

Nutrient limitation of oligotrophic sockeye salmon lakes of Idaho (USA)

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Introduction

Phytoplankton production in lake ecosystems is frequently controlled by amounts of nitrogen and phosphorus (SMITH 1982, ELSER et al. 1990), as well as minor- and micro-nutrients (WURTSBAUGH & HORNE 1983, WURTSBAUGH 1988, LOVSTAD & BJORNDALEN 1990). Nutrient limitation is often studied to determine which nutrient(s) should be reduced to control lake eutrophication (SCHINDLER 1974). Conversely, nutrients have been used for decades to stimulate plankton and, subsequently, fish production in aquaculture (BARDACH et al. 1972).

More recently, lake fertilization has been used to augment salmon runs for commercial exploitation (HYATT & STOCKNER 1985, KYLE et al. 1988), and it has been suggested for reversing losses in lake productivity due to decreases in anadromous salmon populations (KOENINGS & BURKETT 1987). After returning to their natal lakes, adult salmon spawn, die, and decompose, often releasing significant amounts of marine-derived nutrients into the freshwater ecosystems (JUDAY et al. 1932, KLINE et al. 1990). KOENINGS & BURKETT (1987), for example, calculated that sockeye salmon carcasses contributed nearly 60% of the annual phosphorus loading to an Alaskan lake. Because phosphorus loading is often important in determining phytoplankton abundance in lakes (VOLLENWEIDER 1976), declines in returning salmon can lead to decreases in lake productivity, and lower production of the juvenile salmon that rear in the lake for 1-2 years.

In the Sawtooth Valley of Idaho, USA, runs of the endangered Snake River sockeye salmon (*Oncorhynchus nerka*) to five rearing lakes in Idaho have declined more than 99% over the last century, primarily because of dams constructed along their migration route (RIEMAN et al. 1991, BEVAN et al. 1994). Thousands of salmon once returned to these lakes (BJORN et al. 1968). The decline of the Snake River sockeye has undoubtedly reduced nutrient loading and may have contributed to the current low fish production in the lakes. Although the primary threat to these salmon is mortality during downstream migration, it may be possible to help save this race of salmon by fertilizing the rearing lakes to elevate them a higher level of productivity. This remedy

should increase the growth rates and abundances of wild and hatchery-produced sockeye salmon that will be introduced into the lakes. Here we report on laboratory and field nutrient-addition bioassays to determine if lake fertilization could be used to stimulate phytoplankton production and aid in the recovery Snake River sockeye salmon.

Study area and methods

The five study lakes, Redfish, Alturas, Pettit, Stanley, and Yellow Belly are located at elevations near 2000 m in the granitic Sawtooth Mountains of central Idaho (44°N, 115°W). Although their watersheds lie mostly within a pristine wilderness area, the lakes are popular regional destinations for recreation. The lower portions of the drainages support mixed aspen and fir forests. The lakes are generally similar, but Redfish Lake, our primary study site, is the largest (615 ha), and deepest (91 m). It has an average water residence time of 3 yr, alkalinities near 180 $\mu\text{Eq} \cdot \text{L}^{-1}$, and mean summer TP and TN concentrations of 8 and 51 $\mu\text{g/L}$, respectively. Secchi depths range from 9-20 m. Mean summer epilimnetic chlorophyll *a* concentrations average 0.5-1.0 $\text{mg} \cdot \text{m}^{-3}$, but deep chlorophyll layers exist in the metalimnia of all the lakes where concentrations frequently reach 2-3 $\text{mg} \cdot \text{m}^{-3}$ (GROSS 1995, BUDY et al. 1995).

