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Reservoir fertilisation and fishery response in a highly managed reservoir with uncertain flows: Ecosystem-based management using decision analysis

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Abstract

Inland fisheries managers must account for multiple competing uses for aquatic resources; using methods such as ecosystem-based management allows for different priorities for aquatic ecosystems to be accounted for. Declining abundance of kokanee salmon *Oncorhynchus nerka* (Walbaum) in Arrow Lakes Reservoir in the 1990s led to the use of large-scale nutrient addition to improve productivity of kokanee and large piscivores. However, it is unclear what effect these measures had on the system given high discharge and highly variable annual flow regime throughout the watershed. An Ecopath with Ecosim model of the ecosystem was fitted to the available data and used to predict ecosystem structure and reservoir objectives under different nutrient addition strategies and varying annual flow regimes. Results from the model indicate that nutrient addition is an important driver in the system, with lower flows resulting in higher biomass for higher trophic levels. Decision analysis demonstrated the importance of maintaining nutrient additions to achieve management objectives despite losses in some high-flow years.

KEYWORDS
bottom-up control, decision analysis, EcoPath with EcoSim, flow, food web, nutrient addition

1 | INTRODUCTION

Reservoirs are highly managed systems that can result from the conversion of riverine habitat or smaller lake systems into something that more closely resembles a large lake. However, lakes and reservoirs often have different physical, ecological and hydrological characteristics (Gloss *et al.*, 1980; Kennedy, 1984). Because reservoirs are designed to hold water until needed by society for uses such as irrigation, flood control and hydropower generation, flows are carefully managed and quite distinct from that which would occur naturally (APFM, 2011). Nutrient cycles in reservoirs can also be quite different from that of lakes, especially if there is a series of impoundments: while lakes import and mobilise nutrients from upstream, reservoirs downstream of other impoundments can have a nutrient deficit, which can result in oligotrophic conditions (Gloss *et al.*, 1980; Anders and Ashley, 2007). Annual nutrient loading tends to decrease in aquatic areas downstream of a reservoir (Elser and Kimmel, 1985; Matzinger *et al.*, 2007). A lack of nutrients in reservoirs results in low fish abundance, due in part to the strong correlation between phytoplankton productivity and fish production (Adams *et al.*, 1983; Anders and Ashley, 2007).

Freshwater fisheries management should consider the social, economic and cultural benefits provided by recreational fisheries, as well as a variety of other values and services derived from the ecosystem when making management decisions (Cowx and Gerdeaux, 2004; Lynch *et al.*, 2017). Ecosystem-based management strategies,

Informative: A model of a managed reservoir with uncertain flows was constructed in Ecopath with Ecosim, to look at the outcomes on different trophic levels of different management policies regarding nutrient addition.

and tools that can support this concept, can take conflicting priorities into account, such as the values gained from recreational fisheries and conservation limits (Cowx and Gerdeaux, 2004; Pikitch *et al*., 2004; Lynch *et al*., 2017). Fisheries management generally includes actions such as habitat restoration and fisheries regulations; however, it is not well known how these policies may interact with one another or what impact they have on the aquatic ecosystem as a whole (Cowx and Gerdeaux, 2004). While fisheries managers are able to regulate harvest, they are generally not able to regulate other activities that can impact fisheries production if the priority is for other uses such as hydropower and flood control (Lynch *et al*., 2017); therefore, these activities and their impacts must be treated as uncertainties rather than management levers.

The addition of inorganic nutrients to increase productivity of oligotrophic and ultra-oligotrophic freshwater systems was first proposed by Foerster (1968). Initial attempts with coastal sockeye salmon (*Oncorhynchus nerka* (Walbaum)) lakes appeared to show bottom-up transfer of nutrients up the food web to fish stocks, with higher biomass and survival of sockeye salmon smolts (Foerster, 1968; LeBrasseur *et al*., 1978). Fertilisation has also been applied to steep-sided reservoirs, such as Kootenay Lake on the Columbia River, to rebuild fish stocks and allow for recreational harvest (Ashley *et al*., 1997). However, in some cases fertilisation did not appear to have a major effect, and in others it appears to benefit less-desired species (Hyatt *et al*., 2004; Hyatt *et al*., 2005). An additional concern with nutrient addition in reservoirs is that high flows due to water management practices will result in nutrients being swept out of the system, resulting in a large expense and no real benefit (Scott *et al*., 2017). There is also the question of which ecological process, top-down, bottom-up or a combination of both, is more important in stimulating productivity and maintaining a healthy, sustainable fishery (McQueen *et al*., 1989; Power, 1992; Benndorf *et al*., 2002). Some systems have found that other management options (such as stocking, habitat enhancement or predator control) have been required in addition to fertilisation to provide the desired results (McCubbing and Ward, 2002; Perrin *et al*., 2006; Bassett *et al*., 2018d). The benefits of nutrient addition in an interior reservoir with competing water priorities have not been well studied.

