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Life-cycle model reveals sensitive life stages and evaluates recovery options for a dwindling Pacific salmon population

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[A] Abstract

Population models, using empirical survival rates estimates for different life stages, can help managers explore whether various management options could stabilize a declining population or restore it to former levels of abundance. Here we used two decades of data on five life stages of the Cedar River, USA Sockeye Salmon, *Oncorhynchus nerka*, population to create and parameterize a life-cycle model. This formerly large but unproductive population is now in steep decline, despite hatchery enhancement. We gathered population-specific data on survival during five stages: 1) egg-to-fry, 2) fry-to-presmolt, 3) presmolt-to-adult return from the ocean, 4) adult *en route* from the ocean to the spawning grounds, and 5) reproduction. We ground-truthed the model to ensure its fit to the data, and then we modified survival and other parameters during various stages to examine future scenarios. Our analyses revealed that low survival of juveniles in Lake Washington (stage 2: averaging only 3% over the last 20 years), survival of adults returning to fresh water to spawn (stage 4), and survival of adults on spawning grounds to reproduce (stage 5) are likely limiting factors. Combined increases in these stages and others (specifically, the proportion of fish taken into the hatchery to be spawned) might also recover the population. As in other integrated hatchery populations, managers must weigh options relating to balancing the fraction of natural- and hatchery-origin fish, and our results showed that increasing the fraction of fish taken into the hatchery alone will not recover the population. Our model brings together population-specific data to help managers weigh conservation strategies and understand which stages and habitats are most limiting and how much survival must increase to achieve recovery targets. By extension, our analyses also reveal the utility of such models in other cases where stage-specific data are available.

[A] Introduction

Evaluating limiting life stages for declining salmonid populations helps managers focus efforts and determine cost-effective measures for recovery (Shuter et al. 1998, Good et al. 2007, Sweka and Wainwright 2014), following approaches that have been applied to wildlife species (e.g., Hitchcock and Gratto-Trevor 1997). Models used to evaluate limiting factors must accurately reflect the spatial and temporal scales of biological processes and management actions affecting the species (Green et al. 2005). Modeling these scales can be especially challenging for diadromous fishes because their life histories expose them to different abiotic and biotic sources of mortality in freshwater, estuarine, and marine habitats at discrete life stages. Pacific salmon and trout (*Oncorhynchus* spp.) and Atlantic Salmon and Brown Trout (*Salmo* spp.) often travel vast distances and reside in distinctly different environments during discrete phases of their life cycles, experiencing biotic and abiotic influences on survival in each ecosystem they occupy (Elliott 1994, Jonsson and Jonsson 2011, Quinn 2018). They are affected by local environmental conditions within lakes (e.g., Goodlad et al. 1974, Griffiths et al. 2014) and small streams (e.g., Elliott et al. 1997), predation in freshwater habitats (Hansen and Beauchamp 2015), inter-specific competition at sea (e.g., Ruggerone and Connors 2015), and climate-driven processes in freshwater (Winder and Schindler 2004) and marine environments (e.g., Thomson et al. 2012, Friedland et al. 2014, Dorner et al. 2018). Given the diversity of habitats occupied sequentially by diadromous fishes during their life history stages, it can be difficult to discern which stage or stages limit population stability and restoration. This is especially the case if data are limited to simple spawner-recruit relationships or short periods of record, as year-to-year variability in the population may be high. Consequently, life-cycle models can help identify key life stages limiting a population.

Given the costs of habitat enhancement and remediation, hatchery production, and other actions to sustain and restore populations, and with the timeframes typically needed to detect changes in salmonid survival or productivity (Lichatowich and Cramer 1979, Bisson et al. 2008, Dauwalter et al. 2009, Beechie et al. 2015), data-driven life-cycle models can be a useful tool to explore alternative scenarios, design sampling to address key uncertainties, and inform management decisions (e.g., Greene et al. 2005, Scheuerell et al. 2009, Beebe et al. 2021, Crozier et al. 2021). Specifically, such life-cycle models can explore life-stage-specific impacts on overall population dynamics, measured from an adult abundance perspective.

While many salmon populations are monitored for abundance and survival during at least one discrete stage (e.g., egg to emerging fry, representing the embryonic stage; fry-to-smolt, representing survival of juveniles in freshwater habitats; smolt-to-adult, representing the marine phase; or ocean to spawning grounds, representing the return to breed), data for at least one stage are often lacking and thus two stages are combined (e.g., egg-to-smolt survival; Crozier et al. 2021). This can introduce uncertainty because considerable variation in survival at each stage is common (Bradford 1995, Quinn 2018), resulting from combinations of density-dependent and density-independent processes (Jonsson 1998, Dochtermann and Peacock 2013, Grossman and Simon 2020, Matte et al. 2020). Moreover, climate-driven factors can influence survival in freshwater and marine habitats (e.g., Lawson et al. 2004). Consequently, life-cycle models for populations with extensive data can provide perspectives for modeling other populations with shorter time series or gaps in life stages.

