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Limnology of Sawtooth Valley Lakes with Respect to Potential Growth of Juvenile Snake River Sockeye Salmon

Abstract

Recovery efforts for Snake River sockeye salmon were initiated in 1991 in response to a decline in the number of returning adults and listing of this population under the Endangered Species Act. We examined limnological conditions in five nursery lakes within the historical range of this population and emphasized factors that likely affect the growth potential of juvenile sockeye salmon. Results of this sampling were intended to facilitate management decisions concerning strategies for restocking progeny from a capture brood-stock program. Temperature, oxygen, light, chlorophyll, phytoplankton, and zooplankton were sampled in each lake from May through October of 1992. Results from limnological sampling indicated that all five lakes would be suitable for rearing juvenile sockeye, but that the lakes varied considerably in the species composition and abundance of zooplankton. Our results indicated that sockeye salmon would not be limited by oxygen or temperature conditions in any of the five lakes. Light levels were suitable for visual feeding to near bottom depths in three of the lakes (Pettit, Stanley, and Yellow Belly) and through 70-90% of the water column in the other two lakes (Redfish and Alturas Lakes). We ranked the five lakes based on growth potential of juvenile sockeye using published relationships of limnological variables and fish growth. Zooplankton food among lakes resulted in pronounced differences in the growth potential of juvenile sockeye salmon suggesting the zooplankton foraging/bioenergetics model was more suited for predictions of sockeye growth in these systems than the other relationships compared. Although growth potential for juvenile sockeye appeared better in three of the lakes, all five lakes are relatively unproductive. Thus a whole-lake fertilization, similar to nutrient enhancement approaches used in Alaskan and British Columbian sockeye nursery lakes, and the impact of piscivory should be considered before final recommendations for recovery plans are evaluated.

Introduction

In 1991 the National Marine Fisheries Service listed the Snake River stock of sockeye salmon (*Oncorhynchus nerka*) as endangered under the Endangered Species Act. Five high-elevation lakes in the Sawtooth Valley of Idaho were formerly habitat for these anadromous fish. After residing in the lakes for 1-2 years, the juvenile sockeye smolted and began their 1400 km migration to the Pacific Ocean via the Salmon, Snake and Columbia Rivers. After 2-3 years in the ocean, mature adults returned to the rearing watersheds to spawn (Bjornn *et al.* 1968; Idaho Fish and Game, pers. comm). Historically, returning adult sockeye salmon likely exceeded 10,000 fish (Evermann 1896, cited in Bjornn *et al.* 1968), and returned to at least five lakes in the Sawtooth Valley. As late as the 1950's numbers exceeding 4,000 were reported (Bjornn *et al.* 1968). Since that time the number of returning adults has declined such that only four individuals returned in 1991 and one

in 1992. The decline of this stock is likely due to a combination of problems associated with passage through dams on the Columbia, Snake and Salmon River systems and commercial and recreational fishing pressure.

In the fall of 1991 we began an assessment of the rearing habitats for juvenile sockeye salmon in five Sawtooth Valley Lakes (Redfish, Alturas, Pettit, Stanley and Yellow Belly Lakes). We examined a variety of limnological conditions that could affect the ability of each of the lakes to support growth and improve survival of juvenile sockeye salmon. Progeny from the four returning adult fish and the out-migrant smolts in 1991 comprise a captive brood-stock for this endangered species unit. One of the goals of our research program was to compare the rearing environments of each of the five lakes to help fisheries managers evaluate strategies for releasing juveniles from the brood-stock program back into the lakes.

Sockeye salmon are cold-water fishes that prefer temperatures less than 15°C and oxygen conditions greater than 5 mg L⁻¹ (Brett 1983; Kyle *et al.* 1988). They are visually feeding zooplanktivores vulnerable to a variety of piscivorous fishes (Burgner 1992). Studies have suggested that

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growth and survival of juvenile *O. nerka* in lakes are closely linked to zooplankton biomass (Hyatt and Stockner 1985), chlorophyll *a* (Reiman and Meyers 1992), and volume of the euphotic zone (Koening and Burkett 1987). In this paper we present information on lake morphometry, temperature, oxygen, and light profiles, and phytoplankton and zooplankton populations in the lakes. We focused on seasonal and depth-related differences. We then compared these limnological conditions among the lakes to assess the potential production of juvenile sockeye salmon in each, and used this comparison to evaluate management strategies designed to assist in the recovery of this population.

Methods

The routine sampling reported here of the five lakes began in May of 1992 and ended in October of 1992. Lakes were sampled 3-4 times in May and June and once every 10 days for the rest of the season. Additional temperature and oxygen profiles were measured in some of the lakes in April and November.

At the deep station in each lake, we sampled temperature, oxygen, and light profiles, chlorophyll concentrations, and phytoplankton and zooplankton populations. Chlorophyll and zooplankton samples were collected at two additional stations on each lake. The methodology used is described in greater detail below for each variable measured.

Lake Morphometry

We used an echo-sounder linked with a global positioning system (GPS) to chart the bathymetry of each lake in October 1992 using the methodology of Cubala *et al.* (1994). Depth data from an American Pioneer Fishscope II echo-sounder (6.5° beam angle, 160 kHz), and position data from a Trimble Pathfinder Professional GPS unit were recorded on a data logger at 2-second intervals as our boat cruised at 2-4 m/s along transects in each lake. For the different sized lakes we recorded between 860 and 1540 depth and position points. Because the U.S. Department of Defense degrades the satellite-transmitted GPS data through Selective Availability, uncorrected location measurements can be up to 100-m in error. Consequently, we corrected our position data by recording deviations of a GPS unit fixed at the Sawtooth National Fish Hatchery which is within 24-km from the furthest lake. The GPS positions recorded in the boat were then differentially corrected for these devia-

tions with Asset Survey software of Tribble Navigation, Ltd. giving a final accuracy of approximately ± 2 -m. In addition to the GPS locations, we added 160-570 points for the perimeters of the lakes by digitizing USGS topographic maps (7.5' series). Because we did our survey in October at the end of the hydrologic year during a six-year drought, we increased each of our depth readings by 0.5-m to more closely represent normal water conditions in the lakes.

Temperature and Oxygen

Vertical profiles of temperature and oxygen were taken at 1-5-m intervals with a YSI Model 58 Dissolved Oxygen Meter. Periodically throughout the field season, the oxygen content of water from three depths was measured with the Winkler method to verify the accuracy of the YSI probe (APHA 1992).

Light Extinction

Vertical profiles of light intensity were measured at the deep station using a submersible Li-Cor Model LI-188B photometer. Measurements were taken at 2-m increments from the surface to 28-m deep. The extinction coefficient (Wetzel 1983) was then calculated as the slope of the regression of \ln (% surface intensity) against depth.

Water transparency was also measured at the deep station with a 20-cm black and white Secchi disk and recorded as the mean of the depth where the Secchi disk disappeared and reappeared.

Chemical Analysis of Nutrients

An integrated epilimnetic lake water sample was collected at the deep station in each lake by lowering a weighted 0.64-cm diameter Tygon® tube 6-m into the water column and emptying the contents into a 1-l bottle for chlorophyll *a*, phytoplankton and chemical analysis. Samples for dissolved inorganic nutrient analyses [nitrate-nitrogen (NO₃) and soluble reactive phosphorus (SRP)] were filtered through a 0.45- μ m membrane filter 2-6 hours after collection and frozen until analysis. Unfiltered samples were analyzed for total phosphorus (TP) and total Kjeldahl nitrogen (TN).

Chlorophyll and Phytoplankton

In addition to the epilimnetic integrated tube samples described above, on some dates we also

collected metalimnetic and hypolimnetic samples with a Kemmerer water bottle for chlorophyll and taxonomic analyses. For routine analyses of chlorophyll we filtered 50-ml aliquots on 0.45- μm cellulose acetate membrane filters. On two dates we also fractionated the water sample by filtering with 0.1- μm and 1.0- μm Nucleopore membrane filters and 30- μm Nitex nylon screens to establish the relative chlorophyll content of different size fractions of phytoplankton. The filters were either temporarily frozen or placed directly into 6 ml of 100% buffered methanol and extracted in the dark for 24-48 hr at room temperature. The extracts were then analyzed fluorometrically (Holm-Hansen and Rieman 1978) with a Turner model 111 fluorometer calibrated with standard chlorophyll *a* (Sigma). After the initial reading the samples were acidified with two drops of 1.0 N HCl, and reread to correct for phaeophytin.

