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Salmon Nutrients: Closing the Circle

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Introduction

The consequences of nutrient loss (oligotrophication) and attendant low productivity on ecosystem biodiversity and fish production have only recently perked the interest of researchers in aquatic science (Ney 1996; Ashley and Slaney 1997; Stockner et al. 2000). Conversely, research on the ecological consequences of 'excess' nutrients (eutrophication) has been a major focus of limnological research for several decades (Forsberg 1998; Vollenweider 1968). Inputs of phosphorus (P) and nitrogen (N) from anthropogenic interventions on the landscape were identified as primary causal factors of eutrophication (Edmondson 1969; Vallentyne 1974). Over the last century, the impact of man, mediated by overfishing, dam construction, and habitat destruction in both coastal and interior regions of the Pacific Rim nations (United States, Canada, Japan, Russia), has led to a marked decline and, in some cases, total loss of adult salmon spawners, which has had a profound impact on the productivity and biodiversity of salmonid ecosystems (Mathisen 1972; Stockner 1987; Larkin and Slaney 1997; Cederholm et al. 2000a; Gresh et al. 2000). Further, the construction of some dams within the Columbia River basin has not only markedly reduced and/or eliminated anadromous salmon runs, but also, in the upper basin within Canada, has had an equally devastating impact on kokanee salmon *Oncorhynchus nerka* stocks, due both to reservoir oligotrophication and introductions of exotic species, for example, mysids (Northcote 1973; Ashley et al. 1997; Pieters et al., this volume).

The roots of this discourse were largely developed in 1997 and 1998 in Sweden, a country where, for most of the populace, phosphorus removal from lakes and streams has become the standard, and any thoughts of purposely adding nutrients to lakes or streams to enhance fisheries are deemed unorthodox. Thus, it was time to introduce a new paradigm of global 'oligotrophication' to limnology and fisheries science, and the subject of nutrient deprivation and its impacts on fisheries and food chains became the subject of the opening address for the first international symposium on 'Restoration of Fisheries by Enrichment of Aquatic Ecosystems,' held in March 1998 in Uppsala, Sweden (Stockner and Milbrink 1999). Here, we briefly summarize some of the factors known to cause oligotrophication of lakes and streams worldwide, but our main objective is to focus only on those factors affecting anadromous salmon and landlocked kokanee ecosystems, discussing some of the consequences of the oligotrophic condition on production, biodiversity, and fish. We conclude with a few salient comments on some of the more promising remedial measures that can reverse oligotrophication and hasten ecosystem recovery, notably fertilization and habitat restoration.

Background

Nutrients

The primary nutrients essential for growth and reproduction of all living matter are carbon (C), nitrogen (N), and phosphorus (P), and they usually occur in a ratio of approximately 102:16:1 by atoms or 40:7:1 by mass (Vallentyne 1974). Carbon is an important component of carbohydrates and lipids, while nitrogen is common in amino acids, the building blocks of proteins, and P is a vital component of mitochondria, important in metabolic processes and in nucleic acids (e.g., DNA, RNA). Because both C and N are ubiquitous in their gas phase, in most ecosystems, inputs of plant utilizable forms of C (HCO_3^-, CO_2) and N (NH_4^+, NO_3^-) can be restored by biogenic reductive assimilation. However P, lacking a gas phase, cannot be renewed and, therefore, is commonly the nutrient in shortest supply and most limiting to biotic phototrophic production in freshwater habitats (Schindler 1980; Stockner 1987). If C and N are present in ecosystems in nonlimiting concentrations, then 1 mg P can produce about 500 mg of periphyton or phytoplankton biomass; said another way, each person on average releases about 2 kg P per year to wastewater that is capable of producing more than a ton of living plants (Vallentyne 1974). A returning adult salmon weighing 4 kg contains about 18 g P that, if in soluble, available form, would be capable of producing 7.5 kg of living autotrophic plant biomass. Though globally there is a large supply of phosphate rock, most is burdened with impurities (heavy metals), and supplies of quality high-grade rock available for fertilizer manufacture are rapidly diminishing and are predicted to be exhausted from most sources within the first half of this century (CEEP 1998; Driver et al. 1999). Therefore, we opine that it is imperative that the populace now commences all economically and technologically feasible means of recycling P, not discarding this scarce but essential element for life (Stockner et al. 2000).

