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REVIEW ARTICLE

Effectiveness of nutrient enhancement as a remediation or compensation strategy of salmonid fisheries in culturally oligotrophic lakes and streams in temperate climates

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Productivity of temperate streams and lakes is often limited by availability of key nutrients, and nutrient-poor habitats are termed oligotrophic. Oligotrophic streams and lakes occur naturally, but often are a product of human activities (cultural oligotrophication), such as the creation of dams. Cultural oligotrophication has resulted in declining productivity in streams and lakes, a condition that can manifest itself in collapsing salmonid fish stocks. To counteract lost productivity as part of restoration or compensation measures, managers often add nutrient via fertilizers to enhance fisheries production. However, these programs are not always successful, and this article reviews available literature to identify patterns that may influence success of nutrient enhancement programs. Overall fertilization of lakes and streams will almost certainly increase primary producer and invertebrate populations. While it is likely that fertilization will also increase fishery production, it is far from certain. The magnitude of this change is unpredictable, and the success of a fertilization program will vary greatly between years, habitat, and microhabitats. Regardless, if fertilization is coupled with holistic monitoring of the food web and ecosystem, then it is likely to be an effective technique to enhance fishery productivity in active restoration of compensation programs. However, the benefits of fertilization will not outlast the fertilization project, and care must be exercised when ceasing active fertilization. When compared to other restoration/compensation strategies such as fish ladders or trap and transport, fertilization may be a cost-effective method to enhance fishery production. Finally, recommendations are discussed to increase the probability of fertilization success.

Key words: compensation, cultural oligotrophy, fertilization, fisheries, remediation

Implications for Practice

- Fertilization of lakes and streams will almost certainly increase primary producer and invertebrate populations.
- Fertilization will likely increase salmonid fishery production, at a cost of $250 CDN per kg of enhanced smolt production. Magnitude of change is unpredictable.
- Benefits of fertilization will not outlast the fertilization project, care must be exercised when ceasing fertilization.
- Monitored variables should include: (1) nutrient availability, (2) abundance and community composition of primary producers, (3) abundance and community composition of zooplankton and invertebrates, and (4) fish fecundity, size, biomass, abundance, and community composition. Hydrology, temperature, clarity, and reservoir operations must be considered to avoid adding nutrients during high-flow periods.
- Managers should adaptively monitor and adjust N:P ratios as well as nitrate levels.

Introduction

Productivity of temperate streams and lakes is often limited by the availability of key nutrients such as nitrogen (N) and phosphorus (P), and these nutrient-poor habitats are termed oligotrophic. In the absence of these key nutrients biota cannot thrive, and the entire food web is limited, from primary producers (diatoms, algae, and phytoplankton) to invertebrate and fish consumers (Slaney & Ashley 1998; Pieters et al. 2003; Hyatt et al. 2004). Oligotrophic streams and lakes occur naturally in temperate climates, but low-nutrient conditions are created or exacerbated by human activities, such as the creation of

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dams, that often decrease nutrient availability downstream of the impoundment (Pieters et al. 2003; Stockner & Ashley 2003; Stockner & Slaney 2006; Minshall et al. 2014). Oligotrophic conditions as a result of human activities are referred to as cultural oligotrophication (Stockner et al. 2000), and cultural oligotrophication, often associated with dams, has resulted in declining productivity in temperate streams and lakes (Stockner et al. 2000; Stockner & Ashley 2003; Stockner & Slaney 2006). This condition often manifests as collapsing fish stocks (Stockner et al. 2000; Pieters et al. 2003; Stockner & Ashley 2003).

In an effort to increase productivity of lakes and streams as part of restoration or compensation programs, managers often add nutrients or fertilizer (Slaney & Ashley 1998; Slavik et al. 2004; Pellett 2011). Essentially, fertilizer is added to increase availability of limiting nutrients—nitrogen (N) and phosphorus (P)—that are taken up by primary producers (diatoms, algae, and phytoplankton) resulting in an increase in primary productivity (Fig. 1). Invertebrates (benthic invertebrates and zooplankton) consume primary producers, therefore increasing invertebrate abundances and/or biomass. Fish predate upon these invertebrates, and an increase in prey items translates to increased fishery production (population abundance, biomass, and fecundity). Increased fishery production results in more nutrients being added to the ecosystem by decomposing fish, potentially inducing a self-sustaining cycle of elevated productivity in once oligotrophic systems (Stockner & Ashley 2003; Wipfli et al. 2003; Janetski et al. 2009).