We collected samples for algal enumeration and biomass estimates from the same 0-6-m tube samples taken for chlorophyll analyses. Additional samples were occasionally taken in the metalimnion and hypolimnion to examine the change in species composition with depth. We preserved the samples using Lugol's solution and subsequently filtered a single 100 ml aliquot from each depth strata sampled on 0.45- μm cellulose acetate membrane filters at low vacuum pressures (0.3 atm.). The filters were then cleared and mounted in methacrylic resin following the procedure of Crumpton (1987). Cells were identified and counted at 400X-magnification in 50-100 fields that transversed the filter to take into account the tendency of cells to concentrate on the edge of the filters (Holmes 1962). The dimensions of a minimum of 10 individuals in each taxa were taken, and biovolumes subsequently calculated assuming the algae conformed to fixed geometric shapes.

Zooplankton

Six vertical zooplankton tows were collected on each date using a Wisconsin style zooplankton net measuring 35-cm in diameter and 80-cm long with 80- μm mesh. A General Oceanics flow meter was used to determine net efficiency and volume sampled. The flow meter was modified on request to General Oceanics to prevent reverse flow of the meter. Zooplankton were sampled over 2 depth ranges, a 10-m to surface tow and a bottom to surface tow, at each of the three stations. Zooplank-

ton were preserved in 10% neutralized formalin solution.

We identified four cladocera (*Daphnia rosea*, *Bosmina longirostris*, *Holopedium gibberum*, *Polyphemus pediculus*), one calanoid copepod (*Epischura nevadensis*) and several species of cyclopoid copepods (Thorp and Covich 1991). Zooplankton were enumerated and measured in replicated 1-5 ml sub samples taken with a Hensen-Stempel pipette and placed in a circular counting dish. Individual lengths of each species were measured from each sample and mean length for each taxa was calculated. Biomass was determined for each species using the procedures and linear regression equations described by McCauley (1984) and Kocnings *et al.* (1987).

In addition to our routine zooplankton sampling, mid-summer vertical distribution and diel migration of zooplankton was examined in Redfish and Stanley Lakes by collecting depth-stratified zooplankton tows during day and night periods. Zooplankton were collected using a closing net equipped with a flow meter. Samples were collected from Redfish Lake between 1100-1230 h on 3 August 1992 and between 0-120 h on 4 August 1992. Two replicate samples were collected from each 5-m depth strata from 0-20 m, each 10-m strata from 20-40 m, and each 20-m strata from 40-80 m. Two samples were collected from the bottom-80-m. Samples were collected from Stanley Lake between 1450-1530 h on 2 August and between 100 h-200 h on 3 August. Two replicate samples were collected from each 5-m depth strata from the bottom to the surface. Density of each crustacean taxa were estimated according to the methods cited above. We used an Anova to compare differences in depth distribution of individual zooplankton species by day and night (time-by-depth interaction).

Results

Lake Morphometry

Morphometric characteristics of the five lakes are described in Table 1. The morphometry map of Redfish Lake is shown in Figure 1, and maps of the other four lakes are available in Spaulding (1993). Redfish Lake had the greatest volume, surface area and mean maximum depth. Yellow Belly and Stanley were the smallest lakes in the basin, containing only 4% of the volume of Redfish Lake.

TABLE 1. Morphological characteristics of the five study lakes.

Lake	Area (km ²)	Volume (m ³ x10 ⁶)	Depth Maximum (m)	Depth Mean (m)
Redfish	6.15	269.9	91	44
Alturas	3.38	108.2	53	32
Pettit	1.62	45.0	52	28
Yellow Belly	0.73	10.3	26	14
Stanley	0.81	10.4	26	13

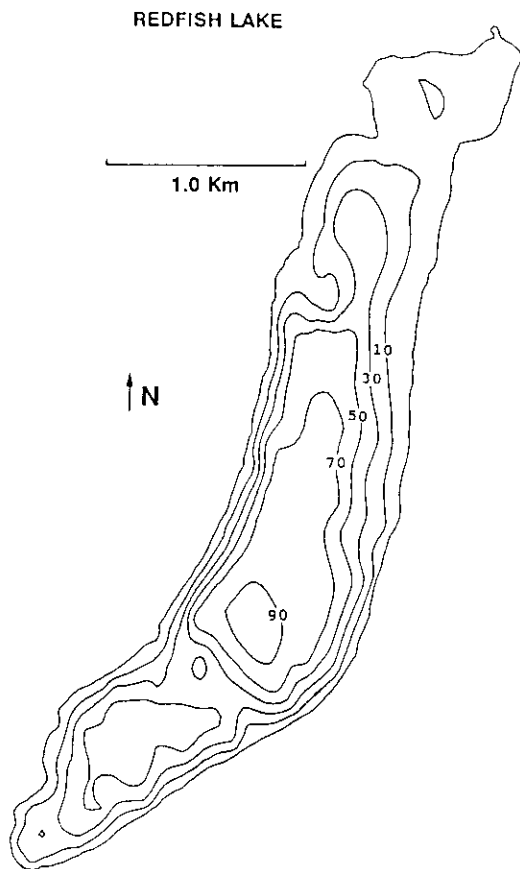


Figure 1. Morphometric map with depth contours in meters for Redfish Lake.

Temperature and Oxygen

Seasonal development of thermal stratification was similar in each of the lakes. Temperature and oxygen profiles for all five lakes on 31 July 1992 are shown in Figure 2. Maximum surface temperatures reached 18°C, while hypolimnetic temperatures

were 4°C over the eight months sampled. Surface temperatures reached a high of 18°C only for a short period in late July and early August and remained between 12-16°C for the majority of the summer. The thermocline developed in mid-May and was generally located between 8-m and 18-m in the deeper lakes (Redfish, Alturas, and Pettit) and between 8-m and 15-m in the shallower lakes (Stanley and Yellow Belly).

Dissolved oxygen levels in mid-May ranged from 10 mg/L near the surface to 4 mg/L near the bottom of all lakes. The YSI meter readings varied within 0-16% of the Winkler measurements when comparing both different depths and lakes. As thermal stratification evolved, oxygen concentrations were reduced in the hypolimnion of all the lakes. Low levels of dissolved O₂ (<3 mg/L) were measured at depth in all lakes except Redfish. The low oxygen levels were located a few meters off the bottom in Alturas (45-50 m), Stanley (22-25 m), and Yellow Belly (21-25 m) but were found as shallow as 40-m in Pettit Lake. Pettit, Stanley and Yellow Belly Lakes exhibited prolonged periods where the bottom water remained below 2 mg O₂ / L.

A metalimnetic oxygen maxima of approximately 10 mg/L developed in Alturas, Yellow Belly, Pettit and Stanley lakes in mid-summer. This maxima lasted for as short as 12 days (Pettit) and as long as 2 months (Alturas). Redfish Lake did not develop a distinct metalimnetic oxygen maxima.

Light Extinction and Transparency

The depth of the nominal photic zone (1% light extinction levels) in each lake was approximately 1.5-2 times the Secchi depth. The relationship between the 1% light level and the Secchi depth was linear when data for all five lakes was combined ($y = 4.5 + 1.5x$; $R^2 = 0.451$). The relationship was much tighter if light extinction and Secchi were examined for each lake individually.

The Sawtooth lakes were quite clear, with Secchi depth transparencies ranging from 5-18 m (Figure 3). In most of the lakes transparencies increased, from May through September. Transparencies in Stanley Lake were lower than in the other lakes and had a different seasonal pattern. Much of the week-week variability in Secchi depths was due to calm versus wavy conditions that affected our measurements.

