



An assessment tool for estimating effects of entrainment at hydropower facilities on adfluvial fish populations

Hsien-Yung Lin¹ · Eduardo G. Martins² · Michael Power³ · James A. Crossman⁴ · Alf J. Leake⁵ · Steven J. Cooke¹

Accepted: 18 April 2022

© The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2022

Abstract

The growing demand for hydropower has influenced the connectivity of freshwater ecosystems. Entrainment through turbines has been identified as one factor which can potentially affect fish populations within and downstream of reservoirs and, in some cases, large numbers of entrained fish are recorded. There is a need to understand and assess species-specific population-level effects of entrainment by considering population growth rate, maturation age, and fecundity. Here, we used field-derived data, life stage-structured population models and Monte Carlo simulations to estimate the influence of the entrainment rate on adfluvial kokanee (*Oncorhynchus nerka*) and bull trout (*Salvelinus confluentus*) populations. Sensitivity and elasticity analyses suggested that entrainment of early life stages have a relatively large effect on long-term population growth. Populations downstream of hydropower facilities may have a relatively high growth rate if fish entrained from upstream survive and downstream habitats are conducive to supporting population growth. Given the same entrainment rates on early life stages, kokanee generally had a lower probability of population decline than bull trout. However, the risk of population decline for kokanee increased more rapidly than bull trout with increasing entrainment rate. Our study provides a framework and assessment tool that could help identifying species-specific critical life stages that require further investigation and management attention to mitigate the negative effect of entrainment on fish population. The relationship between entrainment rate and the probability of population decline could be used to inform threshold setting for acceptable entrainment rate based on management goals. Importantly, field surveys and long-term monitoring will be important to verify model assumptions and reduce the uncertainties in modeling outcomes because of the stage/age-, population-, and reservoir-specific entrainment-related parameters and different facility designs and sizes.

Keywords Assessment tools · Potamodromous · Adfluvial fish · Population dynamics · Entrainment · Hydropower dams

1 Introduction

There is growing demand for hydropower dams because of the increase in human population and economic activities (Zarfl et al. 2014). With ~40,000 existing large dams (height > 15 m) and at least 3700 hydropower dams (capacity > 1 megawatts) that are either planned or under construction worldwide, river connectivity loss and fragmentation are significant issues for fish populations (Barbarossa et al. 2020; Grill et al. 2019). Although hydropower facilities provide important services to human societies such as electricity, water storage, and flood control, they are also considered as one of the largest threats to freshwater biodiversity as a result of creating barriers blocking wildlife and nutrient movement that turn lotic systems into lentic systems (i.e., reservoirs), and modify flow and thermal regimes (Reid et al. 2019; Wu et al. 2019). In tropical and temperate areas, dams

✉ Hsien-Yung Lin
hylin0625@gmail.com

¹ Institute of Environmental and Interdisciplinary Science and Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

² Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada

³ Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada

⁴ Fish and Aquatic Issues, BC Hydro, 601 18th St., Castlegar, BC V1N 2N1, Canada

⁵ Fish and Aquatic Issues, BC Hydro, 6911 Southpoint Drive, Burnaby, BC V3N 4X8, Canada

have also significantly reduced the richness and diversity of fish species, and increased the number of non-native species (Turgeon et al. 2019).

Previous biological studies of dam impacts have focused on the negative effects of dams on migratory and fluvial fish species and associated socio-economic activities like fisheries (Barbarossa et al. 2020; Harrison et al. 2019; Liermann et al. 2012; Wu et al. 2019). However, transitioning from lotic to lentic systems through reservoir creation provides an opportunity for species capable of adapting to the new habitat, such as generalists, large-bodied piscivores, and adfluvial fish (i.e., fish that spawn and hatch in tributaries but feed and mature in lakes) (Arostegui and Quinn 2019; Turgeon et al. 2019). Despite the adaptive potential of some species to remain productive in regulated systems, the operation of reservoirs may predispose some species to elevated risks at certain life stages, in particular when they occupy habitats within the direct operational influence of the dam. For example, fish with life stages utilizing littoral habitats are vulnerable to habitat loss and stranding due to changing reservoir water level, while fish that occupy pelagic forebay areas are susceptible to entrainment, i.e., fish are displaced from reservoirs to downstream reaches through hydropower turbine intakes during hydropower generation, which may cause injury or mortality (Harrison et al. 2019; Hirsch et al. 2017; Martins et al. 2014; Nagrodski et al. 2012). Therefore, it is important to understand the key components of facility design and seasonal operations that affect the persistence of fish populations in upstream reservoirs and reaches downstream of dams.

For resident or adfluvial fishes that utilize reservoirs, dams without fish passage create unidirectional (downstream) passage that fragments habitat and directly removes individuals from the upstream population through entrainment (Ardren and Bernall 2017; Harrison et al. 2019). For example, entrainment through hydropower dams has relocated upstream paddlefish (*Polyodon spathula*), tubenose goby (*Proterorhinus semilunaris*), kokanee (landlocked sockeye salmon, *Oncorhynchus nerka*), and other species to downstream areas (Dawson and Parkinson 2013; Janáč et al. 2013; Pracheil et al. 2015). While entrainment can contribute to the recruitment of downstream populations and population dispersal if some entrained fish survive (Harrison et al. 2019; Janáč et al. 2013), it typically results in an overall loss to the population due to passage mortality (Harrison et al. 2019; Pracheil et al. 2016). Both lab- and field-based studies have been conducted to estimate the entrainment rate (i.e., percentage of population that is lost as a result of passage through turbines and/or spillways) and associated mortality across different species, locations, dam structures and operations (Algera et al. 2020; Harrison et al. 2019; Pracheil et al. 2016). Knowledge of the entrainment and mortality rates alone, however, are not sufficient

to understand population-level responses because population dynamics are also influenced by other vital rates such as growth, maturation rates and fecundity (Power 2007). For example, fish/populations with early maturation and high fecundity may be less vulnerable to entrainment losses (Čada and Schweizer 2012; Harrison et al. 2016). Therefore, long-term monitoring or modeling fish population dynamics and age/size structure changes are needed to appropriately examine the population-level effect of entrainment on fish populations in addition to estimating entrainment and mortality rates (e.g., Underwood and Cramer 2007).

Kokanee and bull trout (*Salvelinus confluentus*) are economically and ecologically important species throughout the Western Cordillera region of North America, and their distributions overlap with areas of hydropower development (Hagen and Decker 2011; Pracheil et al. 2016). The US populations of bull trout have been listed as Threatened under the US Endangered Species Act and several Canadian populations are listed as Threatened or of Special Concern under the Canadian Species At Risk Act (COSEWIC 2012). Although many populations of kokanee are relatively stable and have been stocked in US and Canadian reservoirs to boost local recreational fisheries, entrainment through hydropower plants has the potential to significantly reduce the abundance of kokanee populations in some reservoirs (Baldwin and Polacek 2002; Dawson and Parkinson 2013). Studies have been conducted to estimate entrainment rates for young-of-year kokanee (e.g., 30% in Harrison et al. (2019)) or adult bull trout (e.g., 0.5–3.4% in Harrison et al. (2020) and Martins et al. (2013)). Nevertheless, there remains a lack of understanding regarding the immediate mortality and delayed mortality for these two species. Furthermore, the population-level effects of entrainment in a dam cascade system have rarely been studied as most studies focus on either the population upstream or downstream of a dam, see Pate et al. (2014), Parkinson and Arndt (2014), and Underwood and Cramer (2007).

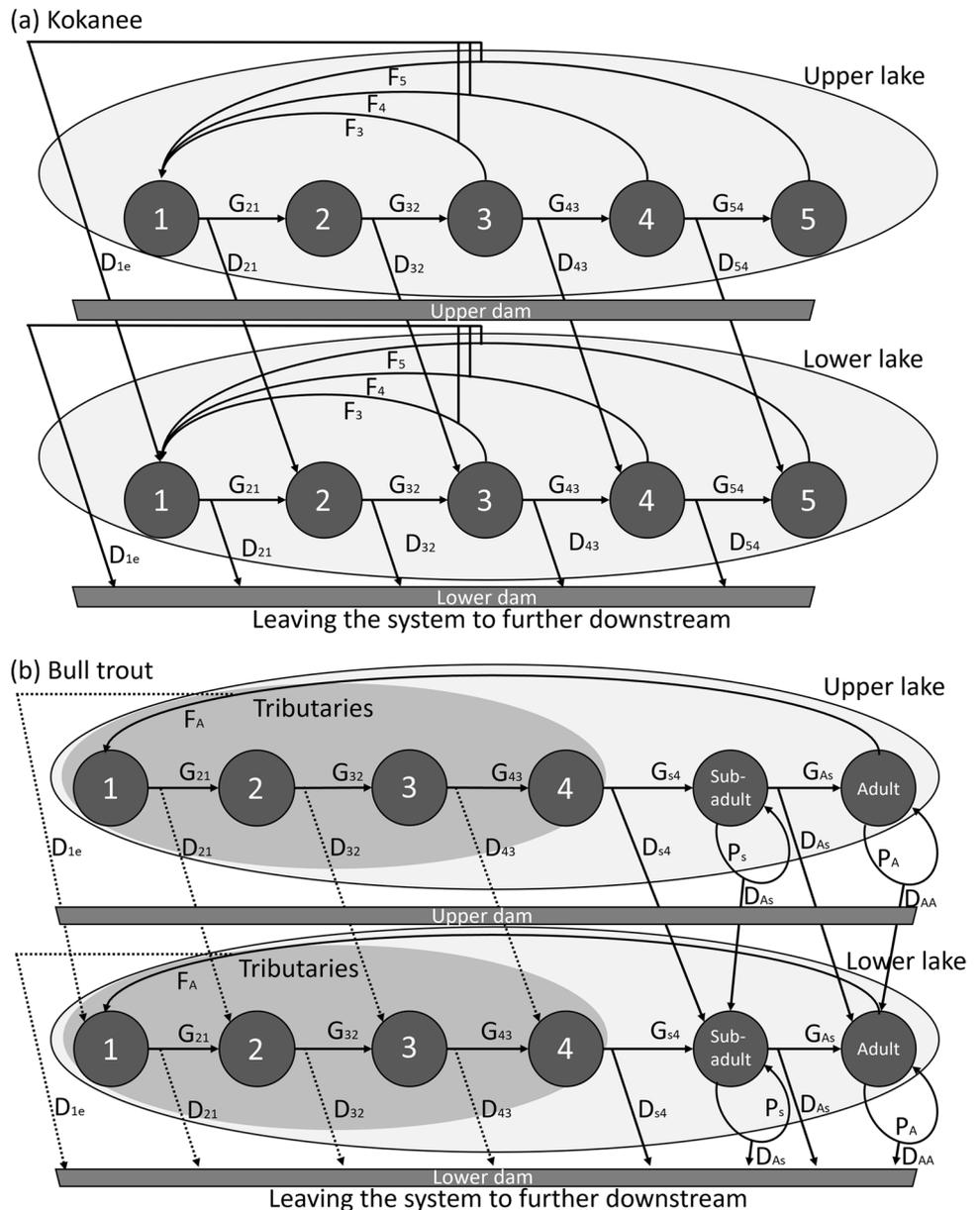
The primary objective of this study was to examine the population-level effects of entrainment and its associated mortality on kokanee and bull trout populations separated by barriers that only permit downstream passage (e.g., hydropower plants without upstream fish passage provisions). We explored how intrinsic rates of population growth varied across a range of demographic parameters, entrainment rates, and entrainment mortality scenarios. While most demographic parameters were collected from previous studies, entrainment parameters were defined by authors (and informed by previous studies) to explore the potential consequences of different entrainment scenarios due to limited empirical data for most hydropower facilities. Testing a range of parameters allows us to address parameter uncertainty, improve the applicability of our results to different reservoir systems, and yields better