The Sockeye Salmon, *O. nerka*, population in the Lake Washington basin's Cedar River provides a case study of the value of comprehensive, multi-stage life-cycle monitoring in guiding management and conservation. Available data, starting in the 1970s, show returns greater than

100,000 in most years (Figure 1), but the run was not sufficiently productive to support sustained, directed fishing and replace itself regularly. Since 2007, adult abundance has declined more than 10-fold despite protective fishing regulations, efforts to improve habitat, and expansion of a supplemental hatchery program. The co-managers (Washington Department of Fish and Wildlife (WDFW) and the Muckleshoot Indian Tribe) have not allowed a recreational fishery since 2006. While the population has some atypical aspects (e.g., Lake Washington is in an urban setting near the southern end of the species' range), rapid declines (and recoveries) are common in Pacific salmon populations, including some large and carefully managed ones such as Sockeye Salmon in Bristol Bay, Alaska (Hilborn et al. 2003) and the Fraser River, British Columbia (Walters et al. 2020).

In this study we modeled the population dynamics of the integrated (i.e., mixed natural and hatchery production), at-risk Cedar River Sockeye Salmon population using two decades of detailed empirical data, identifying critical life stages to guide recovery efforts. Specifically, we developed and parameterized a five-stage, age-structured life-cycle model based on survival and other data collected from this population since 2000. We ran the model into the future to assess the population's probable trajectory and the proportions of hatchery and naturally spawned individuals. We developed seven management scenarios, modifying a) survival at one or more life stage and/or b) the proportion of adults spawned in the hatchery rather than spawning in the river. Based on the model runs for these scenarios, we determined changes in a) life-stage survival and/or b) contribution to the population by hatchery-reared fish needed for the Cedar River sockeye population with the goal of minimizing continued declines in adult abundance and returning to adult abundance levels sufficient to support tribal and recreational fishing.

[A] Methods

[C] *Study site and population.—*

Lake Washington is a natural, urbanized lake 88 km^2 in area, immediately east of Seattle, Washington, USA (Figure 2). Sockeye Salmon were native to the basin as non-anadromous (so-called "kokanee") populations and perhaps anadromous populations (Hendry et al. 1996, Young et al. 2004, Spies et al. 2007). However, the Cedar River, currently the lake's major tributary and primary spawning habitat, did not historically flow into Lake Washington except during flooding (Chrzastowski 1983). In 1912, a new waterway was constructed that diverted the lower Cedar River into Lake Washington (and then into Puget Sound) rather than its original route into Puget Sound via the Duwamish River, thus connecting the extensive spawning habitat in the Cedar River with Lake Washington.

The Cedar River Sockeye Salmon population likely originated from introductions between 1935 and 1945 (Hendry et al. 1996) and expanded to hundreds of thousands of adults. In the late 1960s a valuable fishery began for local tribes and recreational fishers, with a substantial regional economic impact (Mayor 2014). However, as noted above, the population has been declining for several decades and no fisheries have been permitted since 2006.

Like most populations of this species, Cedar River Sockeye Salmon experience mortality in seven habitats and life stages. Mortality at each stage is distinct, though data collection often combines mortality into fewer stages: 1) mortality during the embryonic stage, 2) mortality immediately after emergence from the gravel while fry migrate to the lake where they will feed, 3) mortality in the lake where fry feed prior to seaward migration, 4) mortality during the migration of smolts from the nursery lake to the ocean, 5) mortality at sea; 6) *en-route* mortality of adults in fresh water as they migrate from the ocean to spawning grounds, and 7) mortality on the spawning grounds prior to spawning. The balance of these sources of mortality with egg production determines whether the population grows, is stable, or declines. A final stage, mortality after reproduction, is inherent in their semelparous life history and can be ignored. Mortality at all these stages and habitats has been studied and demonstrated in the Lake Washington basin but assessments here, as in many other salmon populations under study, combine stages 1 and 2, and 4 and 5. Thus there are effectively five monitored stages for Cedar River Sockeye Salmon: 1) deposited eggs to fry entering the lake, 2) fry in the lake for a year prior to seaward migration, 3) presmolts in the lake migrating to sea and surviving there, 4) adults entering fresh water and holding prior to entry onto the Cedar River for spawning, and 5) successful reproduction of adults that reached the Cedar River.