As discussed above, managers often engage in fertilization programs in response to cultural oligotrophication in order to compensate for decreased fishery production and ecosystem services, or as part of restoration programs to restore historic fish populations (Slaney & Ashley 1998; Slavik et al. 2004; Pellett 2011). More specifically, the goal of such programs is usually to enhance salmonid species that support recreational or commercial fisheries. However, these programs are not always successful, nor are they inexpensive (Slaney & Ashley 1998; Pieters et al. 2003; Hyatt et al. 2004). Therefore, this article reviews the available literature in an attempt to identify patterns that may influence success of nutrient enhancement programs. Below, we explore each of the steps described in Figure 1 in more detail (Table 1 further summarizes the available literature), and then describe the potential of fertilization to successfully increase fishery productivity in oligotrophic streams and lakes.

Nutrient Availability

Fertilization of streams and rivers has taken many forms, ranging from pouring liquid nutrients into water to using slow-release fertilizer discs and salmon carcasses (Slaney & Ashley 1998; Slavik et al. 2004; Janetski et al. 2009; Schindler et al. 2011; Minshall et al. 2014). Type of fertilizer also varies greatly (see Table 1), but the most common forms are urea ammonium nitrate for N and ammonium polyphosphate for P (Schindler et al. 2009*a*, 2009*b*; Decker 2010). While the concentration of fertilizer required varies based upon habitat type (lake or river, size, flow rate, temperature, clarity, etc.), ambient nutrient concentrations, and target species (Slaney 1988; Slaney & Ashley 1998; Hyatt et al. 2004; Stockner & Slaney 2006), altering fertilizer concentrations seasonally to mimic natural cycles has been used in successful fertilization programs. For instance, in the Arrow Lakes Reservoir of British Columbia (BC), Canada, quantities and mixtures of fertilizer varied seasonally, resulting in observed increases of all components of the food web (Pieters et al. 2003; Schindler et al. 2006, 2011).

Repeated monitoring of nutrient availability in fertilized streams and lakes is required not only to adaptively alter fertilizer concentrations seasonally, but also to identify potentially dangerous accumulations of fertilizer (Pieters et al. 2003; Schindler et al. 2009*b*; Hoyle et al. 2014). While monitoring is crucial, in some cases fertilization may result in no observed change or even decreases in nutrient availability (Hansen 2003; Ericksen et al. 2009; Hoyle et al. 2014). This may be a result of high flows flushing fertilizer from the system (Hansen 2003) and/or nutrients being consumed quickly by biota (Hoyle et al. 2014). Monitoring of local hydrology as well as the food web will help differentiate between these situations; however, fertilization should generally be timed to avoid periods of high flows (Hansen 2003).

Primary Producers

Increased abundances and biomass of primary producers (algae, diatoms, phytoplankton, periphyton, etc.) is commonly observed following fertilization of streams and lakes (Johnston et al. 1990; Slaney & Ashley 1998; Hyatt et al. 2004; Harris et al. 2007; Janetski et al. 2009; Pellett 2011). Only in a minority of situations has fertilization been observed to have no influence on primary producers (Schindler et al. 2007; Janetski et al. 2009), and this may be a result of invertebrate consumption of primary producers masking elevated primary productivity (Peterson et al. 1993).

Beyond abundance and biomass, fertilization can alter primary producer community composition (Pringle & Bowers 1984; Slavik et al. 2004), and in some situations this results in decreasing abundances of inedible diatoms, increasing availability of edible primary producers as prey for invertebrates (Hoyle et al. 2014). However, fertilization can also stimulate the growth of inedible blue green algae that form dense mats blocking sunlight and consuming oxygen, often directly resulting in mortality of fish and invertebrates (Hyatt et al. 2004). Blue green algae can also produce cyanotoxins that can kill fish and terrestrial invertebrates, including humans, through contact or ingestion (McQueen & Lean 1987; Wiegand & Pflugmacher 2005). Fertilizers with elevated rates of N (high N to P ratios) have been used to control blue green algae (McQueen & Lean 1987; Hyatt et al. 2004); unfortunately, fertilizers with high N to P ratios have also been associated with blooms of ungrazable diatoms such as *Rhizosolenia eriensis*. In these situations, fertilizers with reduced nitrate concentrations are recommended (Hyatt et al. 2004). As such, in-depth monitoring of primary producer communities is required to identify negative changes

Table 1. Summary of fertilization literature.