We used both in vitro laboratory experiments to evaluate the importance of individual nutrients for algal production, and in situ mesocosm experiments to assess seasonal and spatial differences in response to nutrient additions. WATER for the in vitro experiments was collected at 2-5 m from the epilimnion of Redfish Lake. Unfiltered, 0.75-L aliquots of lake water were placed in 1-L polycarbonate flasks and incubated at light intensities of 150 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ with an 18:6 light:dark cycle at the current lake temperature. Nutrient concentrations tested were: 33 $\mu\text{g-atoms} \cdot \text{L}^{-1}$ nitrogen added as NH_4NO_3 , 2.0 $\mu\text{g-atoms} \cdot \text{L}^{-1}$ phosphorus added as KH_2PO_4 , and a minor- and micronutrient mixture composed of micromolar quantities of Mg (1.0 μM), K (14), Si (0.3), S (3), Bo (.004), Cd (.002), Co (.003), Cu (.0005), HEDTA-chelated iron (.007), Mn (.007), Mo (.00015), Ni (.002), and Zn (.005). We also tested and

found no significant differences between the response of phytoplankton to addition of KH_2PO_4 and NaH_2PO_4 . Each flask was swirled and randomly rearranged on the incubation table daily. After 5 and 10-days we took two 50-ml aliquots from each of the three replicate flasks in each treatment and analyzed them for chlorophyll *a* using a methanol extraction and the fluorometric technique of HOLM-HANSEN & RIEMANN (1978). Responses were present after 5 days, but only the results from the 10-day incubations are shown here.

The in situ bioassays were conducted in all of the lakes using translucent, collapsible 10-L polyethylene containers (cubetainers) that transmitted nearly 100 % of incident light. Normally, triplicate cubetainers for each treatment were filled with epilimnetic water and incubated at 5 m and 13–17°C. In these experiments we tested treatments of controls, N+P, and N+P+ micronutrients (M) at the same concentrations noted above. In a September experiment we also tested the response of the metalimnetic water drawn from 13–26 m to N+P additions. In this latter experiment, duplicate treatments were incubated in situ at intensities of 2–5 % of surface light, and 5–9°C. After 10 days chlorophyll *a* samples were collected and analyzed as described previously. In one experiment we preserved phytoplankton in Lugol's solution for subsequent analysis using a filter-concentration procedure described in BUDY et al. (1995).

Results

The results of the in vitro laboratory experiments from Redfish Lake indicated that nitrogen limited algal growth more often than did phosphorus, but that both nutrients were always co-limiting (Fig. 1). In May, neither N or P added alone stimulated chlorophyll levels, but N+P and N+P+M additions stimulated the phytoplankton to 280 % of the controls after a 5-day incubation, and these results (not shown) were significant ($p < 0.02$). In both July and September, nitrogen additions to Redfish Lake water increased chlorophyll levels significantly ($p < 0.001$, 0.02, ANOVA followed by Tukey HSD post-hoc test) while phosphorus had no effect ($p > 0.30$, 0.89) on the algae when it was added alone. The two nutrients together, however, stimulated chlorophyll 500–680 % above control levels during the 10-day incubation, and these effects were significantly greater than when nitrogen was added alone ($p < 0.001$, 0.001). In July, adding minor and micro-nutrients along with nitrogen and phosphorus significantly increased chlorophyll levels above that produced by N+P alone ($p < 0.001$). In

September the minor and micro-nutrients also produced higher mean chlorophyll levels than the N+P treatment, but this increase was not significant ($p = 0.26$).

In the in situ experiments of epilimnetic water, nutrient additions significantly ($p < 0.001$) increased chlorophyll concentrations in all of the lakes (Fig. 2). Initial and control treatments almost always had chlorophyll *a* concentrations $\ll 1 \text{ mg} \cdot \text{m}^{-3}$, suggesting that the lakes were severely nutrient limited. Nitrogen plus phosphorus additions usually stimulated algal growth 200 to >1000 % above control levels after 10 d. Addition of the minor and micro-nutrients increased chlorophyll levels above the NP treatments in 7 of 9 cases, but in most instances these differences were small, and in only two cases did the responses approach significance (ANOVA, Redfish L. in July, $p = 0.06$; Yellow Belly L. in July, $p = 0.10$).

Considerable seasonal differences in the response to nutrient additions were apparent in most lakes (Fig. 2). In Pettit, Redfish, and Stanley Lakes, the responses to all epilimnetic treatments were significantly greater in July than in June or September (1 ANOVA per lake; all p values ≤ 0.025). In Yellow Belly Lake the response was also greater in July than in September ($p = 0.086$), but we did not test this lake in June. Algal response in Alturas Lake was also greater in July than in September, but this difference was not significant.

