Evaluation of Lake Fertilization as a Tool to Assist in the Recovery of the Snake River Sockeye Salmon (Oncorhynchus Nerka)

Howard P. Gross

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EVALUATION OF LAKE FERTILIZATION AS A TOOL TO ASSIST IN THE RECOVERY OF THE SNAKE RIVER SOCKEYE SALMON (*ONCORTHYNCHUS NERKA*)

by

Howard P. Gross

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Watershed Science

UTAH STATE UNIVERSITY
Logan, Utah

1995
ABSTRACT

Evaluation of Lake Fertilization as a Tool to Assist in the Recovery of the Snake River Sockeye Salmon (*Oncorhynchus nerka*)

by

Howard P. Gross, Master of Science
Utah State University, 1995

Major Professor: Wayne A. Wurtsbaugh
Program: Watershed Science

I analyzed lake fertilization (with nitrogen and phosphorus) as a tool to assist in the recovery of the Snake River sockeye salmon (*Oncorhynchus nerka*) in the oligotrophic Sawtooth Valley Lakes in southcentral Idaho. These analyses involved monitoring, manipulating, and modelling several aspects of the lakes' primary producer, nutrient, and light parameters.

In Pettit Lake, I evaluated the effects of metalimnetic and epilimnetic fertilization in 330-m³ mesocosms. The metalimnetic treatment was equal to or more effective than the epilimnetic treatment in increasing chlorophyll a, phytoplankton biovolume, and primary productivity, yet caused smaller changes in periphyton growth and water clarity. Thus, metalimnetic fertilization may provide a tool for increasing lake productivity while minimally
impacting water clarity.

The Sawtooth Valley Lakes had deep chlorophyll maxima (DCM) with mean chlorophyll $a$ peaks 240-1000% of mean epilimnetic concentrations. The DCM existed at low light levels and accounted for 36-72% of the lakes' primary production. Epilimnetic fertilization of 330-m$^3$ mesocosms in Redfish Lake increased levels of primary productivity and chlorophyll $a$, but decreased Secchi depths and light available in the meta- and hypolimnion. I modelled the effects of increased chlorophyll (resulting from epilimnetic fertilization) and decreased light penetration on vertical primary productivity profiles. The simulations showed a large increase in epilimnetic primary productivity due to fertilization, and only a slight decrease in production in the deeper strata due to self-shading.

I also modelled the dependence of Redfish Lake's production on nutrients from the watershed, from lake fertilization, and from marine-derived nutrients from salmon. The model utilized our water budget and nutrient loading measurements. The model and empirical evidence indicated that even before hydropower dams were present in the migration corridor, marine-derived nutrients were not of major importance to lake production, contributing only ~3% of the lake's annual phosphorus load. This contribution was partially offset by the lake's quick flushing rate (3 yr) and phosphorus export by smolts. The model predicted annual adult salmon returns to be 3,800 under pre-dam conditions, 370 under modern conditions, 750 when doubling watershed nutrient loading (simulating lake fertilization), and 780 when doubling migration survival.
ACKNOWLEDGMENTS

I would like to thank my major professor, Wayne A. Wurtsbaugh, for his guidance, encouragement, and hospitality during my years spent at Utah State University. I will always attempt to emulate his work ethic, respectfulness, and good nature. I would also like to thank my committee members, Chris Luecke and Jack Schmidt, for their guidance and support.

I would like to acknowledge several talented individuals at Utah State University for their assistance: Phaedra Budy, Thorsten Blenckner, and Geoff Steinhart foremost, and also Fredrik Norrsell, Darek Staab, Nick Bouwes, Oddette Brandt, John Ossowski, Jim Ruzycki, Rick Orme, and Clyde Lay (all associated with the Limnology Laboratory), and Susan Durham and Nancy Roberts (for statistical assistance). For funding, I would like to thank Utah State University (through a Vice-Presidential Fellowship) and the Shoshone-Bannock Indian Tribes (from the Bonneville Power Administration). In addition, I would also like to thank Mark Moulton, Bob Griswold, Debbie Hunter, Mark Palmer, Patrick Neale, Michael Kimball, Scott Spaulding, Charles Ray, and the employees of the Stanley Ranger Station in the Sawtooth National Recreation Area.

I give a special thanks to my wife, Heidi McIntosh, and my family for making my life a happy and fortunate one.

Howard P. Gross
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CHAPTER 1
INTRODUCTION

In the Sawtooth Valley Lakes of Idaho, anadromous runs of the Snake River sockeye salmon (*Oncorhynchus nerka*) have declined drastically (>99%) since the early 1900's, largely due to increased mortality caused by eight hydroelectric dams on the lower Snake and Columbia Rivers. Because of this decline, the Shoshone-Bannock Indian Tribes successfully filed a petition in 1991 to have the Snake River sockeye salmon protected under the Endangered Species Act. In 1991, Utah State University investigators began to collaborate with a variety of agencies to conduct limnological research specifically pertaining to *O. nerka* in the Sawtooth Valley Lakes. These lakes--Redfish, Alturas, Pettit, Stanley, and Yellow Belly Lakes--are historical rearing habitat for the sockeye salmon. Starting in 1992, I began conducting my graduate research as part of this project, focusing on the linkages between watersheds, nutrients, and algal production in the lakes. Additional work on the zooplankton-fish interactions and winter ecology in the lakes is being conducted, respectively, by Phaedra Budy and Geoff Steinhart, Utah State graduate students in the Department of Fisheries and Wildlife.

The research presented here evaluates lake fertilization as a tool to assist in the recovery of the Snake River sockeye salmon. Because marine-derived nutrients transported by adult salmon can contribute an important portion of a lake's nutrient load (Juday et al. 1932; Krohkin 1967; Stockner 1987; Koenings and Burkett 1987), we speculated that the Sawtooth Valley Lakes had become less productive due to the decline in sockeye escapement. If so, could nutrient additions to stimulate plankton production and,
subsequently, fish growth and survival compensate for the nutrient "deficit" caused by loss of salmon? Regardless of whether the nutrient deficit had a negligible effect on lake productivity, would lake fertilization be a useful tool for increasing the fitness of juvenile sockeye stocked from a broodstock program into one or more of the Sawtooth Valley Lakes? What effects would lake fertilization have on overall lake productivity, water clarity, and the phytoplankton community present in these lakes?

These questions are addressed in three chapters of this thesis. Chapter 2, entitled "The Role of Anadromous Sockeye Salmon (Oncorhynchus nerka) in the Nutrient Loading and Productivity of the Redfish Lake, Idaho," presents water budgets and total nitrogen and phosphorus loading data for Redfish Lake. It also presents a simulation model developed to predict a lake's productivity as a function of nutrient loading from different sources (marine-derived nutrients from adult sockeye, lake fertilization, watershed loading). The model's utility is to help conceptualize the interplay between nutrient loading and sockeye population dynamics, and to make general predictions on how management scenarios might affect sockeye recovery.

Chapter 3 is entitled "Fertilization of an Oligotrophic Lake with a Deep Chlorophyll Maximum: Predicting the Effect on Primary Productivity." This chapter addresses the vertical distribution of primary trophic parameters in the Sawtooth Valley Lakes, and how diminished light penetration resulting from epilimnetic nutrient additions would affect some of these parameters. We used a lake sampling program in all five lakes, as well as large mesocosm (330 m³) experiments in Redfish Lake, to gather the data necessary to model some of the complex effects of lake fertilization.
Chapter 4, entitled "Comparison of Epilimnetic and Metalimnetic Fertilizations on the Phytoplankton and Water Clarity of an Oligotrophic Lake," documents experimental nutrient additions performed in large (330 m³) mesocosms in Pettit Lake. It shows how metalimnetic versus epilimnetic nutrient additions affect periphyton growth, water clarity, chlorophyll a, and phytoplankton biovolume, community structure, and primary productivity. Water clarity and periphyton growth are considered from the perspective of preserving the aesthetics of the Sawtooth Valley Lakes, which are highly used and prized recreational resources.

The result of much of the work completed on the Sawtooth Valley Lakes has been published in two annual reports (Spaulding et al. 1993; Teuscher et al. 1994). All three chapters will be submitted for publication to the Canadian Journal of Fisheries and Aquatic Sciences after final thesis approval. It is my hope that this work contributes to a better understanding of the ecology of the Sawtooth Valley Lakes and their watersheds, specifically the nutrient-primary production dynamics, including the role sockeye salmon. I also hope that this work contributes sound scientific information to be used in the recovery of sizeable, self-sustaining runs of Snake River sockeye salmon and the long-term health of the Sawtooth Valley Lakes.

References


CHAPTER 2
THE ROLE OF ANADROMOUS SOCKEYE SALMON
(ONCORHYNCHUS NERKA) IN THE NUTRIENT
LOADING AND PRODUCTIVITY OF
REDFISH LAKE, IDAHO

Abstract

We constructed a simulation model for Redfish Lake, Idaho, utilizing water budget and nutrient loading measurements, to predict the dependence of lake production on nutrients from the watershed, airshed, lake fertilization, and marine-derived nutrients from salmon. We also used the model to simulate different management scenarios to help restore the endangered Snake River sockeye salmon (Oncorhynchus nerka). The model and other empirical evidence indicate that even before hydropower dams were present in the migration corridor, marine-derived nutrients were not of major importance to lake production, contributing only ~3% of the lake's annual phosphorus load. This contribution was partially offset by the lake's quick flushing rate (3 yr) and phosphorus export by smolts. The model predicted annual adult salmon returns to be 3,800 under pre-dam conditions, 370 under modern conditions, 780 when doubling watershed nutrient loading (simulating lake fertilization), and 750 when doubling migration survival. Although fertilization should stimulate salmon production, this effect was transitory: The model predicted that 8 yr after the end of a 3-yr fertilization period, adult returns were only 5% of baseline conditions. Our

\[\text{Coauthored by Howard P. Gross, Wayne A. Wurtsbaugh, and Chris Luecke.}\]
analysis suggests that to restore self-sustaining anadromous *O. nerka* populations to Redfish Lake, increased smolt-to-adult survival must be achieved.

Introduction

Direct relationships between nutrient loading and lake primary production have been well-studied (Dillon and Rigler 1974, 1975; Vollenweider 1976; Schindler 1977, 1978; Schindler et al. 1978; Smith 1982). Nutrient loading and primary production, to a great extent, also control fish production in lakes (Carline 1986; Downing et al. 1990; Plante and Downing 1993). Thus, control of nutrient loading can be used to reduce eutrophication (Schindler 1974; Schindler et al. 1980), or conversely, to enhance fish production (Nelson 1958; Bardach et al. 1972; Stockner and Shortreed 1985; Kyle et al. 1988).

A substantial portion of nitrogen and phosphorus loading in some lakes can be of marine origin, transported by anadromous salmon (Juday et al. 1932; Krohkin 1967; Mathisen et al. 1988; Kline et al. 1993). In five lakes reviewed by Stockner (1987), sockeye salmon (*Oncorhynchus nerka*) contributed 3-58% of the phosphorus loading. For a single lake, cyclic variations in salmon returns can have a large effect on yearly contribution of marine-derived nutrients (Koenings and Burkett 1987; Stockner 1987). Declining sockeye salmon stocks can lead to a decrease in nutrient loading and lake productivity (Koenings and Burkett 1987). For example, when fishing pressure reduced sockeye runs by 97% in Lake Dalnee (Kamchatka Peninsula, Russia) over a 40-yr period, phosphate levels fell by 75%, primary production by 40%, and smolt output by 86% (Krogius 1979, as cited by Thorpe 1986).
Our study evaluated whether or not a decline of a sockeye salmon run has affected the nutrient loading and productivity of a mountain lake in Idaho, as well as the usefulness of lake fertilization as a tool in the recovery of the run. Numbers of Snake River sockeye salmon returning to their rearing lakes in central Idaho (the Sawtooth Valley Lakes) have declined by >99% since the early 1900's, largely due to the construction of eight dams in their migration corridor (Bevan et al. 1994). Only a total of 16 adults returned between 1989 and 1994. In 1991, the species was listed as endangered under the U.S. Endangered Species Act. In concert with efforts to save this stock, our study addressed the following questions. Had Redfish Lake become less productive as a result of declining sockeye salmon runs (had a nutrient "deficit" developed)? Could short-term nutrient additions trigger enough plankton and subsequent fish production to boost adult returns? Would ensuing increases in adult returns overcome this nutrient deficit and maintain higher production without continuing fertilization? How would improving smolt-to-adult survival compare with lake fertilization as a means for increasing salmon runs?

To meet our objectives, we focused on Redfish Lake, the only lake in the Sawtooth Valley to which sockeye salmon still return. First, we measured the lake's water budget and nutrient loading. Second, we constructed a simulation model that allowed us to predict how the lake's productivity depended on different nutrient sources (marine-derived nutrients from adult sockeye, lake fertilization, and watershed loading). The model conceptualizes the interplay between nutrient loading and sockeye population dynamics, and allows us to make general predictions on how nutrient loading and management scenarios affect populations of sockeye salmon.
Study Area

The Sawtooth Valley Lakes are located in the Sawtooth Valley National Recreation Area in central Idaho (lat. 44°, long. 115°) at elevations of 1996-2157 m (Fig. 2-1). Their pristine watersheds drain the east side of the granitic Sawtooth Mountains (elevations up to 3277 m). The drainage basins were heavily glaciated during the Pleistocene when glaciers advanced just beyond the mouths of the mountain valleys, depositing large moraines behind which the lakes are impounded (Killsgaard et al. 1970; Alt and Hyndman 1989). The lakes are oligotrophic and dimictic, and normally ice-covered from December until May.

Redfish Lake, the focus of this paper, is 6 km long and 1 km wide. It has two perennial inflows, Redfish Lake Creek (a fourth-order stream) and Fishhook Creek (third-order). Mean summer epilimnetic chlorophyll a and nutrient concentrations are low: 0.60 \( \mu g/L \) for chlorophyll a, 65 \( \mu g/L \) for total nitrogen (TN), and 6.8 \( \mu g/L \) for total phosphorus (TP) (Steinhart et al. 1994). Both N and P co-limit algal production (Gross et al. 1993).

Physical characteristics of the lake are:

<table>
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<th>Characteristic</th>
<th>Value</th>
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<tr>
<td>Surface area</td>
<td>6.15 km²</td>
</tr>
<tr>
<td>Lake volume</td>
<td>270 x 10⁶ m³</td>
</tr>
<tr>
<td>Mean depth</td>
<td>44 m</td>
</tr>
<tr>
<td>Maximum depth</td>
<td>91 m</td>
</tr>
<tr>
<td>Drainage area</td>
<td>108 km²</td>
</tr>
<tr>
<td>Mean summer Secchi depth</td>
<td>11.9 m</td>
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Macrophytes are sparse in the lake. The dominant crustacean zooplankton are *Holopedium*
gibberum, Bosmina longirostris, and Daphnia rosea (Budy et al. 1995).

Because Redfish Lake is highly prized for recreation and aesthetics, managers are concerned that lake fertilization might impact water clarity. Campgrounds, a hotel, and marina are present at the lake, but nutrient input from these is limited because sewage is primarily removed by pumping. The lake is accessible by a hard-surface road and has a boat ramp.

The pelagic fish community is dominated by kokanee, the nonanadromous form of *O. nerka*. Juvenile Snake River sockeye salmon from a hatchery broodstock program were stocked into the lake in 1994. Continued stocking through 2003 is envisioned to increase egg-to-smolt survival of these endangered fish and eventually reestablish a self-sustaining population (Bevan et al. 1994).

Four other Sawtooth Valley Lakes included in this study—Alturas, Pettit, Stanley, and Yellow Belly—range in surface area from 0.73 to 3.38 km², mean depth from 14 to 32 m, and mean summer epilimnetic chlorophyll *a* from 0.5 to 1.1 µg/L. Additional limnological characteristics of the lakes are given in Budy et al. (1995) and Steinhart et al. (1994).

Methods

Lake Water Budgets

We measured water budgets of Redfish Lake for two years: 1992, which was a sixth consecutive drought year in the region, and 1993, a normal water year. A lake's annual water budget was expressed as (Likens 1985):
\[ I + P + R + G = O + E + S_p + \delta S_1 \]

where  
I = stream inflows,  
P = precipitation on lake surface,  
R = non-channelized runoff,  
G = groundwater inflows,  
O = stream outflows,  
E = evaporation,  
\( S_p \) = seepage, and  
\( \delta S_1 \) = annual change in lake storage.

G and \( S_p \) were not quantified in this investigation; \( \delta S_1 \) was negligible.

**Stream Inflows and Outflows**

Discharges were measured using a Marsh-McBirney Flo-Mate 2000™ electromagnetic flow meter. Measurements were taken at 15-20 points along a stream cross section. If stream depth was \( \leq 0.75 \) m, flow was measured at six-tenths of depth; if stream depth was \( > 0.75 \) m, flow was averaged between measurements taken at two- and eight-tenths of depth (Rantz 1982). Staff gauges installed on the lake's two inflows (Redfish Lake Creek and Fishhook Creek) and its outflow allowed us to develop a stage-discharge relationship for each stream, and to estimate discharge on several dates when discharges were not measured.