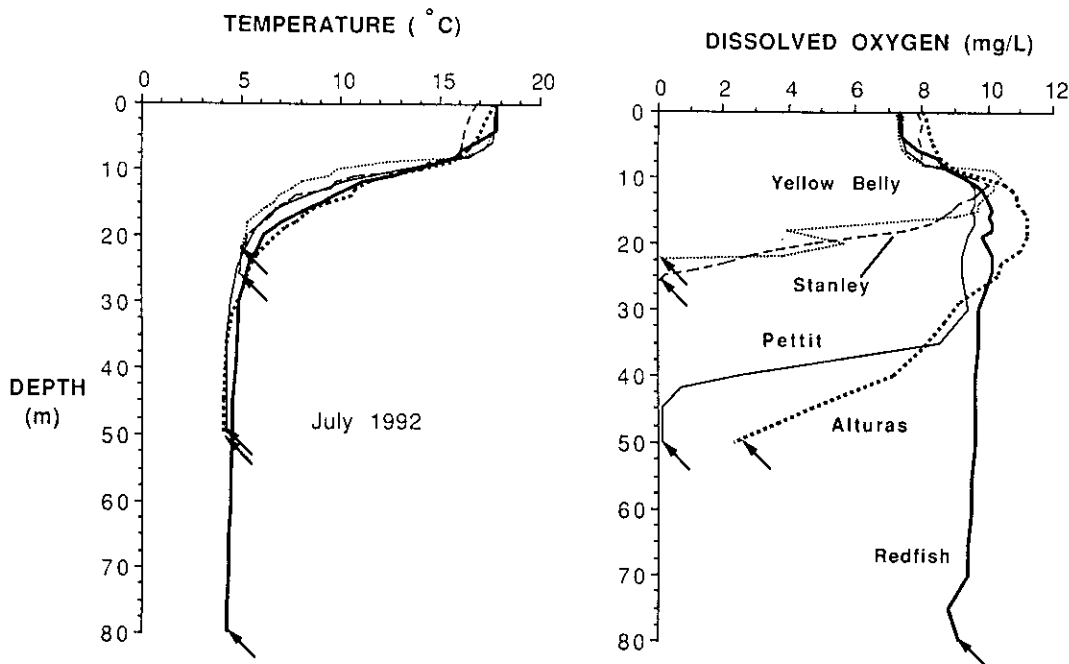


Figure 2. Temperature and oxygen profiles for each lake measured on 31 July 1992 at the deep station in each lake. The arrows point to the approximate bottom depth of each lake. Redfish Lake max depth = 91 m, Alturas Lake max depth = 53 m, Pettit Lake max depth = 52 m, Yellow Belly Lake max depth = 26 m, and Stanley Lake max depth = 26 m.

Chemical Analysis of Nutrients

Mean seasonal epilimnetic TP and TN concentrations ranged from 6-11- $\mu\text{g/L}$ and 66-102- $\mu\text{g/L}$ respectively, and TN:TP ratios ranged from a low of 6:1 to a high of 11.5:1. Mean seasonal concentrations of dissolved nutrients were low with SRP and NO_3 ranging from undetectable values to 2.3 $\mu\text{g/L}$ and 4.0-9.4 $\mu\text{g/L}$ respectively. Inter-year and seasonal fluctuations or climate and limnological conditions have a large effect on Sawtooth Valley Lakes nutrient composition, but these fluctuations do not effect the relative rankings of productivity among the lakes.

Chlorophyll and Phytoplankton

Mean epilimnetic concentration of chlorophyll *a* for the five lakes ranged from 0.44 to 0.90 mg/m^3 , with individual values ranging from 0.22-2.38 mg/m^3 . The highest epilimnetic chlorophyll concentration for each lake occurred on 9 May, when the first measurements were taken (Figure 4) approximately 2 weeks after spring overturn. The minimum epilimnetic chlorophyll concentration for

each lake occurred in July and August. Epilimnetic chlorophyll increased during autumn as the thermocline began to erode.

Depth profiles indicated pronounced increases of chlorophyll *a* in the metalimnia and hypolimnia of the lakes. For example, in mid-September in Redfish Lake, epilimnetic chlorophyll *a* concentrations were 0.49 mg/L , but at 40-m they reached 2.27 mg . In most of these lakes the deep chlorophyll maxima were located near the 1% light level where temperatures were 5-6°C (Figure 5). The deep chlorophyll maxima were located approximately 5-10-m below the metalimnetic oxygen maxima.

Size-fractionation of epilimnetic water revealed a similar size distribution of phytoplankton in each of the five lakes (Figure 6a). Seventy-two to 91% of the chlorophyll in the five lakes was distributed in size classes that would be available to herbivorous crustacean zooplankton (0.45-30 μm ; Reynolds 1984). Only 4 to 12% of the phytoplankton in the five lakes was larger than 30 μm . In Redfish Lake, size-fractionation analysis of samples collected at four depths (0-6 m, 15 m, 35 m, and

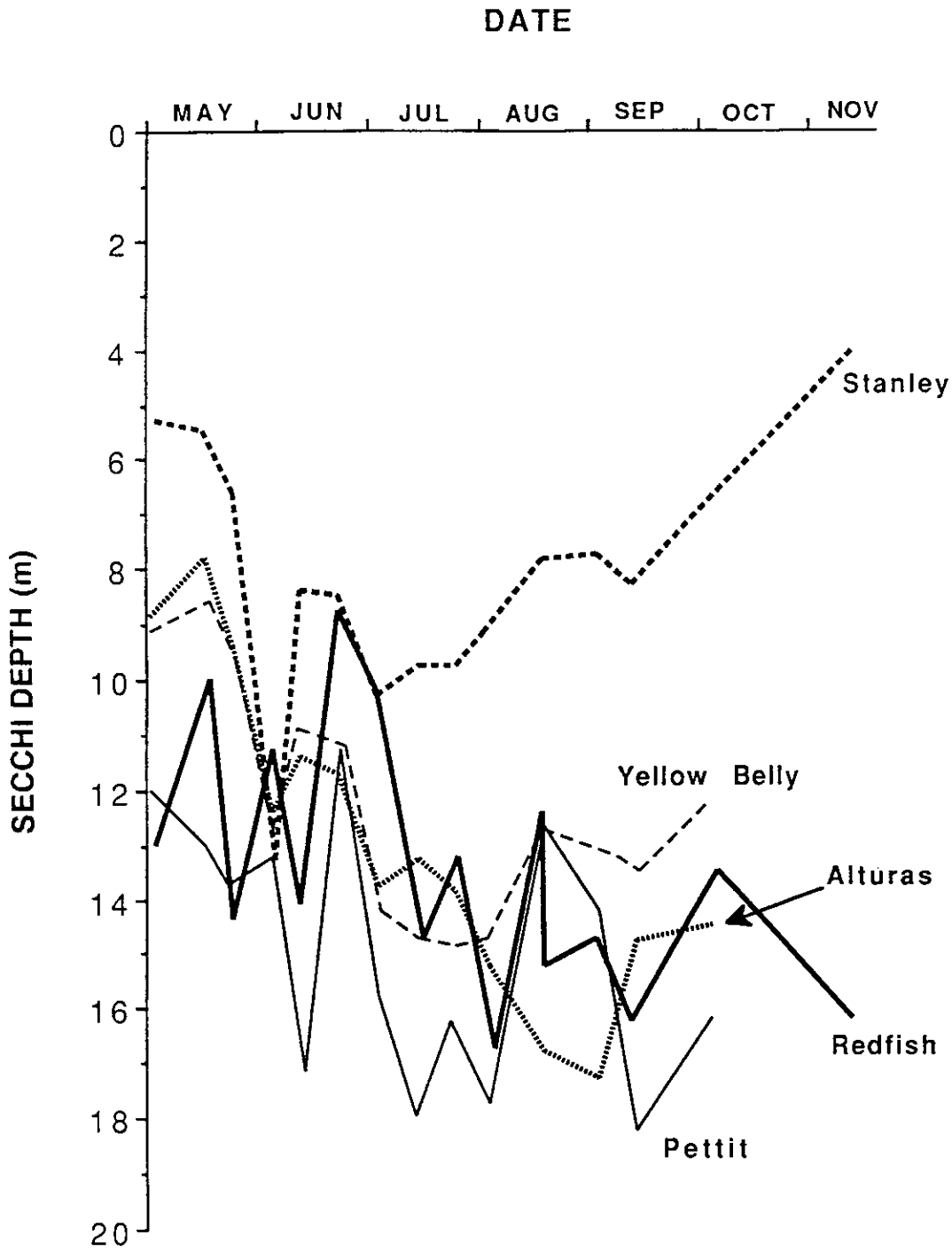


Figure 3. Seasonal distribution of secchi depths measured at the deep station in each lake.