Enumeration and biomass estimates of the phytoplankton from the July in situ experiment indicated that different taxa responded differently to the different nutrients (Fig. 3). The algal biovolume in the initial sample and the controls was dominated by *Dinobryon* sp. In the N+P treatments this taxon nearly disappeared, but was replaced by small unicellular chlorococcales and diatoms that had 8-times greater biovolume than the control treatments. Treatments that received additional minor- and micro-nutrients (N+P+M) had nearly 70-times the biomass of controls after the 10-day incubation. These treatments were also dominated by chlorococcales, the diatoms *Fragilaria* sp. (80 %) and *Amphipleura* sp. (20 %), and a small component of *Chlamydomonas* sp.

Phytoplankton in the metalimnia of the lakes were also nutrient limited, and responded significantly to N and P additions when tested during the September in situ experiment (Fig. 4). Chlorophyll levels in metalimnetic water from

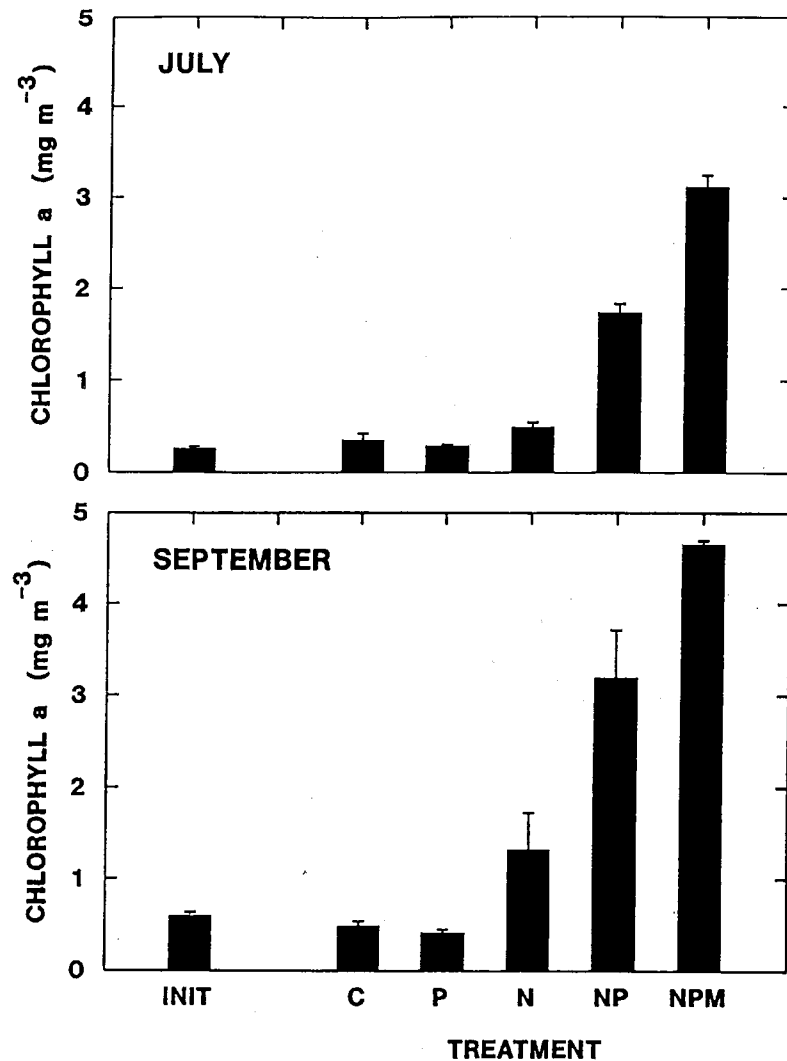


Fig. 1. Effects of additions of nitrogen (N), phosphorus (P), nitrogen + phosphorus (NP), and N+P + minor and micronutrients (NPM) on chlorophyll *a* concentrations in 10-day in vitro bioassays of Redfish Lake water. Initial (INIT) concentrations of chlorophyll are also shown. Above: 22-July to 2-Aug-1992. In July all treatments except +P were significantly different from each other ($p < 0.02$; ANOVA followed by Tukey HSD post-hoc test). Below: 9-19 Sept 1992. All treatments except +P were significantly greater than controls, and all except NP and NPM were significantly different from each other ($p < .003$). Error bars show +1 SE.

