Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: Review and summary of results

K.D. Hyatt, D.J. McQueen, K.S. Shortreed, and D.P. Rankin

Abstract: We reviewed 24 sockeye salmon (*Oncorhynchus nerka*) nursery lake experiments that involved whole-lake fertilization with appropriate treatment and control years. We found that: 21 of 21 studies showed that fertilization was associated with increased chlorophyll *a* concentrations, 16 of 16 showed increased zooplankton biomasses, 16 of 16 demonstrated increased average smolt weights, and 11 of 13 showed increased smolt biomasses. Studies involving assessments of egg-to-smolt survival were rare, but all (4 of 4) showed increased survival rates. Studies involving increased smolt-to-adult survival (i.e., marine survival) were even rarer, but all (3 of 3) showed that lake fertilization and increased smolt size were associated with increased marine survival. Several fertilization studies reported problems, and some offered solutions. For instance, when whole-lake fertilization stimulated the growth of blue-green algae, fertilizer with higher nitrogen to phosphorus ratios was used to control the problem. Conversely, when high nitrogen to phosphorus ratios were associated with blooms of ungrazable diatoms, notably *Rhizosolenia eriensis*, reduced nitrate concentrations were recommended. To date, solutions designed to constrain the growth of both blue-green algae and *Rhizosolenia* blooms remain elusive. Some studies showed that when both mysids (large invertebrate planktivores) and juvenile sockeye inhabit the same lake, sockeye suffer from a competitive disadvantage and mysids consume 80–90% of the available zooplanktonic food production. Similarly, a small number of studies demonstrated that competition from sticklebacks (*Gasterosteus aculeatus*) adversely affected sockeye growth rates, and although the problem remains unresolved, ongoing work in lakes containing kokanee (*O. nerka*), suggests that stocked cutthroat trout (*Salmo clarki*) may be capable of controlling stickleback densities through predation. Despite all of these difficulties, in almost all cases, when lakes were fertilized with various mixtures of inorganic nitrogen and phosphorus, pelagic food web bottom-up control was strong enough and predictable enough to ensure that sockeye smolt biomass increased. We conclude that sockeye nursery lake fertilization is a technique that can contribute usefully to both the enhancement and conservation of sockeye salmon populations.

Key words: sockeye salmon, lake fertilization, bottom-up, aquatic food web.

Received 9 June 2004. Accepted 29 September 2004. Published on the NRC Research Press Web site at http://er.nrc.ca/ on 10 November 2004.

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doi: 10.1139/A04-008

Résumé : Les auteurs ont examiné 24 expériences conduites sur la pisciculture du saumon sockeye en lacs, lesquelles impliquent la fertilisation en vrac avec des traitements appropriés et des années témoins. On constate que : 21 des 21 études montrent que la fertilisation est associée avec une augmentation de la teneur en chlorophylle *a*, 16 sur 16 montrent une augmentation des biomasses de zooplancton, 16 sur 16 conduisent à une augmentation des poids moyens des saumoneaux, et 11 sur 13 se traduisent par une augmentation des biomasses en saumoneaux. Les études impliquant des évaluations de la survie, allant de l'œuf au saumoneau, sont rares, mais toutes (4 sur 4) montrent une augmentation des taux de survie. Les études qui portent sur la survie, allant du saumoneau à l'adulte (i. e. survie en mer), sont encore plus rares, mais toutes (3 sur 3) montrent que la fertilisation des lacs et l'augmentation des dimensions des saumoneaux sont associées à une augmentation de la survie marine. Plusieurs études sur la fertilisation font mention de problèmes, et quelques unes proposent des solutions. Par exemple, lorsque la fertilisation en vrac des lacs stimule la croissance d'algues bleues vertes, on utilise des fertilisants ayant des rapports azote/phosphore plus élevés, pour maîtriser le problème. Réciproquement, lorsque des rapports élevés en azote/phosphore sont associés avec une prolifération de diatomées non pâturables, nommément le *Rhizoselenia eriensis*, on recommande de réduire les nitrates. Jusqu'ici, les solutions conçues pour contrôler la croissance des algues bleues vertes aussi bien que la prolifération des *Rhizoselenia*, demeurent élusives. Quelques études montrent que lorsque les mysis (gros planctivores invertébrés) et les jeunes saumons sockeyes habitent le même lac, les saumons souffrent de la compétition, et les mysis consomment 80–90 % de la production en nourriture zooplanctonique. Dans la même veine, un petit nombre d'études démontrent que la compétition par les épinoches (*Gasterosterus aculeatus*) nuisent aux taux de croissance des saumons, et bien que le problème demeure sans solution, les travaux en cours dans des lacs contenant du saumon kokanee (*O. nerka*) suggèrent que la truite fardée introduite (*Salmo clarkii*) pourrait être capable de limiter la densité des épinoches par prédation. En dépit de ces difficultés, dans presque tous les cas, lorsque les lacs sont fertilisés avec divers mélanges d'azote et de phosphore inorganiques, la maîtrise du réseau de nourriture pélagique est suffisamment grande et prévisible pour assurer que la biomasse des saumons sockeyes augmente. Les auteurs concluent que la pisciculture du saumon sockeye en lacs est une technique qui contribue de façon concrète, à la fois à l'augmentation et à la conservation des populations du saumon sockeye.

Mots clés : saumon sockeye, fertilisation lacustre, de bas en haut, chaine alimentaire aquatique.

[Traduit par la Rédaction]

Introduction

More than 70 years ago, Juday et al. (1932) suggested that biogenic nutrient deposition from the carcasses of spawning salmon was responsible for the unusually luxuriant algal and zooplankton communities found in Karluk Lake, on Kodiak Island, Alaska. Five years later, Ricker (1937) also discussed nutrient contributions from carcasses in Cultus Lake, British Columbia, and wrote "The death and decay of adult salmon has for long been considered as resulting in an important accession of nutrient elements by the lake." Nelson and Edmonson (1955) were the first to actually attempt the artificial fertilization of a sockeye nursery lake. They introduced their ground-breaking study by reviewing data from Karluk Lake (37 km^2), where sockeye returns had declined from approximately 3 million during the late 1800s to less than 1 million during 1944–1953. They attributed this decline to the combined effects of overfishing and changes in the freshwater environment. They hypothesized that during years of high spawner abundance, nutrients from salmon carcasses stimulated algal production, resulting in more zooplankton, increased food consumption by sockeye fry, larger smolts, and (citing Barnaby 1944) therefore better marine survival. Nelson and Edmonson (1955) then went on to suggest that observed declines might be reversed by adding artificial fertilizers during years when returns were low. This suggestion led to a proposed pilot experiment at Bare Lake (0.49 km^2, situated near Karluk Lake). During 1950–1953, Bare Lake was fertilized seven times, and both primary production and algal biomasses increased, but there was no change in zooplankton biomass (Nelson and Edmondson 1955). The result was that Karluk Lake was never fertilized, and Alaskan nursery lake fertilizations were not reinitiated until the 1970s (Kyle et al. 1997).

Activity in British Columbia began in 1969 when a group of scientists from the Pacific Biological Station at Nanaimo put theory into practice at Great Central Lake (GCL), Vancouver Island, B.C. This large-scale lake fertilization experiment was based on the assertion (Barraclough and Robinson 1972) that "Decomposing bodies of anadromous fish, such as sockeye salmon (*Oncorhynchus nerka)* contribute to the fertilization of nursery lakes following spawning in the lake. ... removal of maturing sockeye by the commercial fishery may deny lake waters of their essential nutrients and contribute to lowered productivity." The objective of the Great Central Lake experiment was to test the hypothesis that artificial fertilization could replace nutrient losses associated with sockeye carcasses removed by the commercial fishery. In-lake productivity responses (Parsons et al. 1972; LeBrasseur and Kennedy 1972; Barraclough and Robinson 1972) and subsequent increases in adult returns associated with the first year of fertilization (1970) were judged to be very "positive" and a long-term fertilization program was approved for Great Central Lake. During the late 1970s, a large-scale Lake Enrichment Program (LEP) was established. It began with six lakes and grew until the early 1990s to include 17 (Hilborn and Winton 1993). Since then, priorities within the Department of Fisheries and Oceans have changed, and federally funded lake fertilization has been all but abandoned. In Alaska, during 1979, the Division of Fisheries Rehabilitation, Enhancement, and Development (FRED), a section of the Alaska Department of Fish and Game, initiated a nutrient enrichment and fry outplanting program that included 16 lakes (Kyle et al. 1997). During the 1990s, support for FRED declined and most Alaskan lake fertilization projects were halted.

As we move into the early 21st century, priorities for nursery lake fertilization have begun to change. The emphasis is no longer on stock enhancement for the commercial fishery. Rather, the emphasis has shifted to stock conservation. During the last 50 years, continuous over-fishing, freshwater habitat destruction, and climate-induced marine survival failures have decimated many sockeye stocks. Now, a few government agencies, non-governmental organizations, and First Nations are actively using or considering the use of sockeye nursery lake fertilization to conserve stocks that are depressed, threatened, or near extinction. The review that follows may assist with that important work.

Food web theory

Lake fertilization theory is based on two assumptions. The first is that the size and survival advantages gained by sockeye fry originating from fertilized lakes can be successfully carried into the marine environment, thus ensuring increased returns of adults. The second assumption is that juvenile sockeye biomass in the pelagic zones of lakes is primarily regulated by nutrient availability ("bottom-up" control) and that substantial portions of the nutrient added at the bottom of a food web will successfully make its way from algae, through zooplankton, to fish.

With respect to the first assumption, Ricker (1962) showed that over a broad geographic range there is a positive relationship between sockeye smolt length and marine survival. Similar relationships have also been demonstrated for sockeye from the Karluk River (Barnaby 1944) and Cultus Lake (Foerster 1954). The question is: Do these general patterns apply to sockeye nursery lakes, where artificial fertilization is applied to increase smolt size and production?

With respect to the second assumption, there is general agreement that decomposing bodies of spawning salmon contribute highly variable, but sometimes substantial fractions (0–95%, depending on the lake) of the annual nutrient load to sockeye nursery lakes (Willson and Halupka 1995; Bilby et al. 1996; Larkin and Slaney 1997; Cederholm et al. 1989, 1999; Gresh et al. 2000; Thomas et al. 2002). There is also some consensus that phosphorus and nitrogen availability can be augmented through lake fertilization (Stockner and MacIsaac 1996; Kyle et al. 1997). Nelson and Edmondson (1955) were the first to clearly delineate the fertilizer enhancement theory (carcasses → nutrients → phytoplankton → zooplankton → increased food consumption by fry → larger smolts → increased marine survival) that is generally accepted today. The assumption is that bottom-up control is both predictable and strong. Over the past 30 years, the food web literature has verified the general predictability of bottom-up relationships between (1) nutrients and algae (reviewed in Dillon and Rigler (1975) and Stockner and Shortreed (1985)), (2) algae and zooplankton (reviewed in McCauley and Kalff (1981) and Hanson and Peters (1984)), and (3) zooplankton and planktivorous fish (reviewed in Downing et al. (1990) and Koenings and Kyle (1997)).

