**A quantitative review of nutrient fertilization studies in freshwater ecosystems, and scoping of an experimental program in the Colorado River downstream of Glen Canyon Dam**

Prepared by:

Amy Ker, BSc, University of British Columbia

Ken Ashley, PhD, BC Institute of Technology

Josh Korman, PhD, Ecometric Research

Prepared for:

Western Area Power Administration

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**Executive Summary**

One of the key objectives of the Glen Canyon Dam (GCD) Adaptive Management Program is to understand how fish populations downstream of the dam are influenced by operations controlling the elevation of Lake Powell and flow releases. A better understanding of these effects, and other factors that are not under direct management control, would help identify policies to increase the abundance of endangered Humpback Chub in Grand Canyon, as well as non-native rainbow trout in Glen Canyon that support its blue-ribbon tailwater fishery. Historically, most scientific efforts have focused on understanding direct effects of GCD flows on rainbow trout, and effects of water temperature, turbidity, and non-native fish on humpback chub. More recently, effects of prey availability on native and non-native fish populations are beginning to emerge. Phosphorus is the primary limiting macronutrient in the majority of freshwater ecosystems. Annual variation in soluble reactive phosphorous concentrations (SRP, the biologically active form of phosphorous) in outflows from GCD was found to be a much better predictor of annual variation in rainbow trout recruitment in Glen Canyon since 2000, than flow-based covariates. The factors determining fish prey availability and fish abundance in Glen and Grand Canyons are still uncertain, but the potential importance of phosphorous levels is receiving greater attention.

Phosphorous concentrations in the Colorado River downstream from Glen Canyon Dam are sometimes very low and at limiting levels, and could be increased by dripping liquid fertilizer into the river. The addition of inorganic nutrients like phosphorous and nitrogen to enhance the productivity of freshwater ecosystems is a common fisheries enhancement practice in the Pacific Northwest. Some of the largest and longest-running programs are intended to mitigate losses of phosphorous caused by impoundment and flow regulation resulting from large mainstem dams. The central objective of this report is to review the history and literature on nutrient fertilization in freshwater ecosystems, and to provide a preliminary evaluation of the feasibility of conducting a future experiment below Glen Canyon Dam.

The addition of inorganic nutrients and organic substances to increase the productivity and yield of fish ponds has been an integral part of Asian and Eastern European fish culture for centuries. In contrast, throughout Western Europe and North America, an enormous amount of scientific and regulatory effort in the 1960s and early 1970s was directed at resolving the emerging problem of cultural eutrophication, or excessive anthropogenic loading of limiting nutrients, to inland water bodies. However, in the 1950’s in Alaska, Central Canada, Scotland, and Russia, several limnologists and fisheries biologists noted by observation and experiment, that phosphorus was essential to aquatic life in these nutrient poor environments. After considerable research, it became clear that cultural oligotrophication, excessive elimination of nutrients in some freshwater ecosystems, was having negative effects on fish populations. The limnological duality of phosphorus is now very well established: too much phosphorus causes cultural eutrophication; too little phosphorus results in cultural oligotrophication; and both conditions create nutrient imbalances that are detrimental to aquatic productivity. The cultural eutrophication message was globally acknowledged and acted upon with great conviction by society, whereas the cultural oligotrophication message was largely ignored amongst the deluge of phosphorus (and nitrogen) control efforts and regulations. To date, despite volumes of research, the aquatic ecosystem implications of cultural oligotrophication remain under-appreciated outside of the Pacific Northwest.

We conducted a review of the literature on nutrient fertilization in freshwater ecosystems to better quantify the available evidence of effects of fertilization. Our review characterizes the habitats and geographic locations where fertilization studies have been conducted, the trophic levels that were evaluated and their responses, and the strength of evidence for the responses as determined by experimental design and other characteristics. There are a large number of projects that have evaluated the effects nutrient or salmon carcass additions on various trophic levels. 89% of the 166 studies in our collection were based on a manipulation of nutrient concentration or the number of fish carcasses, with the remaining studies taking advantage of unintended changes in these inputs. 84% of the studies were based on changes in nitrogen or phosphorous levels (nutrients), with the remaining ones evaluating the effects of fish carcasses. Fertilization studies have been conducted on 188 unique water bodies. We identified 111 separate nutrient enhancement projects. The majority of fertilization studies (61%) have been conducted in the Pacific Northwest (Alaska, British Columbia, Washington, Oregon, Idaho, Montana, no studies in Wyoming) with 43, 41, and 20 studies conducted in British Columbia, Alaska, and Idaho, respectively. Globally, the vast majority of studies have been conducted in North America (80%) followed distantly by Europe (17%), and a very small contribution from other continents. The majority of fertilization studies have been conducted in lakes (40%) and streams (36%), followed by mesocosms (21%) and ponds (3%). Phytoplankton or periphyton were the most commonly studied taxa (assessed in 73% of studies), followed by zooplankton (58%) and fish (54%).

The vast majority of fish studies of nutrient fertilization evaluated effects on salmonids (86%), with the majority (60%) of those focusing on *Oncorhynchus nerka* (kokanee and its anadromous morph sockeye salmon) and *Oncorhynchus mykiss* (rainbow trout and its anadromous morph steelhead trout). The focus on salmonids occurred because most studies were conducted in the Pacific Northwest and were intended to enhance commercial (sockeye) or recreational (kokanee and trout) fisheries. Only three studies evaluated effects on brown trout. The majority of studies showed positive responses of desired taxa to increases in nutrients. For example, out of 157 documented fish responses, 68% were positive, with 25% and 6% showing neutral or negative responses, respectively. Within fish taxa, 63 studies (72%) showed positive fish growth responses, and 44 studies (64%) showed positive fish abundance responses. A similar pattern was observed for zooplankton or benthic invertebrates. A higher percentage of phytoplankton/periphyton responses were positive (73%). Bryophytes and macrophytes are an important part of the aquatic plant community in Glen Canyon. There were only two studies of bryophytes and both documented a positive response. The response of macrophytes to nutrient additions was the most variable of all taxa, with 33% of the 12 studies showing a negative response.

Undesired responses to changes in nutrient levels were rare. Out of 166 studies we reviewed, only 13 documented undesired responses of phytoplankton or periphyton, followed by 4 or fewer studies showing unwanted effects for other taxa. Unwanted effects on phytoplankton/periphyton were largely caused by increases in taxa that were not edible to zooplankton or benthic invertebrates. There were only 4 reported cases (2% of studies) of an undesired response resulting from enhancement of a fish species which was either non-native or native predator of a species targeted for enhancement. The strength of inference on effects of nutrient fertilization was generally good. Citations from the primary literature made up 84% of 166 total citations, with the remaining 16% coming from the grey literature. The majority of studies had large sample sizes and were conducted over multiple years, and in a few cases over decades. 34% of the studies used the BACI design (before-after control-impact), which controls for temporal variation in confounding variables. Based on sample size, experimental design, study duration, and the number of trophic levels studied, 16%, 56% and 28% of the studies were classified as having low, moderate, and high inference scores, respectively.

Our review documented largely positive effects of nutrient fertilization on targeted taxa in freshwater ecosystems. In many cases the inferences of fertilization effects were strong owing to adequate experimental design characteristics and measurements of multiple trophic levels. While some undesired responses to nutrient fertilization have occurred, they were rare. Arguably, nutrient fertilization is the most successful and studied fish enhancement technique for oligotrophic (nutrient poor) systems. In spite of the extensive literature on benefits of nutrient fertilization, new efforts should still be considered experimental, and therefore evaluated using an Adaptive Management approach. While the response of lower trophic levels to fertilization were generally positive and predictable, the effects of increased prey on fish communities was less certain. The effects in simple fish communities that are dominated by one species, such as sockeye salmon, may be more predictable owing to the dominance of bottom-up effects. In contrast, effects in more complex fish communities are more challenging to predict owing to a greater influence of top-down effects.

The effects of nutrient fertilization on the fish community in the Colorado River Ecosystem downstream of Glen Canyon Dam should be viewed as uncertain. In Glen Canyon, it is not clear whether rainbow trout or brown trout, or both species, will benefit from elevated phosphorous levels. The existing literature includes numerous cases of positive responses of rainbow trout to fertilization, but positive effects on brown trout from a limited number of studies has also been observed. Uncertainty in fish community response also applies to flannelmouth and bluehead suckers and humpback chub in Grand Canyon. Lower trophic level responses in Glen Canyon are also less certain owing to the extensive bryophyte and macrophyte community. However, given the unsuccessful history of GCD AMP actions to improve the status of desired fish species downstream of GCD, nutrient fertilization may warrant further consideration, especially given the possible future condition of reduced inflows and potentially lower nutrient inputs.

We reviewed phosphorous and nitrogen data from Lake Powell and Glen Canyon Dam to determine if a nutrient fertilization program could potentially enhance primary and secondary productivity. Our analysis of nutrient chemistry data in the Colorado River at or below Glen Canyon Dam was restricted to calendar years 2017-2020 due to better detection limits and more frequent sampling compared to earlier years. Concentrations of soluble reactive phosphorus (SRP) indicate that Glen Canyon was sometimes severely SRP limited (i.e., < 1 ug/L). Approximately 20% of SRP concentrations (19.5% at GCD, 21% at Lees Ferry) were at or below 1 ug/L, with almost all of these observations occurring during the March-August growing season. Average SRP concentration during the growing season was lowest in 2018, with 36% of the 11 observations from the draft tubes at or below 1 ug/l.