Yellow Belly and Stanley Lakes fertilized with N+P reached 8 and 13 mg/m³, respectively. Nutrient additions to epilimnetic water, however, resulted in a greater percent increase in chlorophyll levels than did additions to metalimnetic water in all lakes except Stanley (Fig. 4). The greater response in the epilimnion was significant in Alturas ($p = 0.057$), Redfish ($p = 0.008$), and Yellow Belly ($p = 0.038$) Lakes,

but not Pettit Lake ($p = 0.31$). The greater response in the metalimnetic water in Stanley was not significant ($p = 0.28$).

Discussion

Our results, as well as the low natural levels of algae in the lakes, indicated that phytoplankton in the Sawtooth Valley lakes were severely nu-

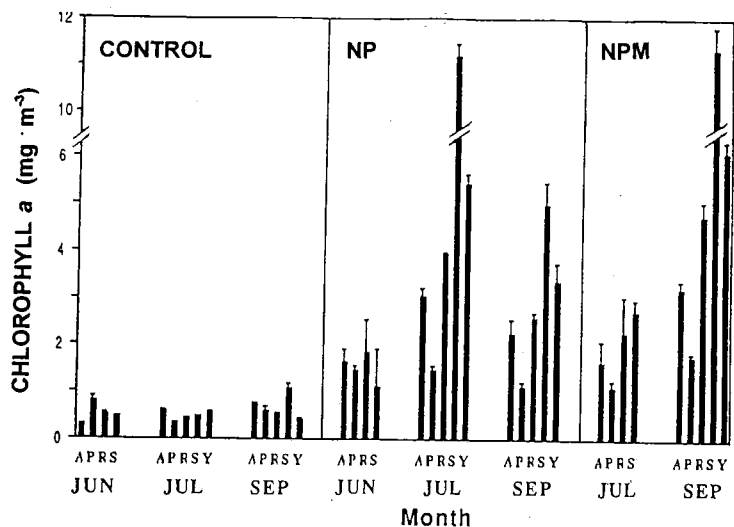


Fig. 2. Seasonal effects of N+P (NP) and N+P+ micronutrient (NPM) additions on chlorophyll *a* levels in 10-day in situ bioassays of epilimnetic water of five Sawtooth Valley lakes during 1992. N=3 for all treatments, except for the five NP treatments in September, when N=2. Error bars show +1 SE. A = Altutes; P = Pettit; R = Redfish; S = Stanley; Y = Yellow belly Lake.

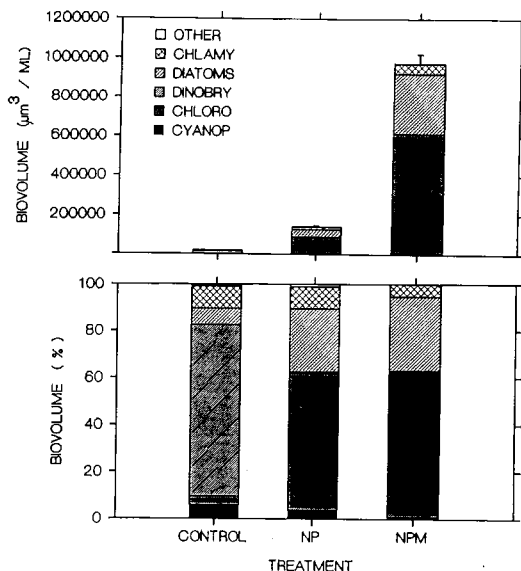


Fig. 3. Effects of nutrient additions on the biovolume (above) and percent composition (below) of the phytoplankton in the July in situ bioassay of epilimnetic water from Redfish Lake, Idaho. Treatments: Control (N=3); N+P (N=3); N+P+ minor and micronutrients - NPM (N=2). Taxa key: CYANOP - Small, unicellular cyanobacteria; CHLORO - Chlorococcales; DINOBYRY - *Dinobryon* sp.; DIATOMS - principally *Fragillaria*, *Tabellaria* and *Amphipleura*; CHLAMY - *Chlamydomonas*. Error bars, when visible, show +1 SE of the total biovolume.

trient-limited, primarily by nitrogen and secondarily by phosphorus. Thus the view that phosphorus alone limits algal growth in lakes (SCHINDLER 1974) is not applicable to the Sawtooth Valley systems. Reviews of bioassay results suggest, in fact, that nitrogen limits phytoplankton growth nearly as frequently as does phosphorus, both in the temperate zone (ELSER et al. 1990) and in the tropics (WURTSBAUGH et al. 1985). The phytoplankton in the lakes were clearly co-limited by N and P, however, as the addition of both nutrients significantly enhanced chlorophyll production.