In the Lake Washington basin, Sockeye Salmon spawn in the fall (September – December), embryos hatch in the winter, and fry emerge from gravel nests and migrate to the lake from January to June (peak in February and March) where they feed on zooplankton in the limnetic zone (Beauchamp et al. 2004). The basin has a complex community of native and non-native fishes (Eggers et al. 1978, Beauchamp et al. 1992, Fayram and Sibley 2000, Nowak et al. 2004, Tabor et al. 2007a, Tabor et al. 2007b, Tabor et al. 2016), some of which prey on Sockeye Salmon during one of more of their life history stages. Sockeye Salmon grow rapidly and leave Lake Washington in the spring about a year after they entered the lake (though some may leave after only a few months as sub-yearling migrants). They quickly exit Puget Sound, feed in the North Pacific Ocean for 2 or 3 years, and then return to fresh water in late spring and early summer (peak in early July; Hodgson and Quinn 2002). This return migration is earlier than most other major Sockeye Salmon populations in the region, and they are apparently not heavily exploited by fisheries in marine waters (Starr and Hilborn 1988).

As adults, Sockeye Salmon transition from Puget Sound to fresh water at the Hiram M. Chittenden Locks (hereafter, "the locks"), migrate 10.4 km through a relatively shallow and urbanized ship canal, and then enter Lake Washington, where they hold below the thermocline all summer (Newell and Quinn 2005). Non-tribal recreational and tribal commercial fishing in Lake Washington has been allowed when > 350,000 Sockeye Salmon are projected to pass the locks based on in-season counts (Ames 2006). Subsequent analyses suggested that this goal is too high for maximum sustainable yield (McPherson and Woodey 2009). We considered 100,000 fish spawning in the Cedar River (i.e., natural spawners) to approximate the escapement level likely to produce maximum sustainable yield (McPherson and Woodey 2009). In the fall, primarily September – November, the Sockeye Salmon ascend the Cedar River to spawn and complete their life cycle (Newell et al. 2007).

The Washington Department of Fisheries (now WDFW) constructed an interim hatchery for Cedar River Sockeye Salmon in 1991 to increase survival during the embryonic stage, and to gather data on survival patterns by thermally marking the otoliths of all hatchery produced fish (Volk et al. 1990, Volk et al. 1994). A larger, permanent hatchery was built in 2011, funded by the City of Seattle, and operated by WDFW. Hatchery production is part of the mitigation agreement for a water supply diversion dam that was constructed in 1901 at river km (rkm) 31.5 (Figure 2; City of Seattle et al. 2000). A weir at rkm 2.9 allows a fraction of the adult Sockeye Salmon (both natural- and hatchery-origin, as they are not externally marked) to be collected and taken to the hatchery, held, and later spawned. Fish not collected there pass upstream of the weir to spawn in the river. The Cedar River Sockeye Salmon population is an integrated hatchery population, consisting of both natural- and hatchery-origin adults (Mobrand et al. 2005), and it is adaptively managed in an effort to produce hatchery-origin salmon that are similar to the natural-origin fish in abundance and phenotype (Tetra Tech/KCM Inc. 2006).

[C] *Data collection.*—

Cedar River Sockeye Salmon have been monitored for many decades, but our model used data collected between 2000 and 2018 as they are the most complete and relevant to current conditions and management regimes. We compiled data to populate egg, fry, presmolt, adult, and spawner abundance and survival metrics. These data were provided as annual point estimates rather than means or median estimates within specified distributions. We recognize that these data are subject to observation and process error, which we could not explicitly estimate and directly include in our modeling process. These sources of error, detailed below, are inherent in the data and could have influenced the survival rates and other metrics estimated and used in our model.

Each year the hatchery reports the numbers of eggs taken and fry that survived to be released into the Cedar River based on the numbers of females spawned, average fecundity, and mortality in the hatchery (WDFW annual hatchery reports; e.g., Sedgwick 2017). Natural-origin fry passing a trap in the lower Cedar River on their way to Lake Washington have also been enumerated annually using first an inclined plane trap and, since 2011, a rotary screw trap (Kiyohara 2017, Lisi 2019). The fraction of the migrating fish sampled is estimated from mark-recapture experiments throughout the season (Lisi 2019).