information to determine the necessity for entrainment mitigation. Specifically, we (1) developed a stage-structured population model for each species, (2) identified the life stages having greatest influence on population growth (“critical life stages” hereafter) by examining the sensitivity and elasticity of population growth rate to change in underlying demographic parameters, (3) assessed the effect of entrainment rate and entrainment mortality on population growth rates, and (4) investigated the probability of population abundance decline under varying entrainment rate scenarios.

2 Materials and methods

We simulated a system with two reservoir habitats and two downstream only pass barriers, each at the most downstream point of each reservoir (Fig. 1), representing a dam cascade system like the Williston Lake-W.A.C. Bennett Dam-Dinosaur Lake-Peace Canyon Dam cascade on the Peace River in northern British Columbia (BC), Canada; nevertheless, the results of our model is not specific for a certain hydropower facility but exploring various possible scenarios, and similar system (i.e., a series of dams along one river) could be found around the world (Barbarossa et al. 2020).

Fig. 1 Stage-structured population models for **a** kokanee and **b** bull trout, in which G_{ji} is the transition probability from stage i to stage j , F_i is the number of age-1 fish produced per spawner at stage i , P_i is the probability of remaining in stage i , and D_{ji} is the proportion of upstream fish joining downstream population, a result of entrainment rate and associated mortality during stage i to j . The grey-shaded areas and dotted lines on bull trout model represent stages when all or part of the population is in tributaries (so less susceptible to entrainment) and the proportion of fish in tributaries gradually decreased as they grow (see Table 2)



2.1 Model structures

Stage-structured population models (Caswell 2001; Kendall et al. 2019) were developed for kokanee (Fig. 1a) and bull trout (Fig. 1b) and both models included two populations separated by barrier which allowed for only downstream passage. The kokanee model included five stages reflective of the age-class distribution for kokanee, in which fish became mature between their third and fifth years depending on body length as observed in most BC lakes (Parkinson and Arndt 2014; Plate et al. 2012; Sebastian et al. 2009). The bull trout model included six stages, in which the first four stages were represented as ages 1 to 4 (i.e., no individuals remained in those stages for more than one year) and the last two stages, subadult and adult, had a probability of remaining in the same stage depending on the age at maturation and maximum age (see details in the next section). The model structure for bull trout was based on other bull trout models (Bowerman 2013; Caskenette et al. 2016), in which the separated early life stages allow us to use age-specific entrainment rates influenced by ontogenetic migration from

tributaries to reservoirs (i.e., higher probability of entrainment for fish living in the reservoir than in tributaries). In contrast, subadult and adult stages were used because the entrainment rates for these stages are relatively low and there is no significant difference in the entrainment vulnerability among adult sized bull trout over a wide range of body length (Harrison et al. 2020; Martins et al. 2013; Underwood and Cramer 2007). As a semelparous species, all kokanee die after spawning while iteroparous bull trout may spawn multiple times in their lifetime but not necessarily every year (Arostegui and Quinn 2019; Benjamin et al. 2020).

2.2 Demographic variables

The values of demographic variables including stage-specific survival rates (s_{ji} , both species), stage-specific length (l_i , both species), annual probability of mature fish spawning (SP , bull trout), asymptotic length (l_{max} , bull trout), growth parameter (k , bull trout), and hypothetical age at length zero (t_0 , bull trout) were extracted from peer-reviewed studies and grey literature (Table 1 and Supplementary File) through Web of Science,

Table 1 Demographic variables extracted from literature, their ranges, and sources used in stage-structured population models

Variable	Range	Sources
Kokanee model		
Survival rate from egg to stage 1, s_{1e}	0.05–0.5	Kootenay Lake, BC (Bell 2009, 2006; Kurota et al. 2011; Neufeld 2018, 2016, 2013); Arrow Lakes, BC (Andrusak 2006; Manson 2005); Okanagan Lake, BC (Webster 2016; Wilson and Andrusak 2005); Kinbasket Lake, BC (Bray et al. 2018); Revelstoke Lake, BC (Bray et al. 2018); Alouette Lake, BC (Andrusak 2013); Williston Lake, BC (E Parkinson, Pers. Comm. 2020)
Survival rate from stage 1 to 2, s_{21}	0.14–0.56	
Survival rate from stage 2 to 3, s_{32}	0.60–0.69	
Survival rate from stage 3 to 4, s_{43}	0.74–0.80	
Survival rate from stage 4 to 5, s_{54}	0.74–0.80	
Length at stage 3	177–275 mm	Kootenay Lake, BC (Andrusak and Andrusak 2015; Peck et al. 2019); Arrow Lakes, BC (Sebastian et al. 2002a, b); Kinbasket Lake, BC (Bray et al. 2018); Revelstoke Lake, BC (Bray et al. 2018); Alouette Lake, BC (Andrusak 2013); Williston Lake, BC (Plate et al. 2012; Sebastian et al. 2009); Skaha Lake, BC (Northcote et al. 1972); Lake Sutherland, WA (Hansen et al. 2016); 10 lakes, ID (Rieman and Myers 1992)
Length at stage 4	207–318 mm	
Length at stage 5	260–278 mm	
Bull trout model		
Survival rate from egg to stage 1, s_{1e}	0.19–0.91	Kootenay Lake, BC (Andrusak and Thorley 2013); Chowade River, BC (Baxter 1996); Metolius River, OR (Bowerman et al. 2014); Estimated stage-specific survival rates from studies in multiple waterbodies in AB, MT, OR, and WA (Caskenette et al. 2016)
Survival rate from stage 1 to 2, s_{21}	0.01–0.14	
Survival rate from stage 2 to 3, s_{32}	0.16–0.52	
Survival rate from stage 3 to 4, s_{43}	0.28–0.67	
Survival rate from stage 4 to subadult, s_{s4}	0.38–0.74	
Survival rate from subadult to adult or remain as subadult, s_{As}	0.45–0.77	
Survival rate during adult stage, s_{AA}	0.50–0.85	
Asymptotic length, l_{max}	768–844 mm	Estimates from von Bertalanffy curves using length-at-age data from waterbodies in AB, BC, ID, MT, NWT, OR, and WA (Caskenette et al. 2016)
Growth parameter, k	0.12–0.14	
Hypothetical age at length zero, t_0	0.17–0.32	
Annual probability of mature fish spawning, SP	0.5–1	Andrusak and Thorley (2013) and Caskenette et al. (2016)

For the kokanee model, stages are equal to ages. For bull trout model, stages 1 to 4 represent ages 1 to 4 while the probability of subadults entering the adult stage depends on age at maturation and maximum age

AB Alberta, BC British Columbia, ID Idaho, MT Montana, NWT Northwest Territories, OR Oregon, WA Washington

Google Scholar, and The Ecological Reports Catalogue (Eco-Cat, <http://a100.gov.bc.ca/pub/acat/public/welcome.do>), a catalogue of reports archived by the British Columbia Ministry of the Environment. In addition to publicly available studies and reports, we also obtained stage-specific survival and length values from an unpublished government database for kokanee (Eric Parkinson, personal communication, 2020). We focused on collecting estimates from studies and reports conducted within the species' native range (BC in Canada, and Washington, Oregon, and Idaho in the US for kokanee; Alberta, BC, and Northwest Territories in Canada, and Washington, Oregon, Idaho, and Montana in the US for bull trout; Table 1). Mean values were calculated for studies with multiyear data to represent the value for populations in those studies. The range of each variable was either the minimum and maximum of recorded values from multiple studies or the lower and upper bounds of 95% confidence intervals from summarized data. While most values could be directly recorded from literature, Web Plot Digitizer (<https://automeris.io/WebPlotDigitizer>) was used when only figures were available (e.g., Fig. 4 in Hansen et al. (2016)). More than 20 studies were used to obtain demographic variables for kokanee while most estimates for bull trout have been summarized in Caskenette et al. (2016). When possible, we used parameters specific for adfluvial bull trout. These variables were then used to calculate the variables in the transitional matrix of stage-structured population models (arrows within each population in Fig. 1).

Overall, variables directly used in the population models included the transition probability of surviving stage i and moving to the next stage j (G_{ji}), number of age-1 fish produced per spawner at stage i (F_i), and the stage-specific annual probability of surviving and remaining in stage i (P_i). Here we used the same set of demographic variables and entrainment-related variables for fish in both upstream and downstream reservoirs. Nevertheless, we acknowledge that biotic and abiotic conditions for cascade reservoirs likely differ and may lead to different demographic variables between populations.