In our in vitro experiments, the minor- and micro-nutrient mixture, when added with N and P, frequently provided additional algal growth, suggesting that one or more of these may limit phytoplankton production. One of the "minor" nutrients added in the mixture was silicate, which is used by diatoms to synthesize their frustules. Diatoms, in fact, responded very strongly to the NPM treatment (Fig. 3), perhaps as the result of the silicate. However, the chlorococcales were also strongly enhanced by the mixture, indicating that some additional micro-nutrient could also have been limiting the total phytoplankton assemblage. It seems unlikely that micro-nutrients alone currently exert much control on the phytoplankton assemblage, because the NP additions always in-

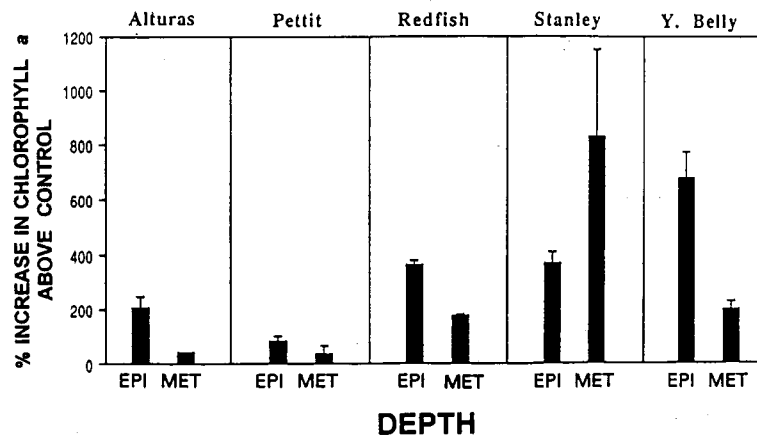


Fig. 4. Relative response of phytoplankton to N+P additions to epilimnetic (EPI) and metalimnetic (MET) water incubated in situ in five Sawtooth Valley Lakes. The results show the percent increase in chlorophyll *a* in treatments (T) above control (C) levels [$\% \text{ increase} = (T \cdot 100 / C) - 100$]. Experimental dates 9–19 September 1992. Error bars show standard errors.

licated that those macro-nutrients were controlling algal growth, and because the micro-nutrient mixture never significantly enhanced production in the in situ experiments. If, however, the lakes are fertilized with nitrogen and phosphorus to alleviate this deficiency, some of the minor and/or micro-nutrients might then become limiting.

Top-down control of the phytoplankton by zooplankton grazing may be relatively unimportant in the Sawtooth lakes, as experiments conducted concurrent to those reported here showed little, if any effect of adding crustacean zooplankton on chlorophyll levels (GROSS et al. 1993). A lack of grazing depression is not surprising, given the very low biomass of zooplankton, which ranged from 10–60 $\mu\text{g/L}$ in the lakes (BUDY et al. 1995). Median grazing rates of crustacean zooplankton are near $0.4 \text{ ml} \cdot \mu\text{g}^{-1} \cdot \text{day}^{-1}$ (PETERS 1984), so that total grazing pressure should have been approximately 0.4 to 2.4 $\% \text{ day}^{-1}$.

In practice, it appears that the phytoplankton production in the Sawtooth Valley lakes can easily be increased by fertilization, as has been done in Alaskan and Canadian sockeye systems (HARDY et al. 1986, STOCKNER 1987). How much, then, should the lakes be fertilized? Answering this question will involve balancing the need to stimulate productivity to protect the endangered sockeye salmon, with the need to protect the aesthetic qualities of these impor-

tant scenic lakes. It should be possible, however, to significantly increase lake productivity and still maintain water clarity within the ranges currently found in the lakes. For example, it might be desirable to fertilize the lakes during summer stratification when chlorophyll levels are low, and when the algae appear to be most nutrient-limited.