For exploratory purposes, the annual volume and cost of liquid inorganic fertilizer required to fertilize the Colorado River at one site below GCD was calculated for the 2017-2020 period. We assumed an in-river target Total Dissolved Phosphorous (TDP) of 3 µg/L between March 1 and August 31. Liquid fertilizer would be released 24 hours per hours/day at a flow volume to fertilizer volume ratio of 70.3 million:1. On average, 21,060 US gallons would be discharged in each year over a six-month period, which is equivalent to a dosing rate of 114 US gallons/day (443 litres/day). This dosing rate is at the low end of the rate applied in the Kootenai River in Montana downstream of Libby Dam (~80-400 US gallons/day). The annual cost for fertilizer for the GCD application averaged ~$65,000 based on flows from 2017-2020. Stream side or in-situ mesocosm studies could be used to reduce uncertainty in periphyton and benthic invertebrate responses to fertilizer addition in Glen Canyon. Alternatively, an experimental fertilization program could be implemented. While this would be a significant step, its annual cost would be small relative to recent efforts to improve secondary productivity by reducing hourly variation in flow on weekends.

**Table of Contents**

[1.0 General Introduction 1](#_Toc90975360)

[1.1 Literature Cited 5](#_Toc90975361)

[2.0 A Brief History of the Development of Nutrient Fertilization Programs and Institutional Hurdles 8](#_Toc90975362)

[2.1 Literature Cited 11](#_Toc90975363)

[3.0 A Quantitative Review of the Effects of Nutrient Fertilization on the Productivity of Freshwater Ecosystems 15](#_Toc90975364)

[3.1 Introduction 15](#_Toc90975365)

[3.2 Methods 16](#_Toc90975366)

[3.3 Results 18](#_Toc90975367)

[3.3 Discussion 22](#_Toc90975368)

[3.4 Literature Cited 25](#_Toc90975369)

[4.0 Preliminary Calculations of Nutrient Loading Rates for Fertilization Downstream of Glen Canyon Dam 29](#_Toc90975370)

[4.1 Assessing nutrient limitation and types of bioavailable nutrients 29](#_Toc90975371)

[4.2 Patterns in Discharge and Macronutrient concentrations in water released from Glen Canyon Dam and at Lees Ferry 31](#_Toc90975372)

[4.3 Conclusions and Recommendations 33](#_Toc90975373)

[4.4 Literature Cited 34](#_Toc90975374)

[Appendix A: Citations for 165 papers used for analysis 50](#_Toc90975375)

# 1.0 General Introduction

One of the key objectives of the Glen Canyon Dam Adaptive Management Program (GCD AMP) is to understand how fish populations downstream of the dam are influenced by operations controlling the elevation of Lake Powell and its outflow (Gloss et al. 2005). A better understanding of these effects, and other factors that are not under direct management control, would help identify policies to increase the abundance of endangered humpback chub in Grand Canyon, as well as non-native rainbow trout in Glen Canyon that support its blue-ribbon tailwater fishery. Historically, most scientific efforts have focused on understanding direct effects of Glen Canyon Dam (GCD) flows on rainbow trout, and water quality effects and other factors on humpback chub. McKinney et al. (2001) concluded that the reduction in hourly variation in flows from GCD in the early 1990’s, to mitigate erosion of beaches and improve recreational boating conditions, was the cause for the increase in electrofishing catch rates of rainbow trout in Glen Canyon between 1991 and 1997 (McKinney et al. 2001). Korman et al. (2012) found that recruitment of rainbow trout in Glen and Marble Canyons between 1991 and 2010 was negatively related to hourly variation in flows, and positively related to annual flow volumes and annual flow maxima. Declines in humpback chub abundance in Grand Canyon have been attributed to indirect effects of GCD operations which include: 1) increased abundance of non-native fish and in particular rainbow and brown trout; 2) cooler water temperatures due to the release of hypolimnetic water from Lake Powell; 3) clearer water resulting from settling of fine sediment in Lake Powell, and 4) loss of backwater habitat due to reduced sediment deposition in Grand Canyon (Gloss and Coggins 2005). In a more recent and quantitative assessment, Yackulic et al. (2018) found that abundance of rainbow trout, water temperature, and turbidity were important determinants of juvenile humpback chub growth or survival.

Quantitative links between prey availability for fish and their abundance have only recently been established. Korman et al. (2021) found that drift concentration of these taxa (prey availability) was the most important factor controlling the somatic growth, abundance, and distribution of rainbow trout in Glen and Marble Canyon between 2012 and 2016. Reduced prey availability in 2014 and 2015, which occurred under drought conditions, led to negative growth in weight and poor condition, especially for larger trout with higher energetic demands. This in turn led to lower survival rates and lower rates of sexual maturation (Korman et al. 2017), which resulted in a 3- to 10-fold reduction in abundance of the population (Korman et al. 2021). The effects of prey availability on native fish are also beginning to emerge. Condition factor of humpback chub near the Little Colorado River was substantially lower in late 2014 and 2015, following the same period of reduced prey availability that had negative impacts on rainbow trout (C. Yackulic, USGS, Flagstaff, AZ, unpublished data). Low condition factor was identified as the likely cause of the low proportion of the chub population that entered the LCR to spawn in 2015, contributing to reduced recruitment in the following year. Similarities in long term trends in condition factor of trout, humpback chub, and flannelmouth sucker over the last two decades in the Colorado River Ecosystem (CRE) suggest that system-wide variation in prey availability can have important effects on both non-native and native fish communities downstream of GCD (C. Yackulic and M. Yard, USGS, Flagstaff, AZ, unpublished data).

The factors determining fish prey availability in Glen and Grand Canyons are still largely uncertain. The food base program within the GCD AMP is tasked with understanding the factors that control prey availability for important fish populations downstream of GCD (Kennedy and Gloss 2005). Early efforts showed that the invertebrate community in Glen and Marble Canyons transitioned from one dominated by large amphipods (*Gammarus lacustris*) in the late 1980s, to one dominated by smaller midges (*Chironomidae*) and black flies (*Simuliidae*) by the mid-1990s (Shannon et al. 2001). The cause for this transition has not been determined. To date, most investigations have focused on effects of fluctuating flows from GCD. Shannon et al. (1996) suggested that low flows with limited fluctuations would increase benthic and drift biomass due to reduced rates of sediment transport which scour and bury benthic invertebrates. Other efforts have focused on the effects of spring high flow experiments on invertebrate production (Shannon et al. 2001, Wyatt et al. 2011). The recent bug flow experiment formalized under the LTEMP (https://ltempeis.anl.gov/), is testing the hypothesis that hourly variation in flows dry-out aquatic insect eggs and larvae and limit aquatic insect production (Kennedy et al. 2016). An unintended result from that experiment was a canyon wide (123-426 river kilometers below the dam) 56% increase in gross primary production rates during steady-low flow days, which was primarily driven by increased water clarity (Deemer et al. In Review). Previous work in the Colorado River has also identified water clarity as a key driver of aquatic primary production (Hall et al. 2015), although more recent investigations suggest that phosphorus also limits gross primary production in much of the Colorado River (but below the macrophyte dominated Glen Canyon Reach).

Effects of nutrient levels from GCD on prey availability and fish populations in the Colorado River ecosystem are beginning to emerge. Korman et al. (2017) identified a correlation between rainbow trout abundance, Lake Powell elevations, and annual flow volumes released from Glen Canyon Dam between 1991 and 2016. They speculated that low concentrations of macronutrients (nitrogen or phosphorus) in the water released from GCD, due to combined effects of low inflows to Lake Powell and low reservoir elevations, was a potential cause of reduced prey availability below the dam, which in turn led to reduced growth and abundance of rainbow trout. Secondary production modelling in Glen Canyon shows a moderate correlation between reservoir elevation, release volumes, phosphorous levels, and energy acquired by rainbow trout (M. Yard unpublished data). Annual variation in soluble reactive phosphorous concentrations (SRP, the biologically active form of phosphorous) in outflows from GCD was found to be a much better predictor of annual variation in rainbow trout recruitment in Glen Canyon since 2000, than flow-based covariates (C. Yackulic, unpublished data). This result suggests that over the last two decades, phosphorous limitation is a more important driver of rainbow trout production then flow volume or flow variation from GCD. If this hypothesis holds, the result represents a major paradigm shift in our understanding of what controls fish abundance, or at least trout abundance, below GCD. This shift has substantive policy implications because it indicates that future actions intended to improve desired fish populations should increase emphasis on strategies that increase nutrient levels, at least in years when they are limiting.

The more recent recognition of the potential importance of phosphorous levels in controlling fish populations downstream of Glen Canyon Dam has led to increased efforts to understand factors that determine phosphorous concentrations in dam releases. To date, limited progress has been made, largely due to the paucity of reliable phosphorous measurements. A non-trivial portion of the historic measurements of SRP in Lake Powell or in GCD outflows are at or below detection limits (detection limit was 5 ug/L until 2000, and has dropped to 1 ug/L in more recent years; Deemer et al. In Prep). In 2017 total dissolved phosphorus was added to the suite of nutrient species that are monitored in GCD outflows, allowing for better quantification of the most biologically available phosphorus. Still, the low levels of SRP in the system have made it difficult to determine which factors control variation in outflow SRP concentrations (B. Deemer, UGSS, Flagstaff, AZ, unpublished data). Currently the best working model predicting outflow SRP concentrations is based on the three-year average total phosphorus loading to Lake Powell (with concentration and flow dominating the loading signal depending on the year, R2=0.55, B. Deemer, UGSS, Flagstaff, AZ, unpublished data). On a yearly basis, pH is also weakly negatively correlated with SRP in dam outflows as well as at Lees Ferry (p=0.007, R2= 0.28, B. Deemer, UGSS, Flagstaff, AZ, unpublished data), a pattern that may be due to co-precipitation of SRP with calcite at high pH since high rates of calcite precipitation do occur in Lake Powell (Deemer et al. 2020). This potential calcite-driven control on SRP is consistent with the positive correlation between reservoir bicarbonate concentrations and outflow SRP (M. Yard, unpublished data). That same modeling exercise identified a positive relationship between reservoir volume and outflow SRP. This relationship suggests the importance of reservoir water level as a driver. In fact, there is almost always depth-specific variation in SRP concentrations and water temperature within Lake Powell, suggesting both the potential for purposeful management and the importance of variation in water storage given a fixed withdrawal point (Korman et al. 2021).