The number of presmolts in Lake Washington in March, approximately two months prior to their seaward migration, has been estimated using combined hydroacoustic-midwater trawl surveys (Hansen et al. 2016) in most (but not all) years. Specifically, the lake is divided into six regions, and the limnetic fish community (juvenile Sockeye Salmon, Long-fin Smelt, and Threespine Stickleback) is sampled with a mid-water trawl in each region to determine the fish species composition. Then, a total of 21 hydroacoustic transects are run perpendicular to the net tows, including all regions of the lake (Hansen et al. 2016).

Returning adult Sockeye Salmon passing the locks between Lake Washington and Puget Sound are estimated by visual counts in the window of a fish ladder (extrapolated for unobserved periods) between June and August, and sex ratio and age composition data are also collected from them (https://wdfw.wa.gov/fishing/reports/counts/lake-washington; Figure 1). There is no explicit adjustment for the low level of interception in commercial fisheries that may occur (Starr and Hilborn 1988), so the "marine mortality" estimated (stage 3) includes that experienced after the presmolt sampling in the lake as the fish migrate to sea, mortality at sea, and any fisheries. The abundance of Sockeye Salmon reaching the Cedar River to spawn is estimated based on repeated visual surveys during the season from rafts. Sex ratio and age composition data are also collected. The observed abundance is translated to a population estimate using tagging data on stream-life to produce area-under-the-curve estimates (Hilborn et al. 1999, Parsons and Skalski 2010; WDFW SCoRE database; https://fortress.wa.gov/dfw/score/score/species/population_details.jsp?stockId=5400). The disparity between counts at the locks and the spawning grounds (including sites other than the Cedar River, which are also monitored) provides an estimate of *en-route* mortality, though observation error and bias (which were not estimated) likely influence the estimates at both the locks and spawning grounds. The prespawning mortality (PSM) rates of Cedar River Sockeye Salmon females spawning naturally in the river were estimated between 2014 and 2018 by Barnett et al. (2020) and annually by hatchery workers who noted when fish died before they could be spawned. A fish subject to PSM was defined as deceased on the spawning ground with

> 50% of the egg complement remaining in the body cavity or dead in the hatchery before it had been spawned (Bowerman et al. 2016). The abundance, age composition data, sex ratio of adult Sockeye Salmon brought into the hatchery for spawning are also reported annually (WDFW annual hatchery reports; e.g., Sedgwick 2017). All hatchery fry were otolith marked to distinguish them from naturally-produced fry.

Our model used sex ratio data from fish collected at the Cedar River weir (which would be transported to the hatchery) as they were available from 2001-2018 and were consistent with data on fish spawning in the river in the four years for which common data were available. Almost all Cedar River Sockeye Salmon mature and spawn at ages 3, 4, and 5, with 4 being most common. For age composition data used in the model, we compared data from fish spawned at the hatchery, passing the locks, and spawning naturally in the river. Data from hatchery-spawned fish and those at the locks encompassed years 2005-2018 and were similar to each other, and they were equally similar to the limited data from fish spawning naturally in the river. To be consistent with the sex ratio data used in the model, in the model we also utilized age composition data from fish spawned in the hatchery, though they include a higher fraction of early-returning ones (Tillotson et al. 2019). Finally, fecundity of a subset of female Sockeye Salmon spawned at the hatchery was measured and averaged annually (WDFW annual hatchery reports; e.g., Sedgwick 2017), and that value was used for all females in that year. Because hatchery- and natural-origin fish spawn annually in the river and in the hatchery (as Cedar River Sockeye Salmon are an integrated population), we did not distinguish between these groups.

[C] *Estimation of survival rate and other variables.—*

We used the data described above to estimate survival rates and other variables from stage to stage. Specifically, for each year the annual (y represents the spawning brood year) number of naturally-spawning (*n*) Sockeye Salmon (S_{n_y}) was multiplied first by the proportion of females in that year and then by the average fecundity to yield the number of naturally-spawned eggs (E_{n_y}). From the number of natural-origin fry produced from that year (F_{n_y}), we estimated annual natural-origin egg-to-fry survival rates (j_{n_y}; equation 1).

Equation 1 $$j_{n_y} = \frac{F_{n_y}}{S_{n_y} * fecundity_y * \%female_y}$$

Hatchery-origin (*h*) egg-to-fry survival in a given year (j_{h_y}) was estimated as the number of fry released from the hatchery from a given brood year (F_{h_y}) divided by the number of eggs spawned in the hatchery in that year (E_{h_y}).

