Adding Nutrients to Enhance the Growth of Endangered Sockeye Salmon: Trophic Transfer in an Oligotrophic Lake

PHAEDRA BUDY,¹ CHRIS LUECKE, AND WAYNE A. WURTSBAUGH

Department of Fisheries and Wildlife and Ecology Center
Utah State University, Logan, Utah 84322-5255, USA

Abstract.—Snake River sockeye salmon *Oncorhynchus nerka*, listed under U.S. law as endangered in 1991 in response to a decline in anadromous adult numbers, spend their first 1–2 years in Redfish Lake, Idaho, before migrating to the sea. To determine how nutrient enhancement might influence phytoplankton, zooplankton, and fish production, we performed fertilization experiments in large enclosures in this oligotrophic lake using juvenile kokanee (lacustrine *O. nerka*) as analogues for endangered sockeye salmon. Fertilization of the metalimnion substantially increased chlorophyll *a* (150%), phytoplankton biovolume (75%), primary productivity (250%), and zooplankton biomass (200%), and moderately increased fish growth (12%) over our control enclosures. Community composition of phytoplankton and zooplankton changed little, and water transparency declined less than 15% compared with controls. Thus, we concluded that metalimnetic fertilization could maintain the aesthetic value of these lakes while increasing zooplankton food resources for juvenile salmon. Our results suggest that whole-lake fertilization would aid in the recovery of Snake River sockeye salmon.

The importance of food resources in controlling the biomass of organisms in a given trophic level has been a dominant theme in community ecology for several decades. These bottom-up effects have been predicted from theory (Fretwell 1977; Oksanen 1988; Liebold 1989; Power 1992), described from empirical relationships (McQueen et al. 1986), and tested with whole ecosystem experiments (McNaughton 1977; Langeland 1982; Peterson et al. 1993). Adding nutrients to enhance ecosystem productivity has been practiced for thousands of years and forms the foundation of agricultural and aquaculture practices. In fisheries sciences, Nelson and Edmondson (1955) demonstrated 40 years ago that lake fertilization increases production of commercially exploited stocks; lake fertilization is now commonly used in Alaska and Canada to increase growth and production of juvenile sockeye salmon *Oncorhynchus nerka* (Stockner 1981, 1987; Stockner and Hyatt 1984; Kyle 1994).

Although bottom-up effects from nutrients are measurable, our ability as ecosystem managers to predict the magnitude of these effects is weak (Power 1992). Much current ecological debate centers on determining when bottom-up effects prevail over top-down effects in defining ecosystem function (Carpenter and Kitchell 1988, 1992;

DeMelo et al. 1992; Matson and Hunter 1992). Primary production has been enhanced in many studies in which nutrients have been added to aquatic systems (Liebold 1989). In some cases, however, intense selective predation on primary consumers can weaken or obliterate the effects of nutrient additions, resulting in a strong top-down control of ecosystem function (Carpenter and Kitchell 1993). Omnivory or diet switching by consumers also can reduce trophic transfer resulting in “middle-out” effects (Polis et al. 1989; DeVries and Stein 1992). Finally, reproductive limitation of key species can uncouple the trophic link between primary producers and consumers (Koenings and Burkett 1987).

In spite of the well-known effects of nutrient additions, we know of no instance in which ecosystem fertilization has been used as a management tool to assist with the recovery of endangered populations. In this paper, we examine the potential for using lake fertilization to enhance growth and survival of endangered sockeye salmon in Redfish Lake, Idaho. Snake River sockeye salmon would probably benefit from an increase in juvenile size in making the long migration from the freshwater nursery lakes to the Pacific Ocean (>1,400 km), a journey that formerly took less than 10 d but now can take over 2 months due to delays associated with dam passage on the Columbia and Snake rivers. Similarly, predation on juvenile salmonids is thought to be highly size-specific, with small increases in growth rate translating to large differences in survival (Luecke et al.

¹ Present address of corresponding author: U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Suite I, Vancouver, Washington 98665, USA; phaedra.budy@mail.fws.gov

1990; Marschall and Crowder 1995). Thus a large-size juvenile sockeye might be better able to avoid piscivorous fish waiting in the reservoirs of these dams (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991).

We conducted a fertilization experiment in large, impermeable enclosures to compare patterns of trophic transfer in control and nutrient addition treatments. We compared nutrient concentration, chlorophyll *a*, phytoplankton biomass and composition, primary production, zooplankton biomass and composition, and fish growth between treatments. We used juvenile kokanee (a conspecific but nonendangered population of *O. nerka*) as a surrogate for sockeye salmon in this experiment and assessed the degree to which nutrient additions were transferred to increases in biomass of organisms at higher trophic levels. Kokanee are the same species as sockeye salmon but remain in the lake for the duration of their life cycle. The anadromous sockeye salmon migrate to the Pacific Ocean after 1–2 years in the nursery lake. Sockeye salmon and kokanee in Redfish Lake are monophyletic and are genetically more similar to each other than to any similar forms in another geographic area (Winans et al. 1996). In addition to their monophyletic origin, juvenile kokanee and sockeye salmon experience the same ecological conditions for the first year of their life, which makes these kokanee ideal surrogates for evaluating the factors that determine growth of endangered sockeye salmon in the freshwater nursery lake. Endangered sockeye salmon were not available for this experiment due to low numbers of broodstock progeny.