Under the 21st century drought (Udall and Overpeck 2017), inflows and elevation of Lake Powell are expected to be low, which could lead to more frequent periods of low phosphorous concentrations in GCD outflows. Given competing demands for water stored in Lake Powell, especially under drier conditions, it may be difficult to manage reservoir elevations and release schedules to maximize SRP concentrations to potentially improve the status of fish populations downstream of the dam. An alternate strategy is to supplement the concentration of phosphorous through nutrient fertilization. This would involve dripping liquid fertilizer into the Colorado River downstream of GCD, to attain a target SRP concentration, during years and seasons when phosphorous is limiting benthic primary production, and hence invertebrate production and prey availability for fish. The addition of inorganic nutrients like phosphorous and nitrogen to enhance the productivity of freshwaters is a common enhancement practice in the Pacific Northwest. Some of the largest and longest-running programs are intended to mitigate losses of phosphorous caused by impoundment and flow regulation resulting from large mainstem dams (e.g. 12% of global riverine phosphorus loads are retained behind dams; Maavara et al. 2012). Given phosphorous limitation in Lake Powell (Gloss 2005) and below Glen Canyon Dam in some years (see section 4.0), this approach has the potential to improve the status of rainbow trout in Glen Canyon, and perhaps humpback chub and other native fishes in Grand Canyon. The action could mitigate the effects of impoundment. Even if long-term implementation of this action is not feasible due to administrative or policy constraints, short-term experimental implementation could lead to a rapid increase in our understanding of the role of phosphorous in controlling the foodbase and fish populations below GCD. This understanding would provide useful context to evaluate the likelihood of success of other flow-based management actions. For example, failure to account for nutrient effects could lead to an underestimation of the benefits of bug flows if those studies were conducted in years when nutrient limitation was dominant (Korman et al. In review). A better understanding of the role of phosphorous would also help interpret the historical record. For example, results from a fertilization study could reduce uncertainty about whether there is a cause-effect relationship between SRP concentration and recruitment of rainbow trout (Yackulic, C., USGS, unpublished data).

The central objective of this report is to review the history and literature on nutrient fertilization in freshwater ecosystems, and to provide a preliminary evaluation of the feasibility of conducting a future experiment below Glen Canyon Dam. The intent is to provide GCD AMP decision-makers with sufficient information to evaluate the merits and risks of this potential experimental action. Chapter two provides a brief history of the nutrient fertilization efforts, and outlines some of the cultural and institutional challenges in implementing these programs. Chapter 3 provides a quantitative review of the extensive literature on nutrient fertilization. The intent is to characterize the habitat and geographic locations where fertilization studies have been conducted, the responses of different trophic levels, and the strength of evidence from these studies. We discuss findings in the context of the Colorado River ecosystem. Chapter 4 uses information on discharge and nutrient concentrations from Glen Canyon Dam to determine how much fertilizer would need to be added, and the costs of this material. This chapter also describes monitoring and mesocosm experiments to better determine the likelihood of success of a larger-scale field experiment.

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# 2.0 A Brief History of the Development of Nutrient Fertilization Programs and Institutional Hurdles

The addition of inorganic nutrients and organic substances to increase the productivity and yield of fish ponds has been an integral part of Asian and Eastern European fish culture for centuries (Nees 1946). In contrast, throughout Western Europe and North America, an enormous amount of scientific and regulatory effort in the 1960s and early 1970s was directed at resolving the emerging problem of cultural eutrophication, or excessive anthropogenic loading of limiting nutrients, to inland water bodies (Edmondson 1969). The seminal book of this era “The Algal Bowl” by Jack Vallentyne (1974) elegantly described how cultural eutrophication had become a major environmental problem throughout the developed world. Following confirmation of phosphorus as the primary limiting macronutrient in freshwater (Edmondson, 1969; Schindler et al., 2008), societal efforts through the remainder of the 1970’s, 1980’s and 1990’s focused on reducing discharges of phosphorus predominately from point-sources, to inland and coastal waters. Hence, the political and regulatory mind-set for the last third of the 20th century was cast, and reduction or elimination of phosphorus (and nitrogen secondarily) discharges to inland and coastal marine waters became the standing regulatory order of the day.

However, in the 1950’s in Alaska (Nelson and Edmondson 1955), Central Canada (Huntsman 1950, Langford 1948), Scotland (Brook 1956, Brook and Holden 1957, Morgan 1966) and Russia (Krokhin 1959 and 1967), several limnologists and fisheries biologists noted by observation and experiment, that phosphorus was essential to aquatic life in these nutrient poor environments. In countries around the North Pacific, the realization that salmon carcass decomposition of biogenically recycled phosphorus and nitrogen sustained high productivity in lakes and rivers that would otherwise have been oligotrophic (low in plant nutrients) offered new insights for management of Pacific salmon. This led to a decision in 1968, by the Canadian Department of Fisheries and Oceans (DFO), to add inorganic nutrients to Great Central Lake on Vancouver Island, British Columbia in an attempt to rebuild a sockeye salmon stock that had been depressed since the turn of the 20th century, yet had failed to recover despite reductions in fishery harvest rates and several decades of positive oceanographic conditions. The rapid recovery of Great Central Lake sockeye (Lebrasseur and Kennedy, 1972; Parsons et al., 1972) led to the creation of a Lake Enrichment Program (LEP) under the direction of DFO’s Salmonid Enhancement Program (SEP) in 1974. In 1979, the Alaska Department of Fish and Game (ADF&G) launched a similar statewide lake enrichment program under the Fisheries Rehabilitation, Enhancement and Development (FRED) Division. In the mid 1980s, the BC Provincial Government’s Fish and Wildlife Branch initiated a comprehensive research program into river and lake fertilization, which evolved into the large-scale river, lake and reservoir fertilization programs that exist today.

In August 1997, a career re-location to Uppsala, Sweden enabled pioneering lake enrichment researcher John Stockner to collaborate with Goran Milbrink, also at the University of Uppsala, who had studied the effects cultural oligotrophication (excessive elimination of nutrients) and conducted innovative fertilization experiments on Swedish hydroelectric reservoirs (Milbrink and Holmgren, 1981; Milbrink et al., 2011). The net result of this Canadian-Swedish collaboration was the first International Workshop on “Restoration of fisheries and enrichment of aquatic ecosystems” in Sweden March 30-April 1, 1998 (Stockner and Milbrink, 1999). The fact that this conference was held in Sweden, and organised by Canadian and Swedish trained limnologists, appears at first glance to be incongruous, as both countries were leaders in the crusade against cultural eutrophication of their inland waters. However, Sweden, like Canada, has long been a leader in the scientific study of factors influencing the productivity of lakes, beginning with pioneering studies of Einar Naumann and Wilhelm Rodhe and later the research programs conducted by the Institute of Freshwater Research at Drottingholm and Institutes of Limnology at the University of Uppsala and the University of Lund.

Scientific recognition of the ecosystem implications of cultural oligtrophication increased dramatically in the late 1980s and 1990s following publication of the first formal papers describing it (Ney 1996, Stockner et al., 2000) and several synopsis papers that quantified the effect of reduced salmonid escapement on Pacific Northwest aquatic ecosystems (Mathisen et al. 1988, Willson and Halupka 1995, Larkin and Slaney 1997, Cederholm et al. 1999, Cederholm et al. 2000, Gresch et al. 2000). Concerns about reductions in marine derived nutrients (MDN) in streams of the US Pacific Northwest (PNW) due to lower returns of wild salmon were also raised (Larkin and Slaney 1997, Gresch et al. 2000). Simultaneously, several researchers in Alaska, BC, Oregon and Washington utilised stable isotope tracers; mainly 15N and 13C, to document the movement of MDNs through the aquatic and terrestrial food webs, which further elucidated the role and importance of salmon nutrients in sustaining production and biodiversity of PNW ecosystems (Bilby et al. 1996, Bilby et al. 2001, Johnston et al. 1997, Kline et al. 1993, Wipfli et al. 1999). In addition, the results of several large-scale lake and river nutrient enrichment experiments were published, which further increased scientific recognition of the issue (Ashley and Slaney 1997, Ashley et al. 1997, Johnston et al. 1990, Slaney et al. 1994, Stockner and MacIsaac 1996, Johnston et al. 1999). This recognition of the critical role of MDNs in salmonid ecology and management culminated in a major international conference in Eugene Oregon in April 2001, which was attended by over 400 participants from North America, Europe and Japan (Stockner 2003).

The limnological duality of phosphorus is now very well established: too much phosphorus causes cultural eutrophication; too little phosphorus results in cultural oligotrophication; and both conditions create nutrient imbalances that are detrimental to aquatic productivity. The cultural eutrophication message was globally acknowledged and acted upon with great conviction by society, whereas the cultural oligotrophication message was largely ignored amongst the deluge of phosphorus (and nitrogen) control efforts and regulations. To date, despite volumes of research, the aquatic ecosystem implications of cultural oligotrophication (as documented in Section 3 of this report) remain under-appreciated outside of the Pacific Northwest except for tacit recognition from individual scientists overseas in Japan, Scotland and Sweden. Consequently, British Columbia, Alaska and most recently northern Idaho are the only centers for large-scale government sponsored lake, reservoir, stream and river fertilization projects.

The causes of cultural oligotrophication, the ‘clear water paradox’, were explored by Anders and Ashley (2007) who asked (1) is there an inherent policy conflict between adding nutrients to watersheds to restore fish populations (and associated ecosystem function) and societal pressure to protect and enhance water quality, given that Western society typically desires both, and (2) is there a regulatory bias toward achieving “distilled water” in lakes, reservoirs, rivers, and streams such that the important beneficial role of waterborne nutrients is not given equivalent consideration and legislative weight? In 2020, most US agencies tasked with water quality management remain conflicted by this paradox, resulting in policy paralysis and inaction, and an unwillingness to explore adaptive management experiments to explore innovative solutions to cultural oligotrophication.

