap confidence interval for this difference ranged from 64 to 127%, indicating statistical significance. Edible phytoplankton was dominated by *Chryptomonas* sp., followed by *Gymnodinium* sp. and *Dinobyron* sp. during untreated years, and by *Chroococcus* sp. and, to a lesser extent, *Komma* sp. and *Chyptomonas* sp. during treated years. Inedible phytoplankton was dominated by *Fragilaria crotenensis* and *Dolichospermum* sp. during both periods.

The proportion of the total phytoplankton biovolume that was composed of *Dolichospermum* sp. was 74% lower for the treated period (mean = 5%) than for the untreated period (mean = 21%; Fig. 6) and the confidence interval for this decrease ranged from 63 to 81%, indicating statistical significance. In general, the proportion of *Dolichospermum* sp. was much lower for treated years, with the exception that 2005 (11%, untreated) and 2007 (13%, treated) were similar (Fig. 6). The proportion of *Dolichospermum* sp. returned to pre-treated levels the first year that N additions were discontinued.

The mean density of total zooplankton was 76% greater for the treated period (mean = 33.2 individuals/L) than the untreated period (mean = 18.9 individuals/L) and confidence intervals for this increase ranged from 53 to 135% (Fig. 7). The mean density of *Daphnia* sp. was 64% higher for the treated period

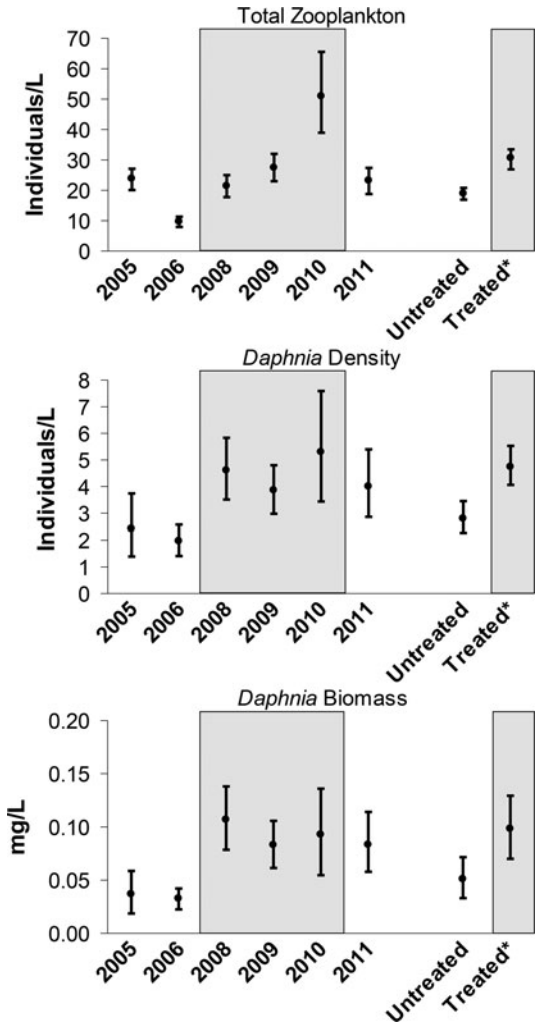

Figure 7. Mean density of zooplankton collected at 4 sampling stations (RK-2, RK-31, RK-56, and RK-72) on Dworshak Reservoir from April through November. Densities are presented for total zooplankton. Both densities and biomass are presented for *Daphnia* sp. Shaded box indicate the treatment period. Error bars represent 95% confidence intervals obtained by bootstrapping. An asterisk indicates that confidence intervals for the observed increase for the treatment period did not include zero.

Table 3. Estimates of age-specific abundance of kokanee in Dworshak Reservoir. Abundance was estimated from acoustic surveys and partitioned into age classes using a combination of target strength and trawl data. A trawl survey was not conducted in 2005.