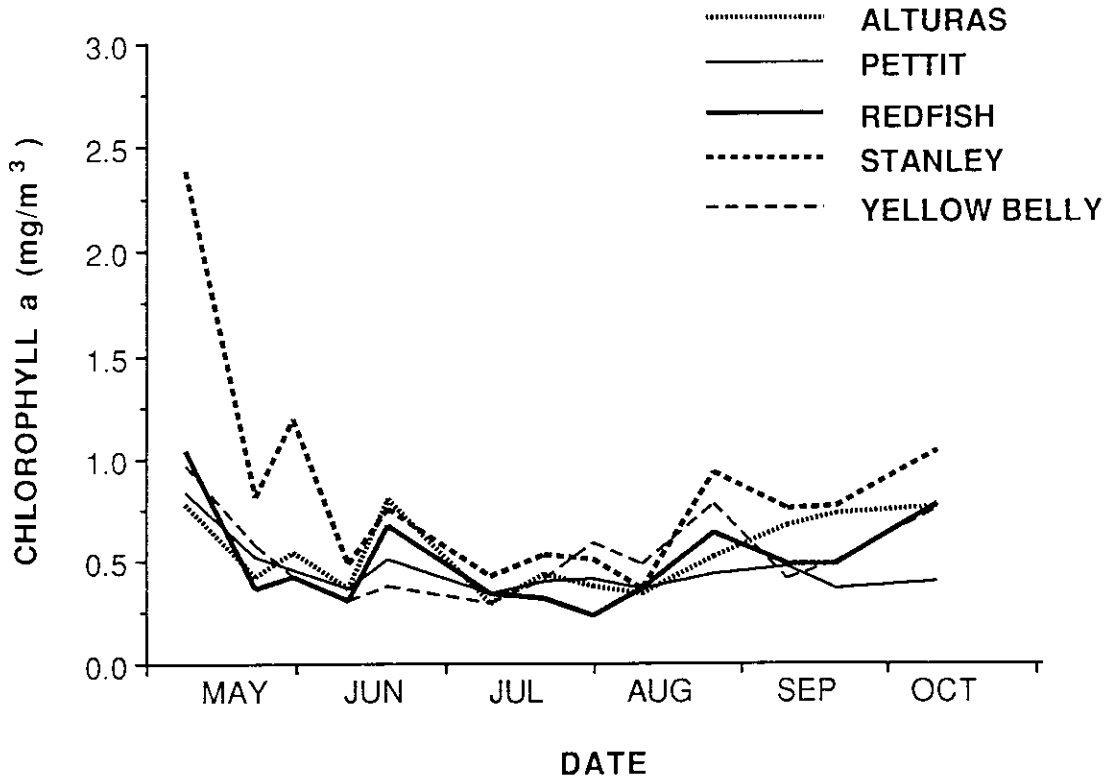


Figure 4. Seasonal distribution of chlorophyll *a* concentrations in the 6-0-m depth strata for all five lakes.

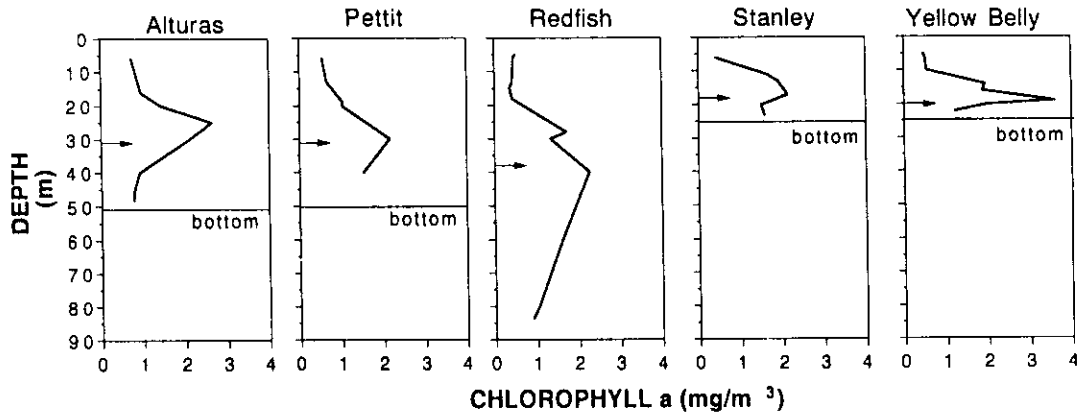


Figure 5. Chlorophyll *a* depth profiles for each lake. The arrows point to the depths of the 1% light extinction depth, and the bottom is shown for the shallower lakes.

80 m) indicated that 60 to 82% of the phytoplankton at each depth was of a grazable size (Figure 6b).

The phytoplankton taxa, exemplified by those in Redfish Lake, were dominated by diatoms (*Cy-*

clotella sp., *Tabellaria* sp., and *Fragilaria* sp.), chrysophytes (*Dinobryon* sp.), chlorophytes (*Chlamydomonas* sp. and small chlorococcales), and a small coccoid cyanobacteria. Nearly all of the phytoplankton were small, and the mean

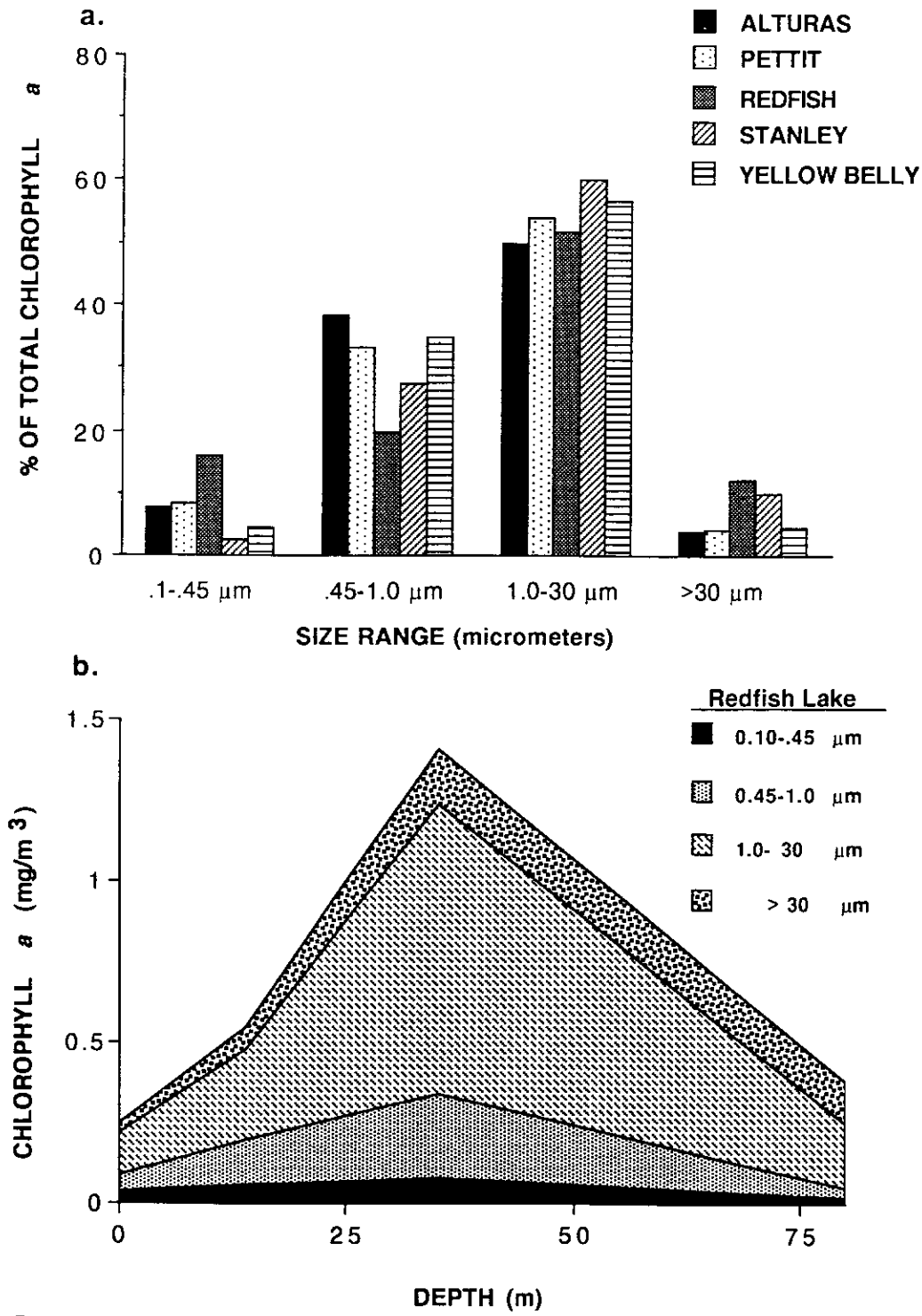


Figure 6. a) Size fractionation of chlorophyll *a* in the epilimnion of all five lakes on 9-11 July 1992. b) Depth-stratified phytoplankton size fractionation for Redfish Lake, 9 July, 1992. Epilimnetic samples were taken with a 0-6 m tube sampler; other discrete samples were collected at 14, 35, and 80-m.

equivalent spherical diameters for all of the taxa ranged from about 4 to 12 μm . Picoplankton ($< 1 \mu\text{m}$) were present and sometimes abundant; however, these microbes were not identified because we were most interested in the primary producers directly available to the macrozooplankton prey of *O. nerka*.