However, during the last 20 years, the same literature has featured considerable disagreement about the relative strength of these bottom-up relations in comparison with top-down processes, which tend to reduce bottom-up control (reviewed in Shapiro and Wright (1984), McQueen (1998), McQueen et al. (1986, 1989), Carpenter et al. (1985, 2001), Mehner et al. (2002), and Jeppesen et al. (2003)). Briefly stated, food web theory supports the general assertion that overall trophic level biomass is regulated by nutrient availability, but there are many top-down processes that can influence energy transfer up pelagic food webs (reviewed in McQueen et al. (2001)). Some of the main factors are (1) the effects of algal cell size and species composition on relative grazability of algae by zooplankton (Hyatt et al. 2004), (2) the effects of algal species composition on availability of fatty acids required for enhanced zooplankton growth (Brett et al. 2000), (3) the influence of regional diversity pools on the availability of the large-bodied zooplankton most favored by planktivorous fish (Matveev et al. 1994), (4) the effects of diel migration on the availability of zooplankton as prey for juvenile sockeye (Levy 1990; Cooper et al. 1992), (5) the effects of grazer body size on rates of phosphorus excretion and recycling by zooplankton (Vanni 1996), (6) the rates of nutrient transport and (or) sedimentation caused by predator-induced changes in zooplankton body size and (or) species composition (Taylor and Carter 1997), (7) abundances of invertebrate planktivores that might be expected to reduce grazer abundance and therefore food availability for planktivorous fish (Benndorf 1995), (8) changes in fish-induced transport of phosphorus from the benthos to the pelagic zone (Perez-Fuentetaja et al. 1996), and (9) potential competitive interactions between juvenile sockeye and other pelagic planktivorous fish (Hyatt et al. 2004). Given the potential effects of these and other top-down factors, there remains considerable uncertainty about the proportion of fertilizer-induced energy captured by phytoplankton that can successfully move from algae to fish. The question remains: Can substantial amounts of the photosynthetically fixed energy stimulated by the addition of fertilizers to lakes make its way up the pelagic food web, causing juvenile sockeye to survive better and (or) grow larger?

Organization of this review

In the pages that follow we have reviewed 24 sockeye nursery lake fertilization experiments. We have divided these studies geographically into those based in Alaska, British Columbia, and the Columbia River, Idaho. In all cases we have summarized relevant lake characteristics, fertilizer quantities, and experimental designs and durations. We have then compared (fertilized vs. unfertilized) averages for epilimnetic nutrient concentrations, phytoplankton biomass and (or) chlorophyll *a* concentrations, zooplankton biomasses, juvenile sockeye growth rates, juvenile sockeye survival, and where available, smolt to adult survival rates. Lake-specific summaries are also provided in Tables 1 to 3. Readers interested in an overview rather than detail may wish to skip these lake-by-lake summaries and move on to the two final sections. The first of these is titled “Cautionary tales” and deals with the problems that have been encountered during various nursery lake fertilizations. The second, titled “Summary of general outcomes”, identifies emergent generalizations and explores the relationship between the quantity of nutrients added and lake responses.

Table 1. British Columbia, Lake Enrichment Program (LEP) data, summarized from Stockner and Hyatt (1984) and Shortreed et al. (2001).

		Treatment years		N and P added ($g\ ha^{-1}\ a^{-1}$)		Mean summer Chl *a* ($\mu g\ L^{-1}$)		Mean zooplankton biomass ($mg\ m^{-2}$ dw)	
Lake	Area (ha)	NF	F	N	P	NF	F	NF	F
Bonilla	230	1979	1980	18 217	2 696	1.00	5.40	280	700
Kennedy Clayoquot Arm	1 700	1977	1978	9 094	1 982			280	400
Kennedy MA	4 700	1978	1979	4 268	649			270	400
Curtis	300	1979	1980	6 067	900	1.24	4.02	100	150
Long	2 100	1981	1982	7 143	1 048	2.24	2.48	150	350
Morice	9 610	1978	1980	3 479	527			750	820
Sproat	4 100		1985–1986	11 139	493	0.60	1.08	285	590
Nimpkish	3 700		1982–1987, 1989	3 327	730	0.80	1.78	73	260
Devon	180	1979, 1981	1980	6 222	944	1.79	4.57	77	108
Lowe	370		1979–1982	7 980	1 169	1.22	1.34	180	815

Note: N, total nitrogen; P, total phosphorus; Chl a, chlorophyll *a*; NF, years when not fertilized; F, years when fertilized.

Table 2. British Columbia, Lake Enrichment Program data summarized from Hyatt and Stockner (1985). Calculation of smolt biomass assumes no mortality from fall fry to smolt.

		Treatment years		Loading rates ($g\ ha^{-1}\ a^{-1}$)		Age 1 smolt weights (g)		Fall-fry densities (ha^{-1})		Smolt biomass (ha^{-1})	
Lake	Area (ha)	NF	F	N	P	NF	F	NF	F	NF	F
Kennedy Clayoquot Arm	1 700	1977	1978	9 094	1 982	1.98	2.55	2 025	3 260	4 010	8 313
Great Central Lake	5 100	1969, 1974–1976	1977–1981	4 029	716	2.78	4.28	2 500	2 103	6 950	9 001
Long	2 100	1980–1981	1977–1979	9 710	1 946	2.47	2.82	4 313	7 016	10 653	19 785
Bonilla	230	1979	1980–1981	20 891	3 196	1.62	2.25	1 222	5 473	1 980	12 314
Devon	180	1979, 1981	1980	6 222	944	2.62	4.35	2 903	2 796	7 606	12 163
Curtis	300	1979	1980–1981	10 867	1 617	1.09	2.78	1 589	4 287	1 732	11 918
Kitlope	1 260	1978	1979–1980	8 944	1 381	2.14	5.20	310	208	663	1 082

Note: N, total nitrogen; P, total phosphorus; Chl a, chlorophyll *a*; NF, years when not fertilized; F, years when fertilized.

Table 3. Multi-year lake fertilization studies. Summary of some data provided in the text. Calculation of smolt biomass assumes no mortality from fall-fry to smolt. All of the comparisons involve the same lake "before and after" treatment. The exception is the Woss–Vernon experiment where Woss Lake was fertilized and Vernon Lake used as an unfertilized reference.

		Treatment years		Loading (g ha^{-1} a$^{-1)}$		TP (μg L^{-1})		Chl a (μg L^{-1})		Zoop biomass (mg m^{-2})		Smolt weight (g)		Smolt biomass (g ha^{-1})	
	Area (ha)	NF	F	N	P	NF	F	NF	F	NF	F	NF	F	NF	F
Great Central Lake	5 100	1969, 1974–1976	1970–1973	5 184	1 227			7.00	11.00	900	7 400	2.78	3.13	6 950	5 822
Hobiton	360	1984	1980–1983	5 840	861	2.1	3.2	1.30	2.20						
Kennedy Clayoquot Arm	1 700	1977, 1985	1978–1984	9 571	1 157	1.5	4.3	0.95	4.70						
Kennedy MA	4 700	1977–1978, 1981–1984	1979–1980, 1985	5 691	613	1.6	2.2	1.14	2.30						
Yakoun	810	1982, 1986–1998[a]	1983–1985	3 563	553	1.9	4.0	1.69	3.28			1.12	2.47	2 700	1 700
Woss–Vernon	1 300	2000–2003	2000–2003	8 579	584	2.90	3.6	0.36	0.92	510	660	2.50	3.30	1 710	2 030
Chilko	18 500	1984–1986, 1989, 1994–1995	1988, 1990–1993	5 480	499	2.7	4.1	0.90	1.20	829	1 119				
Adams	12 900	1986	1997	5 040	540			0.87	0.97	590	743	2.64	3.68		
Leisure	110	1982–1984	1985–1992	31 100	3 455	5.3	9.0	0.65	3.95	70	600	1.70	3.60	2 727	9 544
Fraser	1 660	1985–1987	1988–1992	8 940	982	6.7	8.0	1.00	1.37	150	300	3.60	5.10		

Table 3. *Concluded.*

		Treatment years		Loading (g ha^{-1} $a^{-1)}$		TP (μg L^{-1})		Chl a (μg L^{-1})		Zoop biomass (mg m^{-2})		Smolt weight (g)		Smolt biomass (g ha^{-1})	
	Area (ha)	NF	F	N	P	NF	F	NF	F	NF	F	NF	F	NF	F
Coghill	1 270	1988–1992	1993–1996	3 161	812	8.0	9.8	0.64	2.05	48	92	1.46	1.48	302	641
Packers period 1 vs. 2[a]	210	1981–1983	1984–1986	17 400	1 760	14.7	15.0	1.30	2.00	200	349	5.20	10.40	9 523	14 285
Redoubt	1280	1980–1983	1984–1986	15 600	1 530			0.76	1.20	100	150	4.00	10.00		
Redfish	615	1992	1995–1998	5 265	281			0.50	1.00	348	453				

Note: N, total nitrogen; TP, mean summer total phosphorus; Chl a, mean summer chlorophyll *a*; Zoop biomass, mean summer zooplankton biomass; NF, years when not fertilized; F, years when fertilized.

[a] Yakoun Lake: water chemistry comparison only during 1982–83. Fish comparisons from all other years.

[b] See text for definition of periods 1 and 2.

Field studies in Alaska

Leisure Lake, Alaska

Leisure Lake (latitude 59°35′N, longitude 151°19′W, surface area 1.1 km^2) was stocked with about 2 million sockeye salmon fry per year from 1980–1985 and then stocked and heavily fertilized using a mean loading rate of 31 100 g ha^{-1} a^{-1} of N and 3 455 g ha^{-1} a^{-1} of P during 1985–1992 (Kyle 1994; Koenings and Kyle 1997). Nutrients, chlorophyll, and zooplankton were recorded during both the unfertilized (1985–1992) and fertilized (1982–1984) periods. Fertilization produced almost immediate results. Mean epilimnetic total phosphorus (TP) concentrations increased by 70% from 5.3 $\mu\mathrm{g\,L}^{-1}$ during the unfertilized period to 9.0 $\mu\mathrm{g\,L}^{-1}$ during the fertilized period. Mean chlorophyll *a* concentrations increased by 500% from 0.65 $\mu\mathrm{g\,L}^{-1}$ during the unfertilized period to 3.65 $\mu\mathrm{g\,L}^{-1}$ during the fertilized period. Zooplankton biomass increased more than 700% from 70 mg m^{-2} dry weight (dw) during the unfertilized period to 600 mg m^{-2} dw during the fertilized period. Smolt weights increased 112% from 1.7 g during the unfertilized period to 3.7 g during the fertilized period. Smolt age decreased, and total stocked fry-to-smolt survival almost doubled from 16% during the unfertilized period to 27% during the fertilized period, although between-year variability was high and the differences were not statistically significant. Finally, marine survival, when averaged over three years, increased from 11.4% during the unfertilized period to 14.2% during the fertilized period, but again, between-year variability was very high (13.8%, 6.8%, 13.7% during the unfertilized period and 24.4%, 9.9%, 8.2% during the fertilized period) and the differences were not significant.