	Untreated					
Year	Age-0	Age-1	Age-2	Age-3	Total	≥ Age-1
2003	373,000	281,000	356,000	0	1,010,000	638,000
2004	449,000	273,000	47,000	27,000	796,000	347,000
2006	1,997,000	1,550,000	1,082,000	0	4,630,000	2,633,000
2011	494,000	361,000	231,000	1000	1,087,000	592,000
mean	828,000	616,000	429,000	7000	1,881,000	1,052,000
	Treated					
	Age-0	Age-1	Age-2	Age-3	Total	≥ Age-1
2007	532,000	147,000	457,000	0	1,136,000	605,000
2008	1,359,000	233,000	71,000	22,000	1,686,000	326,000
2009	1,022,000	1,109,000	119,000	0	2,250,000	1,228,000
2010	2,331,000	1,177,000	1,030,000	1500	4,539,000	2,209,000
mean	1,311,000	667,000	419,000	6000	2,403,000	1,092,000

(mean = 4.6 individuals/L) than the untreated period (mean = 2.8 individuals/L) and confidence intervals for this increase ranged from 18 to 97% (Fig. 7). Mean lengths of *Daphnia* sp. were >1.00 mm in 2 out of 3 treated years and <1.00 in all untreated years. The mean biomass of *Daphnia* sp. was 85% higher for the treated period (mean = 0.094 mg/L) than the untreated period (mean = 0.051 mg/L) and the confidence interval for this increase ranged from 32 to 131% (Fig. 7).

Kokanee abundance ranged from 796,000 in 2004 to 4.6 million in 2006 (Table 3). Mean abundance was 2.3 million and median abundance was 1.7 million. The abundance of age-1 and older kokanee, which accounted for the bulk of the biomass, ranged from 326,000 in 2008 to 2.6 million in 2006, with a mean of 1.1 million and median of 600,000. Means were similar for the treated (mean = 1.1 million) and untreated (mean = 1.0 million) periods.

The mean TL of every age class of kokanee was slightly higher for the treated period than the untreated period (Table 4). On average, age-1 fish were 4% longer during the treated period and age-2 fish were 6% longer. Mean weights were also greater for the treated period, although the differences were larger. Age-1 fish were 12% heavier during the treated period, while age-2 fish were 21% heavier. Age-3 fish were not encountered every year, or in high numbers for those years when they were.

During the first 3 yr of N addition, estimates of kokanee biomass fell within the range estimated for untreated years. However, in the fourth treatment year,

Table 4. The mean age-specific total length (TL) in mm and mean body weight in g for age-1 and age-2 kokanee captured during trawl surveys on Dworshak Reservoir during July. S tandard errors are shown in parentheses. A trawl survey was not conducted in 2005.

	Untreated			
	Mean TL (mm)		Mean weight (g)	
Year	Age-1	Age-2	Age-1	Age-2
2003	204 (2.4)	262 (1.8)	71 (3.0)	159 (4.3)
2004	202 (1.6)	295 (2.7)	74 (1.8)	231 (6.5)
2006	145 (2.0)	196 (2.1)	24 (1.0)	60 (2.4)
2011	170 (1.1)	220 (1.2)	46 (1.0)	98 (1.8)
mean	180 (1.6)	243 (1.5)	54 (1.5)	137 (5.3)
	Treated			
	Mean TL (mm)		Mean weight (g)	
	Age-1	Age-2	Age-1	Age-2
2007	198 (2.5)	241 (1.2)	67 (2.3)	125 (2.0)
2008	209 (2.2)	303 (1.4)	85 (3.3)	262 (4.7)
2009	169 (0.7)	272 (2.4)	43 (0.6)	178 (5.4)
2010	172 (0.4)	219 (0.9)	45 (0.3)	94 (1.4)
mean	187 (0.7)	259 (1.7)	60 (0.6)	165 (3.1)

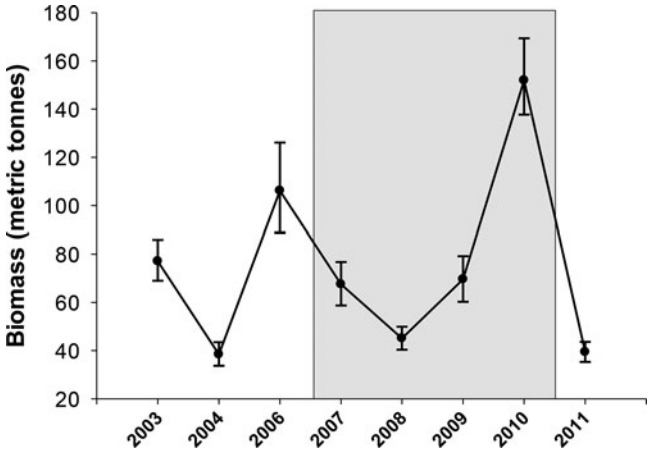

Figure 8. Estimated biomass of kokanee in Dworshak Reservoir derived from July acoustic and trawl surveys. Error bars represent 95% confidence intervals obtained by bootstrapping. The shaded box indicates the period when nutrients were added to the reservoir. A trawl survey was not conducted in 2005, therefore a biomass estimate is not available.

the biomass estimate was 43% higher than the highest biomass estimate for an untreated year and 2.3 times the mean for the untreated period (Fig. 8).

