

# Simulated Growth and Production of Endangered Snake River Sockeye Salmon:

## *Assessing Management Strategies for the Nursery Lakes*

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### ABSTRACT

We examined the potential of employing a series of lake management strategies to enhance production of endangered Snake River sockeye salmon (*Oncorhynchus nerka*) in its historical nursery lakes in central Idaho. We used a combination of limnological sampling, experimentation, and simulation modeling to assess effects of lake fertilization and kokanee reduction on growth and survival of juvenile sockeye salmon. Juvenile sockeye salmon from a broodstock of this endangered species are being introduced into the lakes from 1995 to 1998. Results of our analyses indicated that several lakes were suitable for receiving broodstock progeny. Field experimentation and simulation modeling indicated that lake fertilization, coupled with a program of kokanee reduction, provided the management option most likely to enhance the survival of stocked juvenile sockeye salmon. Simulation models that encompass physiological requirements, ecological interactions, and life-history consequences could be used as templates to help develop recovery plans for other endangered fishes.

**S**nake River sockeye salmon historically spawned and reared in five nursery lakes in the Sawtooth Valley of central Idaho. Currently, anadromous fish return to Redfish Lake, the largest and only lake in the system that has not had local barriers to migration constructed on outlet streams. These juvenile salmon generally smolt at age-1 and migrate down the Salmon, Snake, and Columbia rivers, where they must pass through eight dams and associated reservoirs to reach the Pacific Ocean. Most individuals spend two years at sea before returning through the migration corridor to Redfish Lake (Bjornn et al. 1968).

In 1991, the National Marine Fisheries Service (NMFS) listed the Snake River stock of sockeye salmon as endangered under the Endangered Species Act (ESA) (Bevan et al. 1994). Runs had declined so precipitously that only a handful of anadromous adults were returning to Redfish Lake annually. Previous fishery assessments indicated that up to 5,000 anadromous sockeye salmon returned to Redfish Lake in the 1950s (Bjornn et al. 1968) and that perhaps 20,000 adults returned to nursery lakes in the

Sawtooth Valley near the turn of the century (Evermann 1896). This stock was listed under the ESA because its unique geographical distribution, as the most-southerly and highest-elevation stock of sockeye salmon, provided status as an evolutionarily significant unit. In this paper we evaluated a number of management options for these nursery lakes regarding production of juvenile sockeye salmon.

Although eventual recovery of this stock will depend on modifying the design and operation of mainstem dams on the Columbia and Snake rivers, some immediate steps have been taken or are being considered to enhance numbers and production of juvenile salmon in their rearing environments. The Idaho Department of Fish and Game and NMFS have established a short-term broodstock program to rapidly rebuild sockeye numbers. As part of this effort, approximately 100,000 juveniles from this broodstock program were released into nursery lakes in 1995, and several hundred-thousand juveniles are slated to be released from 1996 through 1998.

The growth and survival of progeny from this broodstock program may be compromised by large populations of native kokanee (also *O. nerka*) in the lakes. These lake-resident kokanee derive from the anadromous sockeye salmon populations in each lake (Robin Waples, National Marine Fisheries Service, Seattle, Washington, personal communication) and may have subsumed much of the lakes' capacities for rearing juvenile *O. nerka*. We evaluated the potential of using lake fertilization and/or

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kokanee reduction strategies to enhance the growth and production of juvenile sockeye salmon released from the broodstock program.

Our goals in this paper were threefold: (1) to assess the limnological conditions of five nursery lakes in the Sawtooth Valley as suitable for sockeye salmon growth and survival, (2) to evaluate the potential of lake fertilization to enhance this production potential, and (3) to evaluate the effect of resident kokanee populations in the lakes on growth of introduced juvenile sockeye salmon. Our approach combined limnological sampling, field experimentation, and simulation modeling to evaluate lake management options. Initially, we analyzed juvenile salmon growth potential and carrying capacity of each lake given information on nutrient content, phytoplankton, zooplankton, and kokanee biomass. We compared estimated carrying capacity of Redfish Lake under current and fertilized conditions using results from field experiments and simulation models. Finally, we used simulation models encompassing life-history traits of anadromous sockeye salmon and kokanee to assess relative fitness in both populations under various management scenarios. We believe this approach helped identify the relevant tradeoffs associated with different management options and could serve as a template to evaluate management options associated with restoring other fish stocks.

### Assessing Lake Carrying Capacity

Our approach in assessing lake carrying capacity was not to produce a single estimate of stocking rate for each of the lakes but rather to evaluate the likely tradeoffs that would occur between individual growth and stocking density. We evaluated the growth potential of individual sockeye salmon based on the limnological conditions of each lake, and then we assessed how increasing the density of juvenile sockeye would decrease this growth potential in each lake.