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# 3.0 A Quantitative Review of the Effects of Nutrient Fertilization on the Productivity of Freshwater Ecosystems

## **3.1 Introduction**

There is an extensive literature documenting generally positive results from nutrient fertilization experiments intended to enhance productivity of freshwater ecosystems. Although nutrient fertilization is one of the best documented fish enhancement techniques, fertilization efforts are largely isolated to the Pacific Northwest. This paradox could be due to biases, such as ‘cultural oligotrophication’, which is a reluctance to enhance nutrient levels in oligotrophic systems owing to the long history of research and regulatory efforts to limit negative eutrophication effects (Stockner et al. 2000). However, there are other potential reasons for the poor uptake of nutrient fertilization as a broad scale fish enhancement method in oligotrophic systems, including: 1) limited evidence of positive effects on higher and targeted trophic levels (fish); 2) weak inferences about positive effects on higher trophic levels; or 3) greater documentation in the grey rather than primary literature, limiting the broadscale dissemination of results. We conducted a review of the literature on nutrient fertilization in freshwater ecosystems to better quantify the available evidence of effects of fertilization and to better define the cause of the poor uptake of this enhancement method.

Our review characterizes the habitats and geographic locations where fertilization studies have been conducted, the trophic levels that were evaluated and their responses, and the strength of evidence for the responses as determined by experimental design and other characteristics. The available literature is vast, and the intent here is to summarize that information in a succinct way. We took a quantitative approach where we enumerated the number of studies and projects by various strata, such as the number in lakes and rivers, or that evaluated the responses of particular trophic levels such as zooplankton or fish. We also quantified the number of studies that showed negative, neutral, or positive trophic level responses to characterize how successful fertilization has been in various situations. We also quantify and discuss studies that showed negative unwanted effects. We evaluate the strength of inference of trophic level responses based on experimental design characteristics and the number of trophic levels studied. Finally, we highlight studies and findings that have more relevance to the Colorado River Ecosystem (CRE), such as effects of fertilization in large rivers, on rainbow trout, brown trout, suckers, and minnows, and on bryophytes and macrophytes which are important elements of primary production in Glen Canyon.

## **3.2 Methods**

***Compilation of the Literature***

We searched a variety of databases for primary and grey literature with one or more words from the categories ‘habitat’ (lake, reservoir, stream, mesocosm), ‘action type’ (fertilization, nutrients, nutrient enrichment, nutrient addition, salmon subsidies, nutrient enhancement, nitrogen, carcass addition, nitrogen, phosphorous), and ‘response type’ (food web, fish production, salmon, zooplankton, salmonid, trout, growth) categories. We used the Google Scholar search engine, but also searched more local databases which included the Province of British Columbia Ecological Reports Catalogue (<https://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/libraries-publication-catalogues/ecocat>) and the Alaska Department of Fish and Game Management and Research Publications and Reports database (<https://www.adfg.alaska.gov/index.cfm?ADFG=research.publications>). Searches in these latter two databases provided much of the grey literature summarized in this review. The abstract of each paper identified from this search process was reviewed and used to determine if the paper would be included in our initial list. For each paper that made the initial list, we reviewed their citation list, and latter papers that had cited the paper, to identify other papers to review.

This process yielded a total of 302 papers, which were then reviewed to determine if they

would be included in our final reference list to be analyzed. Papers were included for further evaluation if the effects of either a purposeful manipulation or unintended change in nutrient levels was evaluated. The following criteria were used to excluded papers: 1) focus on process or on methodology; 2) focus on eutrophication or aquaculture; or 3) where results from a particular project had been more thoroughly reported in a different paper. We also classified 23 of the 302 papers as reviews because they summarized the results of multiple years of results from a single fertilization project, or reviewed papers from the primary literature or grey literature. Findings from review papers were only used in our main analysis if they were the only source of information for a fertilization project. Applying our removal criteria, and removing review papers, reduced our initial list of 302 papers to 166 (Appendix A).

We often encountered a sequence of annual reports from the same projects (study location) in the grey literature. In these cases, we used the most recent publication and/or the publication encompassing the longest duration of study. If two papers reported data over the same time period, we included the paper that provided the most thorough description of the experimental design and results. Multiple papers studying the same waterbody would be included in our final list only if there was no overlap in the time period studied or if the papers focused on different aspects of trophic responses (e.g., zooplankton vs. fish). However, these instances were rare, so the majority of the 166 papers we analyze represent unique fertilization studies.

***Analysis***

We created a database that catalogued the characteristics of each of the 166 papers in our collection (Appendix A). This included the name of the authors, year of publication, project identifier (unique water body and author), journal name and type (primary or grey literature), geographic location, water body name, number of water bodies studied, habitat type, type of manipulation, trophic levels assessed, direction of response of each trophic level to fertilization, the presence of an undesired response, statistical design, study duration, and number of samples.

Information on location, habitat type (stream, lake, pond, mesocosm), and the type of manipulation (unintended change in nutrients inputs to streams or lakes, experimental addition of nutrients, natural or experimental addition of fish carcasses as the nutrient source) allowed us to describe the geographic distribution of studies and the types of habitats they were conducted in. We determined the number of unique fertilization projects based on waterbody names. Information on the trophic levels studied, and their responses to fertilization (negative, neutral, or positive) was used to characterize overall patterns in response. For the fish trophic level, we further classified responses into effects on fish growth and fish abundance. Unwanted effects of fertilization were defined as those resulting in an undesired ecosystem response, such as an increase in blue green algal density, or in the abundance of a non-native fish species.

Information on publication type (primary or grey), statistical design, study duration, and sample size allowed us to evaluate the strength of inference on trophic level responses. Statistical designs were classified into one of four categories: BACI (Before After Control Impact); BA (Before After); CI (Control Impact); or NA (not applicable, e.g., in the case of a modelling study). To summarize the strength of inference about effects of fertilization, we assigned each paper an overall rank score (1=low; 2=moderate; 3=high). This rank score was determined based on the statistical design, duration of the experiment, number of sample locations, and number of trophic levels studied. Studies with the more informative BACI design, where multiple trophic levels were studied, with a longer study duration, and/or more sampling locations, were given a higher overall score.

## **3.3 Results**

There are a large number of projects that have evaluated the effects nutrient or salmon carcass additions on various trophic levels. 89% of the 166 studies in our collection were based on a manipulation of nutrient concentration or the number of fish carcasses, with the remaining studies taking advantage of unintended changes in these inputs. 84% of the studies were based on changes in nitrogen or phosphorous levels (nutrients), with the remaining ones evaluating the effects of fish carcasses. Fertilization studies have been conducted on 188 unique oligotrophic water bodies. We identified 111 separate nutrient enhancement projects as defined by groups of water bodies and author associated with each study. In a few cases these projects studied different periods of time or taxa in the same waterbody. For example, there were six citations describing different aspects of the Kootenai River fertilization effort, and another six describing the Kootenay Lake effort.

The majority of fertilization studies (61%) have been conducted in the Pacific Northwest (Alaska, British Columbia, Washington, Oregon, Idaho, Montana, no studies in Wyoming) with 43, 41, and 20 studies conducted in British Columbia, Alaska, and Idaho, respectively (Table 1). Globally, the vast majority of studies have been conducted in North America (80%) followed distantly by Europe (17%), and a very small contribution from other continents. The majority of fertilization studies have been conducted in lakes (40%) and streams (36%), followed by mesocosms (21%) and ponds (3%). There are a large number of aquaculture-related fertilization studies in ponds, but these studies were excluded from our analysis which focused on ecosystem responses.

Phytoplankton or periphyton were the most commonly studied taxa (assessed in 73% of studies, Table 2a), followed by zooplankton (58%) and fish (54%). The majority of studies (68%) evaluated the response of more than one taxa (Table 2b) which included 36 cases where nutrients, phytoplankton/periphyton (P), zooplankton/benthos (Z), and Fish (F) were jointly evaluated, and 16 studies that jointly evaluated P, Z, and F. These studies provide stronger inference because the effects of changes in nutrients can be tracked across multiple trophic levels.

The vast majority of fish studies (Table 3) evaluated effects on salmonids (86%), with the majority (60%) of those focusing on *Oncorhynchus nerka* (kokanee and its anadromous morph sockeye salmon) and *Oncorhynchus mykiss* (rainbow trout and its anadromous morph steelhead trout). The focus on salmonids occurred because most studies were conducted in the Pacific Northwest and were intended to enhance commercial (sockeye) or recreational (kokanee and trout) fisheries. Only two studies evaluated effects on brown trout.

The majority of studies showed positive responses of desired taxa to increases in nutrients (Table 4). For example, out of 157 documented fish responses, 68% were positive, with 25% and 6% showing neutral or negative responses, respectively. A similar pattern was observed for zooplankton or benthic invertebrates. A higher percentage of phytoplankton/periphyton responses were positive (73%). Bryophytes and macrophytes are an important part of the aquatic plant community in Glen Canyon. There were only two studies of bryophytes and both documented a positive response. The response of macrophytes to nutrient additions was the most variable of all taxa, with 33% of the 12 studies showing a negative response. Within fish taxa, there were 63 studies (72%) which showed positive fish growth responses, and 44 studies (64%) which showed positive fish abundance responses (Table 5).