Study Site and History

Redfish Lake, one of five historical rearing lakes of endangered Snake River sockeye salmon, is located in the Sawtooth Range of central Idaho. These sockeye salmon migrate over 1,400 km from the Pacific Ocean up the Columbia, Snake and Salmon rivers to spawn in Redfish Lake. The juveniles spend 1–2 years in the nursery lake before migrating back to the Pacific Ocean. Several thousand adults once returned to the lake, but when returns diminished to less than 10 per year, the Snake River strain of Sockeye Salmon was listed under U.S. law as an endangered species (Bevan et al. 1994). The few adults that have returned in recent years were captured, and their progeny are being raised as part of an emergency broodstock program for future stocking back into the nursery lakes.

Redfish Lake, the only nursery lake that endangered sockeye have returned to in recent times, is a small, glacially formed lake situated at 1,996 m elevation. The lake is 6.15 km², 91 m in maximum depth, 44 m in mean depth, and has a 108-km² watershed. In addition to Redfish Lake, four other nearby lakes historically supported sockeye salmon. All of the lakes are ultraoligotrophic, with mean summer chlorophyll values ranging from 0.5 to 1.0 µg/L, mean summer Secchi depth transparencies ranging from 8 to 16 m, and total crustacean zooplankton biomass ranging from 1 to 120 µg/L (Budy et al. 1995). See Budy et al. (1995) for detailed limnological information on Redfish Lake and the other four historical sockeye lakes.

Methods

Fertilization experiments were performed in nine large enclosures called limnocorrals (350 m³, 5 m in diameter, and 17 m deep), made of impermeable, polyethylene plastic. The limnocorrals were slowly dropped from the surface with the bottom open, allowing each to fill with lake water during 24 h. Thus, initial conditions within each limnocorral were similar to the lake. When the limnocorral was filled, scuba divers closed the bottom section.

Three treatments were established: control (C), fish (F), and nutrients and fish (NF), each with three replicates. Treatment C received neither fish nor nutrients, and treatment F was stocked with juvenile kokanee. Treatment NF received regular additions of nitrogen and phosphorus fertilizer and was also stocked with juvenile kokanee. In a previous experiment in which we added nutrients and fish to limnocorrals at the same time, we observed large increases in chlorophyll *a* but no subsequent increase in zooplankton biomass, probably because of intense planktivory by the fish (Budy et al. 1994). Therefore, in this experiment, we added nutrients to the limnocorrals for 2 months before the fish were added. This treatment allowed the phytoplankton and zooplankton communities to respond to the fertilizer addition and overcome the time lag between fertilizer addition and zooplankton production before the planktivorous kokanee were added. Thus, the experiment was conducted in two parts. In part 1 (13 June 1994–12 August 1994), nutrients were added to three of nine limnocorrals (NF), and in part 2 (13 August 1994–11 September 1994), nutrient additions continued and fish were added to three fertilized (NF) and three unfertilized limnocorrals (F).

During the first 9 weeks of the experiment (part

1), we compared the six limnocorrals that received no nutrients (C and F) to the three nutrient addition limnocorrals (NF). In the NF treatment, nitrogen and phosphorus fertilizer was added every 10 d to the metalimnion of each limnocorral. We chose metalimnetic fertilization because Redfish Lake has a pronounced deep chlorophyll maximum in that zone and because deep fertilizations can effectively stimulate plankton production while minimizing decreases in water transparency (LeBrasseur et al. 1978; Gross et al. 1994). Nutrients were added at 11 m during part 1 of the experiment and at 12 m in part 2 of the experiment because the thermocline moved deeper.

Nitrogen and phosphorus were added to the metalimnion (11–12 m) of the NF treatment in the form of $(\text{NH}_4)_2\text{HPO}_4$ and NH_3NO_3 every 10 d at a 30:1 ratio (total nitrogen:total phosphorus, by mass; 13.5:1 molar ratio). The addition of 5 μg phosphorus/L and 150 μg nitrogen/L was designed to increase the total nutrient levels approximately 50% over levels in lake water. Similarly, the high total nitrogen:total phosphorus (TN:TP) ratio was used to reduce the likelihood of stimulating nitrogen-fixing cyanobacteria (Schindler 1977).

Juvenile kokanee were used as surrogates for the endangered sockeye salmon in these experiments. Kokanee were trapped shortly after emergence in May from Fishhook Creek, a Redfish Lake tributary, and retained in permeable mesh net-pens in Redfish Lake until addition to limnocorral fish treatments on 13 August 1994.

Limnocorrals were sampled immediately before fertilization, and every 10 d thereafter, for limnological variables including, chlorophyll *a*, zooplankton, Secchi depth transparency, temperature, and oxygen. Where applicable, data from samples taken in the lake during the experiment were provided for comparison. Water for the measurement of profiles of dissolved and total nutrients (total phosphorus, soluble reactive phosphorus (SRP), total Kjeldahl (TKN), and nitrate (NO_3)) was collected four times during the experiment (13 June, 2 July, 2 August, and 31 August).

