

Evaluating benefits of stocking on sockeye recovery projections in a nutrient-enhanced mixed life history population

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Abstract: Dam construction often blocks migration of anadromous sockeye salmon (*Oncorhynchus nerka*), resulting in a residualized population that is often managed as landlocked kokanee. Anadromy resumes when a reconnection to the ocean is established; however, there may be selective pressure acting on threshold trait(s) affecting smolt timing and probability. While there may be interest in predicting persistence of anadromous and residual sockeye forms, this is difficult because the heritability of smolting in these populations is poorly known. We develop a fully density-dependent age-structured model to project abundances for both anadromous and resident sockeye. The model considers trophic interactions due to nutrient variation and the density-dependent consequences for smolting and adult returns. Moreover, it asks how each life history type will persist if a hatchery were used to promote anadromous sockeye through artificial selection. We show hatchery supplementation is unlikely to impact anadromous or resident sockeye significantly, although there is substantial prediction uncertainty suggested in projections. Our study suggests that providing passage for previous land-locked anadromous populations will lead to the return of anadromous fish in the short term, but long-term prospects are far from certain.

Résumé : La construction de barrages entrave dans bien des cas la migration des saumons rouges (*Oncorhynchus nerka*) anadromes, produisant du coup une population résiduelle souvent gérée comme s'il s'agissait de kokanis non anadromes. Si l'anadromie reprend quand la connexion à l'océan est rétablie, il peut y avoir une pression de sélection agissant sur des caractères seuils qui influencent le moment de la smoltification et la probabilité de cette dernière. Il peut être intéressant de prédire la persistance de formes anadromes et résiduelles de saumons rouges, mais cela est difficile parce que l'héritabilité de la smoltification dans ces populations n'est pas bien connue. Nous développons un modèle structuré par âge entièrement dépendant de la densité pour prédire les abondances de saumons rouges tant anadromes que résidents. Le modèle intègre les interactions trophiques dues aux variations de nutriments et les conséquences dépendantes de la densité sur la smoltification et les retours d'adultes. Il demande en outre comment chaque type de cycle biologique persistera en cas d'utilisation de lâchers de poissons d'élevage pour favoriser les saumons rouges anadromes par la sélection artificielle. Nous démontrons qu'il est peu probable que des lâchers de poissons d'élevage aient une incidence significative sur les saumons rouges anadromes ou résidents, bien qu'une incertitude considérable caractérise les projections. L'étude donne à penser que, si l'aménagement de passes pour les populations anadromes piégées dans des eaux intérieures mènera au retour de poissons anadromes à court terme, les perspectives à long terme sont très incertaines. [Traduit par la Rédaction]

Introduction

Dams and reservoirs are an important component of the landscape, and while they serve an important socioeconomic function, they also pose a threat to ecological integrity of the watershed (Freeman et al. 2003; Liermann et al. 2012). Dams and reservoirs disrupt littoral habitat and productivity, alter hydrodynamic processes, alter reservoir nutrient dynamics, and complicate or remove connectivity within the watershed (Friedl and Wüest 2002; Hall et al. 2011). The loss of connectivity is especially important in systems that have traditionally supported anadromous fish species, which annually transport large quantities of marine-derived nutrients to support freshwater and surrounding terrestrial ecosystems (Schindler et al. 2005; Scheuerell et al. 2007; Hall et al. 2012). Additionally, the impact of dams to the cultural identity of indigenous communities is substantial, as members of First Nations who were traditionally connected to the fish and flowing water must look elsewhere to satisfy this cultural and spiritual loss (Baxter 1977; Gregory and Trousdale 2009). Restoration of fish passage is often technically feasible but can often

be expensive, and decisions on whether and where to invest in passage must appropriately weigh environmental, economic, social, and cultural values.

Managing fish populations usually involves taking actions that directly or indirectly affect the numbers or size of animals in the system. This can occur either due to stocking, changes in fisheries management, which results in selective harvest of fish, or due to enhancement of stocks or habitat (Walters and Martell 2004). However, the implications for size structure and abundance are not independent (He et al. 2015). Density-dependent processes mean that changes in the abundance or size structure of the population result in changes in the food resources available per individual, which in turn result in growth or survival implications (Lorenzen 2008). On longer time scales, changes in size-at-age of mature individuals could result in more or larger eggs produced per female, which affects density-dependent survival of resulting larvae in the next generation (Beverton and Holt 1957). Moreover, these simple changes can be propagated through the food web through competitors, predators, and prey. The outcomes of any

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management decision can be complex and counterintuitive (Hilborn and Walters 1992).

Augmenting fish populations with hatchery-reared, wild-stock fish is a frequently used tactic in recovering low abundance populations. The basic idea is to improve survival of young fish and augment abundance, but the detrimental effects of hatcheries are often overlooked (Levin et al. 2001; Araki and Schmid 2010). Negative consequences of stocking include increased competition with wild-spawned fish, inbreeding depression, introgression, and disease transfer, among others (Fleming and Gross 1993; Reisenbichler and Rubin 1999; Weber and Fausch 2003; Araki et al. 2007; Araki and Schmid 2010). Many of these impacts are often not observed in the hatchery; persistent differences between wild and hatchery fish are often only evident by their performance following release in the wild (Araki et al. 2008; Thrower and Hard 2009). Among anadromous species like Pacific salmon (*Oncorhynchus* spp.), the goal of stocking is often to improve abundance of adults once stocked fish smolt to the ocean, grow, and return, but impacts of increased densities of presmolting juveniles (i.e., rearing juveniles in the donor stream or lake) on the remainder of the freshwater ecosystem are often overlooked. This is particularly poignant given uncertain density-dependent responses in growth and recruitment.

Sockeye salmon (*Oncorhynchus nerka*) have a broad suite of life history types due to a combination of phenotypic and genotypic differences among populations and individuals. Anadromous sockeye salmon rear in fresh water for 1–3 years prior to smolting, migrate to the ocean, and remain there for 1–3 years before returning to fresh water to spawn and die, typically between age-3 and age-5. Some sockeye, termed residents, may delay smolting or mature early without migrating to the ocean (this predominantly occurs in males). Early maturing resident sockeye males interbreed with anadromous sockeye by sneaking fertilization, but are morphologically distinct in that they are much smaller and do not attain the typical red colouration at spawning because they are inefficient at utilizing the lower concentration of carotenoids in a freshwater diet (Craig and Foote 2001). Finally, there are kokanee salmon (i.e., the freshwater form of *O. nerka*) that do not smolt and may live sympatrically with sockeye (Taylor et al. 1996). Kokanee live for 3–5 years in fresh water before spawning. Kokanee are thought to maintain genetic isolation from sockeye due to differences in spawning habitat and size; while they have re-evolved the ability to turn red at maturity, they are much smaller (Wood and Foote 1996; Craig and Foote 2001; Dodson et al. 2013).