Undesired responses to changes in nutrient levels were rare (Table 6). Out of 166 studies, there were only 13 which documented undesired responses of phytoplankton or periphyton, followed by 4 or fewer studies showing unwanted effects for other taxa. Unwanted effects on phytoplankton/periphyton were largely caused by increases in taxa that were either not edible to zooplankton or benthic invertebrates (Squires et al. 2008, Hyatt et al. 2004a, Hyatt et al. 2004), and/or caused harmful blooms that were toxic or led to anoxia (Daniels et al. 2015, Bogard et al. 2017a), or substantively reduced water clarity (Miracle 2007). There were only three reported cases (2% of studies) of an undesired zooplankton or benthic invertebrate response. Two of these responses were caused by enhancement of species that were not edible to higher trophic levels (Hyatt et al. 2004, Davis et al. 2010). The third response was a decrease in nematode species diversity at higher nutrient enrichment concentrations (Ristau et al. 2013). There were only 4 reported cases (2% of studies) of an undesired fish response. The responses were enhancements of undesired fish species which were either non-native (Preston et al. 2018) or native but predators of targeted fish species (Perrin et al. 2006, Hyatt et al. 2004, Peck et al. 2019). The one instance of undesired macrophyte response, documented by two studies in the same system, was due to an in increase in inedible macrophyte species that limited the benefit to other trophic levels (Ristau et al. 2012 and 2013). The one undesired bryophyte response resulted from increased bryophyte dominance which had a negative effect on some species of benthic invertebrates (Bensted et al. 2007). The undesired bacterial response resulted from nitrogen addition which reduced bacterial N2 fixation (Gettel et al. 2013). Across taxa, about 1/3rd of the studies documenting undesired effects occurred in mesocosms, often when high levels of nutrients were purposefully applied to determine dose-response relationships.

The strength of inference on effects of nutrient fertilization was generally good. The year of publication for the 166 citations ranged from 1979-2020, with the vast majority (82%) published in the last 20 years (Table 7). Citations from the primary literature made up 84% of 165 total citations, with the remaining 16% coming from the grey literature. The majority of studies had large sample sizes and were conducted over multiple years, and in a few cases over decades (Table 8a). 34% of the studies used the BACI design, which controls for temporal variation in confounding variables (Table 8b). Based on sample size, experimental design, study duration, and the number of trophic levels studied, 16%, 56% and 28% of the 166 studies had low, moderate, and high overall rank inference scores, respectively (Table 9a). This pattern was generally consistent across trophic levels (Table 9b). There were no concerning trends in the direction of response of various taxa and inference rank, where rank would be worse for more challenging taxa to study (Table 10). For example, 48% of the 44 studies that documented a positive response of fish abundance to increases in nutrients were given a high inference level rank, while 50% had a moderate inference level. The majority (57%) of the seven studies documenting a negative response of fish abundance were given a high inference rank.

We report on details of the effects of fertilization on macrophytes and bryophytes owing to their abundance in the Glen Canyon tailwater. Nine studies measured effects of nutrient addition on macrophytes whereas only two studied the effects on bryophytes. Both bryophyte papers reported on long term projects conducted in the Kuparuk river in Alaska. Slavik et al. 2004 found phosphorous fertilization of the Kuparuk River increased bryophyte growth, with bryophytes replacing diatoms as the dominant primary producers but then slowly returned to pre-fertilization levels after treatment ended (Benstead et al. 2007).

Macrophyte studies was predominantly conducted in mesocosms (7), with the remaining two conducted in ponds. Nutrient addition resulted in 7 increased growth responses, 4 decreased growth or die-off responses, and one instance of no change. Negative effects could be attributed to increased turbidity causing macrophyte disappearance (Miracle 2007), high nutrient levels potentially being toxic to macrophytes (Becares et al. 2008) and macrophyte growth being limited by periphyton and phytoplankton growth (Hietala et al. 2004, Daoust and Childers 2004). Two of the 7 positive responses were increased growth of predominantly inedible macrophyte taxa, but this response only occurred in high nutrient mesocosm conditions (Ristau et al. 2012, Ristau et al. 2013).

We further analyzed the effects of nutrient addition on brown trout, rainbow trout, sucker species, peamouth chub, pikeminnow, and silver carp, because these species are either present in Glen or Grand Canyons, or may have similar characteristics to some of the species that live there. Rainbow trout were the most frequently studied of these fish, with 17, 2, and 4 studies showing positive, negative, and no responses. Three studies reported positive effects of fertilization on both rainbow trout growth and abundance (Wilson et al. 2003, Ashley et al. 1999, Slaney & Ward 1993). Studies showing positive responses of rainbow trout growth to fertilization (10) were more common than ones documenting positive fish abundance responses (7), and there were two studies reporting an increase in fish growth but no effect on fish abundance (Johnston et al. 1999, Collins & Baxter 2020). Growth rates of juvenile rainbow trout declined at higher nutrient levels in a mesocosm study (Taipale et al. 2018). One study showed a decline in rainbow trout abundance under fertilization, potentially caused by benefits accruing to non-target species including pikeminnow, peamouth chub, sucker, and kokanee (Squires et al. 2008). Three studies investigated the effects of nutrient addition on brown trout, and two found that nutrient additions led to increases in brown trout growth and abundance (Wilson et al. 2003, Milbrink et al. 2008). The other study reported no effect on brown trout growth after short term (<1 month) addition of nutrients to mesocosm habitats (Bruder et al. 2017).  Two studies reported positive growth of sucker species to nutrient additions (Watkins et al. 2017, Holderman et al. 2009a). Silver carp growth increased in response to phosphorous addition in a short-term study (Zhang et al. 2015).

## **3.3 Discussion**

Our review summarizes an extensive literature documenting largely positive effects of nutrient fertilization on targeted taxa in freshwater ecosystems. In many cases the inferences of fertilization effects were strong owing to good experimental design characteristics and measurements of multiple trophic levels. While some undesired responses to nutrient fertilization have occurred, they were rare and often reversable. Arguably, nutrient fertilization is the most successful and studied fish enhancement technique available, though it is limited to oligotrophic systems. In spite of these benefits, the geographic locations where large-scale field trials of fertilization, or where fertilization is now a management action, is very constrained, with most effort occurring in the Pacific Northwest. Our preliminary hypotheses for this paradox which included: limited benefits on higher trophic levels; weak inferences on higher trophic levels; and a dominance of documentation in less accessible grey literature, were not supported by our analysis. In the discussion which follows, we describe the probable causes for this paradox, limitations of our analysis, and challenges in predicting fish community responses to nutrient fertilization.

The first cause for the paradox of constrained geographic location of fertilization efforts has been termed ‘cultural oligotrophication’ (Stockner et al. 2000), which recognizes the range of phosphorous effects in freshwater ecosystems: too much phosphorus from anthropogenic (‘cultural’) sources causes eutrophication because inputs are too high; too little phosphorus resulting from anthropogenic effects, such as impoundment and isolation of flood plains, causes oligotrophication. Both conditions create nutrient imbalances that are detrimental to the productivity of freshwater systems. Despite the considerable body of literature summarized in this and past reviews, the aquatic ecosystem implications of cultural oligotrophication remain under-appreciated outside of the Pacific Northwest. It is likely that the decades of research and regulatory efforts to limit eutrophication has created a bias among scientists and decision-makers against adding nutrients for enhancement purposes, even in systems where nutrient limitation has been well established. Apparently, this bias can only be overcome in locations where fertilization research effort is prevalent, a surprising result given the large number of papers available in the primary literature.

Natural system model bias is a probable second cause for the paradox of constrained geographic location of fertilization efforts. The influential Natural Flow Regime (NFR) concept proposes that the integrity of rivers depends on their natural dynamic character, and that restoration of natural flow characteristics is essential to improve conditions for biota in regulated systems (Poff et al. 1997). Proponents of the NFR argue that the historical focus on water quality (e.g., water temperature) and minimum flows, intended to improve conditions for biota, has been unsuccessful because of the failure to recognize the importance of other aspects of the natural flow regime, such as the frequency and magnitudes of floods or low flow periods. Although impoundment and flood plain isolation can reduce natural levels of macronutrients, restoring those levels in the absence of dam and dyke removal, requires very un-natural restoration methods. Phosphorous in inorganic fertilizer is manufactured from mined rock phosphate, and nitrogen comes from petroleum or natural gas. This material is dispensed to the receiving environment from a large storage tank using a metering device. Owing to these characteristics, nutrient fertilization would be viewed by natural system model advocates as an un-natural and engineering-based solution, even in systems where the objective is to restore nutrient concentrations to a more natural pre-impoundment or pre-dyke level. While the idea of unshackling natural river processes for restoration is intuitive and appealing to many, the challenge of accomplishing restoration goals through this approach is great.

Our classification of fertilization effects and inference level was coarse owing to the large number of studies we reviewed. Classification of a positive or negative response does not necessarily imply that the effect was large. Similarly, a high level of inference does not necessarily imply an unequivocal linkage between fertilization and the observed response, especially for fish growth and abundance responses. The Kootenai River fertilization project provides an illustrative example of these challenges. We identified six publications that documented positive lower trophic level responses, including one which was given a high inference rank. However, there was only one study of fish populations, which showed a positive growth response for largescale sucker and negative growth response for mountain whitefish (Watkins et al. 2017). Strong inferences about fertilization effects on fish populations is harder to achieve given a larger number of potential confounding effects, such as density-dependent growth and movement between control and experimental reaches. Absent from this paper was any mention of the responses of the targeted species of the fertilization effort, which include rainbow trout, bull trout, and white sturgeon. In our view these findings indicate that the response of the fish community to fertilization in the Kootenai River has been underwhelming. This general conclusion also applies to Kootenay Lake, one of the longest running nutrient fertilization studies every conducted. This study was classified as having positive effects on the growth and abundance of the prized Gerrard rainbow trout and their forage base of kokanee. This classification was based on the initial responses of these populations to fertilization, and more recently kokanee and then rainbow trout populations have collapsed (Peck et al. 2019). The cause of the collapse is uncertain but is suspected to be the result of an in-balance between top predators (rainbow trout and bull trout) and their prey (kokanee). The role that fertilization played in this collapse is uncertain, but it is concerning that there were no collapses prior to fertilization efforts. We developed a database which characterizes the 166 papers covered in our review, and we encourage interested readers to use it to quickly identify the most relevant research for their application so they can more thoroughly determine the nature of the responses and the strength of the inferences.