Fraser Lake, Alaska

Fraser Lake (57°5′N, 154°10′W, surface area 16.6 km^2) was first seeded with sockeye eggs in 1951. During 1964–1986, sockeye escapement increased from 14 000 to 257 000 a^{-1} and mean annual smolt lengths and weights decreased from 148 to 89 mm and 29.5 to 5.9 g (Kyle et al. 1988; Kyle 1994; Koenings and Kyle 1997). In an attempt to increase sockeye lengths and weights, Fraser Lake was fertilized during 1988–1992 using a mean loading rate of 8940 g ha^{-1} a^{-1} of N and 982 g ha^{-1} a^{-1} of P. Data for nutrients, chlorophyll, zooplankton, and fish were recorded for the unfertilized (1985–1987) and fertilized (1988–1992) periods. Mean epilimnetic TP concentrations increased by 19% from 6.7 $\mu\mathrm{g\,L}^{-1}$ during the unfertilized period to 8.0 $\mu\mathrm{g\,L}^{-1}$ during the fertilized period. Mean chlorophyll *a* concentrations increased by 37% from 1.00 $\mu\mathrm{g\,L}^{-1}$ during the unfertilized period to 1.37 $\mu\mathrm{g\,L}^{-1}$ during the fertilized period. Mean zooplankton biomass doubled from 150 mg m^{-2} dw during the unfertilized period to 300 mg m^{-2} dw during the fertilized period. Smolt weights increased 42% from an average of 3.6 g during the unfertilized period to 5.1 g during the fertilized period. During years when escapement exceeded a "target" derived from the eutrophic olume model (see the section "Euphotic volume model" below), fry size declined. When escapement was below or near the euphotic volume (EV) escapement goal, the average length of fry remained stable at approximately 65 mm, and smolt weights increased. The authors concluded that, within limits, fertilization of Fraser Lake counterbalanced top-down effects of fish on zooplankton, so that fry densities could increase without obvious density-dependent declines in smolt weights.

Coghill Lake, Alaska

Edmundson et al. (1997) described trophic-level responses to the nutrient treatment of Coghill Lake (61°4′N, 147°54′W, surface area 12.70 km^2). During 1980–1990 total returns of sockeye to the Coghill Lake system were the highest in Prince William Sound, but during 1990–1994 run sizes declined, possibly in response to earlier over-grazing of the zooplankton forage base. Coghill Lake was fertilized during 1993–1996 using a mean loading rate of 3161 g ha^{-1} a^{-1} of N and 812 g ha^{-1} a^{-1} of P, and it was stocked with sockeye fry during 1995–1996. Fertilizer additions accounted for 40–60% of the mean annual total phosphorus loading. Sockeye salmon carcasses accounted for about 10%. A comparison of seasonal means for unfertilized years (1988–1992) with fertilized years (1993–1996) showed that mean epilimnetic TP concentrations increased from 8.0 μg L^{-1} during the unfertilized period to 9.8 μg L^{-1} during the fertilized period. Mean epilimnetic NO$_3$ concentrations decreased from 18.8 μg L^{-1} during the unfertilized period to 13.4 μg L^{-1} during the fertilized period. Mean epilimnetic chlorophyll *a* concentrations increased from 0.64 μg L^{-1} during the unfertilized period to 2.05 μg L^{-1} during the fertilized period. In response to fertilization, zooplankton biomass (comprising >90% cyclopoids, some bosminids, and little else) roughly doubled from 48.1 mg m^{-2} dw during the unfertilized period to 92.4 mg m^{-2} dw during the fertilized period (Note, this difference was evident only when the authors removed from the comparison the 1988 pre-fertilization data, which may have been influenced by a sampling error). Mean smolt weights remained unchanged at 1.46 g during the unfertilized period and 1.48 g during the fertilized period, but average abundance of smolts doubled from 207 ha^{-1} during the unfertilized period to 433 ha^{-1} during the fertilized period, and average smolt biomass increased from 302 g ha^{-1} to 641g ha^{-1}. In two of the fertilization years, increases in smolt densities were attributed to increased spawner abundance or increased spawners plus stocking. However, during 1 year (1995) higher smolt densities resulted from a 600% increase in smolt survival from 25 to 150 smolts per spawner. In summary, the data suggest that although Coghill Lake was relatively unproductive (meromictic and glacially influenced), and although smolt weights did not change, fertilization was associated with a doubling of smolt densities and therefore a doubling of smolt biomass.

Packers Lake, Alaska

Packers Lake (60°28′N, 151°55′W, surface area 2.1 km^{-2}) is located on Kalgin Island, Cook Inlet, Alaska. Kyle (1994) analyzed the first 12 years of data, and Mazumder and Edmundson (2002) reanalyzed those data and added an additional four years of observations. In an attempt to concisely summarize this complex 16 year data set, we have divided the chronology into four sections: During period 1, comprising years 1 and 2 (1981–1982), baseline data were collected and there was no stocking and no fertilization. During period 2, comprising years 3–6 (1983–1986) the lake was fertilized but not stocked. During period 3, comprising years 7–12 (1987–1992), the lake was both fertilized and stocked. During period 4, comprising years 13–16 (1993–1996), the lake was fertilized and stocked, but N loading and stocking rates were reduced.

Comparisons of time periods 1 and 2: (unfertilized vs. fertilized but not stocked). During period 2, fertilization rates were very high, averaging 17 400 g of N and 1760 g of P ha^{-1} a^{-1}, and this was reflected in higher values for TP, chlorophyll *a*, zooplankton, and fish. Epilimnetic, summer TP concentrations averaged 14.7 μg L^{-1} during the unfertilized period 1 (control) and increased to 15.0 μg L^{-1} during fertilized, but not stocked, period 2. Chlorophyll *a* concentrations averaged 1.3 μg L^{-1} during unfertilized period 1 and increased to 2.0 μg L^{-1} during fertilized period 2. Zooplankton biomasses averaged 200 mg m^{-2} dw during unfertilized period 1 and increased to 349 mg m^{-2} dw during fertilized period 2. These increases were associated with gains in average age 1 smolt weights from 5.2 to 10.4 g and increases in mean smolt biomass from 2000 kg per lake during unfertilized period 1 to 3000 kg per lake during fertilized period 2. Smolt age composition changed from 8% age 1 smolts during unfertilized period 1 to 42% age 1 smolts during fertilized period 2, and marine survival measured as percent smolts returning as adults increased from 9.5% during unfertilized period 1 to 13.6% during the fertilized and not stocked period 2.

Comparisons of time periods 2 and 3: (heavily fertilized vs. reduced fertilization and stocked). During period 3, (1987–1992) fertilization rates were reduced to 619 mg ha^{-1} a^{-1} of P, and this was reflected in declining biomass values for algae, zooplankton, and fish. Summer epilimnetic TP concentrations declined from a mean 15.0 μg L^{-1} during fertilized but not stocked period 2 to 13.0 μg L^{-1} during fertilized and stocked period 3. Chlorophyll *a* concentrations remained stable at 2.0 μg L^{-1}. Mean summer zooplankton biomasses declined from 349 mg m^{-2} dw during period 2 to 200 mg m^{-2} during period 3. Age 1 smolt weights declined from an average of 10.4 g during period 2 to 3.4 g during period 3. Smolt age composition greatly favored age 1 smolts early in period 3 but declined back to near pre-fertilization levels dominated by older age groups by the end of that period. During period 3, fry stocking rates averaged 3 000 000 fry a^{-1}, but because mean smolt size decreased. Mean annual smolt biomass also decreased from 3000 kg per lake during period 2, when the lake was fertilized but not stocked, to 2700 kg per lake during period 3, when the lake was both stocked and fertilized. Marine survival data for period 3 were unavailable.

Comparisons of time periods 3 and 4: (stocked and fertilized vs. stocked and less fertilizer added). During period 4 (1993–1996), fertilization rates were further reduced to 480 mg ha^{-1} a^{-1} of P. Epilimnetic TP concentrations continued to decline from an average of 13.0 μg L^{-1} during period 3 to 9.0 μg L^{-1} during period 4. Chlorophyll *a* concentrations remained unchanged at 2.0 μg L^{-1}. Mean summer zooplankton biomasses declined from an average of 200 mg m^{-2} dw during period 3 to 149 mg m^{-2} dw during period 4. Smolt weights and biomass remained about as they were in period 3. Marine survival data were unavailable.

In summary, during period 2, when Packer Lake was fertilized but not stocked, smolt weights and biomasses were the highest recorded. During periods 3 and 4, when the lake was stocked and fertilizer loads were reduced, smolt weights and biomasses fell. The conclusion is that at Packers Lake fertilization alone produced much better overall results than fertilization plus stocking.

Redoubt Lake, Alaska

Kyle et al. (1997) summarized a portion of the Redoubt Lake (56°53′N, 135°15′W, surface area 12.8 km^2) data set for 1980–1983 (unfertilized) and 1984–1986 when it was fertilized with an average of 15 600 g ha^{-1} a^{-1} of N and 1530 g ha^{-1} a^{-1} of P. Fertilization was associated with increased concentrations of chlorophyll *a*, higher zooplankton biomasses, and larger smolts. Mean epilimnetic chlorophyll *a* increased from 0.76 μg L^{-1} during the unfertilized period to 1.20 μg L^{-1} during the fertilized period. Mean summer zooplankton biomass increased from 100 mg m^{-2} during the unfertilized period to 150 mg m^{-2} during the fertilized period. Mean weights of age 2 smolts increased from 4 g during the unfertilized period to 10 g during the fertilized period. Data analysis for additional years is in progress.

Pass Lake and Esther Pass Lake, Alaska

The objective of the Pass and Esther Pass experiment (Koenings and Kyle 1997) was to test the hypothesis that overgrazing by strong sockeye year classes could restructure the zooplankton assemblages of fertilized lakes to such an extent that they were slow or even unable to respond to lake fertilization. Their results clearly demonstrate the effects of overstocking.

The Esther Pass (60°52′N, 147°56′W, surface area 0.2 km^2) experiment lasted 4 years and included one un-stocked control year (1985), two years (1988–1989) of stocking averaging approximately 600 000 fry per year, and one year (1990) when stocking was discontinued. The lake was never fertilized, but it has been included here because the authors compare outcomes with those obtained from Pass Lake, which was fertilized. During the stocked years, mean summer zooplankton biomasses declined from 402 mg m^{-2} in the control year to an average of approximately 65 mg m^{-2} during stocking. During the stocked years, mean smolt weights remained about constant at 5.4 and 4.8 g, and mean smolt biomasses also remained similar at 69 and 72 kg per lake. When stocking was halted (1990), zooplankton biomass rebounded to 184 mg m^{-2}. The authors concluded that Esther Pass Lake was not stocked beyond the carrying capacity derived from their EV model (see text below), and the post-stocking zooplankton community was able to retain its normal species composition and size frequency characteristics.

The Pass Lake (60°55′N, 148°3′W, surface area 0.5 km^2) experiment also lasted 4 years and included an unstocked control year (1985), two years (1988–1989) of stocking averaging approximately 154 000 fry per year, and one year (1990) when stocking was discontinued. Fertilizer additions occurred during the final two years (1989–1990), which included one year of supplemental fry additions (1989) and one year without (1990). During the stocked years, mean smolt weights were low, equaling 2.2 and 2.1 g. Mean smolt biomass declined from an average of 158 kg per lake during the control year to 45 kg per lake during the stocked year. Mean summer zooplankton biomasses also declined, averaging 783 mg m^{-2} during the control year (1985) and only 13 mg m^{-2} during the stocked year (1989). When stocking was halted and fertilizers applied (1990), zooplankton biomass remained depressed at 10 mg m^{-2}. The authors concluded that Pass Lake had been overstocked and that the zooplankton community was unable to retain its normal species composition and size distribution. The severe degradation of the Pass Lake zooplankton community may have been because Pass Lake TP was lower (2.6 μg L^{-1}) than Esther Pass Lake TP (3.2 μg L^{-1}), and more importantly, during the first year of stocking Pass Lake smolt biomass was higher than Esther Pass Lake smolt biomass. The response was almost complete elimination of all cladocerans from Pass Lake, and the authors concluded that the bottom-up effects of fertilization were unable to counterbalance the top-down, density-dependent effects of overstocking.