Location	*Aquatic Habitat*	*Fertilizer*	*Response Variable*	*Impact*	*Citation*
Japan, Alaska, Pacific Canada, and United States	Streams and rivers	Salmon carcasses	Nutrient availability	Increased	Janetski et al. (2009)
			Primary producers	Abundances increased or decreased	
			Invertebrates	Populations increased or decreased	
Alaska, British Columbia, Canada, and Idaho, United States	Lake	Various	Primary producers	Increased abundance	Hyatt et al. (2004)
			Invertebrates	Increased biomass	
			Sockeye Salmon	Increased average smolt weights, biomass, and survival	
British Columbia, Canada	Rivers	Various	Primary producers	Increased abundance	Slaney and Ashley (1998)
			Invertebrates	Increased abundance and biomass	
			Steelhead Trout	Increased biomass and no change, increased smolt numbers and biomass, but minor impact upon smolt length	
			Coho Salmon	Increased biomass, no impact upon length	
			Rainbow Trout	Increased abundances, and no change, increased biomass	
			Cutthroat Trout	No change	
			Mountain Whitefish	Increased abundance	
			Bull Trout	Increased abundance	
			Arctic Graylings	Increased abundance	
Keogh River, British Columbia, Canada	River	Nitrogen (30–100 μg/L)	Nutrient availability	Increased	Johnston et al. (1990)
		Phosphorus (10–15 μg/L)	Primary producers	Increased abundance	
			Steelhead Trout	Increased biomass	
			Coho Salmon	Increased biomass	
Salmon River Watershed, British Columbia, Canada	Streams and rivers	Nitrogen (various)	Nutrient availability	Increased and no change	Pellett (2011)
		Phosphorus (various)	Primary producers	Increased abundance	
			Steelhead Trout	Increased abundance, accelerated growth	
			Coho Salmon	Increased abundance, accelerated growth	

Table 1. continued

Location	Aquatic Habitat	Fertilizer	Response Variable	Impact	Citation
Sheep Creek, British Columbia, Canada	Stream	Urea ammonium nitrate (100 μg/L)	Invertebrates	Increased abundance	Decker (2010); Decker and Nellestijn (2015)
		Ammonium polyphosphate (10 μg/L)	Bull Trout	Increased length and biomass	
Kootenay Lake, British Columbia, Canada	Lake	Urea ammonium nitrate (various), and ammonium nitrate (10 μg/L)	Nutrient availability	Increased and no change	Perrin and Johnston (1987); Ericksen et al. (2009); Schindler et al. (2009*a*, 2009*b*)
		Ammonium polyphosphate (various) and phosphoric acid (1.5 μg/L)	Primary producers	Increased abundance	
			Invertebrates	Increases and no change to abundance and biomass	
			Kokanee Salmon	Increased abundance, biomass, and length. No change to abundances in some tributaries.	
Kootenai River, Canada, United States	River	Ammonium polyphosphate (3 μg/L)	Nutrient availability	Increases and no change	Ericksen et al. (2009); Hoyle et al. (2014); Minshall et al. (2014)
			Primary producers	Increased abundance	
			Invertebrates	Abundance and biomass increased. Community composition changed	
Arrow Lakes Reservoir, British Columbia, Canada	Reservoir/lake	Ammonium polyphosphate (various)	Nutrient availability	Adaptively altered but increased concentrations and no changes	Pieters et al. (2003); Thorp et al. (2003); Sebastian et al. (2004); Andrusak (2006); Schindler et al. (2006); Schindler et al. (2007); Ericksen et al. (2009); Schindler et al. (2009*a*, 2009*b*); Schindler et al. (2011)
		Urea ammonium nitrate (various)	Primary producers	Increased, decreased, and no change to abundances	
			Invertebrates	Increased and decreased density and biomass	
			Kokanee Salmon	Growth rate increased initially but then decreased. Abundances increased and plateaued, some decreases observed. Number and size of spawners showed increases and decreases. Average biomass increased (3×) and decreased. Fecundity increased slightly.	