Among resident and anadromous sockeye, the choice to smolt is thought to be a function of a threshold trait(s) that initiates physiological changes to the body once certain conditions are met (Dodson et al. 2013); however, when anadromy is blocked, sockeye may all become residents, as anadromy is not obligatory for their life history (Ricker 1959). Interestingly, even kokanee populations that have been isolated for thousands of years are capable of smolting and surviving in the marine environment before returning to their native rivers, albeit with lower marine survival than their anadromous sockeye counterparts (reviewed in Godbout et al. 2011). Godbout et al. (2011) reported the return of anadromy in a previously isolated *O. nerka* population after passage was allowed after nearly 90 years. This population is a deepwater spawner, so neither resident nor anadromous individuals develop red colouration, calling into question whether these are true sockeye or kokanee. Although elders of the Katzie First Nation tell stories of red sockeye being caught in the upper Alouette River (above what is now the Alouette Reservoir; Jenness 1955), this phenotype no longer exists. Interestingly, only a low proportion of this population smolts each year, calling into question the heritability and selective pressure of smolting. While several First Nations and stakeholders wish to see strong annual sockeye returns to the reservoir each year, the decision to invest in perma-

nent fish passage (e.g., a fish ladder) will partially depend on heritability of smolting and, in turn, projected sockeye returns.

This study examines the density-dependent consequences of stocking in a reservoir with a mixed anadromous–resident sockeye population. We use existing data to estimate various key population parameters, including density-dependent growth and survival rates. We project anadromous sockeye returns and abundance of resident sockeye given the full range of uncertainty in all parameters as well as heritability of smolting. Here, heritability of smolting is used as a surrogate for heritability on liability traits, which are a component of complex and relatively uncertain threshold traits leading to alternative migratory tactics (Dodson et al. 2013). The model will be used to provide an evaluation of the value of stocking to promote smolting and provide medium-term (25-year) projections for recovery of the anadromous life history phenotype.

Methods

Study system

This study centers on the sockeye population rearing in Alouette Reservoir (49°17'N, 122°29'W), in southwestern British Columbia. This population exhibits both freshwater resident and anadromous phenotypes. To underline ambiguity in true origins of the population, we refer to all *O. nerka* in the population as “nerkids”. Alouette Reservoir is a medium-sized reservoir (1666 ha at full-pool) approximately 50 km west of Vancouver, Canada. The reservoir is 17 km long, consisting of two basins separated by a shallow isthmus. The lake is home to numerous cool- and cold-water species and supports a recreational fishery on rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarkii*), bull trout (*Salvelinus confluentus*), and resident nerkids, although the majority of fishing effort targets nerkids.

Alouette Reservoir was created in 1928 by completion of the Alouette Dam at the south end of the lake, effectively blocking access to the reservoir from the lower Alouette River. Most flow is now redirected north to a 1 km long tunnel linking to Stave Reservoir, where stored water is used for hydroelectric power generation. The remainder of water is released through a low-level outlet in the dam to the Alouette River, although water can also be released over a crest gate and a free crest weir when water levels exceed 125.5 m above sea level. Completion of the dam meant a cessation of anadromy for several Pacific salmon species, including sockeye salmon, as there was no provision for passage at the dam. Most salmon species were extirpated from the reservoir following completion of the dam with the exception of sockeye, where only obligate residents remained. This also resulted in a loss of annual salmon returns to the local Katzie First Nation.

Productivity in Alouette Reservoir is thought to have followed the typical boom-and-bust nutrient cycle of reservoir formation (“cultural oligotrophication”; Stockner et al. 2000) following dam construction primarily due to a disruption of natural hydrology, sedimentation in the new reservoir, and loss of carbon production from the littoral community. Additionally, the loss of marine-derived nutrients transported by anadromous salmon have also contributed to declines in productivity (Larkin and Slaney 1996; Cederholm et al. 1999). Nutrient restoration in Alouette Reservoir began in 1999 with the primary objective of improving the recreational fishery for resident nerkids. Since that time, inorganic agricultural-grade fertilizer has been added weekly from approximately May to September each year.

The Alouette system has been carefully monitored to promote production of a food web that leads to production of nerkids. Phosphorus and nitrogen levels, as well as phyto- and zooplankton densities and composition, were monitored bimonthly in the first 4 years and monthly thereafter in an attempt to maximize edible phytoplankton while minimizing the risk of plankton bloom. The amount and ratio of phosphorus to nitrogen has var-

ied over the course of the program to adjust to varying annual growing conditions and adaptively determine the optimal strategy aimed at promoting the growth of edible plankton and therefore fish. Gill nets are used in the fall to monitor resident nerkid size structure, and hydroacoustic surveys have been conducted concurrent with gill net sampling to provide an index of abundance. A single beam hydroacoustic survey was used from 1998 to 2001, but this was switched to a split beam survey thereafter. Finally, access point creel surveys have been conducted in 1996 and 2014, providing estimates of total harvest from recreational anglers; there is no other fishery on the reservoir.

Annual spills of water over the free crest weir began in 2005 and continued annually from approximately 15 April to 15 June in an effort to re-establish smolting in the nerkid population. Abundance of smolting nerkids was monitored with mark-recapture using two rotary screw traps in the lower Alouette River. Numbers of nerkid smolts emigrating from the reservoir has varied annually from 720 to 62 000 (Borick-Cunningham and Smith 2016), and returns have varied annually from 0 to 115 (Mathews et al. 2016). Returning adult nerkids have been transported to the reservoir through a trap and truck system. Genetic comparisons of smolting and resident nerkids has shown these two phenotypes to be considered the same population and not genetically distinct. Examination of the next generation does not conclusively demonstrate intermixing of the two phenotypes (Godbout et al. 2010). Re-anadromization of sockeye was originally seen as a great success for members of the Katzie First Nation and local stakeholders, but the lack of improvement in the annual number of smolts and the low mean marine survival (<1%) has been disappointing and led to calls by the Katzie people and local stakeholders for further action to be taken.