The Arrow Lakes Reservoir (Figure 1) was created in 1967 with the construction of the Hugh L. Keenleyside Dam (Schindler *et al*., 2010; Bassett *et al*., 2018a). The reservoir was created by increasing the storage capacity of a natural lake (Hamblin and McAdam, 2003) to prevent downstream flooding and control flows for downstream hydropower generation. Two further dams on the Canadian portion of the Columbia River were completed subsequent to the formation of Arrow Lakes Reservoir: the Mica Dam in 1973 (which formed Kinbasket Reservoir) and the Revelstoke Dam in 1983 (forming Revelstoke Reservoir) (Hamblin and McAdam, 2003). These dams, together with most dams on the Columbia River, work in conjunction to generate power and provide a coordinated flood control, so that flows in one reservoir may be in response to rainfall in another part of the watershed entirely, meaning that high-flow years may

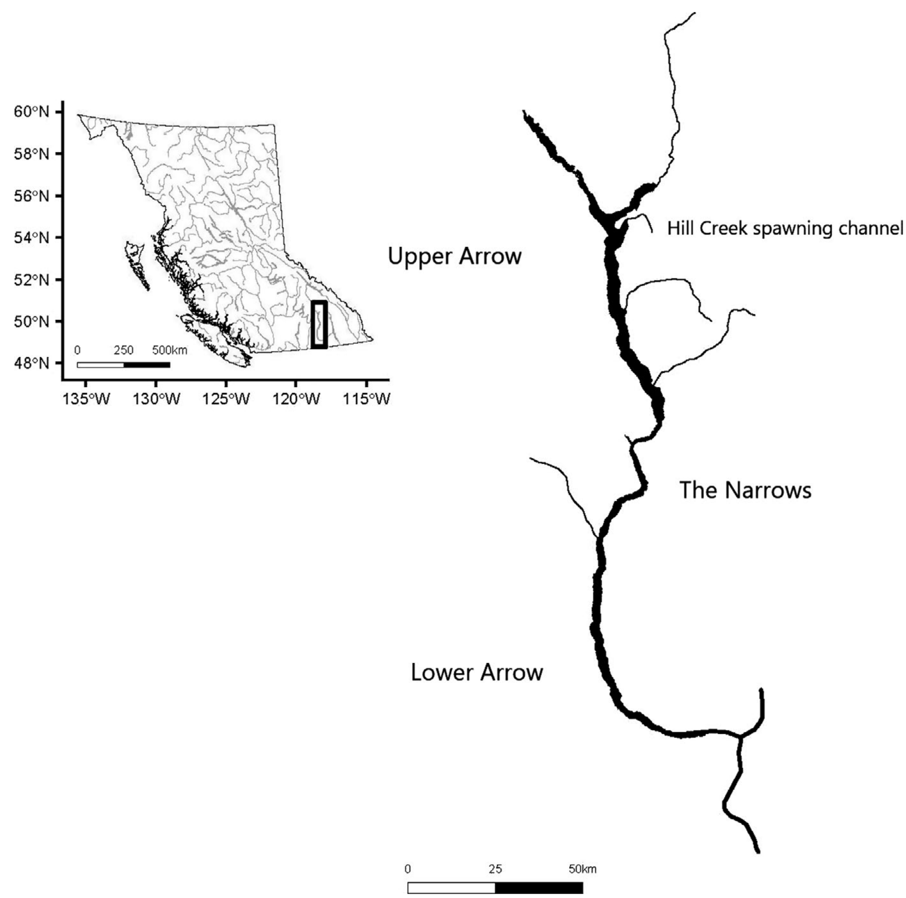

FIGURE 1 The location and map of Arrow Lake Reservoir within British Columbia, Canada

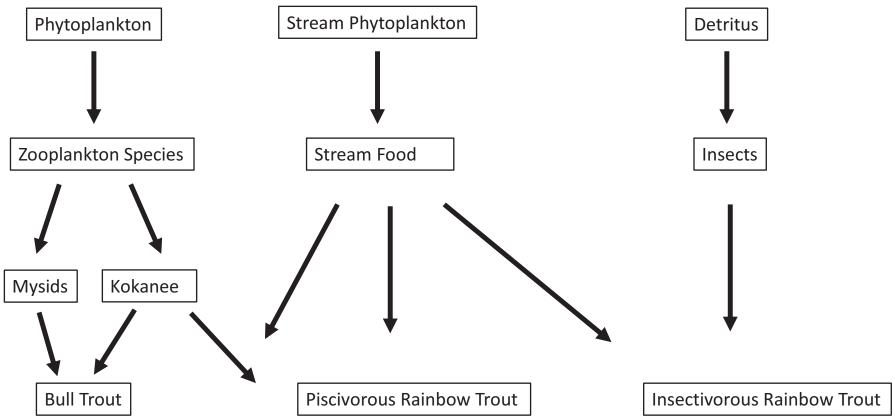

FIGURE 2 A simplified version of the food web as used in the Ecopath model of Arrow Lakes Reservoir