Oligotrophication

Oligotrophic ecosystems are nutrient-poor and are characterized by their low annual rates of biogenic production. This nutrient-poor or 'oligotrophic' status is the antithesis of the nutrient-rich or 'eutrophic' condition. Since most actions leading to either nutrient gain or loss (i.e., nutrient 'imbalances') are mediated by anthropogenic causes, it makes sense to term these processes ' cultural' oligotrophication and eutrophication. Though some lakes, rivers, and streams can become oligotrophic from natural events, most of the documented cases originate from cultural oligo-trophication and can be traced to man's activities, some examples of which include the following (after Stockner et al. 2000):

- **Excessive removal of anthropogenic nutrients**. The consequence of the near total elimination or diversion of direct (point) sources of anthropogenic nutrients (e.g., sewage treatment plant [STP] effluents, stormwater, and/or agricultural drainage).
- **Dam construction.** Reservoirs behind dams on rivers or at lake outflows retain water either for irrigation or hydroelectric power generation or both. Dams, by increasing water retention, increase biogenic reduction of organic matter, increase sedimentation rates and excessive water level fluctuations (drawdown), and destabilize the littoral zone, thereby creating effective P-sinks and low production habitat.
- **Drainage of wetlands.** Land drainage schemes result in increased P-export, due to soil erosion, diminished water retention in soil, wetlands, and streams, and lower and enriched ground water. The newly created agrarian lands eventually require annual fertilizer application (P-import) to sustain production, which further exacerbates P-export to streams and lakes.
- **Fish reductions.** When migratory adult fish leave a large lake or ocean rearing ground and migrate to lakes, rivers, and tributary streams to spawn, they become effective conveyers of nutrients from one ecosystem to another. This salmon mediated nutrient transport system or 'nutrient pump' can be an important C, N, and P source for the maintenance of ecosystem productivity and biodiversity in salmonid lakes and streams where most salmon die after spawning, enriching their natal freshwater and riparian habitats with marine-derived nutrients (MDN) (Kline et al. 1990; Kline, Reimchen et al., Schoonmaker et al., all this volume). Overfishing can remove large

quantities of these nutrients and even moderate fishing extracts nutrients from the ecosystem, and in nutrient-limited habitats, the impacts of these lost nutrients are particularly severe.

- **Acidification.** There is growing evidence that acidification of lakes and streams by acidic precipitation leads to oligotrophication (Jansson et al. 1986; Kopacek et al. 1995; Turner et al. 1995). Processes that increase adsorption of P to aluminum and decrease P-recycling from sediments and littoral margins are implicated.
- **Deforestation.** A clear-cut logged coniferous forest can represent a significant loss of P (P-export) from forested landscapes, not only in log (biomass) removal, but also from erosion of humus and mineral soil layers, due to road construction, log skidding, and related activities. Most deforested lands have decreased soil water retention capacities that initially increase run-off and often turbidity (P-export). After vegetative colonization, a vigorous second growth of young trees and shrubs create high P demands that reduce P supplies to streams and lakes.
- **Climate change.** Recent studies suggest that continued climate warming will reduce carbon production in lakes, due to more protracted periods of stratification that will create severe phytoplankton nutrient limitation within the euphotic zone. With the increased likelihood of milder winters with little or no ice-cover, the water circulation period of an increasing number of temperate dimictic lakes will become warm-monomictic and, as a consequence, will be less productive and experience oligotrophication (Schindler et al. 1990; Henderson et al. 1992; Stockner 1987, 1998).

Among the many causes of oligotrophication, those that have most compromised the efficiency and production of food webs of PNW salmonid ecosystems over the past century are fish reductions (overfishing, habitat loss), construction of hydroelectric and irrigation dams, deforestation (logging), and climate change.

Impacts of Oligotrophication

Extinguishing the Salmon Nutrient Source. As smolts young salmon migrating to the Pacific Ocean take some of their natal lake's or stream's nutrients with them to the sea, but as adults migrating back to the ecosystem of birth, they return much larger quantities of marine nutrients from their vast oceanic rearing grounds; as such, they become effective conveyers of marine nutrients into freshwater and estuarine ecosystems. For example, in many coastal B.C. sockeye *O. nerka* lakes, smolt out-migrations represent from less than 1% to 5% of the total annual TP load from the drainage basin, while marine TP in returning adult spawners can return from 15% to 40% of the annual TP load (Stockner 1987). This marine TP 'interest' payment accrues largely to the ecosystem and supports annual autotrophic aquatic and riparian production cycles while promoting species biodiversity (Cederholm et al. 2000a, 2000b; Jauquet, Reimchen et al., both this volume). Some of the largest salmon P inputs accrue to sockeye, chinook *O. tshawytscha*, and coho *O. kisutch* ecosystems, where some migrations reach great distances inland to mountain lakes and streams where freshwater rearing is a requisite to growth and survival of the species (Murota, this volume). Most juvenile chum *O. keta* and pink salmon *O. gorbuscha* have a short freshwater residency and rear mainly in estuaries and nearshore marine waters. As adults, chum salmon spawners travel far shorter migratory pathways to their natal spawning grounds than pinks, but both are eclipsed by sockeye and chinook migrations. Thus, a larger portion of chum and pink salmon nutrients, if not physically removed in carcasses from streams by large salmon consumers (e.g., bear, mink, raccoon, and eagles), often provide greater nutrient supplementation to lower-gradient reaches of rivers and to estuaries and nearshore coastal regions. The large annual influx of marine nutrients from adult salmon carcasses to river estuaries and coastal embayments over many centuries is certainly one of the more compelling reasons why most estuaries of salmonid river ecosystems are considered highly productive and biologically diverse. Clearly, it has been the gradual loss of adult salmon through the past century, the anadromous nutrient pump, that has resulted in the oligotrophication of a vast majority of PNW salmonid ecosystems. Of course, there are exceptions to this generalization, ecosystems that have been compensated, often to excess, for salmon losses by input of nutrients from anthropogenic sources (e.g., sewage, agricultural drainage), often contaminated by suspended sediments, metals, and so on, which can negate nutrient benefits. However, we opine that in the uppermost reaches of river and lake drainage basins, where salmon are able to spawn and their fry rear, annual supplements of marine nutrients in organic and inorganic form become vitally important to the carbon metabolism of these ecosystems because they are inherently nutrient poor and remain exceptionally so today.