The fry-to-presmolt survival rate (p_y) in Lake Washington for a given brood year was estimated from the number of Sockeye Salmon presmolts in Lake Washington during the March hydroacoustic survey (D_y) divided by the total number of fry (natural and hatchery origin) that entered the lake from that brood year cohort (equation 2).

Equation 2 $$p_y = \frac{D_y}{F_{n_y} + F_{h_y}}$$

We estimated cohort-specific marine survival—(pre)smolt-to-adult return (SAR_y) rates—as the number of adults from a given brood year cohort (A_y) returning to the locks one, two, and three years later divided by the number of presmolts during the March hydroacoustic survey (D_y) (equation 3).

Equation 3 $$SAR_y = \frac{A_y}{D_y}$$

When projecting different scenarios through time, we estimated the number of adults returning to the locks in a given year, A_y, by multiplying the number of presmolts (D_y) by the marine survival rate associated with their brood year cohort (SAR_y) and the proportion of fish of ocean age (*PropOAge*) 1, 2, or 3 (equation 4).

Equation 4 $$A_{y+5} = (D_{y+2} * SAR_{y+2} * PropOAge1) + (D_{y+1} * SAR_{y+1} * PropOAge2) + (D_y * SAR_y * PropOAge3)$$

Annual *en-route* survival (x_y) of adults from the locks to the Cedar River was calculated from the estimated number of spawners in the Cedar River (spawning naturally and in the hatchery; S_y) plus the estimated Cedar River proportion of harvest (if there was a fishery) each year—in sum, the total run size to the Cedar River—divided by the number of adults estimated at the locks that year (A_y). Adjustments were made for the fraction of adults spawning in tributaries and beaches of the basin other than the Cedar River (2000-2008 average = 11%).

A fraction (g_y) of adults returning to Cedar River are taken into the hatchery for spawning each year. This fraction was estimated annually from the number taken into the hatchery and the number spawning in the river. For the model, we developed a standardized rule on the percent of fish taken into the hatchery to spawn based on numbers of fish returning to the Cedar River. This rule, representative of the observed fractions in recent years, was that if < 5,000 fish return to the river, 50% are taken; if 5,000 - 15,000 fish return, 40% are taken; if 15,000 - 25,000 fish return, 30%; if 25,000 - 40,000 fish return, 20%; if 40,000 - 50,000 fish return, 10%; if > 50,000 fish return, 5% are taken to the hatchery. For these percentages, we could not draw values at random, as we did for other model variables, as they depend on the numbers of returning adults. These shifting proportions reflect a management strategy designed to achieve two goals that can be at odds with each other. One goal is to minimize the probability that the majority of returning adults be first-generation hatchery origin fish; this is achieved when returns are abundant by keeping the fraction taken into the hatchery low. The other goal is to keep the run from becoming too low or extinct; this is achieved by taking a higher proportion of the return into the hatchery (where they achieve greater reproductive success compared to fish spawning in the river) when few adults return.

Annual PSM rates for females spawning naturally in the river (PSM_{n_y}) were estimated as the number of females spawning in the river (S_{n_y}) divided by the number of fish that died with > 50% of eggs remaining (Barnett et al. 2020). Hatchery PSM rates were measured as the total numbers of fish taken into the hatchery (S_{h_y}) divided by the numbers of fish that died prior to being spawned; they were measured and reported separately each year for males ($PSM_{h,male_y}$) and females ($PSM_{h,female_y}$). All variables used in the model are listed and described in Table 1 and their estimates from 2000-2018 are provided in Table 2.

[C] *Life-cycle model.*—

We constructed a life stage-structured, heuristic, simulation-based population model for Cedar River Sockeye Salmon with variability for key parameters (Table 1, Figure 3). Model life stages of natural- and hatchery-origin fish were defined to align with empirical estimates of abundance and survival and facilitate analysis of likely management and conservation actions. The model was developed in R (R development core team 2020) to allow for rapid and efficient result acquisition for an annual time step.

Intra-specific density-dependent factors likely play at most a minor role in the future dynamics of the population, given its very low abundance, and were not included in our model. Returns to the Lake Washington basin have been below their escapement goal in almost every year between 2000 and 2018, and sufficiently large future runs will be subjected to fishing. As discussed above, stock-recruit analysis of Cedar River Sockeye Salmon suggests that a lower escapement goal than used in the past may be appropriate (McPherson and Woodey 2009). If the co-managers were to adopt this suggestion, future densities of spawning Sockeye Salmon in the Cedar River are would be lower than those seen in the past, even if full recovery were to occur. Additionally, juvenile Sockeye Salmon rearing in Lake Washington are also unlikely to experience density dependent factors there; they grow very rapidly in the lake and are a small fraction of the planktivorous fish community (Quinn et al. 2012).