also occur in hot, dry years for some reservoirs (Shuai *et al*., 2019). The construction of the two dams upstream of Arrow Lakes reservoir resulted in the loss of productive stream habitat, as well as a disruption of nutrient flows (Matzinger *et al*., 2007). The large water fluctuations due to drawdowns in the reservoir have also disrupted the natural nutrient cycling, with nutrients being potentially unavailable for uptake in the food web (Matzinger *et al*., 2007; Bassett *et al*., 2018c). The reservoir also has a high flushing rate, with an average residence time of 230 d in the north basin and 90 d in the lower basin (Matzinger *et al*., 2007). Even with nutrient addition, the reservoir is classified as oligotrophic due to the low phosphorus concentrations (Bassett *et al*., 2018c). To compound these effects, mysid shrimp, *Mysis diluviana* (Audzijonyte and Vainola, 2005) were added to Arrow Lakes Reservoir in 1968, in a mistaken attempt to provide an additional food source for kokanee salmon, *Oncorhynchus nerka* (Walbaum), and rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Sparrow *et al*., 1964; Sebastian *et al*., 2000); instead, these shrimp have proven to be a competitor with kokanee for zooplankton prey by grazing on available zooplankton at night and vertically migrating out of the euphotic zone during the day, making them largely unavailable to kokanee (Martin and Northcote, 1991).

There are 24 native fish species in the Canadian portion of the Columbia River, including kokanee salmon, rainbow trout and bull trout (Sebastian *et al*., 2000; Hamblin and McAdam, 2003). Kokanee are the primary pelagic species (Schindler *et al*., 2009) and are an important forage fish for larger trout (*Oncorhynchus* spp.) and char (*Salvelinus* spp.) in this reservoir (van Poorten *et al*., 2014). There have been multiple attempts to recover and enhance the population to sustain a piscivore fishery and secondarily a directed kokanee fishery. A kokanee spawning channel was installed in 1980 to address the loss of kokanee spawning habitat due to reservoir construction (Sebastian *et al*., 2000). The spawning channel is actively managed by regulating the number of returning kokanee allowed into the channel; those not allowed have lower spawning success (Andrusak, 2007). To compensate for the upstream loss of nutrients, a reservoir nutrient restoration programme, in which inorganic nutrients (nitrogen and phosphorus) are added to the system, was established in 1999 (Bassett *et al*., 2018a), but the efficacy of this programme, especially in years of high discharge, has been questioned. The nutrients are applied weekly during the growing season (end of April to the beginning of September) and the ratio of nitrogen to phosphorus is varied throughout the season, to approximate the pre-impoundment spring freshet conditions for phosphorus and the biological uptake of nitrogen (Bassett *et al*. 2018c). Due to the multiple interacting management actions, it has been difficult to determine the direct and interactive effects these compensation measures are having on the overall productivity of the system, and kokanee, rainbow trout and bull trout, *Salvelinus confluentus* (Suckley), production of Arrow Lakes Reservoir (Parkinson and Arndt, 2014). There are concerns that the benefits from nutrient additions do not always continue through the food web and that an increase in predator biomass can lead to a collapse of the forage fish populations (Baxter, 2020).

The objective of this study was to characterise the Arrow Lakes Reservoir ecosystem and use this framework to suggest strategies on how to manage into the future, given uncertainty about interactions among abiotic drivers and various trophic levels. An ecosystem model was constructed to represent the biological dynamics of the Arrow Lakes Reservoir. This model was used to explore how various management actions and variable reservoir discharge interact and affect each modelled component of the ecosystem, and therefore the system as a whole, through forward projection. As there is considerable uncertainty about flow impacts due to increasingly uncertain annual precipitation patterns, Monte Carlo simulations were used that incorporate such uncertainty to evaluate how various management policies regarding nutrient restoration affect harvestable biomass of targeted species. Findings from interactions among policy options and uncertainty in future flow scenarios were framed within a decision analysis, which allows communication and justification of management actions amid uncertainty.

2 | METHODS

The Arrow Lakes Reservoir ecosystem was simulated using the Ecopath with Ecosim (EwE) software. EwE notably includes two sub-models: a static mass-balance model (Christensen and Pauly, 1992), which describes initial abundances, productivities and interactions of various components, and a dynamic model (Walters *et al*. 1997; Walters *et al*. 2000), which simulates changes in all components over time. Ecopath is parameterised using a combination of observations and literature values, while tuning in Ecosim due to density-dependent factors can be based on time series of abundance available through population surveys (Christensen and Walters, 2004). All available data were used to create a realistic representation of the Arrow Lakes Reservoir ecosystem (Figure 2) and its interactions with management interventions.