Table 1. continued

Location	*Aquatic Habitat*	*Fertilizer*	*Response Variable*	*Impact*	*Citation*
Ash River, British Columbia, Canada	River	Nitrogen (3 μg/L)	Nutrient availability	Small increases or no change	Hansen (2003)
		Phosphorus (2.5 μg/L)	Steelhead Trout	No change	
Wahleach Reservoir, British Columbia, Canada	Reservoir/lake	Ammonium polyphosphate ($200\ \mathrm{mg\cdot m^2}$)	Nutrient availability	Increased	Harris et al. (2007)
		Urea ammonium nitrate ($200\ \mathrm{mg\cdot m^2}$)	Primary producers	Increased abundance and biomass	
			Invertebrates	Increased abundance and biomass	
			Kokanee Salmon	Increased spawner numbers, but decreased abundances	
Mesilinka River, British Columbia, Canada	River	Does not specify	Primary producers	Increased abundances	Blackman (2000)
			Rainbow Trout	Increased abundances and biomass	
			Mountain Whitefish	Increased abundances	
Cedar Creek, Alaska, United States	Stream	Salmon carcasses	Invertebrates	Increased abundance	Wipfli et al. (2003)
			Coho Salmon	Increased biomass and length	
			Cutthroat Trout	Increased growth rate and biomass	
			Dolly Varden	Increased growth rate and biomass	
Kuparuk River, Alaska, United States	River	Phosphoric acid (10 μg/L)	Primary producers	Biomass and productivity increased, community composition changed or stayed the same, abundances increased and did not change	Peterson et al. (1993); Rublee and Partusch-Talley (1995); Slavik et al. (2004)
		Ammonium sulfate (100 μg/L)	Invertebrates	Growth rates increased but abundances and productivity increased and decreased. Community composition varied	
			Arctic Graylings	Increased growth rates	
Central Idaho, United States	Streams	Pasteurized salmon carcass analogue	Primary producers	Increased abundance	Kohler and Taki (2010)
			Invertebrates	Increased abundance	
Central Idaho, United States	Streams	Pasteurized salmon carcass analogue	Primary producers	Increased abundance	Kohler et al. (2008)
			Invertebrates	Increased abundance	
RedFish Lake, Idaho, United States	Lake	Ammonium nitrate (150 μg/L) Ammonium phosphate (5 μg/L)	Sockeye Salmon	Increased abundance	Luecke et al. (1996)
Carp Creek, Michigan, United States	Stream	Various	Primary producers	Increased abundance and changed community composition	Pringle and Bowers (1984)
La Choza Stream, Argentina	Stream	Nitrofoska (12% nitrogen, 12% phosphorus, 17% potassium)	Invertebrates	Increased abundance and biomass, increased diversity, and changed community composition	Armendáriz et al. (2012)

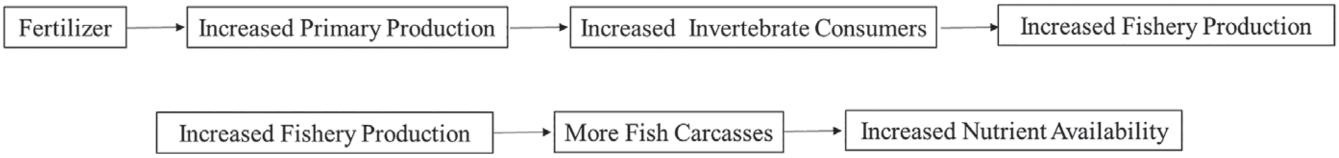

Figure 1. Conceptual model of how adding fertilizer to a stream or lake would result in increased fishery productivity and nutrient availability.

in community composition early enough to allow for correction via alteration of fertilizer composition or component ratios.