Discussion

Water quality

While the goal of this project is to restore lost productivity to the reservoir, it is imperative to do so without degrading overall water quality. A legal Consent Order for the project, provided by IDEQ, stipulated that the median Secchi depth must not fall below 3.0 m. Although the mean Secchi depth was greater for the untreated period, the difference was small and cannot be confirmed with a great deal of statistical certainty. Furthermore, means for treated years were within the range observed for untreated years, and the only year in which the median Secchi depth was below the minimum stipulated by IDEQ was a year in which no N was applied to the reservoir (2011). Therefore, nutrient additions may be resulting in reduced water clarity, but not to the extent that it has been degraded for recreational purposes (<3.0 m) as defined by IDEQ.

A common concern in lakes and reservoirs, particularly those with heavy recreational use, is the prevalence of toxin-forming cyanobacteria (Downing et al. 2001, Paerl et al. 2001, Harris et al. 2014). During the summer months, when recreational use is at its peak, Dworshak Reservoir is typically dominated by *Dolichospermum* sp., a potentially toxin-forming cyanobacteria. However, the reduction in *Dolichospermum* sp. we observed concurrent with N additions, followed by its immediate rebound when N additions were suspended, was compelling. While some researchers have found absolute concentrations of N and P to be better predictors of cyanobacteria dominance than N limitation alone (Downing et al. 2001, Paerl and Scott 2011), others have found evidence that N:P ratio is an important predictor of cyanobacterial dominance (Smith 1983, Graham et al. 2004, Harris et al. 2014). This may be particularly true in the case of N-fixing cyanobacteria. For example, Stockner and Shortreed (1988) found that densities of *Dolichospermum* sp. were greatly reduced by increasing N:P ratios. These observations support the hypothesis that nutrient additions resulted in reduced prevalence of this potentially toxin-forming cyanobacteria, culminating in improved water quality and safety for recreational users.

For this project, we added known quantities of ammonium nitrate to the reservoir without observable changes in several metrics commonly used to monitor water quality. We did not observe increases in nutrient concentrations, Secchi depth, or Chl-*a* concentration, all of which are commonly used by management agencies to monitor water quality (NDEP 2008, USEPA 2011, IEPA 2015). From our study, it cannot be determined how much ammonium nitrate could be added before a change could be detected in these metrics. However, there were observable changes at many of the trophic levels we monitored, such as increased picoplankton, shifts in the phytoplankton community, and increased zooplankton. Monitoring multiple trophic levels may provide clues to detect changes in nutrient loading before water quality has been impaired.

Trophic responses

Nutrient addition appears to be having favorable effects at every trophic level in Dworshak Reservoir. While we did not observe increases in the standing stock of phytoplankton, such results are neither desirable nor a prerequisite for success. We did, however, observe an increase in the density of zooplankton, which may have been the result of shifts in the phytoplankton community (i.e., a higher food quality can result in an increase

in secondary production; Cole et al. 2002). We further observed increases in multi-year means for kokanee size and biomass concurrent with these increases, which may have resulted from increased prey availability. While these results are consistent with other nutrient addition projects in regional lakes and reservoirs, Dworshak may be unique in that P additions were discontinued after the second year, and only N was added thereafter. In contrast, most other nutrient addition projects involve the addition of both N and P (Stockner and MacIsaac 1996, Hyatt et al. 2004).

Aside from nutrient additions, a variety of environmental factors also had the potential to influence trends in the metrics we observed. Multi-year means for these variables were also similar between periods, with the exception that 2011, an untreated year, experienced unusually high inflow due to a heavy snowpack. Therefore, while our observations from this study are promising, additional years will be needed to fully separate the effects of nutrient additions from environmental variation.

We did not observe an increase in available nutrients, particularly N, in years that nutrients were applied. Trends in nutrient concentrations can be difficult to elucidate from our data due to the high number of non-detections. However, if nutrient additions had resulted in a significant increase in concentrations, we would expect the number of non-detections to decrease. Assuming uniform mixing throughout the epilimnion, theoretical concentrations from weekly treatments ranged from 2 to 20 μg/L. Non-uniform mixing might have resulted in higher concentrations at sampling stations due to their close proximity to the applications. Brandt (2013) found that N+N levels were elevated immediately after applications, but could no longer be detected after 8 h. While we cannot confirm the fate of the supplemented N, this is consistent with the rapid uptake of added N by the plankton community and has been observed in other systems (Suttle et al. 1991, Stockner and MacIsaac 1996).