In spite of the extensive literature on nutrient fertilization, new efforts should still be considered experimental, and therefore evaluated using an Adaptive Management approach. While the response of lower trophic levels to fertilization were generally positive and predictable, the effects of increased prey on fish communities is less certain. The effects in simple communities that are dominated by one species, such as sockeye salmon, may be more predictable owing to the dominance of bottom-up effects. In contrast, effects in more complex communities, such as those in Kootenay Lake or the Kootenai River, are more challenging to predict owing to a greater influence of top-down effects. Thus, the effects of nutrient fertilization on the fish community in the Colorado River Ecosystem downstream of Glen Canyon Dam should be viewed as uncertain. In Glen Canyon, it is not clear whether rainbow trout or brown trout, or both species, will benefit from elevated phosphorous levels. The existing literature includes numerous cases of positive responses of rainbow trout to fertilization, but a positive effect on brown trout from a limited number of field trials has also been observed. Uncertainty in fish community response also applies to flannelmouth and bluehead suckers and humpback chub in Grand Canyon. Lower trophic level responses in Glen Canyon are also less certain owing to the extensive bryophyte and macrophyte community. However, given the unsuccessful history of GCD AMP actions to improve the status of desired fish species downstream of GCD, nutrient fertilization may warrant further consideration, especially given the possible future condition of reduced inflows and potentially lower nutrient inputs.

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# 4.0 Preliminary Calculations of Nutrient Loading Rates for Fertilization Downstream of Glen Canyon Dam

## **4.1 Assessing nutrient limitation and types of bioavailable nutrients**

Phosphorus and nitrogen are the primary limiting macronutrients in the majority of freshwater ecosystems (Wetzel, 1975). Micronutrient limitation does occur in freshwater, but is rare (e.g., molybdenum; Axler et al., 1980). In order to determine if macronutrient limitation is constraining higher trophic level production in rivers and streams, it is necessary to assess several factors including ambient nutrient concentrations, nutrient ratios, molecular form of nutrients, periphyton community composition, ecosystem metabolism, and trophic state of the lotic ecosystem. Multiple techniques are available to assess trophic state and ecosystem metabolism, and determine if macronutrient limitation is occurring, either individually, or via co-limitation:

1. Conduct bioassays to measure the periphyton biomass accrual rates over time using in-situ floating or streamside mesocosms in which limiting nutrients are applied over several weeks at known concentrations, molecular form and N:P ratios;
2. Conduct open stream gas exchange measurements of oxygen and carbon dioxide in streams to estimate gross primary production (GPP), respiration (Ra) and net primary production (NPP);
3. Measure stream primary productivity based on 14C uptake;
4. Conduct synoptic stream surveys to measure community composition and biomass of periphyton to classify trophic state (e.g., oligotrophic, eutrophic);
5. Obtain samples for low-level water chemistry analyses for soluble reactive and total dissolved phosphorus (SRP and TDP) and dissolved inorganic nitrogen (DIN = NO3-N + NO2-N + NH3-N) during the growing season to determine ambient nutrient concentrations and ratios. The minimum detection concentration required is 1 μg.L-1 forSRP; 2-3 μg.L-1 forTDP and 4-5 μg.L-1 for DIN; pr
6. A strictly qualitative assessment of the general “slippery feel” and relative abundance of periphyton on natural substrates, and density of aquatic insects beneath stones in streams during the growing season.

Technique 6 is very basic, however, during preliminary stream reconnaissance surveys it can be surprisingly informative and reliable when conducted by an experienced stream ecologist. Technique 5, i.e., low-level water chemistry analyses, will likely form the basis of most nutrient assessments owing to the relatively low cost. Techniques 1-4 require considerable investments in time and resources, and are typically conducted by university researchers or stream ecologists on behalf of natural resource management agencies.

Phosphorus is considered limiting in rivers when concentrations during the growing season are routinely at or below the detection limit of modern water chemistry laboratories (< 1 μg.L-1 SRP and <2-3μg.L-1 TDP). Lotic ecosystems are remarkably efficient at extracting phosphorus at low concentrations, and experimental studies have demonstrated that SRP concentrations as low as 0.3-0.6 μg.L-1 are sufficient to saturate specific growth rates of unicellular periphytic diatoms (Bothwell 1988). However, biomass accrual continues to increase with increasing SRP as the relationship shifts from cellular to community-controlled growth rates, albeit with diminishing effects above surprisingly low SRP concentrations (Bothwell 1989; Quamme and Slaney 2002). Ambient DIN in rivers is dominated by NO3-N, as NO2-N is ephemeral, and like ammonium, is usually present under anoxic conditions. Ammonia (NH3-N) is not as mobile as NO3-N in groundwater, and is generally at or below detection limits (i.e., 5 µg/L) in well-oxygenated river water.

Nitrogen is generally not considered limiting in rivers if the background concentration of DIN is between 30-50 µg/L and becomes limiting at < 20 µg.L-1 (Bothwell 1988). However, in some situations, DIN concentrations near the low range (~30 µg/L) can become co-limiting during enrichment experiments due to the increased biological uptake of DIN caused by addition of P. Macronutrient co-limitation can change during the growing season, due to variations in ambient N and P loading, e.g., shifting from snow melt spring runoff to ground water dominated base flows in summer. Co-limitation by N and P is a dynamic process by which surplus additions of N can drive the periphyton community to a P limited condition, and the addition of surplus P can drive the community into an N limited state (Perrin, 1993).

Phosphorous always exists in a phosphate molecule (i.e., PO4-3), as elemental phosphorus does not occur naturally on earth (Emsley 2001). The molecular form of P most rapidly assimilated by periphyton is PO4-3, and measured as SRP. The form of DIN most rapidly assimilated by periphyton is NH3-N, rather than NO3-N. When ammonium (NH4+) is present over a certain threshold concentration, it either inhibits NO3− uptake or is preferred over NO3− (Dortch 1990; Glass et al. 2012). In rare situations where Mo is limiting, nitrogen assimilation can be constrained as Mo is present in nitrogenase, the enzyme that performs N2 fixation, and in nitrate reductase, the enzyme that performs the first step in nitrate (NO3−) assimilation, reduction of NO3− to nitrite (NO2−) (Glass et al., 2012). Organic forms of N are ubiquitous in fresh-waters; however, the majority of components are refractory (e.g., tannins, lignins, and humates), and require a slow microbial reduction before their N components can be utilized. Urea is the exception, and is an excellent nutrient source readily assimilated after hydrolytic reduction by phytoplankters and bacteria (Antia et al. 1975).

## **4.2 Patterns in Discharge and Macronutrient concentrations in water released from Glen Canyon Dam and at Lees Ferry**

Our analysis of nutrient chemistry data in the Colorado River at or below Glen Canyon Dam is restricted to calendar years 2017-2020 due to higher detection limits and less frequent sampling in earlier years. The phosphorus concentration detection limit decreased from 5 µg/L to 1 µg/L beginning in 2000, and the regularity of the sampling improved starting in 2017, as did the phosphorus fractionation analysis (i.e., TDP was added to TP and SRP). Monthly nutrient sampling from GCD draft tubes and at Lees Ferry was conducted over the 2017-2020 study period.

Although our analysis is limited to only four years, conditions which likely have an important influence on nutrient concentrations were typical of those over the last two decades, as influenced by the 21st century drought (see section 1.0). The average inflow to Lake Powell in water years 2017-2020 was very similar to the average since 2000, which is considerably lower than the average from 1980-2020 (Fig. 1, top-left panel). A similar pattern was observed for the average flow released from GCD during the growing season, which we define as March 1 – August 30 (Fig.1, bottom-left panel). Water surface elevations during the growing season in Lake Powell since 2002 have been substantively lower than the 1980-2020 average, and the elevation over our four study years was even lower than the 2000-2020 average (Fig. 1, top-right panel).

***Analysis of water chemistry data from Glen Canyon Dam Draft Tubes***

Nutrient measurements at the GCD draft tube and at Lees Ferry indicate DIN was not limiting periphyton growth in Glen Canyon between 2017 and 2020 (Figure 2, top). Nitrate concentrations rarely declined below 200 µg/L during the March 1 to Aug 31 growing season, and N limitation occurs in rivers when NO3-N is < 20 µg/L. Thus, there is no requirement to add nitrate-nitrogen should a future whole-river nutrient enrichment experiment be considered. However, 10-34-0 (N-P2O5-K2O) liquid fertilizer that would be used contains 10% N by weight, which amounts to a 2:3 N:P loading rate. Fertilizers without nitrogen are considerably more expensive.

Concentrations of soluble reactive phosphorus (SRP) indicate that Glen Canyon was occasionally SRP limited between 2017 and 2020 (i.e., < 1 ug/L, Fig. 2, bottom). Over the four-year study period, approximately 20% of SRP concentrations (19.5% at GCD, 21% at Lees Ferry) were at or below 1 ug/L with almost all of these observations occurring during the March-August growing season. Average SRP concentration during the growing season was lowest in 2018, with 36% of the 11 observations from the draft tubes at or below 1 ug/l. Thus, of the four study years (2017-2020), P-limitation was greatest in the year that coincided with the lowest inflow to Lake Powell (Fig. 1). However, inflows are clearly not the only driver of SRP concentrations from GCD, given similar inflows and lake elevations in 2020.

