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Nutrient dynamics in a highly managed reservoir system: considering anadromous sockeye salmon (*Oncorhynchus nerka*) and nutrient restoration

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ABSTRACT

Scott DC, Harris SL, Hebert AS, van Poorten BT. Nutrient dynamics in a highly managed reservoir system: considering anadromous sockeye salmon (*Oncorhynchus nerka*) and nutrient restoration. Lake Reserve Manage. 00:1–9.

Modeling nutrient flux in Alouette Reservoir, British Columbia, allowed us to (1) determine the relative importance of key factors that influence its nutrient dynamics and (2) evaluate the potential value of returning anadromous salmon to this highly altered reservoir. Annual surface water releases over the dam spillway have facilitated out-migration of juvenile sockeye salmon (*Oncorhynchus nerka*) produced by resident kokanee parents since 2005, and these juveniles have returned as adult sockeye annually since 2007, thus restoring an anadromous run lost for nearly 90 years. This re-anadromization program may have an effect on the nutrient restoration program, which includes annual additions of nitrogen and phosphorus designed to enhance the recreational kokanee fishery within the reservoir. High flow release to facilitate juvenile out-migration resulted in a net export of nutrients because few adults returned, and a portion of nutrients added to the reservoir were flushed downstream. If only anadromous sockeye are considered, however, nutrient flux was positive in 5 of 6 years for nitrogen (average 2.30 kg; range −1.06 to 5.97), and in 4 of 6 years for phosphorus (average 0.24 kg; range −0.15 to 0.62). Overall, our results show the export of nutrients by the anadromy restoration project represents an average of just 1.54 and 0.60%, respectively, of the seasonal nitrogen and phosphorus budget for the system. Therefore, although the anadromy restoration results in a net loss of nutrients from the system, its effect on the nutrient restoration project is minimal.

Understanding nutrient flux in managed aquatic ecosystems allows managers to determine how decisions influence nutrient dynamics and should inform future decision making. The loss of nutrients in in reservoir systems due to operations that export water complicate nutrient dynamics (Matzinger et al. 2007) and commonly lead to undesired consequences such as decreased recreational fishing opportunities. To avoid these consequences, whole-lake nutrient additions are undertaken in some systems to increase primary productivity and ultimately the food base for harvested fish species (Johnston et al. 1999, Perrin et al. 2006). Ensuring these nutrients are transferred to higher trophic levels presents challenges, and considerable work may be needed to ensure that the target management species (i.e., one targeted by a fishery) is indeed the benefactor (Hyatt et al. 2004). Physical flow dynamics of water through a managed reservoir present additional challenges, such as nutrient export either through powerhouse operations that generate revenue, through spill to the outflowing river, or through sedimentation when reservoir elevations are held constant (Matzinger et al. 2007). Importantly, nutrient addition utilizes agricultural grade fertilizer and is an increasingly costly management tool (Huang 2009). Therefore, tracking the fate of added nutrients and quantifying each of the inputs and outputs of the overall system are important tasks for the agencies that manage reservoirs and must balance multiple, and sometimes competing, objectives.

Impoundments that result in the extirpation of anadromous salmon that can deliver large quantities of marine-derived nutrients to their natal freshwater systems (Cederholm et al. 1999, Schindler et al. 2003) has also prompted the implementation of nutrient addition programs in which agricultural fertilizer is added

to waterbodies. This return of adult salmon fertilizes both freshwater and nearby terrestrial ecosystems, boosting productivity for juvenile salmon emerging the following spring (Naiman et al. 2002, Schindler et al. 2003). Conversely, the seaward migration of juvenile salmon represents a loss of nutrients from freshwater systems, and it has been demonstrated that low adult returns can result in a net nutrient loss from freshwater systems (Scheuerell et al. 2005, Kohler et al. 2013). In nutrient-managed freshwater systems, anadromous salmon may therefore play an important role in nutrient flux dynamics.

Alouette Reservoir in southwestern British Columbia, Canada, is a managed hydropower reservoir with a nutrient addition program and a historically extirpated sockeye salmon (*Oncorhynchus nerka*) population, which was reestablished in 2005 after a 90-year absence (Godbout et al. 2011). To compensate for reservoir operations, each year agricultural grade fertilizer is added to the lake during the spring and summer season (Apr–Sep) to increase productivity of the kokanee fishery. Each spring since 2005, water has been released over the dam spillway to facilitate the release of juvenile *O. nerka*. This spillway release represents a loss not only of juvenile *O. nerka* from the resident kokanee fishery but also lost nutrients carried by water and fish and a loss of potential hydropower production. Overall, the anadromy restoration project may have a negative effect on the nutrient addition project; therefore, determining the fate of nutrients in the system is critical for managers and stakeholders.