To further promote smolting in Alouette nerkids, stakeholders are proposing hatchery intervention. The annual supplemental stocking of nerkid fry is proposed to occur over the short term (two generations) using returning adult Alouette ocean-run nerkids as parental stock. The expectation is that annual stocking of fry derived from anadromous nerkids may artificially select for smolting, with the objective of increasing the proportion of nerkids that smolt. Before investing considerable time and money on a stocking program, it is important to evaluate the potential success and effects of the program to resident and anadromous nerkids. At present, the density-dependent impacts of additional age-0 fry on the growth and abundance of resident nerkids and the resultant fishery are unknown. Likewise, with no prior information on the heritability of smolting and the potential outcome of artificially selecting for smolting, it is difficult to predict how anadromous nerkid returns will continue over time.

Model development

A two-phenotype nerkid model was developed to predict the strength of density-dependent processes and evaluate the potential outcomes that stocking and changes in the probability of smolting may have on both the anadromous phenotype and the freshwater recreational fishery. Derivation of Beverton–Holt recruitment parameters and state dynamics model are described in Table 1, and parameters of the models are listed in Table 2. The state dynamics model is conditioned on smolt estimates from the downstream smolt mark-recapture program (Mathews et al. 2016), returning smolting nerkid count data from the trap and truck program below the Alouette dam (Borick-Cunningham and Smith 2016), and zooplankton densities (Hebert et al. 2015) from the nutrient restoration program. The model is fit to hydroacoustic, gill net, and fishery data collected as part of the nutrient restoration program to parameterize the demography of the nerkid population. The fitted model was then used to make projections of both phenotypes for 25 years considering uncertainty in the heritability of smolting.

A key component of this model is the stock–recruitment function, which is driven by density-dependent compensation and carrying capacity in juvenile mortality as conditions change in the reservoir (eqs. T1.3–T1.6). This model is derived from arguments in Walters and Korman (1999) and fully described in van Poorten et al. (2018). In it, the maximum survival rate, α , is a function of a base mortality and a food-dependent mortality rate, causing maximum juvenile survival to increase in years of abundant food supply. The carrying capacity parameter, β , is also influenced by food density, with maximum recruitment increasing as a quadratic function of food density.

The model includes a combination of parameters that are estimated (eq. T1.1) and assumed constant (eq. T1.2). All indices, parameters, and variables are described in Table 2. Recruitment from eggs to age-1 is divided into two stanzas (Moussalli and Hilborn 1986): one predicts the number of fry (age-0.5; eqs. T1.3–T1.4) and the second predicts the number of yearlings (age-1; eqs. T1.5–T1.6). In both functions, recruitment is limited by zooplankton availability and competition among the recruiting cohort using functions suggested in Walters and Korman (1999) and van Poorten et al. (2018). Recruitment to age-0.5 fry is multiplied by a lognormally distributed process error term. Initial growth is assumed to have been constant resulting in length-at-age following a standard von Bertalanffy function (eq. T1.7). Numbers at age are predicted for two annual time periods: one in the autumn to correspond with timing of smolting, which is initialized using estimated abundances ($N_{t,a}$; eq. T1.8), and one the following spring ($N_{(sp)t,a}$; eq. T1.9) to correspond to sampling dates. Consumption each year is assumed to vary in response to available zooplankton and competition among nerkids, assuming all size classes feed on the same zooplankton resource. This results in asymptotic size varying over time, while metabolic rate remains constant (Walters and Post 1993; van Poorten and Walters 2016; eq. T1.10), resulting in size-at-age varying each year (eq. T1.11). Vulnerability to harvest is assumed to be a logistic function of length (eq. T1.12). The fishery is assumed to occur primarily in summer, so total mortality during summer is half of annual natural mortality and all of size-adjusted fishing mortality (eq. T1.13). Nerkids spawn in autumn and hatch in spring; therefore, number of fry in fall is calculated based on egg abundance the previous year using the first recruitment stanza calculation adjusted with lognormal process error (eq. T1.14). Yearlings the following spring are calculated based on predicted fall fry abundance and the second recruitment stanza calculation (eq. T1.15). In subsequent years, fall abundance of nerkids in the reservoir is reduced as some fish smolt out of the system in early spring. Egg production the following year is based on size-based fecundity of age-3 and age-4 resident nerkids (eq. T1.16; McGurk, 2000) plus eggs contributed by returning anadromous nerkids (eqs. T1.17–T1.18). Anadromous nerkid fecundity is based on a power function with length using parameters from Pitt Lake sockeye (McGurk 2000). Because resident nerkids are semelparous, the model assumes a fixed proportion of fish mature at age-3 (m_3 , set at 0.9) and the remaining fish spawn the following year (eq. T1.19).

Annual numbers of smolting fish are modelled as normally distributed random variables with means and standard deviations set based on annual Peterson mark-recapture estimates of abundance based on rotary screw traps set downstream of the dam (Mathews et al. 2016). Trapping downstream of the dam was not conducted in 2015; therefore, no estimate of smolt outmigration was available for that year. Smolt abundance in 2015 was set as a normally distributed random variable with prior distributions of mean and standard deviation based on the empirical distributions of each over the entire time series of smolt estimates for the system.

Model parameters (eq. T1.1) were estimated using a state-space Bayesian approach that jointly fit to observations of length-at-age, hydroacoustic estimates of abundance, and annual estimates of

Table 1. Statistical catch-at-age model of the mixed resident–anadromous nerkid system including two-stage Beverton–Holt recruitment and density-dependent growth.