2.1 | Data

The Ecopath model included 24 functional groups: bull trout, large (piscivorous) and small (insectivorous) rainbow trout populations, kokanee, mysid shrimp, insects, various zooplankton taxonomic groups, stream-based food and phytoplankton, phytoplankton in the reservoir and detritus (Table 1). Data used directly for biomass calculations included phytoplankton, zooplankton, mysid shrimp and kokanee. Phytoplankton, zooplankton and mysid data were taken from monthly surveys during the growing season, April-November (Bassett *et al.*, 2018a). Phytoplankton were collected in an integrated sampling tube; macrozooplankton were collected in a Clarke–Bumpus sampler over three replicate oblique tows; and mysid shrimp were collected in three vertical hauls using a 1 m^2 square-mouthed net (Bassett *et al.*, 2018a). Kokanee abundance indices were collected through autumn hydroacoustic and trawl surveys (Bassett *et al.*, 2018a); rainbow trout and bull trout abundances were modelled predictions (van Poorten and Woodruff, 2019). The estimated biomass was then divided by the habitat area in km^2, incorporating the water level to obtain an estimate of pelagic area (Bassett *et al.*, 2018a). Estimates of P/B (production to biomass ratio; equal to instantaneous mortality at equilibrium) and Q/B (consumption to biomass ratio) were obtained from Thompson (1999) and tuned to balance the model. Diet composition was estimated from Thompson (1999), Arndt (2004) and indirect assessments of diet based on stable isotope ratios measured in various species (van Poorten *et al.*, 2014; Tables 2–4). Parameter values for biomass, P/B and Q/B ratios are shown in Table 1; diet proportions for each functional group are shown in Tables 2–4.

Forcing functions were used in Ecosim to represent the impact of physical and environmental factors on ecosystem groupings (Christensen and Walters, 2004). Nutrient loading rates from natural inputs and nutrient additions (from agricultural grade liquid fertiliser) and water flow data were both used as forcing functions (Figure S1); these forcing functions were both applied to phytoplankton and zooplankton to include the effects of nutrient additions and possible entrainment, respectively. Flow data were also applied as a forcing function to kokanee fry to simulate entrainment. It was assumed that high flows would have a negative effect and low flows would have a positive effect. Total dissolved phosphorus and dissolved inorganic nitrogen information were estimated from nutrient surveys of ambient concentrations, in combination with monthly nutrient additions.

Time series for rainbow trout and bull trout were predicted using fishery-dependent and fishery-independent data. Fishery-dependent data were taken from annual angler interviews; these data included lengths of captured fish, effort and harvest (expanded to incorporate the whole system: S. Arndt, Pers. Comm.) as well as length-at-age data. Length-at-age data, as determined by scale ages, were used to reconstruct age-specific catch and harvest for each species and year. Redd surveys on key spawning streams were included as fishery-independent data. Redd surveys were used as an index of adult abundance, although there may be some non-linearities between true abundance and redd counts due to redd superposition at high spawner abundance. These data were used in statistical catch-at-age stock assessment models (Hilborn and Walters, 1992) to estimate age-specific abundance and biomass for these two species. The Ecosim model was fitted to predicted age-specific time series for each species. Details of each catch-at-age model were provided in van Poorten and Woodruff (2019).

Prey species exist in two states according to Foraging Arena theory: one in which they are vulnerable to predation and one in which they are

TABLE 1 Functional groups and the Ecopath parameters used for the Arrow Lakes Reservoir model

Group name	Biomass (t/km^2)	P/B or Z (year)	Q/B (year)	Ecotrophic efficiency
Bull trout 6+	0.160	0.35	1.1	0.179
Bull trout 3–5	0.103	0.35	1.6	0.028
Bull trout 0–2	0.0403	0.70	3.0	0.000
Large rainbow trout 6+	0.0130	0.80	2.1	0.115
Large rainbow trout 3–5	0.0289	0.50	2.8	0.043
Large rainbow trout 0–2	0.0190	1.00	5.6	0.000
Small rainbow trout 6+	0.0100	0.50	2.5	0.200
Small rainbow trout 3–5	0.0126	0.50	3.5	0.079
Small rainbow trout 0–2	0.00827	1.00	7.0	0.000
Kokanee spawners	0.0500	2.00	5.5	0.653
Kokanee 2+	0.12	1.20	6.4	0.588
Kokanee 1+	0.21	1.70	8.6	0.437
Kokanee 0	0.098	1.90	16.1	0.645
Insects	3	10	40	0.001
Mysid adults	2	5	8	0.000
Mysid juvenile	0.744	4	16.8	0.056
Other zooplankton	10	11	120	0.099
Epischura	4	3	15	0.582
Daphnia	6	10	40	0.225
Leptodiaptomous	4	3	15	0.328
Phytoplankton	30	113		0.376
Stream food	65	10	40	0.000
Stream phytoplankton	100			0.260
Detritus	100			0.036

TABLE 2 Diet matrix for bull trout and rainbow trout in Arrow Lakes Reservoir

	Bull trout			Piscivorous rainbow trout			Insectivorous rainbow trout		
Prey/Predator	Age 6+	Age 3–5	Age 0–2	Age 6+	Age 3–5	Age 0–2	Age 6+	Age 3–5	Age 0–2
Kokanee spawners	0.200	0.100		0.200	0.100				
Kokanee 2+	0.300	0.100		0.300	0.100				
Kokanee 1+	0.300	0.400		0.300	0.400				
Kokanee 0	0.198	0.300		0.200	0.390				
Insects							0.500	0.500	
Mysid adults	0.00200	0.00100							
Other zooplankton		0.0900			0.0100		0.500	0.500	
Stream food			1.00			1.00			1.00

Note: Numbers refer to the proportional contribution of prey (rows) to each age class of bull trout, piscivorous and insectivorous rainbow trout (columns).