Euphotic volume model

At the International Sockeye Salmon Symposium held at Nanaimo, British Columbia, during the fall of 1985, Koenings and Burkett (1987) reported results of stock density and lake fertilization manipulations in a series of Alaskan lakes. The experiments involved both reduction of food competition through lake fertilization and increased food competition through increased stocking. The objective was to develop an "empirical classification of sockeye salmon smolt production based upon the population characteristics of density, freshwater age and mean size." They used data from 13 Alaskan Lakes (Kyle et al. 1997), and their conclusions were based on a mix of historical data and some of the whole-lake manipulations described above. As noted, the experiment involving fertilization of Leisure Lake produced especially clearcut results. Comparisons of data from pre-fertilized (1981–1983) with fertilized years (1984–1986) showed that the system exhibited strong bottom-up control and that well-fed smolts grew much larger. In general, Koenings and Burkett (1987) reported that "reduced intraspecific competition for food in fertilized lakes resulted in younger and larger smolts, whereas increased intraspecific competition under high stocking regimes resulted in older and smaller ones." In addition, they used their data to derive a simple empirical model (euphotic volume model) based on the volume of a lake capable of photosynthesis. One EV unit was defined to equal 1 000 000 m^3 of water receiving sufficient irradiance to support photosynthesis, and this was used to predict lake-specific optima for smolt numbers (23 000 smolts per EV unit), smolt biomasses, and adult escapement (2500 adults per EV unit).

Field studies in British Columbia

Great Central Lake, British Columbia, 1969–1976

The Lake Enrichment Program grew out of a series of forward-looking experiments started in 1969 at Great Central Lake (49°22′N, 125°15′W, surface area 51 km^2). The early work reported by Parsons et al. (1972), LeBrasseur and Kennedy (1972), and Barraclough and Robinson (1972) suggested that during the first year of fertilization, Great Central Lake algae, zooplankton, and fish all responded positively to fertilizer additions. These early reports were followed by others summarizing data collected during 1969–1976 (LeBrasseur et al. 1978). The lake was fertilized for 4 years (1970–1973) using a mean loading rate of 5184 g ha^{-1} a^{-1} of N and 1227 g ha^{-1} a^{-1} of P. It was not fertilized during 1969 and 1974–1976. Comparisons between the fertilized and unfertilized periods revealed that fertilization was associated with higher mean summer epilimnetic primary production of C averaging 5 g^{-2} a^{-1} during the unfertilized period and 11 g^{-2} a^{-1} during the fertilized period, mean epilimnetic chlorophyll *a* averaging 7 mg m^{-2} during the unfertilized period and 11 mg m^{-2} during the fertilized period, and mean growing season zooplankton biomass averaging 0.9 g^{-2} during the unfertilized period and 7.4 g^{-2} during the fertilized period. Age 1 smolt weights were slightly (but not significantly) higher, averaging 2.78 g during the unfertilized period and 3.13 g during the fertilized period. Age 1 smolt fork lengths were also only slightly higher, averaging 68 mm during the unfertilized years and 70 mm during the fertilized years. Average age 2 smolt weights were significantly higher, averaging 4.3 g during the unfertilized period and 9.9 g during the fertilized period, but age 2 smolts comprised only an average of 3.5% of the population during the fertilized years. There was also some uncertainty about smolt aging, so that some of the age 2 smolts could have been age 3. In-lake survival (i.e., percent egg-to-fry survival) was almost twice as high, averaging 5.2% during the unfertilized period and 10.3% during the fertilized one. However, average acoustic estimates of juvenile sockeye numbers were higher during the unfertilized period (2500 juveniles ha^{-1}) than during the fertilized period (1860 juveniles ha^{-1}). LeBrasseur et al. (1978) stated that marine survival increased from approximately 58 000 adult returns per year produced during the unfertilized years, to approximately 218 000 per year originating from fertilized years. However, because the fry were less than 5% larger during fertilization, it is difficult to explain how increased marine survival could have resulted from fertilizer-induced increases in smolt weights. In addition, the authors noted that during the 1970s returns to nearby Sproat Lake also increased. This observation was confirmed by Hyatt and Steer (1987), who showed that commencing in 1973 the entire Barkley Sound sockeye stock aggregate increased approximately five-fold and that the pattern observed for the Sproat Lake stock closely followed the pattern seen for Great Central Lake. Although juvenile sockeye survival increases at Great Central Lake were readily attributable to lake fertilization, increased marine survivals were not, since nearby Sproat Lake was not fertilized, yet still exhibited coincident increases in returns. Hyatt and Steer (1987) concluded that “there are many unanswered questions concerning the role of lake fertilization in promoting the increased returns of sockeye to GCL and in the intervening years many alternate hypotheses have been suggested as explanations for the increase.”

Combined results from other British Columbia Lake Enrichment Program nursery lakes

An expanded Lake Enrichment Program (LEP) began in 1977, lasted for more than 10 years, and involved various levels of fertilization of 17 sockeye nursery lakes (summarized in Stockner and Hyatt (1984), Stockner and Shortreed (1985, 1988, 1994), Hyatt and Stockner (1985), Hyatt and Steer (1987), Hardy et al. (1986), Stockner (1987), Stockner and MacIsaac (1996)). Summary reports (Stockner and Hyatt 1984; Shortreed et al. 2001) compared the results of short-term pre- and post-fertilization limnological conditions in several of these sockeye nursery lakes (summarized in Table 1). Stockner and Hyatt (1984) also anecdotally noted the following. (1) Kennedy-Clayoquot developed blue-green algal blooms that were reduced by increasing the N:P ratio of the fertilizer (i.e., more nitrogen). (2) Nimpkish Lake developed blooms of *Rhizosolenia*, a large diatom that acted as a nutrient sink, and Stockner and Hyatt (1984) predicted these blooms could be corrected by reducing fertilizer N:P ratios. (3) Great Central Lake was prone to the development of hypolimnetic blue-green algal plates, and they predicted that this problem could be corrected by increasing fertilizer N:P ratios. (4) During 3 years of fertilization, Long Lake developed such large populations of sticklebacks that juvenile sockeye growth rates no longer responded positively to fertilization.

Additional LEP data on limnological responses to lake fertilization were reported in a series of papers published during the 1980s. Stockner and Shortreed (1985) analyzed 1980–1983 phosphorus, nitrogen, chlorophyll, and primary production data from 17 fertilized coastal nursery lakes and verified highly significant bottom-up relationships (Dillon and Rigler 1975) between phosphorus concentrations and various measures of algal biomass and production. Stockner (1987) noted that coastal food chains (picoplankton → protozoans → microzooplankton → zooplankton → sockeye) tended to be longer and therefore perhaps less efficient than food chains found in more eutrophic interior British Columbia nursery lakes. Also focusing on lower trophic levels, Stockner and Shortreed (1988) provided a detailed analysis of water chemistry and algal data from Kennedy Lake. The Clayoquot Arm of Kennedy Lake was fertilized from 1978 to 1984. During 1978 fertilizer with a 10:1 molar N:P ratio was used, and in 1979–1981 the ratio was increased to 15:1. In 1981–1982 a fall bloom of *Anabaena circinalis* was observed. *Anabaena circinalis* was undesirable (i.e., relatively inedible by zooplankton) and known to be a nitrogen fixer, so it was assumed that *A. circinalis* blooms reflected a nitrogen shortage limiting other more desirable algae. Therefore, during 1982 the molar N:P ratio of the fertilizer was increased to 26:1 and during 1983–1984 increased again to 35:1. The result was that during 1983–1984 *Anabaena* disappeared almost entirely but was replaced by large blooms of *Rhizosolenia* sp., a non-grazable diatom. This bloom disappeared in 1985 when fertilization was suspended. Finally, at Sproat Lake, Shortreed and Stockner (1990) reported that *Rhizosolenia eriensis* was the dominant species in the epilimnion during the spring, but during the summer was restricted to a deep chlorophyll maximum (DCM) at the bottom of the epilimnion (20–25 m), and consequently was not influenced by fertilization during 1985 when fertilizers were added slowly over 18 weeks. However, during 1986, when the entire fertilizer load was applied over 8 weeks, epilimnetic algal densities (*R. eriensis* plus other edible species) increased to such an extent that the light penetration into the upper hypolimnion was reduced and production at the DCM declined, resulting in a net loss of algal biomass available to grazers. The authors concluded that fertilization at Sproat Lake may have decreased rather than enhanced food availability for sockeye.

Sockeye data from the LEP experiments were summarized in Hyatt and Stockner (1985). Combined results from 38 lake-years showed significant correlations between age 1 smolt weight and mean summer zooplankton biomass ($r^2 = 0.22$, $n = 38$, $p < 0.003$) and between age 1 smolt weight and mean summer zooplankton biomass per juvenile sockeye ($r^2 = 0.44$, $n = 38$, $p < 0.001$). Hyatt and Stockner (1985) also reported a negative relationship between age 1 smolt weight and summer–fall juvenile density ($r^2 = 0.52, n = 38$, $p < 0.001$), and they found that average smolt sizes in unfertilized lakes were smaller than in fertilized lakes having similar juvenile densities (summarized in Table 2). Taken together, these relationships all strongly suggest that no matter what problems may have occurred with algae, lake fertilization was almost always associated with the production of larger age-1 smolts. Although the authors gave several examples from lakes such as Owikeno and Babine, demonstrating a positive relationship between sockeye smolt size and increased marine survival, comparable data were not available from any of the fertilized or unfertilized LEP lakes.

Hobiton Lake, British Columbia

Hobiton Lake (48°45′N, 124°49′W, surface area 3.6 km^2) is located on the west coast of Vancouver Island. This lake was fertilized using a mean loading rate of 5840 g ha^{-1} a^{-1} of N and 861 g ha^{-1} a^{-1} of P during 1980–1983, and it was not fertilized in 1984–1986 (Hardy et al. 1986). In general, fertilization was associated with higher TP and chlorophyll concentrations but no significant differences in zooplankton and sockeye densities. Mean epilimnetic TP concentration was 2.1 μg L^{-1} during the unfertilized year and 3.2 μg L^{-1} during the fertilized years. Mean summer chlorophyll *a* concentration was 1.3 μg L^{-1} during the unfertilized year and 2.2 μg L^{-1} during the fertilized years. The authors note that during the fertilized years summer TN:TP (weight) averaged 50:1 and picoplankton was abundant. When fertilization was discontinued in 1984, TN:TP increased to 129:1 (weight) and there was a large post-fertilization bloom of *Rhizosolenia* sp. Because both picoplankton and *Rhizosolenia* are resistant to zooplankton grazing, it was not surprising that zooplankton abundances changed little, averaging 4300 and 3700 m^{-3} during unfertilized and fertilized years, respectively. Juvenile sockeye density also remained relatively unchanged, averaging 1576 ha^{-1} during the unfertilized year and 1623 ha^{-1} during the fertilized years. As with the original Great Central Lake experiment, mean smolt size in fertilized years increased by only about 25% by weight, but egg-to-fry survivals in fertilized years were approximately double those in unfertilized years.[2]

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[2] K.D. Hyatt and D.P. Rankin. Unpublished observations.