We directly measured flows or gauge readings to estimate discharge for each stream at least weekly from May through September 1992, and from late-April through September 1993. Several additional measurements were also made during baseflow conditions on the
other months in both years. Additionally, one to three gauge readings were taken daily on Fishhook Creek in 1992 and 1993 during the rising limb, peak, and falling limb of the local hydrograph each year. Additional discharges were estimated for Redfish Lake Creek from a log-log linear regression of discharges ($r^2=0.97$) with the more accessible and intensively measured Fishhook Creek. A regression to United States Geological Survey streamflow data (USGS, Boise, ID) for the Salmon River at Salmon, ID (located 230 km downstream from Redfish Lake) was used to augment the hydrographs during winter baseflow periods.

**Precipitation**

Because Redfish Lake is ice-covered several months each year, precipitation input was partitioned into precipitation received when the lake was open, $P_o$, and during the ice-cover season, $P_i$. $P_o$ was an immediate input into the lake and was derived from recordings made at two weather stations. One station, 8.3 km from the lake (Fig.1-1), is part of the Idaho State Climatologist's network (Station ID 108676, M. Molnau, State Climatologist, University of Idaho, Moscow, ID 83843). The second gauge was 3.4 km from the lake. Precipitation at these two sites differed by only 6%.

$P_i$ accumulates on the frozen lake; some of it sublimates or evaporates. The rest does not become a direct water input to the lake until the ice cover melts in the spring (April or May). In order to determine this amount, data from the U.S. Soil Conservation Service (SCS, Boise, ID) snow courses were used. The snow water equivalent (SWE) of the snowpack for April 1 at the Redfish Lake Flat (RFL) snow course (1 km from the lake) was used to estimate the quantity of the precipitation input which accumulated on the lake before
Because the RFL snow course became inactive in 1990, we predicted the SWE for Redfish Lake by using regressions based on 30 yr of data (1961-1990) from two other snow courses in the region, Banner Summit (BS) and Vienna (VM), located 31 and 40 km, respectively, from Redfish Lake. Linear regressions between each site and the RFL site yielded the following equations:

\[ RFL_{SWE1} = 0.492 \times BS_{SWE} - 1.58, \quad r^2 = 0.82, \quad p = 0.0001 \text{ and} \]
\[ RFL_{SWE2} = 0.346 \times VM_{SWE} - 0.561, \quad r^2 = 0.85, \quad p = 0.0001. \]

The means of \( RFL_{SWE1} \) and \( RFL_{SWE2} \) were used to estimate SWE at Redfish Lake. In 1992, \( RFL_{SWE1} \) and \( RFL_{SWE2} \) were equal; in 1993 they differed by <2%.

**Non-Channelized Hillslope Runoff (NHR) and Lake Evaporation**

Redfish Lake's watershed has portions that drain directly into the lake and are not accounted for when lake inflows are measured. Total watershed and NHR areas were measured by digitizing 1:24,000 topographic maps. Most of the NHR areas are forested, rising only a few hundred meters above the lake. Unit runoff from these areas was computed as measured precipitation minus the percent lost to evapotranspiration from a sub-alpine/alpine watershed (53% for Fraser Experimental Forest, Colorado, Alexander et al. 1985).

We estimated lake evaporation at 74 cm yr\(^{-1}\), based on a map from the U.S. Department of Commerce (1968). This compared with 63-86 cm yr\(^{-1}\) for six mountain reservoirs in Colorado (Spahr and Ruddy 1983).
Water Balance and Lake Flushing Rates

The percent difference between water inputs and outputs to the lake was calculated as:

\[
\frac{[(I+P+R)-(O+E)] \times [O+E]}{100}
\]

Although this calculation does not include groundwater inflows or seepage losses, it gives an indication of the accuracy of our streamflow and precipitation measurements. Lake flushing rate was calculated as the lake volume divided by annual average outflow.

Lake Nutrient Loading

We computed TN and TP fluxes for each component of the water budget by multiplying nutrient concentration by volume. The results were integrated over time to provide volume-weighted annual fluxes. The TN loading estimate does not include autochthonous loading. Since nitrogen-fixing cyanobacteria are largely absent from the pelagic zone of Redfish Lake (chapter 4 of this thesis), autochthonous loading is believed to be minimal.

Stream Inflows

For each inflow, we collected water samples about three times per month from May through September 1992, and weekly from late-April through September 1993. Additional samples were collected during the snowmelt season. During other months of these years, we collected samples at 1- to 3-mo intervals.

Stream samples were collected with a DH-48 depth-integrating sampler with the intake nozzle lowered (sideways) to within 3 cm of the substrate so that we sampled a
portion of the bedload as well as the suspended load. The DH-48 was lowered and raised at a steady rate at 5-10 locations evenly spaced along a stream cross section. Samples were stored in acid-washed (0.1-N HCl) polyethylene bottles in an ice cooler and then frozen within 4 h.

Each sample was analyzed for TN and TP. TN was calculated from the sum of total Kjeldahl Nitrogen (TKN) and nitrate+nitrite nitrogen (NO$_3$-N). Unfiltered water was used for TKN and TP analyses; samples analyzed for (NO$_3$-N) were filtered through a 0.45-$\mu$m membrane filter. TP samples were digested with persulfate and then analyzed colorimetrically using the molybdate-absorbic acid method (APHA et al. 1992). Nitrogen analyses were done colorimetrically using a Kjeldahl digestion for TKN and the hydrazine method for NO$_3$ (APHA et al. 1992).

Because we used a DH-48 to collect stream water, the size of particles we collected were limited by the 6-mm diameter opening of the DH-48's nozzle. Other investigators have shown that streams transport 0.3-19% of TP load (Munn and Prepas 1986; Meyer and Likens 1979) and 3-4% of TN load (Meyer et al. 1981; Triska et al. 1984) in the coarse particulate fraction (>1 mm diameter). With our sampling technique, we collected part of the coarse particulate fraction. Visual inspection of water samples from the peak snowmelt period showed particles up to ~3 mm in diameter. Since some of these particles probably hit the rim and were deflected away from the DH-48's nozzle, we may have underestimated TP loading by <10% and TN loading by <3%.

Our nutrient sampling interval in 1993 (~1 wk) could have over- or under-represented important intermittent pulses of nutrients. Munn and Prepas (1986) found that
weekly sampling underestimated P loading for two streams by averages of 15% and 34%.

Our analysis of 1987 data from Halfmoon Creek, Colorado (USGS's Water Data and Storage Retrieval Information System, WATSTORE, Denver, Colorado) indicated that weekly measuring overestimated TP loading by 1.5% when compared to daily sampling.

Based on these error ranges, and considering the nutrient load we missed using a DH-48, we used a ±25% perturbation for nutrient loading in the sensitivity analysis of our simulation model to account for effects our sampling methods may have had on the accuracy of the nutrient loading data.

**Precipitation**

From April-December 1993, we periodically collected precipitation samples 3.4 km from Redfish Lake using a bulk sampler, which consisted of a polyethylene funnel (30-cm diameter), 2-L reservoir, vapor barrier, and tubing. These samples were coordinated with precipitation measurements. Samples were proportionally pooled, based on precipitation totals, into three mixtures from the open lake \( (P_0) \) period and one mixture from the ice-covered \( (P_i) \) period. Samples were analyzed for TN and TP as described above in order to compute annual \( P_0 \) and \( P_i \) nutrient fluxes. Since precipitation samples were not collected in 1992, we used the nutrient concentrations from the 1993 samples to compute the 1992 precipitation nutrient load.

**Non-Channelized Hillslope Runoff (NHR)**

We did not measure nutrient concentrations in NHR, but rather estimated them by using the mean annual nutrient concentration for the inflow(s) (annual nutrient load ÷ annual
water discharge). NHR volume was multiplied by these concentrations to determine NHR nutrient loads.

Water budgets and nutrient loading for the other Sawtooth Valley Lakes, which are potential sites for reestablishment of sockeye salmon, were measured using similar methodology and are reported in Appendix A.

Simulation Model

The simulation model (Fig. 2-2) takes a "bottom-up" approach to determining lake production. Mean summer chlorophyll $a$ concentration is predicted from TP concentration at spring overturn ($TP_{sp}$). The resultant chlorophyll concentration is used to predict production of $O. \text{nerka}$ smolts. The number of returning adults is determined by the number of smolts and their migration survival rates to and from the ocean, as well as their marine survival rate.

For each yearly iteration, the simulation model determines $TP_{sp}$ by summing the current year's TP inputs ($P_L$) and TP retained from previous years ($P_R$), using the following formulas:

$$P_L = P_W + P_A + P_F - P_S,$$

and

$$P_R = \sum_{i=1}^{j-1} P_{Li} * (1 - \tau_w^{-1})^i,$$

where $P_W$, $P_A$, and $P_F$ equal TP loading from the watershed, returning adult salmon, and fertilizer, respectively, $P_S = TP$ export by age-1 migrating smolts, $\tau_w =$ lake flushing rate, and $j =$ the year number of the current model iteration.
Phosphorus content of sockeye salmon was computed using the following figures:

1. an adult weight of 2.24 kg, based on the mean fork length of salmon returning to Redfish Lake (561 mm; Bjornn et al. 1968), and an adult length-weight relationship derived from Burgner (1991);
2. a smolt weight of 9.6 g, based on a mean length of 101 mm when 100% of smolts migrate from Redfish Lake as yearlings (derived from Bjornn et al. 1968), and a juvenile length-weight relationship (see below); and
3. 0.3364% P in sockeye salmon (Koenings and Burkett 1987).

We derived an empirical relationship for the Sawtooth Valley Lakes to predict mean summer chlorophyll concentration based on TP<sub>sp</sub>. We determined TP<sub>sp</sub> for 1992 and 1993 from samples collected just after ice out from Redfish, Alturas, Pettit, and Stanley Lakes. Samples were handled and analyzed as described above. Mean summer chlorophyll concentration for each lake was determined from samples collected two-three times per month from May to October in 1992 and 1993. Chlorophyll and nutrient samples were collected using a 0-6 m tube sampler. For chlorophyll analysis, two duplicate 50-ml aliquots per sample were filtered through 0.45-µm cellulose acetate membrane filters, which were extracted in 6-ml of 100% methanol in the dark for 24-48 h. The extracts were then analyzed before and after acidification (Holm-Hansen and Riemann 1978) using a Turner model 111 fluorometer. Corrections were made for phaopigments.

We then predicted *O. nerka* smolt production from mean summer chlorophyll a concentration using an empirical relationship between chlorophyll concentrations and kokanee biomasses in ten Idaho lakes and reservoirs (Rieman and Myers 1992). We calculated salmon production in each lake as the product of mean standing stock biomass...
and growth rates between year classes according to:

\[ \sum_{i=1}^{2} \left[ \frac{(B_i + B_{i+1})}{2} \right] \times \frac{(\ln W_{i+1} - \ln W_i)}{1 \text{ year}} \]

where:  
- \( B_i \): Standing stock biomass (density \(*\) mean weight) of year class \( i \) in the lake.  
- \( W_i \): Mean weight (g) of fish in year class \( i \), calculated from fork length (FL, in mm) data using the following length-weight relationship for juvenile \( O. \ \text{nerka} \) (unpublished data, P. Budy, Dept. of Fisheries & Wildlife, Utah State University, Logan, UT 84322):  
  \[ \log(W_i) = -4.803 + 2.886 \log(\text{FL}_i), \quad r^2 = 0.97. \]

Rieman and Myers' (1992) data allows us to approximate \( O. \ \text{nerka} \) production from age 1 to 3, but since it does not include the densities and sizes of the young-of-the-year in the lakes, the production of salmon moving from age class 0° to 1 could not be included. To account for production of age-0 fish, which is often a substantial portion of total production, we doubled the age 1 to 3 production estimates (Morgan 1980).

Migration and marine survival rates were taken from Bowles and Cochnauer (1984), who modelled potential sockeye production in Alturas Lake. They estimated that sockeye salmon spent 2 yr in the ocean (Bjornn et al. 1968), and that overall ocean and coastal survival was 0.344. For pre-dam conditions, they estimated survival rates of 0.13 for downstream migration and 0.90 for upstream migration, yielding a smolt-to-adult survival rate of 0.040. The survival rates they used for modern conditions, accounting for eight hydroelectric dams, were 0.0253 for smolts migrating downstream and 0.462 for adults migrating upstream, yielding a smolt-to-adult survival rate of 0.0040.
We used the model to simulate the following five scenarios:

(1) In scenario 1, we simulated sockeye production under pre-dam migration conditions.

(2) In scenario 2, we modelled modern conditions.

(3) Scenario 3 was the same as scenario 2, except that we doubled the smolt-to-adult survival rate, representing improvements in migration survival.

(4) Scenario 4 was also the same as scenario 2, except that we doubled watershed P loading to simulate the potential benefits of a lake fertilization program.

(5) In scenario 5, we simulated a 3-yr fertilization program to see if a short-term fertilization program would boost smolt production and the subsequent return of enough nutrients in adults to trigger a permanent increase in lake productivity that would make the stock self-sustaining without further fertilizations.

In all scenarios, we assumed that all *O. nerka* production went into sockeye salmon and none went into kokanee salmon.

We performed a sensitivity analysis on the model by perturbing the following parameters: nutrient loading (both watershed and fertilizer loading), smolt-to-adult survival, and lake flushing rate. Each parameter was perturbed individually, and then collectively, by +25% and -25%.
Results

Water Budgets

In 1993, near-normal precipitation resulted in near-normal total discharge in the upper Salmon River Basin: mean annual discharge for 1993 on the Salmon River at Salmon, ID, was 54.2 m$^3$/s, compared to the average mean annual discharge of 55.0 m$^3$/s for 78 years of record (Gross and Wurtsbaugh 1994). This contrasted with 1992, which was the sixth year of a drought period and had the lowest stream flows on record. Water input to Redfish Lake in 1992 was only 53% of that in 1993. Mean annual flows for Redfish Lake Creek and Fishhook Creek in 1993 were 1.84 and 0.81 m$^3$/s, respectively.

The water budgets were dominated by stream inflows and outflows (Table 2-1). In 1992 and 1993, inflows were 91% of the inputs, and outflows were 92-95% of the measured losses. The percent differences between measured inputs and outputs were -13% and -2% in 1992 and 1993, respectively.

Precipitation in 1992 was 10.7 cm during the open-lake period ($P_o$) and 16.2 cm when the lakes were ice covered ($P_i$). In 1993, $P$ and $P$ were 23.7 and 29.2 cm, respectively. The 30-yr averages of $P_o$ and $P_i$ are 18.7 cm and 30.2 cm, respectively. Thus, for 1993, precipitation for the basin was close to average.

The flushing rate in Redfish Lake was 3.0 yr based on the 1993 outflow and 5.4 yr using the drought year outflow of 1992. Because 1993 was nearly an average flow year, we used 3.0 yr as the flushing rate in the simulation model.
Nutrient Loading

Nutrient loading to Redfish Lake was much higher in 1993 than in 1992, although the relative contributions from inflows, NHR, and precipitation were similar in the two years (Table 2-2). TP loading in 1993 was 0.15 g/m², almost twice as much as the 0.08 g/m² TP in 1992. TN nutrient loading in 1993 was 1.95 g/m², which was 2.6 times the 0.75 g/m² TN in 1992. Nutrient concentrations of stream samples used to derive these figures, as well as stream nutrient data for the other lakes, are reported in Appendix B.

Nitrogen and phosphorus entered the lake primarily through the tributaries. The majority of tributary nutrient loading occurred during the snowmelt runoff period. Between 12 May and 30 June 1993, only 13% of the calendar year, Fishhook Creek and Redfish Lake delivered 67% of their annual TP load and 62% of their annual TN load.

Precipitation on the surface of Redfish Lake contributed 7% of annual TP and 18-24% of annual TN loads (Table 2-2). The volume-weighted TP and TN concentrations of the three pooled samples from the open-lake period were 18 and 850 µg/L, respectively, while the one pooled sample from the ice-covered period had TP and TN concentrations of 20 and 487 µg/L, respectively.

Simulation Model

Mean summer chlorophyll a concentrations were linearly related to spring TP in the Sawtooth Valley Lakes (Fig. 2-3, r²=0.83, p=0.0018). Based on a spring TP concentration in Redfish Lake of 10 µg/L in 1993, this relationship predicts a mean summer chlorophyll concentration of 0.57 µg/L.
Although there was considerable scatter in the data, there was a significant, linear log-log relationship between chlorophyll $a$ concentration and the production of O. nerka in Idaho lakes (Fig. 2-4, $r^2=0.52$, $p=0.018$). The production data is shown in units of kg ha$^{-1}$ yr$^{-1}$, and as the equivalent number of smolts (# ha$^{-1}$ yr$^{-1}$) that could be produced, if all of the current kokanee production in these lakes was realized by sockeye salmon that grew to smolt size (9.6 g, Bjornn et al. 1968) in one year. The relationship predicts that as chlorophyll levels rise from 0.5 to 5 mg m$^{-3}$, O. nerka production increases from 1.20 to 13.2 kg ha$^{-1}$ yr$^{-1}$, or in terms of potential smolts, from 125 to 1370 fish ha$^{-1}$ yr$^{-1}$.

