



# Recovery tactics for sockeye blocked from anadromy evaluated through decision analysis and value of information



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## ABSTRACT

Choosing among recovery tactics for fish populations is challenged by high costs and uncertain outcomes. Depressed populations of salmonids are often supplemented using hatchery propagation; these strategies may involve releasing fish at different locations, densities, and life stages. We describe a unique decision context where supplementation is used to improve anadromous returns of a mixed anadromous-resident coastal sockeye salmon (*Oncorhynchus nerka*) population. Current anadromous returns in this system are declining, while resident abundance is stable. The recovery of anadromous sockeye salmon depends on depends in part on the heritability of anadromy, since anadromous sockeye are used as hatchery broodstock. Managers have long assumed that anadromy is a heritable trait, but the mounting evidence shows that both genetic and environmental processes shape the expression of migratory phenotypes. We use decision analysis to evaluate a series of decisions regarding whether to allow fish passage above the dam, whether to stock anadromous progeny above or below the dam, at what life stage, and by how much. We further conduct a value of perfect information analysis to evaluate whether outcomes can be improved with an experiment aimed at estimating anadromy. When model projections are integrated over uncertain heritability, the optimal solution is to stock into the reservoir at a high rate and allow passage of adults back into the reservoir. Value of perfect information suggests that this decision is insensitive to heritability, implying that restoration decisions should not wait for a time-intensive experiment. This work emphasizes careful consideration of objectives and the value of experimentation in driving decisions regarding population recovery and management.

## 1. Introduction

Dams are found in most watersheds worldwide where they are used for hydroelectric power generation, irrigation, human consumption, flood control or industrial use. The economic value generated by dams is often offset by impacts to natural aquatic systems upstream and downstream of the dam, as well as in the surrounding terrestrial ecosystem (Baxter, 1977; Liermann et al., 2012). In coastal watersheds, these impacts are especially pronounced in migratory fish species such as Pacific salmon (*Oncorhynchus* spp.) because a dam either blocks access to essential upstream spawning habitat, traps portions of the population above the dam, or results in the flooding of upstream spawning habitat. Salmon are highly valued economically as the basis for important commercial and recreational fisheries and culturally by local First Nations, for which anadromous salmon are an important part of their identity (Lichatowich, 1999). Within this context, increasing attention is being paid to reducing or mitigating losses to salmon as a result of dams (Whitney et al., 2005; Williams, 2008).

A variety of tactics are considered to restore salmon populations blocked from anadromy. Allowing fish passage, either through the construction of permanent facilities or through trap-and-truck methods, is the most direct mitigative tactic (McLaughlin et al., 2013). Permanent fish passage may be purpose-built to facilitate free movement of fish, but passage efficiency is not 100 % and the energetic cost of ascending the ladder may impact reproductive success (Caudill et al., 2013; Roscoe et al., 2011; Roscoe and Hinch, 2010). Hatchery supplementation and artificial spawning substrate are other tactics used to increase population abundance, but may lead to a variety of unintended genetic and ecological risks (Levin et al., 2001; Tringala and Bert, 1998). Nutrient restoration is another mitigation technique, where inorganic nutrients are added to increase primary production and provide more food for higher trophic levels (Perrin et al., 2006). Nutrient restoration has been used in many nursery lakes for Pacific salmon to increase smolt size and abundance from freshwater rearing systems (Compton et al., 2006; Hyatt et al., 2004) and is also used in reservoirs as a restoration technique following nutrient collapse common

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following dam construction (Stockner et al., 2000). Each of these tactics may be considered to compensate for impacts of dams, but which to use and in what combination is a decision problem with large potential risks and rewards (McLaughlin et al., 2013).

Decisions with clear objectives and high risks and rewards are often addressed with formal decision analysis, which breaks decisions down into a series of logical components. The steps of decision analysis include (adapted from Peterman and Anderson, 1999; Robb and Peterman, 1998): (1) identify management objectives; (2) identify possible management actions; (3) identify unknown aspects of the system that may affect outcomes, referred to as a state of nature, such as future fishing effort, productivity, or water flow; (4) assign probabilities to each possible state of nature; (5) calculate outcomes of each combination of management action and state of nature; and (6) evaluate management tactics. The decision analysis approach allows decision makers to see how management tactics compare against one another while understanding trade-offs between different management objectives. Proceeding through a decision analysis may suggest that outcomes are sensitive to one or more parameters. Decision analysis can be extended through a expected value of information analysis (Fielder et al., 2016; Hilborn and Walters, 1992), which examines how reducing uncertainties may affect the decision on how to act and/or improve outcomes. In this way, a decision-maker may evaluate whether reducing uncertainty in a parameter will result in improved management outcomes that offset the investment in research (Fielder et al., 2016).

One such decision that could benefit from decision analysis involves increasing the proportion of anadromous sockeye salmon (*O. nerka*) in Alouette Reservoir, British Columbia, Canada. Sockeye spawning in Alouette River were blocked from anadromy when the Alouette Dam was constructed in the lower river in 1928 with no allowance for passage over the dam (Godbout et al., 2011). Sockeye were no longer able to migrate to the ocean and became freshwater resident sockeye, which persist to present day. Resident sockeye have become the focus of a targeted recreational fishery, largely due to a nutrient restoration program aimed at increasing recreational catch rates of sockeye in the reservoir (Hebert et al., 2015). Access was reconnected in 2005 when annual springtime surface spills facilitated smolting and a trap and truck program allowed adults back into the reservoir (Godbout et al., 2011), however, numbers of returning adults have declined to fewer than 15 sockeye each year (Borick-Cunningham and Smith, 2017).

Improving anadromous returns to the Alouette Reservoir has had two primary challenges. The first is a low smolting rate of approximately 25 % of age-1 sockeye in the reservoir, and much fewer of older age-classes (Mathews et al., 2016). The second is a persistently low marine survival rate of smolts; currently 0.025 % relative to 2.1 % for nearby Cultus Lake sockeye (DFO, 2010; van Poorten et al., 2018a, 2018b). In an effort to improve smolting, springtime flows over the spillway have been varied within and across years to improve attraction efficiency for fish that wish to smolt, resulting in a 20 % smolting rate. A hatchery has been proposed to raise progeny of returning anadromous sockeye in an effort to select for anadromy, assuming it is a heritable trait; that is, some proportion of phenotypic expression is due to additive genetic variation. The decision to smolt in salmonines is actually dependent on a variety of factors including maternal influence, growth and metabolism, and can be influenced by body condition, lipid load, food availability, density-dependence, water temperature and stream flow (Kendall et al., 2015; Quinn and Myers, 2004). However, most of what we know about partial migration in salmonines comes from other species: very little has been studied regarding partial anadromy in sockeye. Therefore, determining how stocking decisions will affect anadromous returns and the resident sockeye population are unknown, especially since the genetic and environmental drivers of anadromy are uncertain.