Parameters	
T1.1	$\theta = (L_{\infty,1}, K, L_0, c^{(1)}, c^{(2)}, c^{(3)}, p_1, p_2, p_3, \{N_{0,a}\}_{a=1}^{a=A}, M, F, \lambda, \tau, \xi, \psi, \chi, \{\varepsilon_t\}_{t=1}^T)$
T1.2	$\varphi = (a_e, b_e, L_{50(f)}, \sigma_{(f)}, m_3, \rho)$
Multistanza stock–recruit variables	
T1.3	$\alpha_{(1)t} = \exp\left\{\left[-c^{(1)}p_1 - \frac{c^{(2)}p_2}{z_t}\right] \times 0.5\right\}$
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	$\alpha_{(1+t)} = \exp\left\{\left[-c^{(1)}(1 - p_1) - \frac{c^{(2)}(1 - p_2)}{z_t}\right] \times 0.5\right\}$
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	$\hat{t}_{t=1,a} = \begin{cases} L_0 & a = 0 \\ L_0 \exp(-Ka) + L_{\infty,1}[1 - \exp(-Ka)] & a \geq 1 \end{cases}$
T1.8	$\hat{N}_{t=1,a} = N_{0,a}$
T1.9	$\hat{N}_{(sp)t=2,a} = \begin{cases} \frac{N_{0,a}\alpha_{(1+1)}}{1 + N_{0,a}\beta_{(1+1)}} & a = 1 \\ N_{0,a-1} \exp(-M/2) & a \geq 2 \end{cases}$
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	$\hat{t}_{t,a} = \begin{cases} L_0 & a = 0 \\ \hat{t}_{t-1,a-1} + L_{\infty,t}[1 - \exp(-K)] & a \geq 1 \end{cases}$
T1.12	$v_{t,a} = \left(1 + \exp\left\{-\frac{[\hat{t}_{t,a} - L_{50(f)}]}{\sigma_{(f)}}\right\}\right)^{-1}$
T1.13	$Z_{a,t} = M/2 + v_{t,a}F$
T1.14	$\hat{N}_{t,a} = \begin{cases} \frac{\hat{E}_{t-1}\alpha_{(1)t}}{1 + \hat{E}_{t-1}\beta_{(1)t}} \exp[\varepsilon_t - 0.5\sigma_{(R)}^2] & a = 0; \quad \varepsilon_t = N(0, \sigma_{(R)}) \\ [\hat{N}_{(sp)t,a-1} - \hat{s}_{t,a-1}] \frac{v_{t,a}F}{Z_{a,t}} \exp(-Z_{a,t}) & 1 < a < A \\ \hat{N}_{(sp)t,a-1} \frac{v_{t,a}F}{Z_{a,t}} \exp(-Z_{a,t}) & a = A \end{cases}$
T1.15	$\hat{N}_{(sp)t+1,a} = \begin{cases} \frac{\hat{N}_{t,a}\alpha_{(1+t)}}{1 + \hat{N}_{t,a}\beta_{(1+t)}} & a = 1 \\ \hat{N}_{t,a} \exp(-M/2) & 1 < a < A - 2 \\ \hat{N}_{t,a}(1 - m_3) \exp(-M/2) & A - 1 \end{cases}$
T1.16	$\hat{f}_{t,a} = a_e + \hat{t}_{t,a} \exp(b_e) \quad \{a = A - 1, A\}$
T1.17	$\hat{E}_{(S)t} = \hat{f}_S \hat{N}_{(S)t} / 2$
T1.18	$\hat{E}_t = (\hat{f}_3 \hat{N}_{t,3} m_3 + \hat{f}_A \hat{N}_{t,A}) / 2 + \hat{E}_{(S)t}$
Fishery catch-at-age observations	
T1.19	$\hat{C}_{t,a} = \hat{N}_{t,a}[1 - \exp(-v_{t,a}F)]$
Process and observation error	
T1.20	$\sigma_{(R)} = \rho\psi$
T1.21	$\sigma_{(1)t,a} = \hat{t}_{t,a}c v_1$
T1.22	$\tau_{(1)t,a} = \sigma_{(1)t,a}^{-2}$
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	$\tau_{(H)a=1+} = \sigma_{(H)a=1+}^{-2}$

Table 2. Notation for the statistical catch-at-age models.

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 (year^{-1})
L_0	++	Age at age-0 (mm)
$c^{(1)}$	++	Base mortality parameter
$c^{(2)}$	++	Mortality per time spent foraging (N_{prey}^{-1})
$c^{(3)}$	++	Carrying capacity parameter (fish^{-1})
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 (year^{-1})
F	++	Instantaneous fishing mortality rate (year^{-1})
λ	++	Food dependence parameter of density-dependent growth ($\text{mm} \cdot N_{\text{prey}}^{-1}$)
τ	++	Alternate food parameter of density-dependent growth (N_{prey})
ξ	++	Competition dependence parameter of density-dependent growth (mm^{-2})
ψ	++	Total error (observation + process)
χ	++	Proportion of acoustic observation error attributed to age-0
a_e	-7.151	Egg-length multiplier ($\text{egg} \cdot \text{FL}^{-1}$)
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
ρ	0.75	Proportion of total error attributed to process error
Sv_m	0.0025	Marine survival for sockeye from smolt to return
Derived variables		
$L_{\infty,t}$		Asymptotic length in year t (mm)
$\hat{l}_{t,a}$		Length-at-age in year t (mm)
$\hat{F}_{t,a}$		Fecundity at age in year t (eggs-female $^{-1}$)
$V_{t,a}$		Length-based vulnerability to angling in year t
$\alpha_{(1)t}, \alpha_{(1+t)}$		Maximum survival to age-1 or age-1+, respectively
$\beta_{(1)t}, \beta_{(1+t)}$		Carrying capacity parameter to age-1 and age-1+, respectively (fish^{-1})
$Z_{a,t}$		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 age-1+ abundance, respectively
$\sigma_{(l)t,a}$		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 eggs in year t (i.e., sockeye + kokanee)
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

Note: Parameter descriptions include units in parentheses. Values of ++ indicate estimated parameters.

fishery harvest. Annual length-at-age observations for individual fish captured in gill net sampling ($l_{t,a,i}$) were assumed to be normally distributed with observation error $\tau_{(l)t,a}$ (eqs. T1.21–T1.22):

$$(1) \quad l_{t,a,i} \sim N(\hat{l}_{t,a}, \tau_{(l)t,a})$$

Log-transformed hydroacoustic abundance estimates were assumed to follow a normal distribution. Annual autumn hydroacoustic estimates of abundance were divided into age-0 and age-1

and older nerkids based on modal separation of annual target strength distributions. Therefore model predictions of log-transformed autumn abundance were fit separately to each age group based on abundance in autumn:

$$(2) \quad \log(N_{(H)t,0}) = N(\log(N_{t,a=0}), \tau_{(H)0})$$

$$(3) \quad \log(N_{(H)t,1+}) = N\left(\log\left(\sum_{a=1}^A N_{t,a}\right), \tau_{(H)1+}\right)$$

Table 3. Prior probability density functions (PDFs) and posterior predictive distributions for each estimated parameter.

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 (9033.4)	999.7–33 249.2
$N_{0,2}$	U(0, 500 000)	5701.3 (4682.9)	161.2–17 468.1
$N_{0,3}$	U(0, 500 000)	6399.4 (4677.5)	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
λ	U(0, 50)	16.8 (12.3)	0.6–45.1
τ	U(0, 10 000)	751.1 (131.4)	549.3–1019.8
ξ	U(0, 10)	6.4 (1.8)	3.4–9.8
ψ	U(0, 10)	2.8 (0.3)	2.3–3.4
χ	B(1, 1)	0.5 (0.1)	0.4–0.6
CV_I	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

Note: Prior PDFs are described as either normal $N(\mu, \tau)$, uniform U (upper, lower), beta $B(\alpha, \beta)$, or gamma G (shape, rate) distributions. Posterior distributions for parameters are reported with mean and standard deviation with upper and lower 95% credible intervals.

where precisions for age-0 and age-1+ groups observation errors are described in eqs. T1.23–T1.26.