To move the fish through their life cycle, we first multiplied the number of spawners (*S*) by a given year's fecundity value and % female value to estimate the number of eggs (*E*) for brood year *y*. For naturally-spawning fish producing natural-origin eggs (E_{n_y}), the equation is:

Equation 5 $$E_{n_y} = S_{n_y} * fecundity_y * \%female_y$$

A similar equation was used for hatchery-spawning fish producing hatchery-origin eggs (E_{h_y}).

To estimate the numbers of natural- and hatchery-origin fry (F_{n_y} and F_{h_y}), we multiplied the number of natural- or hatchery-origin eggs by the natural- or hatchery-specific egg-to-fry survival rates (j_{n_y} or j_{h_y}). Specifically, the number of natural-origin fry can be estimated as:

Equation 6 $$F_{n_y} = E_{n_y} * j_{n_y}$$

Next, the abundance of natural- plus hatchery-origin presmolts (D_y) were estimated as the number of natural- plus hatchery-origin fry multiplied by the fry-to-presmolt survival rate (p_y; Equation 7). This rate was found to be similar for both natural- and hatchery-origin fish (Hovel et al. 2019).

Equation 7 $$D_{n_y} = (F_{n_y} + F_{h_y}) * p_y$$

The numbers of natural- and hatchery-origin adults at the locks (*A*) were estimated as in Equation 4 (the number of presmolts [*D*] multiplied by the presmolt-to-adult survival rate and the proportion of ocean age fish). To get the number of age-3, 4, and 5 (freshwater age 1 plus ocean age 1, 2 or 3) adults returning in a given year, starting in year 5 of the simulation we added up the total number of ocean age 1, 2, and 3 Sockeye Salmon associated with that return year. In years 1-4 we waited for all age classes to contribute to a full age composition for adult returns as we seeded the model with ocean ages 1, 2, and 3.

The number of natural- and hatchery-origin adults returning to Cedar River associated with a given brood year was estimated by multiplying the number of natural- and hatchery-origin adults at the locks (A) by the *en-route* survival. To estimate the number of natural-origin, natural spawners, we multiplied the number of natural-origin adults returning to Cedar River by the percent of fish not taken into the hatchery and the prespawning survival rate for sockeye spawning naturally in the river during year 5 (Equation 8).

Equation 8 $$S_{n_{y+5}} = ((D_{n_{y+2}} * SAR_{y+2} * PropOAge1) + (D_{n_{y+1}} * SAR_{y+1} * PropOAge2) + (D_{n_y} * SAR_y * PropOAge3)) * x_{y+5} * \left(1 - g_{y+5}\right) * PSM_{n_{y+5}}$$

This estimate was also made for hatchery-origin, natural spawners, and then total natural spawners (S_n) was the sum of these values. To estimate numbers of fish taken to the hatchery to be spawned ("hatchery spawners"; S_h), Equation 8 for natural-origin, hatchery spawners and the equivalent for hatchery-origin, hatchery spawning fish was used with (g_{y+5}) rather than $(1 - g_{y+5})$.

Combining the above equations, the model predicting the number of natural-origin spawners produced from effective natural spawners in brood year y can be written as:

Equation 9 $$S_{n_{y+5}} = S_{n_y} * fecundity * \%female * j_{n_y} * p_y * ((SAR_{y+2} * PropOAge1) + (SAR_{y+1} * PropOAge2) + (SAR_y * PropOAge3)) * x_{y+5} * \left(1 - g_{y+5}\right) * PSM_{n_{y+5}}.$$

When a variable's value was not available for a given year, the average value of all available years of data was used.

[C] *Ground-truthing the model and input data.—*

Prior to running forward-projection scenarios, we evaluated whether our model, using the 2000-2018 input data, could predict the numbers of fish from one generation to the next that were actually observed, a process known as "ground truthing" (Köhler and Huth 2010, Krelling et al. 2017). We started with observed number of fish spawning in the river and the number taken to the hatchery in the year 2000. We multiplied these numbers with that year's PSM for in-river and hatchery spawners to estimate the number of effective natural and hatchery spawners. We then moved natural- and hatchery-origin fish through their life cycle to estimate the number of spawners that they would produce (Equation 9). We continued this cycle to 2018. For years when data were not available, we used the average value for all years with data. We compared observed data to the modeled data at various life stages.