Zooplankton and Benthic Invertebrates

As with primary producers, increases of invertebrate abundances and biomass are commonly observed following fertilization (Slaney & Ashley 1998; Hyatt et al. 2004; Schindler et al. 2006; Janetski et al. 2009; Decker 2010; Kohler & Taki 2010; Minshall et al. 2014; Decker & Nellestijn 2015). In some situations fertilization had no effect upon invertebrates, or even led to decreased abundances (Slavik et al. 2004; Schindler et al. 2007; Janetski et al. 2009); however, these responses were postulated to be the result of community interactions such as competition or predation that complicated the invertebrate community's response to fertilization (Peterson et al. 1993). Monitoring of abundances, biomass, and community composition of benthic invertebrates and zooplankton over multiple years is recommended to better understand site-specific invertebrate responses to fertilization.

Fertilization of streams and lakes has also been observed to alter invertebrate community composition (Slavik et al. 2004; Armendáriz et al. 2012; Minshall et al. 2014). Unlike community composition changes observed in primary producers, it is currently unclear if changes in community composition of invertebrates influence how fish communities respond to fertilization treatments. Specifically, it is unclear if changing species assemblages within an invertebrate community limits or enhances prey availability to fish, even if the invertebrate community overall increases in abundance due to fertilization. To the best of our knowledge this has never been investigated directly, and variation in invertebrate prey availability could explain the variability (detailed below) in fishery responses to fertilization (Slaney & Ashley 1998; Kohler & Taki 2010; Minshall et al. 2014). Further research is required to clarify if fertilization enhances or decreases invertebrate availability as prey to fish consumers.

Fish

Fish responses to lake and stream fertilization vary by species. Fertilization has been observed to increase abundance, biomass, and survival of Sockeye Salmon (*Oncorhynchus nerka*) (Luecke et al. 1996; Hyatt et al. 2004); increase or not change abundance and biomass, as well as increase growth rates, and smolt length of Steelhead Trout (*Oncorhynchus mykiss*) (Johnston et al. 1990; Slaney & Ashley 1998; Hansen 2003; Pellett 2011); increase biomass and abundance, increase and not impact length of Coho Salmon (*Oncorhynchus kisutch*) (Johnston et al. 1990; Slaney & Ashley 1998; Wipfli et al. 2003; Pellett 2011); increase and decrease growth rates, and abundance, increase biomass, fecundity, and length of Kokanee Salmon (*O. nerka*) (Perrin & Johnston 1987; Pieters et al. 2003; Thorp et al. 2003; Sebastian et al. 2004; Andrusak 2006; Harris et al. 2007; Schindler et al. 2007, 2009*a*, 2009*b*, 2011; Ericksen et al. 2009); increase biomass and growth rates of Dolly Varden (*Salvelinus malma malma*) (Wipfli et al. 2003); increase or not change abundances, and increase biomass of Rainbow Trout (*O. mykiss*) (Slaney & Ashley 1998); increase or not impact growth rate and biomass of Cutthroat Trout (*Oncorhynchus clarkii*) (Slaney & Ashley 1998; Wipfli et al. 2003); increase abundance of Mountain Whitefish (*Prosopium williamsoni*) (Slaney & Ashley 1998); increase abundance, biomass, and length of Bull Trout (*Salvelinus confluentus*) (Slaney & Ashley 1998; Decker 2010; Decker & Nellestijn 2015); and increase abundances and growth rates of Arctic Grayling (*Thymallus arcticus*) (Peterson et al. 1993; Slaney & Ashley 1998; Slavik et al. 2004). Despite this variation, Grant et al. (1998) postulated that increases in salmonid abundance resulting from fertilization was caused by an increase in growth rates rather than an increase in population density, therefore increasing over-winter survival and/or smolt production (Grant et al. 1998). Finally, while many studies have observed a positive influence of fertilization upon fish, only a single study has observed a direct link between fertilization, an increase in fish numbers (Steelhead), and increased catch by anglers (Slaney & Ashley 1998).