Total fishery harvest has only been evaluated twice since 1998 in Alouette Reservoir using creel surveys: once in 2002 (McCusker and Wilson 2002) and once in 2014 (Hebert et al. 2016). Log-transformed total annual harvest estimates were assumed to be normally distributed:

$$(4) \quad \log(C_t) = N\left(\log\left(\sum_{a=0}^A \hat{C}_{t,a}\right), \tau_{(C)}\right)$$

where harvest precision in observation is directly estimated.

Prior probability distributions for all estimated parameters are shown in Table 3. We used JAGS 3.4.0 (Plummer 2003) to numerically approximate the posterior probability distribution using Markov chain Monte Carlo (MCMC) simulation. 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 1000 from three separate chains. Convergence could not be rejected using Gelman–Rubin convergence diagnostics and visual inspection of MCMC chains.

Future projections

The two-phenotype nerkid model was used to project the system 25 years into the future using estimated parameters. Zooplankton densities were assumed to remain constant at a level equal to the mean densities observed from 2011 to 2015. This is consistent with the goals of the nutrient restoration program. Anadromous nerkid-derived offspring are assumed to be stocked as fry directly into the reservoir for the entire 25 years. All smolts leaving the system are assumed to be age-1 for simplicity.

Nerkid fry descended from returning adults stocked into the reservoir are assumed to smolt at a rate dictated by the narrow-sense heritability (h^2) of smolting (Morrisey et al. 2014; Table 4). The proportion of stocked fry that will smolt is given in eq. T4.1. Note that returning anadromous nerkids are selected as brood-

Table 4. Calculation of phenotypic response to selection for smolting and resulting sockeye returns in a mixed kokanee–sockeye system.

Phenotypic expression	
T4.1	$Sm^H = p_{(smolt)t-4} + h^2[1 - p_{(smolt)t-4}]$
T4.2	$Sm^K = p_{(smolt)t-4} + h^2\left[\frac{E_{(S)t-2}}{E_{t-2}} - p_{(smolt)t-4}\right]$
Smolts and sockeye returns	
T4.3	$\hat{s}_{t,1} = [Sm^H x_t + Sm^K N_{(sp)t,1}] \frac{N_{(sp)t,1}}{N_{t-1,1}}$
T4.4	$\hat{N}_{(S)t} = \hat{s}_{t-2,1} S v_m$

stock in the hatchery; therefore, the proportion of hatchery fry that smolt is related to the difference between the proportion of the previous generation that smolted from selected parents (= 1.0) and the general population (= $p_{(smolt)t-4}$). Resident nerkids in future generations will also be influenced by the selection differential for smolting based on the difference between the proportions of resident nerkids that smolted the previous generation and the relative genetic success of smolting (the proportion of eggs laid that were derived from anadromous nerkids; eq. T4.2). The number of smolts each year is then a combination of hatchery and resident nerkid smolts (eq. T4.3). The number of anadromous nerkids returning 2 years later are given by the smolts leaving the reservoir multiplied by a total marine survival rate (eq. T4.4).

Projected dynamics of the age-structured model proceed as in Table 1, except additional fish may be stocked into the reservoir as fry to the 0+ population. These fish then compete for resources with natural-spawned offspring, thereby reducing survival to age-1 through increased density-dependent competition. For ease of interpretation, all smolts are assumed to be age-1.

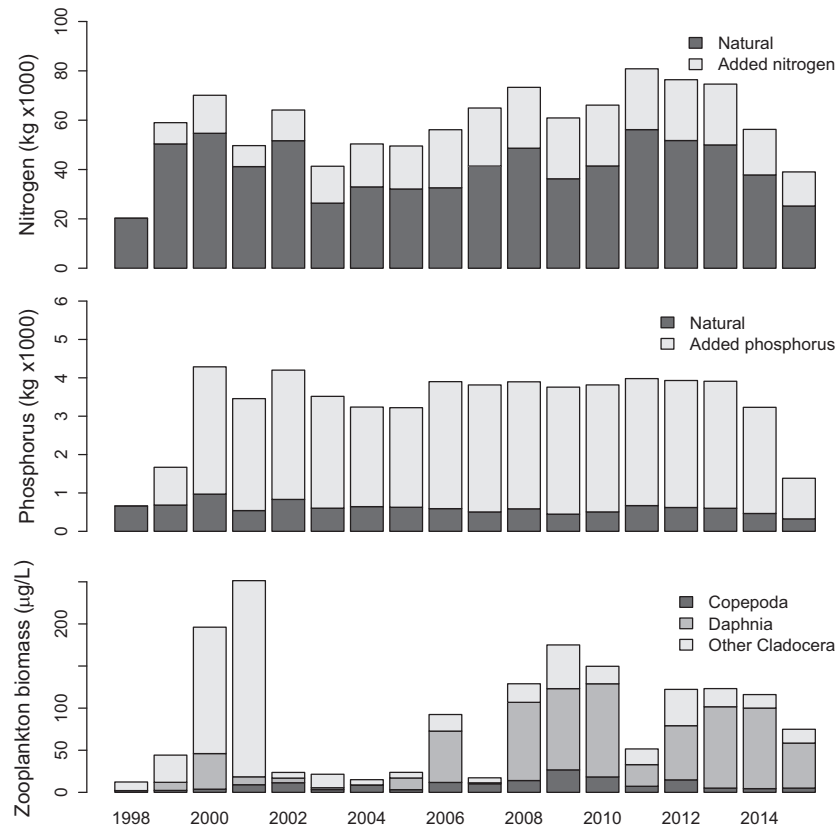
Future projections of anadromous nerkid returns and the resident nerkid population are dependent on two key parameters: marine survival rate and heritability of smolting. Marine survival was fixed at 0.25% based on the geometric mean observed marine survival rate for Alouette anadromous nerkids (Alouette River Management Society 2015). We are not aware of any estimates of heritability of smolting in sockeye; heritability was therefore assumed to be a uniform beta distributed random variable with both shape parameters set to 1.0 (i.e., uniform from 0 to 1).