[C] *Forward projections.*—

We ran each model scenario for 60 years with 1,000 simulation runs to examine how the results responded to variation in the input parameters. If the input data were available as a distribution that would describe some of their inherent observation and process error, we could draw from the distribution to get annual input parameters for each model scenario. However, because the input data provided to us were point estimates, we could not explicitly include stochasticity in our life-cycle model. We acknowledge that observation and process error are inherent in these input data, but they cannot be explicitly quantified in our model.

To start each forward projection, we used the average numbers of female and male spawners in the river (naturally spawning) and in the hatchery from the most recent five years with complete data (2014-2018), which were 7,028, 5,010, 2,066, and 1,794, respectively. We plotted model results starting in year 5 to allow all age classes to contribute to adult returns. For all scenarios, we present results for the number of fish spawning in Cedar River (i.e., natural spawners) before PSM, because they are influenced by almost all inputs evaluated in the model and can be compared with the 100,000 fish escapement level likely to produce maximum sustainable yield.

We first developed a baseline future scenario that reflected no changes in management and drew from observed 2000-2018 values. While future conditions may differ from those in 2000-2018, we developed this baseline to compare with other future scenarios. To generate matrices of the input data for use in the model runs, we sampled, at random and with replacement, 60 values (one for each year) of each input variable as data were available between 2000 and 2018 1,000 times. The exception was adult survival in fresh water, which only included input values from years 2014-2018 because the markedly lower survival in those years compared to earlier years seemed most appropriate for the future (Figure A1). Because conditions in a given year could affect survival rates in multiple life stages and thus survival rates may co-vary, we sampled the same brood year's input variables when they were available. Input data on the percent of females in the population, their fecundity, and natural- and hatchery-origin egg-to-fry survival were obtained from brood years 2001-2018.

[C] *Model scenarios.—*

We developed seven alternative scenarios in which input values were modified at one or more life stage as listed and described in Tables 3 and A1. Cedar River Sockeye Salmon stakeholder groups have discussed management options to help stabilize and recover the population and meet the goals of current management plans. We used the list of options they developed in addition to others that match the parameters in our model (and thus can be modified in our model) to develop the list of scenarios. We did not assess the efficacy of specific strategies, only the consequence of increased survival at the stages when they might have an effect.

Management options to improve fry-to-presmolt survival include predator suppression in Lake Washington, extended rearing of juvenile Sockeye Salmon in the hatchery to a larger size (to reduce their vulnerability to predators), and reduction of introduced aquatic littoral vegetation in the lake to hinder predation. Fry-to-presmolt survival rates (average of 3% in 2000-2018) are much lower than average values from other Sockeye Salmon populations but within the observed range (Foerster 1968, Eggers et al. 1978, Stober and Hamalainen 1980, Macdonald et al. 1987, Roos 1991, Bradford 1995; annual or average values ranging from 2.4% to 49% and averaging 27%), suggesting that there may be scope for improvement at this stage. Therefore, we increased fry-to-presmolt survival from the 2000-2018 average value of 3% to 4-22% (Tables 3 and A1).

Next, management actions reducing ambient light pollution (e.g., Mazur and Beauchamp 2006), predator abundances, and introduced aquatic littoral vegetation in the Lake Washington ship canal might improve presmolt survival on their way to the ocean and thus increase overall presmolt-to-adult survival. Studies of marine survival rates from Sockeye Salmon populations across their range showed that annual or average values ranged from 3.8 to 33% with an average of 13% (Ricker 1962, 1981, Hyatt and Stockner 1985, Macdonald et al. 1987, Thorne and Ames 1987, Henderson and Cass 1991, Woolington et al. 1991, Koenings et al. 1993). Thus, the Cedar River Sockeye Salmon presmolt-to-adult survival rates (average of 14% between 2000 and 2018 when data were available) are similar to other populations, suggesting less scope for improvement. For this stage we increased survival from the 2000-2018 average value of 14% to 15-33%, which were on the high side of the range reported for other populations (Tables 3 and A1).

Third, strategies including introducing cold water into the ship canal and transporting Sockeye Salmon from the locks directly to the hatchery might decrease *en-route* mortality and, later, PSM of adults. It may be possible to modify the hatchery to decrease PSM of adults held there, thus increasing adult survival in fresh water. The precise causes of adult mortality in freshwater are uncertain but this mortality has been seen in conspecifics elsewhere (e.g., Quinn et al. 2007, Tillotson and Quinn 2017, Atlas et al. 2021), and also in other salmon species (Bowerman et al. 2016), so they are neither unique to the Lake Washington basin nor to Sockeye Salmon, and the scope for improvement in these survival rates is uncertain. For this scenario, values for the adult survival in freshwater variables were increased 20-100% or up to a set survival rate of 90%. There was less scope for increases in these variables as their starting values were higher than those in the first two scenarios and survival rates cannot exceed 100%.