We calculated the nutrient flux of the Alouette Reservoir with a mass balance approach to determine the mass of nitrogen and phosphorus transported in association with juvenile and adult migrations of anadromous *O. nerka*. This nutrient flux model will provide insight into the net flux of nutrients in nutrient-managed systems with a low abundance of returning salmon and potentially provide guidance on future management decisions regarding the yearly release of juvenile *O. nerka* from this and other similar systems.

Study system

Alouette Reservoir (49°17′N, 122°29′W) is located within a steep-sided glacial valley in the Coast Mountains, about 50 km northeast of Vancouver, British Columbia (Fig. 1). The Alouette Dam was originally constructed in 1925 to 1928, joining 2 small upstream lakes into a single 17 km long, 1666 ha reservoir with a maximum depth of 152 m. Dam construction extirpated anadromous populations of cutthroat trout (*O. clarkii clarkii*) and steelhead (*O. mykiss*), chum (*O. keta*), coho (*O. kisutch*), Chinook (*O. tshawytscha*), pink (*O. gorbuscha*), and sockeye salmon runs that historically spawned upstream of the dam (Harris et al. 2011). Sockeye remained as a "residual" population of resident kokanee that have persisted in the reservoir (Godbout et al. 2011). In this paper, we refer to anadromous sockeye as either juvenile *O. nerka* or *O. nerka* returns and resident fish as kokanee. Inflows are unregulated, whereas water flowing out of the reservoir has 3 outlets: through a subsurface tunnel that connects the upstream end of Alouette Reservoir to Stave Reservoir (Fig. 1), through a low-level outlet into the Alouette River, or over the dam spillway each spring to facilitate juvenile *O. nerka* outmigration (Fig. 1). The Alouette River Water Use Plan has required an average base flow of 2.60 cubic meters per second (cms) be released from the low-level outlet into the Alouette River through the dam (BC Hydro 1996). Since 2005, the majority of water discharge has been through the tunnel into Stave Reservoir (average 79.9%), followed by the dam outlet (13.3%), with the spillway release responsible for the remaining 6.8%.