Secchi depth measurements were recorded in each limnocorral to estimate water clarity. Temperature and oxygen profiles were measured with a Hydrolab® meter in one randomly chosen limnocorral from each of the three treatments every 10 d. Previous sampling indicated that little variation in temperature and oxygen occurred among limnocorrals in these types of experiments (Budy et al. 1994).

Water for chlorophyll-*a* analysis and nutrients

was collected with weighted polyethylene tubes for integrated depth samples and a 4-L Van Dorn bottle sampler for discrete depth samples. Epilimnetic water samples were taken with a 6-m tube, and whole limnocorral water column samples were taken with a 17-m-long (0.02-m-diameter) tube every 10 d. Discrete water samples were collected from the metalimnion (11 or 12 m) every 10 d and from near the bottom of each limnocorral (17 m) on selected dates.

Water for nutrient analyses (TP, SRP, TKN, and $\text{NO}_3 + \text{NO}_2$) was placed in polyethylene bottles previously rinsed with 0.1 N HCl and then rinsed three times with aliquots of the sample water. Nutrient samples were frozen until analysis. Unfiltered water was used for TKN and TP analyses; samples analyzed for ($\text{NO}_3 + \text{NO}_2$) and SRP were filtered through 0.45- μm membrane filters. The TP samples underwent a persulfate digestion and were then analyzed colorimetrically by the molybdate-ascorbic acid method (APHA et al. 1992). Nitrogen analyses were conducted by the University of California at Davis (Limnology Laboratory); a Kjeldahl digestion was used for TKN and the hydrazine method was used for $\text{NO}_3 + \text{NO}_2$ (APHA et al. 1992). The TN was the sum of TKN and $\text{NO}_3 + \text{NO}_2$. One randomly chosen sample for each nutrient analyzed, and for each sample date, was replicated and spiked, and standard solutions were used for quality assurance and quality control (APHA et al. 1992). Differences among mean nutrient concentrations for the two unfertilized treatments summed (C + F) versus the fertilized limnocorrals (NF) were statistically analyzed with analysis of variance (ANOVA) for each nutrient sampled (TP, SRP, TKN, and $\text{NO}_2 + \text{NO}_3$).

Chlorophyll-*a* measurements were used as a measure of phytoplankton standing crop. Two 50-mL aliquots per sample were filtered through 0.45- μm cellulose acetate membrane filters. Filters were either temporarily frozen or placed directly into 6 mL of 100% methanol for chlorophyll pigment extraction in the dark for 24 h. Extracts were then analyzed before and after acidification (Holm-Hansen and Rieman 1978) with a Turner model 111 fluorometer with corrections made for phaeopigments.

We preserved water for phytoplankton enumeration from the chlorophyll-*a* and nutrient water samples described above. One to two limnocorrals per treatment per date were selected randomly for analysis to represent each treatment on that date. Phytoplankton samples were preserved with Lugol's (iodine) solution, and a 100-mL aliquot from

each phytoplankton sample was filtered through a 0.45- μm cellulose filter. The filters were cleared and permanently mounted (Crumpton 1987). Cells were counted in a minimum of 10 fields per slide at 400 $\times$ magnification; 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 Cyanophyta (blue-green algae), Chlorophyta (green algae), Chrysophyta (*Dinobryon* sp. was the dominant chrysophyte), Bacillariophyta (diatoms), and Dinophyta (*Peridinium* sp. was the dominant dinophyte). Low numbers of replicate phytoplankton biovolume counts prevented statistical analysis of this variable.

Rates of in situ primary production (PPR) were also measured on two dates, 1 August 1994 (before fish) and 31 August 1994 (after fish), by using the ^{14}C technique (Wetzel and Likens 1991). Water from each of four depths (0.5, 6, 11 or 12, and 17 m) in all nine limnocorrals was incubated in three 25-mL glass scintillation vials. Each vial was inoculated with 80 μL of 25-microcuries $^{14}\text{CHO}_3/\text{mL}$, and one vial at each depth was inoculated with 150 μL of a saturated solution of photosynthetic inhibitor, diuron (N' -(3,4,-dichlorophenyl)-N, N-dimethyl-urea; DCMU) to measure nonphotosynthetic ^{14}C uptake. The vials were incubated at the appropriate depth in their respective limnocorrals for 4 h in clear acrylic plastic tubes. At the end of the incubation, the entire contents of each vial was filtered through a 0.45- μm cellulose nitrate filter and rinsed with 0.01 N HCl. They were then air dried and subsequently counted by liquid scintillation spectrometry. Production rates were calculated by subtracting carbon uptake in the DCMU treatments from the light treatments. Dissolved inorganic carbon was estimated from pH and alkalinity measurements determined with the Gran procedure (Wetzel and Likens 1991). Differences in primary productivity among treatments were statistically analyzed with an ANOVA for the two dates sampled.

Periphyton accumulation on the walls of the limnocorrals was evaluated by suspending weighted 17-m-long $\times$ 10-cm-wide strips of the same polyethylene limnocorral material in the center of each corral. At every other sampling period (~ 21 d), we removed two 10-mm squares from four depths (1, 6, 11–12, and 17 m) on each strip. These squares were placed immediately in 6 mL of methanol, left to extract in the dark for 24 h, and then analyzed fluorometrically for chlorophyll *a* according to the methods described above.