Yakoun Lake, British Columbia

Yakoun Lake (53°19′N, 132°17′W, surface area 8.1 km^2), located on the Queen Charlotte Islands, was fertilized during 1983–1985 at an average loading rate of 3563 g ha^{-1} a^{-1} of N and 533 g ha^{-1} a^{-1} of P. Water chemistry (Stockner and Shortreed 1985) was reported for one control year (1982) and for the first year of fertilization (1983). Sockeye data (Hyatt and Rankin 1996; Rankin and Hyatt 2002) were reported for several years between 1982 and 1998. Fertilization was associated with increased concentrations of nutrients and chlorophyll *a*. The summer epilimnetic TP average was 1.9 μg L^{-1} during the unfertilized year and 4.0 μg L^{-1} during the fertilized year. The summer epilimnetic TN average was 187 μg L^{-1} during the unfertilized year and 288 μg L^{-1} during the fertilized year. The epilimnetic chlorophyll *a* concentration average was 1.69 μg L^{-1} during the unfertilized year and 3.28 μg L^{-1} during the fertilized year. The general conclusion was that all the limnological variables increased significantly because of fertilization.

The fish data were more difficult to interpret. The first complication was that average brood-year escapement was 13 300 adults during fertilized years and only 7 800 adults during unfertilized years. Therefore, average potential egg deposition was 16.6 million during fertilized years and 9.9 million during unfertilized years. Also, during 1982–1986 Yakoun Lake had exceptionally large populations of sticklebacks. During this period stickleback densities averaged 1846 ha^{-1}, and juvenile sockeye densities averaged only 922 ha^{-1}. The expected effect of both increased sockeye fry recruitment and high stickleback densities was increased competition for food leading to potentially lower growth rates for both during the fertilized period. This prediction proved to be true. When total fish density (sockeye fry plus stickleback) exceeded 1800 fish ha^{-1}, sockeye growth rates declined (Hyatt and Rankin 1996). Therefore, to make meaningful comparisons for juvenile sockeye responses to fertilized (1983–1986) and unfertilized periods (1982, 1986–1999), we restricted our unfertilized data set to years when total fish densities were greater then 1500 ha^{-1}. Comparisons between the fertilized data set (1983–1986) and the selected unfertilized data set (including 1981, 1986–1989, 1995) indicated total fish density (sockeye + stickleback) averaged 2775 ha^{-1} during the fertilized years and 2214 ha^{-1} during the unfertilized years. The density of sockeye alone was 709 ha^{-1} during the fertilized years and 1528 ha^{-1} during the unfertilized years, and the density of stickleback alone was 2066 ha^{-1} during the fertilized years and 686 ha^{-1} during the unfertilized years. Sockeye fall fry weights averaged 2.47 g during the fertilized years compared with only 1.12 g during the unfertilized years, but egg-to-fry survival during the fertilized years averaged only 6.7% compared with 11.2% during the unfertilized years. The overall result was that juvenile sockeye production averaged only 1.7 kg ha^{-1} during the fertilized period compared with 2.7 kg ha^{-1} during the unfertilized period. Note that average fish production (sockeye plus stickleback) was higher at 4.2 kg ha^{-1} during fertilized years compared with only 3.7 kg ha^{-1} during unfertilized years. Although fertilization was associated with increased overall total fish production and with larger sockeye fall-fry, the differences were not statistically significant. Also, during fertilized years sockeye densities and sockeye production were lower than during the unfertilized years.

Chilko Lake, British Columbia

Chilko Lake (51°16′N, 124°04′W, surface area 18.5 km^2) situated in the interior of British Columbia, was fertilized for 5 years (1988, 1990–1993) using a mean loading rate of 5480 g ha^{-1} a^{-1} of N and 499 g ha^{-1} a^{-1} of P. Results from the fertilized years, were compared with measurements from 6 unfertilized years (1984–1986, 1989, 1994–1995) (Bradford et al. 2000). There was a significant increase in mean epilimnetic TP concentration from 2.7 μg L^{-1} during the unfertilized period to 4.1 μ g L^{-1} during the fertilized period. Average summer epilimnetic primary production increased from 102 mg C m^{-2} d^{-1} during the unfertilized period to 175 mg C m^{-2} d^{-1} during the fertilized period. Mean summer chlorophyll *a* increased from 0.9 μg L^{-1} during the unfertilized period to 1.2 μ g L^{-1} during the fertilized period. Mean summer zooplankton biomass increased from 829 mg m^{-2} dw during the unfertilized period to 1119 mg m^{-2} dw during the fertilized period, but variability was high and the difference was not statistically significant. During the fertilized years, the mean weight of age 1 smolts increased by 34% and the mean weight of age 2 smolts increased by 58%. The average number of recruits per spawner was 73% higher during fertilized versus unfertilized years, but the confidence interval was large (−2% to 174%). Finally, marine survival was positively associated with smolt size.

Adams Lake, British Columbia

Adams Lake (51°15′N, 119°30′W, surface area 12.9 km^2) located in south-central British Columbia, was fertilized for 1 year (1997) using a loading rate of 5040 g ha^{-1} a^{-1} of N and 540 g ha^{-1} a^{-1} of P (Hume et al. 2003). Water chemistry data were reported for a control year (1986) and for the fertilized year (1997). Mean summer epilimnetic particulate P averaged 1.2 μg L^{-1} during the unfertilized year and 2.7 μg L^{1} during the fertilized year. Mean summer epilimnetic NO_3 averaged 77.1 μg L^{-1} during the unfertilized year and 61.6 μg L^{-1} during the fertilized year. The average of summer chlorophyll *a* was 0.87 μg L^{-1} during the unfertilized year and 0.97 μg L^{-1} during the fertilized year. During fertilization there was an increase in all of the major zooplankton species (*Daphnia thorata*, *Eubosmina longispina*, *Diacyclops bicuspidatus thomasi*, and *Leptodiaptomus ashlandi*), and mean summer zooplankton biomass was higher, averaging 590 mg m^{-2} dw during the unfertilized year and 743 mg m^{-2} dw in the fertilized year. During the fertilized year sockeye diets comprised $>$ 80% *Daphnia* plus 10% other cladocerans. Copepods were seldom consumed. Comparisons of age 1 smolt weights from an unfertilized brood year (1992) with age 1 smolt weights from the fertilized brood year (1996), suggested that mean smolt weight increased from 2.64 to 3.58 g.

Muriel Lake, British Columbia

Muriel Lake (49°08′N, 125°36′W, surface area 1.5 km^2), is located on the west coat of Vancouver Island. The lake was fertilized during 1984 using slow release pellets maintained in floating cassettes at the lake surface. Loading rate records have been lost, but were calculated to maintain summer N and P values similar to those observed in other fertilized British Columbia lakes.[3]

The objective of the Muriel Lake experiment (Hyatt et al. 2005) was to investigate potential competitive interactions among juvenile sockeye, threespine stickleback, and *Neomysis mercedis*. Smolt samples taken during 1982–1989 suggested that age 1 and age 2 smolt weights and lengths did not increase during fertilization. Also, bioenergetic assessments of the 1985–1986 data sets suggested that *N. mercedis* could consume 7% to 8% of the zooplankton standing stock per day, while sockeye younger then 1 year old (0+) and sockeye younger than 2 years old (1+) could consume only 0.8% d^{-1}. Threespine stickleback could consume less than 0.2% d^{-1}. Although *N. mercedis* was the main consumer of zooplankton, they were themselves consumed by fish. During the second summer of the study (1986) an increase in the relative numbers of 1+ sockeye was associated with substantial declines in *Neomysis* biomass. Although this came too late in the season to benefit 1986 Muriel Lake sockeye fry, it did serve to highlight the importance of pelagic food web “trophic triangles” (Hyatt et al. 2005). The authors suggested that during years when exogenous recruitment events result in high sockeye biomasses, *Neomysis* populations could be held in check by 0+ and especially 1+ sockeye. During years when sockeye biomasses were low, zooplankton consumption rates by *Neomysis* would be so high that sockeye could gain little benefit from fertilizer-induced enhancement of their zooplankton food base. The authors concluded that *Neomysis* lakes should only be fertilized when sockeye densities are high enough to reduce *Neomysis* densities and mitigate the effects of competition from *Neomysis*.

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[3] K. Stephens. Personal communication.

Woss Lake, British Columbia

Woss Lake (50°07′N, 126°37′W, surface area 13.6 km^2) is located on the north-east side of Vancouver Island. Woss Lake was fertilized during 2000–2003, using an average loading rate of 8579 g ha^{-1} a^{-1} of N and 584 g ha^{-1} a^{-1} of P. Nearby Vernon Lake (surface area 8.4 km^2) was maintained as an unfertilized reference lake. The experimental protocol (Hyatt et al. 2004) was to quantify species compositions, densities, and biomasses for phytoplankton, zooplankton, and sockeye and then to use these data to estimate the proportion of species-specific zooplankton production and standing stock consumed by sockeye. In the fertilized lake (Woss), epilimnetic TP averaged 3.6 μg L^{-1}, and in the unfertilized control (Vernon), epilimnetic TP averaged only 2.9 μg L^{-1}. In the fertilized lake, average chlorophyll *a* was 0.92 μg L^{-1} and in the unfertilized lake, 0.36 μg L^{-1}. Similarly, average edible algal biovolume (algae 2–30 μm diameter) was 300 mm^3 m^{-3} in the fertilized lake but only 100 mm^3 m^{-3} in the unfertilized control. Average biomass of edible zooplankton (zooplankton found in stomach content samples) was dw of 22 μg L^{-1} in the fertilized lake compared with 17 μg L^{-1} in the unfertilized control. In December, average weight and total biomass of juvenile sockeye was 3.3 g and 2.03 kg ha^{-1}, respectively, in the fertilized lake compared with 2.5 g and 1.71 kg ha^{-1} in the unfertilized control.

The authors note that these "treatment" vs. "control" comparisons should be viewed with caution! During the first year of the experiment (2000), both Woss (fertilized) and Vernon (unfertilized) had about equal volumes of edible algae and zooplankton; and fish densities and growth rates in both lakes were almost the same. During the next three years (2001–2003) edible algal biomass in the unfertilized control lake remained about the same, but zooplankton biomasses declined and 0+ sockeye growth rates also declined. Given available 0+ sockeye weights and densities, bioenergetics-based consumption estimates suggested that the 0+ sockeye could not have caused the observed declines in Vernon Lake (unfertilized) zooplankton biomasses. Because the algal biomass did not change, the only other logical explanation was that some of the targets assessed during the Vernon Lake acoustic surveys must have been fish that were larger than 0+ sockeye. In fact, larger fish (kokanee) were found in the Vernon Lake trawl nets during 2001–2003, and bioenergetic simulations suggested that during all of those years they competed significantly with 0+ sockeye and were, in part, responsible for the reduced sockeye growth rates observed in Vernon Lake. Kokanee catches in Woss Lake remained very low throughout the experiment (Hyatt et al. 2004).