Methods

Nutrient restoration project

Since 1999, the Alouette Reservoir has been fertilized with inorganic nitrogen and phosphorus at weekly intervals over a 20-week period from late April until early September (Harris et al. 2011) to improve the kokanee fishery. The desired annual nitrogen (N) loading rate is 1520 mg/m^2 (total 24,656 kg/yr) and the phosphorus (P) loading rate is 204 mg/m^2 (total 3309 kg/yr), which aims to satisfy the phosphorus loading rate of at least 200 mg/m^2 established by Perrin et al. (2006; Harris et al. 2011). Because of logistical issues, however, this loading rate is not accomplished in all years. The Alouette kokanee population has responded to nutrient enhancement as expected, with a significant increase in the size and abundance of age 3+ fish (Harris et al. 2011). Since the inception of the nutrient restoration program, the cost of fertilizer has more than doubled from an average of $26,203 per year over
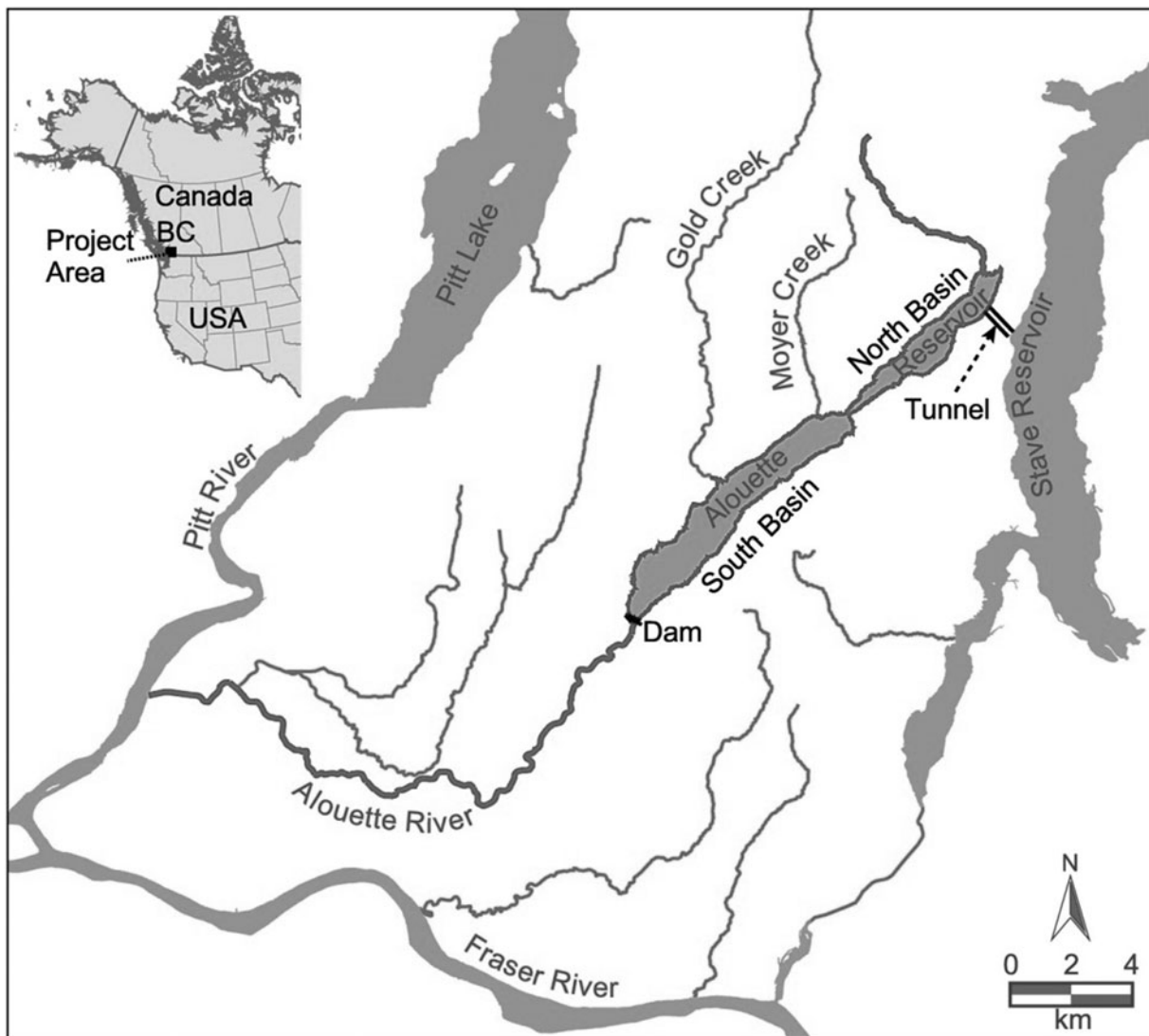
Figure 1. Location of the Alouette Reservoir (outlined), including surrounding watershed. Inset displays location of the Alouette River watershed in western North America.

the first 5 years (1999–2003) to $60,568 over the past 6 years (2009–2014), potentially jeopardizing the cost-effectiveness of employing fertilization as a management tool.

Anadromy restoration project

In spring 2005, we conducted an experiment to determine the feasibility of restoring anadromous fish populations to the Alouette basin. Spillway releases were allowed over the Alouette Dam to determine if marked hatchery-produced coho salmon smolts could successfully out-migrate (Baxter and Bocking 2006). Unanticipated was the outmigration of juvenile *O. nerka* produced by resident kokanee, with an estimated 7900 juveniles leaving the system in the first year

(Baxter and Bocking 2006; Fig. 2a). This surface release occurred again in spring 2006 to test outmigration success of steelhead smolts, and again juvenile *O. nerka* were captured, with an estimated 5064 migrating out of the reservoir (Humble et al. 2006). Surface release flows have since continued annually to restore anadromous *O. nerka* to the reservoir. In fall 2007, for the first time in nearly 90 years, 28 adult sockeye returned to the Alouette River; genetic and scale analysis confirmed they were from the 2005 outmigration group that originated in the basin (Godbout et al. 2011). Adult sockeye have returned each year since, with the exception of 2014, with an average of 37 (range 0–115) individuals returning annually (Fig. 2b).