Zooplankton were sampled from two depth strata, 10–0 m and 17–10 m, every 10 d in each limnocorral. Two replicate samples were taken over each depth stratum with a closing 80- μm -mesh net that was 35 cm in diameter and 150 cm long and was equipped with an antireverse General Oceanics® flowmeter. Samples were immediately preserved in a 10% formalin-sucrose solution and subsequently counted and measured. The zooplankton taxa identified included four cladoceran species (*Daphnia rosea*, *Bosmina longirostris*, *Holopedium gibberum*, *Polyphemus pediculus*), one calanoid copepod (*Epischura nevadensis*), and at least two species of cyclopoid copepods. Dry biomass was calculated with length-mass regressions (McCauley 1984; Koenings et al. 1987), and densities were corrected for the volume sampled. To measure diel vertical migration of zooplankton in the limnocorrals, we sampled in the depth strata (6–0, 12–6, 17–12) both during the day (1200 hours) and then again 12 h later at night (2400 hours) on 6–7 September 1994.

Five juvenile kokanee were added to each of the three nutrient addition treatment limnocorrals (NF) and three of the fish-only control limnocorrals (F) on 12 August 1994. This density of 0.014 fish/L is slightly higher than densities of planktivores measured by means of combined hydroacoustic and trawling estimates of population abundance for localized habitats of juvenile salmon (Steinhart et al. 1993; Teuscher and Taki 1994; Beauchamp et al., in press). Fish were anesthetized with tricaine methanesulfonate (MS-222), measured for total length (TL, nearest millimeter), weighed (nearest 0.01 g), and given a unique fin clip in order to measure individual growth rates. The mean size ($\pm$ SE) of stocked fish was 0.34 g $\pm$ 0.07 and 39 mm $\pm$ 4. Fish were allowed to recover for several hours before addition to each limnocorral. At the end of the experiment, 87% (26 of 30) of the initially stocked kokanee were removed from the experiment by using dry ice asphyxiation (~ 45 kg/limnocorral). The fish were then measured and weighed. Differences in fish growth (g gained $\cdot$ g $^{-1}$ initial weight $\cdot$ d $^{-1}$) were analyzed for statistical significance with a one-way ANOVA.

Repeated-measure ANOVAs, accounting for time and initial differences among treatments, were used to analyze most limnological variables for statistical significance (Wilkinson 1990). The experiment was statistically analyzed as the two parts described above (part 1 = nutrient additions, part 2 = nutrient and fish additions). Thus, there were two treatments for part 1 with three replicates

FIGURE 1.—Temporal changes in mean ($\pm$ SE) Secchi depth in the three enclosure treatments and in Redfish Lake, Idaho. For part 1 of the experiment (pre-fish) there were only two treatments: controls (C, solid circles) and nutrient additions (N, solid squares). For part 2 of the experiment, after fish were added, there were three treatments: controls (C), fish (F, solid triangle), and nutrients and fish (NF, solid squares). The vertical dashed line indicates the start of part 2, the day the fish were added (13 August 1994). Lake values (starred points and dashed lines) are included for comparison.

for the nutrient additions (NF) and six replicates for the control treatments (C and F). For part 2, there were three replicates of the C treatment, three replicates of the F treatment, and three replicates of the NF treatment. Because of the low power of our experimental design, we chose to use an α of 0.10 to evaluate the effects of the nutrient additions.

Results

Temperature and Oxygen

Temperature and oxygen conditions in each treatment were similar and showed the same pattern observed in the lake for the duration of the experiment (Budy et al. 1994). Dissolved oxygen ranged from 6 to 9 mg/L during the experiment. Epilimnetic temperatures ranged from 11 to 15°C, metalimnetic (11–12 m) temperatures ranged from 6.5 to 12°C, and temperatures at the bottom of the limnocorral remained below 7.5°C.

Water Transparency

On any date, Secchi depth transparencies were 2–4 m shallower in fertilized limnocorrals (NF) than in the control limnocorrals (F and C; Figure 1). All limnocorrals showed a general pattern of increasing water clarity through the summer that

was similar to that observed in the lake. Before the fish were added, there was no significant difference in Secchi depth among treatments, but there were significant time and treatment $\times$ time effects (Table 1). After fish were added, time and treatment $\times$ time effects disappeared, but a significant treatment effect occurred. These results indicated that significant differences in water transparency between fertilized and unfertilized treatments arose through time and were maintained throughout part 2 of the experiment (Table 1). Secchi depth transparencies in control treatments were similar to those observed outside of limnocorrals in the open water of the lake (Figure 1).

Nutrient Analyses

Nutrient additions to the limnocorrals had relatively little effect on phosphorus levels or N:P ratios (Table 2). Total nutrient concentrations (TP and TKN) appeared slightly higher in nutrient addition treatments, but differences were not statistically significant (TP: $F = 2.27$; $df = 1,16$; $P = 0.15$; TKN: $F = 3.31$; $df = 1,8$; $P = 0.11$). Soluble nutrient concentrations were also similar in all treatments (SRP: $F = 0.03$; $df = 1,6$; $P = 0.88$; $\text{NO}_2 + \text{NO}_3$: $F = 1.48$; $df = 1,6$; $P = 0.27$). Soluble nutrient concentrations remained low throughout

TABLE 1.—Analysis of variance (ANOVA) by treatment for the limnological variables analyzed with repeated measures for the two parts of the experiment (part 1 = prefish; part 2 = postfish). Statistics for other variables analyzed with regular ANOVAs are provided in the text.