There are other sources of marine nutrients uploaded to freshwater and estuarine ecosystems, such as the eulachon *Thaleichthys pacificus* or candlefish along the Pacific Coast, some species of herring, and several species of sea bird, but salmon, by their adult size and population abundance, represent one the most important vectors of marine nutrients to freshwater habitats (Murota, this volume). Though we focus on Pacific salmon in this discourse, we would be remiss not to mention Atlantic salmon *Salmo salar*. Roughly half of adult Atlantic salmon die after spawning, so several centuries ago, Atlantic salmon nutrient uploads must have cast a far-reaching shadow across the northeastern coasts of North America, Northern Europe, Scandinavia, Great Britain, and Ireland that sadly has now been largely extinguished. On the Pacific Coast of North America, in Japan, and in the Kamchatka Peninsula of Russia, commencing in the latter half of the 19th century, the anadromous Pacific salmon nutrient pump (shadow) has also been slowly attenuated by overfishing, dams, and loss of habitat, now to such an extent that in the remotest salmon ecosystems, the shadow has either been obscured or completely extinguished by reduced escapements and/or complete extinction of runs (Larkin and Slaney 1997; Nakajima and Ito, Schoonmaker et al., both this volume). A case in point would be the extinction of all chinook runs to the Upper Columbia Basin in Northeast Washington and all of Northeastern British Columbia in the early 1940s by closure of the Columbia River after construction of the Grand Coulee Dam, extirpating anadromous salmon forever to these vast, wild regions. Notable, also, is the loss of most anadromous chinook and sockeye salmon runs to large portions of eastern Oregon, Idaho, and Nevada by the construction of multiple Snake and Columbia river dams (Griswold et al., Thomas et al., both this volume).

Some sense of how great the nutrient reduction has been to British Columbia's freshwaters, since the inception of commercial fishing and habitat disruption, can be seen by converting the historic record of B.C. salmon catches into phosphorus equivalents (Figure 1). Losses of adult salmon P to catch since the turn of the century have averaged between 225–275 tons, enough phosphorus to produce more than 100,000 tons of living autotrophic plant biomass! Said another way, sufficient nutrients to 'green' the beds of rivers, estuaries, and margins of salmon lakes throughout the province.

But to better view the direct impact of oligotrophication imparted by nutrient loss to salmon ecosystems, it is more realistic to com-

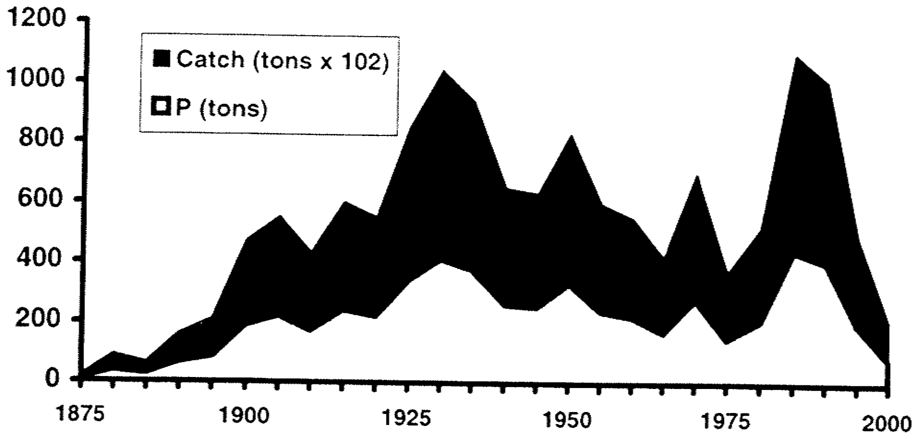

FIGURE 1. British Columbia salmon catch expressed in biomass and phosphorus equivalents (Canadian Department of Fisheries and Oceans, Vancouver, B.C., unpublished data)

pare estimates of early returns and escapement with those of the 20th century (Figure 2).