The parameters in the simulation model approached equilibrium conditions quickly. Spring TP, chlorophyll concentrations, and numbers of smolts and returning adults reached 99% of the equilibrium values within 2-7 yr for scenarios 1-3 and in 12 yr for scenario 4.

The simulation model indicates that marine-derived nutrients are not very important for Redfish Lake's productivity. The simulations indicate that the amount of nutrients transported to the lake by returning adults was between 0.1-1.5% (depending on scenario) of loading from the lake's watershed (Figs. 2-5a & b). Nutrients from adult salmon were largely offset by a combination of (1) high washout of nutrients through the lake's outflow (due to the lake's 3-yr flushing rate), and (2) departure of nutrients with out-migrating smolts (Fig. 2-5a). In fact, in scenarios representing modern migration survival rates (scenarios 2 and 4), the smolt-to-adult survival rate of 0.40% is lower than the smolt-to-adult mass ratio of 0.43% (9.6 g:2240 g). Consequently, under modern survival rates, more nutrients leave the lake with smolts than return with adults.

Spring TP, chlorophyll concentration, and smolt production were highest under the
lake fertilization simulation (Fig. 2-5c). Under the other scenarios, the values for these parameters varied by <2%.

The number of returning adult salmon was greatest in simulations where pre-dam survival estimates were used (Fig. 2-5d, scenario 1). This simulation indicated that 3,800 adults could have returned annually to Redfish Lake before the dams were constructed on the Columbia and Snake Rivers-930% more than predicted for modern conditions.

The simulation of modern conditions indicated that with present production and sockeye survival estimates, 370 returning adult salmon could be produced. Doubling watershed P loading increased returns by 110% to 780, while doubling migration survival increased returns by 100% to 750.

In scenario 5, where watershed P loading was doubled for 3 yr to simulate temporary lake fertilization, chlorophyll concentrations and numbers of sockeye smolts and returning adults increased to levels similar to those when fertilization was continuous (scenario 4). After fertilization ceased, however, phosphorus, chlorophyll, smolt production, and adult sockeye salmon numbers returned to within 5% of modern conditions within 8 yr, and within 1% in 16 yr (Figs. 2-6a & b). The TP from the fertilizer was flushed from the lake while the TP levels resulting from the continual watershed loading were sustained. The model thus indicates that a 3-yr fertilization would not trigger a self-sustaining return of salmon and nutrients to the lake.

The sensitivity analysis showed that a given change in the value of a parameter generally resulted in a similar change in the number of returning adult salmon. The relative differences in adult returns under each scenario, however, remained the same (Table 2-3).
Regardless of the perturbation, returns under modern conditions always were 9-10% of pre-dam conditions, while returns under conditions of increased downstream survival or lake fertilization always were 19-21% of pre-dam escapement. Perturbation of ±25% of each parameter resulted in changes in returns of ±24-29%. When all parameters were simultaneously increased or decreased by 25%, adult returns increased by 100-108% or declined by 59-60%, respectively.

Discussion

Our simulation model predicted that under equilibrium conditions when 3,800 sockeye salmon returned to Redfish Lake, they would have contributed only 3% of the lake's annual TP load. Empirical estimates also suggest that marine-derived nutrients transported by sockeye salmon were relatively unimportant to the overall nutrient load. From 1953-1964, Bjornn et al. (1968) found a mean of 769 and a maximum of 4,361 adult sockeye salmon returning to Redfish Lake. If 4,361 salmon returned in the normal water year of 1993, they would have contributed 3% of the TP and 2% of the TN budget (Table 2-4). This estimate is not substantially different than that predicted by the model. The number of sockeye that returned in the 1950's and 1960's was, however, according to Bjornn et al. (1968, p. 360), "probably only a small fraction of the number which returned during the 1800's....There is no reliable information on the numbers of sockeye salmon spawning in Redfish Lake at those early times." To demonstrate another possible scenario, we have therefore assumed a return of 25,000 adults, which gives a spawner density (4065/km²) similar to that reported for Karluk Lake, Alaska, a system with some limnological
characteristics similar to those in Redfish Lake. If 25,000 spawners returned to Redfish Lake, we estimate that they would have contributed 17% of the TP and 11% of the TN coming into the lake (Table 2-4).

The estimated low contribution of marine-derived nutrients to lake production in Redfish Lake, compared to other sockeye salmon nursery lakes, is likely a consequence of the low smolt-to-adult survival rate of migrating Snake River sockeye salmon. The 4.0% smolt-to-adult survival rate estimated by Bowles and Cochnauer (1984) is lower than the rate for six other Pacific sockeye salmon stocks, which ranged from 5-34% (Ricker 1962). While the relative rapid washout of nutrients is also a factor, Redfish Lake's 3-yr flushing rate is comparable or slightly greater than that of most other sockeye salmon nursery lakes. Water residence time for 31 oligotrophic sockeye salmon nursery lakes ranged from 0.2-34.7 yr, but 23 of the lakes had residence times <3.0 yr (Stockner and Shortreed 1985; Koenings and Burkett 1987; Kyle et al. 1988). Thus, Redfish Lake's smolt-to-adult survival rate differentiates it more from other sockeye salmon nursery lakes than does its rapid flushing rate.

The low smolt-to-adult survival rate may be partially caused by the long migration to and from Redfish Lake, which is the longest (1450 km) and represents the greatest elevation gain (1996 m) of any sockeye salmon stock in the world (Bevan et al. 1994). Of the 54 sockeye nursery lakes listed by Burgner (1992), the longest migration was 1064 km, and 74% of the lakes had migration distances of ≤100 km.

As the smolt-to-adult survival rate and/or flushing rate increase from one lake to the next (and nutrient loading remains the same), our model predicts an increase in the number
of returning adults (Fig. 2-7). Since Redfish Lake's rates of flushing (3 yr) and modern smolt-to-adult survival (0.40%) are both low, adult returns predicted by the model are much lower than if the migration survival rates and/or flushing rates were higher.

In model scenarios where hypothetical flushing and smolt-to-adult survival rates were both high enough, returning adults transported enough marine-derived nutrients to cause escalating increases each year in smolt production and subsequent adult returns. Such a scenario occurred when the model was run with a flushing rate of 30 yr and a smolt-to-adult survival of 40%. In this scenario, an equilibrium level of adult returns was never reached, as the marine-derived nutrients were transported to the system faster than they were flushed out. Thus, they accumulated, causing higher levels of chlorophyll, smolt production, and adult returns. Under these scenarios, however, some other factor, such as spawning habitat, would eventually limit the population of salmon in Redfish Lake. This model indicates that smolt-to-adult survival rates of 0.20, lake flushing rates of 20 yr, and sustained watershed nutrient loading are necessary before returning salmon cause productivity to escalate "unchecked."

Results of the 3-yr lake fertilization simulation show that a short-term lake fertilization program would have little long-term impact on sockeye recovery under the modern migration survival rate. While the fertilization augmented the numbers of migrating smolts and returning adults for three years, these increases decreased when fertilization was halted, largely due to the lake's fast flushing rate. Thus, a short-term nutrient addition would not trigger enough plankton and subsequent fish production to return Redfish Lake to a hypothesized earlier condition supporting larger sockeye runs.
Short-term fertilization, however, may increase growth and survival of juvenile sockeye salmon returned to Redfish Lake from the ongoing broodstock program. If so, short-term lake fertilization could decrease continued erosion of the stock which, in concert with improvements in mainstem dam passage, could contribute to the prevention of the stock's extinction. Lake trophic status is, however, inversely related to water clarity (Dillon and Rigler 1975; Carlson 1977; Goldman 1988), so the impact of lake fertilization on Redfish Lake's aesthetic values will require careful monitoring.

Although our model is useful for conceptualizing nutrient dynamics and comparing the effects of different management strategies in sockeye salmon lakes, many of our measurements and relationships were not exact and limit us from making precise predictions. Our measurement of nutrient loading in the drought year 1992 was not a good indicator of annual nutrient loading, and thus was not used in the model. The 1993 loading values depict data for an average flow year, but higher than average loading may have resulted due to flushing of nutrients accumulated in the watershed during the preceding 6-yr drought. Nutrient export from Redfish Lake's watershed in 1993 (10.3 mg P/m² and 115 mg N/m²) was, however, consistent with ranges for temperate forests of 1.5-51 mg P/m² and 60-230 mg N/m² (Likens et al. 1977).

Although our calculation of phosphorus retention and the relationship between spring TP and mean summer chlorophyll a concentration may also have contributed to inaccuracies in our prediction, we are confident that the simulation model gives reasonable predictions for total phosphorus in the system. Under modern conditions, the spring TP in Redfish Lake predicted by the model (10.6 µg/L) was very close to that observed during the normal water
year in 1993 (10 \( \mu g/L \)). Although a more refined model of phosphorus retention might incorporate phosphorus sedimentation and turnover, our simple approach appears to have captured the dynamics of the system reasonably well.

The relatively poor fit of the relationship between chlorophyll concentration and \( Q \) _nerka_ production (Fig. 2-4) potentially introduced the greatest inaccuracy into our model. The poor fit likely results from (1) other factors besides chlorophyll affecting fish production and (2) the imprecision of the trawling methods used to measure fish biomass (Parkinson et al. 1994). Although the relationship we derived was variable, the increases in fish production associated with increases in primary producer surrogates is consistent with many other studies (reviewed by Carline 1986; Plante and Downing 1993). Consequently, although the model's predictions of salmon numbers may not be highly accurate, the trends predicted are reasonable.

The chlorophyll-smolt relationship indicates that ambient chlorophyll levels in Redfish Lake could produce substantial numbers of sockeye salmon smolts, but much of the production may now go into kokanee due to the construction of eight dams on the Snake and Columbia Rivers during the past 60 years. Increased mortality imposed on anadromous strains of \( Q \) _nerka_ during this period decreased the numbers of adult sockeye returning from the ocean. With fewer progeny from anadromous adults entering the lakes, the natural production potential likely was subsumed by kokanee populations. Gross (1987) has provided a conceptual model of how changes in mortality or growth during various stages of a fish's life can favor anadromous or nonanadromous life-history strategies. This explanation suggests that artificial reductions of the kokanee population might facilitate the
reestablishment anadromous sockeye salmon due to the reduction of competition between the two *O. nerka* groups for food in the lake. However, if the kokanee numbers are reduced and the sockeye recovery fails, unforeseen stochastic events could eradicate the *O. nerka* populations in Redfish Lake.

The simulation model's predicted escapement of 370 adults under modern conditions is high when considering that the mean annual return between 1989-1994 was 2.7 fish. This is partially due to the model's assumption that all *O. nerka* production goes into sockeye salmon and none goes into kokanee. Another reason for this difference may be that the migration survival rates we used (Bowles and Cochnauer 1984) were probably too high for the drought conditions that existed during 7 of the 8 yr between 1987-1994 in much of the Columbia River Basin.

Predicted escapement of 3,800 spawners under pre-dam conditions compares to a mean return of 769 from 1954-1964, a time when returns were "probably only a small fraction of the number which returned during the 1800's" (Bjornn et al. 1968, p. 360). Bjornn et al. (1968) recorded a peak return of 4,361 adults in 1957. Our model operates under equilibrium conditions and does not portray the fluctuating, cyclic nature of sockeye returns often observed between generations (Mathisen and Poe 1981; Kyle et al. 1988; Burgner 1991). Thus, it would be possible to see peak annual returns greater than 10,000 in a sockeye population with a mean escapement of 3,800.

It is not our intent, however, to predict exact sockeye salmon escapement figures—the imprecision of our model's relationships precludes this. The primary utility of our model, then, is to help understand the mechanisms driving nutrient loading and smolt production in
Redfish Lake and compare different management scenarios. The model allows us to analyze in an iterative fashion the role returning adults played in lake P loading and overall lake productivity.

Ultimately, to restore self-sustaining populations of anadromous sockeye salmon to the Sawtooth Valley Lakes, increased survival during mainstem passage must be achieved. Efforts to enhance production of juvenile sockeye salmon in the rearing lakes through fertilization should only be viewed as a tool to increase the forage base, survival, and growth of juvenile salmon produced naturally and those from the broodstock program. The potential successes of recovery activities in the rearing environment will be tempered by problems facing sockeye smolts in the migration corridor.

References


Table 2-1. Water budgets for Redfish Lake, 1992 and 1993. All quantities are 10^6 m³, except for \( \Delta \), which is in \% \( (\Delta = \text{[Sum of inputs-sum of outputs]} \times \text{[sum of outputs]}^{-1} \times 100) \). NHR = non-channelized hillslope runoff.

<table>
<thead>
<tr>
<th></th>
<th>Gains</th>
<th>Losses</th>
<th>( \Delta ) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inflows</td>
<td>Precipitation</td>
<td>NHR</td>
</tr>
<tr>
<td>1992</td>
<td>43.2</td>
<td>1.6</td>
<td>2.7</td>
</tr>
<tr>
<td>1993</td>
<td>83.4</td>
<td>3.3</td>
<td>5.2</td>
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</table>
Table 2-2. Total nitrogen (TN) and phosphorus (TP) loading for Redfish Lake in 1992 and 1993. Ppt. = precipitation, NHR = non-channelized hillslope runoff.

<table>
<thead>
<tr>
<th></th>
<th>Total (g/m²)</th>
<th>% of TP</th>
<th>% of TN</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>0.08 0.75   88  6  7</td>
<td>72  4  24</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.15 1.95   88  6  7</td>
<td>78  5  18</td>
<td></td>
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</tbody>
</table>
Table 2-3. Sensitivity analysis of equilibrium numbers of adult sockeye salmon spawners predicted by the simulation model. The results show predicted adult returns when each parameter was perturbed individually -25% and +25%, and then collectively. The scenarios are described in the methods section of the text. The results for scenario 5 (3-yr lake fertilization) are the same as for scenario 2.

<table>
<thead>
<tr>
<th>Parameter perturbed</th>
<th>Scenario(s)</th>
<th>% Change due to perturbation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>(pre-dam conditions)</td>
<td>(modern conditions)</td>
</tr>
<tr>
<td>None</td>
<td>3800</td>
<td>370</td>
</tr>
<tr>
<td>Nutrient loading</td>
<td>2800, 4900</td>
<td>270, 470</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake flushing rate</td>
<td>2800, 4900</td>
<td>270, 470</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smolt-to-adult survival</td>
<td>2900, 4800</td>
<td>270, 470</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All parameters simultaneously</td>
<td>1500, 7900</td>
<td>150, 750</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2-4. Annual total phosphorus (TP) and total nitrogen (TN) budgets for Redfish Lake, in kg, including two different run sizes of adult sockeye contributing nutrients.  
1993 fluvial inputs have been used to represent an average year.

<table>
<thead>
<tr>
<th>Input:</th>
<th>TP</th>
<th>%</th>
<th>TN</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>4,361 adults in 1955 (Bjornn et al. 1968)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fluvial inputs</td>
<td>890</td>
<td>91</td>
<td>9,920</td>
<td>81</td>
</tr>
<tr>
<td>Precipitation</td>
<td>62</td>
<td>6</td>
<td>2,110</td>
<td>17</td>
</tr>
<tr>
<td>Adult sockeye</td>
<td>33(^{1,2})</td>
<td>3</td>
<td>261(^{1,3})</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>985</td>
<td>100</td>
<td>12,291</td>
<td>100</td>
</tr>
</tbody>
</table>

| **25,000 adults, pre-1900's, hypothetical** |       |      |       |      |
| Fluvial inputs  | 890   | 78   | 9,920 | 73   |
| Precipitation   | 62    | 5    | 2,110 | 16   |
| Adult sockeye   | 190\(^{1,2}\) | 17   | 1,495\(^{1,3}\) | 11   |
| Total           | 1,142 | 100  | 13,525| 100  |

\(^{1}\) Mean weight of Redfish Lake adult sockeye of 2.24 kg (Bjornn et al. 1968).
\(^{2}\) 0.3364% P in an adult sockeye (Koenings and Burkett 1987).
\(^{3}\) 2.67% N in an adult sockeye (Mathisen et al. 1988).
Figure 2-1. Map showing Pacific Northwestern states and the location of the study lakes in the Sawtooth Valley, ID. Location of rain gauges shown by '•'.
Figure 2-2. Flow diagram of the simulation model. Model was used to predict spring total phosphorus concentration, mean summer chlorophyll \( a \), and smolt and adult sockeye production under different survival and lake fertilization scenarios.
Figure 2-3. Relationship between spring total phosphorus concentration and mean summer chlorophyll a levels in the Sawtooth Valley Lakes, Idaho. R=Redfish Lake, A=Alturas Lake, P=Pettit Lake, and S=Stanley Lake, while 92=1992 and 93=1993.
Figure 2-4. Relationship between mean chlorophyll a levels and kokanee salmon production in ten Idaho lakes. The growth rate data were derived from estimates of fish biomass and growth reported by Rieman and Myers (1992). The right scale indicates the number of 9.6 g smolts that could be produced if all of the kokanee production was channeled into sockeye salmon production.
Figure 2-5. Predicted parameter values for Redfish Lake using different model scenarios under equilibrium conditions. (a) Total phosphorus (TP, in $\mu g \ L^{-1} \ yr^{-1}$) gained from returning adult salmon versus TP exported with migrating smolts, (b) TP loaded from the watershed and fertilization, (c) spring TP and chlorophyll a concentrations, and number of smolts produced, and (d) number of returning adults are shown. Shown are four simulation scenarios: pre-dam and modern conditions, doubling of downstream migration survival, and doubling of watershed phosphorus loading by lake fertilization.
Figure 2-6. Simulated effects of a 3-yr lake fertilization program. Parameters shown are:
(a) spring total phosphorus (current year's input plus that retained from previous years)
originating from the watershed and from fertilizer, and mean summer chlorophyll a, and (b)
annual smolt production and adult sockeye salmon returns. The simulated fertilization
occurred in years 2 through 4.
Figure 2-7. Model predictions of equilibrium numbers of returning adult salmon to Redfish Lake under different combinations of smolt-to-adult survival rate and flushing rate. The column with an '•' shows expected returns under pre-dam conditions. Histogram columns with '†' on top indicate conditions where numbers of returning adults would not reach equilibrium due to continually escalating salmon returns. The text describes such a scenario.
CHAPTER 3
COMPARISON OF EPILIMNETIC AND METALIMNETIC
FERTILIZATIONS ON THE PHYTOPLANKTON AND
WATER CLARITY OF AN OLIGOTROPHIC LAKE²