In the epilimnion of Redfish Lake, algal biomass was moderately high from April to May, with a peak in the last two weeks of June (Figure 7a). During spring the community was dominated by *Dinobryon* sp., very small unidentified spherical green algae of the order chlorococcales, and diatoms (principally *Cyclotella* sp., *Tabellaria* sp., and *Fragilaria* sp.). In early July the algal biovolume plunged by an order of magnitude from the spring maximum high, and became dominated by small cyanobacteria and *Dinobryon* until the end of August when diatoms and the green algae *Chlamydomonas* sp. appeared (Figure 7b).

Algal biovolume was lowest in Redfish Lake, and highest in Yellow Belly Lake (Figure 7a). Seasonal changes in algal biovolume in all lakes were variable, but generally indicated higher algal abundance in spring and lower biovolume by mid-summer (Figure 7a). Phytoplankton in the deeper waters of Redfish Lake were more abundant and had a different taxonomic composition than those in the epilimnion. In July, the epilimnetic biovolume was dominated by cyanobacteria (78%), *Dinobryon* sp. (10%), and diatoms (8%). At the top of the metalimnion (14 m), algal biovolume increased slightly due to an increase in *Dinobryon* sp. In the hypolimnion (80 m), the total biovolume was nearly nine times greater than in the epilimnion and was dominated by diatoms. In August, the epilimnion community was composed of diatoms (38% by volume), *Chlamydomonas* sp. (48%) and small chlorococcales (11%). *Chlamydomonas* sp. disappeared in the upper metalimnion (14 m), as diatoms increased to represent 89% of the community. Near the deep chlorophyll maxima (35-m) (Figure 6b), the biovolume was nearly eight times higher than in the epilimnion, and the relatively large or colonial diatoms, *Asterionella* sp., *Synedra* sp., and *Cyclotella* sp. represented 99% of the biovolume (Figure 6b).

Zooplankton

Seasonal patterns of crustacean zooplankton density and biomasses indicated that the epilimnion

of Redfish and Alturas Lakes contained the lowest biomass throughout the season compared to the other lakes (Figure 8). Pettit Lake had a high density but low biomass of crustaceans early in the season owing to the dominance of small-bodied *Bosmina*. The dominance of *Bosmina* in Alturas Lake throughout the season resulted in moderately high densities of total crustacean zooplankton but consistently low biomass when compared to the other lakes. All five lakes appeared more similar in zooplankton abundance when only density was considered, but total biomass estimates indicated differences among the lakes (Figure 8 a,b).

Redfish and Alturas Lakes had very low biomasses of crustacean zooplankton with *Holopedium* dominating most of the season in Redfish and *Bosmina* dominating in Alturas (Figure 9 a,b). Total crustacean zooplankton biomass remained below 25 $\mu\text{g/l}$ in these lakes in mid-summer. The carnivorous cladoceran *Polyphemus* exhibited a substantial increase in Alturas immediately after the mid-summer decline of *Bosmina* and *Holopedium*. Neither of these two lakes had abundant populations of *Daphnia* or copepods in the epilimnion.

Pettit, Stanley, and Yellow Belly lakes had higher cladoceran densities than Alturas or Redfish (Figure 9 c,d,e). Pettit and Stanley Lakes exhibited a distinct seasonal succession of cladoceran species in which *Holopedium* comprised most of the biomass in early summer, and *Daphnia* dominated during late summer and early fall. The predatory copepod *Epischura* contributed to the crustacean biomass of Stanley Lake, and *Daphnia* dominated the zooplankton of Yellow Belly throughout the year.

Zooplankton densities estimated from bottom to surface tows were generally lower than values estimated in the epilimnion in all lakes. Cyclopoid copepods, however, were much more abundant in the hypolimnion in each of the lakes. *Holopedium* and *Epischura* were more abundant in the epilimnion than in the hypolimnion. Densities of *Bosmina* and *Daphnia* were similar in epilimnetic and whole water column tows. Whole water column tows may have over-emphasized zooplankton taxa that occurred in the hypolimnion because of the decrease in net efficiency as the net was pulled through the deep chlorophyll maxima that contained net-clogging filamentous algae (Figure 6 b).

Vertical distribution of zooplankton in Redfish Lake on 3 August 1992 indicated that different zooplankton taxa segregated according to depth

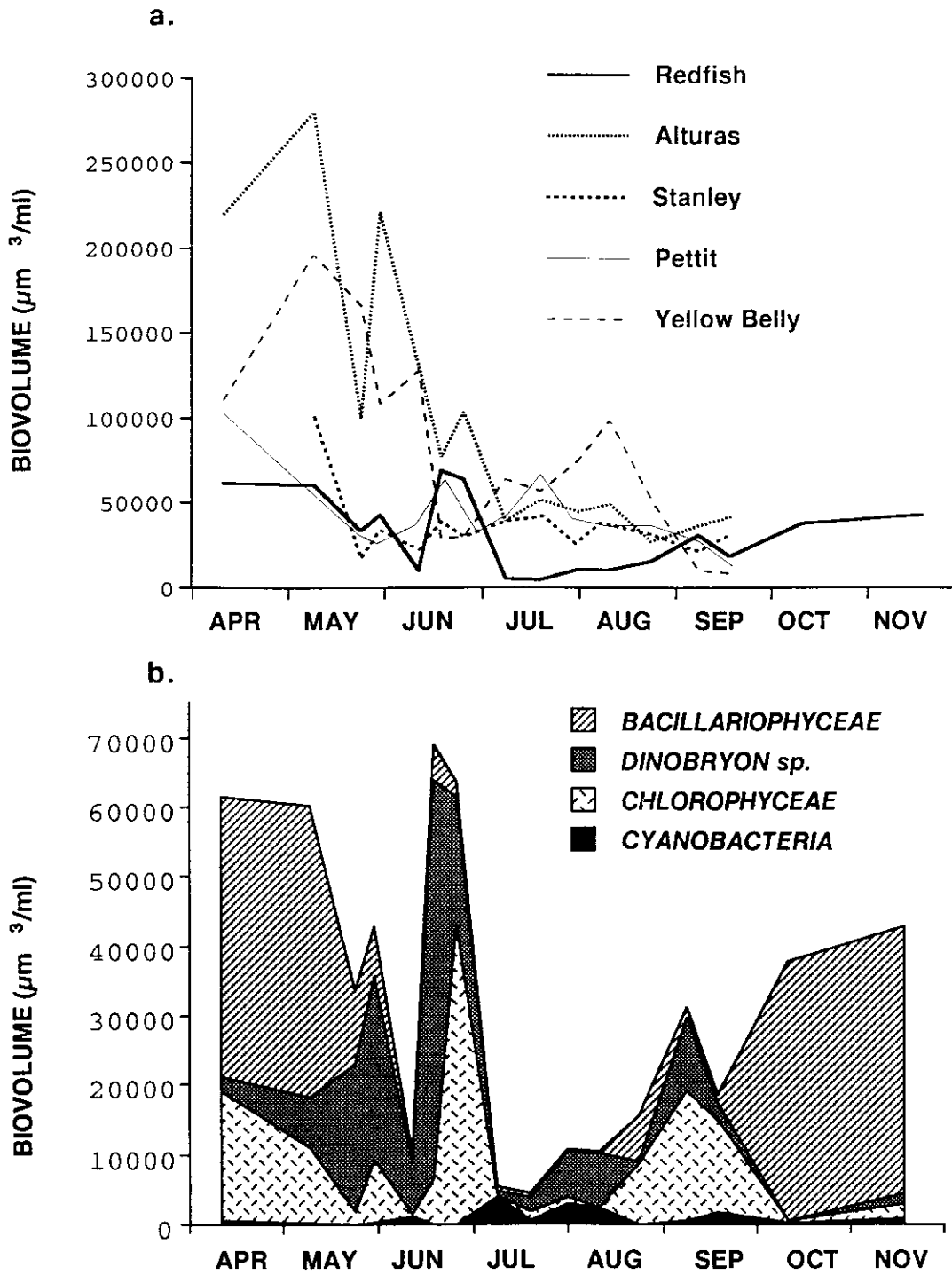


Figure 7. a) Seasonal changes in total epilimnetic algal biovolume in the five lakes, 1992. b.) Seasonal changes in the biovolume of different phytoplankton taxa in the epilimnetic water of Redfish Lake, 1992.