To improve outcomes for Alouette sockeye, I evaluated 14 recovery tactics to explore how each affected anadromous and resident sockeye. Specifically, the impacts of allowing fish passage and stocking at

various rates and sizes above and below the dam were evaluated. A decision analysis was used to evaluate long-term impacts of each tactic on the abundance of resident and anadromous components of the population, recognizing and accounting for uncertainty in the heritability of anadromy and uncertainty in future marine survival. As part of the decision analysis, it was important to understand how resident and anadromous sockeye might trade off against each other across tactics. Heritability of anadromy was an important management parameter because of the intention to raise only offspring of anadromous parents. Therefore, I further explored how further studies to estimate the magnitude of heritability may improve management outcomes by calculating the expected value of perfect information (EVPI) to determine how this information may change the ultimate decision of population recovery.

## 2. Methods

### 2.1. Decision analysis

To evaluate tactics for improving anadromous sockeye returns while minimizing losses to the recreational fishery on resident sockeye, the steps of decision analysis as identified in Robb and Peterman (1998) were followed. The first step of decision analysis is to identify quantitative objectives and specifying their performance measures. Fish passage decisions on the Alouette watershed fall under the BC Hydro Fish Passage Decision Framework, which separates biological objectives from technical and economic objectives. The decisions considered here fall within the step dealing with biological issues, therefore, the decision analysis considered here focuses on recovery (biological) objectives alone. Objective functions were based on informal discussions with the Alouette River Salmon Reanadromization Project committee, which is focused on restoring anadromous sockeye while maintaining the resident sockeye for the benefit of recreational anglers. The committee includes approximately 15 members total from federal and provincial governments, the local Katzie First Nation and local stakeholders. Members of the committee were informally questioned regarding perceived utility of acceptable end-points and performance measures. It was agreed that the appropriate performance measures should be anadromous returns, which are important for Katzie First Nation and local stakeholders and abundance of resident sockeye vulnerable to the recreational fishery, which are important to local anglers and the provincial government who manages the fishery. Resident sockeye vulnerable to the fishery, referred to here as vulnerable sockeye, were calculated as the sum of abundance at age multiplied by vulnerability to the fishery at age. There were two complementary objectives for anadromous sockeye: persistence and recovery. Persistence was defined as achieving 200 returning sockeye per year; recovery would be achieved if there were 2000 returning sockeye per year. These were used as upper 95 % utility, while 10 and 100 annual returns were used as lower 5% endpoints for persistence and recovery, respectively. These endpoints were used to calculate logistic utility curves for persistence and recovery. The final anadromous sockeye utility was the equally weighted average of the existence and recovery functions based on input from the committee (Fig. 1; top panel). Most participants were ambivalent to the resident sockeye population; utility measures from this component came from members of the provincial government who manage the nutrient restoration program in part to support the recreational fishery on resident sockeye. These members stated there was a very low perceived utility for scenarios where abundance of resident vulnerable sockeye dropped to levels estimated prior to initiation of the nutrient restoration program in 1999. Similarly, provincial representatives achieved a high utility from the current vulnerable sockeye in the reservoir, which generates substantial fishing effort. These endpoints were used to define 5 and 95 % utility, respectively, which were then used to calculate utility for resident sockeye (Fig. 1; bottom panel). The objective of the sockeye recovery

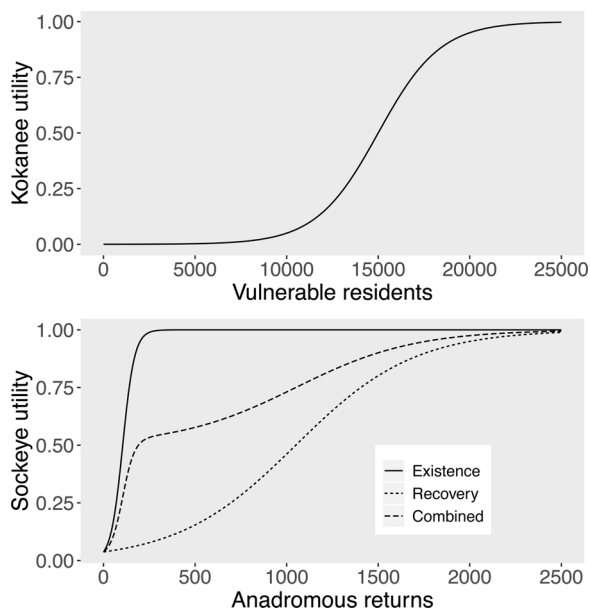


Fig. 1. Logistic utility functions used to describe perceived utility of returning anadromous sockeye (bottom panel) and perceived utility of resident vulnerable sockeye (top panel).

committee is not to maximize utility of anadromous and resident sockeye collectively, but to maximize both phenotypes individually. Therefore, the multi-attribute utility function was the product of the two utilities, which recognizes the trade-off between these two phenotypes and ensures maximizing the total objective does not sacrifice one of the two values. Members of the committee agreed to the shape and calculation of each sub-objective and the final objective function.

The second step of a decision analysis is to identify possible management actions. Three types of recovery actions, or tactics, were considered. The first tactic evaluated related to whether to return anadromous adults back into the reservoir. If returning sockeye were not returned to the reservoir, it would keep strays from neighbouring stocks out, still allow screened anadromous Alouette progeny to be used in the hatchery and allow community harvest by community members of the Katzie First Nation. The second tactic evaluated explored whether to stock and at what life stage. Rearing fish in hatcheries can have genetic and demographic repercussions, which should be considered carefully before stocking begins (Araki and Schmid, 2010). The impacts of stocked fish will vary with density and size at stocking (Taylor et al., 2013). Fish may be stocked as age-0+ fry in the reservoir or as age-1 smolts below the dam. The third tactic evaluated was related to the stocking rate for fry or smolts. Stocking rates for fry were 25,000, 50,000 or 75,000 and rates for smolts were 5000, 10,000 or 15,000 per year. Smolts must be held in the hatchery for longer and cost more to raise, so are typically released at lower numbers (Leber et al., 2005; Varkey et al., 2016). It was assumed that 80 % of fish raised in the hatchery will survive to release. Therefore, returning adults carrying eggs equal to 1.25 times the specified stocking rate were removed from wild returns and used in hatchery propagation; the remaining returning sockeye were placed in the reservoir if passage was allowed. All combinations of passage, stocking location and rate were considered.