Part and source of variation	Mean square	F	df	P
Secchi depth				
Part 1				
Treatment	18.9	0.19	1	0.67584
Time	174.19	2.01	6	0.08526
Treatment $\times$ time	259.13	2.99	6	0.01584
Part 2				
Treatment	42.66	59.99	2	0.00036
Time	1.01	1.55	2	0.25843
Treatment $\times$ time	0.14	0.22	4	0.92146
Epilimnetic chlorophyll <i>a</i>				
Part 1				
Treatment	6.16	56.53	1	0.00014
Time	2.93	32.15	6	0.00000
Treatment $\times$ time	1.02	11.17	6	0.00000
Part 2				
Treatment	0.66	2.54	2	0.15852
Time	18.41	24.82	2	0.00005
Treatment $\times$ time	0.17	0.22	4	0.91953
Metalimnetic chlorophyll <i>a</i>				
Part 1				
Treatment	24.49	20.88	1	0.00258
Time	12.39	28.46	6	0.00000
Treatment $\times$ time	3.42	7.84	6	0.00001
Part 2				
Treatment	3.12	5.80	2	0.03958
Time	0.59	0.48	2	0.62806
Treatment $\times$ time	0.55	0.45	4	0.76785
Overall chlorophyll <i>a</i>				
Part 1				
Treatment	42.67	56.72	1	0.0001
Time	4.44	3.10	2	0.1029
Treatment $\times$ time	3.26	2.28	2	0.1619
Part 2				
Treatment	1.20	25.23	2	0.0012
Time	0.16	1.16	2	0.3361
Treatment $\times$ time	0.16	1.22	4	0.3569
Zooplankton biomass				
Part 1				
Treatment	3,364.64	4.43	1	0.07325
Time	3,038.16	14.39	6	0.00000
Treatment $\times$ time	826.90	3.92	6	0.00339
Part 2				
Treatment	7,145.24	4.91	2	0.05452
Time	804.47	2.89	2	0.09451
Treatment $\times$ time	479.94	1.72	4	0.20921

the experiment, indicating that nutrient uptake by phytoplankton was rapid in all treatments. The SRP concentrations remained near our analytical detection limits (1 $\mu\text{g/L}$). The ratio of total nitrogen to total phosphorus differed little between treatments. Nutrient concentrations in control treatments were generally similar to nutrient concentrations observed in lake samples (summer lake

TABLE 2.—Treatment means and SEs of nutrient concentrations in integrated water column samples (17–0 m) for the duration of the experiment in the nutrient (NF) and control (C + F) treatments for measured nutrients and for the N:P ratio. All values are in $\mu\text{g/L}$; TP = total phosphorus, SRP = soluble reactive phosphorus, TKN = total Kjeldahl nitrogen, NO_3 = nitrate, NO_2 = nitrite, N:P = total nitrogen to total phosphorus ratio.

Variable	C + F		NF	
	Mean	SE	Mean	SE
TP	10.3	0.7	12.08	0.8
SRP	2.3	0.3	2.4	0.6
TKN	52.5	7.5	84.4	16.0
$\text{NO}_3 + \text{NO}_2$	1.1	0.4	5.4	3.05
N:P	5.8		5.4	

means, $\mu\text{g/L}$: TP = 8.9, SRP = 0.5, TKN = 66.4, $\text{NO}_2 + \text{NO}_3$ = 0.8).

Phytoplankton

Nutrient additions markedly increased chlorophyll-*a* levels in the limnocorrals (Figure 2). Epilimnetic chlorophyll in the nutrient addition limnocorrals (NF) was generally 70–100% greater than in control treatments, with the exception of a peak in chlorophyll near the start of the experiment (Figure 2a). Nutrient additions significantly increased epilimnetic chlorophyll-*a* concentrations before fish were added to the experiment (Table 1). After fish were added, there was a significant time effect but no significant treatment or treatment $\times$ time effect on epilimnetic chlorophyll, indicating that the addition of fish did not influence epilimnetic algal abundance. Epilimnetic chlorophyll *a* in control limnocorrals paralleled values observed in the epilimnion of the lake (Figure 2a). Nutrient additions increased metalimnetic chlorophyll-*a* levels 150–300% over levels observed in control limnocorrals (Figure 2b). Metalimnetic chlorophyll-*a* concentrations showed the same high peak near the start of the experiment in both nutrient addition and control treatments as observed in the epilimnion. The difference in metalimnetic chlorophyll concentrations among treatments was statistically significant before fish were added (Table 1).