Sockeye escapements to Chilko Lake in the central interior of British Columbia, expressed as percent of total returns since commercial fishing, illustrates the general trend of salmon nutrient reduction to many of the large, sockeye nursery lakes in the Fraser River system. For nearly a century, adult sockeye returning to Chilko Lake ($0.08–0.25 \times 10^6$) were less than 15% of estimated historic levels (1.1×10^6), but in recent years, they have improved (1990–2000) ($>0.6 \times 10^6$) to about 20% of total returns, owing to implementation of lake fertilization in the late 1980s and early 1990s and to restricted harvest policies in the 1990s (Bradford et al. 2000).

Only about one-third of the total Chilko Lake sockeye escapement actually enters the lake from the river below, but when the P content of the lake escapement is normalized to lake surface area, some sense of the impact of oligotrophication by loss of salmon nutrients and its effects, past and present, on lake biogenic production can be seen (Figure 3).

The Keogh River provides an example of changes in salmon nutrient income to a small coho, steelhead, and pink salmon stream prior to and after the onset of 20th century commercial fishing and logging activities (Figure 4).

The Keogh River is typical of small, B.C. coastal salmon rivers, and its loss of salmon nutrients offers some perspective on local impacts of oligotrophication on biotic production potentials of stream and estuary ecosystems common throughout the Pacific Rim. On average, there has been about a 25-fold decline in adult salmon nutrients to the ecosystem with major losses accruing to the mid to lower reaches of the river and to the estuary, due to pink salmon losses. Prior to anthropogenic disturbance in the early 20th century, coho and steelhead P contributions were estimated to be about 1,300 kg P, about 8–10-fold higher than recent returns from these two species (165 kg P). Large declines in salmon nutrients, since the turn of the century, have also been estimated for the larger, interior Salmon River Basin of Idaho (Thomas et al., this volume).

The Freshwater Nutrient Shadow. A less recognized component of biogenic nutrient recycling in the PNW is the freshwater nutrient shadow. In many interior lakes and reservoirs, landlocked kokanee salmon convey thousands of kilograms of lake-derived N and P into tributary streams during autumn spawning migrations. Nutrients, physiologically released during these migrations, temporarily increase tributary nutrient concentrations and stimulate microbial, algal, and invertebrate production (Richey et al. 1975). Upon decomposition, carcasses provide vital carbon, nitrogen, and phosphorus to a variety of terrestrial and aquatic vertebrates and invertebrates dependent on this seasonal supply of kokanee nutrients. A striking example of the keystone role of landlocked salmonids is the case

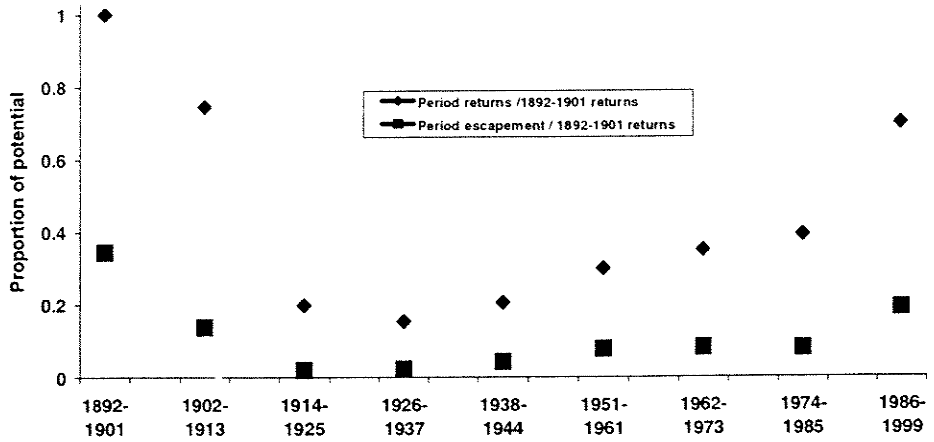

FIGURE 2. Depiction of change in total return and escapement in the 20th century from Chilko Lake 'optimal' potential sockeye return (3+ million) and escapement (1+ million) from 1892–1901 to present (Data from Pacific Salmon Commission, Vancouver, B.C., and J. Hume, Canadian Department of Fisheries and Oceans, Cultus Lake, B.C., unpublished data.)