The five historical nursery lakes in the Sawtooth Valley were oligotrophic, with total phosphorus and total nitrogen concentrations in the epilimnion averaging less than 15 µg/l and 100 µg/l, respectively (Table 1). Mean summer chlorophyll concentrations in epilimnetic water remained below 1.5 µg/l for all lakes, but a substantial productivity difference was apparent, with Stanley and Yellow Belly lakes having the highest phytoplankton abundance and Redfish and Pettit lakes having the lowest (Budy et al. 1995a). Diatoms, chlorophytes, and dinofytes comprised most of the phytoplankton biovolume in 1992 and 1993

(Teuscher and Taki 1994). Biomass of crustacean zooplankton varied ten-fold in these lakes, with mean summer epilimnetic values ranging from 4 µg/l to 50 µg/l. Crustacean zooplankton was dominated by *Daphnia rosea*, *Bosmina longirostris*, and *Holopedium gibberum* (Budy et al. 1994; Teuscher and Taki 1994). In addition to kokanee and sockeye salmon, naturally reproducing pelagic fish species in Redfish, Alturas, Pettit, and Stanley lakes include redbside shiners (*Richardsonius balteatus*), northern squawfish (*Ptychocheilus oregonensis*), bull trout (*Salvelinus confluentus*), and brook trout (*S. fontinalis*). Lake trout (*S. namaycush*) are present in Stanley Lake, and cutthroat trout (*O. clarki*) are present in Yellow Belly Lake (Teuscher and Taki 1994). Rainbow trout (*O. mykiss*) are stocked annually into Redfish, Alturas, Pettit, and Stanley lakes.

The oligotrophic nature of these lakes dictates that fish production will be low. To assess the density of juvenile sockeye salmon these lakes could support, we developed a series of simulation models to estimate growth of stocked juvenile sockeye salmon. Initially, we combined a bioenergetics simulation model (Beauchamp et al. 1989) with a foraging model (Budy et al. 1995a) to assess the growth potential of a given sockeye salmon placed into the limnological characteristics of each of the five nursery lakes (Figure 1). Inputs to the model were initial fish mass and seasonal information on water temperature and crustacean zooplankton biomass, the primary food source for juvenile sockeye salmon. In model simulations, we estimated the proportion of a fish's maximum consumption at a given temperature from zooplankton biomass according to the empirically derived relationship for kokanee salmon reported in Budy and Luecke (1994).

$$P = (0.035 * ZB) / (1 + 0.077 * ZB) \quad (1)$$

where  $P$  is the temperature-specific proportion of maximum consumption, and  $ZB$  is crustacean zooplankton biomass in µg/l.  $P$  is equivalent to the  $p$ -value of Beauchamp et al. (1989). Daily consumption for each fish was

**Table 1** shows limnological conditions of Sawtooth Valley lakes in 1992–1993. Area is in hectares. Total phosphorus (TP), total nitrogen (TN), chlorophyll a (Chl), and zooplankton biomass are in µg/l and represent epilimnetic values for June–September. We estimated kokanee densities (No./Ha) from hydroacoustic surveys conducted in September 1993.

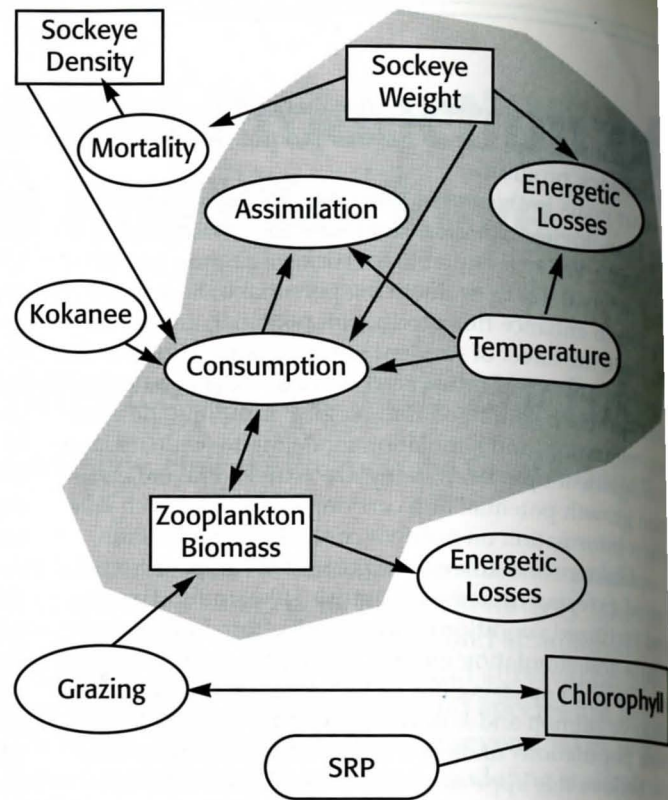
Lake	Area	TP	TN	Chl	Zooplankton Biomass	Kokanee Density
Redfish	615	7.6	58	0.52	13.0	341
Alturas	338	8.3	85	0.63	3.4	591
Pettit	162	6.2	82	0.47	38.5	162
Stanley	81	8.0	93	0.83	26.0	394
Yellow Belly	73	6.3	95	0.54	49.4	0

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determined from  $P$ , fish mass, and temperature according to the bioenergetics equations in Beauchamp et al. (1989). Energetics losses due to food processing, basal metabolism, and activity were calculated using Beauchamp et al. (1989). We used energetics gains and losses to derive a daily change in mass of an individual fish.