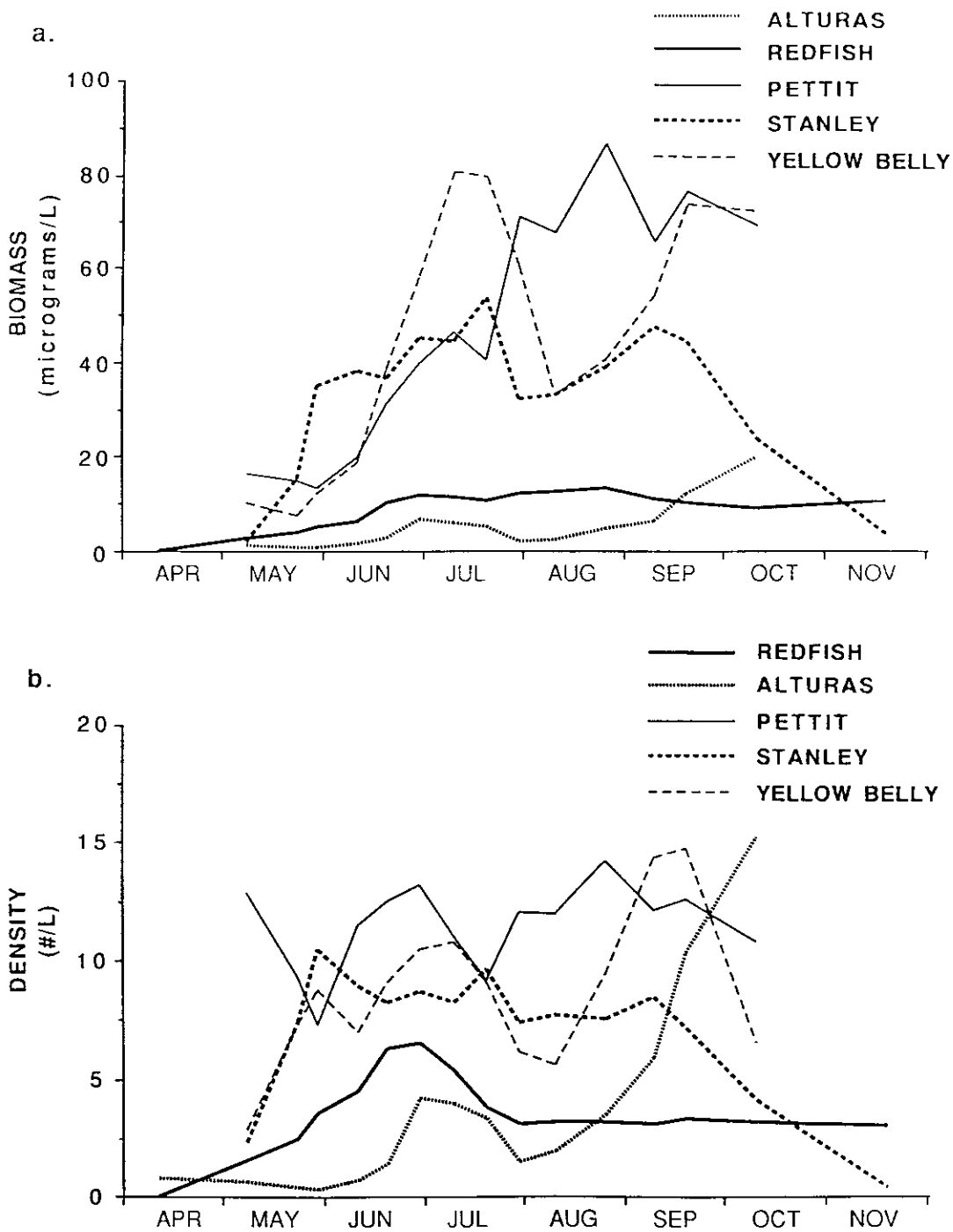


Figure 8. Seasonal distribution of total crustacean zooplankton in epilimnetic tows in the five lakes: a) biomass b) density. Data were smoothed with a 3-point running mean.

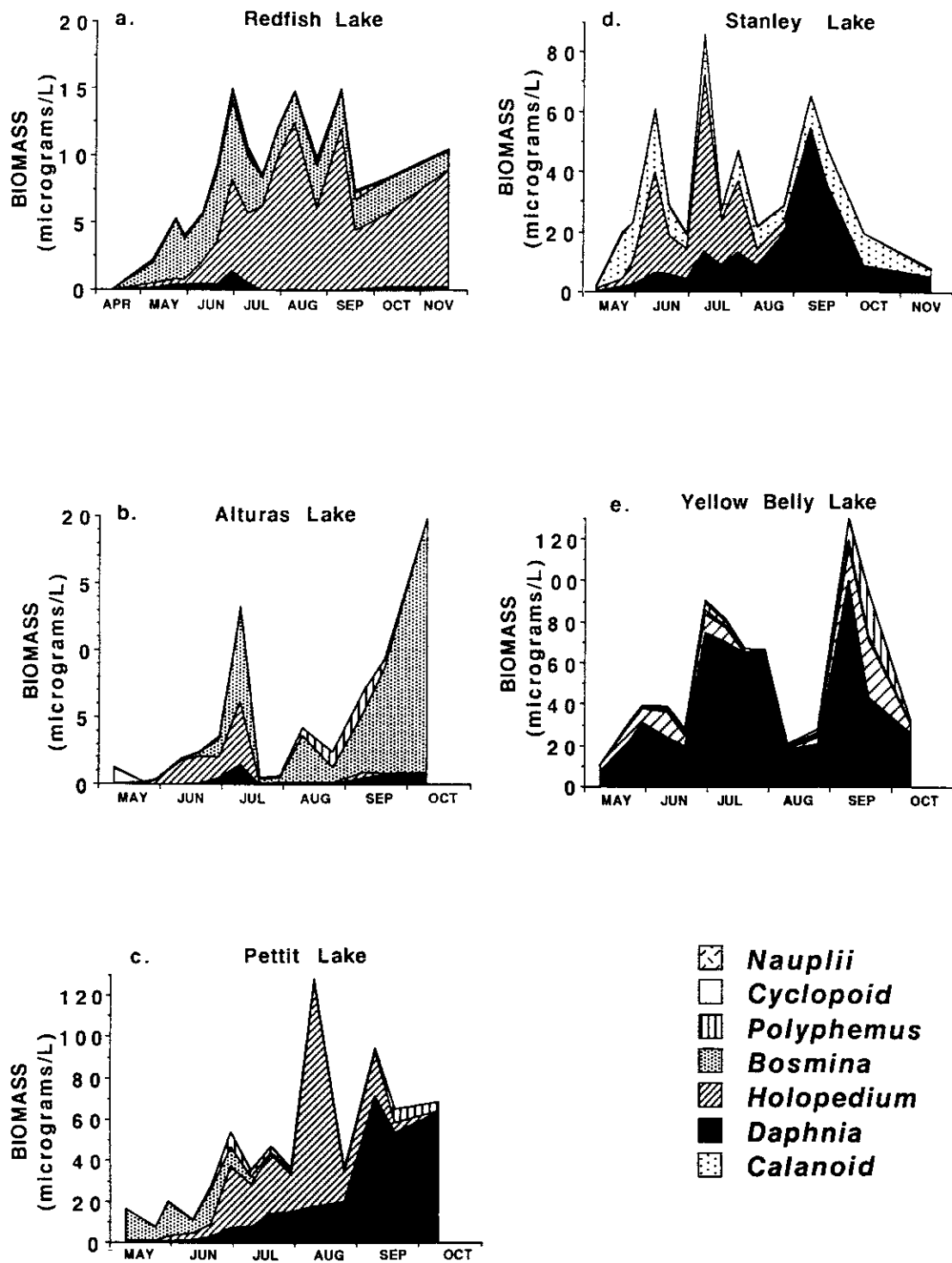


Figure 9. (a-e). Seasonal distribution of zooplankton species biomass composition in the epilimnion of all five lakes. Note the different y-axis scales used: (0-20 $\mu\text{g/l}$) on the Redfish and Alturas Lakes, (0-120 $\mu\text{g/l}$) on the Pettit, and Yellow Belly Lakes graphs, and (0-90 $\mu\text{g/l}$) on the Stanley Lake graph.