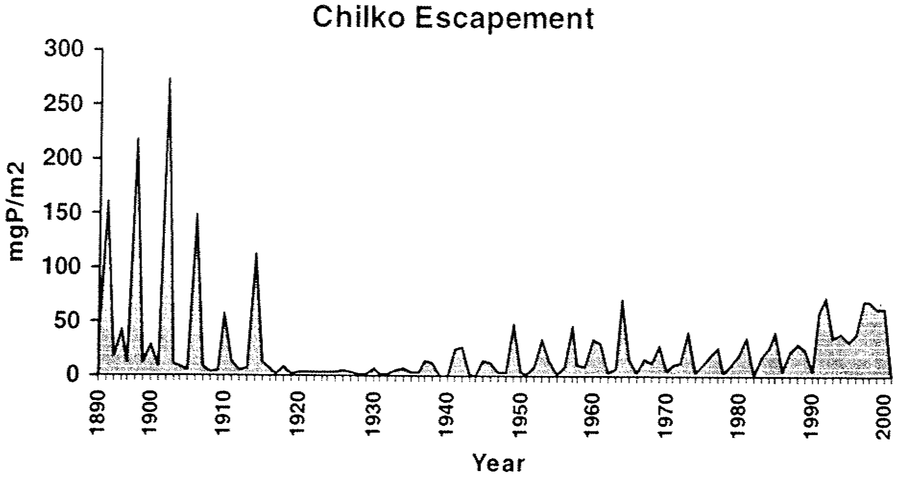

FIGURE 3. Total P content of Chilko Lake sockeye escapement (30% total escapement) from 1890 to present normalized to lake surface area. (Data from Pacific Salmon Commission, Vancouver, B.C., and J. Hume, Department of Fisheries and Oceans, Cultus Lake Laboratory, Cultus Lake, B.C., unpublished data).

study of Flathead Lake, Montana, that once supported large escapements of kokanee and a diverse terrestrial megafauna dependent on their seasonal spawning migrations. Following introduction of mysid shrimp *Mysis relicta*, the kokanee population collapsed, followed by a complete disappearance of bald eagles and grizzly bears from the carcass-deficient tributary drainage basins (Spencer et al. 1989). Although reproductively isolated from their anadromous relatives for thousands of years, kokanee and other landlocked semilparous salmonids represent the inland extension of the anadromous nutrient shadow and provide the same positive ecological benefits of increased production and biodiversity to interior, large-lake ecosystems.

Managing Climate Change

Many have warned of impending global warming with increasing concentrations of greenhouse gases and their potential impacts on terrestrial and aquatic habitats (Schneider 1989). It is clear that changes in circulation patterns and processes that deliver nutrients to euphotic regions of oceans have created large-scale events and that these have affected ocean temperatures, plankton production, and associated salmon population cycles in the past and are likely to continue to do so in the future, perhaps with greater intensity and more profound effects (Venrick et al. 1987; Beamish and Bouillon 1993). So, now superimposed upon documented declines of adult salmon, due to anthropogenic interventions (e.g., overfishing, habitat loss), we must also consider the significance of climate-imposed variability on forage production in the ocean rearing grounds of adult salmon and its impact on their marine survival. To scientifically document such effects is expensive and often imprecise because of scale (i.e., magnitude of the oceanic rearing ground), but thanks to recent paleolimnological studies, we have been given some compelling evidence of long-term, major climate oscillations and their impact on adult sockeye salmon production in some large Alaskan lakes (Finney et al. 2002). Unfortunately, apart from 'riding a bicycle' instead of 'driving an SUV', there is little we can do as fish ecologists or salmon managers to mollify the influence of these global, mesoscale oceanic events on North Pacific salmon production. Nonetheless, it is important that we understand that these ocean events have in the past and will continue in the future to influence salmon populations. A warmer climate is sure to impact salmonid freshwater rearing habitats as well, and preliminary studies suggest potential impacts on juvenile sockeye from warmer nursery lakes (Levy 1992; Henderson et al. 1993). But we must not lose focus on the requirement for further work in fresh water habitat restoration and in creative ecosystem management to rehabilitate salmonid freshwater early life stages. We need, also, to use inno-