Abstract

The effects of nitrogen and phosphorus fertilization applied to the epilimnia and metalimnia were evaluated in large mesocosms (330 m³) during a 10-wk experiment to Pettit Lake, Idaho, an oligotrophic mountain lake. The metalimnetic (META) fertilizations were equal to or more effective than epilimnetic fertilizations (EPI) in increasing chlorophyll a, phytoplankton biovolume, and primary productivity, yet caused smaller changes in periphyton growth and water clarity. Weekly mean water column chlorophyll concentrations were 0.91, 1.42, and 2.56 µg/L for the control (CNTL), EPI, and META treatments, respectively. Primary productivity, stimulated 2.5-4 fold by fertilization, was similar in the EPI and META treatments, with production peaks in each treatment occurring at the depth where nutrients were added. Increases in phytoplankton biovolume were mostly from diatoms and were more sustained in the META than the EPI treatments. Cyanobacteria were more abundant in the EPI treatments. Periphyton growth was stimulated 10-100 times more by the EPI than the META treatments, and diverted nutrient addition effects from the planktonic autotrophs. Fertilization significantly decreased water transparency in both treatments, as measured by Secchi depth, which were deeper in the META treatments than

²Coauthored by Howard P. Gross, Wayne A. Wurtsbaugh, Chris Luecke, and Phaedra Budy.
in the EPI treatments on 8 of 11 dates. Thus, metalimnetic nutrient additions show promise for managers evaluating lake fertilization as a tool for increasing lake productivity while minimally impacting water clarity.

Introduction

Lake fertilization has been used for decades in aquaculture, and more recently as a management tool to increase salmon production in many Alaskan and British Columbian lakes (Nelson 1958; Hyatt and Stockner 1985; Kyle et al. 1988; Stockner 1987). This bottom-up approach to boosting the limnetic food chain strives to increase the productivity of the phytoplankton and zooplankton communities, and ultimately, fish production. Increases in the trophic status of a lake are associated with decreases in water clarity and, sometimes, water quality (Carlson 1977; Goldman 1988). Thus, improving lake productivity and preserving water clarity as management goals may involve a trade-off.

Numbers of adult Snake River sockeye salmon (Oncorhynchus nerka) that return to the oligotrophic Sawtooth Valley Lakes in central Idaho have declined drastically (>99%) since the 19th century. In 1992, managers began a hatchery broodstock program to avert extinction of the species (Bevan et al. 1994). Resource managers are considering fertilizing the Sawtooth Valley Lakes to increase the growth and survival rates of juvenile sockeye introduced from the broodstock program. These lakes are in a pristine setting and are highly valued for recreational and aesthetic purposes. Ideally, a fertilization program to help recover this endangered salmon should minimally impact water clarity, but increase primary and secondary productivity.
One approach that may minimize the effect on water clarity is to inject nutrients into the metalimnia. LeBrasseur et al. (1978) experimented with this approach and were able to increase primary productivity at a depth of 10 m in Great Central Lake, British Columbia. This is an appealing strategy for the Sawtooth Valley Lakes because it may allow for preservation of water clarity and an increase in sockeye production at the same time. Consequently, in 1993 we used large mesocosms in one of the Sawtooth Valley Lakes, Pettit Lake, to test whether epilimnetic and metalimnetic nutrient additions have different effects on water clarity, primary productivity, chlorophyll \(a\) concentrations, periphyton growth, and phytoplankton community structure.

**Study Area**

Pettit Lake is located in the Sawtooth National Recreation Area in central Idaho (lat. 44°, long. 115°) at 2132 m elevation. Its watershed lies in the pristine, granitic Sawtooth Mountains. The steep-sided lake formed behind a large terminal moraine deposited by glaciers during the Pleistocene. It is dimictic and oligotrophic, with low mean summer epilimnetic nutrient levels: 82 \(\mu g/L\) for total nitrogen (TN) and 6.2 \(\mu g/L\) for total phosphorus (TP) (Steinhart et al. 1994). Mean summer epilimnetic chlorophyll \(a\) concentrations are near 0.5 \(\mu g/L\). Physical characteristics of the lake are:

<table>
<thead>
<tr>
<th>Surface area</th>
<th>1.62 km(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean depth</td>
<td>28 m</td>
</tr>
<tr>
<td>Max. Depth</td>
<td>52 m</td>
</tr>
<tr>
<td>Drainage area</td>
<td>27.4 km(^2)</td>
</tr>
</tbody>
</table>
Mean summer Secchi depth 14.4 m

Macrophytes are sparse. The dominant crustacean zooplankton is *Daphnia rosea*, followed by *Holopedium gibberum* and *Bosmina longirostris* (Budy et al. 1995). The fish community includes kokanee salmon (*O. nerka*), brook trout (*Salvelinus fontinalis*), bull trout (*S. confluentus*), rainbow trout (*Oncorhynchus mykiss*), and redside shiners (*Richardsonius balteatus*) (Beauchamp et al. 1993). The lake is highly prized for its recreational and aesthetic values.

**Methods**

The nutrient addition experiments were conducted over a 10-wk period in six 330 m$^3$ mesocosms, or limnocorals. Each limnocorral was 5 m in diameter and approximately 17 m deep with tops that floated above the lake surface. They were constructed with weighted curtains of impermeable, fiber-reinforced polyethylene. The limnocorals were unfurled slowly (12 h) through the water column with the bottoms open; thus the initial conditions were similar to those in the lake. Once filled, scuba divers tied the bottoms closed. Each limnocorral was randomly assigned one of three treatments ($n=2$):

1. Control (CNTL),
2. Nitrogen (N) and phosphorus (P) added to the epilimnion (EPI), and
3. N and P injected into the metalimnion at a depth of 14.5 m (META).

At the start of the experiment on 3 July, TP and TN concentrations in the limnocorals were 4.4 (range of 3.9-5.2) µg/L and 84 (range of 67-95) µg/L, respectively. Over the course of the summer we added 6 and 120 µg/L, respectively, of P and N to the
EPI and META treatments. Nutrients were added in the form of \((\text{NH}_4)_2\text{HPO}_4\) and \(\text{NH}_4\text{NO}_3\), at a 20:1 mass TN:TP ratio. This high ratio was used to reduce the likelihood of stimulating cyanobacteria (Schindler 1977). Weekly, EPI nutrient solutions were stirred in at the surface, while META nutrient solutions were injected at 14.5 m through a hose (using limnocorral water of a temperature equal to that at 14.5 m). Fifty percent of the nutrients were added during the first week of the experiment; the remaining 50% were added in equal parts over the following 9 wk. We would have preferred a more even distribution of nutrient additions starting at a date earlier than 3 July, but logistical difficulties caused the fertilization to start over 2 wk later than planned. In an attempt to stimulate zooplankton production, we made the early, large addition of nutrients so that these organisms would have sufficient time to respond to increased phytoplankton production.

In each limnocorral, we measured temperature and oxygen biweekly at 1-m intervals (from 0 to 17 m) with a Hydrolab® H20 Multiparameter Water Quality Data Transmitter. Water transparency measurements were made weekly with a 25-cm diameter Secchi disk.

On three dates (initially, and at 4 and 8 wk into the experiment) we collected epilimnetic, metalimnetic, and near-bottom water with a Van-Dorn bottle for nutrient analyses. Samples collected for nutrient analyses were placed in polyethylene bottles that were first rinsed with 0.1 N HCl and then three times with aliquots of the actual sample. Nutrient samples were stored in an ice chest and then frozen upon return to our field laboratory. Total nitrogen was calculated from the sum of total Kjeldahl Nitrogen (TKN) and nitrate+nitrite nitrogen \((\text{NO}_3^-\text{N})\). Unfiltered water was used for TKN and TP analyses; samples analyzed for nitrate were filtered through 0.45-µm membrane filters prior to
freezing. TP samples underwent a persulfate digestion and were then analyzed colorimetrically using the molybdate-absorbic acid method (APHA et al. 1992). Nitrogen analyses were conducted colorimetrically using a Kjeldahl digestion for TKN and the hydrazine method for NO$_3$-N (APHA et al. 1992).

On the same dates and depths when we collected nutrient samples, we also preserved samples with Lugol's iodine solution for phytoplankton enumeration. A 100-ml aliquot from each phytoplankton sample was filtered through a 0.45-µm cellulose acetate filter. Each filter was cleared and permanently mounted, according to the method of Crumpton (1987). Cells were counted in a minimum of 10 fields per slide at 400x; the dimensions of a minimum of 10 individuals in each taxon were measured to calculate biovolume (Wetzel and Likens 1991). Phytoplankton were taxonomically classified as Cyanobacteria (blue-green algae), Chlorophyta (green algae), Chrysophyta (primarily Dinobryon sp.), Bacillariophyta (Diatoms), and Dinophyta (primarily Peridinium sp.).

At weekly intervals we collected water for chlorophyll a analysis from the epilimnion and from 0 to 17 m in each limnocorral with depth-integrating vinyl tubes. Biweekly, we collected additional chlorophyll samples from the metalimnetic and near-bottom waters with a 4-L Van Dorn bottle. We sampled additional depths for chlorophyll a analysis concurrent with $^{14}$C primary productivity measurements (see below). Two 50-ml aliquots per sample were filtered through 0.45-µm cellulose acetate membrane filters, extracted into 6 ml of 100% methanol, and analyzed fluorometrically using a Turner Model 111 fluorometer (Holm-Hansen and Riemann 1978). Corrections were made for phaopigments. The fluorometer was calibrated using chlorophyll a standards that were verified
At 2 d, 4 wk, and 8 wk into the experiment, $^{14}$C primary productivity measurements were made at five depths in each limnocorral (Wetzel and Likens 1991). Water from each depth was placed into three 25-ml glass scintillation vials, taking care not to expose the plankton to direct sunlight. Each vial was inoculated with 80 µL of 25 µCi/ml of $^{14}$CHO$_3^-$. To measure nonphotosynthetic $^{14}$C uptake, we inoculated one vial from each depth with 150 µL of a saturated solution of Diuron (dichloro-phenyl-dimethylurea; DCMU), a photosynthetic inhibitor. The vials were resuspended in the water column in clear acrylic plastic tubes hung from a line and incubated for approximately 4 h near midday. The vials were then removed and stored in a light-tight box. Within 2 h of the end of the incubation, the entire contents of each vial were filtered through 0.45-µm cellulose nitrate filters and rinsed with 0.01-N HCl. They were then air dried, and subsequently counted by liquid scintillation spectrometry using Readysafe® cocktail. Production rates were calculated by subtracting carbon uptake in the DCMU treatments from the light treatments. Dissolved inorganic carbon was estimated from pH and temperature, and alkalinity measurements were determined with the Gran procedure (Wetzel and Likens 1991).

To quantify periphyton growth, we suspended a weighted 10-cm wide strip of polyethylene limnocorral material from the center of each corral to the bottom. At approximately 4, 8, and 11 wk into the experiment, we carefully bored two 14-mm diameter disks from each periphyton strip with a cork borer at five to six depths. The disks were kept on ice until returned to our field laboratory, where they were placed directly into 6 ml of 100% methanol, extracted in the dark for 24-48 h, and then analyzed for chlorophyll a and spectrophotometrically.
phaeophytin as described above.

Because resident O. nerka were unavailable in Pettit Lake, we attempted to use age-0 redside shiners in the limnocorrals to evaluate effects of nutrient additions on fish growth. Fifteen fish (0.3-0.5 g) were placed in each corral. Unfortunately, the fish were extremely sensitive to handling and few survived (Gross et al. 1994). Because over 90% of these fish could not be accounted for, no conclusions about planktivory or fish growth in response to nutrient additions could be made.

Results

Water Clarity, Temperature, and Oxygen

Fertilization significantly decreased water transparency over controls (repeated measures ANOVA, Table C-1, $F_{2,3} = 35.7$, $p=0.008$). The Secchi depths were deeper in the META treatments than in the EPI treatments on 8 of 11 dates (Fig. 3-1), but the difference was not significant (post hoc Tukey's, $\alpha=0.05$). The mean Secchi depths for the CNTL, EPI, and META treatments, respectively, were 13.7, 10.9, and 11.4 m. Water transparency was deeper than 8 m in all of the treatments throughout the experiment (Fig. 3-1).

Temperature and oxygen profiles closely paralleled the conditions observed in the lake, and there was little difference among treatments on each date. Throughout the experiment, the limnocorrals (and lake) were thermally stratified, with a 4-6-m thick epilimnia with a temperature of 11-16 °C, and a metalimnia that reached 5.5-6.0 °C at 17 m. Dissolved oxygen conditions in all of the corrals were suitable for fish growth (>5.0 mg/l at all depths, Brett et al. 1969).
Both the EPI and META nutrient additions increased TN and TP concentrations over initial and CNTL concentrations (Fig. 3-2). While the TP increases were significant (repeated measures ANOVA, Table C-2, F_{2,3}=27.2, p=0.012), the TN increases were not (repeated measures ANOVA, Table C-3, F_{2,3}=3.87, p=0.148). The nutrient profiles indicated that there was considerable movement of the added nutrients between strata. The highest nutrient concentrations in the META treatments were at 17 m, but epilimnetic nutrient levels also increased in this treatment (Fig. 3-2, c-f). In the EPI treatments, the highest nutrient concentrations were in the epilimnion on 31 July (Fig. 3-2, b & e). However, on 29 August, they were highest at 17 m (Fig. 3-2, c & f). Higher concentrations of nutrients at 17 m was probably partially caused by the depth boundary condition imposed by the limnocorral, allowing the accumulation of sinking phytoplankton, detritus, and other particulates near the bottoms of the mesocosms.

Mean chlorophyll levels in the EPI and META treatments were greater or equal to CNTL treatments throughout the experiment (Figs. 3-3 & 3-4). The means of the epilimnetic chlorophyll levels were 0.31, 0.74, and 0.67 $\mu$g/L for the CNTL, EPI, and META treatments, respectively (Fig. 3-3a). While there was a significant treatment effect (repeated measures ANOVA, Table C-4, F_{2,3}=223, p<0.001), the EPI and META means were not significantly different from each other (post hoc Tukey's comparison, $\alpha = 0.05$). The mean chlorophyll concentrations in the weekly 0-17 m tube samples were 0.91, 1.42,
and 2.56 μg/L for the CNTL, EPI, and META treatments, respectively (Fig. 3-3b). While there was a significant treatment effect (repeated measures ANOVA, Table C-5, \( F_{2,297} = 26.2, p=0.013 \)), only the META means were significantly different from the CNTL means (post hoc Tukey's comparison, \( \alpha = 0.05, \) CNTL = A, EPI = AB, META = B). However, the mean 0-17 m chlorophyll values for the META treatments were greater than those in the EPI treatments on all 10 weekly samplings after nutrient additions began (Fig. 3-3b).

Nutrient additions markedly increased primary productivity in the limnocorral, and the stimulation was greatest in the strata where the nutrients were added. Primary production was first measured two days after nutrient additions began (Fig. 3-4d). On this date productivity was generally similar among the treatments, except at 0.5 m in the EPI treatments, where algal growth was over 50% greater than the CNTL treatments. This suggests that the phytoplankton responded quickly to the nutrient additions in surface waters where light levels were high. By the end of July the spatial differences in productivity among the three treatments were well established (Fig. 3-4e). Productivity in the CNTL treatments remained low throughout the water column. In the EPI treatments, production in the epilimnion was approximately 200% greater than in the controls. This enhanced productivity extended to 10 m, but declined in the deeper water. In the META treatments, production in the deeper waters was 400% greater than in the controls, whereas in the epilimnia the stimulation was less pronounced. By the end of August, the spatial differences in productivity among the treatments were less distinct, but the pattern established in July was still evident (Fig. 3-4f).

We integrated the primary productivity profiles to compare how the different
fertilization strategies affected primary production through the entire limnocorral water column. On 5 July total integrated productivity was similar in all three treatments (ANOVA, Table C-6, $F_{2,3}=0.27$, $p=0.780$), indicating that there had been insufficient time for significant response to the fertilizations. However, in late July and late August, mean rates of primary production were approximately 190% higher in the EPI and META treatments than in the controls (ANOVA, Table C-6; 31 July: $F_{2,3}=30.7$, $p=0.010$; 28 August: $F_{2,3}=154$, $p<0.001$). Overall rates of primary productivity were not significantly different in the EPI and META treatments (post hoc Tukey's, $\alpha=0.05$).