***Estimate of volumes and costs to fertilize the Colorado River below Glen Canyon Dam***

For exploratory purposes, the annual volume and cost of liquid inorganic fertilizer required to fertilize the Colorado River at one site below GCD was calculated for the 2017-2020 study period (Table 4.1). We assumed an in-river target Total Dissolved Phosphorous (TDP) of 3 µg/L between March 1 and August 31. We used the dilution discharge formula described by Ward et al. (2018) to calculate the 10-34-0 liquid fertilizer volume needed to achieve this target given the average monthly discharge for each of the six months of the growing period in each of the four study years. Liquid fertilizer would be released 24 hours per hours/day at a flow volume to fertilizer volume ratio of 70.3 million:1. This ratio is very large because the P concentration in the liquid fertilizer is very high relative to the target in-river concentration. Although there is no need to add nitrogen given high background rates, the N:P concentration in the fertilizer is 2:3, so some N loading will occur. On average, 21,060 US gallons would be discharged in each year over a six-month growing period (March – September), which is equivalent to a dosing rate of 114 US gallons/day (443 litres/day). This dosing rate is at the low end of the dosing rate applied in the Kootenai River in Montana downstream of Libby Dam (~80-400 US gallons/day)

The annual cost for fertilizer for the GCD application averaged ~$65,000 across the four study years (Table 4.1). Annual estimates were calculated as the product of the annual mass of liquid fertilizer that would be discharged and a unit cost of $570 per metric ton . Given similar flows from GCD among study years, the fertilizer volumes and costs were similar. Therefore, from a fertilizer-only cost perspective, a whole-river fertilization experiment is feasible. There would be a one-time setup cost for the tank and metering equipment to dispense the fertilizer. Dispensing the fertilizer from the base of Glen Canyon Dam would be the simplest and most cost-effective location. However, from a scientific perspective it would be better to have the release point further downstream so that the section of river upstream of the release point could act as a control site to better evaluate trophic responses to fertilizer addition. This option would likely require a large storage tank at Lees Ferry, and weekly trips with a jet boat to fill a smaller storage tank located at the release site.

## **4.3 Conclusions and Recommendations**

The available water chemistry data collected from the GCD draft tubes and Lees Ferry indicate that Glen Canyon is not nitrogen limited, but is occasionally phosphorus limited. Little more can be concluded from the available data. The potential for P-limitation in the Colorado River Ecosystem is supported positive correlations between SRP, invertebrate drift density and fish growth in Glen (Korman et al. 2021) and Grand Canyons (C. Yackulic, M. Yard, and B. Deemer, USGS, Flagstaff, AZ, unpublished data).

A stream side or in-situ mesocosm study (Bothwell 1988, Quamme and Slaney 2002 Hoyle 2003) in Glen Canyon could be used evaluate biotic responses of Colorado River periphyton and invertebrate communities to controlled additions of 10-34-0 liquid inorganic fertilizer at various target concentrations (e.g., 1.5, 3 and 5 µg/L of phosphorus). The results from these mesocosm studies, and from the enhanced whole-river monitoring program, would inform the regulatory agencies as to whether a whole-river fertilization experiment below CGD would be worth further consideration. The required steps and procedures for a whole-river enrichment are outlined in detail in Ashley and Stocker (2003). Wilson et al. (2003) provides a nice example of a well-designed multi-year BACI-type whole-river enrichment experiment.

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**Table 1.** Number of nutrient fertilization studies (N) by province (Canada), state (US), or country.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Country or Continent** | **Location** | **N** |  | **Country or Continent** | **Location** | **N** |
|  |  |  |  |  |  |  |
| Canada | British Columbia | 43 |  | Europe | Sweden | 10 |
|  | Saskatchewan | 3 |  |  | Spain | 5 |
|  | Ontario | 2 |  |  | Finland | 3 |
|  | Quebec | 1 |  |  | Germany | 3 |
|  | Total | 49 |  |  | Netherlands | 3 |
|  |  |  |  |  | UK | 3 |
| United States | Alaska | 41 |  |  | Poland | 2 |
|  | Idaho | 20 |  |  | Norway | 1 |
|  | North Carolina | 7 |  |  | Scotland | 1 |
|  | California | 5 |  |  | Total | 30 |
|  | Michigan | 4 |  |  |  |  |
|  | Montana | 4 |  | Africa | Tanzania | 1 |
|  | Wisconsin | 3 |  |  | Zambia | 1 |
|  | Oregon | 2 |  |  | Total | 2 |
|  | Arizona | 1 |  |  |  |  |
|  | Colorado | 1 |  | South | Brazil | 1 |
|  | Florida | 1 |  | America | Venezuela | 1 |
|  | Kentucky | 1 |  |  | Total | 2 |
|  | Massachusetts | 1 |  |  |  |  |
|  | Minnesota | 1 |  | Other | China | 1 |
|  | Nevada | 1 |  |  | New Zealand | 1 |
|  | Utah | 1 |  |  | Total | 2 |
|  | Washington | 1 |  |  |  |  |
|  | Total | 95 |  | Grand Total |  | 181 |

**Table 2.** Number (N) and percentage (%) of nutrient fertilization studies by trophic level (a) and for combinations of trophic levels evaluated in the same study (b). Note that more than one trophic level could be evaluated in a study, thus the N in a) represents the number of times a taxa was studied, while N in b) represents the number of studies.

a)

|  |  |  |
| --- | --- | --- |
| **Trophic Level** | **N** | **%** |
|  |  |  |
| Nutrients (N) | 73 | 44% |
| Bacteria (B) | 9 | 5% |
| Phytoplankton/Periphyton (P) | 122 | 74% |
| Macrophytes (M) | 9 | 5% |
| Bryophytes (Br) | 2 | 1% |
| Benthic Invertebrates/Zooplankton (Z) | 97 | 59% |
| Fish (F) | 89 | 54% |
| Amphibians (A) | 1 | 1% |

b)

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Trophic Level** | **N** | **%** |  | **Trophic Level** | **N** | **%** |
|  |  |  |  |  |  |  |
| N P Z F | 35 | 21% |  | M P Z | 1 | 1% |
| P | 24 | 15% |  | M Z F | 1 | 1% |
| F | 19 | 12% |  | N B P | 1 | 1% |
| P Z F | 17 | 10% |  | N B Z | 1 | 1% |
| N P | 13 | 8% |  | N M | 1 | 1% |
| P Z | 7 | 4% |  | N P B | 1 | 1% |
| Z | 7 | 4% |  | N P M | 1 | 1% |
| Z F | 6 | 4% |  | N P R Z F | 1 | 1% |
| N P Z | 5 | 3% |  | N P Z F A | 1 | 1% |
| N P F | 4 | 2% |  | P F | 1 | 1% |
| N | 3 | 2% |  | P M | 1 | 1% |
| N Z | 3 | 2% |  | P N | 1 | 1% |
| B P Z | 2 | 1% |  | P R Z F | 1 | 1% |
| N P B Z F | 2 | 1% |  | P Z M | 1 | 1% |
| Z M | 2 | 1% |  | P Z Z F | 1 | 1% |
| B P M Z | 1 | 1% |  |  |  |  |
| B Z | 1 | 1% |  | Total | 166 | 100% |

**Table 3.** Number of nutrient fertilization studies (N) that evaluated the fish trophic level by species and type of response. Note in some cases both growth and abundance were assessed in a single study

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **N** | **Growth** | **Abundance** |
|  |  |  |  |
| sockeye | 25 | 16 | 18 |
| rainbow trout | 20 | 15 | 16 |
| kokanee | 16 | 12 | 12 |
| coho | 12 | 4 | 12 |
| steelhead/rainbow trout | 9 | 4 | 8 |
| cutthroat trout | 8 | 5 | 6 |
| arctic grayling | 6 | 1 | 6 |
| stickleback | 6 | 4 | 4 |
| mountain whitefish | 5 | 4 | 5 |
| bull trout | 3 | 2 | 3 |
| sculpin | 3 | 1 | 3 |
| brown trout | 3 | 2 | 3 |
| chinook | 2 | 1 | 1 |
| dolly varden | 2 | 0 | 2 |
| largescale sucker | 2 | 1 | 2 |
| salmonid | 2 | 2 | 1 |
| arctic char | 1 | 0 | 1 |
| atlantic salmon | 1 | 1 | 1 |
| brook trout | 1 | 1 | 1 |
| lake trout | 1 | 0 | 1 |
| mosquito fish | 1 | 0 | 1 |
| mummichog | 1 | 1 | 1 |
| peamouth chub | 1 | 1 | 1 |
| pikeminnow | 1 | 1 | 1 |
| striped bass | 1 | 1 | 0 |
| silver carp | 1 | 0 | 1 |
| sucker | 1 | 1 | 1 |
| threadfin shad | 1 | 1 | 0 |
|  |  |  |  |
| Total | 136 | 82 | 112 |
| Total for salmonids | 117 | 70 | 97 |

**Table 4.** Number (a) and percentage (b) of studies that showed a negative, neutral, or positive response to nutrient fertilization by trophic level.

a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Trophic Level** | **Negative** | **Neutral** | **Positive** | **Total** |
|  |  |  |  |  |
| Nutrient (N) | 6 | 17 | 58 | 81 |
| Bacteria (B) | 1 | 4 | 7 | 12 |
| Phytoplankton/Periphyton (P) | 15 | 22 | 101 | 138 |
| Macrophytes (M) | 4 | 1 | 7 | 12 |
| Bryophytes (Br) | 0 | 0 | 2 | 2 |
| Benthic Invertebrates/Zooplankton (Z) | 13 | 33 | 77 | 123 |
| Fish (F) | 10 | 40 | 107 | 157 |
| Amphibians (A) | 1 | 0 | 0 | 1 |
|  |  |  |  |  |
| Total | 50 | 117 | 359 | 445 |

b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Trophic Level** | **Negative** | **Neutral** | **Positive** | **Total** |
|  |  |  |  |  |
| Nutrient (N) | 7% | 21% | 72% | 100% |
| Bacteria (B) | 8% | 33% | 58% | 100% |
| Phytoplankton/Periphyton (P) | 11% | 16% | 73% | 100% |
| Macrophytes (M) | 33% | 8% | 58% | 100% |
| Bryophytes (Br) | 0% | 0% | 100% | 100% |
| Benthic Invertebrates/Zooplankton (Z) | 11% | 27% | 62% | 100% |
| Fish (F) | 6% | 25% | 68% | 100% |
| Amphibians (A) | 100% | 0% | 0% | 100% |
|  |  |  |  |  |
| Total | 11% | 26% | 81% | 100% |