We used the foraging and energetics model to estimate the growth potential of juvenile sockeye salmon in each of the nursery lakes given seasonal temperature and zooplankton biomass measured in 1992. Results of these simulations suggested that introduced sockeye salmon would exhibit much higher growth rates in Stanley, Pettit, and Yellow Belly lakes than in Redfish and Alturas lakes (Figure 2). To assess the reasonableness of these model predictions we used resident kokanee as analogues for endangered sockeye salmon and compared mass of age-0 kokanee captured in trawls from Redfish, Alturas, and Stanley lakes to model predictions (Figure 2). Predictions from the foraging and energetics model were similar to growth of kokanee in the three lakes, indicating that this model was a useful tool for assessing growth potential of juvenile *O. nerka* in Sawtooth Valley lakes. A more complete description of the validation and sensitivity analysis of this model is presented in Budy and Luecke (1994).

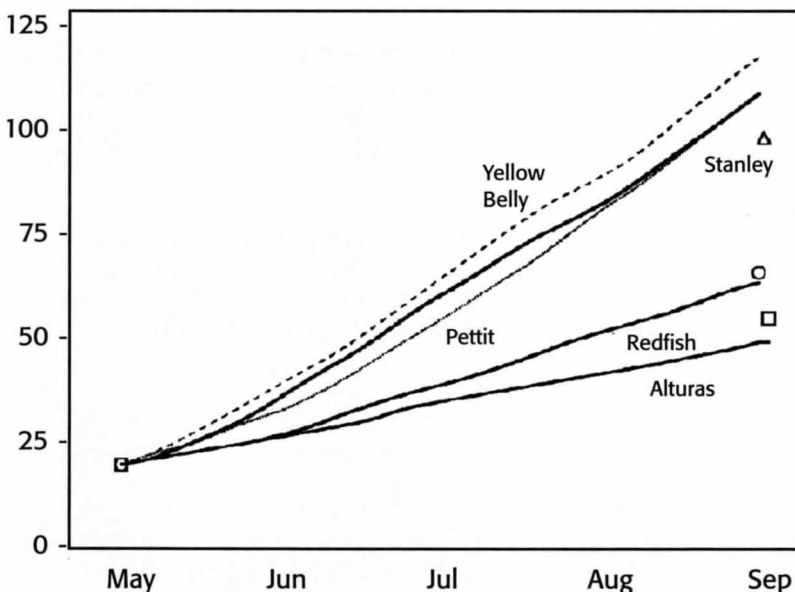
The simulated low growth potential for *O. nerka* in Alturas Lake indicated that it would be a poor candidate to receive broodstock progeny (Figure 2). The higher growth potentials in Pettit, Stanley and Yellow Belly lakes caused managers to consider these lakes as viable options, in addition to Redfish Lake, for stocking juvenile sockeye salmon. Large numbers of piscivorous lake trout captured in Stanley and cutthroat trout captured in Yellow Belly Lake (Spaulding 1993) reduced their appeal; thus, managers chose Pettit Lake to receive broodstock progeny in 1995. Even though the growth potential of individual sockeye salmon stocked into Redfish Lake was low, the lake has recently produced sockeye salmon that successfully returned from the sea, indicating that current limnological conditions are suitable for sockeye-rearing. The large size of Redfish Lake compared



**Figure 1** presents the conceptual diagram of the bioenergetics and lake carrying capacity model used to predict sockeye salmon growth and production. Components of the bioenergetics module are enclosed within the shaded area. Initial fish mass, zooplankton biomass, and temperature are inputs for the energetics simulations; temperature, soluble reactive phosphorus (SRP), and initial concentrations of chlorophyll, zooplankton, and kokanee are inputs for the carrying capacity model. Rectangles designate state variable and ovals designate functions. Model simulations began with varying densities of 1-g sockeye salmon stocked on 1 June.

with the other four lakes (Table 1) is also an advantage in efforts to produce a large number of sockeye smolts.