Results

Inorganic fertilizer added into Alouette Reservoir starting in 1999 accounted for a substantive proportion of the total nitrogen and phosphorus in the system (Fig. 1). Total nitrogen and phosphorus loading in the reservoir varied as researchers refined the relative amounts of nitrogen and phosphorus to best produce edible phytoplankton. This had an impact on zooplankton densities, although seasonal averages varied widely across years. Increased nutrient load in the reservoir resulted in marked increases in mean annual zooplankton densities, initially in all cladocerans and later focused on *Daphnia* spp. (Fig. 1). Nerkid growth and size-at-age immediately increased as a result of increased zooplankton densities (Fig. 2). Larger nerkids released more eggs, resulting in a lagged increase in abundance of age-0 nerkids due to both increased egg abundance and increased survival of age-0 fish. Older age classes also increased over time due to improved abundance and survival of age-0 nerkids (Fig. 2). As abundance of both zooplankton and nerkids began to stabilize, nerkid body size also stabilized with size-at-age slightly larger than before nutrient restoration.

The model was able to estimate density-dependent processes relating to survival from egg to fry and survival from fry to smolt. Carrying capacity for both stanzas increased threefold in the first

Fig. 1. Total nitrogen (top panel) and phosphorus (middle panel) loads in Alouette Reservoir from 1998 to 2015, separated into natural loading and mass added through the nutrient restoration program. Bottom panel shows the associated zooplankton biomass over the same years, broken up into copepods, *Daphnia*, and other cladocerans.



2 years following the onset of nutrient restoration, declined as zooplankton densities declined and fry density increased, and stabilized at an intermediate level after 2008 (Fig. 3). Carrying capacities closely track zooplankton density, with the strength of the zooplankton effect influenced by density of age-0+ or age-1. Carrying capacity for both stanzas was similar, which reflects the difficulty in updating the prior prediction of p_1 - p_3 , which allocate Beverton-Holt parameters across the two stanzas.

If the nutrient restoration program maintains zooplankton density at densities seen in recent years, the model predicts resident nerkid vulnerable abundance to remain approximately similar to what has been seen to date (Fig. 4). Unfortunately, median anadromous nerkid returns are projected to decline over time due to low marine survival. However, these projections include uncertainty in heritability, which contribute variation in the annual distribution of predicted vulnerable resident and anadromous nerkid returns. If heritability of smolting is actually low, anadromous nerkid returns will persist over time despite lower survival in the marine environment, albeit at low abundance (Fig. 5; left panels). In this scenario, returning fish are primarily smolts from the abundant resident nerkid phenotype, rather than a persistent anadromous phenotype. If heritability is actually high, anadromous nerkid returns will rapidly decline and that life history form will be lost because marine survival is too low to maintain a sustainable anadromous run for this population. Both scenarios show minimal influence on resident nerkid persistence because of low inputs from anadromous nerkids each year (Fig. 5; top panels).

If fry derived from anadromous nerkids are stocked into the reservoir, abundance of resident nerkids vulnerable to the recreational fishery is projected to decline over 25 years and the extent of the decline is directly related to stocking rate (Fig. 6A). Note that

vulnerable abundance is a function both of numbers, which decline with increased competition among fry, and size, which increases with reduced competition following smolting. Once stocking rate exceeds 35 000 anadromous nerkid fry, there is a 5% probability of extirpation of the resident phenotype, and this probability increases with stocking. The range of projected resident nerkid abundance is substantial, with 95% credible intervals ranging from a high of approximately 50 000 vulnerable resident nerkids at a stocking rate of 80 000 nerkid fry, down to complete extirpation. Mean anadromous nerkid returns 25 years in the future are projected to moderately increase with stocking rate, though again, uncertainty around projections is substantial (Fig. 6B). For example, stocking 50 000 anadromous nerkid fry results a 95% probability that anadromous nerkid returns in 25 years may range between 10 and over 3300. Even at this high stocking rate, there is a 50% chance that projected returns 25 years in the future will be 161 anadromous nerkids or less.

Discussion

Marine-derived nutrients are an important subsidy to oligotrophic coastal systems. This is especially so for reservoirs such as Alouette Reservoir, which are nutrient-deprived due to the effect of dams on within-reservoir nutrient dynamics (Scott et al. 2017). Ordinarily, additional sockeye returning to the system would increase natural nutrient levels and consequent prey density resulting in improvements to production and carrying capacity (Cederholm et al. 1999; Naiman et al. 2002; Schindler et al. 2003). However, the nutrient restoration program offsets this benefit because nutrient levels are managed to maximize edible phytoplankton concentrations. Additional marine-derived nutrients would be largely matched by a decline in added inorganic fertilizer. In

Fig. 2. Median (lines) and 95% credible interval (shaded area) of predicted length-at-age (top panel) for nerkids in Alouette Reservoir from 1998 to 2015. Observed (circles) and predicted (lines and shaded area) abundance of age-0 (middle panel) and age-1 to age-4 nerkids (bottom panel) in the hydroacoustic surveys from 1998 to 2015. Hydroacoustic surveys are assumed to be nonselective for age.

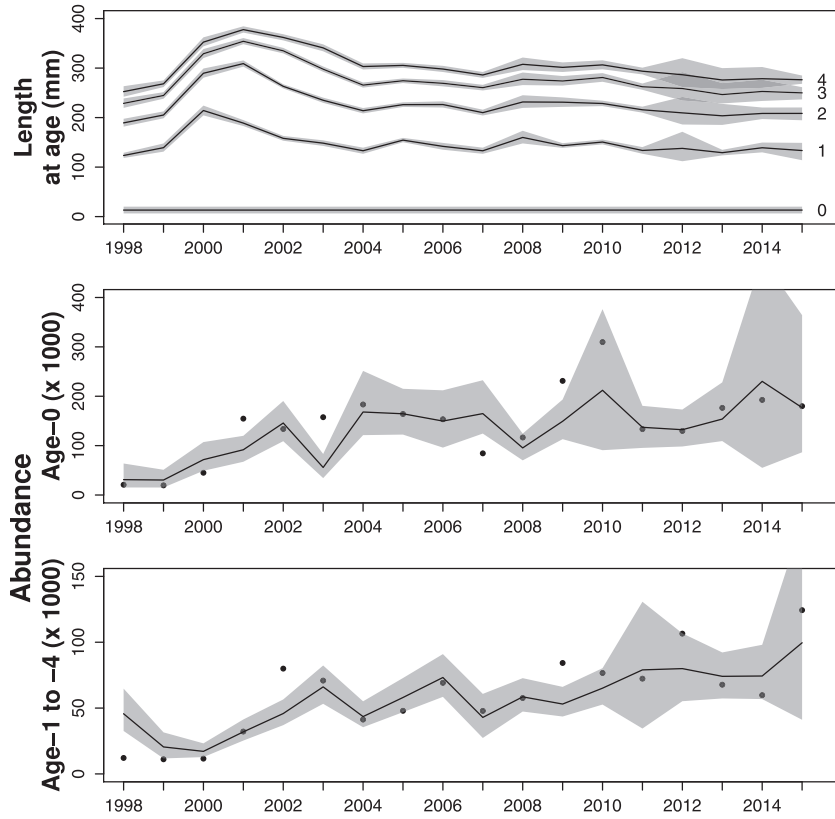


Fig. 3. Log-transformed carrying capacity for nerkids in Alouette Reservoir from 1998 to 2015 for two stanzas: (top panel) egg to fry and (bottom panel) fry to age-1.