For the kokanee model, stage-specific transition probability G_{ji} was calculated as

$$G_{ji} = (1 - m_i) \times s_{ji} \times (1 - E_{ji}), \tag{1}$$

in which m_i is the maturation probability at stage i , s_{ji} is the survival rate from stage i to j , and E_{ji} is the entrainment rate from stage i to j . There is no m_1 and m_2 because no kokanee became mature at the first two stages (i.e., first 2 years), and m_5 was 1 because all individuals became mature at stage 5 (see "Model structures" section). The maturation probability in stage 3 and 4 (m_3 and m_4) was calculated as

$$m_i = l_i^{15} / (l_i^{15} + L50_i^{15}), \tag{2}$$

where l_i is fish length at stage i and $L50_i$ is the length at which 50% of a cohort of stage i fish matures. $L50_i$ is 280

and 200 mm for stage 2 and 3 kokanee, respectively (Parkinson and Arndt 2014).

The F_i for kokanee was calculated based on sex ratio, maturation probability, fecundity, and early survivorship and entrainment, as in following equation,

$$F_i = 0.5 \times m_i \times Fecundity_i \times s_{1e} \times (1 - E_{1e}), \tag{3}$$

in which sex ratio is set as 1:1 [i.e., 50% are females, see Bell (2009) and Webster (2016)], s_{1e} is the survival rate from egg to stage 1, and E_{1e} is the entrainment rate from egg to stage 1. Fecundity at stage i was calculated using equations from McGurk (2000) that depend on fish length and latitude.

For bull trout, stage-specific transition probabilities G_{ji} were calculated based on stage-specific survival rates (s_{ji}), entrainment rates (E_{ji}), and the probability of moving forward to the next stage (r_i).

$$G_{ji} = s_{ji} \times (1 - E_{ji}) \times r_i. \tag{4}$$

r_i is set to 1 for the initial four stages (stage 1, new recruit, to stage 4, juvenile), which equate to ages 1 to 4 (Caskenette et al. 2016). For subadult and adult stages r_i can be computed assuming the population is stationary as:

$$r_i = \frac{(s_{ji})^T - (s_{ji})^{T-1}}{(s_{ji})^T - 1}, \quad i = s \text{ (subadult) or } A \text{ (adult)}, \tag{5}$$

where s_{ji} is survival rate between stage i and j and T is the duration of the stage in years (Caskenette et al. 2016; Caswell 2001; Lefkovitch 1965). For subadult (r_s), T is the duration between entering the subadult stage and age at maturity (t_{mat}) and for adult (r_A), T is the duration between t_{mat} and the maximum age of the population (t_{max}). The use of r_A for adults represents survival adjusted by maximum age (t_{max}) as in Caskenette et al. (2016). Age at maturity was calculated as:

$$t_{mat} = -\frac{\log\left(1 - \frac{l_{mat}}{l_{max}}\right)}{k} + t_0, \tag{6}$$

where l_{mat} is length at maturity, l_{max} is asymptotic length, k is the growth parameter from the von Bertalanffy model, and t_0 is hypothetical age at length zero, and maximum age was calculated as:

$$t_{max} = e^{(0.5498+0.9571\log(t_{mat}))}, \tag{7}$$

(Caskenette et al. 2016; Froese and Binohlan 2000).

Number of age-1 fish produced per mature adult bull trout (F_A) was calculated from the three equations below,

$$Fecundity_A = 0.0001 \times (l_A)^{2.7326} \tag{8}$$

and

$$F_i = 0.5 \times SP \times \text{Fecundity}_A \times s_{1e} \times (1 - E_{1e}). \quad (9)$$

The first equation was estimated from empirical length and fecundity data from Fig. 4 in Caskenette et al. (2016) and l_A was the length of adult bull trout. The second equation then integrated fecundity, annual probability of mature fish spawning (SP), survival rate from egg to stage 1 (s_{1e}), and entrainment rate from egg to stage 1 (E_{1e}) into the number of age-1 fish produced. Sex ratio was set as 1:1 (i.e., 50% females) based on previous observation (Hagen and Weber 2019). Because the adult stage of bull trout includes several age classes and a range of lengths, the length of adult fish was randomly selected from a uniform distribution between length at maturity and maximum length with Monte Carlo simulation for 10,000 times. Length at maturity was calculated from

$$l_{\text{mat}} = 10 \times e^{(0.8979 \times \log(\frac{l_{\text{max}}}{10}) - 0.0782)}, \quad (10)$$

in which l_{max} is the asymptotic length (Caskenette et al. 2016; Froese and Binohlan 2000).

Finally, the annual probability of surviving and remaining as subadult (P_s) or adult (P_A) bull trout was calculated as

$$P_i = s_{ji} \times (1 - r_i) \times (1 - E_{ji}), \quad i = s \text{ (subadult) or } A \text{ (adult)}, \quad (11)$$

in which s_{ji} is the survival probability, r_i is the probability of moving forward to the next stage (see Eqs. 6–8), and E_{ji} is the entrainment rate.

We used two stage-specific variables to represent the effect of entrainment, the entrainment rate (E_{ji}) and entrainment survival (p_{ji}). Therefore, the proportion of upstream fish joining downstream population was calculated as

$$D_{ji} = E_{ji} \times p_{ji}, \quad (12)$$

in which the passage mortality included both short-term and delayed mortality (Harrison et al. 2019) and these two values (E_{ji} and p_{ji}) were set as described below.

2.3 Identifying critical life stages (sensitivity analyses)

To identify those life stages critical to population growth, we first ran the models with no entrainment rate and examined the sensitivity and elasticity of population growth rate (λ) to the demographic variables (all variables in Table 1) for each life stage of each species (see Fig. 1). The initial population of kokanee consisted of 80% stage 1, 15% stage 2, 3% stage 3, 2% stage 4, and < 1% stage 5 (Supplementary file), based on the observation in Williston and lakes across BC (Sebastian et al., 2009). Same initial stage structure with similar composition (Supplementary File) was used for bull

trout for the sake of simplicity because there is a lack of stage/age structure data for adfluvial bull trout (Hagen and Weber 2019; Plate et al. 2012; Sebastian et al. 2009). We used Monte Carlo simulations to capture the variations and uncertainties in variables, in which model input were randomly drawn from the range of each variable shown on Table 1 (Morris and Doak 2002). For each species, 10,000 matrices with variable values randomly drawn from uniform distributions within their ranges were used to project population dynamics for 50 years. Then, we calculated the population growth rate λ of each projection to examine the potential range of population growth rate. The λ examined in this study was the finite annual rate of increase between the first and last simulated time (i.e., geometric mean of λ over 50 years, λ_g hereafter). Overall, 10,000 estimates of λ were produced per species and the distributions of λ were examined. We also ran simulations with the same set of variables and variable ranges for 50,000 and 100,000 times and found identical distributions of λ . Thus, we only present the results of 10,000 repeated simulations here and for following scenario analyses.

Multiple regression was used to examine the influence of absolute change (i.e., sensitivity) and proportional change (i.e., elasticity) in each demographic variable on λ , in which population growth (i.e., 10,000 different λ) was the dependent variable and modeled by an additive linear function of different variable inputs (Meehan et al. 2018). Variables were centered on the mean and the original scales were maintained for sensitivity analyses. In contrast, to examine the elasticity, variables were centered and scaled by the standard deviation as standardization across variables. We defined critical life stages as the stages that have variables with highest sensitivity and elasticity values (i.e., coefficients) because this indicates that disturbances (e.g., entrainment) occurring on these life stages may have a relatively large influence on population growth rate. Two critical life stages were identified for each species.

2.4 Examining the effects of entrainment and passage mortality

We developed four scenarios to compare the effect of entrainment rate and mortality on kokanee and bull trout populations. Stage-specific entrainment rate and mortality derived from literature and assumptions were used to build the baseline scenario (Table 2). In general, earlier life stages are more likely to be entrained but with higher survival rates, while adults may entrain at lower rates but suffer higher entrainment mortality (Harrison et al. 2019). We used 30% as the entrainment rate for the two earliest life stages of kokanee for the baseline scenario, which is the value estimated for age 1 kokanee through Mica Dam (BC, Canada, Harrison et al. 2019). An additional modifier (1/3) was

Table 2 The value of life stage-specific entrainment variables used in baseline scenarios for kokanee and bull trout

Variable	Value	Justification and assumption
Kokanee		
Entrainment rate from egg to stage 1, E_{1e}	$0.30 \times 1/3$	(1) 0.3 entrainment rate for young-of-year kokanee (Harrison et al. 2019); an additional modifier was added for larval stage to represent a lower entrainment risk of this stage because part of this stage is attached to substrate and some stream-spawning kokanee spend most of this stage in tributaries; (2) The age composition of entrained kokanee (Arndt 2009) was comparable to the age composition of kokanee in reservoirs (Sebastian et al. 2009); (3) Generally, larva and juveniles might be more susceptible to entrainment (Harrison et al. 2019) and adults will leave reservoirs during spawning season
Entrainment rate from stage 1 to 2, E_{21}	0.30	
Entrainment rate from stage 2 to 3, E_{32}	0.25	
Entrainment rate from stage 3 to 4, E_{43}	0.20	
Entrainment rate from stage 4 to 5, E_{54}	0.20	
Passage survival from egg to stage 1, P_{1e}	0.469	The short-term mortality was calculated from an empirical relationship between mortality and fish length: mortality (%) = $0.0772 \times \text{length (mm)} + 1.7715$ (Parkinson and Arndt 2014). An assumed moderate delayed mortality 50% was added
Passage survival from stage 1 to 2, P_{21}	0.438	
Passage survival from stage 2 to 3, P_{32}	0.411	
Passage survival from stage 3 to 4, P_{43}	0.396	
Passage survival from stage 4 to 5, P_{54}	0.387	
Bull trout		
Entrainment rate from egg to stage 1, E_{1e}	0.30×0	(1) 0.015 entrainment rate for adult (average of numbers from three studies Harrison et al. 2020; Martins et al. 2013; Underwood and Cramer 2007)); (2) around trebling for subadult from adult (Underwood and Cramer 2007); (3) assumed the same entrainment rate for the early life stages of kokanee and bull trout; however, additional modifiers were added for bull trout to represent the fact that most (80%) bull trout enter reservoirs at age 2 and 3 (Arostegui and Quinn 2019; Downs et al. 2006); (4) Generally, larva and juveniles might be more susceptible to entrainment (Harrison et al. 2019) and adults will leave reservoirs during spawning season
Entrainment rate from stage 1 to 2, E_{21}	0.30×0.1	
Entrainment rate from stage 2 to 3, E_{32}	0.25×0.5	
Entrainment rate from stage 3 to 4, E_{43}	0.20×0.9	
Entrainment rate from stage 4 to subadult, E_{s4}	0.10	
Entrainment rate from subadult to adult or remain as subadult, E_{As}	0.045	
Entrainment rate during adult stage, E_{AA}	0.015	
Passage survival from egg to stage 1, P_{1e}	0.467	
Passage survival from stage 1 to 2, P_{21}	0.426	
Passage survival from stage 2 to 3, P_{32}	0.368	
Passage survival from stage 3 to 4, P_{43}	0.335	
Passage survival from stage 4 to subadult, P_{s4}	0.305	For adult stage: The short-term mortality was set as 0.56, which is the average of (1) the mortality calculated from the above empirical relationship based on fish length at age 6 to 13, (2) 0.57 for <i>Salvelinus</i> sp. (Pracheil et al. 2016), and (3) 0.5625 for adult salmonids (Pracheil et al. 2016). An assumed moderate delayed mortality 50% was added
Passage survival from subadult to adult or remain as subadult, P_{As}	0.220	
Passage survival during adult stage, P_{AA}	0.220	