Limnological measurements and model simulations suggested that Redfish and Pettit lakes were the best candidates for broodstock introductions. To estimate the effects of stocking densities of juvenile sockeye salmon in each lake, we augmented the simulation model to include phytoplankton, zooplankton, and fish production (Figure 1). State variables for zooplankton biomass, chlorophyll, and kokanee and sockeye biomass varied according to differential equations describing the gains and losses of each component. State variables were expressed as wet biomass in  $\mu\text{g}/\text{l}$  using a 0.2 day time step. We modeled zooplankton production using energetics relationships for *Daphnia* (McCauley et al. 1990) and smaller crustaceans (Richman 1964).



**Figure 2** (left) illustrates bioenergetics simulations of age-0 *O. nerka* growth in five Sawtooth Valley lakes for 1992. Solid (Alturas, Redfish and Stanley) and dotted (Pettit and Yellow Belly) lines represent simulation runs for each lake; the square, circle, and triangle represent the mean total length of age-0 kokanee captured in trawls from Alturas, Redfish, and Stanley lakes in late September.

Zooplankton consumed phytoplankton based on a type-II functional response:

$$\text{Grazing} = (0.36 \text{ Chla}) / (0.8 + \text{Chla}) \quad (2)$$

where Grazing is zooplankton consumption (g/g/day), and Chla is the concentration of chlorophyll in µg/l. We assumed zooplankton assimilation of ingested algae to be 66%. Losses to metabolism were 12% of body mass per day, and additional losses came from kokanee and sockeye consumption (Luecke et al. 1992). These losses from fish predation were calculated from the foraging and energetics model described earlier.

Chlorophyll production varied as a function of dissolved phosphorus and algal biomass according to the modified Monod equation of Vanni et al. (1992):

$$\text{Ppr} = (1.37 \text{ SRP} / (1.2 + \text{SRP})) / (\text{Chla} / 0.82) \quad (3)$$

where Ppr is specific production of chlorophyll (g/g/day), and SRP is soluble reactive phosphorus (µg/l). The constants 1.37, 1.2, and 0.82 describe the maximum daily algal reproductive rate, the half-saturation constant of algae for phosphorus, and a self-shading coefficient, respectively.

Daily mortality of stocked juvenile salmon was modeled as a size-dependent process according to the relationship of Miller et al. (1988):

$$\text{Mort} = 0.01 (10^{-0.185 W}) \quad (4)$$

where Mort is the proportion of the population dying per day, and W is the mass of individual sockeye salmon (g).

Grazing by zooplankton reduced chlorophyll concentrations (Equation 2). We used seasonal information on dissolved phosphorus as an input to the simulations. When measured dissolved phosphorus was below detection limits (1.0 µg/l), we assumed a value of 0.7 µg/l. This assumption provided chlorophyll concentrations in model simulations that were similar to lake values.

Results of these simulations indicated that density dependence of salmon growth was strong in both lakes (Figure 3). In Redfish Lake stocking 200,000 juvenile sockeye salmon (325 per Ha) in June reduced growth of each individual by 30% compared to baseline simulations (5 per Ha). In Pettit Lake, stocking a similar density of juvenile sockeye salmon reduced individual growth potential by 38%. The greater density dependence exhibited in Pettit occurred because of lower nutrient concentrations and subsequent lower primary and secondary production in Pettit Lake. Results of these simulations suggested that stocking more than 200,000 (325 per Ha) juvenile sockeye salmon into Redfish and 20,000 (125 per Ha) sockeye into Pettit would substantially

reduce zooplankton populations in each lake. Model simulations indicated that stocking 300 juvenile sockeye salmon per hectare into Redfish and Pettit lakes would reduce growth of individuals to 70% of values currently observed in Redfish Lake.

### Evaluating Lake Fertilization

Growth and production of juvenile sockeye salmon have been enhanced in other systems by adding inorganic nutrients to nursery lakes (Hyatt and Stockner 1985; Stockner 1987; Kyle et al. 1988). To evaluate the potential of using lake fertilization to enhance sockeye salmon production in Sawtooth Valley lakes, we conducted an *in situ* mesocosm experiment in 1994 and incorporated these results into the simulation model to compare trophic transfer in Redfish Lake under natural and fertilized conditions (Budy et al. 1995b). Six large, impermeable limnocorrals (5 m in diameter by 17 m deep) were placed in Redfish Lake and allowed to fill with lake water. After the bottoms were sealed to prevent any additional water exchange, we added nutrients in the form