Chlorophyll-*a* concentrations measured from integrated samples from the whole water column (17–0 m) showed the same general pattern of nutrient stimulation observed in the epilimnetic and metalimnetic chlorophyll measurements (Figure 2c). Nutrient additions increased water column chlorophyll *a* 100–350% over control treatments. This increase in chlorophyll *a* in whole water col-

FIGURE 2.—Mean ($\pm$ SE) chlorophyll-*a* concentrations for the C, NF, and F limnocorals: (a) epilimnion values (6–0 m) for limnocorals and for Redfish Lake (starred point); (b) metalimnion (11–12 m) values for the limnocorals; and (c) whole water column tow (17–0 m) values for the limnocorals. Symbols and vertical dashed line are defined as in Figure 1.

umn samples was statistically significant for part 1 and part 2 of the experiment; there was no significant treatment $\times$ time effect for part 1 and no significant time or treatment $\times$ time effects for part 2 (Table 1). Depth profiles of chlorophyll *a* (0.5, 6, 11–12, and 17 m) taken on 2 July, 1 August, and 1 September 1994 indicated greatest chlorophyll-*a* concentrations near the metalimnion of the nutrient addition treatments. On 2 July and 1 Au-

gust, 1994, chlorophyll-*a* concentration was greatest in the metalimnion of nutrient addition treatments and greatest at the bottom of control treatments (17 m). By 1 September, however, the chlorophyll-*a* profile revealed little difference in chlorophyll-*a* concentration with depth.

Nutrient additions appeared to enhance phytoplankton biovolume in whole water column samples (17–0 m) on seven of eight dates analyzed

FIGURE 3.—Seasonal changes in the mean biovolume of identified phytoplankton taxa from integrated water column samples (17–0 m) for the three limnocorral treatments: (a) C = controls; (b) F = fish; and (c) NF = nutrient and fish. The top line in each graph corresponds to total phytoplankton biovolume. Vertical dashed line indicates date that fish were added.

(Figure 3). Early in the experiment, nutrient additions stimulated the already dominant Dinophyta and Bacillariophyta twofold to threefold above control treatments. Nutrient additions also appeared to stimulate Chlorophyta biovolume as the experiment progressed. By late August, a small peak in cyanobacteria biovolume was observed in nutrient addition treatments (NF), while chrysophytes appeared in both unfertilized treatments (C and F). Both total phytoplankton biovolume and taxonomic composition of the phytoplankton were similar among control treatments and phytoplankton sampled in the lake.

Depth profiles of phytoplankton biovolume on three dates (2 July, 1 August, and 31 August 1994) showed higher (10–350%) biovolume at all depths

in the nutrient addition treatments than in the control treatments. General trends of increasing depth of maximum phytoplankton biovolume and an overall decline in biovolume at all depths through time were observed in all treatments. The greatest phytoplankton biovolume was observed at 17 m in control treatments (C and F) and at 11 m in nutrient addition treatments (NF) on 2 July 1994. This pattern switched on 1 August 1994 when biovolume was considerably reduced at all depths in the controls, and the greatest biovolume was observed at 17 m in nutrient addition treatments.

Periphyton was not abundant in any of the limnocorrals until August and remained negligible in control (C and F) treatments throughout the experiment. A comparison of the total amount of

FIGURE 4.—Primary productivity in limnocorrals before fish were added (pre-fish, 1 August 1994) and after fish were added (post-fish, 31 August 1994) at four depths (0.5, 6, 12, 17 m). The values shown represent the mean ($\pm$ SE) of the three treatments (C = controls, F = fish, NF = nutrient and fish).

chlorophyll *a* in each limnocorral from periphyton versus that from phytoplankton shows a switch from higher phytoplankton chlorophyll *a* (phytoplankton = 1.0 $\mu\text{g/L}$; periphyton = 0.1 $\mu\text{g/L}$) early in the experiment to dramatically higher periphyton chlorophyll *a* in nutrient addition treatments by late August (phytoplankton = <1 $\mu\text{g/L}$; periphyton = 9 $\mu\text{g/L}$). Nutrient additions stimulated periphyton at all four depths sampled, and the metalimnetic (11 and 12 m) samples showed the greatest periphyton accumulation. The least amount of periphyton growth was observed in epilimnetic samples (1 and 6 m) in all treatments.

Primary production ($\text{mg C} \cdot \text{m}^{-3} \cdot \text{h}^{-1}$) was greater in the nutrient addition limnocorrals than in control limnocorrals both before and after fish were added and at all depths sampled (Figure 4). Before fish were added, primary production in the control treatments was higher in the epilimnion (0.5 m and 6 m) than the metalimnion (11–12 m) and hypolimnion (17 m). In the nutrient addition treatments, rates of primary production were greatest in the hypolimnion, followed by the metalimnion. After fish were added, rates of primary production remained higher in the nutrient addition limnocorrals than in the fish (F) or control (C) treatments. Depth-integrated mean primary production in nu-

trient addition treatments was statistically higher than in control treatments for part 1 (mean square = 6.37, 0.32; $F = 20.20$; $\text{df} = 1, 6$; $P = 0.004$) and part 2 (mean square = 1.73, 0.26; $F = 6.59$; $\text{df} = 2, 9$; $P = 0.017$) of the experiment.

Zooplankton

Zooplankton total biomass clearly responded to nutrient additions, increasing overall during the experiment (Figure 5). Total zooplankton biomass was greater in nutrient addition treatments than in control treatments from 12 July 1994 to the end of the experiment. Zooplankton biomass was very low at the start of the experiment in both treatments (<1 $\mu\text{g/L}$) but then increased 200–300% in control treatments (C and F) and 900% in nutrient addition treatments (NF). Zooplankton biomass showed significant treatment, time, and treatment $\times$ time effects for part 1 of the experiment (Table 1). The increase in zooplankton in nutrient addition limnocorrals over control limnocorrals continued after fish were added, as indicated by significant treatment and time effects. After the fish were added, total zooplankton biomass slightly increased in the F treatment compared to the C treatments. Total zooplankton biomass in control limnocorrals was generally 5–10 $\mu\text{g/L}$ higher than in

FIGURE 5.—Mean ($\pm$ SE) total zooplankton biomass for the three treatments (C = controls, F = fish, NF = nutrient and fish) and for Redfish Lake (starred points and dashed lines). Vertical dashed line indicates date that fish were added.

the lake for the duration of the experiment (Figure 5).