Key assumptions and calculations used for variables are described for both species

added to the first stage (egg to age 1) to represent a lower entrainment risk of this stage (than the next stage) because part of this stage is attached or living close to substrate and some kokanee (i.e., stream-spawners) spend most of this stage in the tributary. Entrainment rates for later life stages were assumed to be similar but slightly lower than 30% (i.e., 25% for stage 2 and 20% for stages 3 and 4) because (1) generally, younger fish are more susceptible to entrainment (Harrison et al. 2019), (2) adfluvial mature kokanee will leave reservoirs and enter tributaries to spawn, and (3) the age composition of young (ages 1 and 2) entrained kokanee collected in downstream areas in one study (Arndt 2009) is similar to the age composition of kokanee in reservoirs (Sebastian et al. 2009) but with fewer old fish.

In contrast, a few studies estimate the entrainment rates of adult bull trout while no values are available for young-of-year bull trout. Therefore, the average of entrainment rates (1.5%) from three different studies were used for adult bull trout for the baseline scenario (Harrison et al. 2020; Martins et al. 2013; Underwood and Cramer 2007). Based on the same assumption for kokanee and other fish, higher entrainment rates were applied on earlier life stages (but see additional modifiers below). Entrainment rate was slightly higher for subadult (4.5%) similar to Underwood and Cramer (2007). We used the same entrainment rates (30%, 25%, and 20%) for kokanee and bull trout in their early life stages for simplicity's sake because of the unavailability of data for young bull trout. However, additional modifiers (0, 0.1,

0.5, 0.9) were added on the first four stages of bull trout to simulate 0% of the fish before age 1, 10% before age 2, 50% before age 3, and 90% before age 4 leaving their natal tributaries and entering reservoirs. Based on literature, most (80%) bull trout enter reservoirs and become exposed to entrainment at age 2 and 3 (Arostegui and Quinn 2019; Downs et al. 2006). Combining stage-specific entrainment rate and addition modifiers, 0% entrainment rate was given to egg to stage 1 bull trout, 3% to stage 1 to 2, 12.5% to stage 2 to 3, and 18% to stage 3 to 4, which were much lower than kokanee.

In the absence of stage/age-specific entrainment mortality data for kokanee and young-of-year bull trout, the empirical relationship between mortality and fish length (mortality (%) = $0.0772 \times \text{body length (mm)} + 1.7715$) provided by Parkinson and Arndt (2014) was used. We further compared the values calculated from the above equation with (1) estimates using equations in Gloss and Wahl (1983) and (2) 61 field-based mortality rates for salmonids (mostly *Oncorhynchus* spp.) recorded in a systematic review (Algera et al. 2020) and found similar survivorship values especially for early stages (Supplementary File). Generally, the short-term mortality rates are higher for larger fish because the probability of blade contact is positively correlated with fish length (Table 2; Cada 1991). Scenarios (see next paragraph) were then used to cover differences among mortality estimates. Because the adult stage of bull trout covered a relatively wide range of body length, we compared the estimated mortality calculated from the above empirical relationship using body lengths at age 6 to age 13 (average: 55.4%) with two values recorded in the literature [57% for *Salvelinus* sp. and 56.25% for adult salmonids, Pracheil et al. (2016)]. The average of these three comparable values was used as the short-term mortality for adult bull trout. We incorporated an assumed 50% delayed mortality for all entrained fish to represent a moderate risk of delayed effects as in Harrison et al. (2019) but acknowledged that there is no currently available data for delayed mortality.

After developing the baseline scenario, we varied entrainment rate and passage survival to explore the potential outcomes if these two variables used in baseline scenario were underestimated (i.e., populations may experience higher entrainment rates and/or lower passage survival than we thought). First, we doubled the entrainment rate or reduced the passage survival to half to create one high entrainment and one high entrainment mortality scenario, respectively. A worse-case scenario was developed for both species, where we both doubled the entrainment rate and reduced the passage survival to half. As shown on Fig. 1, entrained fish from the upstream population may survive and join the downstream population while entrained fish from downstream population would leave the system. Similar to the previous step, we ran the

simulations 10,000 times using uniform distributions of variables (ranges see Table 1) and fixed entrainment rate and entrainment mortality (but different combination) for each scenario to examine the distribution of the geometric mean of λ , λ_g .

2.5 Investigating the probability of declining populations

Lastly, we investigated the probability of declining populations across a range of entrainment rates, which could be used to identify acceptable/threshold entrainment rate for managers. A declining population was defined as a population with a geometric mean of the population growth rate smaller than 1 ($\lambda_g < 1$) and the probability of population decline was taken as the proportion of $\lambda_g < 1$ among the 10,000 simulations of each scenario. To better inform future studies and guide management alternatives, we focused on changing the entrainment rate of the two critical life stages that we identified in the previous section. Specifically, entrainment rates varied for (1) the life stage with the highest sensitivity and elasticity, (2) the stage with the second highest sensitivity and elasticity, and (3) both life stages. First, we varied one quarter of the baseline entrainment rates (baseline values see Table 2) each time cumulatively (i.e., relative change of entrainment rate; 1st: baseline minus 25%, 2nd: baseline, 3rd: baseline plus 25%, 4th: 3rd plus 25% of 3rd, 5th: 4th plus 25% of 4th, 6th: 5th plus 25% of 5th) and recorded λ_g . Then, we examined changes in λ_g given a range of entrainment rates (0.05, 0.15, 0.30, 0.45, 0.60, 0.75) on both critical life stages for both species (i.e., absolute change of entrainment rate) and the results were compiled for both upstream and downstream populations. All calculations were conducted in R 3.6.3 (R Core Team 2020) and population models were projected using the *Popbio* package (Stubben and Milligan 2007).

3 Results

3.1 Critical life stages

Critical life stages identified for both species were the earliest life stages, with entrainment-related changes in the numbers of individuals occurring at early life stages having a large influence on long-term population growth rate relative to changes occurring at later life stages (Table 3). For kokanee, variables having the highest sensitivity and elasticity values were survival rates from egg to stage 1 and from stage 1 to 2. The critical life stages for bull trout were from stage 1 to 2 and stage 2 to 3.

Table 3 Sensitivity and elasticity (i.e., coefficients in regression models) of kokanee and bull trout population growth rate in relation to variables in population models

Variable	Sensitivity	Elasticity
Kokanee model		
<i>Survival rate from egg to stage 1, s_{1e}</i>	1.773	0.230
<i>Survival rate from stage 1 to 2, s_{21}</i>	1.233	0.148
Survival rate from stage 2 to 3, s_{32}	0.614	0.016
Survival rate from stage 3 to 4, s_{43}	0.417	0.007
Survival rate from stage 4 to 5, s_{54}	0.061	0.001
Length at stage 3	0.002	0.053
Length at stage 4	0.004	0.117
Length at stage 5	0.0004	0.002
Bull trout model		
Survival rate from egg to stage 1, s_{1e}	0.351	0.073
<i>Survival rate from stage 1 to 2, s_{21}</i>	2.446	0.092
<i>Survival rate from stage 2 to 3, s_{32}</i>	0.488	0.051
Survival rate from stage 3 to 4, s_{43}	0.349	0.039
Survival rate from stage 4 to subadult, s_{s4}	0.303	0.031
Survival rate from subadult to adult or remain as subadult, s_{As}	0.450	0.041
Survival rate during adult stage, s_{AA}	0.129	0.013
Asymptotic length, l_{max}	0.001	0.016
Growth parameter, k	5.272	0.030
Hypothetical age at length zero, t_0	-0.081	-0.004
Annual probability of mature fish spawning, SP	0.236	0.034

Significant sensitivity or elasticity values are bolded (all p value < 0.00001). Rows with bold italic represented critical life stages we identified for kokanee (from egg to stage 1, and 1 to 2) and bull trout (from stage 1 to 2, and 2 to 3), and all sensitivity and elasticity values for critical life stages are significant

3.2 Entrainment and entrainment mortality

For both species, doubling entrainment rate shifted the distribution of λ towards the left, which indicated that there will be a higher probability of reduced population growth ($\lambda_g < 1$; Figs. 2 and 3). For example, for the upstream kokanee population, the λ_g at 50% quantile reduced from 1.20 to 0.77 (Fig. 2a baseline scenario and 2b high entrainment scenario). Nevertheless, the effects of reducing downstream passage survival rate to half on downstream population growth rate were negligible (between baseline and high entrainment mortality scenario, or between high entrainment and worse-case scenario in Figs. 2 and 3). While the effects of increasing entrainment rate were similar to both upstream and downstream populations (between (a) and (b) scenario, or between (c) and (d) in Figs. 2 and 3), the probability of $\lambda_g < 1$ was lower for downstream population (e.g., 20% for upstream and 13% for downstream populations under baseline scenario in Fig. 2a; 56% for upstream

and 27% for downstream populations under worse-case scenario in Fig. 3d). Under the baseline scenario, kokanee had a lower probability of $\lambda_g < 1$ than bull trout (20% in Fig. 2a and 32% in Fig. 3a); nevertheless, doubling entrainment rates had a relatively large effect on kokanee (e.g., 20 to 95% for upstream kokanee and 32 to 55% for upstream bull trout).