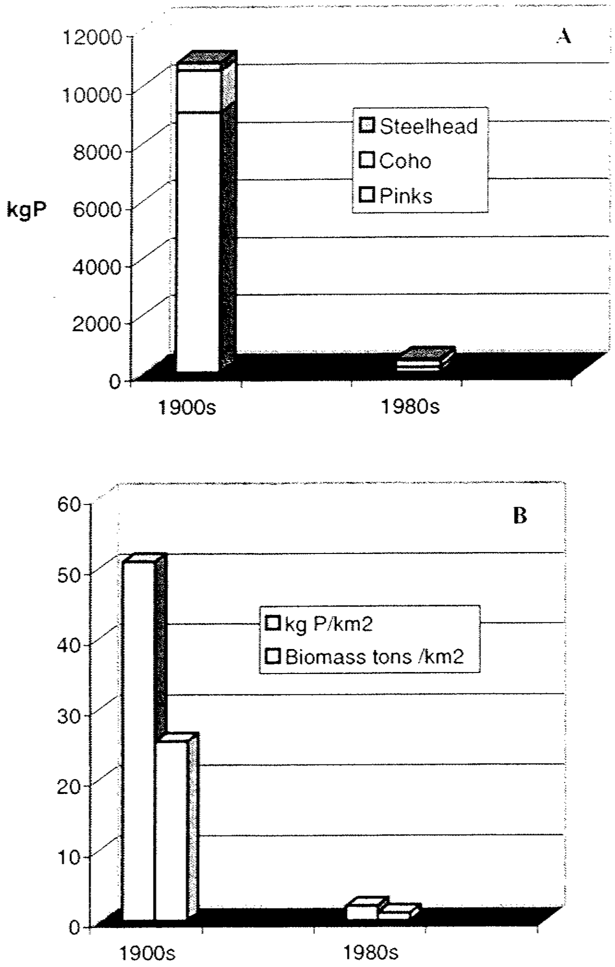

FIGURE 4. A. Estimated total P contributions from adult salmon accruing to the Keogh River and estuary in the predisturbance early 1900s and in the 1980s. B. Total kg P input and autotrophic biomass production potential in Keogh River normalized to km^2 wetted area before and after disturbance. (B. Ward, B.C. Ministry of Fisheries, UBC, Vancouver, B.C., personal communication).

vative management approaches that recognize the value of curtailing harvest and allowing sufficient adult salmon escapement to assure that ecosystem production and biodiversity are sustained and/or further enhanced by salmon nutrients (Knudson et al., Michael, both this volume).

Some Hope for the Future

Lake and Stream Fertilization in the Pacific Northwest

In an attempt to reverse the oligotrophication of sockeye salmon nursery lakes and to increase juvenile growth and survivals, the Canadian Department of Fisheries and Oceans (DFO) began a large lake enrichment program (LEP) in 1975. Selected sockeye nursery lakes were aerially fertilized to increase primary and secondary production, so as to increase juvenile sockeye forage base and improve growth and survival (Stockner 1981; Stockner and MacIsaac 1996). The lakes chosen for treatment varied from small (<200 ha) warm-monomictic coastal lakes to very large (>15,000 ha) dimictic, interior lakes. Over the last 3 decades, about 25 lakes were fertilized weekly during the growing season with liquid N and P fertilizer at an atomic N:P ratio greater than 25:1. Fertilizer loads to lakes averaged about 3.0–4.5 mg P/m^2 per week, equivalent to a weekly epilimnetic addition of 0.2–0.7 μg P/L. The treated lakes have shown a positive production response at all trophic levels, with an increase in activity and doubling of bacterial abundance, a 50–60% increase in autotrophic picoplankton abundance and phytoplankton biomass (chlorophyll), and a greater than 2-fold increase in primary production and zooplankton biomass (Stockner and MacIsaac 1996). This enhanced lake production has increased growth and survival of lake-rearing juvenile sockeye and increased the weight of seaward migrant smolts by more than 60%, resulting in improved marine survival and larger adult sockeye returns (Hyatt and Stockner 1985; Bradford et al. 2000). The Alaskan Fisheries Research and Enhancement Division (FRED) followed with a similar program to restore productivity to Alaskan sockeye lakes that were showing signs of decreased fertility caused by several decades of intensive commercial harvest (Kyle et al. 1997). In addition, lake enrichment is a key part of the recovery strategy for the imperiled Redfish Lake, Idaho, sockeye population (Gris-wold et al., this volume).

Many large interior lakes that have been impounded for hydroelectric purposes have experienced major disruptions to kokanee populations and the inland nutrient shadow as a result of hydropower operations (Stockner et al. 2000). The impoundment process initiates a downward spiral in reservoir productivity (oligotrophication), eventually leading to collapse of large piscivores (*Oncorhynchus mykiss* and *Salvelinus confluentus*) heavily dependent on kokanee populations. In 1992, the B.C. Ministry of Environment, Land and Parks (MELP) initiated an experimental reservoir fertilization program to reverse this trend in selected B.C. reservoirs. Kootenay Lake (39,500 ha) was chosen for the initial enrichment experiment, due to concerns about the effect of declining kokanee stocks on their major predator—the famous Gerrard rainbow trout strain (Ashley et al. 1997). The program was expanded in 1997 to include the upper and lower Arrow reservoirs (46,450 ha) and two coastal reservoirs—Wahleach (320 ha) and Alouette (1,670 ha), all of which were experiencing catastrophic declines in kokanee abundance because of a combination of cultural oligotrophication and species introductions (mysid shrimp and three-spine sticklebacks—*Gasterosteus aculeatus*). Each reservoir has been fertilized weekly during the 20-week growing season with a variable N:P ratio loading schedule, starting at 0.67:1 (weight:weight) ratio in late April and incrementally increasing to about 7.5:1 towards the end of the growing season (Ashley et al. 1997). Fertilizer loading averaged 13.6 mg P/m^2 per week and 60 mg N/m^2 per week in the large Columbia Basin reservoirs.