during the day (Figure 10). At mid-day, *Holopedium* was concentrated in the epilimnion and metalimnion attaining peak densities of 4 individuals L^{-1} in the 5-10-m strata. Cyclopoid copepods were most abundant in the hypolimnion attaining peak densities of 1.7 individuals L^{-1} in the bottom strata. *Bosmina* was present throughout the water column but was more concentrated in the deeper waters. *Daphnia* and *Polyphemus* were present in very low numbers throughout the water column.

An ANOVA examining the time-by-depth interaction suggested that the common crustaceans moved up in the water column during the night. *Holopedium* moved slightly from a mean depth of 10-m during the day to 7-m at night ($F_{1/8} = 17.8$, $P < 0.001$). *Bosmina* migrated extensively from a mean depth of 46-m during the day to 15-m at night ($F_{1/8} = 28.8$, $P < 0.001$). Cyclopoid copepods exhibited small movements, migrating from a mean depth of 71-m during the day to 58-m at night, but this difference was not significant ($F_{1/8} = 0.38$, $P > 0.05$).

The vertical distribution of crustacean zooplankton in Stanley Lake was similar to that of Redfish. During the day *Holopedium* was concentrated in the epilimnion, whereas cyclopoid copepods were concentrated in the hypolimnion. *Daphnia* was present throughout the water column but most abundant in the 10-15-m strata. *Epischura* was most abundant in the upper portion of the water column. An ANOVA indicated that diel differences in vertical distribution were significant for *Daphnia* which occupied a mean depth of 11.8-m during the day and 7.9-m during the night than during the day ($F_{1/4} = 4.70$, $P < 0.05$). *Holopedium* also was located higher in the water column during the night ($F_{1/4} = 8.46$, $P < 0.05$). Cyclopoid copepods became more concentrated near the bottom of the lake during the night ($F_{1/4} = 21.5$, $P < 0.01$). No significant differences in diel changes in the vertical distribution of *Epischura* was apparent in Stanley Lake.

Discussion

Results from the limnological sampling indicated that all five lakes are suitable for rearing juvenile sockeye salmon. Temperature and oxygen conditions within a large portion of each lake fell within the tolerance range of sockeye ($< 17^{\circ}C$, > 5 mg O_2/L , LeBrasseur *et al.* 1978). In Redfish Lake

nearly all of the water column was within these tolerance ranges throughout the season. In the other lakes the bottom 5-15-m of water contained insufficient oxygen to support permanent occupation by sockeye salmon. Subsequent sampling in these lakes has indicated that the low deep hypolimnetic oxygen levels are due to incomplete mixing of the water column in the spring and/or fall (Luecke and Wurstbaugh, unpublished data).

The ample volume of water with suitable temperature and oxygen conditions suggests that sockeye salmon could behaviorally select water depths that provide best conditions for growth and survival. Brett *et al.* (1969) suggest that sockeye should choose water temperatures around $15^{\circ}C$ to optimize conversion efficiency of food. This hypothesis would predict that juvenile sockeye salmon would reside in epilimnetic waters in the five lakes. Brett (1971) subsequently showed, however, that salmon seldom use temperatures of $15^{\circ}C$.

Light conditions indicated that sockeye salmon could feed visually during the day near the bottom of Stanley, Pettit and Yellow Belly Lakes (0.1% of surface light, Ali 1959, Levy 1990). Conversely, fish would cross the 0.1% surface light isolume at approximately 45-m in Alturas and 55-m in Redfish Lake. Although zooplankton densities are low in all the lakes, the high light environment should facilitate foraging juvenile sockeye salmon.

Levy (1990) indicated that juvenile sockeye salmon in lakes with piscivorous fish populations were concentrated during the day at depths (and light levels) that could be predicted from light extinction (k) according to the relationship:

$$\text{Depth (m)} = 15.4 k^{-1} + 1.23$$

These results caused Levy (1990) to hypothesize that juvenile sockeye salmon should behave so as to avoid visual predators during the day and choose an energetically efficient temperature at night. His hypothesis predicts that juvenile sockeye salmon would reside at the bottom of all five lakes during the day, and move to epilimnetic areas at night. The high light environment in the Sawtooth Valley Lakes may make juvenile sockeye salmon particularly vulnerable to fish piscivores in that little day-time refuge exists for these prey fish.

The nutrient and chlorophyll data suggest that all of the Sawtooth Valley lakes are oligotrophic, and that fish production will consequently be

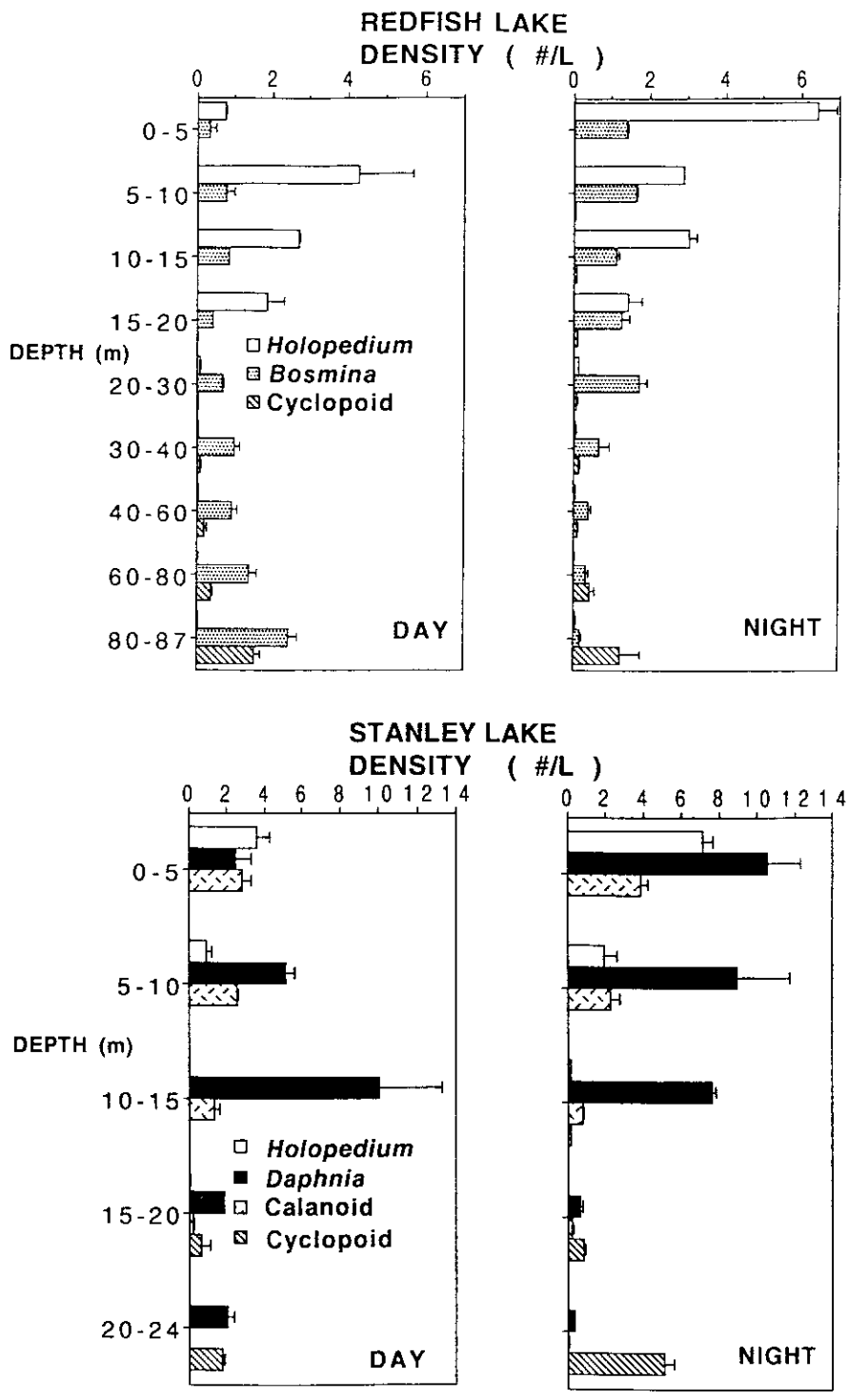


Figure 10. Diel vertical distribution of zooplankton densities from Redfish Lake (above) and Stanley Lake (below). 3-4 August 1992. Error bars denote the one-half range of two samples.