Chlorophyll *a* has often been used to assess the trophic state of lakes and reservoirs (Carlson 1977). In Dworshak Reservoir, mean Chl-*a* did not increase in response to N addition. However, Chl-*a* is an instantaneous measure of standing stock and by itself yields no information on rates of production or grazing. It follows that Chl-*a* is not always correlated with primary production (Brylinsky and Mann 1973). Furthermore, the relationship between Chl-*a* and phytoplankton biovolume is complex and may be altered by shifts in species composition (Felip and Catalan 2000). Likewise, Mazumber and Havens (1998) found that the presence of large *Daphnia* sp. could alter the relationship between nutrient concentrations and Chl-*a* yield. If the composition of the phytoplankton community in Dworshak Reservoir has shifted to more edible species, those species may be grazed off by zooplankton at a higher rate (Lynch and Shapiro 1981), thus masking effects of increased productivity if Chl-*a* is used as the primary metric.

Picoplankton are known to play an important role in aquatic food webs, particularly oligotrophic lakes or reservoirs, where they can be responsible for up to 90% of primary production (Stockner 1988). Stockner and Brandt (2006) reported a predominance of picoplankton in the plankton communities of Dworshak Reservoir during the early spring pre-treatment. Therefore, the picoplankton response to N addition was of some interest. Dworshak Reservoir exhibited an initial picoplankton response similar to that seen during the early years of nutrient additions to several British Columbia lakes and reservoirs (Stockner and Shortreed 1994, Stockner and MacIsaac 1996, Pieters et al. 2003). However, picoplankton densities did not return to previous levels in 2011 when nutrient applications were suspended. The reason for this is unclear. Either 2006 densities were much lower than average, meaning the actual response at this trophic level was not as strong as what we observed, or productivity did not drop as quickly as we thought it would. Other environmental variables, such as high inflow observed that spring, may account for this trend, but we did not have a sufficient number of years to draw firm conclusions.

The greatest observed differences in the phytoplankton community were shifts in the community structure. As with Chl-*a*, the weak response in standing stock of total phytoplankton is inadequate for assessing potential changes, or lack thereof, in reservoir productivity. The relationship between primary productivity and algal standing stock is not always straightforward (Oglesby 1977). We observed minimal increases in total phytoplankton at best, and standing stock appeared to be higher in years of higher mean solar radiation (e.g., 2009). On the other hand, the standing stock of edible phytoplankton and the percentage of edible phytoplankton were greater for treated

years. If productivity increased in edible species, it could have been masked by increased grazing from zooplankton (Lynch and Shapiro 1981). Supplemented N can be used by edible and inedible species alike, but some inedible species (i.e., *Dolichospermum* sp.) can fix N and have a competitive advantage when the available N is nearly exhausted (Barica et al. 1980, Stockner and Shortreed 1988, Schindler et al. 2008). These taxa tended to dominate the phytoplankton community of Dworshak Reservoir during the late summer and fall in untreated years. Although *Dolichospermum* sp. were among the more prevalent inedible taxa during the course of the study, they were less prevalent during treated years, which likely contributed to the increased proportion of edible species. Moreover, when N additions were halted, the proportion of *Dolichospermum* sp. immediately increased concurrent with a decline in overall edibility of the phytoplankton community. These observations support the hypothesis that nutrient additions led to shifts in the phytoplankton community structure.

We also observed an increase in available prey for kokanee during treated years. Kokanee have been found to prey preferentially on *Daphnia* sp., both in Dworshak Reservoir (Stark and Stockner 2006) and other systems (Johnson and Martinez 2012). The biomass of *Daphnia* sp. we observed during treated years was nearly double what we observed during untreated years, which was similar to the response for British Columbia lakes reported by Stockner and MacIsaac (1996). Cole et al. (2002) found that food quality was more important than food quantity or temperature for production of *Daphnia rosea*. This suggests that observed shifts in the structure of the phytoplankton community may be more important in determining increases in *Daphnia* sp. than the lack of observed increases in standing stock.