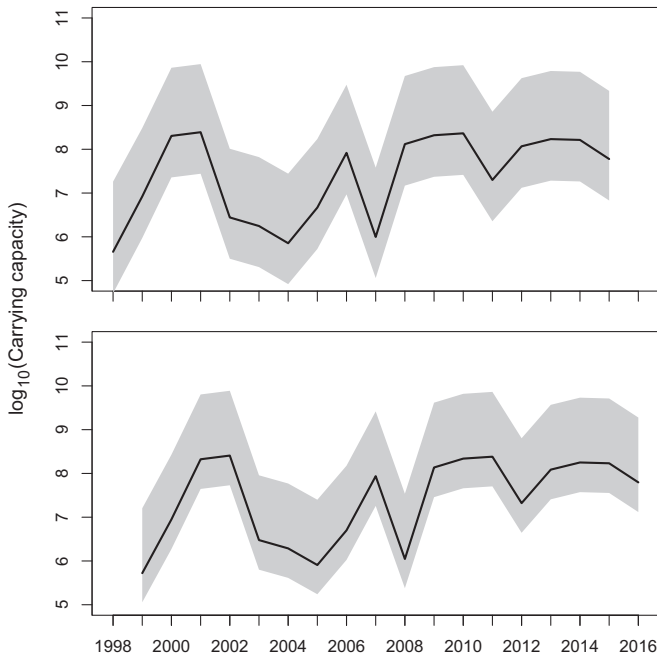


Fig. 4. Time series of vulnerable resident nerkid abundance (top panel) and anadromous nerkid returns (bottom panel) from 1998 to 2040. Posterior distributions of each are characterized by median estimates (solid line) and projections (dotted line) and 95% credible intervals (shaded area). Resident nerkid returns from 1998 to 2015 (circles) are observed data. Projections assume uniform distribution of heritability from 0 to 1.

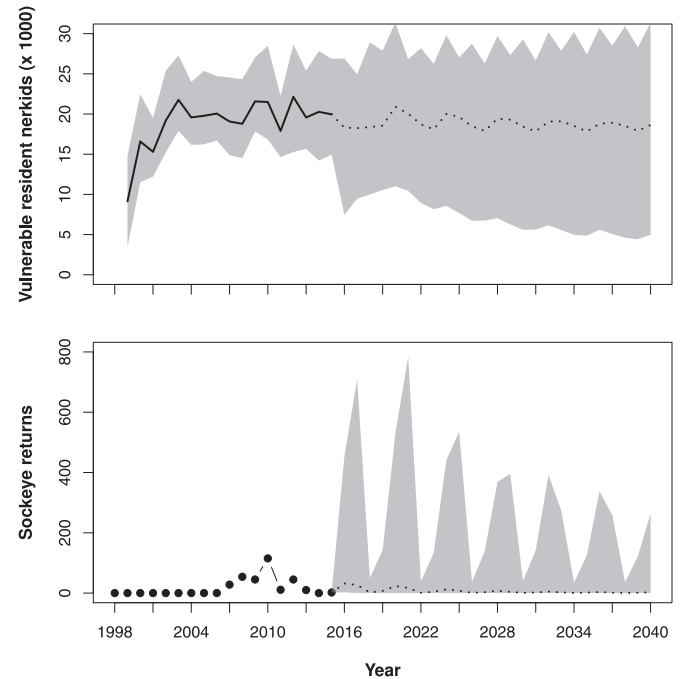


Fig. 5. Time series of vulnerable resident nerkid abundance (top panels) and anadromous nerkid returns (bottom panels) from 1998 to 2040. Posterior distributions are characterized as above. Projections assume heritability is known at either 0.2 (left panels) or 0.8 (right panels).

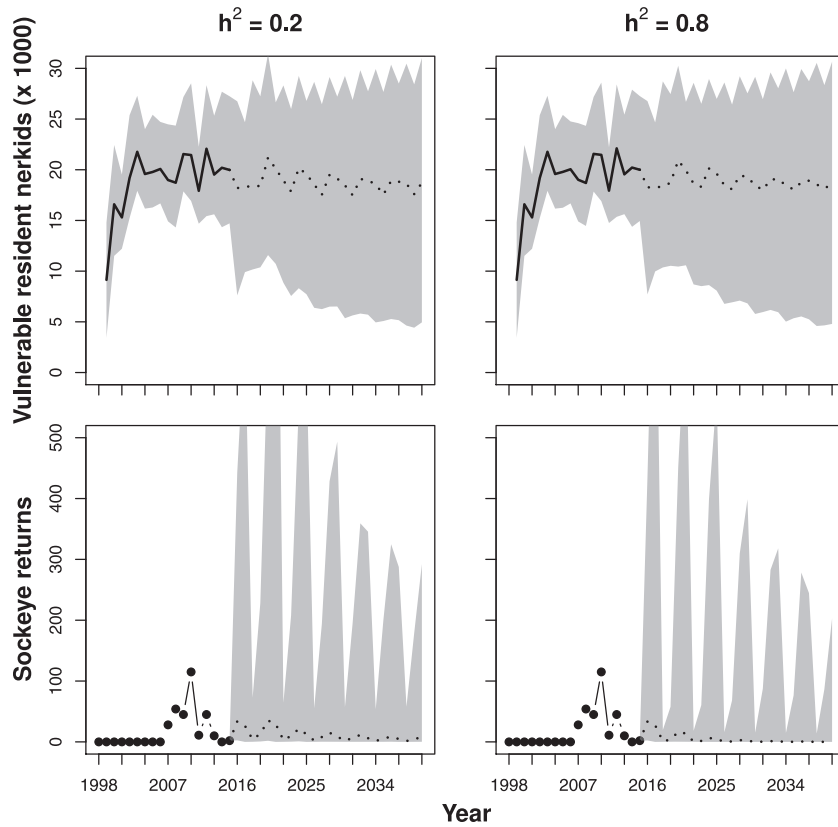
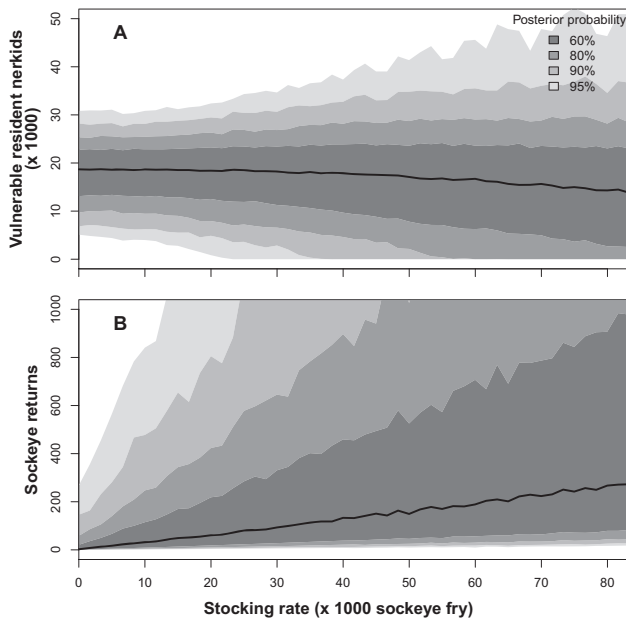