Alternatively, nutrients could be added to the metalimnia of the lakes where phytoplankton are also nutrient-limited (Fig. 4). Metalimnetic additions would have the advantage of stimulating algal growth, yet minimally affecting water clarity. Metalimnetic fertilization has been demonstrated to enhance phytoplankton production in another oligotrophic sockeye salmon lake (LEBRASSEUR et al. 1978). If metalimnetic fertilizations are attempted, however, care must be taken that the nutrients remain in the photic zone where phytoplankton could be stimulated, as deeper additions may result in nutrient immobilization (SCHINDLER et al. 1980).

Although short-term fertilization may help recover the endangered salmon, it will not likely restore lake productivity for the long-term, because added nutrients are relatively quickly washed from the lakes due to their low retention rates. Furthermore, because of high natural and dam-induced mortality of the migrating salmon, more nutrients leave with emigrating smolts, than return with adult salmon (WURTSBAUGH & LUECKE 1994, GROSS

1995). Consequently, any long-term solution for recovering sockeye salmon in the Sawtooth Mountain lakes will require solving the salmon passage problems on the Columbia and Snake Rivers.

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References

- BARDACH, J. E., RYTHER, J. H. & McLARNEY, W. O., 1972: *Aquaculture*. - Wiley-Interscience, New York, 868 pp.
- BJORN, T. C., CRADDOCK, D. R. & CORLEY, D. R., 1968: Migration and survival of Redfish Lake, Idaho, sockeye salmon, *Oncorhynchus nerka*. - *Trans. Am. Fish. Soc.* 97: 360-373.
- BUDY, P., LUECKE, C., WURTSBAUGH, W. A., GROSS, H. P. & GUBALA, C., 1995: Limnology of Sawtooth Valley lakes with respect to potential growth of juvenile Snake River sockeye salmon. - *Northwest Sci.* 69: 133-150.
- BEVAN, D., HARVILLE, J., BERGMAN, P., BJORN, T., CRUTCHFIELD, J., KLINGEMAN, P. & LITCHFIELD, J., 1994: Snake River salmon recovery team: Final recommendations to National Marine Fisheries Service. - *Nat. Marine Fish. Service*, Seattle, Washington, 491 pp.
- ELSER, J. J., MARZOLF, E. R. & GOLDMAN, C. R., 1990: Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. - *Can. J. Fish. Aquat. Sci.* 47: 1468-1477.
- GROSS, H. P., 1995: Evaluation of lake fertilization as a tool to assist in the recovery of the Snake River sockeye salmon, *Oncorhynchus nerka*. - *M. S. thesis*, Utah State University, Logan, Utah. 195 pp.
- GROSS, H. P. & WURTSBAUGH, W. A., 1994: Water and nutrient budgets of the Sawtooth Valley lakes. - In: TEUSCHER, D. & TAKI, D. (eds.): *Snake River sockeye salmon habitat and limnological research*: 7-29. - Bonneville Power Administration (DOE/BP-22548-2), Portland, OR.
- GROSS, H. P., WURTSBAUGH, W. A., LUECKE, C. & BUDY, P., 1993: Nutrient limitation of phytoplankton in oligotrophic lakes of the Sawtooth Valley, Idaho. - In: SPAULDING, S. (ed.): *Snake river sockeye salmon (Oncorhynchus nerka) habitat/limnologic research*: 29-52. - Bonneville Power Administration (DOE/BP-22548-1), Portland, OR.
- HARDY, F. J., SHORTREED, K. S. & STOCKNER, J. G., 1986: Bacterioplankton, phytoplankton, and zooplankton communities in a British Columbia coastal lake before and after nutrient reduction. - *Can. J. Fish. Aquat. Sci.* 43: 1504-1514.
- HOLM-HANSEN, O. & RIEMANN, B., 1978: Chlorophyll *a* determination: improvements in methodology. - *Oikos* 30: 438-447.
- HYATT, K. D. & STOCKNER, J. G., 1985: Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia lakes. - *Can. J. Fish. Aquat. Sci.* 42: 320-331.
- JUDAY, C., RICH, W. H., KEMMERER, G. I. & MANN, A., 1932: Limnological studies of Karluk Lake, Alaska, 1926-1930. - *Fish. Bull.* 47: 407-436.
- KLINE JR., T. C., GOERING, J. J., MATHISEN, O. A. & POE, P. H., 1990: Recycling of elements transported upstream by runs of Pacific salmon: I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin Creek, southeastern Alaska. - *Can. J. Fish. Aquat. Sci.* 47: 136-144.
- KOENINGS, J. P. & BURKETT, R. D., 1987: An aquatic rubic's cube: restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*). - In: SMITH, H. D. & MARGOLIS, L. & WOOD, C. C. (eds.): *Sockeye salmon (Oncorhynchus nerka) population biology and future management*: 419-434. - *Can. Spec. Publ. Fish. Aquat. Sci.* 96: 486 p.
- KYLE, G. B., KOENINGS, J. P. & BARRETT, B. M., 1988: Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. - *Can. J. Fish. Aquat. Sci.* 45: 856-867.
- LEBRASSEUR, R. J., McALLISTER, C. D., BARRACLOUGH, W. E., KENNEDY, O. D., MANZER, J., ROBINSON, D. & STEPHENS, K., 1978: Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. - *J. Fish. Res. Board Can.* 35: 1580-1596.
- LØVSTAD, O. & BØRNDALLEN, K., 1990: Nutrients (P, N, Si) and growth conditions for diatoms and *Oscillatoria* spp. in lakes of south-eastern Norway. - *Hydrobiol.* 196: 255-263.
- PETERS, R. H., 1984: Methods for the study of feeding, grazing and assimilation by zooplankton. - In: DOWNING, J. A. & RIGLER, F. H. (eds.): *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Water*: 2nd ed: 336-412. - Blackwell Scientific, Oxford, 501 pp.