3.3 Probability of declining populations

Similar to the results in previous section, the population growth rates of kokanee populations (both upstream and downstream) varied with changing entrainment rates more than bull trout populations (relative change of entrainment rate, Fig. 4), even when the same set of entrainment rate were applied on the two critical life stages (absolute change of entrainment rate, Fig. 5). However, given the same entrainment rate on critical life stages (Fig. 5), bull trout experienced higher probability of population decline than kokanee, except under high entrainment rate (0.75, Fig. 5).

4 Discussion

Using stage-structured population models, we identified critical life stages (same as ages in these cases) and examined the effects of entrainment rate and mortality on upstream and downstream populations for kokanee and bull trout considering the variations within each demographic variable. For both species, early life stages were identified as critical stages that could have relatively large influences on long-term population growth. Compared to the baseline scenario, doubling entrainment rates reduced the population growth rates for upstream and downstream populations while the effect of halving passage survival on downstream population growth rates were negligible. Lastly, varying entrainment rates on critical stages had a relatively large effect on the population growth rate of kokanee; nevertheless, given the same entrainment rates, the probability of population decline was generally higher for bull trout, except under very high entrainment rates. The results of this assessment tool could provide information for hydropower facility management, such as identifying focal life stages for assessing entrainment impacts, helping regulators and hydropower operators to set quantitative objectives to mitigate the effect of entrainment on fish populations, and developing species-specific mitigation options where entrainment effects can't be resolved. For example, if a goal is to keep the risk of population decline for kokanee within a reservoir lower than 25%, mitigation actions may be required to reduce entrainment rates if the estimated rates for critical life stages are over 0.3 (Fig. 5).

Similar to previous modeling (e.g., Bowerman 2013; Carim et al. 2017; Caskenette et al. 2016; Caskenette and Koops 2018; Cox et al. 2013; Ng et al. 2016) and field-based

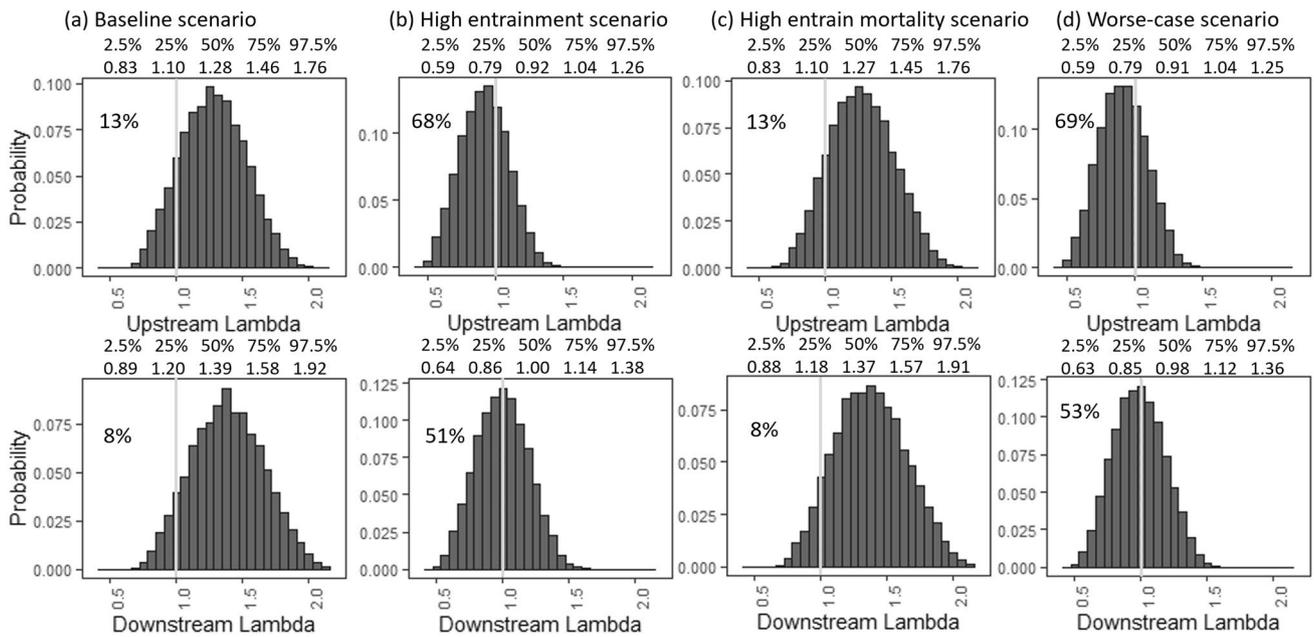


Fig. 2 The probability distribution of kokanee population growth (λ) in upstream (1st row) and downstream (2nd row) under baseline (a), high entrainment (b), high passage mortality (c), and worse-case scenarios (d). The percentages (2.5, 25, 50, 75, and 97.5%) and numbers

below represented the quantiles and corresponding λ for each distribution. The vertical line represents a stable population ($\lambda = 1$). The percentages beside bars are the proportion of $\lambda_g < 1$ among 10,000 simulations

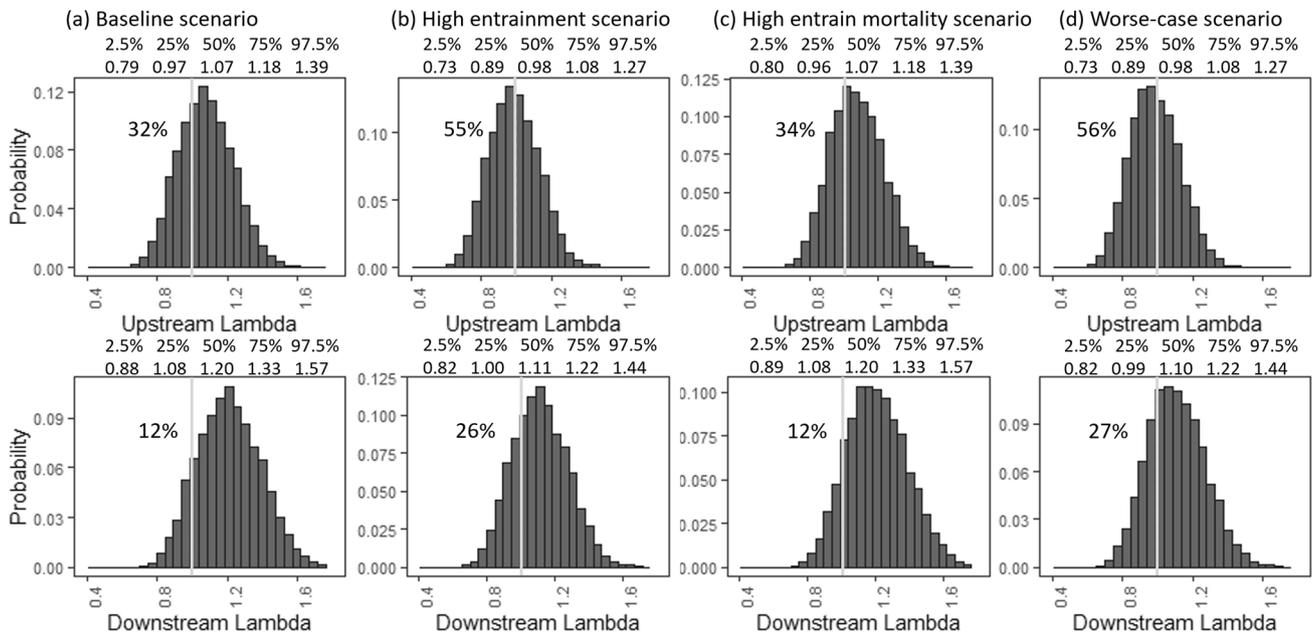


Fig. 3 The probability distribution of bull trout population growth (λ) in upstream (1st row) and downstream (2nd row) under baseline (a), high entrainment (b), high entrainment mortality (c), and worse-case scenarios (d). The percentages (2.5, 25, 50, 75, and 97.5%) and num-

bers below represented the quantiles and corresponding λ for each distribution. The vertical line represents a stable population ($\lambda = 1$). The percentages beside bars are the proportion of $\lambda_g < 1$ among 10,000 simulations

studies (e.g., Bassar et al. 2016; Hilborn et al. 2003) on salmonids, our results indicated that changing the numbers of individuals in early life stages could have relatively large

effects on population dynamics. Indeed, studies have found large amount of young-of-year and juvenile fish being entrained through hydropower turbines at rates that may

Fig. 4 The probability of declining population ($\lambda_g < 1$) with decreasing or increasing entrainment rates 25% at a time from baseline cumulatively on critical stages. Three lines represented that changing the entrainment rate on the life stage with the highest sensitivity and elasticity (1st only: egg to stage 1 for kokanee and stage 1 to 2 for bull trout), with the second highest sensitivity and elasticity (2nd only: stage 1 to 2 for kokanee and stage 2 to 3 for bull trout), or both stages (both). Two additional x-axes on the top of each plot represent the actual values of entrainment rate for the 1st (Act E 1st) and 2nd (Act E 2nd) inputted in the model. The curved arrows below plots represent the cumulative changes