The next steps in decision analysis are identifying unknown states of nature and assigning probabilities to them. Current marine survival rate is known for this population because annual abundance of smolts is estimated using in-river mark-recapture monitoring below the dam (Mathews et al., 2016) and returns are enumerated when they are trapped below the dam (Borick-Cunningham and Smith, 2017). Marine survival of anadromous Alouette sockeye has been anomalously low, with a geometric mean of approximately 0.025 %, whereas other Fraser

River stocks, such as Cultus and Chilko lakes are 2.1 % and 2.6 %, respectively (DFO, 2010). Stakeholders wonder whether marine survival will improve with continued stocking and selection for anadromy due to either improvements in homing or selection for predator avoidance. Stakeholders did not consider reductions in marine survival due to climate impacts or persistent degradation of marine conditions, partly because these impacts will happen on time-scales beyond the scope of this study. Therefore, two marine survival scenarios were evaluated: (1) marine survival is a random variable across simulations and year-classes with a lognormal distribution equal to the observed marine survival observations; and (2) marine survival is a random variable as above but increases each year by 0.05, so that the geometric mean in the final year is approximately 0.008. I assigned an equal prior probability of 0.5 to each scenario.

The next decision analysis step is to calculate outcomes of each combination of management tactic and state of nature. I first estimated parameters of an age-structured model of the system using a statistical catch-at-age model, fully described in van Poorten et al. (2018a). The model begins by predicting initial abundance-at-age and size-at-age. Annual recruitment is predicted using a zooplankton-dependent stock recruitment model (van Poorten et al., 2018a, 2018b), which allows Beverton-Holt recruitment predictions to vary with available food density. A food-dependent stock recruitment function is necessary to account for the dramatic increase in primary productivity that occurred following initiation of a nutrient restoration program, which involved additions of phosphorus and nitrogen, starting in 1999. The density-dependent function is broken into two phases, where the first predicts the number of age-0+ fall fry and the second predicts the number of age-1 the following spring at the time of smolting. This was necessary because hatchery fry are likely to be stocked in the fall, but smolts leave in spring, so the model separates the time prior to, and following stocking. These two times may have different densities, which will act on juvenile survival in those stages. The model then proceeds annually by calculating density-dependent asymptotic length, length-at-age, fishing mortality, abundance and egg deposition from predicted fecundity and abundance of resident sockeye and observed anadromous sockeye returns each year (Table A1; A2). The model was fit to annual hydroacoustic abundance indices for age 0 and age 1+ sockeye, gill net catch-at-age and fishery catch data. An informative prior probability was used for natural mortality with mean and precision of 0.6; an uninformative prior probability on age-0 length was used with mean of 60 mm and precision of 6. All other parameters had uninformative uniform or beta distributions (Table A3). The posterior probability distribution was numerically approximated using Markov chain Monte Carlo (MCMC) simulation in JAGS 3.4.0 (Plummer, 2003). Posterior distributions were calculated from 2,500,000 iterations after a burn-in of 1,000,000 and thinned to provide a final sample of 3000 across three separate chains (van Poorten et al., 2018a, 2018b). All model equations can be found in Table A1, a list of parameters and variables can be found in Table A2 and prior and posterior distributions can be found in Table A3.

The fitted model was used to make forward projections for both phenotypes for 25 years, which was a time frame that stakeholders were satisfied with. Projections were made assuming zooplankton densities equal to the mean from the last five years of data. Naturally reproducing sockeye survive and grow at a density-dependent rate through the first summer based on the first phase Beverton-Holt model used above. Depending on the management tactic chosen, hatchery-reared sockeye may be stocked as fry into the reservoir at the end of the summer, or as age-1 yearlings below the dam in the spring. A 10 % release mortality is applied to hatchery-reared fish to account for lower fitness of fish raised in captivity (Araki et al., 2008). Both wild and hatchery-origin fry in the reservoir then survive at a second density-dependent rate through to the following spring using the second phase Beverton-Holt model above at which point they may smolt at a rate based on the assigned heritability of anadromy, or may remain in the reservoir. Phenotypic

expression of anadromous and resident age-1 sockeye in the reservoir is calculated in equations T1.27 and T1.28 in Table A1. Heritability is assumed to be constant within each simulation, but uniform random across simulations. Density-dependence is not considered here as an antecedent to smolting because the nutrient restoration program will maintain constant competition in future years by adjusting nutrients to ensure consistent residual food density after sockeye consumption. Yearlings stocked below the dam experience no density-dependent mortality and immediately smolt. Anadromous sockeye return two years later at a rate set by the random density independent marine survival rate for the year and simulation, as set out in step 2 of the decision analysis. Returning adults may be removed for hatchery propagation or may be returned to the reservoir to spawn naturally.

Simulations were used to evaluate how different tactics affect resident and anadromous components of the sockeye population. Simulations were repeated 3000 times, corresponding to each sample from the posterior distributions of the estimation model and for each recovery tactic. Utility for each recovery tactic was calculated based on the mean abundance of vulnerable sockeye or number of annual anadromous returns over the 25 projection years, and averaged across the 3000 simulations. Because heritability was randomly chosen for each simulation and marine survival was randomly chosen for each year and simulation, outcomes accounted for uncertainty in these parameters. The optimal recovery tactic ( $X$ ) that resulted in the highest overall utility given no knowledge ( $N$ ) of heritability was termed  $X_{N,h^2=U(0,1)}$ .

## 2.2. Value of information

The following steps were used to assess the value of information gained by conducting an experiment to assess heritability of anadromy. First, model projection simulations were repeated with heritability set at  $Y_i = 0.0, 0.1, \dots, 1.0$ , where  $i$  indexes over heritability options. Each model run represents hypothetical cases of having perfect information about heritability. For each combination of recovery tactic ( $X$ ) and heritability, utility was calculated based on average vulnerable sockeye and average number of returning anadromous sockeye. The recovery tactic with the highest utility under a particular smolting heritability ( $h^2 = Y_i$ ) given perfect information about heritability ( $PI$ ) was termed  $X_{PI,h^2=Y_i}$ . The expected gain in knowledge from knowing heritability of anadromy was calculated as the difference in expected utility achieved for  $h^2 = Y_i$  if the recovery tactic used,  $X$ , is the optimal choice given perfect information or the optimal choice given no information (Mäntyniemi et al., 2009):

$$L(h^2 = Y_i) = E(U|X_{PI,h^2=Y_i}) - E(U|X_{N,h^2=Y_i}) \quad (1)$$

This same calculation was repeated for each 'known' heritability option. The value of perfect information was calculated by summing the product of prior probabilities for each heritability option ( $P(Y_i)$ ) and the expected gains in knowledge for each heritability option

$$VoPI = \sum_{i=1}^I P(Y_i)L(h^2 = Y_i) \quad (2)$$

Prior probabilities were uniform across each heritability option (i.e.  $P(Y_i) = I^{-1}$ ).