All reservoirs have shown strong, positive responses at each trophic level, with significant increases in zooplankton biomass and kokanee populations (Ashley et al. 1999; Wilson et al. 2001; Pieters et al., this volume). For example, in Kootenay Lake, the escapement of North Arm kokanee has increased from a record low of 237,100 in 1991 to 1,204,700 in 1999, after 8 years of enrichment (Ashley et al. 1999 and K. Ashley, B.C. Ministry of Fisheries, Vancouver, unpublished data). A similar recovery has been recorded on the Columbia's upper and lower Arrow reservoirs, where the amount of phosphorus translocated into tributary streams by spawning kokanee has increased from a prefertilization (1989–1998) mean of 130 kg to more than 430 kg (1999 and 2000 average; Figure 5), demonstrating the partial recovery of the long-attenuated freshwater nutrient shadow (Pieters et al., this volume). In Alouette Reservoir, kokanee size has increased from a mean prefertilization weight of 122 g in 1998 to 587 g in 2001, after three years of enrichment, even though hydroacoustic estimates indicate the pelagic fish population has increased from 57,600 in 1998 to 265,500 in 2001 (Wilson et al. 2001; Scholten and Woodruff 2002).

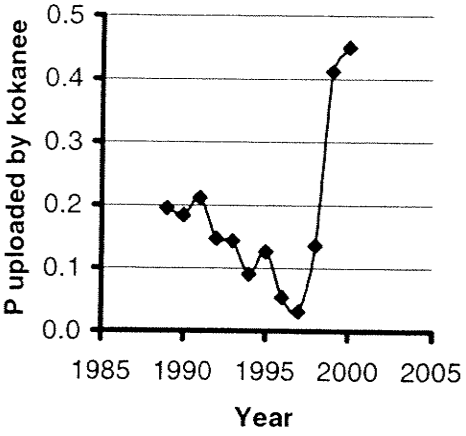

FIGURE 5. Metric tonnes of phosphorus uploaded by spawning kokanee into tributary streams in upper and lower Arrow reservoirs. Note: nutrient enrichment experiment started in 1999.

Research on stream fertilization has occupied a central theme within British Columbia for nearly two decades. Pioneering studies on the Keogh River, in the early 1980s, demonstrated the role of autotrophic production in maintaining the productivty of steelhead *O. mykis* and coho salmon in coastal rivers (Perrin et al. 1987; Johnston et al. 1990). The Keogh River served as the principle research site to investigate various fertilizer loading rates and formulations and habitat restoration techniques (Slaney et al., this volume). Instream mesocosm studies, here, have demonstrated that phosphorus loadings (solu-able P) of 3–5 µg/L were sufficient to restore autotrophic production and maintain high water quality, even though increased insect production was detected at higher nutrient loading rates (Quamme and Slaney, this volume). A multiyear paired watershed experiment at the Keogh River has been intrumental in quantifying the synergistic effect of stream habitat structures and inorganic nutrient treatment on steelhead and coho salmon production, thus providing the scientific rationale for ecologically-based watershed restoration activities (Ward et al., this volume). Knowledge gained from the Keogh River experiments have been applied to several B.C. rivers with similar positive results, demonstrating the importance of nutrient supply and autotrophic production in rebuilding fish populations in nutrient deficient coastal river systems (Slaney et al., Wilson et al., both this volume). Stream studies on the Olympic Pennisula in Washington have convincingly demonstrated the important role of native alder trees *Alnus rubra* in supplementing nutrients in oligotrophic salmonid streams (Volk et al., this volume)

A variety of innovative application systems has been developed to facilitate nutrient application to rivers, including flow proportional fertilizer injection systems using real–time stage-discharge information, and pre-programmed units designed for metering fertilizer into snowmelt dominated river systems (Wilson et al., this volume). The most promising technique has been the development and testing of slow release inorganic nutrient briquettes (Sterling et al. 2000), thus allowing once per year treatments, which are particulary useful in remote regions (Sterling and Ashley, this volume). All of these treatments are designed as *temporary* treatments to restore stream productivity and structure awaiting the return of carcasses to rebuild salmonid populations, thus 'priming' the anadomous nutrient pump.