TABLE 3 Diet matrix for kokanee in Arrow Lakes Reservoir. Numbers refer to the proportional contribution of prey (rows) to each class of kokanee (columns)

Prey/Predator	Kokanee spawners	Kokanee 2+	Kokanee 1+	Kokanee 0
Other zooplankton	0.150	0.150	0.100	0.100
Epischura	0.100	0.100	0.100	0.100
Daphnia	0.700	0.700	0.700	0.700
Leptodiaptomous	0.0500	0.0500	0.100	0.100

TABLE 4 Diet matrix for mysids and zooplankton in Arrow Lakes Reservoir. Numbers refer to the proportional contribution of prey (rows) to predators (columns)

Prey/Predator	Mysid adult	Mysid juvenile	Other zooplankton	*Epischura*	*Daphnia*	*Leptodiaptomous*
Mysid juvenile	0.0104	0.00	0.00	0.00	0.00	0.00
Other zooplankton	0.156	0.150	0.00	0.00	0.00	0.100
Epischura	0.104	0.150	0.00	0.00	0.00	0.0500
Daphnia	0.156	0.150	0.00	0.00	0.00	0.100
Leptodiaptomous	0.104	0.150	0.00	0.00	0.00	0.00
Edible phytoplankton	0.208	0.300	0.800	0.800	0.900	0.750
Detritus	0.260	0.100	0.200	0.200	0.100	

not (Ahrens *et al*. 2012). The rate at which prey species move between these two states affects the mortality caused by predators, and is a density-dependent factor. If vulnerabilities are low (i.e. close to 1), an increase in the abundance of predators will not result in a corresponding increase in the predation mortality of the prey; this is an example of a bottom-up control situation. Conversely, if vulnerabilities are high, there is very little density dependence and an increase in predators will cause an increase in predation mortality; there is a top-down control by the predator in this situation. The fit of the model to the various data sources (evaluated using the sum of squared deviations between available time series for various species groups and model predictions) was improved by iteratively changing the vulnerability exchange rates using a numerical search routine (Christensen and Walters, 2004). The Ecosim component of the model includes a function that allows the program to adjust the vulnerabilities to obtain the closest fit of the model to the available data (Christensen and Walters, 2004).

2.2 | Model

An EwE model was constructed for the Arrow Lakes Reservoir ecosystem for the years 1998 to 2018. The starting year of 1998 was used to represent the initial state for Ecopath. The Ecopath model assumes mass balance and is constructed using two master equations: the first equation is for production:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \quad (1)$$

where P_i is production of species i, Y_i is the fishery catch rate, $M2_i$ is the instantaneous predation rate, B_i is the biomass, E_i is the net migration rate, BA_i is the biomass accumulation rate, and $M0_i$ is the mortality rate from all other sources. The second equation is for energy balance:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food.} \quad (2)$$

The input parameters used for the Ecopath model of Arrow Lakes Reservoir were biomass, P/B (production to biomass ratio), Q/B (consumption to biomass ratio) and the proportional diet composition of each consumer. The fish species and mysid shrimp species included in the model were separated into different age stanzas to incorporate ontogenetic changes in diet; these were entered into the model as multi-stanza groups, and an estimate of total mortality (Z; equivalent to P/B) was used for the production component of each stanza.

Ecosim provides dynamic simulations for the model, where initial conditions are established through the Ecopath mass-balance solution. The time series of relative biomass estimates (based on the starting year of 1998) was included from 1998 to 2018. Nutrient inputs (1998–2018) and flow measurements (1998–2018) were used as forcing functions on phytoplankton and zooplankton groups, while flow measurements were also applied to age 0 kokanee. The recorded flow measurements were inverted to reflect an increased flushing rate with flow. The model treated the two basins of Arrow Lakes Reservoir as one system.

2.3 | Predictions of environmental effects on ecosystem function

Once the model was fitted to existing data, the system was projected forward to the year 2060 under different combinations of nutrient delivery and flow through the reservoir. Nutrient addition scenarios included a baseline natural nutrient level with average fertilisation (average of nutrient additions by month, from 1999 to 2018) projected forward; using only a baseline nutrient level (natural nutrient level; no nutrient additions); and using an average nutrient addition regime only until June in years that have begun as high-flow years. This final scenario was to examine the effect of stopping nutrients in years of high flow due to the likelihood of additional nutrients being flushed out of the reservoir with little to no beneficial effect, and could be used as a potential cost-saving measure. However, there is no guarantee that flows will continue to be high for the remainder of the year. This scenario represents a strategic gamble made by managers. The time series used as forcing functions are provided in the Supplementary Material.