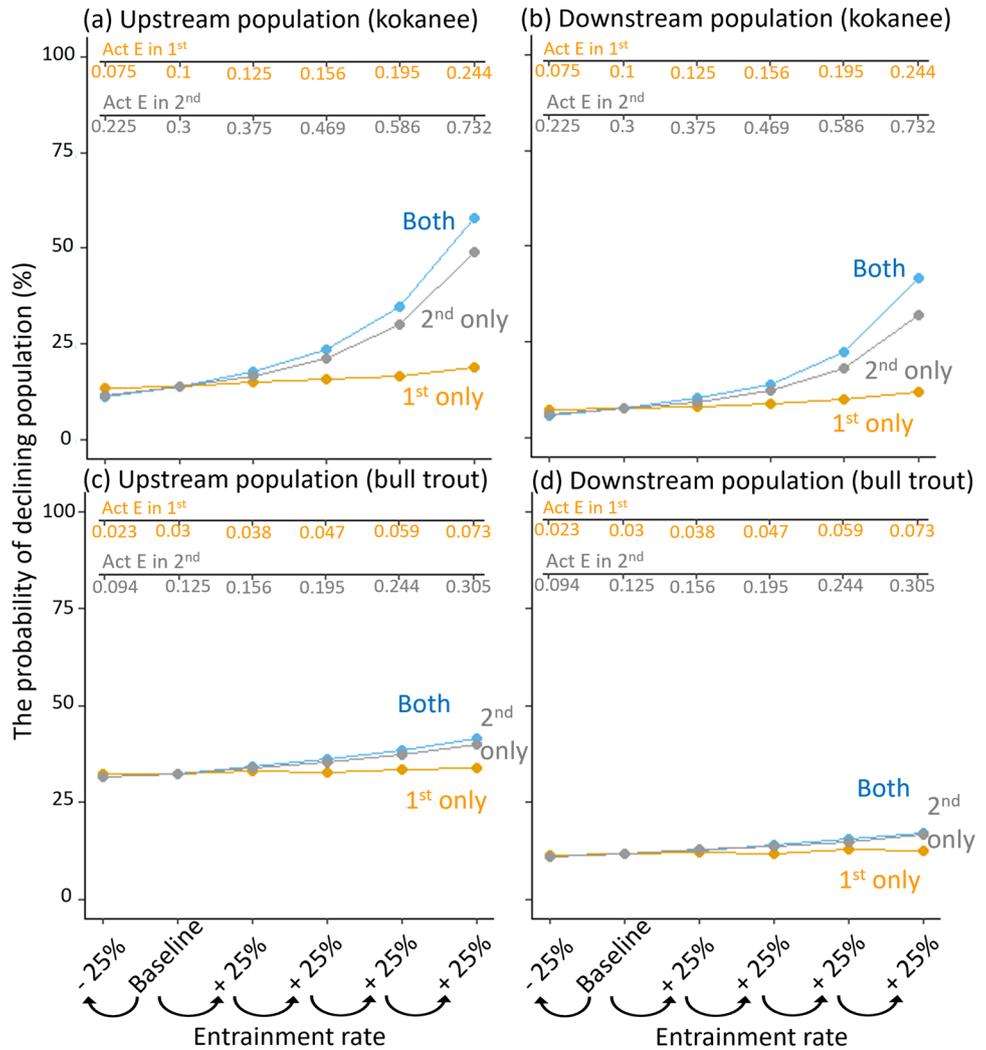
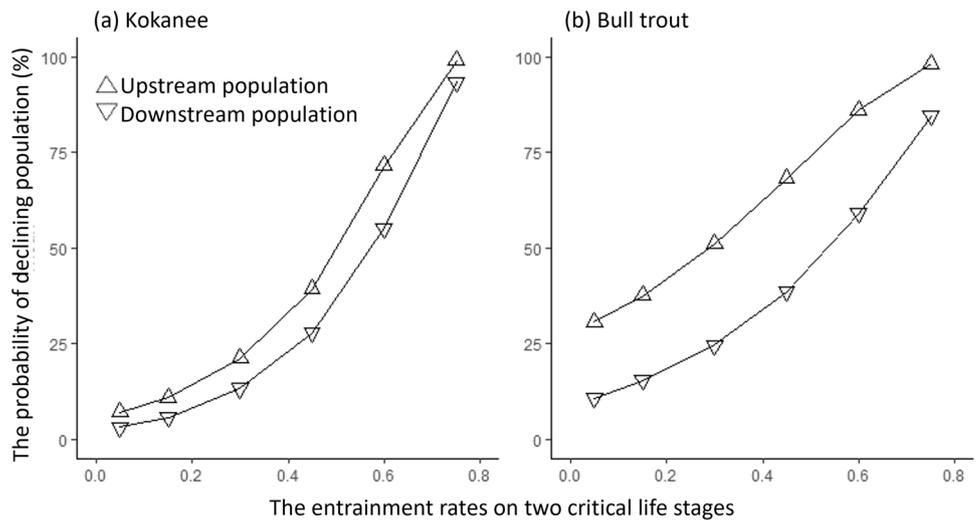


Fig. 5 The probability of declining population ($\lambda_g < 1$) with low to high (0.05, 0.15, 0.30, 0.45, 0.60, 0.75) entrainment rates on both critical stages



affect upstream populations (reviewed in Harrison et al. 2019) and our results suggested that the probability of population decline in upstream reservoirs could be higher than

50% when the entrainment rates on two critical life stages were over 0.5 (Fig. 5). While species with high reproductive output might be less susceptible to the removal of young

individuals (e.g., burbot, see Harrison et al. 2016; kokanee comparing to bull trout in this study), the relationship between entrainment rate and the probability of population decline could be an exponential-like curve (Fig. 5). Because site-specific entrainment rates are expected depending on facility characteristics (e.g., size, turbine type, operation timing/season, flow rates, head height, intake velocities, and amount spillage), habitat characteristics, and fish traits and the numbers of juvenile fish entrained vary across facilities (e.g., from 80,000 to 4.47 million per year; Harrison et al. 2019), it is important to assess and mitigate entrainment rates at facility-specific level (detailed discussion see Harrison et al. 2019). This is even more critical for facilities that may have species-specific effects during early life stages, as efforts to maintain a stable or increasing upstream fish population will be most sensitive to entrainment rates early in life.

Downstream dispersal is important for many potadromous fish species especially during their early life stages (O'Hanley et al. 2013; Wolter and Sukhodolov 2008). Fish that survive entrainment could play a significant role on maintaining downstream population when the recruitment of downstream population is weak, such as reservoirs with limited numbers of suitable spawning or nursery tributaries (e.g., in Arrow Lakes, Parkinson and Arndt 2014 and Dinosaur Lake, Pattenden and Ash 1993, BC, Canada). The effect of entrainment mortality on downstream population growth rate was negligible in this study, which may be because we did not assign different carrying capacity values for upstream and downstream populations, and both upstream and downstream reservoirs were able to sustain a growing fish population if there is no entrainment (making the situation different from Arrow Lakes and Dinosaur Lake). In addition, while we used the same set of entrainment rates for both upstream and downstream barriers for simplicity's sake, upstream and downstream barriers may have different entrainment rates based on reservoir characteristics, dam structure, and turbine operating regimes. When applying this modeling framework to a specific case, reservoir-specific carrying capacity and facility-specific entrainment rate for the target species should be incorporated when data is available.

The seasonal or diel movement and ontogenetic migration of fish could influence the potential risk of being entrained and consequently, the probability of population decline. The relative high risk of population decline for kokanee in high entrainment scenarios might be because of the different early life histories between kokanee and bull trout. Compared to adfluvial bull trout that usually spend their first 2 to 3 years in natal tributaries, kokanee spend most of their early life stages in the lake/reservoir either with an adfluvial (stream-spawning) or lake resident (lake-spawning) life history (Arostegui and Quinn 2019). Therefore, most stages and especially critical early life stages of lake-spawning kokanee could be susceptible to entrainment. Presumably

the population will start to decline when reproductive output could not compensate the loss under high entrainment rates. However, the proportion of lake-spawning kokanee varies across lakes (from 20 to 95%, see Chang et al. 2021; Lemay and Russello 2015; Ward et al. 2019) and this life history diversity may influence the overall susceptibility of kokanee populations in a given lake/reservoir to entrainment. Our study indicated the importance of using fish life history traits and behavior to compare the relative risk of entrainment among species (as in Čada and Schweizer 2012). In addition to the residence time in reservoirs, the spatio-temporal pattern of fish utilizing areas close to turbine intake after entering reservoirs and the pattern of turbine operation could provide more direct information (Harrison et al. 2019; Martins et al. 2014).

The main uncertainties in this study may come from (1) variables used in stage-structured population models and (2) entrainment-related parameters. Monte Carlo simulations were used to incorporate the effect of uncertainties in variables for stage-structured models as in previous studies (Meehan et al. 2018; Smart et al. 2017; Wong and Dowd 2016). While this method enabled us to explore the range of all possible outcomes (i.e., λ), the relatively broad ranges (e.g., kokanee, Fig. 2, comparing to bull trout, Fig. 3) might be less informative and less specific for local reservoir managers. Using other types of distribution (e.g., beta, Poisson, or normal distribution) informed by data from local surveys (e.g., survival rate directly estimated from the focal reservoir) rather than using uniform distributions for life history variables may reduce the range of uncertainties (see DuFour et al. 2020; Meehan et al. 2018). In contrast, there was less information available for entrainment-related parameters. These data were either unknown (e.g., the entrainment rate for large kokanee and young-of-year bull trout, and species- and stage-specific entrainment mortality) or required to be derived from low number of studies (e.g., the entrainment rate for young-of-year kokanee). The use of parameters from other species or a low number of studies (Table 2) can introduce uncertainties to the modeling outputs, especially when variations among populations are observed (Hernández-Camacho et al. 2015). Beside fish length, other factors such as turbine characteristics, bar rack spacing, flow rates, and barotrauma could also influence fish entrainment and associated mortality (Pracheil et al. 2015). However, Algera et al. (2020) indicates that except two major turbine types (Francis and Kaplan), there is insufficient data to quantify the effect of other facility and hydrological characteristics on entrainment injury and mortality. While direct research on entrainment at large hydropower facilities can be challenging, estimates from the field could be used as input to make the results of our model more accurate for specific facility and to quantify the relationship between fish

stage-specific entrainment rate and mortality with different facility and hydrological characteristics.

In order to resolve or mitigate impacts associated with fish entrainment, there is a demonstrated need to estimate the potential population consequences from entrainment through hydropower operations for new or existing facilities (Harrison et al. 2019). However, a lack of species-specific entrainment-related estimates and variations among ages, populations, and reservoirs hinder the development of effective mitigation strategies. Using stage-structured population models and Monte Carlo simulations, we projected the potential population-level effects across a range of demographic variables and entrainment-related parameters for kokanee and bull trout in North America. Using assumed entrainment parameters derived from different studies might make our results more generalized for scenario exploration than specialized for specific hydropower facility. Nevertheless, using entrainment estimates directly measured from a specific facility as input could make the results more specialized to a local condition. Our results suggested that for both species, entrainment of early life stages has a larger effect on long-term population growth that when entrainment principally affects older life stages. While bull trout generally had a higher probability of population decline than kokanee under baseline scenario and associated parameters, the long-term growth rate of bull trout was less influenced by changing entrainment rates because they have a later lake/reservoir entry. These findings are of direct relevance to regulators and hydropower operators as they may help inform operational alternatives to mitigating life stage-specific entrainment or highlight compensation efforts (e.g., habitat enhancement) that benefit life stages most likely to be impacted. Importantly, knowledge gaps such as species-, age-, population-, and reservoir-specific entrainment-related parameters should be addressed to improve the accuracy and applicability of the model results.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10669-022-09858-y>.