## 3. Results

Each recovery tactic had different and often opposing impacts on resident and anadromous Alouette sockeye. If passage was no longer allowed and stocking was not used to improve anadromy, resident sockeye would remain at approximately 18,600 sockeye vulnerable to the recreational fishery (Table 1). Anadromous sockeye returns would average about 30 fish per year. Simply allowing passage for returning anadromous sockeye back into the reservoir, which is the current tactic, increases expected annual returns to nearly 150 sockeye. Allowing

returning anadromous sockeye passage back into the reservoir generally leads to marginal improvements for resident sockeye but leads to greater than four-fold improvements in anadromous sockeye returns. Stocking fry in the reservoir leads to greater improvements in abundance of both anadromous and resident sockeye despite increased competition with wild sockeye hatched in the reservoir. Increasing stocking rate leads to proportional increases in return rates. If marine survival were to increase at 0.05 per year, resident sockeye will decline somewhat if passage is allowed, while anadromous returns will increase regardless of whether passage is allowed or not. Note that in tactics allowing stocking, there will be many years where all returning sockeye will be used for hatchery propagation, so no fish will be returned to the reservoir even if passage is permitted. It is important to note that while allowing passage of returning anadromous sockeye does not have a significant effect on resident sockeye, stocking in the reservoir increases variability in the resident sockeye leading to an increased probability of losing the phenotype (Table 1).

Predicted utility for resident and anadromous sockeye demonstrate the trade-off expected between the two phenotypes (Fig. 2). Across all tactics, there is little risk to resident sockeye while there is a four-fold range in utility for anadromous sockeye. Increased stocking rate leads to the greatest increase in anadromous utility, while stocking in the reservoir leads to the greatest loss in utility for resident sockeye. All recovery tactics led to expected utilities greater than 0.6 for resident sockeye abundance, while no tactics are expected to have a drastic negative impact on the expected utility for the recreational fishery. Allowing returning anadromous sockeye passage into the reservoir and stocking fry at a high rate leads to the greatest utility for anadromous sockeye while also resulting in the lowest utility for resident sockeye.

The decision table evaluates all recovery tactics across the uncertain trend in marine survival, allowing decision-makers to see which tactic leads to the greatest utility for both phenotypes (Table 2). The multi-attribute utility consistently increases across recovery tactics if marine survival increases at 5% per year, but there is no change in the ranking of tactics across scenarios with and without changes in mean marine survival. Expected value for each recovery tactic represents the mean utility expected irrespective of the rate of change in marine survival. Across recovery tactics, the highest expected utility comes from allowing passage and stocking fry into the reservoir at a high rate despite potential losses to the resident sockeye phenotype. Other combinations of actions resulted in similar expected utility; these consistently involved high stocking rates, though different combinations of passage decisions, stocking locations and ages.

The value of perfect information analysis demonstrates that taking time to better understand heritability of anadromy will not change the choice of which recovery tactic to use to balance anadromy and residency for the population. Regardless of heritability of anadromy, the highest expected multiattribute utility was obtained by allowing returning anadromous sockeye back into the reservoir and stocking fry into the reservoir at high rates. This analysis shows that while better understanding heritability of anadromy will reduce uncertainty in the future of the system, it will not affect the management decision being considered, which is only focused on which tactic will increase anadromous returns while having little impact on the recreational fishery.

## 4. Discussion

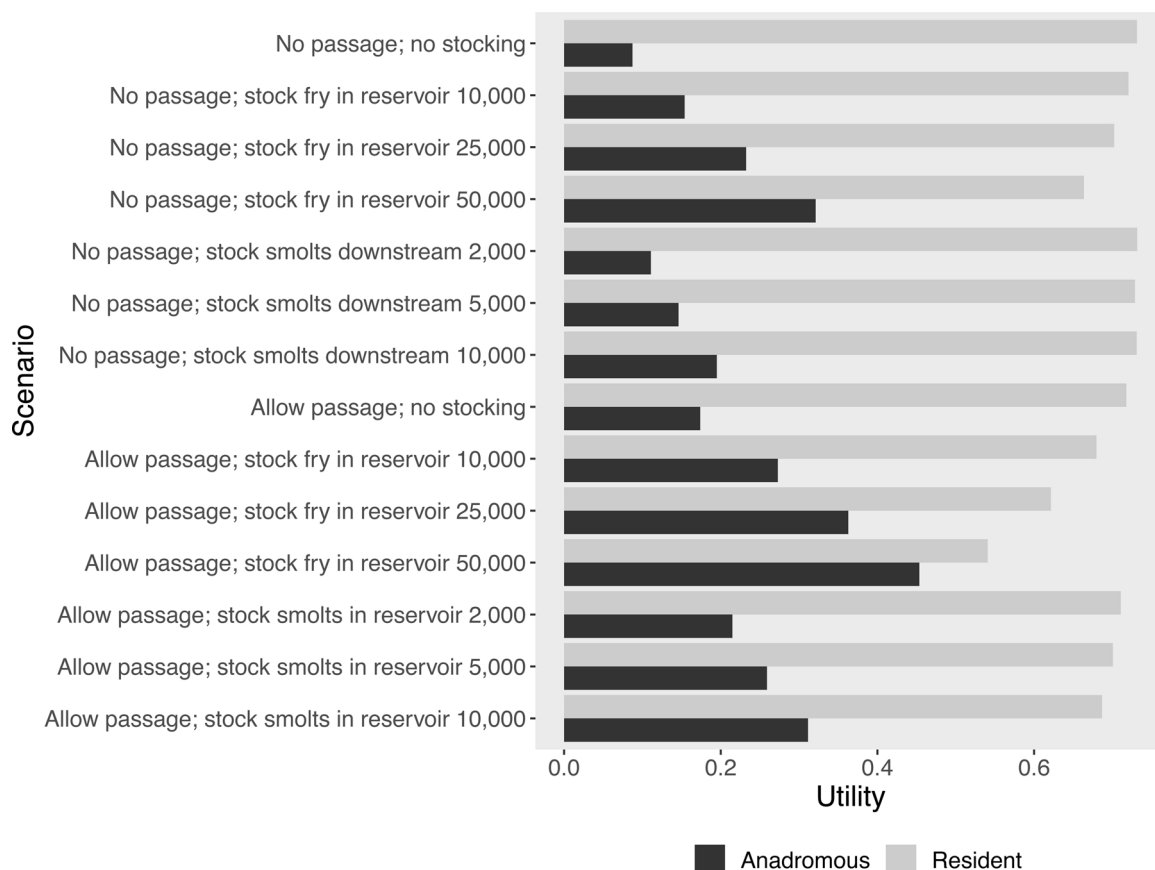
The best way to improve anadromous returns to the Alouette while not compromising the existing recreational fishery on resident sockeye is predicted to occur with high stocking rates of fry into the reservoir while ensuring returning anadromous adults are allowed back into the reservoir. Understandably, there was a trade-off between the resident and anadromous phenotypes: tactics that increased anadromy led to higher risk of low abundance or even extirpation to the resident phenotype due to increased competition in early life. Interestingly, this work revealed that there was little change in the best decision when