Fig. 6. Projected abundance at year 25 of vulnerable of resident nerks (A) and anadromous nerkid returns (B) after constant stocking at a particular rate. Solid line represents median predictions, shaded areas represent different credible intervals.



fact, it would take substantial anadromous nerkid returns to exceed added nutrient concentration in the system (Scott et al. 2017). The overall impact is that improved anadromous returns only add competitors to the system without improving growing conditions. An important lesson from the Alouette Reservoir case study is that sockeye restoration targets should carefully consider trophic interactions, especially in systems already undergoing nutrient restoration.

Despite nearly 10 years of anadromous nerkid returns, smolting rates from Alouette Reservoir are often still low, suggesting this is either a kokanee population with low smolting heritability or a sockeye population where conditions favour residency over anadromy. This work highlights the substantial value of information with respect to understanding the mechanisms and thresholds related to smolting when considering restoring or enhancing anadromous sockeye stocks (Hansen et al. 2016). Barriers to migration are being re-examined, and solutions such as dam removal, trap-and-truck, and fish ladders are being considered at many dams throughout North America (Anderson et al. 2014). Predicting outcomes of reintroductions is difficult in light of uncertainty in heritability and often only includes extreme possibilities (e.g., 100% anadromy or 100% residency; Hansen et al. 2016). We expect this work will guide future efforts to restore anadromy using stranded nerkid phenotypes.

Kokanee and sockeye populations occur sympatrically throughout their range, yet these pairs are consistently genetically distinct, partially because of reproductive isolation due to their sexual dimorphism (Foote et al. 1989; Taylor et al. 1996). Taylor et al. (1996) suggested that although male kokanee may sneak fertilizations with female sockeye (Foote and Larkin 1988), there must be substantial selective pressure against kokanee–sockeye “hybrids”. Although there is a substantial polymorphism in body size between resident and anadromous nerks in Alouette Reser-

voir, there is no difference in colour (both are drab olive or silver), presumably because of deepwater spawning (Moreira and Taylor 2015). Performance of sockeye–kokanee hybrids has been shown to be inferior in salinity tolerance, swimming performance, growth, and development rate (Wood and Foote 1990; Taylor and Foote 1991; Foote et al. 1992). Although Alouette nerkids have smolted, returned, and been released back into the reservoir for almost 10 years, there have been no observations from genetic analysis of offspring from these anadromous fish and no conclusive evidence of hybrids, although sample sizes were low (Godbout et al. 2011; Alouette River Management Society 2015). The model presented here assumes no intermixing, but neither does it assume Allee effects. Given the low anadromous nerkid return rates, it may be that re-establishment in the Alouette Reservoir may only be possible following one or more anomalously good smolting or marine survival events or through hatchery supplementation.

Our results show that sustained stocking is unlikely to dramatically improve anadromous nerkid returns over the first 25 years, even at substantial stocking rates. Sockeye salmon are particularly difficult to culture largely due to the potential for disease outbreak (Meyers et al. 1990). While stocking may be used as a tool to select for anadromy if there is some heritability in smolting, selective pressure for smolting will return to normal once hatchery supplementation is ceased. If heritability were known to be high and marine survival even marginally improved, the chance of successful restoration of anadromy may be higher, though this would also likely spell the demise of the resident nerkid life history. Similar instances where previously landlocked steelhead (*O. mykiss*) were allowed to smolt revealed a low prevalence of smolting due to low heritability (Thrower et al. 2004; Pearse et al. 2009). This highlights the need to determine heritability of smolting to evaluate the benefits (in terms of sockeye returns) against costs of restoration or installation of permanent fish passage.

Arguably the most uncertain process in any Pacific salmon life cycle model is marine survival, which is essentially a catch-all for multiple but unmeasured impacts on anadromous fish. Alouette Reservoir anadromous nerkids migrate outside times of major commercial fishery openings (Godbout et al. 2011), so the causes of marine survival variation are largely unknown. Marine survival for Alouette anadromous nerkids has ranged from 0% to 1.3% since outmigration began, which is low among nearby stocks (DFO 2010, 2017). If marine survival for Alouette anadromous nerkids were to improve, the outcome for this phenotype would be better than the median prediction from our models. This again serves to underscore the tremendous uncertainty in restoration potential for this stock and the need to invest in determining heritability to reduce this uncertainty.

Our work clearly demonstrates high uncertainty in expected anadromous nerkid returns if smolting continues. This suggests that from a purely ecological and economic standpoint, investing in permanent upstream fish passage infrastructure may not be prudent. However, this is one of many examples where the historic construction of dams has directly affected one or more First Nations (Notzke 1994). The decision to invest in anadromy should and does weigh ecological, economic, social, and cultural values; the cultural benefit to restoring anadromy would be substantial. This work highlights not only the uncertain ecological benefit of stocking anadromous nerkids into this system, but also the uncertain cultural gain. Results here should reinforce how important it is to understand the factors that contribute to smolting to provide a more certain and predictable outcome, both for the hydroelectric utility, who must invest in fish passage, but also for the Katzie First Nation, which has waited so long for salmon to return.

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