Acknowledgements We thank T. Meehan for recommendations in population modeling and E. Parkinson and T. Weir for providing life history data.

Funding Funding was provided by BC Hydro as well as an NSERC CRD Grant to S. Cooke and M. Power. We thank several anonymous referees for providing thoughtful comments on the manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

- Algera DA, Rytwinski T, Taylor JJ, Bennett JR, Smokorowski KE, Harrison PM, Clarke KD, Enders EC, Power M, Bevelhimer MS, Cooke SJ (2020) What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review. *Environ Evid* 9:3. <https://doi.org/10.1186/s13750-020-0184-0>
- Andrusak GF, Andrusak H (2015) Gerrard rainbow trout growth and condition with kokanee prey at low densities. Report prepared for Fish and Wildlife Compensation Program – Columbia Basin (Nelson, BC) by Redfish Consulting Ltd. Nelson, BC. FWCP Report No. F-F15-15. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Andrusak GF, Thorley JL (2013) Kootenay Lake exploitation study: Fishing and natural mortality of large rainbow trout and bull trout—2013 annual report. A Poisson Consulting Ltd. and Redfish Consulting Ltd. Report prepared for the Habitat Conservation Trust Foundation and Fish and Wildlife Compensation Program. HCTF Report No. CAT13-4-413. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Andrusak G (2006) Hill Creek spawning channel kokanee fry production-2006. Report prepared for the Fish and Wildlife Compensation Program—Columbia Basin, Nelson BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Andrusak GF (2013) Alouette kokanee age structure analysis (ALUMON#6)-2014. Year 6 of Alouette project water use plan monitoring plan #6. A Redfish Consulting Ltd. Contract report for Ministry of Environment and BC Hydro. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Ardren WR, Bernall SR (2017) Dams impact westslope cutthroat trout metapopulation structure and hybridization dynamics. *Conserv Genet* 18:297–312. <https://doi.org/10.1007/s10592-016-0906-6>
- Arndt S (2009) Footprint impacts of BC Hydro dams on kokanee populations in the Columbia River Basin, British Columbia. Fish and Wildlife Compensation Program—Columbia Basin, File 132-83. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Arostegui MC, Quinn TP (2019) Reliance on lakes by salmon, trout and charr (*Oncorhynchus*, *Salmo* and *Salvelinus*): an evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish Fish* 20(4):775–794. <https://doi.org/10.1111/faf.12377>
- Baldwin C, Polacek M (2002) Evaluation of limiting factors for stocked kokanee and rainbow trout in Lake Roosevelt, WA. Report FPA 04–03. Washington Department of Fish and Wildlife, Olympia
- Barbarossa V, Schmitt RJP, Huijbregts MAJ, Zarfl C, King H, Schipper AM (2020) Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proc Natl Acad Sci USA* 117:3648–3655. <https://doi.org/10.1073/pnas.1912776117>
- Bassar RD, Letcher BH, Nislow KH, Whiteley AR (2016) Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. *Glob Chang Biol* 22:577–593. <https://doi.org/10.1111/gcb.13135>
- Baxter JS (1996) Bull trout egg to fry survival studies in the Chowade river: 1995/96. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Bell J (2006) 2006 North arm kokanee escapement/fry production summary report. Ministry of Environment, BC, Canada. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Bell J (2009) 2009 North arm kokanee escapement/fry production summary report. Ministry of Environment, BC, Canada. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Benjamin JR, Videgar DT, Dunham JB (2020) Thermal heterogeneity, migration, and consequences for spawning potential of female

- bull trout in a river–reservoir system. *Ecol Evol* 10(9):4128–4142. <https://doi.org/10.1002/ece3.6184>
- Bowerman T, Neilson BT, Budy P (2014) Effects of fine sediment, hyporheic flow, and spawning site characteristics on survival and development of bull trout embryos. *Can J Fish Aquat Sci* 71:1059–1071. <https://doi.org/10.1139/cjfas-2013-0372>
- Bowerman T (2013) A multi-scale investigation of factors limiting bull trout viability. Dissertation, Utah State University.
- Bray K, Weir T, Pieters R, Harris S, Brandt D, Sebastian D, Vidmanic L (2018) Kinbasket and Revelstoke reservoirs ecological productivity and kokanee population monitoring—2008–2016 (Years 1 to 9) synthesis report. Prepared for BC Hydro under the Columbia River Water Use Plan, Water licence requirements study Nos. CLBMON-2, CLBMO
- Cada GF (1991) Effects of hydroelectric turbine passage on fish early life stages. In: Darling DD (ed) *Waterpower '91: A new view of hydro resources*. American Society of Civil Engineers, American Society of Civil Engineers, New York, pp 318–326
- Čada GF, Schweizer PE (2012) The application of traits-based assessment approaches to estimate the effects of hydroelectric turbine passage on fish populations. Oak Ridge National Laboratory, Oak Ridge. <https://doi.org/10.2172/1038082>
- Carim KJ, Vindenes Y, Eby LA, Barfoot C, Vøllestad LA (2017) Life history, population viability, and the potential for local adaptation in isolated trout populations. *Glob Ecol Conserv* 10:93–102. <https://doi.org/10.1016/j.gecco.2017.02.001>
- Caseknette AL, Koops MA (2018) Recovery potential modelling of rainbow trout, *Oncorhynchus mykiss* (Athabasca River populations). DFO Can Sci Advis Sec Res Doc 2018/021. <http://publications.gc.ca/pub?id=9.854809&sl=0>
- Caseknette AL, Young JAM, Koops MA (2016) Recovery potential modelling of bull trout (*Salvelinus confluentus*) (Saskatchewan—Nelson rivers populations) in Alberta. DFO Can Sci Advis Sec Res Doc 2016/099. <http://publications.gc.ca/pub?id=9.828497&sl=0>
- Caswell H (2001) *Matrix population models: construction, analysis, and interpretation*, 2nd edn. Sinauer, Sunderland
- Chang SL, Ward HG, Russell MA (2021) Genotyping-in-Thousands by sequencing panel development and application to inform kokanee salmon (*Oncorhynchus nerka*) fisheries management at multiple scales. *PLoS ONE* 16(12):e0261966. <https://doi.org/10.1371/journal.pone.0261966>
- COSEWIC (2012) COSEWIC assessment and status report on the bull trout *Salvelinus confluentus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa
- Cox BS, Guy CS, Fredenberg WA, Rosenthal LR (2013) Baseline demographics of a non-native lake trout population and inferences for suppression from sensitivity-elasticity analyses. *Fish Manag Ecol* 20:390–400. <https://doi.org/10.1111/fme.12024>
- Dawson J, Parkinson E (2013) Revelstoke Reservoir kokanee behavior and entrainment rate assessment project final report: 12-87057-001. MCA/REV FESMON#2. Report submitted to BC Hydro, Burnaby
- Downs CC, Horan D, Morgan-Harris E, Jakubowski R (2006) Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. *N Am J Fish Manag* 26:190–200. <https://doi.org/10.1577/m04-180.1>
- DuFour MR, Robinson KF, Jones ML, Herbst SJ (2020) A matrix population model to aid agency response to grass carp (*Ctenopharyngodon idella*) in the Great Lakes Basin—Lake Erie. *J Great Lakes Res.* <https://doi.org/10.1016/j.jglr.2020.06.022>
- Froese R, Binohlan C (2000) Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *J Fish Biol* 56:758–773. <https://doi.org/10.1111/j.1095-8649.2000.tb00870.x>
- Gloss SP, Wahl JR (1983) Mortality of juvenile salmonids passing through Ossberger Crossflow Turbines at small-scale hydroelectric sites. *Trans Am Fish Soc* 112:194–200. [https://doi.org/10.1577/1548-8659\(1983\)112%3c194:mojspt%3e2.0.co;2](https://doi.org/10.1577/1548-8659(1983)112%3c194:mojspt%3e2.0.co;2)
- Grill G, Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere H, Ehalt Macedo H, Filgueiras R, Goichot M, Higgins J, Hogan Z, Lip B, McClain ME, Meng J, Mulligan M, Nilsson C, Olden JD, Opperman JJ, Petry P, Reidy Liermann C, Sáenz L, Salinas-Rodríguez S, Schelle P, Schmitt RJP, Snider J, Tan F, Tickner K, Valdujo PH, van Soesbergen A, Zarfl C (2019) Mapping the world's free-flowing rivers. *Nature* 569:215–221. <https://doi.org/10.1038/s41586-019-1111-9>
- Hagen J, Decker S (2011) The status of bull trout in British Columbia: A synthesis of available distribution, abundance, trend, and threat information. Fisheries Technical Report No. FTC 110. Province of British Columbia, Ministry of Environment, Ecosystems Protection & Sustainability Branch, Aquatic Conservation Science Section Victoria, British Columbia. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Hagen J, Weber S (2019) Limiting factors, enhancement potential, critical habitats, and conservation status for bull trout of the Williston Reservoir Watershed: Information synthesis and recommended monitoring framework. Report prepared for the Fish and Wildlife Compensation Program—Peace Region, Prince George, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Hansen AG, Gardner JR, Beauchamp DA, Paradis R, Quinn TP (2016) Recovery of sockeye salmon in the Elwha River, Washington, after dam removal: dependence of smolt production on the resumption of anadromy by landlocked kokanee. *Trans Am Fish Soc* 145:1303–1317. <https://doi.org/10.1080/00028487.2016.1223752>
- Harrison PM, Gutowsky LFG, Martins EG, Patterson DA, Cooke SJ, Power M (2016) Burbot and large hydropower in North America: benefits, threats and research needs for mitigation. *Fish Manag Ecol* 23:335–349. <https://doi.org/10.1111/fme.12178>
- Harrison PM, Martins EG, Algera DA, Rytwinski T, Mossop B, Leake AJ, Power M, Cooke SJ (2019) Turbine entrainment and passage of potadromous fish through hydropower dams: Developing conceptual frameworks and metrics for moving beyond turbine passage mortality. *Fish Fish* 20:403–418. <https://doi.org/10.1111/faf.12349>
- Harrison PM, Ward T, Algera DA, Culling B, Euchner T, Leake A, Crossman JA, Cooke SJ, Power M (2020) A comparison of turbine entrainment rates and seasonal entrainment vulnerability of two sympatric char species, bull trout and lake trout, in a hydropower reservoir. *River Res Appl* 36:1033–1045. <https://doi.org/10.1002/rra.3617>
- Hernández-Camacho CJ, Bakker VJ, Aurióles-Gamboa D, Laake J, Gerber LR (2015) Use of surrogate data in demographic population viability analysis: a case study of California sea lions. *PLoS ONE* 10:139158. <https://doi.org/10.1371/journal.pone.0139158>
- Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. *Proc Natl Acad Sci USA* 100:6564–6568. <https://doi.org/10.1073/pnas.1037274100>
- Hirsch PE, Eloranta AP, Amundsen PA, Brabrand Å, Charmasson J, Helland IP, Power M, Sánchez-Hernández J, Sandlund OT, Sauterleute JF, Skoglund S, Ugedal O, Yang H (2017) Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish. *Hydrobiologia* 794:287–301. <https://doi.org/10.1007/s10750-017-3105-7>
- Janáč M, Jurajda P, Kružíková L, Roche K, Prášek V (2013) Reservoir to river passage of age-0+ year fishes, indication of a dispersion pathway for a non-native species. *J Fish Biol* 82:994–1010. <https://doi.org/10.1111/jfb.12037>