The phytoplankton community structure was similar in all three treatments at the start of the experiment (Fig. 3-5, see 3 July 1993), with a mixture of chlorophyta, diatoms, and Dinobryon spp. at all depths. The chlorophytes were Oocystis sp., Chlorella spp., and small Chlorococcales spp., while the dominant diatom was a Cyclotella sp.

The nutrient additions significantly increased total phytoplankton biovolumes (repeated measures ANOVA, Table C-7, $F_{2,3}=8.82$, $p=0.055$). After 4 wk (Fig. 3-5, see 31 July 1993), phytoplankton biovolumes had increased most in each treatment at the depths where the nutrients had been added. The dominant increase was in the diatoms, primarily due to blooms of Fragilaria. The subdominant Tabellaria, Asterionella, and Synedra spp. also increased. The Cyclotella and Dinobryon spp. declined in all three treatments. The phytoplankton community structure in the CNTL treatments remained similar to that of 3 July 1993, but the biovolume declined by 15-60%, with the largest decrease at 17 m. In the EPI treatments, biovolumes increased from 3 July 1993 in the epilimnia (an enormous 4300%) and at 10 m (52%), but decreased slightly (14%) at 17 m. The cyanobacteria
Oscillatoria also increased in the epilimnia, but only made up 6% of the total biovolume. Epilimnetic increases in the chlorophyta were due to Spondylosium sp. In the META treatments, increases in mean algal biovolumes over 3 July 1993 were greatest at depth (37% in the epilimnion, 76% and at 10 m, and 150% at 17 m). Chlorophyta increases of ~100% in the META treatments were primarily from Oocystis.

After 8 wk (Fig. 3-5, see 29 August 1993), the Fragilaria sp. bloom from 31 July 1993 was virtually gone from the EPI treatments, but had increased by 45% in the META treatments. The biovolumes in the CNTL treatments increased at all depths by between 30-160% from 31 July 1993, attaining levels comparable to the EPI and META treatments in the epilimnia and at 10 m. In the EPI treatments, increases in biovolume of the chlorophytes of up to 130% consisted primarily of Spondylosium and Gloeocystis spp. The chlorophyte increase at 17 m in the META treatments was primarily due to Chlorella spp., although a Spondylosium sp. was also present.

Periphyton Growth

Periphyton biomass inside the limnocorrals (as indicated by chlorophyll levels) was significantly increased by nutrient additions (repeated measures ANOVA, Table C-8, $F_{2,3}=123$, $p=0.001$), varying at times by up to three orders of magnitude (Fig. 3-6, a-c). Periphyton was barely detectable by eye in the CNTL treatments, but in the EPI treatments 5-20 mm thick patches developed on the limnocorral walls. Chlorophyll concentrations were always significantly lower in the CNTL treatments than in the nutrient addition treatments (post hoc Tukey's comparison, $\alpha = 0.05$). Periphyton levels were significantly higher in the
EPI than the META treatments on two of three dates; on the third date, they were not significantly different from each other (post hoc Tukey's comparison, $\alpha = 0.05$). In the EPI treatments, periphyton developed first in the epilimnion (Fig. 3-6a) and then spread deeper into the water column as the experiment progressed (Fig. 3-6b). By the end of the experiment, however, EPI periphyton levels had begun to decline (Fig. 3-6c). Overall, epilimnetic periphyton chlorophyll was always greatest in the EPI treatments (Fig. 3-6, a-c).

In the META treatments periphyton was stimulated throughout the water column, but particularly in the lower depths. Periphyton levels in the META treatment increased as the experiment progressed, eventually exceeding EPI treatment levels at 13 and 17 m on 14 September 1993 (Fig. 3-6, a-c).

For comparison, we calculated total chlorophyll a in each limnocorral's phytoplankton and periphyton component by depth-integrating the chlorophyll profiles (Fig. 3-6, d-f). Throughout the experiment the amount of periphyton chlorophyll in the CNTL treatments was $<4\%$ of the total chlorophyll. In the EPI treatments, however, between 20 and 50\% of the chlorophyll in the limnocorral was in the periphyton community. In the META treatments, periphyton developed slowly, and it never represented more than 20\% of the chlorophyll in these limnocorral.

Discussion

The metalimnetic fertilization strategy was better overall than the epilimnetic strategy for achieving the dual goals of stimulating phytoplankton and minimizing aesthetic impacts. The two strategies resulted in similar enhancement of primary production, but metalimnetic
fertilization resulted in less periphyton and cyanobacteria growth, deeper Secchi depths, and higher phytoplankton biovolume increases than the epilimnetic fertilization.

For lake fertilization to increase sockeye growth, the phytoplankton stimulated by the added nutrients must benefit zooplankton species preferred by sockeye. In Pettit Lake, *Daphnia rosea*, and to a lesser extent *Bosmina longirostris* and *Holopedium gibberum*, are favored by the sockeye. From our monitoring, we can generalize what effect changes to the phytoplankton community observed in the limnocorrals would have on Pettit Lake cladocera by focusing on *Daphnia* (Sterner 1989).

Size is the predominant factor affecting cladoceran feeding selectivity (Sterner 1989). In both the control and fertilized limnocorrals, much of the phytoplankton was <40 µm in diameter (H. Gross, unpublished data), a size range grazable by *Daphnia* (Porter 1973; Sommer 1988).

Phytoplankton taxa vary in their utility to cladocera. Diatoms (*Synedra* spp. and colonial *Fragilaria*, *Tabellaria*, and *Asterionella* spp.) contributed most of the biovolume increases in the fertilized limnocorrals. While *Daphnia* can separate individual diatoms from their colonies in order to ingest them (Lampert 1978; Infante and Litt 1985; Sarnelle 1986), cladocera handling colonial algae can experience a lower total algal clearance rate (Gliwicz and Siedlar 1980). Although *D. rosea* has not been evaluated, several investigators have shown the above diatoms to be of varying food quality for several other *Daphnia* spp. (Schindler 1971; Porter 1973; Lehman and Sandgren 1985; Infante and Litt 1985; Knisely and Geller 1986; Sommer 1988). Also, it is possible that low cladoceran grazing pressure in the limnocorrals on colonial diatoms resulted in their high abundance.
Chlorophytes stimulated by the metalimnetic treatments were of higher quality for
*Daphnia* than those present in the epilimnetic treatments. For instance, the chlorophyta
increases at 17 m in the metalimnetic treatments were primarily due to *Chlorella* sp. >5 µm
in diameter, which are of medium to high food quality for *Daphnia* (Knisely and Geller
1986). Conversely, a *Gloecystis* sp. with a gelatinous sheath, a poor planktonic food
source (Porter 1973; Sarnelle 1986; Sommer 1988), comprised a large portion of the
chlorophyte biovolume in the epilimnetic treatments on 29 August 1993. We note that our
4-wk sampling interval for taxonomic identifications may have missed some phytoplankton
community dynamics which can occur within shorter durations.

The periphyton was stimulated much less in the metalimnetic than the epilimnetic
treatments. Thus, more of the added nutrients in the metalimnetic treatments were available
for phytoplankton production than in the epilimnetic treatments, and hence, more likely to
benefit cladoceran zooplankton and, ultimately, juvenile sockeye salmon. Additionally,
increased periphyton biomass is probably more visually noticeable than is increased
phytoplankton (Goldman 1974). Thus, it appears that a metalimnetic fertilization would
have less of an impact on lake aesthetics than would an epilimnetic fertilization.

The stimulation of periphyton by nutrient additions is consistent with other research
indicating that this algal community is nutrient and/or light limited (Fairchild et al. 1985;
Mazumder et al. 1989; Marks and Lowe 1993). We hypothesize that in the epilimnetic
treatments, the fertilization enabled the periphyton to overcome nutrient limitation and
bloom in the epilimnetic waters, where light was not limiting. In the metalimnetic
treatments, the periphyton was likely still limited by nutrients in the epilimnetic waters and
by light in the metalimnetic waters. Light intensity at a depth of 15 m was <2% of surface light on the four dates it was measured between 17 July and 11 September 1993 (H. Gross, unpublished data).

Caution must be exercised when using periphyton growth observed in the limnocorral experiments to qualify periphyton growth that might result from a whole-lake fertilization. The relative amount of nutrients diverted by the periphyton in a whole-lake fertilization would probably be much less than in the limnocorral experiment due to the lake's smaller littoral zone to lake surface area ratio.

In addition to stimulating periphyton, whole-lake fertilizations may increase cyanobacteria. We observed a cyanobacteria bloom (Oscillatoria sp.) in the epilimnion of the EPI treatments on 31 July 93. While this bloom comprised only 6% of the total epilimnetic biovolume, its absolute biovolume exceeded the total epilimnetic biovolume in the META and CNTL treatments by over 100%. Thus, a metalimnetic fertilization also appears more promising in limiting cyanobacteria blooms.

Cyanobacteria often do well when TN:TP ratios are low (Schindler 1977; Flett et al. 1980). We used a TN:TP ratio in our fertilizer of 20:1 (atomic weight), hoping to preclude the occurrence of cyanobacteria, yet Oscillatoria still bloomed in the EPI treatments. If fertilizations are attempted in the Sawtooth Valley Lakes, it may be desirable to use an even higher TN:TP ratio than we used in the limnocorral experiment.

The difference in water clarity between the EPI and META treatments (Fig. 3-1) may have been reduced by the apparent vertical mixing of nutrients in the treatments resulting from our sampling activities (hauls with sampling bottles, Secchi depths, etc.). While we
were cautious to avoid unnecessary mixing during our sampling activities, some mixing was unavoidable. On a whole lake basis, where anthropogenic mixing would not be a factor, we would expect the difference in water clarity between the two treatments to be more substantial.

If whole-lake fertilizations are attempted, a more evenly spaced addition of nutrients would be desirable to the early, large addition we used in the 1993 experiments. Distributing the nutrients evenly over the summer would likely decrease the strong pulse in chlorophyll that we observed in the fertilized limnocorrals in July (Fig. 3-3), and better maintain production above controls later in the summer. This might be particularly important in the Sawtooth Valley Lakes because small-scale in situ bioassay experiments conducted in 1992 indicated that the phytoplankton were more nutrient limited in mid summer than in June (Gross et al. 1993).

Overall, the metalimnetic fertilization strategy showed more promise for minimizing water quality impacts and increasing primary production in a manner that would benefit the food web of juvenile sockeye salmon. While lake fertilization is routinely used in Alaska and British Columbia to benefit juvenile sockeye salmon, metalimnetic fertilization has rarely been employed. One vulnerability of metalimnetic fertilization is the potential for greater nutrient loss to the hypolimnion than in an epilimnetic fertilization scenario. Also, additional economic costs would be incurred implementing metalimnetic fertilization on a whole lake basis. However, the higher cost and level of uncertainty may be worth undertaking in order to lessen the impact on water quality.
References


Figure 3-1. Mean Secchi depth (n=2) by treatment in the Pettit Lake limnocorral for the duration of the experiment (10 wk). Control (CNTL), epilimnetic (EPI), and metalimnetic (META) treatments shown.
Figure 3-2. Depth profiles of total phosphorus (TP) and total nitrogen (TN) in Pettit Lake limnocorrals on three dates in 1993. Control (CNTL), epilimnetic (EPI), and metalimnetic (META) treatments shown; error bars show range (n=2). Integrated epilimnetic samples (0-4 and 0-6 m) were collected with a Tygon tube.
Figure 3-3. Mean chlorophyll a levels for Pettit Lake limnocorrals for the duration of the experiment, 1993. Concentrations in epilimnetic (a) and 0-17 m tube samples (b) are shown. Control (CNTL), epilimnetic (EPI), and metalimnetic (META) treatments shown; error bars show range (n=2). Nutrient additions began on 3 July.
Figure 3-4. Vertical profiles of mean chlorophyll $a$ and primary productivity in Pettit Lake limnocorrals on three dates in 1993. Control (CNTL), epilimnetic (EPI), and metalimnetic (META) treatments shown; error bars show range (n=2).
Figure 3-5. Mean algal biovolumes for Pettit Lake limnocorals at epilimnetic, metalimnetic, and near-bottom depths on three dates in 1993. Treatments are control (CNTL), and epilimnetic (EPI) and metalimnetic (META) nutrient treatments.
Figure 3-6. Mean chlorophyll a periphyton (above), and limnocorral periphyton versus phytoplankton chlorophyll a (below) on three dates in Pettit Lake limnocorals, 1993. Control - CNTL, epilimnetic - EPI, and metalimnetic - META treatments. (a-c) Mean chlorophyll a periphyton profiles. Treatment profiles for same date with different letters (A, B, and C) are significantly different (post hoc Tukey's, $\alpha = 0.05$, n=2). (d-f) Total phytoplankton and periphyton chlorophyll a in each limnocorral (one bar = one limnocorral).
CHAPTER 4
FERTILIZATION OF AN OLIGOTROPHIC LAKE WITH A DEEP CHLOROPHYLL MAXIMUM: PREDICTING THE EFFECT ON PRIMARY PRODUCTIVITY³

Abstract

Epilimnetic nutrient additions to large mesocosms (330 m³) in Redfish Lake, Idaho, increased levels of primary productivity and chlorophyll a, but decreased Secchi depths and light available in the meta- and hypolimnion. Redfish Lake and other Sawtooth Valley (Idaho) Lakes had deep chlorophyll maxima (DCM) in which the mean chlorophyll a peaks were 240-1000% of mean eplimnetic chlorophyll a concentrations. The DCM existed at low light levels and accounted for 36-72% of the lakes' primary production. We developed photosynthesis-irradiance (P-I) curves to predict the effects of increased chlorophyll (resulting from epilimnetic fertilization) and decreased light penetration on vertical primary productivity profiles. The simulations showed a large increase in epilimnetic primary productivity due to fertilization, and only a slight decrease in production in the deeper strata due to self-shading. Fertilization approximately doubled predicted water column primary productivity.

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Introduction

Managers have used lake fertilization to increase the productivity of sockeye salmon (Oncorhynchus nerka) rearing lakes in North America, primarily for commercial purposes (Nelson 1958; Hyatt and Stockner 1985; Stockner 1987; Kyle et al. 1988). This approach attempts to enhance trophic transfer throughout the limnetic food chain: Increases in a lake's nutrient load cause increases in the productivity of the phytoplankton community, which leads to increases in zooplankton, and ultimately, sockeye production.

We evaluated lake fertilization as a tool to help prevent the extinction of the endangered Snake River sockeye salmon (Gross et al. 1993; Budy et al. 1994; Gross et al. 1994). Due to a drastic decline (>99%) in the numbers of anadromous sockeye salmon in the Sawtooth Valley Lakes, central Idaho, USA, resource managers began a hatchery broodstock program to propagate more sockeye salmon than would otherwise survive in the lakes (Bevan et al. 1994). As pre-smolts from this broodstock program are outplanted into the Sawtooth Valley Lakes, managers may use lake fertilization to increase the fish's growth and survival rates.

The Sawtooth Valley Lakes have deep chlorophyll maxima (DCM) (Budy et al. 1995) that may be affected by lake fertilization. Chlorophyll a concentrations in these lakes can be up to 10 times greater in the meta- and hypolimnia than in the epilimnia (Steinhart et al. 1994).

DCM in lakes and oceans have varying characteristics that suggest multiple processes contributing to their formation and maintenance (Steele 1964; Anderson 1969; Hobson and
Lorenzen 1972; Venrick et al. 1973; Brooks and Torke 1977; Richerson et al. 1978; Cullen 1982; Gasol et al. 1992). DCM occur in or below the thermocline where light, temperature, and turbulence are low, but nutrients are relatively rich (Moll and Stoermer 1982). Some investigators (Shortreed and Stockner 1990; Gasol et al. 1992) maintain that most of the DCM is controlled by differential sinking rates of algal cells generated in the epilimnion, while others (Fee 1976; Abbott et al. 1984) conclude that the DCM is generated in situ by substantial levels of primary production. Investigators must exercise caution when assigning ecological significance to the DCM because phytoplankton will often increase pigment production under the low-light conditions of deeper waters (Steele 1964; Hobson and Lorenzen 1972; Kiefer et al. 1976).

In some sockeye salmon rearing lakes, juvenile *O. nerka* may primarily reside at metalimnetic depths during part of the growing season due to temperature limitations (Foerster 1968), consuming a large portion of the metalimnetic zooplankton standing stock (LeBrausser et al. 1978; Shortreed and Stockner 1990). This reduction in metalimnetic zooplankton and corresponding reduction in grazing rate on phytoplankton may also contribute to the maintenance of the DCM.

The DCM in the Sawtooth Valley Lakes are located at depths where the light levels are near or below 1% of surface light. While this light level is nominally given as the bottom of the photic zone, substantial primary production has been measured at lower light levels (Anderson 1969; Venrick et al. 1973). Increases in phytoplankton which would result from lake fertilization should decrease light available in the DCM and lead to a compression of the photic zone (Goldman 1988). Thus, we were interested in the effect this shading could have
on the phytoplankton assemblage in the DCM, and resultant effects on water column primary production.