The authors concluded that because Woss Lake (fertilized) fish densities were low (mean 646 ha^{-1}), juvenile sockeye consumed only a portion of the available zooplankton production and had no long-term density dependent effects on zooplankton biomass. Also, because Woss Lake was subject to blooms of *Rhizosolenia*, an algae that is large and therefore resistant to zooplankton grazing, an average of less than 20% of the algal production was available to zooplankton. For both these reasons, less than 0.1% of the fertilizer added to Woss Lake was incorporated into fish biomass. On the other hand, even this small amount of fertilizer stimulated an additional 3–19% increase (depending on the year) in sockeye production. These increases translated into 69 kg of additional 0+ sockeye production in 2000, 114 kg in 2001, 399 kg in 2002, and 206 kg in 2003. Given the unused zooplankton production capacity that was generated by Woss Lake fertilization, the authors suggested that 0+ sockeye production could have been 2–3 times greater had the sockeye fry densities been greater.

Photosynthetic rate model

Development of the photosynthetic rate (PR) model (Hume et al. 1996; Shortreed et al. 2000, 2001) to determine production potential of juvenile sockeye in both fertilized and unfertilized lakes served to underscore the importance of bottom-up biological control mechanisms over juvenile sockeye production in British Columbia lakes. The PR model is a modification of the EV model (Koenings and Burkett 1987), which was developed for Alaskan lakes where abiotic factors such as glacial silt and organic stain varied widely but nutrient loading varied relatively little. Consequently, euphotic zone depths were positively and strongly ($r = 0.9$) correlated with areal primary production rates, and euphotic zone depth could be used as an index of primary production in Alaskan lakes (Koenings and Burkett 1987). In British Columbia sockeye lakes there was a greater range in nutrient loading, so biotic factors (phytoplankton biomass and productivity) played a greater role in determining euphotic zone depth. Hume et al. (1996) demonstrated that in British Columbia lakes there was a negative correlation between euphotic zone depth (EZD) and areal primary production rates such that EZD does not readily index productive capacity of a lake for planktivorous fish. However, the PR model of Hume et al. (1996) demonstrates direct linkages between measured primary production rates and nursery lake capacity to support juvenile sockeye salmon production. Practical applications of the PR Model are found in Shortreed et al. (2000, 2001) and Cox-Rogers et al. (2004).

Field studies in Idaho

Redfish Lake, Columbia River system

(Gross et al. 1998, Budy et al. 1998, Luecke et al. 1996, Griswold et al. 2003). Declining returns of sockeye to the Snake and Salmon Rivers (headwaters of the Columbia River) have been largely attributed to the construction of eight dams in the Columbia corridor. Only 16 spawners returned between 1989 and 1994. In 1991, Snake River sockeye were listed under the U.S. Endangered Species Act (ESA). The ESA listing prompted several preliminary studies of the potential for lake fertilization to contribute to sockeye stock recovery at Redfish Lake (44°N, 115°W, surface area 6.15 km^2).

Gross et al. (1998) constructed a nutrient loading model for Redfish Lake and then predicted the likely long-term consequences of lake fertilization. The model suggested that under pre-dam conditions the annual return to Redfish Lake would have been 3800 sockeye and that this would have contributed about 3% of the annual nutrient load received by the lake. The model also suggested that 3 years of lake fertilization would stimulate sockeye production but that the effects would almost disappear after 8 post-fertilization years. They concluded that permanent effects could be achieved only by solving migration problems in the Columbia River to increase smolt-to-adult survival.

Budy et al. (1998) reported results from Redfish Lake enclosures (350 m^3) treated with fish (juvenile kokanee) and nutrients (added to the metalimnion). The objectives were to assess the potential impacts of fertilization on water clarity (Redfish is a highly valued recreation area) and to assess the potential to increase juvenile sockeye growth rates. They found that fertilization substantially increased chlorophyll (150%), primary production (250%), zooplankton biomass (200%), and that water clarity was reduced by 2–4 m (Secchi disk). However, fish growth increased very little (15%), and even then it was likely that increased growth rates were because the enclosures were fertilized (and zooplankton biomasses increased) for several weeks before fish were added. The authors concluded that fertilization in conjunction with removals of kokanee could benefit anadromous sockeye.

Luecke et al. (1996) used a food web model to assess various management strategies for Redfish Lake and also concluded that fertilization in conjunction with removals of kokanee could benefit anadromous sockeye. They knew from earlier cage studies that kokanee densities in Redfish Lake were near carrying capacity, and the model suggested that if the kokanee were left unchecked, more than 98% of the extra nerkid (juvenile sockeye and kokanee) production stimulated by fertilizer addition would accrue to kokanee. They recommended that if the lake was fertilized at a rate of 715 kg a^{-1} of P, a reduction of 50–70% of the 0+ kokanee would be required to ensure that increased fertilizer-induced zooplankton biomass would benefit stocked anadromous sockeye fry.

In conjunction with the above studies, Redfish Lake was fertilized during 1995–1998 (Griswold et al. 2003). The data comprised three pre-fertilization years (1992–1994) and four fertilized years (1995–1998) and included both an experimental lake (Redfish) and an unfertilized control lake (Stanley). The nerkid population in both lakes was a mix of kokanee and stocked anadromous juvenile sockeye. Fertilizer was added at an average rate of 5265 g ha^{-1} a^{-1} of N and 281 g ha^{-1} a^{-1} of P. Comparisons of pre- and post-fertilization years showed that during fertilization Secchi depth declined and chlorophyll *a* increased from a mean of 0.5 μg L^{-1} during the pre-fertilization period to 1.0 μg L^{-1} during the fertilized period. During fertilization mean summer zooplankton biomass increased from 7.9 to 10.3 μg L^{-1} dw, and *Daphnia* biomass increased from 0.8 to 2.6 μg L^{-1} dw. Owing to sockeye stocking, fish density increased from 240 ha^{-1} during pre-fertilization to 301 ha^{-1} during fertilization. The authors noted that post-manipulation nerkid survival improved from 6.7% during pre-fertilization to 19.7% during the fertilization period, but they also stated that these changes could have been due to changes at the hatchery that produced higher quality fish during the fertilization period. Changes in juvenile lengths and weights were not assessed.

Stanley Lake was monitored as a control, and during the pre- and post-manipulation time periods Stanley Lake chlorophyll increased slightly, *Daphnia* biomasses declined slightly, total zooplankton biomass did not change, and fish density (kokanee plus a few stocked sockeye) increased from about 100 to 400 ha^{-1}. Changes in juvenile lengths and weights were not assessed. The authors stated that climatic changes influencing snow pack and discharge rates coincided with the pre- and post-fertilization periods and confounded experimental outcomes. They also noted that it was possible that the kokanee in Redfish Lake may have disproportionately benefitted from lake fertilization (see Luecke et al. (1996)) and the planned 1999 fertilization was suspended for that reason. Also, because of concerns for esthetic values (clear water), the amount of fertilizer added (200 kg a^{-1} of P) was less than recommended (see Luecke et al. (1996)), and this may have weakened the anticipated bottom-up response by sockeye salmon.

Cautionary tales

Although virtually all the studies summarized above suggest that lake fertilization is likely to yield positive gains in smolt biomass and may even contribute to increased marine survival, they also suggest that problems are possible — even likely. This is not surprising. Freshwater food webs are relatively complex, and when entire lakes are fertilized to enhance the production and survival of anadromous sockeye, it is almost certain that unexpected results will emerge. Based on the preceding literature review, seven potential "issues" have been identified. The first two deal with some of the myths and realities of phosphorus loading. The last five with technical problems, some resolved, others not.

(1) The very first lake fertilization at Great Central Lake (1969) was prompted by the suggestion that declines in sockeye might be partially explained by the "smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners" (Foerster 1968). Recently, stable isotope studies (reviewed in Cederholm et al. (1999)) have shown that marine-derived N and C is found in lake, stream, and terrestrial biota and that watersheds with higher escapements have more marine-derived N in some terrestrial species (Reimchen et al. 2003). These data, combined with escapement and mass-balance analyses, leave little doubt that sockeye salmon carcasses contribute to the nutrient regimes of *rivers and streams* of watersheds containing sockeye (reviewed in Naiman et al. (2002)). For sockeye nursery *lakes*, there is also evidence suggesting that carcasses can make significant contributions to nutrient budgets, but conclusions seem to be very lake-dependent. The evidence that is generally cited (Kyle et al. 1997; Naiman et al. 2002) to support the case for the importance of carcasses to nursery lakes is primarily based on data from two lakes. Krokhin (1967) used a 24-year (1937–1960) data set to estimate phosphorus inputs and losses from Lake Dalnee, Kamchatka, Russia, and he concluded that low sockeye returns during 1948–1960 were associated with negative phosphorus balances (inputs – losses) to the lake. Even more intensive data are available from Karluk Lake, Kodiak Island, Alaska. Juday et al. (1932) were among the first to suggest that primary and secondary production at Karluk Lake was strongly influenced by sockeye salmon carcasses. This early work was followed by an overview of the Karluk Lake data up to 1953 (Nelson and Edmondson 1955) and by a recent analysis by Schmidt et al. (1998), who concluded that carcasses could account for 40% or more of the phosphorus in Karluk Lake. They also found that there was a clear relationship (although

confounded by fertilizer additions during the mid-1980s) between July–August TP concentrations and fertilizer derived from carcasses deposited during the pervious year.

Ricker (1937) acknowledged the Karluk Lake data (Juday et al. 1932), but stated that at Cultus Lake “even the largest runs would not be sufficient to add greatly, on decomposition, to the dissolved supply [of nutrients] already available.” He pointed out that this was because run density (per cubic metre of lake water) was 10 times higher in Karluk Lake than in Cultus Lake and that the Cultus Lake water turnover rate is high, resulting in the loss of at least one half of the nutrient load each year. Gross et al.(1998) used the Redfish Lake simulation model (see above) to estimate that carcasses accounted for only about 3% of the annual historical total nutrient load to the lake, even before the advent of hydroelectric dams, and Edmundson et al. (1997) estimated that Coghill Lake carcasses contributed only 10% of the annual load. From these data, it may be wise to conclude that the contribution of carcasses varies considerably from lake to lake. Factors such as spawner numbers, redd locations, lake volumes, watershed areas, turnover times, the timing of flushing events, and the effectiveness of a variety of nutrient retention and recycling processes influence historical and current contributions made by carcasses. Additional mass-balance studies for sockeye nursery lakes are much needed. In the meantime, it should be noted that in all the case-studies reviewed here artificial fertilizer was added during the spring and summer, when it was most needed, and that fertilizer-loading rates often exceeded carcass-loading rates by an order of magnitude or more.

(2) One of the stated objectives of this review was to determine whether substantial amounts of fertilizer-induced primary production could make its way up a nursery lake food web, to increase juvenile sockeye growth and survival. Even the most basic calculations show that if a four-step food chain (TP → algae → zooplankton → sockeye) and an average ecological efficiency of 20% are assumed, less than 1% of the nutrients added to a lake are expected to end up in sockeye. To our knowledge only one study (Hyatt et al. 2004) has addressed this question in detail. In Woss Lake during 2000–2003, the amount of fertilizer-P incorporated into new sockeye tissue varied from 0.04 to 0.14% of the fertilizer-P added to the lake. Conversely, 99.9% of the fertilizer-P added to the lake was *not* incorporated into sockeye tissue. Given these estimates, one must ask how fertilization could have contributed significantly to increased juvenile sockeye biomass? The answer is that fish contain relatively small amounts of phosphorus. In Woss Lake during 2000–2003, a very small portion (average 0.14%) of the phosphorus added as fertilizer contributed to an additional 200 kg (150 g ha^{-1}) of juvenile sockeye production per year. This translated to a cost of approximately CAN$200 per kg of enhanced smolt production. It should be noted that during 2000–2003 Woss Lake fry abundance (average 645 sockeye ha^{-1}) was low, and edible zooplankton were always underused. Fertilization coincident with higher sockeye densities observed during the 1980’s (1500–3000 sockeye ha^{-1}) would have substantially reduced smolt production costs per koligram, but still the cost would be high.