The Alouette system is novel in that the juvenile *O. nerka*, which continue to out-migrate from the
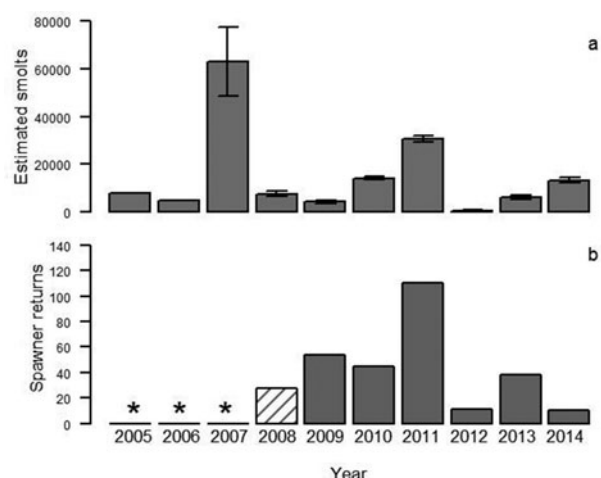
Figure 2. Migration of *O. nerka* from the Alouette Reservoir. (a) Estimated number of *O. nerka* smolts leaving the system based on field mark–recapture estimates; bars indicate 95% confidence intervals for these estimates. Mark–recapture methods for 2005 and 2006 were not used, and therefore no confidence estimate exists. (b) Number of adult sockeye captured at the ALLCO Fish Hatchery fish trap, transported above the dam, and then released into the southern basin. The exception was in panel (b) in 2008, denoted by the hashed bar, when the fish were counted but not transported into the lake. In panel (b), * indicates years prior to the reestablishment of adult sockeye returns. Adult sockeye that return in fall contribute to the nutrient budget for the following spring and are therefore attributed to the year following their return.

reservoir, are the offspring of resident kokanee (Godbout et al. 2011). Although determining if juvenile *O. nerka* are intentionally outmigrating or if a portion is simply being entrained is not possible, we assumed the vast majority are making a directed outmigration based on the distribution of their observed migration timing.

The anadromy restoration program consists of surface water release of ~3.0 cms, typically occurring between mid-April to mid-June with an average of 58 days of flow per year (2007–2014). Juvenile *O. nerka* are captured, weighed, and marked each spring using a rotary screw trap operated downstream of the dam in the Alouette River. Captured fish are then released below the Alouette Dam, and juvenile *O. nerka* recaptured in the rotary screw trap allow abundance to be estimated using a pooled Petersen estimator (Mathews et al. 2015). Although out-migration occurs at relatively the same time each year, peak timing and duration have been variable across years. The mark–recapture methods used have estimated an average 15,500 (range 720–63,000) *O. nerka* out-migrating annually (Fig. 2a). Returning adult *O. nerka* are captured and enumerated at the ALLCO Fish Hatchery fish trap, where fork length is measured. Adults are then transported above

the dam and released into the southern basin of the reservoir.

Nutrient flux data

We calculated a seasonal (Apr–Sep) nutrient budget for nitrogen and phosphorus in Alouette Reservoir to assess the relative importance of nutrient gains and losses from sockeye migrations and nutrients conveyed downstream with additional water spilled to facilitate outmigration. The quantity of nutrients in Alouette Reservoir is controlled by a number of natural inputs as well as yearly fertilizer additions; export of water through the low-level outlet, the powerhouse, and the spillway; and *O. nerka* migrations. Natural inputs of nitrogen and phosphorus are delivered from the watershed at an annual rate determined by surface runoff. Natural watershed loading was determined from a combination of gauged tributary inflow (BC Hydro daily inflow data) and ungauged inflow. Water chemistry sampling at tributary sites was conducted from 1998 to 2002 and from 2003 onward, and the 5-year mean nutrient concentrations for each stream were used. Nitrogen and phosphorus concentrations for ungauged inflow were estimated using the 5-year mean of water chemistry results from the Alouette River, Moyer Creek, and Gold Creek (Fig. 1). Phosphorus and nitrogen are also deposited from the atmosphere at an average annual rate of 50 kg (Harris et al. 2011) and 7164 kg per season, respectively, with nitrogen based on 8.6 kg/ha/yr for atmospheric nitrogen contribution from Belzer et al. (1997). Entrainment of juvenile *O. nerka* through the tunnel may also represent a loss of nutrients from the reservoir; however, its estimation was beyond the scope of the current study.

To estimate nutrient export, concentrations of total nitrogen (TN) and total phosphorus (TP) were measured monthly and used with discharge volume for the entire month (Table 1). Analysis was completed by Maxxam Analytics laboratory in Burnaby, BC (Table 1), and samples were dropped off the same day they were taken. For additional details on methods used refer to Harris et al. (2011). We subtracted the base flow requirement (2.60 cms) from the spillway volume because during spillway releases the low-level outlet is closed; therefore, a significant portion of the water used to transport juvenile *O. nerka* is required to be released regardless. Detailed body size information and estimates of abundance for outmigrating juvenile and returning adult salmon exist for each year, allowing

Table 1. Details of water chemistry samples collected during limnology field program using Maxxam Laboratory, 2014, Alouette Reservoir BC.