Here we describe: (1) the DCM's relative contribution to overall lake primary production; (2) if the DCM were an artifact of increases in pigment production under low-light conditions; and (3) the effect of epilimnetic nutrient additions on primary production in the epilimnion and in the DCM. We examined these objectives by implementing a lake sampling program, conducting fertilization experiments in large-scale mesocosms, and constructing a primary productivity prediction model. Our work focused on one of the Sawtooth Valley Lakes, Redfish Lake, because it is the focus of the sockeye salmon recovery program. Data from other Sawtooth Valley Lakes are presented for emphasis of certain findings.

Study Area

The five study lakes are located in the Sawtooth National Recreation Area in southcentral Idaho (lat. 44°, long. 115°) at elevations between 1985 and 2157 m (Table 4-1). The lakes drain the east sides of the pristine, granitic Sawtooth and Smoky Mountains. These deep, steep-sided lakes were formed behind large moraines deposited by glaciers during the Pleistocene.

Nutrient levels in the lakes are low: Mean summer total nitrogen (TN) and total phosphorus (TP) concentrations in their epilimnia ranged from 65-95 and 6.5-8.6 µg/L, respectively. Correspondingly, water clarity is high, with Secchi depths ranging up to 19 m (Steinhart et al. 1994). Macrophyte abundance is low. The lakes and their watersheds are
highly prized for their recreational and aesthetic values.

Redfish Lake has a very low zooplankton biomass, dominated by *Bosmina longirostris* and *Holopedium gibberum*, with small contributions from *Daphnia rosea*, *Polyphemus pediculus*, *Epischura nevadensis*, and at least two species of cyclopoid copepods (Budy et al. 1995). The fish community includes sockeye and kokanee salmon (both *O. nerka*), bull trout (*Salvelinus confluentus*), northern squawfish (*Ptychocheilus oregonensis*), and rainbow trout (*Oncorhynchus mykiss*) (Beauchamp et al. 1993).

**Methods**

**Lake Sampling**

Sampling of Sawtooth Valley Lakes in 1993 began in March when all of the lakes were sampled through a hole sawed through 50-70 cm of ice. Redfish, Alturas, Pettit, and Stanley were sampled biweekly from mid-May (ice-out) until the beginning of October, and then again in November. Yellow Belly Lake was sampled in March, and monthly from June through September.

A Hydrolab H2O® Multiparameter Water Quality Data Transmitter was used to take vertical profiles of temperature. Vertical profiles of light extinction were measured using a Li-Cor Model LI-1000 DataLogger, a deck cell, and an underwater spherical sensor that measured photosynthetic active radiation (400-700 nm; PAR). Measurements were taken at 2-m intervals until 36 m, or to the bottom of the shallower lakes. The extinction coefficient was then calculated from the slope of the regression of the natural log of the percentage of surface intensity against depth (Wetzel 1983). The extinction coefficients
were then used to compute the depth where 1% of surface light remained. Water transparency measurements were made with a 25-cm diameter Secchi disk.

In most of the lakes chlorophyll samples were collected biweekly from the epilimnion with a tube sampler at three stations. These stations were separated by 200-500 m near the deepest part of each lake. At the central index station additional samples were taken at the 1% light level. At monthly intervals, samples from 5 to 13 other depths were collected at the index station. For chlorophyll analysis, two 50-ml aliquots per sample were filtered through 0.45-µm cellulose acetate membrane filters. Filters were placed into 6 ml of 100% methanol in the dark for 24-48 h to extract chlorophyll a. The extracts were then analyzed before and after acidification (Holm-Hansen and Riemann 1978) using a Turner model 111 fluorometer. Corrections were made for phaopigments. The fluorometer was calibrated using commercial chlorophyll a standards that were verified spectrophotometrically.

Phytoplankton samples were collected monthly from the epilimnion and 1% light level and preserved using Lugol's iodine solution. Additional epilimnetic samples were collected at biweekly intervals from some lakes. A 50- or 100-ml aliquot from each sample was filtered through a 0.45-µm mixed-ester filter (Millipore® HAWP), cleared and permanently mounted, according to the method of Crumpton (1987). Cells were counted in a minimum of 10 fields per slide at 400x; the dimensions of a minimum of 10 individuals in each taxon were measured to calculate biovolume (Wetzel and Likens 1991). Phytoplankton were taxonomically classified as follows: Cyanobacteria (blue-green algae), Chlorophyta (green algae), Chrysophyta (primarily Dinobryon sp.), Bacillariophyta (diatoms), and Dinophyta (primarily Peridinium sp.).
In situ primary production rates (PPR) of phytoplankton were measured with the $^{14}$C-technique (Wetzel and Likens 1991). Measurements were made on three dates in Redfish and Pettit Lakes, and once in Stanley and Alturas Lakes. Water from each of 8 to 9 depths was placed into three 25-ml glass scintillation vials, taking care not to expose the plankton to direct sunlight. Each vial was inoculated with 80 $\mu$L of 25 $\mu$Ci/ml of $^{14}$CHO$_3^-$. To measure nonphotosynthetic $^{14}$C uptake, we inoculated one vial from each depth with 150 $\mu$L of a saturated solution of Diuron (dichloro-phenyl-dimethylurea; DCMU), a photosynthetic inhibitor. The vials were resuspended in the water column in clear acrylic plastic tubes hung from an incubation line. Incubations were normally conducted from 10:00 a.m. to 14:00 p.m. (Mountain Standard Time). After the incubation, the vials were kept in the dark and within 2 h the entire contents of each vial was filtered through 0.45 $\mu$m cellulose nitrate filters and rinsed with 0.01N HCl. They were then air dried, and subsequently counted by liquid scintillation spectrometry using Readysafe® cocktail. Production rates were calculated by subtracting carbon uptake in the DCMU treatments from the light treatments. Dissolved inorganic carbon was estimated from pH and temperature, and alkalinity measurements determined with the Gran procedure (Wetzel and Likens 1991). Productivity in the water column was partitioned into that occurring in the epilimnion and in the lower strata. Because the lakes were not clearly stratified for much of the summer, we used a nominal depth stratum of 0-7.5 m for calculating the production that occurred in the epilimnion.

**Limnocorral Experiment**

Nutrient addition experiments took place in Redfish Lake in six cylindrical
mesocosms (limnocorrals, designed by Aquatic Research Instruments, Seattle, WA) over an 11-wk period. The 330-m³ limnocorrals were 5 m in diameter and approximately 17 m deep with open tops floated above the lake surface. They were constructed with weighted curtains of impermeable, fiber-reinforced polyethylene. The limnocorrals were unfurled slowly (12 h) through the water column with the bottoms open; thus, the initial conditions were similar to those in the lake. Once filled, scuba divers tied the bottoms closed. Each limnocorral was randomly assigned one of three nutrient treatments (n=2):

1. controls, which received no nutrient additions (CNTL),
2. low levels of nitrogen (N) and phosphorus (P) additions (LOW), and
3. high levels of N and P additions (HIGH).

At the start of the experiment, on 29 June, mean total P (TP) and total N (TN) concentrations in the limnocorrals were 5.6 (range of 5.1-5.9) µg/L and 67 (range of 63-76) µg/L, respectively. In the LOW nutrient treatment we increased P by 75% and N by 125% over the 11-wk experiment (i.e. 4.2 µg-P/L and 84 µg-N/L were added). In the HIGH nutrient treatment P and N concentrations were increased by 150% and 250%, respectively (8.4 µg-P/L and 168 µg-N/L). Nutrients were added in the form of (NH₄)₂HPO₄ and NH₄NO₃, at a 20:1 mass TN:TP ratio. The high TN:TP ratio was used to reduce the likelihood of stimulating nitrogen-fixing cyanobacteria (Schindler 1977). Weekly, nutrient solutions were stirred into each limnocorral at the surface. In order to promote rapid initial growth of the plankton community, 40% of the nutrients were added during the first week of the experiment; the remaining 60% were added in equal parts over the following 10 wk.

Since the experiment was also designed to determine whether zooplankton and fish
growth could be enhanced by nutrient additions, we added native kokanee (*O. nerka*) in lieu of endangered sockeye salmon to each of the limnocorals. The results of the nutrient additions on zooplankton and fish growth are reported in Budy et al. (1994).

We monitored chlorophyll \(a\), primary production, and light in each limnocorral. Monitoring was conducted 7 d after a nutrient addition and immediately before the subsequent addition. Samples were collected weekly for chlorophyll \(a\) analysis from the epilimnion (0- to 4, 5, or 6 m, deepening during the summer) with a depth-integrating vinyl tube. Biweekly, we collected additional chlorophyll samples from the metalimnion and near the bottom of the limnocorral with a 4-L Van Dorn bottle. At 1, 4, and 8 wk of the experiment, \(^{14}\text{C}\) primary productivity measurements were made at five depths using the methodology described above. Additional depths were sampled for chlorophyll \(a\) analysis concurrent with the primary productivity measurements. Water transparency measurements were made weekly with a 25-cm black and white Secchi disk. Vertical profiles of light intensity were measured every 2-4 wk as described above, except that measurements were taken at 1-m intervals from 0 to 17 m depth.

**Primary Production Prediction Modelling**

Because the DCM peaked below 20 m in Redfish Lake, the 17-m bottom-boundary of the limnocorals prevented us from determining, in situ, what effects shading caused by epilimnetic fertilization would have on the DCM. Therefore, we used a modelling approach to: (1) simulate the decline in PPR in the DCM that might result from shading associated with fertilization; (2) compare the reduction in PPR in the DCM to the enhancement of PPR
in the epilimnion; and (3) compare total simulated water column PPR under fertilized and unfertilized conditions.

In order to predict PPR depth profiles for Redfish Lake under the altered light and chlorophyll conditions expected with fertilization, we used photosynthesis-irradiance curves (P-I curves; Reynolds 1984). These curves relate irradiance (I) to photosynthetic rate (P, normalized to chlorophyll a biomass). They were produced using PPR, chlorophyll a, and irradiance data generated during the lake sampling and 14C measurements. The average depth-specific irradiance for the duration of each 14C measurement was used. Data from six of the eight PPR profiles measured in the Sawtooth Valley Lakes were used; two profiles were excluded (Redfish Lake, 04 July 1993 and Pettit Lake, 07 Aug 1993) due to incomplete data.

Parameters of the P-I curve, such as the initial slope of the light-limited portion of the curve (α) and the maximum photosynthetic rate (Pm B), are affected by factors such as temperature, nutrient conditions, and the species comprising the algal community. In addition, photoinhibition (characterized by β) can occur above a threshold light intensity (I T). β and I T also can vary with environmental conditions.

To partially account for the variations of the P-I curves' parameters with depth, we used two P-I curves. We separated our samples into two groups using the bottom of the thermocline, which provides an impediment to mixing, as the delineator (Platt et al. 1982; Gallegos et al. 1983). The P-I curve for samples from below the thermocline was fit using Eqn. 8 from Jassby and Platt (1976), which is based on two parameters, α and Pm B:

\[
P_z^B = P_m^B \cdot \tanh(\alpha \cdot I_z / P_m^B),
\]

(1)
where $P^B_z = P^B$ at depth $z$ and $I_z = \text{light intensity at depth } z$. The samples above the bottom of the thermocline were fit using the method of Neale and Richerson (1987), which includes $\beta$ and $I_T$, thus accounting for photoinhibition, which was frequently observed in the shallower depths of the Sawtooth Valley Lakes:

$$P^B_z = P^B \cdot \tanh(\alpha \cdot I_z / P^B_m) \cdot e^{\beta \cdot c}, \quad (2)$$

where $c = 0$ if $I_z \leq I_T$,

and $c = I_z - I_T$ if $I_z > I_T$.

The parameters for the $P-I$ curves were derived using primary productivity, chlorophyll, and light data (Table D-1) and Gauss-Newton nonlinear regressions (NLIN procedure, SAS Institute, Inc. 1988).

The $P-I$ curves were then used to predict and compare vertical primary productivity profiles under fertilized and unfertilized conditions. Predictions for unfertilized conditions were made using light and chlorophyll levels observed in the lake. Predictions for PPR profiles under fertilized conditions were based on the following alterations of observed chlorophyll and light levels:

1. The chlorophyll levels in the top 17 m (depths of 0.5, 5, 10, 13, and 17 m) were boosted over values observed in the lake by the increases we saw in the limnocorral due to the LOW levels of nutrient additions. The LOW level was chosen because most closely resembles levels which would be used for a whole-lake fertilization.

2. Light intensity at each depth was computed using the following equation, which modifies the ambient light level in the lake to include the shading caused by increases in phytoplankton resulting from the nutrient treatments:
\[ I_z = I_0 \cdot \left( e^{-\text{LE}_{\text{trt}} \cdot z_1} \right) \cdot \left( e^{-\text{LE}_{\text{cnd}} \cdot z_1} \right)^{-1} \cdot \left( e^{-\text{LE}_{\text{lake}} \cdot z_2} \right) \]  

\( I_z \) = light intensity in water at depth \( z \)  
\( I_0 \) = light intensity in water at depth 0  
\( \text{LE}_{\text{trt}} \) = mean light extinction coefficient in nutrient treatments (e.g. \( \text{LE}_{\text{low}} \) or \( \text{LE}_{\text{high}} \))  
\( \text{LE}_{\text{cnd}} \) = mean light extinction coefficient in CNTL treatments  
\( \text{LE}_{\text{lake}} \) = light extinction coefficient in lake  

For \( z = 0 \) to 17 m, \( z = z_1 = z_2 \),  
\( z > 17 \) m, \( z = z_2 \),  
\( z_1 = 17 \) m.

\( \text{LE}_{\text{trt}} \) and \( \text{LE}_{\text{cnd}} \) were selected to represent the levels of shading observed in the limnocorrals—the greater the difference between \( \text{LE}_{\text{trt}} \) and \( \text{LE}_{\text{cnd}} \), the greater the level of shading. Thus, by using recorded light extinction coefficients representing the upper, intermediate, and lower levels of shading observed in the limnocorrals, we tested the sensitivity of the shading parameter.

This approach assumes that all of the added nutrients remained in the top 17 m of the water column, stimulating the phytoplankton there. In the lake, some of these nutrients would be transported to the DCM through sedimentation and other mixing processes, possibly stimulating phytoplankton growth there (depending on whether this layer is light and/or nutrient limited).
Results

Lake Sampling

Deep chlorophyll maxima (DCM) existed in the Sawtooth Valley Lakes during the ice-free stratified season (Fig. 4-1). In mid-May, Redfish Lake was isothermal and chlorophyll levels nearly homogenous from 0-70 m, indicating that the lake mixed to the bottom in 1993. By 10 June, a DCM was observable, and it persisted through November, when the thermocline began to erode with the approach of fall overturn. The DCM peak was located below the thermocline, near and frequently below the 1% light level (Fig. 4-1). Similar DCM patterns occurred in the other Sawtooth Valley Lakes (Appendix E). The peak levels of chlorophyll a in the DCM of the Sawtooth Valley Lakes from June-October 1993 were 120-1000% higher than those in the epilimnia (Table 4-2).

The seasonal progression of epilimnetic chlorophyll a in the Sawtooth Valley Lakes in 1993 was similar to that of Redfish Lake: the highest values for the ice-free season occurred just after spring overturn in May, followed by a gradual decline to a midsummer minimum, after which levels increased (Fig. 4-2). At the 1% light level, however, chlorophyll a increased after spring overturn in each lake (as exemplified by Redfish Lake in Fig. 4-2; also see Appendix E).

Not only were chlorophyll a concentrations higher near the 1% light level, but greater algal biovolumes were supported there as well (Fig. 4-3 and Appendix F). In Redfish Lake, for example, biovolumes were on the average 170% greater at the 1% light level than in the epilimnion.
Diatoms (Synedra, Cyclotella, Melosira, and Tabellaria) and Dinobryon sp. dominated the lakes' epilimnetic biovolume early in the growing season. By late July, however, the diatoms declined in the epilimnia, and were replaced by chlorophytes and dinophytes, particularly Peridinium (Fig. 4-3 & Appendix F). Cyanobacteria were rare in all lakes (<3% of mean summer epilimnetic biovolume) except in Alturas, where they were present but non-dominant (13%).

In Redfish Lake, the chrysophyte Dinobryon sp. and the diatoms Synedra sp. and Tabellaria sp. made up a considerable portion of the biovolume of the deep algal stratum (Fig. 4-3). Diatom and Dinobryon sp. blooms occurred later in the DCM than in the epilimnion. In the other Sawtooth Valley Lakes, the deep algal stratum consisted primarily of Oocystis and Chlorella spp. (Appendix F).

Rates of primary production in the Sawtooth Valley Lakes were very low, with much of the algal growth occurring in the deep chlorophyll layer. Integrated water column productivity ranged from 9 to 27 mg C m$^{-2}$ h$^{-1}$ on the eight occasions it was measured. In Redfish Lake, 68-72% of the primary production occurred below the epilimnion. In the other Sawtooth Valley Lakes, except Stanley, >62% of the primary production occurred below the epilimnia (Fig. 4-4). Due to Stanley Lake's shallower depth and smaller non-epilimnetic photic volume, the majority of the PPR (64%) occurred in its epilimnion. Photosynthesis was measurable in all lakes to depths of at least 30 m, except in Stanley Lake, which is only 26 m deep (Table 4-1).