Zooplankton taxonomic composition in the limnocorrals was dominated by cladocerans, and cyclopoid copepods usually contributed less than 5% of the total crustacean biomass. Cladoceran zooplankton species composition was dominated by *Bosmina* and *Holopedium* in all treatments early in the experiment (Figure 6). On 22 July 1994, the species composition shifted as the proportion of *Daphnia* began to increase and the proportion of both *Holopedium* and *Bosmina* began to decline. Control treatments showed a small peak in *Holopedium* on 22 August 1994 that was not observed in either the F or NF treatments. *Daphnia* appeared slightly more abundant in the NF treatment than in either the C or F treatments during part 2 of the experiment. Trends in zooplankton taxonomic composition in all treatments closely paralleled those observed in the lake (Budy et al. 1994).

Diel vertical migration of crustacean zooplankton was minimal in all limnocorrals. During both day and night, the highest biomass of zooplankton ($\mu\text{g/L}$) was observed in the epilimnion (6–0 m) in all three treatments (35–63% of the total biomass). At night, zooplankton biomass was lowest in the bottom stratum of each limnocorral, but during the day, zooplankton biomass was similar in metalimnetic and hypolimnetic strata.

Fish Growth

Final mean weight of fish in the nutrient addition treatments was greater than in the control treatments (1.92 g and 1.78 g, respectively). Mean growth rate ($\pm$ SE) was 0.064 ($\pm$ 0.003) in the nutrient addition treatment and 0.057 ($\pm$ 0.005) in the fish treatment, a difference of 12% (Figure 7). An ANOVA indicated that this difference in fish growth was not significant (mean square = 00, 00; $F = 1.1$; $df = 1, 4$; $P = 0.36$). Although the variance for the means in this analysis was small, the power was low (42%) due to the low number of replicates per treatment ($N = 3$) (Peterman 1990).

Discussion

The limnocorral experiment was conducted to assess the likelihood that a whole-lake fertilization would enhance the growth and production of endangered juvenile sockeye salmon stocked into Redfish Lake in 1995. Previous lake fertilization studies revealed that phytoplankton production was almost always stimulated by nutrient additions (Stockner 1987; Shortreed and Stockner 1990; Kyle et al. 1997) but that increases in zooplankton and fish production were more uncertain (Stockner 1981; Koenings and Burkett 1987). Results from our limnocorral experiment showed that addition of inorganic nutrients increased primary production, chlorophyll-*a* concentration, phytoplankton

FIGURE 6.—Cladoceran zooplankton taxonomic composition in the three treatments during the experiment. The three replicate limnocoralls were averaged for each treatment (C = controls, F = fish, and NF = nutrient and fish), and data are shown as percent of total biomass of cladoceran zooplankton. Vertical dashed line indicates date that fish were added.

biomass, and zooplankton biomass. Adding nutrients for a period of time before the addition of fish appeared to stimulate trophic transfer within the food web such that zooplankton rapidly responded to increased phytoplankton food. This increase in zooplankton was available as forage for these juvenile fish.

We view the increase in zooplankton biomass as particularly important in that other analyses we have conducted indicated that zooplankton food

resources strongly affect the growth of juvenile salmon. In three Sawtooth Valley lakes (1992–1995), growth of juvenile kokanee increased with increasing food resources, and in net-pen cage experiments in two of these lakes (1993 and 1995), age-0 kokanee grew faster in the lake that had higher food availability (Figure 8; Budy 1996). The low growth rate of fish in an oligotrophic lake, such as Redfish Lake, coupled with the small number of replicates feasible in our limnocorral ex-

FIGURE 7.—Mean (+ SE) daily growth rate (weight gained, g/initial weigh, g) for kokanees in nutrient addition (filled bar) and control treatments (open bar).

FIGURE 8.—Fish growth (g/d) observed in age-0 kokanee caught in trawls during September (1992–1995) in three Sawtooth Valley lakes (circles) and from juvenile kokanee grown in net-pens in Redfish and Stanley lakes in 1993 and 1995 (squares).

periment, reduced statistical power (42%). Nevertheless, the fish in nutrient addition treatments were growing at a faster growth rate than fish grown in control treatments. We conclude that fertilization of Redfish Lake would probably enhance food resources and growth of juvenile sockeye salmon, particularly if the fertilization was initiated 4–6 weeks before fish were stocked. Currently, endangered juvenile sockeye salmon from the broodstock program are stocked into the nursery lakes in August and September (Idaho Department of Fish and Game, personal communication).