Parameter	Sample frequency	Depths	Preservation	Reportable detection limit	Analytical method
Nitrogen: low level nitrate and nitrite	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold, field filtered 0.45 μm sterile Satorius filter	2 μg/L	SM 22 4500-NO$_{3-}$ I m
Nitrogen: Total	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold	20 μg/L	SM 22 4500-N C m
Nitrogen: total Kjeldahl	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold	20 μg/L	SM 4500N-C
Phosphorus: low level dissolved orthophosphate	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold, field filtered 0.45 μm sterile Satorius filter	1 μg/L	SM 22 4500-P E m
Phosphorus: dissolved	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold, field filtered 0.45 μm sterile Satorius filter	2 μg/L	SM 22 4500-P E m
Phosphorus: total	Monthly Apr–Oct	1, 80; 0 m to mixed layer depth (max 20 m)	Cold	2 μg/L	SM 22 4500-P E m

Note. Discrete and integrated samples taken on each sampling occasion with discrete samples taken at 1 and 80 m depths, and integrated samples were taken from 0 m to mixed layer.

the calculation of mass transport of nutrients due to *O. nerka* migrations. Nutrient flux by *O. nerka* was calculated using the following formulas from Moore and Schindler (2004):

$$\text{Export}_{n,t} = S_t * SM\bar{w} * M_{n,smolt}, \quad (1)$$

where mass of a given nutrient n (either nitrogen or phosphorus) in juvenile *O. nerka* for each year (t) is the product of the number of juveniles in year-t (S_t), the average mass of juveniles that year (SM$\bar{w}$) and the average mass of n by wet weight ($M_{n,smolt}$). Import of a given nutrient n from returning *O. nerka* adults in each year is:

$$\text{Export}_{n,t} = A_t * AM\bar{w} * M_{n,adult} \quad (2)$$

where A_t is the number of returning adults the previous year, AM $\bar{w}$ is the average mass of the adults of the previous year, and $M_{n,adult}$ is the average mass of n by wet weight. Values for $M_{n,smolt}$ and $M_{n,adult}$ are provided in Table 2. Body mass was estimated from fork lengths using a length–weight relationship taken from mature sockeye in Bristol Bay, Alaska (Mathisen 1965). Managers consider the nutrients returned by adult salmon each summer to contribute to the nutrient budget for the following spring; therefore, returning *O. nerka* and

Table 2. Nutrient percentages based on wet weight used for this study.

Life stage	Nutrient	Value	Source
Spawners			
	Nitrogen	3.04%	Larkin and Slaney 1997
	Phosphorus	0.38%	Donaldson 1967
Smolts			
	Nitrogen	2.49%	Kline and Willette 2002
	Phosphorus	0.43%	Donaldson 1967

their associated nutrients are counted toward the year following their return.

To better understand how variation in the abundance of juvenile migrants, adult returns, and marine survival affect the net nutrient flux associated with sockeye, we modeled nutrient flux for numbers ranging from 0 to 100,000 outmigrating juveniles, and adult returns as a function of marine survival, which varied from 0 to 5%. The net flux of nitrogen and phosphorus was modeled using equations 1 and 2, which provided estimates of equilibrium juvenile *O. nerka* output across a range of marine survival rates. Marine survival was assumed to be constant for each modeling run. We also investigated how net nutrient flux varied with and without accounting for nutrient losses in surface water spilled during outmigration. In this calculation, wet weight of juveniles and adults was set to 0.0075 and 3.30 kg, respectively.

Results

If only the migration of *O. nerka* is considered, they represent a net input of nitrogen and phosphorus to the system overall and in most years from 2009 to 2014. Juvenile *O. nerka* represent a minor export, an average of 1.72 kg of nitrogen (range 0.28–3.34) and 0.29 kg (range 0.05–0.59) of phosphorus (Table 3). Similarly, returning adults represented a small import of nutrients, delivering an average of 4.18 kg (range 0.34–9.95) and 0.55 kg (range 0.15–1.33 kg) of nitrogen and phosphorus, respectively. Overall, nutrient flux by migrating *O. nerka* was positive in 5 of 6 years for nitrogen (average 2.61 kg; range −0.60 to 7.16), and in 4 of 6 years for phosphorus (average 0.24 kg; range −0.15 to 0.62;

Table 3. Nutrient inputs and outputs and their average seasonal (Apr–Sep) mass (2009–2014) in the Alouette Reservoir.

Direction	Source	Nitrogen (kg/yr)	Phosphorus (kg/yr)
Inputs			
	Fertilization	23,771.00	3,231.43
	Watershed	45,564.07	503.33
	Atmospheric deposition	7164.00	50.00
	Adult *O. nerka*	4.41	0.55
	Total	76,503.48	3785.31
Outputs			
	Tunnel	36,414.64	873.00
	Low-level outlet	6937.23	190.78
	Spillway	1174.04	22.61
	Juvenile *O. nerka*	1.72	0.30
	Total	44,527.63	1086.68

Note. Nutrients lost via the spillway that would have been lost via the low level outlet per the base flow requirement for the Alouette River have been assigned to the low-level outlet.