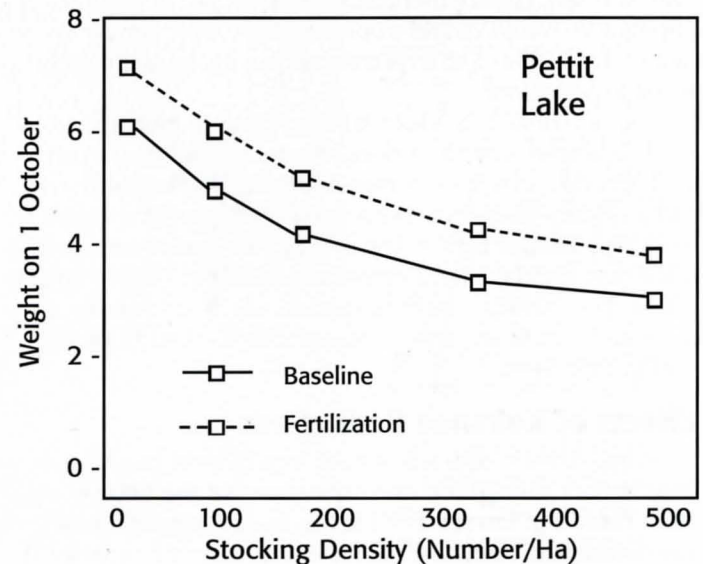
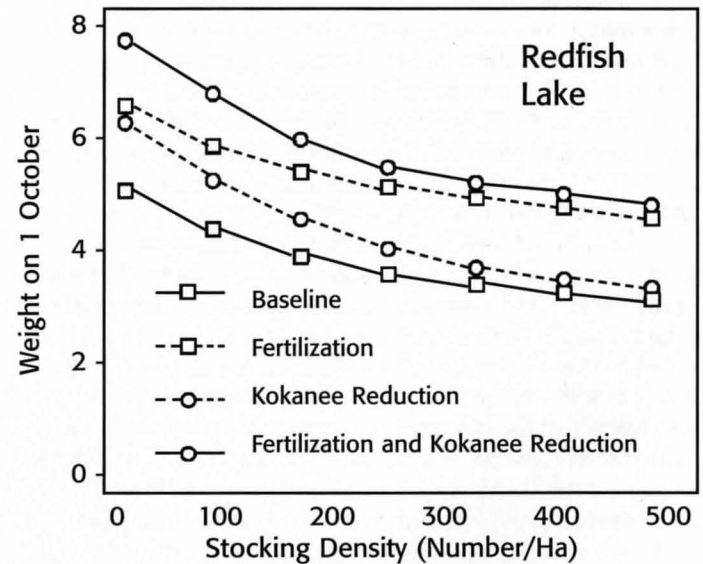


Figure 3 (right) shows effects of sockeye stocking density on growth of individual juvenile sockeye salmon in carrying capacity simulations for Redfish Lake (top panel) and Pettit Lake (bottom panel). Wet weight (g) of individuals on 1 October is plotted for simulations where 1-g fish were stocked on 1 June. Baseline conditions consider only effects of stocking density on growth. Fertilization was modeled as a 50% increase in concentration of soluble reactive phosphorus in the water column. Kokanee reduction was modeled as a 50% decrease in survival of age-0 kokanee.

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of ammonium phosphate and ammonium nitrate to 3 of the corrals every 10 days from 13 June through 11 September (see photograph). These regular additions added 5 µg/l P and 150 µg/l N to the fertilized corrals by the end of the experiment, an increase of 66% and 260% above ambient levels. On 12 August, five juvenile kokanee salmon (mean weight 0.34 g) were added to each of the three fertilized limno-

corrals and to each of the three corrals without nutrient additions. On 13 September, the fish were retrieved from the limnocorrals and measured for length, wet mass, and dry mass.

Additions of nitrogen and phosphorus to the limnocorrals increased chlorophyll concentrations, zooplankton biomass, and fish growth (Table 2). In fertilized limnocorrals, chlorophyll concentrations increased to 160% of nonfertilized treatments. Zooplankton biomass and kokanee growth rate in fertilized treatments increased 222% and 20% respectively over unfertilized values. Budy et al. (1995b) presents a more complete analysis of results from this experiment. Our results indicated that lake fertilization has potential to increase sockeye growth in Sawtooth Valley lakes.

We simulated fertilization of Redfish Lake by running the food web model with enhanced values of dissolved phosphorus (SRP). We assumed baseline values of SRP to be 1.0 µg/l and lake fertilization to increase SRP concentrations by 50%. These baseline values were similar to those measured in Redfish Lake in 1992–1993, and proposed fertilization plans call for increases in nutrients of 30%–50%. Initial simulations were conducted using information from the limnocorral experiment. Predictions from the food web model were similar to experimental results (Table 2). The model underestimated zooplankton biomass and fish growth and overestimated chlorophyll concentrations, but in general, population dynamics and trophic transfer were similar in model simulations and experimental results from the limnocorral experiments.

In simulations of a whole-lake fertilization, nutrient additions enhanced growth of stocked juvenile sockeye salmon at all stocking densities examined (Figure 3). Fertilization had a slightly greater effect on individual growth at high stocking densities than at low ones. These simulations indicated that with lake fertilization an additional 180,000 juvenile sockeye salmon could be stocked into Redfish Lake and maintain individual growth rates similar to conditions present in 1992–1994.