Flow data (in m^3/s) were accessed through Water Survey of Canada (http://wateroffice.ec.gc.ca) based on measurements immediately downstream of the reservoir. A low-flow scenario was simulated by repeating the monthly flow time series corresponding to flows seen in 2001; the average flow scenario used monthly flows from 2005; and the high-flow scenario used monthly flows from 2012. As it is not realistic to have only all low, average or high flows going forward, flow scenarios were randomly selected for the period 2019 to 2060, leading to one simulation with more average flows, one with more low flows and one with more high flows. A fourth simulation was included to examine the effects of stopping nutrient additions if it appeared that it would be a year of high flow: using the simulation with the greatest number of high flows, the flow was continued until June and then randomly kept as high or changed to either a low or average flow year. As there is a known negative correlation between high flows and phytoplankton biomass (Feiping *et al*., 2013), it was necessary to adjust the low and high flows by taking the inverse values to simulate the positive (from low flows) and negative (from high flows) effects. The time series used as forcing functions are provided in the Supplementary Material.

Different combinations of the timing of nutrient additions and flow through the reservoir were evaluated to see how interactions would affect overall ecosystem fishery performance. To evaluate the various management actions, a Bayesian decision analysis framework was used (Robb and Peterman, 1998). Decision analysis helps determine the performance of different management options amid uncertainty in the system (Walters, 1986). For this purpose, available management actions included every combination of nutrient additions described above. Normally distributed monthly/annual time series of flow were simulated into the future using mean annual flow from the three reference years and a standard deviation of 0.3. Each flow scenario was repeated 100 times across each combination of management intervention.

Fisheries management in Arrow Lakes Reservoir is concerned with satisfying catch expectations for anglers fishing for piscivores (bull trout and large rainbow trout; main priority) and kokanee (a secondary priority). Two management objectives were considered: predator biomass and kokanee biomass. For each combination of flow and management intervention, the proportion of years where piscivore and kokanee biomass exceeded the observed 75th percentile of biomass of the previous 12 years of time series data was calculated. Performance of each management action under each flow scenario was evaluated; the expected performance of each scenario was calculated as the mean performance across flow scenarios. This relative expected performance across management actions is equivalent to the Bayesian posterior estimate of management performance regardless of uncertainty in flow.

3 | RESULTS

3.1 | Ecosystem dynamics: 1998–2018

The Ecosim model did not always capture the variation in observed data (Figures S2-S5). After fitting to time series, vulnerabilities were all greater than 1.0, indicating top-down control (Christensen and Walters, 2004). This was suggested by the data for phytoplankton and zooplankton, which showed little systematic change in relative abundance despite onset of nutrient additions in 1999 (Figure S2).

The model predicted a systematic increase in mysid adults in the years following nutrient additions, whereas juveniles remained relatively constant (Figure S3); this reflects cannibalism in the species, as reflected in the diet composition (Table 4). Kokanee data suggest a response in age-2 and spawner relative abundance immediately after initiating nutrient additions, with increases in age-0 and age-1 the following year (Figure S4). By contrast, the model predicted an increase in abundance in all year-classes immediately after nutrient additions. Model-predicted abundance of all age-classes of kokanee declined by the mid-2000s as predation pressure by piscivores reached a peak.

Although the piscivorous rainbow trout and bull trout data indicated that the age 3–5 groups declined after fertilisation, the model suggested a progressive increase across the species due to increasing zooplankton and then increasing kokanee abundance for the years 2000–2005 (Figure S5). Inter-annual flow variability (Figure S1) led to variation in the abundances of piscivores once they entered the reservoir around the age of 3 (Figure S5).

3.2 | Model projections: 2019–2060

The current nutrient addition regime had poorer performance for kokanee in high-flow years and years where flow was high in spring (Table 5). Maintaining nutrient additions consistently resulted in higher kokanee outcomes than if nutrient additions were eliminated. Cessation of the nutrient restoration programme resulted in few to no years with abundance greater than the 75th percentile (Table 5). The management option where nutrients were halted in summer and autumn after high spring flow years had moderate success, but the uncertainty of whether flows in the remainder of the year would be high or low meant the kokanee objective was still lower than maintaining nutrients at the average rate. The best management option for kokanee, irrespective of annual flow (expected value in Table 5), was to maintain an average nutrient addition regime.

The highest bull trout outcomes were observed with an average fertilisation regime and more average flows, followed by having fertilisation and more low flows (Table 6). A scenario with more high flows or high flows until at least June resulted in fewer years with abundance greater than the 75th percentile. Cessation of the nutrient restoration programme resulted in few years with abundance greater than the 75th percentile (Table 6). Overall, given uncertainty in annual flows from upstream, the best management option was to maintain nutrient outputs regardless of early season flows.

Large rainbow trout age 6+ performed best under low-flow conditions (Table 7). Rainbow trout had the best response when nutrients were halted in the spring of high-flow years, likely due to a decrease in competition from bull trout (which were predicted to have lower biomass under those conditions; Table 6). However, given uncertainty in annual flow variation, the best management option overall was to maintain an average nutrient addition regime (Expected flow column in Table 7).