Primary production was usually greatest near the top of the thermocline at depths of 5-10 m (Fig. 4-4). Lowered productivity at the surface (photo inhibition) was observed in
all profiles, except for Pettit Lake on 7 August, which was an overcast, stormy day. Secondary peaks in productivity in the metalimnion were found on two of three dates in Redfish Lake, and on all three dates we made measurements in Pettit Lake. In Alturas and Stanley Lakes, secondary peaks in productivity were absent on the days measurements were taken, but both analyses were done on partially cloudy days.

**Limnocorral Experiment**

Nutrient additions to the limnocorrals caused a significant increase in chlorophyll (repeated measures ANOVA, Table C-9, $F_{2,3}=57.8$, $p=0.004$). The means (and ranges) of the weekly epilimnetic chlorophyll levels were 0.65 (0.36-1.16), 1.94 (1.49-3.41), and 2.19 (1.20-4.32) µg/L for the CNTL, LOW, and HIGH treatments, respectively (Fig. 4-5). While there was an overall significant treatment effect, the LOW and HIGH means were not significantly different from each other (post hoc Tukey's comparison, $\alpha = 0.05$). The epilimnetic chlorophyll levels in the CNTL treatments followed a trend similar to, although slightly higher than, the lake during the experiment (Fig. 4-5).

The nutrient additions caused increased chlorophyll at all depths, particularly at 17 m (Fig. 4-6, a-c). The high concentrations at 17 m may have been an artifact of the 17 m depth boundary imposed by the limnocorral bottoms. Samples collected from 17 m may have contained some phytoplankton that had sedimented out of the water column.

Nutrient additions to the limnocorrals significantly stimulated primary production (repeated measures ANOVA, Table C-10, $F_{2,3}=75.6$, $p=0.003$). Fertilization significantly increased epilimnetic production more than metalimnetic production (Fig. 4-6, d-f) (repeated
measures ANOVA, Table C-10, F_{3,9}=19.9, p<0.001). Six days after the experiment began (4 July), increased production in the epilimnia of both the LOW and HIGH treatments was apparent (ANOVA, Table C-11, F_{2,3}=9.16, p=0.053). Metalimnetic production rates, however, were similar in the control and fertilized treatments. Three weeks later (25 July) epilimnetic production was further stimulated in both the LOW and HIGH treatments (ANOVA, Table C-11, F_{2,3}=146, p=0.001), and the effects extended into the metalimnia. After four additional weeks (22 August) primary production was still enhanced by the nutrient additions (ANOVA, Table C-11, F_{2,3}=8.82, p=0.055), but the differences among treatments were less distinct.

When we integrated the phytoplankton productivity profiles through the water column, we found that nutrient additions significantly increased primary production 110-290% in the LOW treatment, and 90-490% in the HIGH (repeated measures ANOVA, Table C-12, F_{2,3}=51.1, p=0.005). A post hoc Tukey's comparison, however, showed that the increases in primary productivity resulting from the LOW and HIGH treatments were not significantly different from each other (α = 0.05).

Water transparency, as measured by Secchi depth, was significantly decreased by the nutrient additions (repeated measures ANOVA, Table C-13, F_{2,3}=57.6, p=0.004). The means of the weekly Secchi depth measurements were 11.3, 8.0, and 7.9 m for the CNTL, LOW, and HIGH treatments, respectively (Fig. 4-7). The LOW and HIGH Secchi means were significantly different from the CNTL Secchi mean but not significantly different from each other (post hoc Tukey's comparison, α = 0.05).

The LOW and HIGH treatments had 22-46% less light available at 17 m depth than
did the CNTL treatments on 25 July and 9 August (Table 4-3). On 11 July, 35-37% less light was available at 17 m, but these differences were not significantly different from the controls. Measurement of the light profiles was problematic due to shading caused by infrastructure supporting the limnocorral (e.g. docks, float tubes, sampling platforms) and this contributed to the variability in the light data. Nevertheless, it is apparent from the light, Secchi, and chlorophyll data that substantial shading was caused in the limnocorral by the nutrient additions.

**Primary Productivity Predictions**

The results of the lake sampling, the limnocorral experiment, and the P-I curves (Fig. 4-8), were used to predict primary production (PPR) depth profiles under fertilized and unfertilized conditions for two dates in Redfish Lake (Fig. 4-9). The predictions were made using a range of light extinction coefficients from Table 4-3. By using a range of light coefficients in Eq. 3, the sensitivity of this modelling approach to different levels of shading was tested. A low level of shading in the fertilized versus unfertilized scenario was modelled using $\text{LE}_{\text{high}}$ (0.212) and $\text{LE}_{\text{end}}$ (0.197) from 09 August 1993; intermediate shading was modelled using $\text{LE}_{\text{low}}$ (0.221) and $\text{LE}_{\text{end}}$ (0.197) from 09 August 1993; high shading was modelled using $\text{LE}_{\text{low}}$ (0.223) and $\text{LE}_{\text{end}}$ (0.188) from 25 July 1993. Under the low, intermediate, and high shading scenarios, 22%, 33%, and 46% less light, respectively, was available at the 17-m depth in the fertilized versus unfertilized scenario.

The simulations demonstrated a large increase in epilimnetic PPR due to fertilization, and only a slight decrease in production in the deeper strata due to self-shading (Fig. 4-9).
Depending on the level of shading used, the simulations predicted integrated water column PPR for fertilized conditions to be 183-201% of predicted PPR for unfertilized conditions for 8 August, and 175-190% for 3 September. Predicted integrated PPR for unfertilized conditions was 91% and 117%, respectively, of the actual PPR observed in the lake on 8 August and 3 September (Table D-2).

Discussion

Our results demonstrate that there are broad deep chlorophyll maxima (DCM) in the Sawtooth Valley Lakes and that higher phytoplankton biovolumes are present in these DCM than in the lake's epilimnetic waters. Furthermore, these deeper waters contribute over 60% of the primary productivity in the lakes.

The limnocorral experiment demonstrated that lake fertilization would decrease water clarity and increase shading of the DCM, thus compressing the photic zone. However, our modelling indicated that the resulting loss of primary production in the DCM under fertilized conditions would be more than offset by higher productivity in the epilimnion. Primary production in the limnocorral's 17-m water column was 90-490% greater in treatments than in the controls.

Compression of the photic zone in association with cultural eutrophication has been documented in other lakes. Coastal British Columbian sockeye-rearing lakes that received nutrient additions had shallower Secchi depths than unfertilized lakes (Stockner 1987). Goldman (1988) showed that water transparency decreased and the photic zone compressed during the onset of cultural eutrophication of ultraoligotrophic Lake Tahoe. He also found
that water column primary productivity rates increased as Secchi depth decreased.

Our approach to comparing water column primary productivity under fertilized and unfertilized conditions using P-I curves may be useful in other situations. For instance, Martin et al. (1990a, 1990b, 1991) have proposed that increased atmospheric \( \text{CO}_2 \) concentrations resulting from anthropogenic activities may be partially offset by fertilizing the ocean with iron to stimulate algal uptake of carbon. Because DCM are prominent in many of the world's oceans (Anderson 1969; Venrick et al. 1973; Kiefer et al. 1976; Cullen 1982), our approach to evaluating the effect of shading of the DCM could be incorporated into attempts to model the effects of iron enrichment of the oceans.

For lake fertilization to help in the recovery of the Snake River sockeye salmon, nutrient additions must stimulate the zooplankton that occupy waters in which sockeye salmon reside, thus allowing the energy captured in increased PPR to be transferred to the juvenile sockeye. Because juvenile sockeye often avoid water temperature >16°C (Foerster 1968), Shortreed and Stockner (1990) concluded that the effectiveness of surface fertilization of Sproat Lake (a British Columbian lake with a DCM) might be reduced because the zooplankton there did not display diel vertical migrations. Thus, the epilimnetic zooplankton that would benefit from nutrient additions would not be available to the juvenile sockeye.

These concerns are less applicable to Redfish Lake. The distribution of zooplankton in Redfish Lake's water column suggests that they may be able to convey energy gains resulting from epilimnetic nutrient additions to juvenile sockeye (Steinhart et al. 1994). Also, epilimnetic temperatures in Redfish Lake exceeded 16°C for a much shorter period of
the year than in Sproat Lake, and thus the epilimnetic zooplankton should be more available to the sockeye salmon.

An approach that might circumvent spatial and temporal concerns about juvenile sockeye habitation of the water column is to inject nutrient additions into deeper waters (metalimnetic fertilization) (LeBrasseur et al. 1978; Chapter 3 of this thesis). This approach may be more effective than surface fertilization in facilitating sockeye growth.

Although our studies were not specifically designed to isolate mechanisms responsible for the DCM's presence, we may have identified a factor contributing to their maintenance in the Sawtooth Valley Lakes. With the onset of thermal stratification following spring overturn in 1993, stream inflow temperatures (auto-logged every 36 min) were almost always colder than lake epilimnetic temperatures (H.P. Gross and W.A. Wurtsbaugh, unpublished data). Based on temperature, we estimated that the inflow water would plunge to the meta- or hypolimnion during most of the ice-free season. Diel fluctuations in the stream temperatures indicated that the entering stream water may plunge across a wide range of depths on a given day. Fluoroscene dye tracer studies in the Sawtooth Valley Lakes have confirmed the plunging inflow phenomenon (W.A. Wurtsbaugh, unpublished data), although dye entering the lake did not plunge as deeply as temperature alone would predict. Nevertheless, it appears that nutrients brought into the lake through inflow streams during the ice-free stratified period (the primary nutrient input source to lakes during this time) are first delivered to meta- and hypolimnetic waters. This may result in an improved nutrient climate over the lakes' epilimnetic waters, thus nourishing the DCM.
During the second half of our limnocorral experiment, the LOW treatments influenced primary productivity, epilimnetic chlorophyll a, and Secchi depth more than the HIGH treatments did. Although not statistically significantly, these results were unexpected, but may have been caused by differences in periphyton and zooplankton biomass between the LOW and HIGH treatments. Periphyton chlorophyll a inside the limnocorrals was 90-720% greater in the HIGH than in the LOW treatments (Budy et al. 1994). Thus, the periphyton growth in the HIGH treatments most likely deprived the phytoplankton of more added nutrients than did periphyton in the LOW treatments. In addition, the LOW treatments had greater zooplankton biomass in July, while the HIGH treatments had greater zooplankton biomass in August and September (Budy et al. 1994). Thus, dissimilar grazing pressure between treatments probably contributed to greater epilimnetic chlorophyll levels occurring in the HIGH treatments in July and in the LOW treatments in August and September.

In conclusion, decreases in light and increases in primary trophic conditions should be expected as a result of fertilization of Redfish Lake. Decreased PPR in the DCM would be more than offset by increases in the epilimnetic waters. In order for lake fertilization to be used as a tool to assist in the Snake River sockeye salmon recovery effort, energy captured in increased PPR must be effectively transferred to the zooplankton, and ultimately to the juvenile sockeye salmon, without causing adverse effects on the aquatic community and trophic structure of the Sawtooth Valley Lakes.


Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the


Kiefer, D.A., R.J. Olson, and O. Holm-Hansen. 1976. Another look at the nitrite and


Table 4-1. Physical and morphometric characteristics of the Sawtooth Valley Lakes.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Surface Area (km²)</th>
<th>Mean Depth (m)</th>
<th>Max. Depth (m)</th>
<th>Drainage Area (km²)</th>
<th>Mean Summer Secchi Depth, 1993 (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redfish</td>
<td>6.15</td>
<td>44</td>
<td>91</td>
<td>108.1</td>
<td>11.9</td>
</tr>
<tr>
<td>Alturas</td>
<td>3.38</td>
<td>32</td>
<td>53</td>
<td>75.7</td>
<td>10.4</td>
</tr>
<tr>
<td>Pettit</td>
<td>1.62</td>
<td>28</td>
<td>52</td>
<td>27.4</td>
<td>13.2</td>
</tr>
<tr>
<td>Stanley</td>
<td>0.81</td>
<td>13</td>
<td>26</td>
<td>39.4</td>
<td>7.3</td>
</tr>
<tr>
<td>Yellow Belly</td>
<td>0.73</td>
<td>14</td>
<td>26</td>
<td>30.4</td>
<td>9.2</td>
</tr>
</tbody>
</table>
Table 4-2. Chlorophyll \( a \) concentrations (\( \mu \text{g/L} \)) in the epilimnion and at the deep chlorophyll maxima (DCM) peak in the Sawtooth Valley Lakes during June-October, 1993.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Mean Epilimnetic Chl. a</th>
<th>Mean DCM Peak</th>
<th>DCM Peak Range</th>
<th>% Increase in Mean DCM Peak Over Mean Epilimnetic Chl. a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redfish</td>
<td>0.6</td>
<td>3.1</td>
<td>2.2-4.8</td>
<td>420%</td>
</tr>
<tr>
<td>Alturas</td>
<td>0.8</td>
<td>2.7</td>
<td>2.0-3.4</td>
<td>240%</td>
</tr>
<tr>
<td>Pettit</td>
<td>0.5</td>
<td>3.3</td>
<td>2.0-4.4</td>
<td>560%</td>
</tr>
<tr>
<td>Stanley</td>
<td>1.1</td>
<td>2.4</td>
<td>1.6-4.5</td>
<td>120%</td>
</tr>
<tr>
<td>Yellow Belly</td>
<td>0.6</td>
<td>6.6</td>
<td>2.6-8.2</td>
<td>1000%</td>
</tr>
</tbody>
</table>
Table 4-3. Mean light extinction coefficients, % of surface light at 17 m depth, and % shading in nutrient treatments (LOW and HIGH) compared to the control (CNTL) treatments for the Redfish Lake limnocorral, 1993. Statistics were performed on the light extinction coefficients. P-values are from ANOVAs (d.f.=2) for each date (Table C-14). Treatments with the same letter were not significantly different (Tukey’s post hoc comparison with α = 0.10).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean Light Extinction Coefficient @ 17 m Depth</th>
<th>% of Surface Light @ 17 m than CNTL Treatment</th>
<th>% Less Light @ 17 m than in CNTL Treatment</th>
<th>Tukey's</th>
</tr>
</thead>
<tbody>
<tr>
<td>CNTL</td>
<td>04 July 1993 (p=0.697)</td>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>LOW</td>
<td>0.241</td>
<td>1.68</td>
<td>--</td>
<td>A</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.247</td>
<td>1.53</td>
<td>9</td>
<td>A</td>
</tr>
<tr>
<td>HIGH</td>
<td>11 July 1993 (p=0.264)</td>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>CNTL</td>
<td>0.242</td>
<td>1.69</td>
<td>--</td>
<td>A</td>
</tr>
<tr>
<td>LOW</td>
<td>0.266</td>
<td>1.10</td>
<td>35</td>
<td>A</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.268</td>
<td>1.06</td>
<td>37</td>
<td>A</td>
</tr>
<tr>
<td>CNTL</td>
<td>25 July 1993 (p=0.068)</td>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>LOW</td>
<td>0.188</td>
<td>4.17</td>
<td>--</td>
<td>A</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.223</td>
<td>2.27</td>
<td>46</td>
<td>B</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.221</td>
<td>2.48</td>
<td>41</td>
<td>B</td>
</tr>
<tr>
<td>CNTL</td>
<td>09 August 1993 (p=0.080)</td>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>LOW</td>
<td>0.197</td>
<td>3.53</td>
<td>--</td>
<td>A</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.221</td>
<td>2.36</td>
<td>33</td>
<td>B</td>
</tr>
<tr>
<td>HIGH</td>
<td>0.212</td>
<td>2.76</td>
<td>22</td>
<td>AB</td>
</tr>
</tbody>
</table>
Figure 4-1. Chlorophyll a concentration (µg/L) and temperature (°C) profiles for Redfish Lake, 1993. When present, a '*' represents the 1% light level.
Figure 4-2. Mean chlorophyll a concentration (µg/L) in the epilimnion (n=3) and at the 1% light level (n=2) in Redfish Lake, 1993. Error bars show range.
Figure 4-3. Seasonal changes in the biovolumes of different phytoplankton taxa in Redfish Lake, 1993. (a) epilimnetic water, and (b) at the 1% light level.
Figure 4-4. Vertical profiles of primary productivity (PPR) and temperature in the Redfish, Pettit, Alturas, and Stanley Lakes in 1993. Mean and range of duplicate measurements are shown. Curves for PPR fit with spline function.
Figure 4-5. Mean chlorophyll a (µg/L) from epilimnetic tube samples (0-6 m) collected from Redfish Lake limnocorrals, 1993. Control (CNTL), low, and high fertilization treatments are shown. Lake epilimnetic chlorophyll a (µg/L) is also shown for comparison. Error bars for limnocorrals show range (n=2).
Figure 4-6. (a-c) Vertical profiles of mean chlorophyll $a$ ($\mu$g/L) and (d-f) primary productivity (mg C m$^{-3}$ hr$^{-1}$) in the Redfish Lake limnocorals, 1993. Control (CNTL), low, and high fertilization treatments are shown; error bars show range ($n=2$).
Figure 4-7. Mean Secchi depth (n=2) by treatment in the Pettit Lake limnocorrals for the duration of the experiment. Control (CNTL), low, and high fertilization treatments are shown.
Figure 4-8. Relationship between irradiance ($I_z$) and photosynthetic rates normalized to chlorophyll a ($P_z$) from six 1993 dates in the Sawtooth Valley Lakes. The curve in (a) was fit through data points measured below the bottom of the thermocline using the method of Neale and Richerson (1987). The curve in (b) was fit through data points measured above the bottom of the thermocline using the method of Jassby and Platt (1976). The curves were used to predict primary production depth profiles under fertilized and unfertilized conditions in Redfish Lake. (Data for points plotted on Fig. 4-8 are listed in Table D-1.)
Figure 4-9. Primary production profiles for Redfish Lake on two dates in 1993. (a-b) Observed and predicted primary production (P) profiles under fertilized and unfertilized conditions using intermediate shading levels. (c-d) Chlorophyll a concentrations observed in the lake under unfertilized conditions and predicted for fertilized conditions. (e-f) Light levels (I) observed in the lake under ambient conditions and predicted for fertilized conditions under intermediate shading levels.
This thesis evaluates lake fertilization of the Sawtooth Valley Lakes from two perspectives. The first perspective is of *O. nerka*’s entire ecosystem, emphasizing nutrient loading (from the lakes’ watersheds, returning adult sockeye salmon, and nutrient additions), juvenile production in the rearing habitat, and other life stages affecting smolt-to-adult survival. The second perspective is more narrow, focusing on how nutrient additions affect primary production parameters in the lakes, and the implications of these changes on *O. nerka*’s food web and lake aesthetics.