### Effects of Kokanee Reductions

Strong density-dependent effects on *O. nerka* growth evident in both simulations and cage experiments (Budy et al. 1994; Budy and Luecke 1994) led us to conclude that kokanee densities in Redfish Lake were near carrying capacity. It

**Table 2.** Mean limnological conditions in Redfish lake limnocorral experiment conducted in 1994 are compared with predictions from the simulation model. Control enclosures received no added nutrients, whereas fertilized treatments received additions of 5 µg/l P and 150 µg/l N during the course of the experiment.

Treatment or Simulation	Chl a (µg/l)	Zooplankton biomass (µg/l)	Fish growth (%/day)
Control corrals	0.42	20.1	3.3
Control simulation	0.62	22.3	2.6
Fertilized corrals	1.10	64.7	4.0
Fertilized simulation	0.78	42.5	3.5

populations have collapsed (Budy et al. 1994). During the past 40 years, increased mortality on the anadromous form of *O. nerka* could have shifted relative fitness to favor lake resident kokanee (Gross 1991). These suppositions indicate that reducing the current number of kokanee in Redfish Lake may be a necessary and appropriate strategy to restore a population of anadromous sockeye salmon.

To evaluate the impact of reducing kokanee abundance on growth of stocked sockeye salmon, we conducted two types of modeling simulations. First, we examined the immediate impact of reducing kokanee recruitment on juvenile sockeye growth by running the food web model assuming a 50% reduction in age-0 kokanee under both unfertilized and fertilized conditions. Second, we were concerned that lake fertilization might benefit lake resident kokanee to a greater extent than anadromous sockeye salmon. To evaluate how lake fertilization might differentially affect kokanee and sockeye populations through longer time scales, we developed a life history simulation.

Results from the food web simulations suggested that a one-year reduction in age-0 kokanee would have a small impact on individual sockeye growth (Figure 3). Model simulations indicated that lake fertilization alone would have a much greater effect on enhancing sockeye growth compared with kokanee reduction. The combination of lake fertilization and kokanee reduction was additive in its effect on sockeye growth potential. Only at very low stocking rates did the relative impact of kokanee reduction approach the effect of lake fertilization. These simulations suggest that an additional 210,000 juvenile sockeye could be stocked into Redfish Lake with lake fertilization and kokanee reduction and still maintain *O. nerka* growth rates similar to those existing during the 1992–1994 period.

The kokanee-sockeye life-history simulations derive from simple life-history models (Gross 1991) and a relationship between indices of lake productivity and kokanee production (Gross and Wurtsbaugh 1994 as calculated from Riemann and Meyers 1992). In model simulations, total phosphorus loading determines mean summer chlorophyll concentrations, according to Vollenwieder (1976) (Table 3). We determined production of juvenile *O. nerka* from mean summer chlorophyll concentrations. *Oncorhynchus nerka* production was divided into kokanee and sockeye production based on

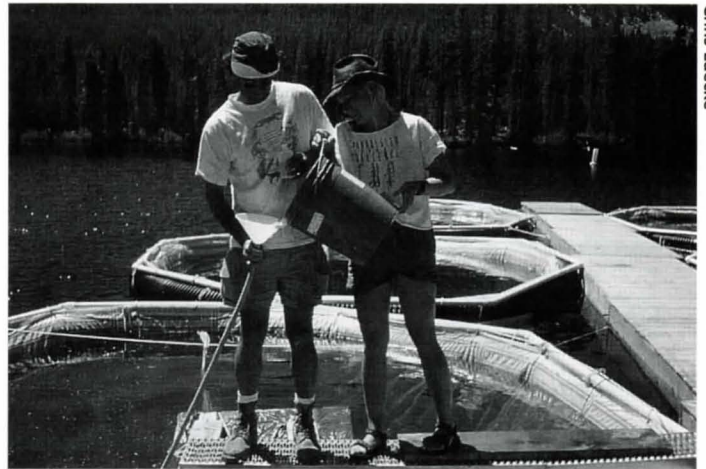
seems unlikely that current kokanee densities (360 individuals per Ha, Teuscher and Taki 1994) were present when several thousand anadromous sockeye salmon spawned in the lake, resulting in upward of half-a-million fry (Bjornn et al. 1968). The high density of kokanee estimated for Alturas Lake in 1993 (Table 1) appears to have exceeded carrying capacity in that crustacean zooplankton

the number of eggs deposited by each population each year. Age-specific rates of mortality and egg deposition were estimated from Snake River sockeye salmon (Bowles and Cochnauer 1984) and are presented in Table 3. Phosphorus loading was 715 kg annually as calculated from the mean of 1992–1993 nutrient budgets (Gross and Wurtsbaugh 1994). We assumed that lake fertilization would increase total phosphorus concentrations by 50% in model simulations.