Five additional cautionary issues involve technical problems that have been encountered and often solved. The first three deal with nutrients and algae.

(1) In Great Central Lake, Stockner and Hyatt (1984) reported the development of hypolimnetic blue-green algal plates, and they suggested that this problem could be corrected by increasing the N:P ratio of added fertilizer.

(2) Also, Stockner and Hyatt (1984) and Stockner and Shortreed (1988) reported that when fertilizer with low N:P ratios (low N) was added to Kennedy-Clayoquot, an *Anabaena* bloom developed. When the fertilizer having a higher N:P ratio (increased N) was applied, the blue green bloom disappeared.

(3) Finally, Stockner and Hyatt (1984) and Stockner and Shortreed (1988) reported that when higher N:P ratio fertilizer was added to Kennedy-Clayoquot, a *Rhizosolenia* bloom developed. Stockner and Hyatt (1984) also reported that during 1982, when fertilizer having an N:P ratio of 15:1 (mass) was added to Nimpkish Lake, *Rhizosolenia* bloomed, but when the mass ratio was reduced to 1:1 (unpublished data), *Rhizosolenia* became far less abundant. *Rhizosolenia eriensis* also appeared at Woss Lake during both 2000 and 2003. *Rhizosolenia eriensis* cells resemble large "glass-like" cylinders, measuring approximately 75 μm × 6 μm × 4 μm with spines at each end. Their shape ensures that they are non-grazable and it also allows individual cells to absorb considerable quantities of nutrients that might otherwise fuel the growth of grazable species. Over the 4-year fertilization period at Woss Lake, only 20% of the available algae were grazable, and during *R. eriensis* blooms, percent grazable algae fell to 2–5% by volume. *Rhizosolenia* was also reported at Mohun Lake (Perrin et al. 1986), where densities increased when fertilizer was added, and also at Hobiton Lake, which was fertilized during 1980–1983 (Hardy et al. 1986). At Hobiton Lake, during fertilization the epilimnetic TN:TP mass ratio was 50:1. When fertilization stopped in 1984, mean summer TN:TP mass ratio increased to 129:1, and this was associated with a large bloom of *Rhizosolenia* sp. Finally, MacIsaac[4] found that in the laboratory *Rhizosolenia* grew better with a high TN:TP ratio. It appears that the potential key to *Rhizosolenia* control is to reduce the N:P ratio in the fertilizer. The obvious problem is that too little N is widely associated with the growth of blue-green algae. However, this also appears to be partially controlled by the fact that blue-green algae like *Anabaena* are most common in lakes with warm, shallow, stable epilimnia and are seldom found in lakes subject to more wind, such as Henderson, Chilko, and Woss lakes, even when TN:TP ratios are low (less nitrogen). Clearly, before additional coastal-lake fertilizations are attempted, lake-specific information pertaining to algal species composition and preferences for physical-chemical conditions is highly recommended. Some of the relevant information pertaining to appropriate nutrient ratios is available in Ashley and Stockner (2003).

The final two cautionary issues deal with fish and zooplankton.

(4) Hyatt and Stockner (1985) reported that after the onset of fertilization Long Lake developed a very large stickleback population that appeared to suppress juvenile sockeye growth responses to fertilization. O'Neill (1986) and O'Neill and Hyatt (1987) used enclosure manipulations to compare food preferences and consumption rates of threespine sticklebacks and juvenile sockeye. They found that both ate roughly the same food types and that consumption rates were about equal. As noted in the preceding case-study review, stickleback also caused competitive problems at Yakoun Lake. During the fertilization years stickleback accounted for more than half of the fish in the lake, and the result was reduced sockeye yields. To date, there is no clear understanding of the factors that cause stickleback "outbreaks". Their appearance tends to be sporadic, lasting a few years, after which they may virtually disappear, sometimes for 10–20 years at a time. Potential solutions to the stickleback–sockeye competition problem require more work. Currently, scientists from the British Columbia Ministry of Water Land and Air Protection are involved in several whole-lake fertilization projects designed to increase kokanee production (Ashley et al. 1999; Pieters et al. 2003). One innovative solution to the stickleback problem comes from the work of Ashley and Rosenau,[5] who addressed a kokanee collapse in Walheach Reservoir (British Columbia), by introducing 25-cm sterilized cutthroat trout, which preyed on resident stickleback, thus reducing the effects of stickleback–kokanee competition for zooplankton.

Kokanee (a sibling species of "landlocked" sockeye salmon) are potential competitors and are common in relatively productive nursery lakes. For that reason, only two sockeye nursery lakes

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[4] E.A. MacIsaac. Personal communication.

[5] K.I. Ashley and Rosenau. Personal communication.

containing kokanee have been fertilized to date. At Redfish Lake, Griswold (2003) suggested that fertilization may have benefitted kokanee more than sockeye. At Vernon Lake (Hyatt et al. 2004), fertilization has just begun (2004), and results are still unavailable, but the expectation is that 0+ sockeye and 0+ kokanee may be able to compete equally, although sockeye may be at a competitive advantage in the early spring because they originate from larger eggs than kokanee. Predictions involving competition among 0+ sockeye and older kokanee (1+ and 2+) are less certain. Lakes having large pelagic invertebrates such as mysids could tip the competitive balance in favor larger and older kokanee. However, in Vernon Lake, zooplankton tend to be small-bodied and relatively unproductive, suggesting that older, larger kokanee may be at a competitive disadvantage. During the next 2 years production, consumption, and fish bioenergetics methods will be used to assess competitive outcomes between sockeye and multiple age classes of kokanee during fertilization of Vernon Lake.

(5) Finally, Cooper (1988), Cooper et al. (1992), Ashley et al. (1999), and Hyatt et al. (2005) have commented on the problems associated with competition between mysids (*Mysis relicta* and *Neomysis mercedis*) and juvenile sockeye. Concern is based on the fact that in Kennedy and Muriel lakes, the mysid population (*N. mercedis*) has been estimated to consume 5–10 times as much zooplankton as the juvenile sockeye population (Hyatt et al. 2005). No solutions have been offered, but Hyatt et al. note that sockeye (especially 1+ juveniles) consume substantial quantities of *Neomysis*, and they recommend that lakes containing mysids should be fertilized only when sockeye densities are relatively high or *Neomysis* densities are low. The expected outcome is that sockeye could benefit directly by consuming these large invertebrate planktivores and indirectly by reduced competition for food.

In general, the problems associated with algae (blue-green algae or large diatoms) appear to be manageable. Partially because alterations of fertilizer N:P ratios have been shown to be effective (for blue-green algae at least), and also because even when algal problems have been encountered, increased biomasses of zooplankton have still been associated with the fertilization of coastal lakes (Hyatt and Stockner 1985). Briefly stated, when fertilizers are added to lakes, increased zooplankton biomass and production is almost guaranteed. The more serious problems have occurred at the zooplankton → sockeye link in the food web. Aside from the obvious difficulties associated with temperature effects and competition from mysids and sticklebacks, one must ask why the literature shows so much variation in fertilizer-induced increases in smolt sizes. It seems likely that the answer to this problem must involve the amount of energy that juvenile sockeye are able to derive from available zooplankton species compositions and production levels. Stockner (1987) noted that food chains tend to be long in oligotrophic coastal lakes including substantial fractions of picoplankton, protozoans, and microzooplankton. In addition, coastal nursery lakes tend to have simple macrozooplankton food webs, usually dominated by *Cyclops bicuspidatus thomasi* and *Skistodiaptomus oregonensis*, which are too small and fast to yield optimum food value to sockeye. Coastal food webs also frequently lack the large cladoceran species typically found in the more productive interior nursery lakes. To date, the geographical and bottom-up factors that regulate the zooplankton species compositions of coastal lake food webs have not been clearly identified. Thus, basic zooplankton research is needed here.

Given the structure of the planktonic food webs of coastal lakes dominated by small cladocerans and copepods, it seems likely that sockeye smolt weights and yields will be limited no matter how much fertilizer is added. On the other hand, some interior British Columbia lakes, such as those in the Fraser River system (reviewed in Shortreed et al. (2001)), are known to have *Daphnia*-dominated food webs capable of producing very large smolts, but these systems are also susceptible to strong density dependence. For example, at Quesnel Lake smolt weights averaged 2.7 g at a density of 2590 ha^{-1} and increased to 9.4 g at a density of 201 ha^{-1}. Similarly at Chilko Lake, smolt weights averaged 3.3 g at a density of 1990 ha^{-1} and increased to 6.2 g at a density of 279 ha^{-1}. Not surprisingly, when Chilko Lake

(Bradford et al. 2000) was fertilized, the result was increased phytoplankton, increased zooplankton including *Daphnia*, larger smolts, and improved in-lake and marine survival. Again, more work is needed to determine the unique mix of algal species composition and perhaps physical conditions that characterizes these *Daphnia*-dominated "interior lake" food webs. Given observed differences in food web structure, it seems likely that the cost-benefits of "interior lake" fertilization will be substantially greater than for "coastal lake" fertilization.

Summary of general outcomes

At the outset we noted that the potential success of sockeye nursery lake fertilization is predicated on the assumption that bottom-up trophic transfers between nutrients → algae → zooplankton → fish can be shown to be both predictable enough and strong enough to yield increased smolt survival and size. We also noted that nursery lake fertilization is based on the assumption that the size and survival advantages gained by sockeye fry, originating from fertilized lakes, can be successfully carried into the marine environment, thus ensuring increased total returns.