On average, kokanee tended to be larger during the treated period. However, Reiman and Meyers (1992) found kokanee growth was density dependent. Therefore, fish densities or abundance need to be taken into account when assessing the effects of nutrient additions on growth. Although age-2 kokanee were small in 2010, the density was quite high. When comparing the size of these fish to those in 2006, the only untreated year with similar abundance, age-2 kokanee were more than 50% heavier on average in 2010. While additional years of data will be needed to determine the extent to which nutrient addition can influence kokanee growth, this observation suggests there is potential for significant gains.

As a result of increased weight at a given level of abundance, we observed a record biomass of kokanee during the fourth year of N addition. However, it remains uncertain if this level of biomass was an anomaly, or if it will be sustained through continued nutrient addition. In Kootenay Lake, British Columbia, kokanee biomass averaged 5.3 kg/ha over 6 yr prior to nutrient addition. During the first year of treatment in Kootenay Lake, biomass did not increase above what had been previously documented, but did increase to about 2.5 times the pre-treatment mean by the third year. From 1992 through 2012, the after-treatment biomass has averaged 13.8 kg/ha, or 2.6 times the pre-treatment mean. Biomass in Kootenay Lake did not peak until the seventh year of treatment, at almost 5 times the pre-treatment mean (Schindler et al. 2014). Observations for Dworshak Reservoir are thus far encouraging and consistent with those from Kootenay Lake, although the ultimate magnitude of the increase in biomass is yet to be determined.

Another uncertainty unique to Dworshak is how kokanee entrainment losses will affect biomass trends under nutrient addition. 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). Entrainment is believed to be a significant source of this mortality, as the number of dead and dying kokanee in the river below the dam prompted the opening of a salvage fishery. Therefore, the biomass would likely have dropped off substantially in 2011 even if nutrient addition were continued. Regular entrainment losses of this magnitude could limit long-term gains in kokanee biomass, despite anticipated improvements due to nutrient addition.

While nutrient additions have been used successfully to mitigate for oligotrophication in lakes of Alaska (Hyatt et al. 2004), British Columbia (Stockner and MacIsaac 1996, Ashley et al. 1999, Pieters et al. 2003), and Scandinavia (Milbrink et al. 2008), this tool may not be ubiquitously appropriate or effective. When used as a means to restore fisheries, it is assumed that fish production is limited by forage, and that forage is limited by nutrients. However, Peltz and Koenings (1989) found that growth of juvenile sockeye salmon in Hugh Smith Lake, Alaska, did not improve with nutrient additions, despite increases to phytoplankton

and zooplankton, because fish growth was limited by temperature rather than forage. On the other hand, primary production in many oligotrophic lakes may be limited by light penetration rather than nutrient loading (Karlsson et al. 2009). Reservoirs with low retention times, particularly for the epilimnion, may also be poor candidates for nutrient additions as added nutrients may not be sufficiently retained. Finally, it may not be desirable to increase productivity in lakes that are already mesotrophic to eutrophic (Stockner et al. 2000). Therefore, candidate lakes should be carefully evaluated before nutrient addition is considered as a restoration tool.

Conclusions

Through the first 4 yr of this study, nutrient addition has shown promise as a management tool for enhancing fish stocks in Dworshak Reservoir. Standing stock of phytoplankton did not increase, but instead appears to have shifted to edible species, and away from inedible, and potentially harmful, cyanobacteria (e.g., *Dolichospermum* sp.). *Daphnia* sp., an important prey for kokanee, has increased, along with both kokanee size and biomass. While a single year of post-treatment monitoring may not be sufficient to confirm these results, continued nutrient addition has shown potential to increase the productivity of fish stocks without adversely affecting water quality.

While additional years of study will be conducted to confirm these results, the unintended suspension of N addition in 2011 strengthens these conclusions, as a clear shift to higher abundance of cyanobacteria was observed. As with all observational studies, assigning causality is problematic (Oehlert 2000). In studies such as this, comparisons with a reference lake can be useful to separate annual variation due to other factors (e.g., climate) from treatment effects. Unfortunately, a suitable reference was not available. However, inference can be strengthened by combining evidence from observational studies and controlled experiments that elucidate mechanistic interactions (Clements et al. 2002). Therefore, we recommend that in future years this study be paired with a mesocosm experiment, including replicated addition of various N concentrations and controls. Such a study would provide direct evidence of the effect of N addition on the reservoir food web, including changes to primary production, phytoplankton composition, and zooplankton standing stock. Comparing responses to different levels of N addition could also provide useful information to refine the N additions to Dworshak Reservoir.

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