4 | DISCUSSION

Biomass for each of the focal fish species: kokanee, bull trout and rainbow trout, responded positively to nutrient additions. These three key species responded differently to the different flow regimes because of differences in competition and prey availability. Bull trout was predicted to have the highest biomass with average flows, likely due to a higher abundance of kokanee prey. By contrast, piscivorous rainbow trout was predicted to have higher biomass in years when bull trout biomass declined, possibly due to a predicted lack of competition with bull trout. Bull trout is considered to be one of the top predators in their native ecosystems (Lowery and Beauchamp, 2015). Since the overall objective is to maintain high biomass and catch of all three fish species, the best management action is to maintain nutrient additions throughout the season regardless of what flows occur.

For all trophic levels, the potential productivity of a system was partly determined by nutrient supply (Carpenter *et al*., 1985). Nutrient addition was by far the strongest external driver of system productivity and discontinuing nutrient additions would cause a near-collapse of all fisheries, similar to the initial state of the system, which prompted the programme in the first place. Importantly, quickly discontinuing nutrient additions will result in rapid short-term depletion of large piscivores, which would be quickly noted by anglers. This highlights the importance nutrients play in naturally ultra-oligotrophic systems such as Arrow Lakes Reservoir. Large-scale nutrient restoration programmes have become less common in recent years (Hyatt *et al*., 2004); this is partly due to increased costs of inorganic fertiliser. However, the direct and immediate benefits of these programmes are highlighted by these findings: all objectives suffered when nutrient additions were halted and systems persisted on natural inputs alone.

Scenarios that contained more average or low flows were predicted to result in more years of increased biomass of the higher trophic levels. Hydrological aspects such as water residence time

TABLE 5 Proportion of simulations where the biomass of kokanee spawners was above the 75th quartile of biomass for the years 2007–2018

Scenario	Average flow	High flow	High flow to June, then random	Low flow	Expected value
Average nutrient addition regime	0.46	0.21	0.37	0.45	0.37
No additional nutrients	0.01	0.00	0.02	0.01	0.01
Average nutrient addition regime only to June in high-flow years	0.41	0.16	0.22	0.29	0.29

Note: Expected value is the weighted average of values in each flow scenario weighted by their relative probability of occurrence in the future.

TABLE 6 Decision table for large (age 6+) bull trout

Scenario	Average flow	High flow	High flow to June, then random	Low flow	Expected value
Average nutrient addition regime	0.89	0.45	0.73	0.83	0.73
No additional nutrients	0.08	0.02	0.03	0.11	0.06
Average nutrient addition only to June in high-flow years	0.77	0.22	0.49	0.62	0.53

Note: Values represent the proportion of simulations where the biomass was above the 75th quartile of documented biomass for the years 2007–2018. Expected value is the weighted average of values in each flow scenario weighted by their relative probability of occurrence in the future.

TABLE 7 Large rainbow trout 6+, percentage of simulations where the biomass was above the 75th quartile of documented biomass for the years 2007–2018

Scenario	Average flow	High flow	High flow to June, then random	Low flow	Expected value
Average nutrient addition regime	0.094	0.091	0.10	0.12	0.10
No additional nutrients	0.047	0.024	0.024	0.072	0.04
Average nutrient addition only to June in high-flow years	0.093	0.055	0.059	0.17	0.09

Note: Expected value is the weighted average of values in each flow scenario weighted by their relative probability of occurrence in the future.

and flow rate have been shown to influence zooplankton dynamics (Obertegger *et al*., 2007), with longer residence times resulting in higher crustacean abundance and biomass. Zooplankton biomass has been shown to be positively correlated with water retention time (Campbell *et al*., 1998), possibly due to the reduced swimming abilities of the larval forms (Dodson and Ramcharan, 1991). Increased zooplankton biomass, especially in preferred prey items such as cladocerans and copepods, would have positive impacts on the planktivorous kokanee populations and thus provide more forage fish for the piscivores (Hansen *et al*., 2010).

Although bull trout had more years of higher biomass in scenarios with more average flow years and showed a strong positive response to fertilisation, piscivorous rainbow trout fared better under low-flow conditions. Bull trout had fewer years with higher biomass under low-flow conditions; it is possible that rainbow trout are at a competitive disadvantage with bull trout, and able to increase in biomass with a reduction in bull trout biomass. In other systems, bull trout is the predominant predator of kokanee (Hansen *et al*., 2010). Other char species, such as lake trout, *Salvelinus namaycush* (Walbaum), which have a similar size, diet and life history to bull trout, have been shown to react to fish prey at greater distances than rainbow trout, and lake trout has been known to cause declines in native trout species when introduced (Mazur and Beauchamp, 2003). If bull trout is a more efficient predator than rainbow trout, any situation where bull trout biomass declines will provide more opportunities for rainbow trout to increase in abundance.

Due to the uniqueness of each freshwater system, it is unlikely that a universal critical flow exists, making it difficult to predict the effects of flows overall (Feiping *et al*., 2013). In reservoirs especially, there tends to be a nutrient gradient, characterised by riverine, lacustrine and transitional zones (Kennedy, 1984). In larger systems, high productivity generally occurs in upstream or mid-reservoir areas, at a distance from the outlet dam (Kennedy, 1984). Despite the size of Arrow Lakes Reservoir (>200 km long), this reservoir has a high flushing rate, (Matzinger *et al*., 2007), which may distort this pattern. The model results suggest that flow has an appreciable impact on overall ecosystem objectives, with high flows resulting in decreases in biomass for both planktivorous and piscivorous fishes.