From the broader, watershed-ecosystem perspective, our monitoring and modelling indicate that Redfish Lake has not become less productive due to the decline of anadromous *O. nerka*. Marine-derived nutrients transported by sockeye salmon were relatively unimportant to the lake’s overall nutrient load. This contrasts with other Pacific Northwest sockeye salmon lakes and is primarily due to the low smolt-to-adult survival rate associated with the long migration to and from Redfish Lake. This migration is the longest and represents the greatest elevation gain of any sockeye salmon stock in the world. While short-term lake fertilization may increase growth and survival of juvenile sockeye salmon returned to Redfish Lake from a broodstock program, it would have little long-term impact on sockeye recovery under the modern migration survival rate. Increased smolt-to-adult survival would be more beneficial to achieving self-sustaining sockeye runs than would lake fertilization.
Taking the narrower, limnetic ecosystem perspective, we found that nutrient additions boosted those parameters we used to monitor the primary producers. Metalimnetic fertilization was equal to or more effective than epilimnetic fertilization in increasing chlorophyll $a$ concentrations, phytoplankton biovolume, and primary productivity, yet caused a smaller change in periphyton growth and water clarity. This is useful for managers trying to balance the aesthetic and recreation utility of the Sawtooth Valley Lakes with their value as rearing habitat for an endangered species. We also found that the lakes' deep chlorophyll maxima were important to overall lake productivity. However, modelling predicted that epilimnetic nutrient additions would result in a large increase in epilimnetic primary productivity, and only a slight decrease in production in the deeper strata due to self-shading.

By combining the two perspectives, we conclude that to restore self-sustaining runs of Snake River sockeye salmon to the Sawtooth Valley Lakes, increased smolt-to-adult survival must be achieved. The growth and survival of juveniles outplanted from the broodstock program may be enhanced through lake fertilization. However, this depends on increased production from the primary producers being effectively transferred to the crustacean zooplankton and the juvenile sockeye. Lake fertilization can assist as a stopgap measure to reduce the rate of erosion of this endangered population, but benefits from fertilization will fade soon after it is halted.
APPENDICES
### APPENDIX A

Water Budgets, Nutrient Loading, and Watershed Statistics for the Sawtooth Valley Lakes

Table A-1. Water budgets for Sawtooth Valley Lakes, 1992 and 1993. All quantities are $10^6$ m$^3$, except for $\Delta$, which is in % ($\Delta = \frac{\text{Sum of inputs} - \text{sum of outputs}}{\text{sum of outputs}} \times 100$). NHR = non-channelized hillslope runoff.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Gains</th>
<th>Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inflows</td>
<td>Ppt.</td>
</tr>
<tr>
<td><strong>1992</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redfish</td>
<td>43.2</td>
<td>1.6</td>
</tr>
<tr>
<td>Alturas</td>
<td>20.3</td>
<td>0.9</td>
</tr>
<tr>
<td>Pettit</td>
<td>7.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Stanley</td>
<td>13.0</td>
<td>0.2</td>
</tr>
<tr>
<td>Yellow Belly</td>
<td>13.2</td>
<td>0.2</td>
</tr>
<tr>
<td><strong>1993</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Redfish</td>
<td>83.4</td>
<td>3.3</td>
</tr>
<tr>
<td>Alturas</td>
<td>55.9</td>
<td>1.8</td>
</tr>
<tr>
<td>Pettit</td>
<td>19.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Stanley</td>
<td>30.0</td>
<td>0.4</td>
</tr>
</tbody>
</table>
Table A-2. Nutrient loading for the Sawtooth Valley Lakes in 1993. Ppt. = precipitation, NHR = non-channelized hillslope runoff. Because some figures are rounded off, % totals may not add up to 100.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Total (g · m² · yr⁻¹)</th>
<th>% of TP</th>
<th>% of TN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redfish</td>
<td>0.15</td>
<td>1.95</td>
<td>88</td>
</tr>
<tr>
<td>Alturas</td>
<td>0.22</td>
<td>1.98</td>
<td>92</td>
</tr>
<tr>
<td>Pettit</td>
<td>0.080</td>
<td>1.52</td>
<td>84</td>
</tr>
<tr>
<td>Stanley</td>
<td>0.49</td>
<td>4.26</td>
<td>93</td>
</tr>
</tbody>
</table>
Table A-3. Ratio of watershed to lake area, nutrient export from each stream (normalized by drainage area), and total nutrient loading per surface area of the Sawtooth Valley Lakes during 1993.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Watershed + Lake Area</th>
<th>mg/m² of drainage area</th>
<th>g/m² of lake surface</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>TP</td>
<td>TN</td>
</tr>
<tr>
<td>Redfish</td>
<td>17.6</td>
<td>10.3</td>
<td>115</td>
</tr>
<tr>
<td>Alturas</td>
<td>22.4</td>
<td>10.5</td>
<td>83</td>
</tr>
<tr>
<td>Pettit</td>
<td>16.9</td>
<td>4.6</td>
<td>80</td>
</tr>
<tr>
<td>Stanley</td>
<td>48.6</td>
<td>11.4</td>
<td>97</td>
</tr>
</tbody>
</table>

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>TP</td>
<td>TN</td>
</tr>
<tr>
<td>Redfish</td>
<td></td>
<td>0.15</td>
<td>1.95</td>
</tr>
<tr>
<td>Alturas</td>
<td></td>
<td>0.22</td>
<td>1.98</td>
</tr>
<tr>
<td>Pettit</td>
<td></td>
<td>0.08</td>
<td>1.52</td>
</tr>
<tr>
<td>Stanley</td>
<td></td>
<td>0.49</td>
<td>4.26</td>
</tr>
</tbody>
</table>
APPENDIX B

Nutrient Concentrations for Stream Inflows to
the Sawtooth Valley Lakes
1992 and 1993

The following abbreviations are used in the tables in Appendix B.

- TP - total phosphorus
- NO$_3$-N - nitrate+nitrite nitrogen
- TKN - total Kjehldahl nitrogen
- TN - total nitrogen

Table B-1. Redfish Lake Creek Inflow nutrient concentrations, 1992. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO$_3$-N + TKN.

<table>
<thead>
<tr>
<th>Date</th>
<th>TP</th>
<th>NO$_3$-N</th>
<th>TKN</th>
<th>TN</th>
<th>TN:TP</th>
</tr>
</thead>
<tbody>
<tr>
<td>26-Mar-92</td>
<td>7</td>
<td>8</td>
<td>52</td>
<td>60</td>
<td>9</td>
</tr>
<tr>
<td>11-Apr-92</td>
<td>10</td>
<td>11</td>
<td>123</td>
<td>134</td>
<td>13</td>
</tr>
<tr>
<td>13-May-92</td>
<td>6</td>
<td>32</td>
<td>21</td>
<td>53</td>
<td>9</td>
</tr>
<tr>
<td>25-May-92</td>
<td>9</td>
<td>43</td>
<td>21</td>
<td>64</td>
<td>7</td>
</tr>
<tr>
<td>31-May-92</td>
<td>6</td>
<td>44</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>12-Jun-92</td>
<td>5</td>
<td>49</td>
<td>62</td>
<td>111</td>
<td>22</td>
</tr>
<tr>
<td>19-Jun-92</td>
<td>9</td>
<td>19</td>
<td>38</td>
<td>57</td>
<td>6</td>
</tr>
<tr>
<td>29-Jun-92</td>
<td>39</td>
<td>35</td>
<td>130</td>
<td>165</td>
<td>4</td>
</tr>
<tr>
<td>09-Jul-92</td>
<td>7</td>
<td>42</td>
<td>21</td>
<td>63</td>
<td>9</td>
</tr>
<tr>
<td>22-Jul-92</td>
<td>8</td>
<td>33</td>
<td>25</td>
<td>58</td>
<td>7</td>
</tr>
<tr>
<td>01-Aug-92</td>
<td>19</td>
<td>44</td>
<td>42</td>
<td>86</td>
<td>5</td>
</tr>
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Table B-2. Redfish Lake Creek Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. \( \text{TN} = \text{NO}_3-\text{N} + \text{TKN} \).

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Table B-3. Fishhook Creek Inflow nutrient concentrations, 1992. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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Table B-4. Fishhook Creek Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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Table B-5. Alturas Creek Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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Table B-6. Pettit Lake South Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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Table B-7. Pettit Lake North Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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Table B-8. Stanley Lake Inflow nutrient concentrations, 1993. All values are in µg/L, except TN:TP ratios, which are by weight. TN = NO3-N + TKN.

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APPENDIX C

Analysis of Variance Tables

Table C-1. Repeated measures analysis of variance of log of Secchi depths in the Pettit Lake limn corrals on 11 dates in 1993.

<table>
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<tr>
<th>Source</th>
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<th>P</th>
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<td>------</td>
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Table C-2. Repeated measures analysis of variance of log of total phosphorus concentrations at 3 depths in the Pettit Lake limnocorrals on 3 dates in 1993.

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<td>0.149</td>
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<td>0.0245</td>
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<td>------</td>
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<td>Date</td>
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<td>0.251</td>
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Table C-3. Repeated measures analysis of variance of log of total nitrogen concentrations at 3 depths in the Pettit Lake limnocorrals on 3 dates in 1993.

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Table C-4. Repeated measures analysis of variance of log of epilimnetic chlorophyll a values in the Pettit Lake limnocorral for 11 dates in 1993. Due to a missing value, only 65 observations were used in this analysis.

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Table C-5. Repeated measures analysis of variance of log of 0-17 m chlorophyll a values in the Pettit Lake limnocrors for 11 dates in 1993.

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Table C-6. Analysis of variance of log of integrated water column primary production in the Pettit Lake limnocorrals for 3 dates in 1993.

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Table C-7. Repeated measures analysis of variance of log of phytoplankton biovolume at 3 depths in the Pettit Lake limnocorrals on 3 dates in 1993. Due to a missing value, only 17 observations were used in this analysis.

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<td>Treatment</td>
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<td>0.174</td>
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<td>0.105</td>
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<td>0.0540</td>
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<td>0.306</td>
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<td>1.26</td>
<td>0.315</td>
<td>8.47</td>
<td>0.012</td>
</tr>
<tr>
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<td>6</td>
<td>0.223</td>
<td>0.0372</td>
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<td>------</td>
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<td>0.0541</td>
<td>0.72</td>
<td>0.598</td>
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Table C-8. Repeated measures analysis of variance of log of integrated water periphyton growth in the Pettit Lake limnocorral on 3 dates in 1993.

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<td>------</td>
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<tr>
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<td>0.361</td>
<td>13.7</td>
<td>0.004</td>
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<td>0.158</td>
<td>0.0263</td>
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Table C-9. Repeated measures analysis of variance of log of epilimnetic chlorophyll a values in the Redfish Lake limnocorrals for 13 dates in 1993.

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<td>0.0780</td>
<td>0.0260</td>
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<td>Treatment*Date</td>
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<td>0.00546</td>
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Table C-10. Repeated measures analysis of variance of log of primary production at 5 depths in the Redfish Lake limnocorrals on 3 dates in 1993.

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<td>------</td>
</tr>
<tr>
<td>Depth</td>
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<td>1.52</td>
<td>0.506</td>
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<td>0.0255</td>
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<td>Date</td>
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<td>0.134</td>
<td>0.0223</td>
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<td>Date<em>Treatment</em>Depth</td>
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Table C-11. Analysis of variance of the log of primary production measured at 5 depths in the Redfish Lake limnocrals on 3 dates in 1993.

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<td><strong>July 4</strong></td>
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<tr>
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Table C-12. Repeated measures analysis of variance of log of integrated water column primary production in the Redfish Lake limnocorrlals on 3 dates in 1993.

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Table C-14. Analysis of variance of the log of light extinction coefficients in the Redfish Lake limnocorals on 4 dates in 1993.

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<td>August 9</td>
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</table>
## APPENDIX D

### Sawtooth Valley Lakes

### Primary Production

Data

Table D-1. Primary productivity, chlorophyll, and light profiles measured in the Sawtooth Valley Lakes, 1993.

<table>
<thead>
<tr>
<th>Lake &amp; Date</th>
<th>Depth (m)</th>
<th>Primary Productivity (mgC·m$^{-3}$·h$^{-1}$)</th>
<th>Chlorophyll a (µg/L)</th>
<th>Assimilation Number (mg C·mg Chl. a$^{-1}$·h$^{-1}$)</th>
<th>Light Extinction Coeff</th>
<th>Light @ Depth ($\mu$E·cm$^{-2}$·s$^{-1}$)</th>
</tr>
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<tbody>
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<td>0.5</td>
<td>0.63</td>
<td>-----</td>
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<td>0.195</td>
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Table D-2. Observed and predicted (unfertilized and fertilized) water column primary productivity (PPR) for two dates in Redfish Lake. The prediction for fertilized conditions was made using 33% as a mean shading level while the figures in parentheses were derived using a range (46% and 22%) of shading.

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<th>Predicted Unfertilized PPR mg C m² hr⁻¹</th>
<th>% of Observed PPR PPR</th>
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APPENDIX E

Chlorophyll and Temperature Profiles

for the Sawtooth Valley

Lakes, 1993
Figure E-1. Chlorophyll a and temperature profiles for Alturas Lake, 1993.
Figure E-2. Chlorophyll $a$ and temperature profiles for Pettit Lake, 1993.
Figure E-3. Chlorophyll $a$ and temperature profiles for Stanley Lake, 1993.
Figure E-4. Chlorophyll a and temperature profiles for Yellow Belly Lake, 1993.
APPENDIX F

Seasonal Changes in Phytoplankton Biovolume,

by Taxa, for the Sawtooth Valley Lakes

1993
Figure F-1. Seasonal changes in the biovolumes of phytoplankton taxa in Alturas Lake, 1993. (a) epilimnetic water, and (b) at the 1% light level.
Figure F-2. Seasonal changes in the biovolumes of phytoplankton taxa in Pettit Lake, 1993. (a) epilimnetic water, and (b) at the 1% light level.
Figure F-3. Seasonal changes in the biovolumes of phytoplankton taxa in Stanley Lake, 1993. (a) epilimnetic water, and (b) at the 1% light level.
Figure F-4. Seasonal changes in the biovolumes of phytoplankton taxa in Yellow Belly Lake, 1993. (a) epilimnetic water, and (b) at the 1% light level.
APPENDIX G - PERMISSION LETTER

September 4, 1995

Department of Fisheries & Wildlife
UMC 5210
Utah State University
Logan, UT 84322-5210
(801) 753-3684

Dear Ms. Budy:

I am in the process of preparing my thesis in the Fisheries and Wildlife Department at Utah State University. I plan on completing in the Fall of 1995. As you know, you are listed as a co-author of two of the three chapters of my thesis. This stems from the joint and multi-faceted nature of the investigations we conducted together during 1992 and 1993 in the Sawtooth Valley of Idaho.

I am requesting your permission to include the two manuscripts described below as part of my thesis. A footnote will be included in the thesis for each of the manuscripts below acknowledging your co-authorship. Please indicate your approval of this request by signing in the space provided below. Thank you for your cooperation and contribution to this work.

Sincerely,

Howard Gross

I hereby give permission to Howard Gross to include the following manuscripts, of which I am a contributing co-author, in his thesis at Utah State University. The manuscript titles are:

“Comparison of Epilimnetic and Metalimnetic Fertilizations on the Phytoplankton and Water Clarity of an Oligotrophic Lake,”

and

“Fertilization of an Oligotrophic Lake with a Deep Chlorophyll Maximum: Predicting the Effect on Primary Productivity.”

Phaedra E. Budy