**Table 5.** Number (a) and percentage (b) of studies that measured fish growth or abundance and showed a negative, neutral, or positive response to nutrient fertilization by trophic level.

a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Type** | **Negative** | **Neutral** | **Positive** | **Total** |
|  |  |  |  |  |
| Growth | 3 | 22 | 63 | 88 |
| Abundance | 7 | 18 | 44 | 69 |
|  |  |  |  |  |
| Total | 10 | 40 | 107 | 157 |

b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Type** | **Negative** | **Neutral** | **Positive** | **Total** |
|  |  |  |  |  |
| Growth | 3% | 25% | 72% | 100% |
| Abundance | 10% | 26% | 64% | 100% |

**Table 6.** Number of studies that showed an unwanted effect by trophic level and habitat type.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Trophic Level** | **Stream** | **Lake** | **Mesocosm** | **Total** |
|  |  |  |  |  |
| Phytoplankton/Periphyton (P) | 2 | 6 | 5 | 13 |
| Fish (F) | 0 | 3 | 1 | 4 |
| Bacteria (B) | 0 | 1 | 1 | 2 |
| Macrophytes (M) | 0 | 0 | 1 | 1 |
| Benthic Invertebrates/Zooplankton (Z) | 1 | 1 | 1 | 3 |
| Bryophytes (Br) | 1 | 0 | 0 | 1 |
|  |  |  |  |  |
| Total | 4 | 11 | 9 | 24 |

**Table 7.** Number of nutrient fertilization studies by source (primary or grey literature) and year of publication.

|  |  |  |  |
| --- | --- | --- | --- |
| **5 Year Block** | **Primary** | **Grey** | **Total** |
|  |  |  |  |
| 1975-79 | 2 | 0 | 2 |
| 1980-84 | 0 | 1 | 1 |
| 1985-89 | 3 | 3 | 6 |
| 1990-94 | 9 | 3 | 12 |
| 1995-99 | 8 | 1 | 9 |
| 2000-04 | 29 | 4 | 33 |
| 2005-09 | 30 | 7 | 37 |
| 2010-14 | 23 | 3 | 26 |
| 2015-19 | 32 | 4 | 36 |
| 2020 | 3 | 1 | 4 |
|  |  |  |  |
| Total | 139 | 27 | 166 |

**Table 8.** Number and percentage of nutrient fertilization studies by duration of study (a) and statistical design (b).

a)

|  |  |  |
| --- | --- | --- |
| **Study Duration** | **N** | **%** |
|  |  |  |
| <1 month | 7 | 4% |
| 1-3 months | 24 | 15% |
| 4-12 months | 6 | 4% |
| 1-4 years | 70 | 42% |
| 5-10 years | 37 | 22% |
| 11-20 years | 13 | 8% |
| 20+ years | 6 | 4% |
| NA | 3 | 2% |
|  |  |  |
| Total | 166 | 100% |

b)

|  |  |  |
| --- | --- | --- |
| **Design** | **N** | **%** |
|  |  |  |
| BACI | 57 | 34% |
| CI | 54 | 33% |
| BA | 48 | 29% |
| NA | 7 | 4% |
|  |  |  |
| Total | 166 | 100% |

**Table 9.** Number (a) and percentage (b) of nutrient fertilization studies categorized by overall inference rank by trophic level.

a)

|  |  |  |  |
| --- | --- | --- | --- |
| **Trophic Level** | **Low** | **Moderate** | **High** |
|  |  |  |  |
| Nutrients (N) | 13 | 40 | 20 |
| Bacteria (B) | 0 | 6 | 3 |
| Phytoplankton/Periphyton (P) | 22 | 67 | 33 |
| Macrophytes (M) | 2 | 5 | 2 |
| Bryophytes (Br) | 0 | 0 | 2 |
| Benthic Invertebrates/Zooplankton (Z) | 14 | 51 | 30 |
| Fish (F) | 12 | 54 | 23 |
| Amphibians (A) | 0 | 1 | 0 |
|  |  |  |  |
| Total | 63 | 224 | 113 |

b)

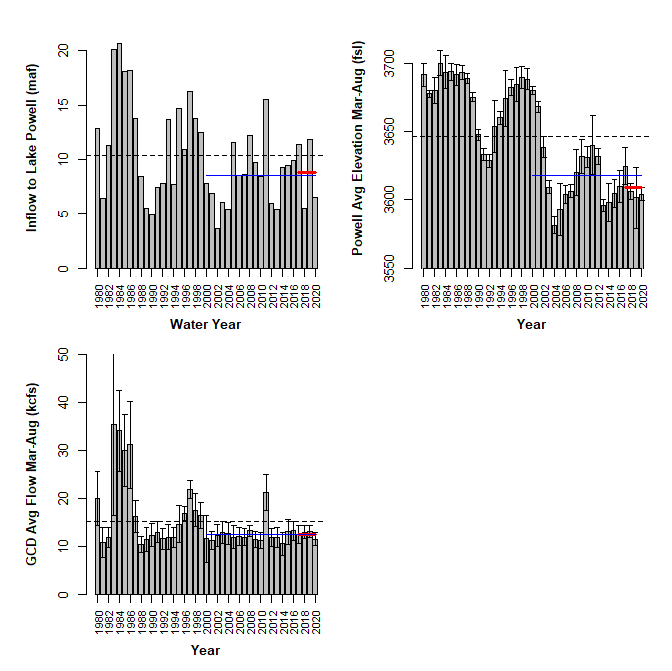
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Trophic Level** | **Low** | **Moderate** | **High** | **Total** |
|  |  |  |  |  |
| Nutrients (N) | 18% | 55% | 27% | 100% |
| Bacteria (B) | 0% | 67% | 33% | 100% |
| Phytoplankton/Periphyton (P) | 18% | 55% | 27% | 100% |
| Macrophytes (M) | 22% | 56% | 22% | 100% |
| Bryophytes (Br) | 0% | 0% | 100% | 100% |
| Benthic Invertebrates/Zooplankton (Z) | 15% | 54% | 32% | 100% |
| Fish (F) | 13% | 61% | 26% | 100% |
| Amphibians (A) | 0% | 100% | 0% | 100% |

**Table 10.** Overall rank inference level by taxa-specific response direction to increased nutrient levels.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Trophic Level** | **Effect** | **Low** | **Moderate** | **High** | **Total** |
|  |  |  |  |  |  |
| Nutrients (N) | Negative | 0% | 50% | 50% | 6 |
|  | Positive | 19% | 55% | 26% | 58 |
|  |  |  |  |  |  |
| Phytoplankton/Periphyton (P) | Negative | 13% | 67% | 20% | 15 |
|  | Positive | 17% | 54% | 29% | 100 |
|  |  |  |  |  |  |
| Benthic Invertebrates/Zooplankton (Z) | Negative | 0% | 46% | 54% | 13 |
|  | Positive | 9% | 55% | 36% | 76 |
|  |  |  |  |  |  |
| Fish Growth | Negative | 0% | 67% | 33% | 3 |
|  | Positive | 13% | 57% | 30% | 63 |
|  |  |  |  |  |  |
| Fish Abundance | Negative | 14% | 29% | 57% | 7 |
|  | Positive | 2% | 50% | 48% | 44 |
|  |  |  |  |  |  |
| Bacteria (B) | Negative | 0% | 0% | 100% | 1 |
|  | Positive | 0% | 71% | 29% | 7 |
|  |  |  |  |  |  |
| Bryophytes (Br) | Negative | 0% | 0% | 0% | 0 |
|  | Positive | 0% | 0% | 100% | 2 |
|  |  |  |  |  |  |
| Macrophytes (M) | Negative | 0% | 75% | 25% | 4 |
|  | Positive | 29% | 43% | 29% | 7 |
|  |  |  |  |  |  |
| Amphibians (A) | Negative | 0% | 100% | 0% | 1 |
|  | Positive | 0% | 0% | 0% | 0 |

**Table 4.1.** Annual volume (US gallons) and cost (US dollars) of 10-34-0 liquid fertilizer to attain a 3 ug/l target Total Dissolved Phosphorous concentration in the Colorado River downstream of Glen Canyon Dam (after full mixing with river water) for the March – August growing season.

|  |  |  |
| --- | --- | --- |
| **Year** | **Volume** | **Cost** |
|  |  |  |
| 2017 | 20,846 | $63,871 |
| 2018 | 21,926 | $67,181 |
| 2019 | 22,035 | $67,514 |
| 2020 | 19,432 | $59,539 |
|  |  |  |
| Average | 21,060 | $64,526 |



**Figure 1.** Annual inflow to Lake Powell (millions of acre-feet, top-left), mean discharge from Glen Canyon Dam (GCD) from March 1 – August 30 (thousands of cubic feet per second, bottom-left), and average water surface elevation of Lake Powell from March 1 – August 30 (feet above sea level, bottom-right). Error bars show the extent of seasonal variation in flow or elevation over the March-August as represented by the standard deviation in mean monthly values. Black-dashed, solid blue, and solid thick red lines represent the averages between 1980-2000, 2000-2020, and 2017-2020, respectively.



**Figure 2.** Nitrate + Nitrite (top) and soluble reactive phosphorous (bottom, SRP) concentrations measured at the Glen Canyon Dam draft tubes and Lees Ferry, 2017-2020 (points). The dashed horizontal line represents the concentration that limits periphyton growth. The black and red horizontal solid lines show the average concentrations over the March 1 – August 31 growing season. The SRP concentration at Lees Ferry on May 22, 2017 was 14 ug/L and is not shown in the bottom panel because the y-axis maximum was set at 10 ug/L to better see variation in concentrations over time and among locations.

# Appendix A: Citations for 166 papers used for analysis

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