Fig. 3a). Juvenile *O. nerka* exported a large proportion of adult nutrients, averaging 53% (8–140%) and 73% (11–193%) of nitrogen and phosphorus, respectively. Individual juvenile *O. nerka* have on average been <0.5% of the mass of individual adults; thus, >99.5% of adult nutrients originate from the marine environment.

Although nutrient flux by *O. nerka* alone is on average positive, nutrient-enriched water conveyed via the spillway represents a loss of nutrients from the system in all years (Fig. 3b and c, Table 3). Nutrient flux from the spillway water and migrating juvenile *O. nerka* combined represents a loss of an average of 1.54 and 0.61% of the seasonal nitrogen and phosphorus budget of the system, respectively (Fig. 3b and c). This amount makes up a relatively minor proportion of the overall nutrient budget of the reservoir, however, with the vast majority of nutrient export via the tunnel (47.60% N, 23.06% P), and a smaller proportion exported via the low level outlet (9.10% N, 5.04% P; Fig. 3b and c). Overall, the seasonal nutrient budget results in net gains of nitrogen and phosphorus to the system (Table 3), increasing the productivity of this oligotrophic reservoir.

Modeling scenarios indicate that as marine survival improves, so too does the gain in nitrogen and phosphorus to the system (Fig. 4). As the number of outmigrating juvenile *O. nerka* increases at a fixed marine survival rate, there is a loss of nutrients but a net gain in nutrients due to the larger quantity of nutrients derived from the marine environment and delivered via returning adults. Alternatively, increases in marine survival for a given abundance of outmigrating juveniles will intuitively also lead to increases in delivered nutrients.
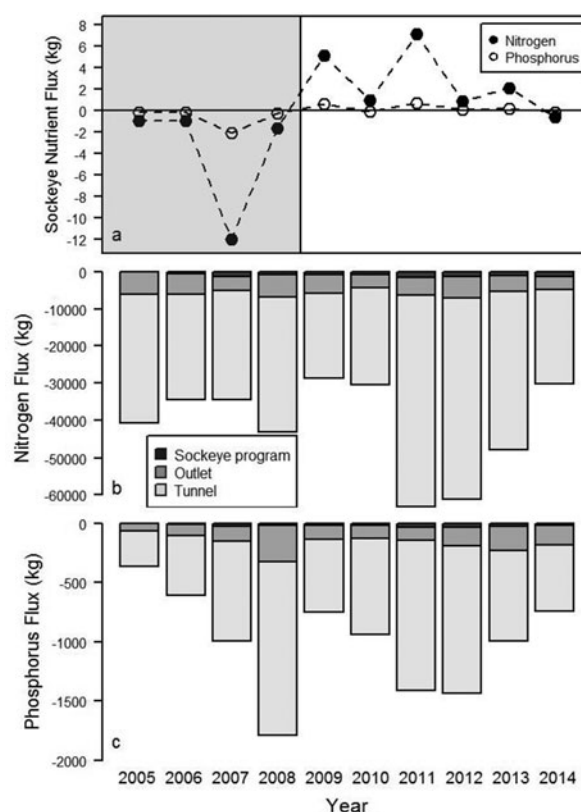

Figure 3. Net nutrient flux associated with the migration of *O. nerka* from the Alouette Reservoir for each season since outmigration began. Shaded and unshaded areas in (a) represent years before and after nutrient addition began in 2009. (a) Net flux of nitrogen and phosphorus, indicated by closed and open circles, respectively. Flux for a given year is calculated using adult returns from the previous fall and smolts from that spring, as a product of weight, abundance estimates, and known nutrient concentrations for different life stages of *O. nerka*. (b and c) Amount of nitrogen and phosphorus flux attributed to the sockeye migration program (net flux by sockeye and additional spillway flows), from the low-level outlet and through the diversion tunnel.

If the nutrients lost with spillway water associated with smolting are accounted for, however, both the number of outmigrating juveniles and marine survival must increase to achieve neutral or positive flux, particularly for nitrogen because the loss via the spillway is much greater in magnitude (Fig. 4c and d). The resulting relationship between nutrient flux, marine survival, smolts, and water export is a linear multiple regression, demonstrated by the concave 3-dimensional pattern (Fig. 4).