The life-history simulations indicated that under current mortality and growth rates of kokanee and sockeye, greater than 98% of the *O. nerka* production would be channeled to kokanee (Figure 4). This extinction pathway has likely operated in the Redfish Lake sockeye population during the past several decades, where the higher growth of marine sockeye salmon compared to that of lake-resident kokanee could not overcome the increased mortality associated with downstream migration in the anadromous life history. Model simulations indicated that most of the benefits of lake fertilization would go toward producing a larger, faster-growing kokanee population (Figure 4). This result occurred because of the survival advantage of kokanee and because each kokanee resided in the more-productive fertilized lake environment for four years, whereas individual sockeye derived benefits from lake fertilization for only one year. Model simulations indicated that the sockeye population would benefit from lake fertilization only if survival of age-0 kokanee was reduced by 50%–70% (Figure 4). Reducing survivorship of age-0 kokanee by 70% resulted in approximately 60% of the *O. nerka* production shifting to the sockeye life history.

## Discussion

Information gathered from lake investigations and simulation modeling produced novel insights into the management of lake environments for juvenile sockeye salmon. Previous attempts to predict lake carrying capacity for fish relied heavily on empirical regression models using lake area (Plante and Downing 1993), euphotic volume (Koenings and Burkett 1987), primary production (Downing et al. 1990), and zooplankton biomass (Schmidt et al. 1994). Our inclusion of the



Howard Gross and Phaedra Budy add fertilizer to one of the limnocorrals in Redfish Lake.

processes of trophic transfer, in simulations of the food webs of our oligotrophic lakes, allowed us to explicitly examine the effects of a variety of interactions unaccounted for in the empirical models.

**Table 3** shows assumptions of the kokanee-sockeye life history model. Values represent mean conditions from 1992 to 1993. P is total phosphorus in  $\mu\text{g/l}$ ; Chl-a is concentration of chlorophyll in  $\mu\text{g/l}$ . Fish biomass and egg deposition is in g. Sockeye survival estimates are from Bowles and Cochnauer (1984). Kokanee survival estimates are based on hydroacoustic surveys of kokanee abundance (Teuscher et al. 1994).

### General assumptions

P-loading is determined from stream inflows (715 kg/year), lake fertilization (357 kg/year), and salmon migration. Chl-a is determined from P-loading according to Vollenweider (1976)  $0.0182 * (\text{P-loading}/\text{lake area})^{0.91}$ . Production of *O. nerka* is determined from Gross (1995)  $10^{(2.12 + 1.04 \log(\text{Chl-a}))} * \text{lake area}$ . *O. nerka* production is partitioned into sockeye and kokanee based on the relative mass of kokanee and sockeye eggs each year. Simulations begin with 100,000 age-0 kokanee and 100,000 age-0 sockeye.

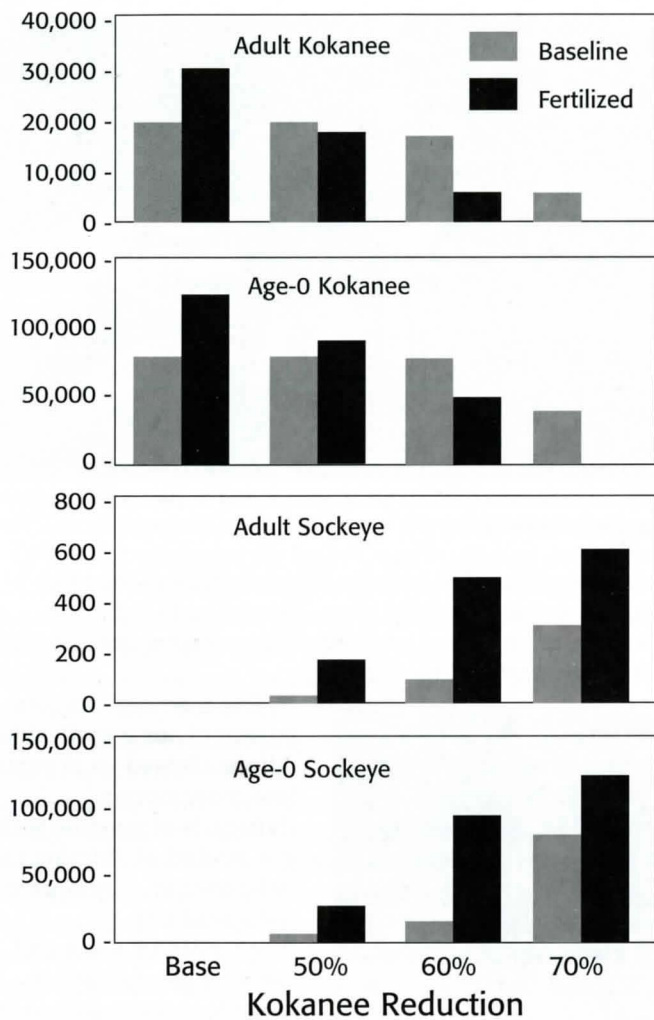
### Kokanee survival and growth

Survival from first September to second September is 0.5. Kokanee reduction scenarios reduce this rate. Subsequent annual survival is 0.7. Individual kokanee mass = age-specific mass  $*(0.88 + 1.12(\text{Chl-a}))$ . Kokanee egg deposition =  $0.11 * \text{kokanee spawning mass}$