Beyond the differences between species, there is considerable variation in fish responses to fertilization between years, habitats, and microhabitats (Peterson et al. 1993; Slavik et al. 2004; Schindler et al. 2006, 2009*a*; Ericksen et al. 2009). One component of the observed variability is the natural annual variability of fish populations (Quinn 2011). However, part of this variability is a density-dependent response to increased nutrient conditions. Generally, with increasing prey abundances, fish populations will initially increase, start to plateau, and then either remain steady or decrease. At the same time individual fish size typically increases at first, then decreases due to a density-dependent response to increasing population numbers. Such a trend was observed for Kokanee Salmon in the Arrow Lakes Reservoir, BC, Canada; Kokanee numbers increased initially with fertilization as the population approached the new carrying capacity and dynamic equilibrium condition, then plateaued, and in some locations decreased (Schindler et al. 2006, 2007, 2009*b*, 2011). Given this natural variability, as well as density-dependent responses to fertilization, monitoring will need to be conducted long term and in multiple locations within a site to elucidate if fertilization is enhancing fishery production.

While fertilization can enhance fisheries (Slaney & Ashley 1998), not all habitats are good candidates for fertilization. Grant et al. (1998) postulated that fertilization will only have positive impacts in nutrient-poor systems that have limited salmonid densities. Further, correct habitats need to be targeted to enhance target species; specifically, habitats in which target species spend the bulk of its time foraging should be enhanced. For instance, fertilization of streams and creeks has successfully enhanced Bull Trout populations (Slaney & Ashley 1998; Decker 2010; Decker & Nellestijn 2015), while fertilization of lakes (or reservoirs) has enhanced Kokanee populations (Perrin & Johnston 1987; Harris et al. 2007; Ericksen et al. 2009; Schindler et al. 2009*a*, 2011). While managers need to target the correct habitat in fertilization projects, considerable knowledge gaps exist for most species. For instance, it is unknown if fertilization of creeks and streams will have any impact on Kokanee Salmon. Current knowledge suggests that Kokanee do not spend much time in rivers or streams after they hatch, as they migrate quickly to lakes in which they rear (Quinn 2011). It is unclear if Kokanee forage in streams during this brief window. If Kokanee are not foraging in streams or rivers, then fertilization in these habitats will have little impact upon Kokanee. However, if foraging is occurring, then enhancing prey populations during this brief period may have large positive impacts upon Kokanee. More research is required to fill this and other species-specific data gaps to optimize fertilization targets.

Nutrient and Biomass Transfer Through the Food Web and Long-Term Success

As detailed in Table 1, fertilization of streams and lakes is almost guaranteed to increase the abundance and/or biomass of primary producers and zooplankton/benthic invertebrates (Hyatt et al. 2004). However, the transfer of nutrients to the fish community (biomass or abundance) is less clear, and upwards of 99% of added nutrients will not be incorporated into fish tissue (Hyatt et al. 2004). Table 1 highlights that in many situations fertilization has not enhanced fishery production, and there is considerable variation in fish responses to fertilization between years, habitats, and microhabitats (Peterson et al. 1993; Slavik et al. 2004; Schindler et al. 2006, 2009*a*; Ericksen et al. 2009). Thus, the link between fertilization and fishery improvements is not yet fully resolved. Moreover, while many studies have observed a positive influence of fertilization upon fish, only a single study has observed a direct link between fertilization and increased catch by anglers (Slaney & Ashley 1998). Despite these uncertainties, there is strong evidence that fertilization can in some situations improve fish numbers, biomass, and fecundity (Slaney & Ashley 1998; Ericksen et al. 2009; Schindler et al. 2009*a*; Pellett 2011; Decker & Nellestijn 2015).

If fisheries enhancements are achieved, any observed improvements to the fishery will likely cease as soon as fertilization ends (Ericksen et al. 2009; Schindler et al. 2009*b*, 2011; Pellett 2011). For instance, Ericksen et al. (2009) experimentally reduced fertilization levels in the north arm of Kootenay Lake, and Kokanee abundances, which had been increasing under higher fertilization levels, declined sharply. This implies that while fertilization of streams and lakes may improve fish abundance, biomass, and fecundity, it has not yet resulted in feedback loops where decomposing carcasses enhance once oligotrophic systems (Ericksen et al. 2009; Schindler et al. 2009*b*, 2011; Pellett 2011). This situation will be further exacerbated if fish are harvested and do not enrich the system with nutrients contained in their carcasses (Stockner & Ashley 2003). Further, elevating fish populations beyond the natural carrying capacity of the system, and then ceasing fertilization could have dramatic negative consequences. Naturally oligotrophic systems would be unable to support elevated fish populations, and any crashes that result could have lasting impacts upon the system (Pellett 2011). As such, the decision to terminate fertilization programs should only be made after careful consideration of monitoring data (nutrient availability, primary producer, invertebrates, and fish communities), and cessation of fertilization should be conducted gradually.