Addition of nutrients to the metalimnion rather than the epilimnion of limnocoarals indicated that enhancement of trophic transfer could occur without dramatically reducing water clarity. In a previous limnocoaral experiment in Redfish Lake, additions of nutrients to the epilimnion of limnocoarals reduced mean Secchi transparencies by 75% compared with values in control limnocoarals (Budy et al. 1994). In our present study, mean Secchi transparency in metalimnetic fertilization treatments averaged about 85% of control and lake values. Metalimnetic fertilization resulted in water transparencies always exceeding 7 m, a value associated with high water quality (Goldman and Horne 1983). Similarly, Gross et al. (1994) reported comparable differences in water transparency between epilimnetic and metalimnetic fertilization experiments.

Although nutrients in our experiments were added to the metalimnion of the limnocoarals, phytoplankton biomass was increased in both epilimnetic and metalimnetic strata. This observation suggests that the added nutrients were transferred to the top 6 m of the limnocoaral by water currents, by the movement and excretion of zooplankton and fish, and by our use of zooplankton nets and other sampling equipment. Nutrient additions stimulated the growth of sizes and species of phytoplankton that are grazeable by most cladoceran zooplankton (Porter 1973; Lampert 1978; Sommer 1988). The species composition of phytoplankton was similar among treatments and in the lake, indicating that the high N:P ratio and modest degree of nutrient addition kept nitrogen-fixing cyanobacteria from becoming dominant, as has been reported in other fertilization studies (Schindler 1977; Stockner and Shortreed 1988).

A comparison of chlorophyll *a* in the phytoplankton versus the periphyton indicated that a substantial amount of nutrients were utilized by periphyton communities growing on the sides of

the limnocoarals in the latter half of the experiment. This accumulation of high levels of periphyton in the second part of the experiment was probably due in part to the lack of periphyton grazers present in our pelagic limnocoarals. The inclusion and increased production of herbivorous zooplankton probably contributed to the decline of phytoplankton in the water column after mid-July. These differences in grazing regimes allowed for more efficient trophic transfer in the pelagic food web than in the periphyton-based community. By the end of the experiment, about 90% of the chlorophyll in the limnocoarals was on the walls. While the stimulation of periphyton is an alternative pathway of energy transfer that may influence whole-lake fertilization (Goldman 1981), the exclusion of periphyton grazers and the high surface area:volume ratio in the limnocoarals compared with the lake suggest that periphyton growth would be much less pronounced during a whole-lake fertilization. Although some nutrients were lost to periphyton in the limnocoarals, primary production of phytoplankton was significantly stimulated by nutrient additions throughout the experiment and provided sufficient food resources to maintain the increased biomass of pelagic zooplankton.

Despite the considerable increase in total zooplankton biomass in nutrient addition treatments, zooplankton taxonomic composition differed little among treatments. The small difference in zooplankton composition in nutrient addition treatments compared with controls was due to an increase in *Daphnia*, a zooplankton species preferred by juvenile salmonids (Lazzarro 1987; Luecke and Brandt 1993). Comparisons of zooplankton biomass in control treatments with that observed in the natural lake environment during similar time periods revealed that ambient densities of zooplankton in the lake were considerably lower than in control limnocoarals. Thus the refuge from fish predation for the first half of the experiment probably contributed to the greater zooplankton biomass observed in limnocoarals over ambient lake densities (Stich and Lampert 1981; Iwasa 1982; Gliwicz 1986; Stirling et al. 1990; Schmidt et al. 1994). However, the increased zooplankton biomass was maintained in nutrient addition treatments after the fish were added.

The stocking of several hundred thousand juvenile sockeye salmon into Redfish Lake over the next 3 years from the broodstock program may cause negative density-dependent effects on fish growth (Rieman and Meyers 1992). The oligotro-

phic nature and current abundance of kokanee in Redfish Lake suggest that lake carrying capacity may be exceeded by the stocking program (Budy et al. 1995; Luecke et al. 1996). The increased zooplankton biomass and fish growth rate in fertilized limnocoralls over control limnocoralls, in addition to the high growth rates demonstrated by all fish in the experiment, suggest that fertilization would increase the carrying capacity of Redfish Lake. Our experiment, in combination with limnological sampling and simulation modeling, suggests that a modest program of lake fertilization, in combination with a reduction of landlocked kokanee, could overcome these negative density-dependent effects expected to accompany the stocking of endangered broodstock individuals (Luecke et al. 1996).

These results suggest that increased growth under lake fertilization may improve the ability of these fish to thrive and ultimately return from the marine environment. If mortality is strongly size dependent, larger juvenile sockeye salmon entering the winter would likely be better able to avoid piscivorous northern squawfish *Ptychocheilus oregonensis* and bull trout *Salvelinus confluentus* in Redfish Lake (Luecke et al. 1990; Marschall and Crowder 1995). An increase in growth rate will also probably increase the survival of these juvenile fish on their perilous migration through the Snake and Columbia rivers and reservoirs (Rieman et al. 1991; Vigg et al. 1991; Peterson et al. 1993). Poe et al. (1991) demonstrated that juvenile salmonids made up 67% of northern squawfish diets in John Day Reservoir on the Columbia River, representing a mean annual loss that Rieman et al. (1991) estimated at 2.7 million juvenile salmonids per year. Further, northern squawfish consistently consumed juvenile salmonids from smaller size-groups, indicating that mortality was size-specific. These suppositions provide further support for the use of lake fertilization as a tool to enhance production of this endangered stock.

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