### Sockeye survival and growth

Juvenile downstream survival is 0.025. Annual ocean survival is 0.59. Upstream survival of adults is 0.46. Adult sockeye mass =  $2240 * (0.8 + \text{Chl-a} * 0.2)$ . Sockeye egg deposition =  $0.15 * \text{adult sockeye mass}$

The bioenergetics component of our growth simulations allowed us to simulate consumption dynamics of juvenile sockeye stocked at differing initial densities. The large initial size of our hatchery-reared fish and the high growth rate of juvenile sockeye salmon in Redfish Lake resulted in differences in predicted carrying capacity between our models and those used in sockeye stocking programs in Alaska (Kyle et al. 1988) and British Columbia (Stockner 1987). Our model simulations suggested maximum stocking rates of 200–300 juvenile sockeye per hectare compared with values two to three times that rate using the empirical approaches of the Alaska and British Columbia programs. This difference occurred because of the relatively large smolt size of sockeye salmon in Redfish Lake (10 g) compared with Alaska and British Columbia programs (2g–5g smolts). This faster growth rate of juvenile sockeye



**Figure 4** presents predicted abundances of age-0 and adult sockeye salmon and kokanee in year 40 of life history simulations for Redfish Lake. Baseline conditions assume current growth and survivorship estimates. Fertilization assumes 50% increases in nutrient income above 1992–1993 values. Fifty- to seventy-percent reduction in survivorship of age-0 kokanee, combined with lake fertilization scenarios, are depicted.


salmon in Redfish Lake places greater predation pressure on zooplankton populations compared with the slower growing sockeye salmon populations.

Our models also allowed us to investigate interactions among lake productivity, kokanee density, and sockeye growth. Unexpectedly, these simulations suggested that kokanee competitors had more impact on sockeye growth at low sockeye stocking densities, and lake fertilization had a greater impact on sockeye growth at high sockeye stocking density. This result occurred because of the shape of the density dependence of growth in Figure 3. This type of density dependence has been found in empirical (Groot and Margolis 1992) and modeling studies (Walters and Juanes 1994). Our results may influence the type of lake management pursued as juvenile sockeye density varies during subsequent years of the recovery plan.

Results from the life history simulations caused us to re-evaluate our interpretation of nutrient cycling regimes in

Redfish Lake. Initially, we assumed that adult salmon returning from the marine environment would add substantial amounts of nutrients to the freshwater environment of Redfish Lake. Our simulations indicated that at current migration and marine survival rates, more nutrients leave the lake as smolts than return in adult carcasses. This result occurred in our simulations whenever the product of smolt-adult biomass increase (10g to 2000g; 200 x) and smolt-adult survivorship (0.002) was less than 1.0. Our results were opposite those observed for sockeye populations with higher smolt-adult survivorship, where adult salmon bring significantly greater amounts of marine-derived nutrients back to the nursery lakes (Koenings and Burkett 1987). The high mortality associated with large riverine migrations suggests that even under pre-dam conditions, when adult salmon returning to Redfish lake may have exceeded 20,000 individuals, nutrients from salmon carcasses likely contributed less than 20% of the nutrient budgets for Sawtooth Valley lakes (Gross and Wurtsbaugh 1994).

### Management Implications

Results of limnological sampling, experiments, and simulation modeling led us to three recommendations for managing endangered sockeye salmon in Sawtooth Valley lakes. First, in addition to Redfish Lake, Pettit Lake appears to be an excellent candidate for establishment of a sockeye population. High ambient zooplankton concentrations suggest that this lake is furthest from *O. nerka* carrying capacity and can support juvenile sockeye from the broodstock population while maintaining growth conditions similar to those observed in Redfish Lake. Second, the negative density-dependent effects on sockeye growth that would likely occur with additional stocking of *O. nerka* into Redfish Lake can be overcome with a modest program of lake fertilization. Third, the impact of a lake fertilization program should be augmented by simultaneous reduction in the density of kokanee in Redfish Lake. High densities of kokanee would likely benefit more from a lake fertilization program than would a nascent sockeye population established from the broodstock program. Our results suggest that offspring from the sockeye broodstock program could be used to establish or augment anadromous sockeye populations in Redfish and Pettit Lakes and that a combination of lake fertilization and kokanee reduction could be used in Redfish to enhance the success of stocked juvenile sockeye in Redfish Lake. Until problems with migratory losses can be solved, these measures may allow us to maintain the Snake River sockeye salmon in these lakes. 

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