Other Factors

Fertilization may not only stimulate the productivity of target fish species, but it will also stimulate other species such as Sticklebacks (family Gasterosteidae). Sticklebacks compete with salmonids for elevated invertebrate prey items, and can limit productivity of salmonids in fertilized habitats (Hyatt et al. 2004; Harris et al. 2007). One previous study successfully controlled Stickleback densities via predation by introducing sterilized Cutthroat Trout, whose predation upon Sticklebacks resulted in the release of Kokanee Salmon from this competitive limit on their growth (Harris et al. 2007). Such competitive interactions have not been reported in other fertilization studies; however, such an interaction would have gone undetected if only salmonid densities were monitored. As such monitoring should include the entire fish community to detect potential competitive interactions.

Differing concentrations of key nutrients beyond those being supplemented (N and P) could also influence the success or failure of fertilization programs. For instance, n-3 PUFA fatty acids enhance metabolism and aid in migration success in mammals and birds (Maillet & Weber 2006, 2007). Fish tissue often contains high concentration of PUFA fatty acids, and dietary PUFA content has been linked to elevated growth and survival, as well as low occurrences of malformations in fish larvae (Sargent et al. 1999). Invertebrates and primary producers can have high concentrations of PUFAs; however, this concentration varies between species (Bigogno et al. 2002; Gressler et al. 2010; Quinn et al. 2017). As nutrient addition can alter primary producer and invertebrate community composition, availability of PUFAs may also vary due to nutrient addition. Similarly, if nutrient addition results in the accumulation of more carbon than N or P in primary producer or invertebrate populations, this may also hinder the enhancement of fisheries production (Sterner & Elser 2002; Hessen et al. 2013). However, these relationships are poorly understood and more research is required.

One technique that could offer insight into the transfer of nutrients throughout the food web is stable isotope analysis (Quinn & Hamilton 2012; Moore et al. 2016; Hertz et al. 2017). If nutrient enhancement stimulates primary producer or invertebrate communities in such a way as to increase fisheries production, primary producer isotope signatures should increase in fish consumers. If fishery production does not increase, isotopic signatures could be used to determine if nutrients are being passed up the food web to fish. If not, the isotopic signatures of primary producers and invertebrate prey items could offer clues as to barriers to nutrient transfer.

Finally, fertilization of streams and lakes will not be successful long term if the quality and quantity of suitable spawning habitats and other key habitat features such as side channels, gravel beds, and large woody debris (LWD) are not able to support enhanced fish populations (Blackman 2000; Stockner & Slaney 2006; Ericksen et al. 2009). Therefore, pre-fertilization assessments must include an evaluation of key habitat feature availability in target ecosystems.

Cost

It is difficult to determine the exact budget required to successfully enhance fishery production without first identifying the number of streams and/or lakes that would be fertilized. Further, we only present estimates of cost if they appeared in peer-reviewed articles, therefore in-depth cost analyses were not possible due to a deficient of available data. However, Hyatt et al. (2004) reported that enhancement of Sockeye Salmon smolt production via fertilization cost approximately \$200 CND (\$250 CND in 2018 dollars) per kg of enhanced smolt production. Even though this value was calculated for Sockeye, \$250 CND per kg of enhanced smolt production is likely a good minimum estimate for most salmonid species. This value, however, does not include the monitoring required to adaptively manage a fertilization program. No budget estimates are provided here for monitoring due to the highly site-specific nature of such a budget. Given the uncertainties associated with nutrient enhancement, and that enhancements will not outlast the fertilization project, fertilization projects would benefit from a cost–benefits analysis over the lifecycle of the project, to determine if fertilization is an appropriate compensation option. However, other compensation or remediation options associated with dams and culturally oligotrophic systems such as fish ladders or trap and transport of fish require infrastructure investments and annual operating budgets that can range from tens of thousands to millions of dollars depending upon the habitat in question and infrastructure required (Abbott 1984; Congleton et al. 2000; Muir et al. 2006; Keefer et al. 2008; Anderson et al. 2012). Even given its uncertainties, when compared to other remediation or compensation strategies, fertilization may be a cost-effective method to enhance fisheries production, but the cost-effectiveness of this method requires further empirical investigation.