- RIEMAN, B. E., BEAMESDERFER, R. C., VIGG, S. & POE, T. P., 1991: Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. - *Trans. Am. Fish. Soc.* 120: 448-458.
- SCHINDLER, D. W., 1974: Eutrophication and recovery in experimental lakes: implications for lake management. - *Science* 184: 897-899.
- SCHINDLER, D. W., RUSZCZYNSKI, T. & FEE, E. J., 1980: Hypolimnion injection of nutrient effluents as a method for reducing eutrophication. - *Can. J. Fish. Aquat. Sci.* 37: 320-327.
- SMITH, V. H., 1982: The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. - *Limnol. Oceanogr.* 27: 1101-1112.
- STOCKNER, J. G., 1987: Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. - In: SMITH, H. D. & MARGOLIS, L. & WOOD, C. C. (eds.) Sockeye salmon (*Oncorhynchus nerka*) population biology and future management: 198-215. - *Can. Spec. Publ. Fish. Aquat. Sci.* 96: 486.
- VOLLENWEIDER, R. A., 1976: Advances in defining critical loading levels for phosphorus in lake eutrophication. - *Mem. Ist. Ital. Idrobiol.* 33: 53-83.
- WURTSBAUGH, W. A., 1988: Iron, molybdenum and phosphorus limitation of N₂ fixation maintains nitrogen deficiency of plankton in the Great Salt Lake drainage (Utah, USA). - *Verh. Internat. Verein. Limnol.* 23: 121-130.
- WURTSBAUGH, W. A. & HORNE, A. J., 1983: Iron in eutrophic Clear Lake, California: its importance for algal nitrogen fixation and growth. - *Can. J. Fish. Aquat. Sci.* 40: 1419-1429.
- WURTSBAUGH, W. A. & LUECKE, C., 1984: Limnological models of sockeye salmon production in the Sawtooth Valley Lake. - In: TEUSCHER, D. & TAKI, D. (eds.): *Snake River sockeye salmon habitat and limnological research*: 116-125. - Bonneville Power Administration (DOE/BP-22548-2), Portland, OR.
- WURTSBAUGH, W. A., VINCENT, W. F., ALFARO TAPIA, R., VINCENT, C. L. & RICHERRON, P. J., 1985: Nutrient limitation of algal growth and nitrogen fixation in a tropical alpine lake, Lake Titicaca (Peru/Bolivia). - *Freshwat. Biol.* 15: 185-195.

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