**Table 1**

Mean (+/- 95 % credible intervals) abundance of resident sockeye vulnerable to the recreational fishery and abundance of anadromous sockeye returning to the dam over the next 25 years integrated over parameter uncertainty. Results are shown for resident and anadromous performance measures under the assumption that mean marine survival is constant or increases over time at a rate of 0.05 per year.

Recovery tactic			Constant marine survival		Increasing marine survival	
Passage	Stocking stage	Stocking rate	Targeted residents (thousands)	Anadromous returns	Targeted residents (thousands)	Anadromous returns
No passage	No stocking	0	18.6 (6.6–29.7)	30 (0–242)	18.6 (6.5–29.5)	49 (0–355)
No passage	Fry in reservoir	10,000	18.7 (5.1–31.9)	62 (1–381)	18.7 (5.1–31.9)	116 (1–721)
No passage	Fry in reservoir	25,000	19.0 (1.9–38.2)	114 (1–666)	19.0 (2.0–38.4)	228 (2–1,420)
No passage	Fry in reservoir	50,000	19.6 (0.1–57.6)	200 (2–1,195)	19.4 (0.0–54.1)	426 (2–2,614)
No passage	Smolts downstream	5000	18.6 (6.5–29.6)	42 (0–279)	18.6 (6.5–29.4)	71 (1–456)
No passage	Smolts downstream	10,000	18.6 (6.6–29.6)	58 (1–354)	18.5 (6.8–29.6)	106 (1–651)
No passage	Smolts downstream	15,000	18.5 (6.6–29.3)	85 (1–502)	18.5 (6.6–29.6)	163 (2–976)
Allow passage	No stocking	0	18.6 (6.1–30.6)	148 (0–819)	18.8 (5.5–31.6)	1208 (0–4,223)
Allow passage	Fry in reservoir	10,000	18.9 (2.6–37.1)	338 (1–1,459)	18.7 (0.2–41.3)	2338 (1–9,649)
Allow passage	Fry in reservoir	25,000	19.1 (0.0–54.7)	492 (1–2,435)	18.3 (0.0–58.2)	3549 (2–16787)
Allow passage	Fry in reservoir	50,000	18.7 (0–74.0)	914 (2–4,725)	17.1 (0.0–70.0)	4894 (2–28945)
Allow passage	Smolts downstream	5000	18.7 (6.0–31.0)	185 (1–985)	18.8 (4.6–33.0)	1438 (1–5,560)
Allow passage	Smolts downstream	10,000	18.6 (5.6–31.7)	217 (1–1,162)	18.6 (3.1–34.0)	1618 (2–7,665)
Allow passage	Smolts downstream	15,000	18.6 (4.8–32.5)	299 (1–1,602)	18.4 (0.6–3573)	2286 (2–10683)



**Fig. 2.** Utility achieved for abundance of resident vulnerable sockeye and abundance of anadromous returns under each recovery tactic. Each bar represents the expected value across marine survival scenarios and across all simulations for the resident or anadromous utility.

heritability of anadromy was known with perfect information, suggesting little advantage in spending time and money understanding this variable (Mäntyniemi et al., 2009; Walters, 1986). By evaluating different tactics and comparing their impact on the existing recreational fishery and the potential increase in anadromous returns, it is possible to move forward with mitigating for the loss of anadromous sockeye to affected communities and the ecosystem.

A key aspect of this study has been on the genetic influence on anadromy primarily because of the desire to artificially select for anadromy through stocking. While this provides a credible prediction of anadromy in future years if all else is equal, it ignores other drivers such

as food availability and growth rate, which have been demonstrated to influence migratory decisions in other salmonids (reviewed in Kendall et al., 2015). Density-dependent smolting may influence anadromy in a stocked population; greater stocking densities limit per capita food availability, potentially leading to higher smolting rates (Olsson et al., 2006; Wysujack et al., 2008). Food availability influences growth rates and condition factors, which have been shown to influence smolting rates (O’Neal and Stanford, 2011; Tipping and Byrne, 1996). The nutrient restoration program in Alouette Reservoir should minimize density-dependence by adjusting primary production to account for changing fish density (Hebert et al., 2015), making predictions here more

**Table 2**

Decision table evaluating utility of each recovery tactic under assumptions that mean marine survival either stays constant or increases at 0.05 per year. Expected value refers to the mean utility across each marine survival scenario weighted by the prior probability of each and represents expected utility integrated across assumptions of marine survival.

Recovery tactic			Prior = 0.5	Prior = 0.5	
Passage	Stocking stage	Stocking rate	Constant marine survival	Increasing marine survival	Expected value
No passage	No stocking	0	0.06	0.07	0.06
No passage	Fry in reservoir	10,000	0.09	0.13	0.11
No passage	Fry in reservoir	25,000	0.13	0.20	0.16
No passage	Fry in reservoir	50,000	0.18	0.25	0.21
No passage	Smolts downstream	5000	0.07	0.09	0.08
No passage	Smolts downstream	10,000	0.09	0.13	0.11
No passage	Smolts downstream	15,000	0.11	0.17	0.14
Allow passage	No stocking	0	0.09	0.15	0.12
Allow passage	Fry in reservoir	10,000	0.14	0.23	0.18
Allow passage	Fry in reservoir	25,000	0.18	0.26	0.22
Allow passage	Fry in reservoir	50,000	<b>0.21</b>	<b>0.27</b>	<b>0.24</b>
Allow passage	Smolts downstream	5000	0.11	0.19	0.15
Allow passage	Smolts downstream	10,000	0.14	0.22	0.18
Allow passage	Smolts downstream	15,000	0.17	0.26	0.21

credible. However, these extrinsic sources of variation should be accounted for in other systems where prediction of anadromy is important and variation in density-dependence is likely greater.