Recommendations

When nutrient enhancement has failed in the past, it is not always clear as to why. Therefore, holistic monitoring of the entire ecosystem—nutrient availability, primary producers, invertebrates, and fish communities—is important, as it enables adaptive management of fertilization programs. However, previous fertilization programs have struggled to enhance fisheries productivity for a variety of reasons. First, given that upwards of 99% of added nutrients will not be incorporated into fish tissue (Hyatt et al. 2004), sufficient quantities of nutrients must be added. Second, addition of nutrients should mimic natural nutrient cycles, and take into account hydrological conditions so that added nutrients are not flushed from the system before being incorporated (Pieters et al. 2003; Schindler et al. 2006, 2011). Fertilization programs may also fail to transfer nutrients into fish tissue if fertilizer N:P ratios or nitrate levels result in blooms of blue green algae or ungrazable diatoms (Hyatt et al. 2004). Fertilization of microhabitats in which target fish species do not forage (lake vs. stream) may also contribute to poor success rates. Absence of critical habitat features such as side channels, gravel beds, and LWD capable of supporting enhanced fish populations may also limit success (Blackman 2000; Stockner & Slaney 2006; Ericksen et al. 2009). Without these habitat features, it is unlikely that nutrient enhancement will result in increased fishery production. Moreover, many previous studies (Table 1) have only monitored target fish species, often salmonids that support commercial or recreational fisheries. However, nutrient enhancement can also enhance non-target fish species such as Sticklebacks that compete with salmonids for prey items (Hyatt et al. 2004; Harris et al. 2007). Failure to account for this possibility and to monitor the entire fish community could result in failure of nutrient enhancement programs. Finally, natural variability in fishery production as well as density-dependent responses to fertilization (Schindler et al. 2006, 2007, 2009*b*, 2011) are common. As such, failure to monitor fisheries long term may result in increases or plateaus being unobserved.

Based upon the above discussion, if a fertilization program is to be successful it must: (1) mimic natural nutrient cycles, (2) be conducted in areas with key habitat features such as LWD and ample spawning habitat, (3) local hydrology, temperature, turbidity, and reservoir operations must be considered to avoid adding nutrients during high flow periods, and (4) adaptively monitor and adjust N:P ratios as well as nitrate levels to control blue green algae and ungrazeable diatoms. Repeated monitoring will be required over the long term (at least 5 years, if not 15–20). Monitored variables should include: (1) nutrient availability in water, (2) abundance and community composition of primary producers (phytoplankton, algae, diatoms, periphyton, etc.), (3) abundance and community composition of zooplankton and benthic invertebrates, and (4) fish fecundity, size (length), biomass, abundance, and community composition.

Conclusions

In general, fertilization of oligotrophic lakes and streams will almost certainly increase primary producer and invertebrate populations. While it is likely that fertilization will also increase fishery production, it is far from certain. The magnitude of this change is unpredictable, and the success of a fertilization program will vary greatly between years, habitats, and microhabitats. As such, repeated long-term monitoring of nutrient availability, primary producers, invertebrates, and fish communities at multiple microsites within a fertilized area is required for adaptive management, and to maximize success of fertilization programs as a remediation strategy for culturally oligotrophic areas. If funding is available for long-term fertilization and monitoring (at least 5 years, if not 15–20), a fertilization program is likely to enhance fishery production as part of an active restoration or compensation program. However, any benefits accrued because of fertilization will cease following termination of the program. Care must be exercised when terminating the fertilization program, as elevating fish populations beyond natural carrying capacities and then ceasing fertilization could result in population crashes with lasting impacts. Further, a cost–benefit analysis is strongly recommended prior to initiating a fertilization program. Regardless, when compared to other restoration/compensation strategies in oligotrophic habitats, such as fish ladders or trap and transport, fertilization may be a cost-effective method to enhance fishery production.

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