Discussion

We found *O. nerka* returns result in a net input of nutrients in most years when considered alone;
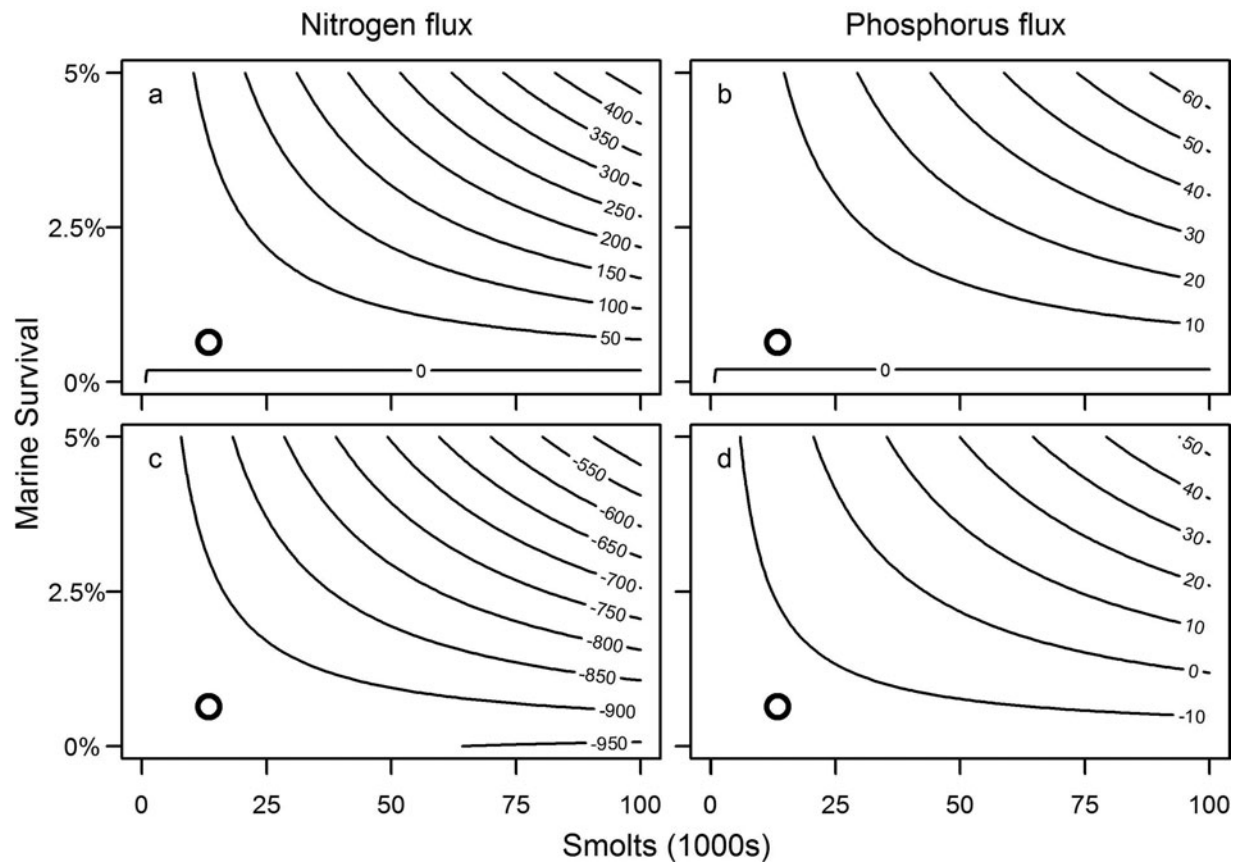
Figure 4. Long-term expected nutrient flux calculated assuming equilibrium conditions for marine survival and smolt abundance. Contour lines represent nutrient flux in kilograms for (a and c) nitrogen and (b and d) phosphorus. (a and b) Flux calculated using *O. nerka* alone; (c and d) Flux of *O. nerka* and spillway water. Black circles indicate the average values for the study period.

however, outmigrating juveniles export a large proportion of these nutrients and out-migrate each spring regardless of the number of returning *O. nerka* adults in previous years. Moore and Schindler (2004) estimated an overall nutrient export by smolts of 5 to 25% of the total imported by their parents; however, we found that at low abundances of returning adults, juveniles can export >100%, resulting in net export. Similarly, Scheuerell et al. (2005) found that low abundance of Chinook spawners in the Snake River resulted in a net export of phosphorus by smolts in 12% of years studied (1962–1984 and 1990–2002), and Kohler et al. (2013) found that during periods of low adult abundance, juvenile Chinook in the Columbia River basin exported up to 194 and 268% of parental nitrogen and phosphorus inputs, respectively. In our system, the proportion of adult nutrients exported by juvenile *O. nerka* the following years was highly variable, averaging 53% (8–140%) and 73% (11–193%) of nitrogen and phosphorus, respectively. Nutrient export by juveniles is novel in our system in that juvenile *O. nerka* are the offspring of resident kokanee parents; annual DNA testing

has yet to identify an outmigrating juvenile that was the product of 2 returning *O. nerka* spawners. Thus, outmigration abundance is decoupled from returning *O. nerka* adult abundance, and nutrients exported by juvenile *O. nerka* are of purely freshwater origin, creating a unique scenario where outmigrating *O. nerka* can export a much greater proportion of nutrients than that returned by adults.