Regardless of the magnitude of the heritability of anadromy, the best tactic identified from the decision analysis was unlikely to change when the magnitude of heritability of anadromy was known with certainty. This suggests that conducting a multi-year experiment on the heritability of anadromy would not improve the process of selecting the best management tactic, and only serves to hamper recovery efforts by delaying the selection process. However, even if the experiment does not benefit Alouette sockeye, understanding genetic and environmental influences of anadromy in sockeye may benefit other systems. Preliminary analysis of Alouette sockeye using this model (results not shown) suggest that if marine survival were similar to other systems (~2.3 %; DFO, 2010) and not limiting recovery, the magnitude of smolting heritability influences the decision on how to recover the system. Specifically, if marine survival were similar to other systems, the impact on resident sockeye would be greater, so the magnitude of heritability would have a greater influence the number of anadromous sockeye returning and impacting the resident sockeye. Regardless, the Alouette system is an ideal system for experiments to better understand genetic and density-dependent influences on anadromy, given consistent monitoring of sockeye residents, smolts and returns. If the final decision made for this system matches the optimal decision recommended through the decision analysis, the experiment on heritability could be conducted concurrently. Fish passage is being considered on dams all over the world as regulations and social norms change (McLaughlin et al., 2013); predicting the impact of improving fish passage is an important part of those decisions as well. The predicted benefits of providing passage for sockeye salmon will partly rely on genetic and density-dependent drivers of anadromy as well as how first-generation migrants and their progeny survive at sea. The value of perfect information calculated here only relates to the impending decision to recover anadromy of Alouette sockeye; it does not speak to the value of estimating heritability of anadromy for other systems where marine survival may be higher and recovery objectives and tactics may be different.

This work does not provide guidance on the type of upstream passage to be considered. The existing trap-and-truck passage does provide passage and can be used to guard against entry of invasive species and stray adult sockeye salmon from other systems entering the reservoir. However trap-and-truck is not a perfect solution and can result in disorientation or mortality (Keefer et al., 2010; Noonan et al., 2012; Schmetterling, 2003). Conversely, permanent fish ladders also cause injury and mortality (Noonan et al., 2012) as well as being relatively

non-selective with respect to species that are allowed access. The decision to allow permanent passage clearly has risks to population genetic (e.g. gene flow) and ecosystem (e.g. energy flow) processes (McLaughlin et al., 2013). Such risks should be carefully considered, as the outcome of these decisions cannot easily be undone (Rahel, 2013).

Alouette stakeholders do not consider delaying passage as an option, whereby the decision to allow fish to smolt out of the system is postponed until ocean conditions and expected marine survival improves. Marine conditions have fluctuated through periods of high and low productivity, which impacts marine survival for anadromous salmon (Beamish et al., 1999). Certainly there is a hope among some stakeholders that the current low marine survival state regime measured among Pacific salmon populations and species (e.g. Kendall et al., 2017) is transitory. This was not considered for two reasons. First, the immediate social benefits of delaying are low; the Katzie First Nation and stakeholders have waited for a long time to see anadromous returns to the system (van Poorten et al., 2018a, 2018b); delay would result in low expected utility for anadromous sockeye. The second reason is that it is difficult to reliably forecast regime shifts, or predict their persistence (DeYoung et al., 2008). Trapping sockeye in Alouette Reservoir has inadvertently protected this low abundance population from risk of extirpation, similar to intentional efforts to protect endangered steelhead in other systems (Thrower et al., 2004). The nutrient restoration program has greatly increased abundance (B. T. van Poorten et al., 2018a, 2018b), thereby further protecting the population from risks due to stochastic events. Delay is a reasonable, precautionary action to consider in situations where there are irreversible risks to consider (Fenichel et al., 2008). However, there is no guarantee that marine survival will increase in the foreseeable future, so the delay tactic is impossible to reliably evaluate in a decision analysis and would be a poor choice for management.

This analysis only considered ecological objectives. Economic measures, such as cost of ongoing trap and truck or capital costs associated with construction of a permanent fish passage facility, as well as ongoing cost of hatchery operation, were not considered. Although the utility gained by members of the Katzie First Nation from anadromous sockeye was considered, this drastically oversimplifies the variety of cultural and spiritual benefits they would gain from both returns of sockeye and potentially, the provision of fish passage on the fish community at large (Lichatowich, 1999). Indigenous values related to culture and spiritual objectives are characteristically difficult to quantify (Raymond et al., 2014), but should necessarily play a role in the decision of how to restore this and other impacted ecosystems (Ortolano and Cushing, 2002). Economic and cultural values were not considered in this analysis because they will be evaluated at a later

stage of the overall decision process (Fish and Wildlife Compensation Program, 2018); it will be important to weight all objectives carefully at that later stage (Gowan et al., 2006). The appropriate weighting of ecological, economic and social aspects of ecosystem recovery is critical to ensuring all groups are respected and accept the final decision regarding passage and recovery.

Dams and other obstructions to passage within watersheds are nearly ubiquitous; many of these obstructions do not properly address the needs of the aquatic ecosystem and should be remediated. Conservation and mitigation dollars are limited and many restoration tactics are very expensive (Null and Lund, 2011). However, the results of our actions or inactions affect ecosystems, fisheries catch and First Nations cultures (Opperman et al., 2011; Williams, 2008) so these decisions must carefully consider mitigation options and uncertainties. We know that populations in partially anadromous species may revert back to anadromy following decades or even centuries of isolation from the ocean (Foerster, 1947; Godbout et al., 2011; Thrower et al., 2004), so past actions such as building dams are not irreversible. Dams and other obstructions to anadromy are widespread, leading to a re-evaluation of the need for these structures. Many systems are being considered for dam removal, such as occurred on the Elwha River (Pess et al., 2008). Appropriately accounting for uncertainties in factors such as marine survival and heritability of anadromy will be important in providing advice to decision makers that promotes recovery of

anadromous stocks in a way that helps mitigate for past impacts on these important species.

**CRedit authorship contribution statement**

**Brett T. van Poorten:** Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing - review & editing, Writing - original draft.

**Declaration of Competing Interest**

The authors declare that there are no conflicts of interest.