Arrow Lakes Reservoir and the Hugh Keenleyside Dam are part of a series of reservoirs along the mainstem of the Columbia River. The location of the reservoir (downstream from two other large hydroelectric reservoirs and upstream from many others, as well as many communities downstream) means that flows are subject to high variability due to precipitation patterns throughout the large Columbia watershed and associated power and water storage demands (Thomson *et al*., 2017). It is reasonable to assume nutrients and resultant phytoplankton and zooplankton might be entrained downstream in high-flow years, suggesting high cost to the Arrow Lakes ecosystem with no local benefit. Further, if flows are high through the spring and the addition of nutrients was stopped, how likely will high flows be through the remainder of the season? These uncertainties and potential actions have large consequences for ecosystem function. If money used to deliver nutrients were used for other mitigative actions, there may be greater benefits to the ecosystem as a whole. These questions are valid and should be considered. Results of this study are only relevant to the specific objectives and scenarios evaluated; there may be greater benefit if nutrient dollars were used for other actions. This decision analysis suggests that continuing nutrient restoration is robust to uncertainty in flow. Future work could expand on these results by exploring alternative mitigative options.

There were several assumptions made when building the model. The model assumes that low flows produce more of a positive effect than high flows. Although there are two basins (Upper and Lower Arrow, separated by The Narrows; Figure 1), the model treated the system as a whole, so that nutrients and flow would have an equal effect throughout the reservoir. Kokanee from the spawning channel and wild fish were combined into one group, which assumes that annual recruitment between the two groups is correlated. The model assumes that kokanee fry would be affected by flow and that zooplankton and phytoplankton would all be affected by nutrient addition and flows. The assumptions on flow and the positive effect of nutrients would then bias the abundance estimates upwards and increase the effect of nutrients and lower flows. While any of these assumptions may be incorrect, the model predictions are consistent with the data. Moreover, previous models of the system (not shown) show that changes to some of these assumptions either do not lead to credible predictions or provide lower impact of flow and nutrients on biomass. Regardless of how the system was modelled, results from the decision analysis were the same, suggesting a robustness of these findings.

This study did not take into account the use of changing recreational fishery regulations to increase sustainable fisheries. It is unlikely that mangers would make substantial changes to fishing regulations to reduce the amount of harvest, due to the likely backlash from the anglers. The fishery management objective for this reservoir is to support a world class recreational fishery for piscivorous rainbow trout, as well as increasing opportunities for a kokanee fishery (FWCP, 2012); the nutrient addition programme is implemented to increase production and allow more harvest (Bassett *et al*., 2018b). Regulations tend to focus on distributing harvest opportunity across anglers (through individual harvest limits) but do not actually control the overall effort or limit the number of anglers (Arlinghaus and Cooke, 2009).

For decades, limnologists have focused on the effects of eutrophication on freshwater systems (Goldman, 1988; Smith, 2003). There are attempts to reduce nutrient loading, and situations where the addition of nutrients to a waterbody is considered pollution (Smith *et al*., 2006). This project examined the opposite situation, in which nutrients had been anthropogenically reduced, leading to a loss of productivity in the reservoir and it was necessary to add inorganic nutrients to the system (Stockner *et al*., 2000). Although the cost of fertiliser is high, having a healthy ecosystem with high fisheries values allows for an economic benefit from recreational angler use (Post *et al*., 2002). Oligotrophic systems are generally considered to be more aesthetically pleasing, due to the clear waters, but these systems are inefficient due to the low levels of algal biomass, and are unable to support high levels of fish production (Stockner *et al*., 2000). Even in the oligotrophic Arrow Lakes Reservoir, the addition of nutrients requires constant monitoring, as an imbalance of the N:P ratio can still lead to either increases in inedible phytoplankton, or blooms of blue-green algae, such as are seen in systems undergoing eutrophication (Hyatt *et al*., 2004). The importance of maintaining a healthy ecosystem must be a primary goal for both eutrophic and oligotrophic systems.

This study shows that greater fishery outcomes are achieved more often when flows were average or low in Arrow Lakes Reservoir. Managers and stakeholders have questioned whether nutrient addition, which is expensive and uncertain, is necessary at all or if nutrient additions can cease in years of high flow. However, the data and the model predictions show nutrient additions are necessary to maintain fishery values and predator biomass. With the trade-off between expensive, uncertain nutrient additions and high-flow events, which are difficult to predict, this work provides an understanding in the efficacy of different nutrient addition options in the face of this uncertainty. The model and associated results were able to show the value in the nutrient restoration programme and demonstrate that the option to cease nutrients in June if high flows have been seen to date is still inferior to continuing nutrient additions. The decision analysis used in this study allows clear communication of the multitude of interacting effects (Walters, 1986), which should help managers understand the important aspects of the system and should lead to improved management and confidence in future management interventions.

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CONFLICT OF INTEREST

We declare that we have no conflict of interest with this research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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