- Kendall BE, Fujiwara M, Diaz-Lopez J, Schneider S, Voigt J, Wiesner S (2019) Persistent problems in the construction of matrix population models. *Ecol Modell* 406:33–43. <https://doi.org/10.1016/j.ecolmodel.2019.03.011>
- Kurota H, McAllister MK, Parkinson EA, Johnston NT, Askey PJ (2011) Progress report: Management reference points for kokanee and salmonid piscivores in large BC lakes. BC Ministry of Environment, Fisheries Project Report RD133, Victoria BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Lefkovich LP (1965) The study of population growth in organisms grouped by stages. *Biometrics* 21:1–18. <https://doi.org/10.2307/2528348>
- Lemay MA, Russello MA (2015) Genetic evidence for ecological divergence in kokanee salmon. *Mol Ecol* 24:798–811. <https://doi.org/10.1111/mec.13066>
- Liermann CR, Nilsson C, Robertson J, Ng RY (2012) Implications of dam obstruction for global freshwater fish diversity. *Bioscience* 62:539–548. <https://doi.org/10.1525/bio.2012.62.6.5>
- Manson H (2005) Hill Creek spawning channel kokanee fry enumeration report—2004. Columbia Basin Fish and Wildlife Compensation Program. Nelson, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Martins E, Gutowsky L, Harrison P, Patterson D, Power M, Zhu D, Leake A, Cooke S (2013) Forebay use and entrainment rates of resident adult fish in a large hydropower reservoir. *Aquat Biol* 19:253–263. <https://doi.org/10.10354/ab00536>
- Martins EG, Gutowsky LFG, Harrison PM, Flemming JEM, Jensen ID, Zhu DZ, Leake A, Patterson DA, Power M, Cooke SJ (2014) Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling. *Anim Biotelemetry* 2:1–13. <https://doi.org/10.1186/2050-3385-2-13>
- McGurk MD (2000) Comparison of fecundity-length-latitude relationships between nonanadromous (kokanee) and anadromous sockeye salmon (*Oncorhynchus nerka*). *Can J Zool* 78:1791–1805. <https://doi.org/10.1139/z00-106>
- Meehan TD, Harvey AL, Michel NL, Langham GM, Weinstein A (2018) A population model exploring factors influencing Black Oystercatcher (*Haematopus bachmani*) population dynamics. *Waterbirds* 41:115–221. <https://doi.org/10.1675/063.041.0202>
- Morris WF, Doak DF (2002) Quantitative conservation biology. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts
- Nagrodski A, Raby GD, Hasler CT, Taylor MK, Cooke SJ (2012) Fish stranding in freshwater systems: sources, consequences, and mitigation. *J Environ Manage* 103:133–141. <https://doi.org/10.1016/j.jenvman.2012.03.007>
- Neufeld M (2013) 2013 North arm kokanee escapement/fry production summary report. Ministry of Forests, Lands and Natural Resource Operations, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Neufeld M (2016) 2016 North arm kokanee escapement/fry production summary report. Ministry of Forests, Lands and Natural Resource Operations, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Neufeld M (2018) 2017 North arm kokanee escapement/fry production summary report. Ministry of Forests, Lands and Natural Resource Operations, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Ng EL, Fredericks JP, Quist MC (2016) Population dynamics and evaluation of alternative management strategies for nonnative lake trout in Priest Lake Idaho. *N Am J Fish Manag* 36:40–54. <https://doi.org/10.1080/02755947.2015.1111279>
- Northcote TG, Halsey TG, MacDonald SJ (1972) Fish as indicators of water quality in the Okanagan Basin Lakes, British Columbia. British Columbia Fish and Wildlife Branch Department of Recreation and Conservation, BC
- O’Hanley JR, Wright J, Diebel M, Fedora MA, Soucy CL (2013) Restoring stream habitat connectivity: a proposed method for prioritizing the removal of resident fish passage barriers. *J Environ Manage* 125:19–27. <https://doi.org/10.1016/j.jenvman.2013.02.055>
- Parkinson E, Arndt S (2014) Results of a workshop on management policy options for Arrow Lakes. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Pate WM, Johnson BM, Lepak JM, Brauch D (2014) Managing for coexistence of kokanee and trophy lake trout in a montane reservoir. *N Am J Fish Manag* 34:908–922. <https://doi.org/10.1080/02755947.2014.923072>
- Pattenden R, Ash G (1993) Fisheries enhancement options for Dinosaur Lake, a review. Peace/Williston Fish and Wildlife Compensation Program, Report No. 72. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Peck K, Johnner D, Bassett M, Weir T, Fox R (2019) Kootenay Lake nutrient restoration program North Arm and South Arm 2017 and 2018 report. Fisheries Project Report No. 164. British Columbia Ministry of Forests, Lands and Natural Resource Operations and Rural Development, Province of British Columbia, Vancouver, British Columbia, Canada. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Plate EM, Bocking RC, Degan DJ (2012) Peace Project water use plan: Monitoring programs for the Peace Spill Protocol (GMSMON-4 WAC Bennett Dam entrainment study) Williston fish index in the vicinity of W.A.C. Bennett Dam an index of fish distribution and abundance in the Peace Arm of Willisto. Prepared for BC Hydro, Burnaby, BC
- Power M (2007) Fish population bioassessment. In: Guy CS, Brown ML (eds) Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, pp 561–624
- Pracheil BM, Mestl GE, Pegg MA (2015) Movement through dams facilitates population connectivity in a large river. *River Res Appl* 31:517–525. <https://doi.org/10.1002/rra.2751>
- Pracheil BM, DeRolph CR, Schramm MP, Bevelhimer MS (2016) A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage. *Rev Fish Biol Fish* 26:153–167. <https://doi.org/10.1007/s11160-015-9416-8>
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol Rev* 94:849–873. <https://doi.org/10.1111/brv.12480>
- Rieman BE, Myers DL (1992) Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. *Trans Am Fish Soc* 121:178–191. [https://doi.org/10.1577/1548-8659\(1992\)121%3c0178:IOFDAR%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1992)121%3c0178:IOFDAR%3e2.3.CO;2)
- Sebastian D, Scholten G, Woodruff P (2002a) Arrow Reservoir kokanee monitoring results of hydroacoustic and trawl surveys in July and October 2000. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Sebastian D, Scholten G, Woodruff P (2002b) Arrow Reservoir kokanee monitoring results of hydroacoustic and trawl surveys in July and October 2001. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Sebastian D, Andrusak G, Scholten G, Langston A (2009) An index of fish distribution and abundance in Peace Arm of Williston Reservoir based on hydroacoustic and gillnet surveys. Report GMS-MON #13, Peace Project Water Use Plan. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>

- Smart JJ, Chin A, Tobin AJ, White WT, Kumasi B, Simpfendorfer CA (2017) Stochastic demographic analyses of the silvertip shark (*Carcharhinus albimarginatus*) and the common blacktip shark (*Carcharhinus limbatus*) from the Indo-Pacific. *Fish Res* 191:95–107. <https://doi.org/10.1016/j.fishres.2017.03.002>
- Stubben C, Milligan B (2007) Estimating and analyzing demographic models using the popbio package in R. *J Stat Softw* 22:1–23. <https://doi.org/10.18637/jss.v022.i11>
- Turgeon K, Turpin C, Gregory-Eaves I (2019) Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. *Ecol Lett* 22:1501–1516. <https://doi.org/10.1111/ele.13283>
- Underwood K, Cramer SP (2007) Simulation of human effects on bull trout population dynamics in Rimrock Reservoir, Washington. *Am Fish Soc Symp* 53:191–207
- Ward HGM, Askey PJ, Weir T, Frazer KK, Russello MA (2019) Genetic stock identification reveals that angler harvest is representative of cryptic stock proportions in a high-profile kokanee fishery. *North Am J Fish Manag* 39(3):415–425. <https://doi.org/10.1002/nafm.10277>
- Webster J (2016) Estimation of adult kokanee escapement, egg deposition, fry abundance and egg-to-fry survival at Mission Creek spawning channel, 2015 brood. Prepared for Ministry of the Environment, Penticton, BC. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Wilson A, Andrusak H (2005) Egg development and fry emergence of Okanagan Lake 2004 shore spawning kokanee with reference to 2001–2003 brood year results. EcoCat. <http://a100.gov.bc.ca/pub/acat/public/welcome.do>
- Wolter C, Sukhodolov A (2008) Random displacement versus habitat choice of fish larvae in rivers. *River Res Appl* 24:661–672. <https://doi.org/10.1002/rra.1146>
- Wong MC, Dowd M (2016) A model framework to determine the production potential of fish derived from coastal habitats for use in habitat restoration. *Estuaries Coasts* 39:1785–1800. <https://doi.org/10.1007/s12237-016-0121-1>
- Wu H, Chen J, Xu J, Zeng G, Sang L, Liu Q, Yin Z, Dai J, Yin D, Liang J, Ye S (2019) Effects of dam construction on biodiversity: a review. *J Clean Prod* 221:480–489. <https://doi.org/10.1016/j.jclepro.2019.03.001>
- Zarfl C, Lumsdon AE, Berlekamp J, Tydecks L, Tockner K (2014) A global boom in hydropower dam construction. *Aquat Sci* 77:161–170. <https://doi.org/10.1007/s00027-014-0377-0>