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**Appendix A**

Tables A1–A3

**Table A1**  
Statistical catch-age model of the mixed resident-anadromous nerkid system including two-stage Beverton-Holt recruitment and density-dependent growth. Reproduced from van Poorten et al., 2018a.

Parameters	
T1.1	$\theta = (L_{\infty,1}, K, L_0, c^{(1)}, c^{(2)}, c^{(3)}, p_1, p_2, p_3, \{N_{0,a}\}_{a=1}^A, M, F, \lambda, \tau, \xi, \psi, \chi, \{\varepsilon_t\}_{t=1}^T)$
T1.2	$\varphi = (a_e, b_e, L_{50(f)}, \sigma(f), m_3, \rho)$
Multi-stanza stock recruit variables	
T1.3	$\alpha_{(1)t} = \exp\left(-c^{(1)}p_1 - \frac{c^{(2)}p_2}{z_t}\right)$
T1.4	$\beta_{(1)t} = \frac{c^{(3)}p_3}{c^{(1)}p_1z_t^2 + c^{(2)}p_2z_t}(1 - a_{(1)t})$
T1.5	$\alpha_{(1+)t} = \exp\left(-c^{(1)}(1 - p_1) - \frac{c^{(2)}(1 - p_2)}{z_t}\right)$
T1.6	$\beta_{(1+)t} = \frac{c^{(3)}(1 - p_3)}{c^{(1)}(1 - p_1)z_t^2 + c^{(2)}(1 - p_2)z_t}(1 - a_{(1+)t})$
Initial population	
T1.7	$\hat{l}_{t=1,a} = \begin{cases} L_0 & a = 0 \\ L_0e^{-Ka} + L_{\infty,1}(1 - e^{-Ka}) & a \geq 1 \end{cases}$
T1.8	$\hat{N}_{t=1,a} = N_{0,a}$
T1.9	$\hat{N}_{(sp)t=2,a} = \begin{cases} \frac{N_{0,a}\alpha_{(1+)1}}{1 + N_{0,a}\beta_{(1+)1}} & a = 1 \\ N_{0,a-1}e^{-M/2} & a \geq 2 \end{cases}$
State dynamics	
T1.10	$L_{\infty,t} = \frac{\tau + \lambda z_t}{1 + \xi \sum_{a=0}^A (N_{t,a} l_{t-1,a}^2)}$
T1.11	$\hat{l}_{t,a} = \begin{cases} L_0 & a = 0 \\ \hat{l}_{t-1,a-1} + L_{\infty,t}(1 - e^{-K}) & a \geq 1 \end{cases}$
T1.12	$v_{t,a} = \left[1 + \exp\left(-\frac{(\hat{l}_{t,a} - L_{50(f)})}{\sigma(f)}\right)\right]^{-1}$
T1.13	$Z_{a,t} = M/2 + v_{t,a}F$
T1.14	$\hat{N}_{t,a} = \begin{cases} \frac{\hat{E}_{t-1}\alpha_{(1)t}}{1 + \hat{E}_{t-1}\beta_{(1)t}} e^{\varepsilon_t - 0.5\sigma_{(R)}^2} & a = 0; \varepsilon_t = N(0, \sigma_{(R)}) \\ (\hat{N}_{(sp)t,a-1} - \hat{S}_{t,a-1}) \frac{v_{t,a}F}{Z_{a,t}} e^{-Z_{a,t}} & 1 < a < A \\ \hat{N}_{(sp)t,a-1} \frac{v_{t,a}F}{Z_{a,t}} e^{-Z_{a,t}} & a = A \end{cases}$

(continued on next page)

**Table A1** (continued)

Parameters	
T1.15	$\widehat{N}_{(sp)t+1,a} = \begin{cases} \frac{\widehat{N}_{t,a}\alpha(1+t)}{1 + \widehat{N}_{t,a}\beta(1+t)} & a = 1 \\ \widehat{N}_{t,a}e^{-(M/2)} & 1 < a < A - 2 \\ \widehat{N}_{t,a}(1 - m_3)e^{-(M/2)} & A - 1 \end{cases}$
T1.16	$\widehat{f}_{t,a} = a_e + \widehat{l}_{t,a} \exp(b_e) \quad \{a = A - 1, A\}$
T1.17	$\widehat{E}_{(S)t} = \widehat{f}_3 \widehat{N}_{(S)t} / 2$
T1.18	$\widehat{E}_t = (\widehat{f}_3 \widehat{N}_{t,3} m_3 + \widehat{f}_A \widehat{N}_{t,A}) / 2 + \widehat{E}_{(S)t}$
Fishery catch-at-age observations	
T1.19	$\widehat{C}_{t,a} = \widehat{N}_{t,a} (1 - e^{-v_{t,a} F t})$
Process and observation error	
T1.20	$\sigma_{(R)} = \rho \psi$
T1.21	$\sigma_{(l)t,a} = \widehat{l}_{t,a} c v_l$
T1.22	$\tau_{(l)t,a} = \sigma_{(l)t,a}^{-2}$
T1.23	$\sigma_{(H)a=0} = (1 - \rho) \psi \chi$
T1.24	$\tau_{(H)a=0} = \sigma_{(H)a=0}^{-2}$
T1.25	$\sigma_{(H)a=1+} = (1 - \rho) \psi (1 - \chi)$
T1.26	$\tau_{(H)a=1+} = \sigma_{(H)a=1+}^{-2}$
Phenotypic expression	
T1.26	$\tau_{(H)a=1+} = \sigma_{(H)a=1+}^{-2}$ Phenotypic expression
T1.27	$Sm^H = p_{(smolt)t-4} + h^2 (1 - p_{(smolt)t-4})$
T1.28	$Sm^K = p_{(smolt)t-4} + h^2 \left( \frac{E_{(S)t-2}}{E_{t-2}} - p_{(smolt)t-4} \right)$
Smolts and sockeye returns	
T1.29	$\widehat{s}_{t,1} = (Sm^H x_t + Sm^K N_{(sp)t,1}) \frac{N_{(sp)t,1}}{N_{t-1,1}}$
T1.30	$\widehat{N}_{(S)t} = \widehat{s}_{t-2,1} S v_m$

**Table A2**

Notation for the statistical catch-age models. Values of ++ indicate estimated parameters. Parameter descriptions include units in parenthesis.