TABLE 2. Potential growth or production of juvenile sockeye salmon in five lakes of the Sawtooth Valley. Chl (chlorophyll) and Secchi relationships are from Rieman and Meyers (1992), the EZ (euphotic zone) model from Koenings and Burkett (1987), and the ZOOPE (zooplankton/energetics) model is from Budy et al. (1994). Values represent predictions of the model in either lengths of age-0 fish in September (mm TL) or production of smolts (# / ha). The number in parentheses refers to the rank given each lake in terms of sockeye production for a particular model. The last row of data refers to *O. nerka* collected in mid-water trawls. NA indicates that no data were collected.

Model	Lake				
	Redfish	Alturas	Pettit	Stanley	Yellow B.
Chl (mm TL)	99	100	98	108	99
(Rank)	(3.5)	(2)	(5)	(1)	(3.5)
Secchi (mm TL)	65	67	43	134	79
(Rank)	(4)	(3)	(5)	(1)	(2)
EZ (smolts/ha)	791	547	780	425	386
(Rank)	(1)	(3)	(2)	(4)	(5)
Zoop (mm TL)	63	50	105	105	112
(Rank)	(4)	(5)	(3)	(2)	(1)
Actual (mm TL)	65	55	NA	95	NA
(Rank)	(2)	(3)		(1)	

limited by basic lake productivity. Although we did not measure primary production directly in this study, subsequent work in Redfish Lake has shown a close correlation between epilimnetic chlorophyll concentrations and primary production (Gross *et al.* 1994), as it often is in oligotrophic lakes (i.e. Stockner and Hyatt 1984). Furthermore, both nutrient and chlorophyll concentrations have been used successfully to predict fish production in lentic systems (Carline 1986). The presence of deep-chlorophyll layers in the lakes may, however, confound predictions based on epilimnetic chlorophyll levels, as a considerable amount of primary production in these lakes may occur in the metalimnia and hypolimnia (Shortreed and Stockner 1990).

A number of authors have derived sockeye growth or production values from nursery lakes given limnological information of the type collected in our study. Rieman and Meyers (1992) indicated that Secchi transparency and epilimnetic chlorophyll levels provided the best predictors of the growth of *O. nerka* in Idaho Lakes. Koenings and Burkett (1987) described a significant positive relationship between the volume of the euphotic zone and the density of sockeye smolts in a series of Alaskan lakes. In addition to these regression approaches, Walters *et al.* (1991) and Budy *et al.* (1993) have constructed simulation models to examine the relationship between zooplankton biomass and juvenile sockeye growth within a bioenergetics context (Beauchamp *et al.* 1989).

These approaches can be used to assess the potential for each of the five lakes to serve as a rearing environment for the endangered stock of sockeye salmon. These models provide a different ranking of the lakes in terms of sockeye growth potential (Table 2). The chlorophyll and Secchi relationships (Rieman and Myers 1992) indicated that Stanley would provide the best conditions for juvenile growth and that Pettit would provide the worst. The euphotic zone model (Koenings and Burkett 1987) predicted that Redfish and Pettit would produce almost 800 smolts per hectare (Table 2), whereas Stanley and Yellow Belly would produce only half that amount. Preliminary simulations of a zooplankton foraging-energetics model (Budy *et al.* 1993) suggest that growth of juvenile sockeye salmon would be greatest in Yellow Belly, Stanley, and Pettit Lakes (descending order) and poorest in Redfish and Alturas (Table 2).

A comparison of the weight of *O. nerka* captured in mid-water trawls in September of 1992 with the rankings of each of the potential sockeye growth or production models suggests that the Secchi and zooplankton models provided the closest fit to the observed growth of juvenile *O. nerka* in the lakes (Table 2). The chlorophyll model predicted larger fish than occurred in trawl catches from the lakes. Predictions from the Secchi model were similar to the observed size of fish captured in Redfish Lake, but predicted larger fish than were captured in Stanley Lake. The zooplankton

simulation model correctly ranked the growth of fish in the lakes, but the range of fish lengths among the lakes was greater than predictions from the simulations. It was unlikely that the euphotic zone production model would provide a good ranking of potential production of sockeye in these highly transparent lakes in that this model was designed for use with stained or glacial lakes where light limitation of phytoplankton is common.

Results of this study indicated that each of the five lakes could support juvenile sockeye salmon, but that the potential growth and therefore survival (Peterson and DeAngelis 1993) of these fishes would vary several-fold among the lakes. Further, based on limnological information presented here, the lakes can all be considered oligotrophic and thus relatively unproductive rearing lakes for sockeye salmon. The higher zooplankton biomasses in Stanley, Pettit and Yellow Belly Lakes indicates that growth of juvenile sockeye salmon would be greater in these lakes compared to Redfish and Alturas. However, Redfish is the only lake that now supports a sockeye population, and Alturas is the only other lake to have had recent adult sockeye returns (Bowles and Cochnauer 1984). Planned modification of low-water dams on the outflow of Stanley and Pettit Lakes, in addition to possible whole lake fertilization aimed at increasing food availability for juvenile sockeye, makes these lakes attractive for reintroduction of endangered Snake River Sockeye Salmon.

The differences in zooplankton biomass in the lakes may be, in part, due to differences in the abundances of zooplanktivorous fish in each lake. Yellow Belly Lake, with a high zooplankton biomass contains only cutthroat trout that often feed preferentially on benthic invertebrates rather than zooplankton (Luecke 1986). Likewise, Pettit Lake is dominated by brook trout (*Salvelinus fontinalis*), bull trout (*S. confluentus*), stocked rainbow trout (*Oncorhynchus mykiss*), and a small population of reidside shiners (*Richardsonius balteatus*). Stanley Lake has several trout species, reidside shiners, and kokanee salmon (resident *O. nerka*). Both Redfish and Alturas Lakes have large populations of kokanee salmon that may prey on larger zooplankton and depress their abundance. Competition between kokanee salmon and reintroduced sockeye salmon may therefore be an important consideration for recovery of the endangered species.

Additionally, the abundance of piscivorous fishes in the lakes may affect survival of juvenile *O. nerka*. Stanley and Yellow Belly lakes appear to have higher abundances of piscivorous fish than are present in Redfish and Alturas lakes (Spaulding 1993). Consequently, there may well be a trade off between growth potential and mortality due to predators. Additional piscivore assessment and modeling efforts are needed before the tradeoffs between sockeye growth and survival can be properly evaluated for these lakes.

Consideration of both the potential growth and survival of juvenile sockeye salmon is essential before plans to rehabilitate this endangered stock are finalized. Our limnological work has provided a template for future management options and research. Investigations of published sockeye models indicated that our bioenergetics/zooplankton foraging model provided the most reasonable results for this system and that future work should include a more rigorous field test of the model. Our limnological data demonstrates these five lakes are relatively unproductive and suggests that the addition of fertilizer, an approach often used to increase the naturally high sockeye production in British Columbia and Alaskan sockeye lakes (Kyle *et al.* 1993; Stockner 1981, 1992; Stockner and Hyatt 1984), may enhance endangered sockeye salmon growth and thus survival.

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