Although anadromous *O. nerka* are a net importer of nutrients to this system, surface spills result in a net loss of nutrients from the system. Adult *O. nerka* have been net importers to this system, despite low abundances, and are widely known to supply nutrients to the freshwater environments in which they spawn (Naiman et al. 2002, Schindler et al. 2003). However, the loss of nutrients from surface water spilled to allow juvenile *O. nerka* out-migration results in an overall nutrient deficit in all years. Although a portion of this water is released through the low-level outlet as part of the minimum flow requirement, additional surface water spilled represents 300 and 35 times the amount of nitrogen and phosphorus, respectively, relative to

those exported by juveniles. Although the overriding loss of nutrients is through the tunnel and low-level outlet, these losses occur to facilitate power production. Thus, the most important factor in the anadromy restoration program that can be controlled by managers is the quantity of water lost over the spillway to facilitate outmigration. Thus, determining the minimum spill needed to achieve out-migration should be a high priority for managers to optimize the cost of fertilizer addition with that lost via spill.

Our results also demonstrate that as marine survival improves, or as juvenile *O. nerka* abundance increases, so too does the gain in nitrogen and phosphorus to the system. If marine survival remains at its current rate, any increase in the number of outmigrating juvenile *O. nerka* will result in a net gain of nutrients, but if adults fail to return at their current survival rate, increases in outmigration abundance will contribute to nutrient losses. When nutrients lost with surface water releases to facilitate outmigration are included, however, marine survival must increase dramatically to achieve neutral or positive nitrogen flux. To achieve positive flux in nitrogen and phosphorus, assuming marine survival is invariant, outmigrating juvenile *O. nerka* would need to increase to at least 2.5 million and 26.8 thousand per year, respectively. If annual juvenile *O. nerka* output remains constant, however, an improvement to 70 and 7.6% marine survival rate is necessary to achieve positive flux in nitrogen and phosphorus, respectively. Even if both outmigrating abundance and marine survival increase, it seems that spills to facilitate the outmigration will inevitably mean the anadromy restoration project results in a net loss of nutrients, particularly for nitrogen. This information allows managers to evaluate the probable long-term impacts of the anadromy restoration program on the nutrient restoration program.

The direct loss of nutrients from the system could result in either reduced kokanee abundance or higher fertilization costs to compensate for lost nutrients. One possibility is that a loss of nutrients will lead to lower primary and secondary production in the reservoir. In Alouette Reservoir and elsewhere (Rieman and Myers 1992), lower primary production has been shown to affect the resident kokanee population through density-dependent growth and/or survival of juveniles. Because the Alouette Reservoir is managed as a recreational fishery for kokanee, the end

result will be reduced angling success. The other consideration is higher costs incurred to maintain primary productivity at a sufficient level to ensure sufficient edible phytoplankton to maintain kokanee at current levels. Although the social and ecological benefits of anadromous *O. nerka* returning to the system are an important management value, they must be formally balanced with the various other aspects of the total system, including both the resident kokanee fishery and power production.

Although considerable year-to-year variability complicates decision making for managers, modeling nutrient flux allows us to better understand the fate of added nutrients and the effects of *O. nerka* migrations on the overall nutrient budget. Little is known about the mechanisms controlling outmigration from the system, which initially occurred accidentally and has been highly variable over the study period. Factors affecting marine survival, which has been low since the return of anadromy (mean survival = 0.64%), are also unknown and a major determinant of total nutrient flux by sockeye (Larkin and Slaney 1997). Further research in our system will look at density dependence, which is known to affect the growth of juvenile sockeye in nursery lakes (Kyle et al. 1988) and may further complicate the effect of juvenile outmigration on resident kokanee dynamics and thus management objectives. Overall, we found modeling nutrient flux allows us to determine the relative importance of key factors that influence nutrient dynamics in our system and demonstrate the potential value to managers of returning anadromous salmon to highly altered reservoirs.

of the trap is managed by Katzie First Nation and LGL Ltd. environmental consultants. The sockeye transplant program is managed by the Alouette River Management Society and the Fraser Regional Corrections Center.

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