Symbol	Value	Description
Indices		
$t$	{1,2,...T}	Time step (T = 15)
$a$	{1,2,...A}	Age-class (A = 4)
Model parameters		
$L_{\infty,1}$	++	Asymptotic length in first year (mm)
$K$	++	von Bertalanffy metabolic parameter (yr <sup>-1</sup> )
$L_0$	++	Age at age-0 (mm)
$c^{(1)}$	++	Base mortality parameter
$c^{(2)}$	++	Mortality per time spent foraging (N <sub>prey</sub> <sup>-1</sup> )
$c^{(3)}$	++	Carrying capacity parameter (fish <sup>-1</sup> )
$p_1, p_2, p_3$	++	Proportion of $c^{(1)}, c^{(2)}, c^{(3)}$ attributed to first or second stanza
$N_{0,a}$	++	Initial abundance at age- $a$
$M$	++	Instantaneous natural mortality rate (yr <sup>-1</sup> )
$F$	++	Instantaneous fishing mortality rate (yr <sup>-1</sup> )
$\lambda$	++	Food-dependence parameter of density-dependent growth (mm N <sub>prey</sub> <sup>-1</sup> )
$\tau$	++	Alternate food parameter of density-dependent growth (N <sub>prey</sub> )
$\xi$	++	Competition-dependence parameter of density-dependent growth (mm <sup>-2</sup> )
$\psi$	++	Total (observation + process) error
$\chi$	++	Proportion of acoustic observation error attributed to age-0
$a_e$	-7.151	Egg-length multiplier (egg fl <sup>-1</sup> )
$b_e$	2.375	Egg-length exponent
$L_{50(f)}$	225	Length-at-50 % vulnerability to angling
$\sigma_{(f)}$	20	Angling vulnerability variance
$m_3$	0.9	Proportion of kokanee mature at age-3
$\rho$	0.75	Proportion of total error attributed to process error
$S v_m$	0.0025	Marine survival for sockeye from smolt to return
Derived variables		
$L_{\infty,t}$		Asymptotic length in year- $t$ (mm)
$\widehat{l}_{t,a}$		Length-at-age in year- $t$ (mm)

(continued on next page)



Table A2 (continued)

Symbol	Value	Description
$\hat{J}_{t,a}$		Fecundity at age in year- $t$ (eggs/female)
$v_{t,a}$		Length-based vulnerability to angling in year- $t$
$\alpha_{(1)t}, \alpha_{(1+)t}$		Maximum survival to age-1 or -1+, respectively
$\beta_{(1)t}, \beta_{(1+)t}$		Carrying capacity parameter to age-1 and 1+, respectively (fish <sup>-1</sup> )
$Z_{a,t}$		Total fishing mortality at age in year- $t$
$\sigma_{(R)}$		Process error in age-0+ recruitment
$\sigma_{(H)a=0}, \sigma_{(H)a=1+}$		Observation error in age-0 and -1+ abundance
$\sigma_{(l)t,a}$		Observation error in length-at-age
$\tau_{(C)}$		Precision in observation error for annual catch
State variables		
$\hat{N}_{t,a}$		Number of age- $a$ fish in fall of year- $t$
$\hat{N}_{(sp)t,a}$		Number of age- $a$ fish in spring of year- $t$
$V_t$		Vulnerable abundance in year- $t$
$\hat{C}_{t,a}$		Catch at age in year- $t$
$\hat{E}_{(S)t}$		Sockeye eggs in year- $t$
$\hat{E}_t$		Total (sockeye + kokanee) eggs in year- $t$
Observations		
$I_{t,a}$		Hydroacoustic survey index in year- $t$ for ages $a=0$ or $a = 1 - 4$ combined
$C_{t,a}$		Catch of age- $a$ fish in year- $t$ in recreational fishery
$l_{t,a,i}$		Length-at-age in year- $t$ for individual $i$
Management Controls		
$x_t$		Spring age-0 stocked fry descended from returning sockeye (fish)
Uncertain states		
$h^2$		Heritability of smolting

Table A3

Prior probability density functions (PDF) and posterior predictive distributions for each estimated parameter from van Poorten et al., 2018a. Prior PDFs are described as either normal  $N(\mu, \tau)$ , uniform  $U(\text{upper}, \text{lower})$ , beta  $B(\alpha, \beta)$  or gamma  $G(\text{shape}, \text{rate})$  distributions. Posterior distributions for parameters are reported with mean and standard deviation with upper and lower 95 % credible intervals.

Parameter	Prior PDF	Posterior PDF	95 % Credible interval
$L_{\infty,1}$	$U(100, 1000)$	287.6 (7.0)	274.6 – 300.7
$K$	$U(0, 2)$	0.5 (0.0)	0.5 – 0.5
$L_0$	$N(60, 6)$	13.1 (3.4)	6.4 – 20.1
$c_1$	$U(0, 10)$	1.8 (6.4)	0.7 – 3.3
$c_2$	$U(0, 10)$	0.1 (0.1)	0.0 – 0.4
$c_3$	$U(0, 1)$	0.0 (0.0)	0.0 – 0.0
$p_1$	$B(2, 2)$	0.4 (0.2)	0.1 – 0.7
$p_2$	$B(2, 2)$	0.6 (0.2)	0.1 – 0.9
$p_3$	$B(2, 2)$	0.5 (0.2)	0.1 – 0.9
$N_{0,0}$	$U(0, 500,000)$	33,164.4 (12,258.4)	15,297.1 – 63,786.8
$N_{0,1}$	$U(0, 500,000)$	14,062.9 (9,033.4)	999.7 – 33,249.2
$N_{0,2}$	$U(0, 500,000)$	5,701.3(4,682.9)	161.2 – 17,468.1
$N_{0,3}$	$U(0, 500,000)$	6,399.4 (4,677.5)	313.0 – 17,543.3
$N_{0,4}$	$U(0, 500,000)$	20,385.6 (4,370.1)	12,060.2 – 29,147.2
$M$	$N(0.6, 0.6)$	0.9 (0.1)	0.6 – 1.1
$F$	$U(1, 1)$	0.1 (0.1)	0.0 – 0.3
$\lambda$	$U(0, 50)$	16.8 (12.3)	0.6 – 45.1
$\tau$	$U(0, 10,000)$	751.1 (131.4)	549.3 – 1,019.8
$\xi$	$U(0, 10)$	6.4 (1.8)	3.4 – 9.8
$\psi$	$U(0, 10)$	2.8 (0.3)	2.3 – 3.4
$\chi$	$B(1, 1)$	0.5 (0.1)	0.4 – 0.6
$cv_t$	$B(1, 1)$	0.1 (0.0)	0.1 – 0.1
$\tau_{(C)}$	$G(0.01, 0.01)$	0.0 (0.0)	0.0 – 0.0

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