Bottom-up processes

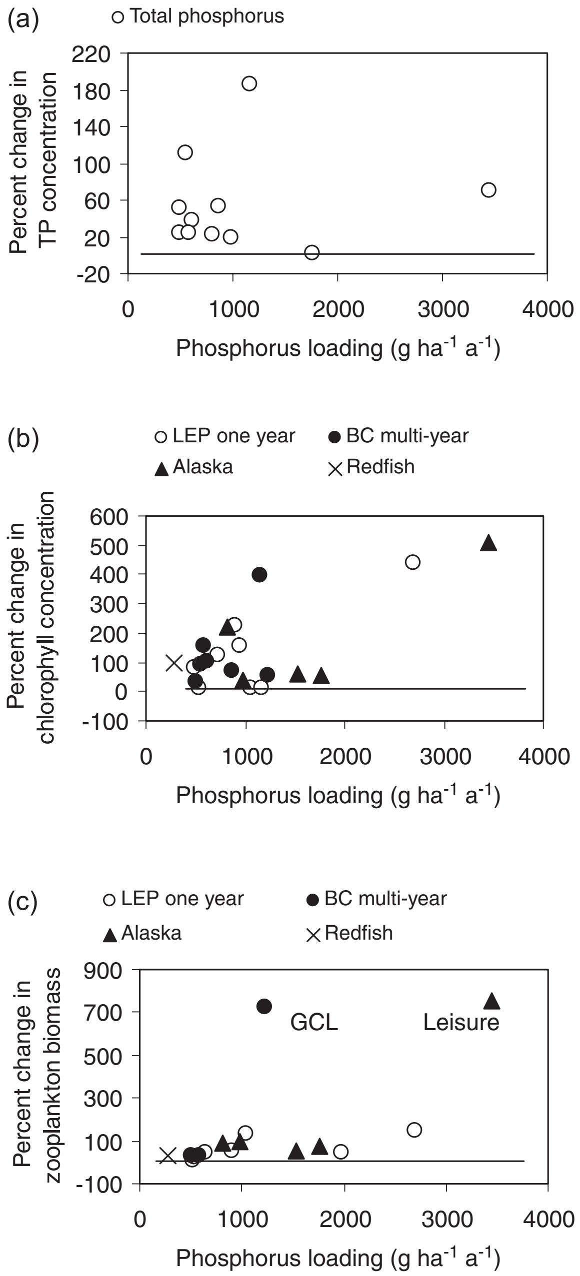
The preceding literature review suggests that lake fertilization is associated with increased biomasses and (or) production of phytoplankton, zooplankton, and juvenile sockeye (Tables 1, 2, and 3). At the base of the food web (Fig. 1*a*) 11 of 11 studies showed that when fertilizers were applied, epilimnetic TP increased. For chlorophyll *a* (Fig. 1*b*), 21 of 21 studies showed positive responses to fertilization. This effect was especially clear for the two most heavily loaded lakes (Leisure, 3455 g ha^{-1} a^{-1} of P and Bonilla 2696 g ha^{-1} $\text{a}^{-1}$of P). For zooplankton (Fig. 1*c*), responses to fertilization were generally more muted, but 16 of 16 studies showed a positive increase in zooplankton biomass following fertilization. Two studies showed exceptionally large increases in zooplankton biomass. In the case of Leisure Lake, the loading rates were very high (3455 g ha^{-1} a^{-1} of P), but in the case of Great Central Lake (LeBrasseur et al. 1978) increased zooplankton abundances were probably associated with sockeye densities and biomasses that were lower during the fertilized years than during the unfertilized years.

In 16 of 16 studies, fertilization was associated with increased weight gains by fall fry and (or) smolts (Fig. 2*a*). Although the relationship between phosphorus loading rate and smolt weight is positive, the trend is not significant (RANOVA based on weight differences from fertilized and unfertilized treatments, df = 15, $p = 0.49$). In some cases this poor correlation is due to unexplained outliers. For example, the highest percentage weight gains came from three lakes (Cultis, Kitlope, and Redoubt) that received intermediate loading rates, and the lake with the second highest rate of fertilization (Bonilla) showed one of the lowest weight gains for smolt. None of the original data explain any of these patterns. In other cases, it is clear that there was a density-dependent trade-off between increased average smolt size and increased smolt densities. For example, at Coghill Lake densities increased and average smolt weight remained stable, while at Great Central, Yakoun, and Kitlope lakes densities declined and smolt weights increased.

In 11 of 13 experiments (Fig. 2*b*), fertilization was associated with increased smolt production, and the trend was significant (RANOVA based on average weight differences from fertilized and unfertilized treatments, df = 12, $p = 0.03$). Leisure Lake was again a standout, showing an increase of more than 250%. Great Central Lake recorded a loss due to poor escapement and little increase in smolt weight, and Yakoun recorded a loss due to competition from sticklebacks.

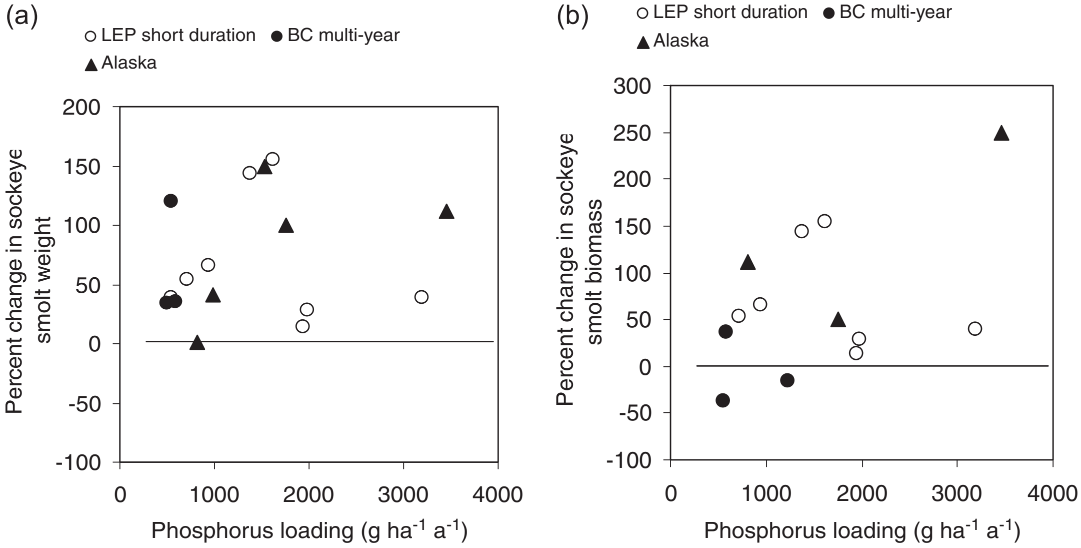
As noted above, smolt biomasses depend on both smolt weight and smolt density. Fertilization can accelerate weight gains, but densities are dependent on both escapement and egg-to-fry survival. Escapement is dependent on many factors that are beyond the control of those adding fertilizer to sockeye nursery lakes, but juvenile survival is likely to be influenced by resource availability. Egg-to-fry survival rates were recorded for four studies. At Leisure Lake, fertilization was associated with an

Fig. 1. (*a*) Percent change in epilimnetic TP for fertilized vs. unfertilized lake-years; (*b*) percentage change in epilimnetic chlorophyll *a* for fertilized vs. unfertilized lake-years; (*c*) percentage change in zooplankton biomass for fertilized vs. unfertilized lake-years. Horizontal line represents 0% change.



average survival increase of 69%. At Coghill Lake, during 1 year (1995), smolts per spawner increased from 25 to about 150 per female, but during the other two years there was no increase. At Chilko Lake, recruits per female increased by 73% and Great Central Lake egg-to-fry survival increased by almost 100%. On balance, although data are sparse, it seems likely that fertilization is associated with increased egg-to-fry survival.

Fig. 2. (*a*) Percentage change in smolt weights for fertilized vs. unfertilized lake-years; (*b*) percentage change in smolt biomasses for fertilized vs. unfertilized lake-years. Horizontal line represents 0% change.



Smolt size and marine survival

We now turn our attention to the second assumption, which is that larger smolts survive better at sea (Koenings et al. 1993). As noted, Ricker (1962) showed that over a broad geographical range there is a positive relationship between sockeye smolt length and marine survival. This pattern has also been observed in between-year data from Owikeno and Babine lakes (Hyatt and Stockner 1985), from the Karluk River (Barnaby 1944), and from Cultus Lake (Foerster 1954). The question is: Do the weight gains that result from fertilization confer survival advantages in the marine environment? At Leisure Lake, smolt weights increased 112% and smolt-to-adult survival increased 25%. At Packers Lake, comparisons of results from the unfertilized period and the 1983–1986 fertilized period (Kyle 1994) show that smolt weights increased by 100% and marine survival increased by 43%. At Chilko Lake, each 1 g increase in smolt weight was associated with a 14% increase in the rate of adult returns. It should be noted that these results depend on rather small numbers of lake-years and that variability in the data is large and statistical significance is weak. On the other hand, there are no studies that show that fertilization is associated with reduced marine survival. On balance, we suggest that it seems likely that lake fertilization is positively associated with increased marine survival of sockeye salmon.

Fishery and climate induced variations

As noted earlier, Nelson and Edmonson (1955) reviewed historical data from Karluk Lake (37 km^2) and attributed an almost continuous decline in lake productivity to a decline in sockeye abundance caused by over fishing. Recently this pattern has been confirmed by Finney et al. (2000, 2002), who used paleolimnological evidence to show that during the 1882–1985 period of rapid development of commercial fishing for sockeye salmon in the eastern Pacific there was a positive correlation between declining sediment concentrations of δ^{15}N originating from sockeye carcasses and declining pelagic productivity at Karluk Lake. Using these δ^{15}N data, Finney et al. (2000, 2002) also demonstrated that Karluk Lake sockeye abundances were low during the early 1700s and again during the period 1810–1835, prior to the advent of industrial scale fishing. Thus, it appears that supplies of marine derived nutrients associated with sockeye salmon returns to freshwater may be disrupted not only by large magnitude removals associated with commercial fishing but also by naturally occurring variations in sockeye stock productivity associated with poorly understood climate variation and change events. Natural climate variations inducing either increases or decreases in stock productivity may have considerable potential to confound effects of some sockeye lake fertilization experiments. Indeed, simultaneous increases and decreases in sockeye returns are now known to occur over decades of time to both fertilized (Great Central Lake) and unfertilized (Sproat Lake) lakes in the Barkley Sound area of British Columbia (Hyatt et al. 2002). These observations suggest that increased returns exhibited by the Barkley Sound sockeye aggregate in the early 1970s were related, in part, to "climate" events that favored increases to marine survival for several local stocks rather than just lake fertilization that doubled freshwater sockeye fry survival in Great Central Lake.

Climatically induced variations in either freshwater or marine production of sockeye salmon clearly have the potential to confound interpretation of outcomes of some lake fertilization events. However, the north–south geographic and temporal scope of lake fertilization trials reviewed here (Alaska to Idaho and 1950s through 2003) provide sufficient temporal and spatial "control" observations to largely discount a pervasive influence of uncontrolled climate variation on biological outcomes of fertilization experiments in general. Accordingly, known effects of lake fertilization from specific nursery lake assessments serve as a more parsimonious explanation of observed sockeye responses than basin-wide production trends associated with shifting climate "regimes" for North Pacific salmon (Beamish et al. 1999), inverse production trends between northern and southern stocks (Hare et al. 1999), or co-variation in stock abundance for salmon populations that are geographically proximal (Mueter et al. 2002).

In summary

The available literature dealing with sockeye nursery lake fertilization, suggests that bottom-up, trophic transfers between nutrients → algae → zooplankton → fish are both predictable and strong enough to increase fry survival and smolt size. Larger smolts also appear to survive better at sea, resulting in increased escapement back to the nursery lake of origin, and that within limits, increased phosphorus loading is associated with increased smolt weights and yields. Although it may be argued that the fertilization of sockeye nursery lakes is interventionist and unnatural, it is important to note that human activities, including habitat destruction by industrial or urban development and over-exploitation of sockeye stocks by the commercial fishery, have been strongly implicated in the decline of many Pacific sockeye populations (Slaney et al. 1996). Currently, a number of depressed or threatened sockeye stocks have been identified in both the United States and Canada. These include sockeye originating from Redfish Lake, Ozette Lake (Gustafson et al. 1997), Cultus Lake, and Adams Lake (Schubert et al. 2002; MacKinlay[6]). Given appropriate conditions, nursery lake fertilization may make significant contributions to the recovery of these and other depressed or threatened sockeye salmon populations.

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