Management for Ecosystem Production and Biodiversity

Given the overwhelming evidence of the importance of salmon nutrients in maintaining productivity in salmonid ecosystems, it is clearly time for a major paradigm shift in fisheries, forestry, and river basin management. Single species stock-recruitment models that failed to recognize the role of salmon nutrients in maintaining stock productivity dominated the previous fisheries paradigm, and most forest managers did not appreciate the ecological function of salmon nutrients in riparian ecosystems. Hydropower interests advocated single-use river systems, primarily to provide flood protection, irrigation water, and low cost energy to industry and often-subsidized agriculture and/or transportation. Urbanization expanded with little or no regard for salmon habitat. As a consequence, high exploitation rates gradually "mined" centuries of accrued phosphorus "interest" from salmonid ecosystems, while bank-to-bank logging disrupted the riparian habitat, flood plains, and estuaries where terrestrial vertebrates previously transported a majority of the salmon nutrients (Reimchen et al., this volume). The loss of large woody debris (LWD) in streams reduced the retention of carcasses and further accelerated the negative spiral towards cultural oligotrophication (Slaney and Martin 1997; Cederholm et al. 2000a, 2000b). The complete anadromous blockage by some dams such as Grand Coulee forever disrupted the social fabric of First Nations communities dependent for millennia on substantial runs of migrating salmon. The biological extinction of numerous stocks, including the famous "June hogs" chinook of the upper Columbia River, was nothing short of an ecological disaster that should never have happened and must never be repeated again. On the ledger of salmon abundance, the 20th century will be recorded by historians as one of a massive net loss for anadromous salmon, worldwide.

It is now time to replace nonsustainable resource management models and adopt holistic, ecologically-based, basin-scale, multispecies management strategies. Fisheries managers must convert to ecosystem-based escapement models that ensure that annual "interest" payments of MDN are allowed to accrue to the ecosystem (Michael, Knudsen, both this volume). Forest management must establish sufficient riparian reserve zones to ensure that logging does not occur in the riparian corridors and that LWD is allowed to recruit to the rivers to trap gravel, create habitat complexity, and retain salmon car- casses (Slaney and Martin 1997). They also must understand the significance of subsurface stream hyporheic zones and the role they play in nutrient retention (O'Keefe and Edwards, this volume). Future hydropower systems must be designed with near-zero upstream and downstream fish mortalities, as new bypass and turbine systems are developed (Cada 2001). Older hydropower dams can be retrofitted during relicensing to minimize anadromous barriers, while careful enrichment of nutrient deficient reservoirs should become standard practice in oligotrophic reservoirs (Stockner et al. 2000). Society, as a whole, must take greater responsibility for the footprint of urbanization and the endless demands for excessive 'paved' land, often at the expense of 'green-belts' for salmonid habitats. Municipal, provincial, and state zoning regulation and policies can be fish friendly and not significantly impede societal progress (Lackey, this volume). If our populace chooses to ignore these warning signs, the alternatives will be a cumulative wasting of salmonid stocks to the point where they resemble much of those of western Europe, eastern North America, and the Asian Far East, where only remnant stocks remain and most have been extirpated. To date, society has shown scant willingness to adopt the policy changes to reverse the long-term downward trend in wild salmon (Lackey 2001). Time is running out for wild salmon; further extinction of stocks is occurring. Is this what we desire for future generations in the PNW? We do not think so.

Conclusions and Summary

The importance of the adult salmon returns to production cycles of lakes and streams of the PNW, Alaska, Japan, and Russia have been elaborated in this volume. Factors such as overfishing, dams, and habitat destruction have markedly reduced adult salmon migrations and have attenuated the once-extensive nutrient shadow cast on freshwater salmonid habitat, diminishing both production and biodiversity. Many of these now salmonless ecosystems have seen an improvement in their aesthetic appeal (water clarity), but what is visually pleasing but unproductive is not necessarily good for fish production or efficient ecosystem function.

In many lakes and streams maintaining viable salmonid fisheries are important, and managers have now begun to recognize the importance of a balanced source of nutrients to support these fisheries. Nutrient enrichment has proven to be an effective habitat restoration and enhancement tool, increasing fish production in oligotrophic lakes and streams in British Columbia and in Alaska. Properly administered nutrient additions to lakes and streams should be viewed as an effective means of *restoration* of ecosystem production and biodiversity. But implementation will require good limnological knowledge and a better understanding of how important it is to maintain a balanced nutrient supply and suitable habitat to optimize production potentials. More importantly, this will require a change in the way the public views and engineers and resource managers design wastewater discharges, hydroelectric and irrigation dams, logging plans, and atmospheric emissions affecting climate change.

As a life form, salmon have demonstrated they are capable of colonizing and thriving in harsh nutrient-deficient ecosystems during the current and previous interglacial periods, partly because of their unique ability to increase the productivity of their natal streams, rivers, and lakes by recycling phosphorus and other carcass nutrients, thus casting a thin but vast nutrient shadow. The importance of this biogenic phosphorus recycling to the aquatic and terrestrial ecosystems cannot be overemphasized. As noted by Asimov (1975), "Life can multiply until all the phosphorus is gone and then there is an inexorable halt which nothing can prevent." The message is clear: a balanced supply of nutrients, reduced fishing pressure, and restoration/protection of suitable habitat is vital to the recovery of salmonids and ultimately humans in the Pacific Northwest. Thus, it is our conviction that modern society must once again 'close the circle' on phosphorus through efficient use and recycling, or we will ultimately experience the same fate as our salmonid sentinels and struggle to find a meaningful existence in a nutrient deficient world.

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