Fourth, we considered increasing the proportion of adult Sockeye Salmon spawned in the hatchery, which could reduce overall egg-to-fry survival and thus produce more fry per female from the integrated population. Variable proportions of returning Cedar River Sockeye Salmon taken into the hatchery for spawning reflect an explicit goal in the Cedar River Sockeye Salmon Adaptive Management Plan (Tetra Tech/KCM Inc. 2006) that, on average, no more than half the returning fish should be of first-generation hatchery origin. Given the higher survival of embryos in the hatchery than in the river, this necessitates that far fewer than half (about 10%) of the adults be spawned in the hatchery. However, in years when returns are very low, the managers can allow a larger proportion (> 10%) of returning adults to be taken into the hatchery, resulting in > 50% of all fry being of hatchery origin. Accordingly, we modeled this option (i.e., higher fractions of spawners taken into the hatchery).

We ran the life-cycle model into the future using modified input values (Tables 3 and A1), including changes in survival during single life stages and combinations of stages. For most non-modified input values, we used observed 2000-2018 values as described above in the baseline scenario. The exceptions were parameters for adult survival in fresh water, for which we used values observed during 2014-2018 the baseline because they were very different than the previous 15 years' values (Table 2; there were insignificant trends from 2000-2018 in the other model input variables). Modified values at the different life stages were uniformly distributed from the smallest to the largest value listed in Table A1. As with the 2000-2018 values, we sampled, at random and with replacement, 60 values (one for each year into the future) of the modified values 1,000 times to generate matrices of the input data for use in the model runs for each version of each scenario.

[A] Results

[B] Ground-truthing the model and input data

Using input data between 2000 and 2018 (Table 2), our life-cycle model predicted Cedar River Sockeye Salmon abundances at various life stages that followed the trends of observed values over that period, decreasing to low levels of abundance (Figure 4). Predicted vs. observed abundance values were most different in adult return and spawning years 2010-2013, corresponding to the years when fry-to-presmolt and presmolt-to-adult survival data were unavailable (brood years 2006-2009; Table 2). When presmolt-to-adult survival rates for these years (2006-2009) were estimated and then included in the ground-truthing effort, the numbers of adults estimated at the locks and in the Cedar River more closely matched the observed values (Figure 4) but these estimated presmolt-to-adult survival values were not included in forward projections. Thus, our model and the available input data effectively predicted (i.e., hindcasted) the trends in Cedar River sockeye over the past two decades, rendering the model structure appropriate in forward-projection simulations.

[B] Forward projections and model scenarios

All scenarios of our life-cycle model produced a large range of possible abundance values over the 60-year run due to the range of input variables (Table 2). For example, the 1,000 runs of the baseline scenario showed that the population could range from zero to > 100,000 adults spawning in the river in the future (Figure 5). This is an important point to remember for each scenario, and there was overlap in potential spawner abundance values among some versions of each scenario. Nevertheless, many patterns were very clear in the general projections. For the baseline scenario (Figure 5), the median number of natural spawners across all model runs declined rapidly from the starting 12,038 spawners (the recent-5-year average number of natural spawners) to 5,500 by year 10 and then down to 2,500 by year 15. The decline slowed thereafter, with an average of 500 spawners for the remaining 45 years.

For the first scenario (Scenario 1; Table 3), different versions of the model increased the average fry-to-presmolt survival rate (i.e., in the lake) from an average of 3% (2000-2018) to an average of 4-22% (see Table A1 for specific details on each version). In versions 1 and 2, spawner abundance declined, but abundance stabilized around 20,000 fish when survival averaged 8% (version 3) and around 70,000 fish when fry-to-presmolt survival averaged 12% (version 4; Figure 6a). Version 5, with an average in-lake survival rate of 17%, increased the projected number of Cedar River spawners to 100,000 by year 27, and version 6 (average survival of 22%) did so by year 16.

Next, for Scenario 2, we ran seven model versions with average presmolt-to-adult survival values ranging from 15-33% (baseline average = 14%; Tables 3 and A1). None of the model versions forecast > 50,000 natural (i.e., in river) spawners over time (Figure 7a). For the two versions with the highest presmolt-to-adult survival values (6 [average = 30%] and 7 [average = 33%]), adult abundance increased or was stable over time whereas average values ≤ 25% resulted in slowly declining abundance.

In Scenario 3, we explored how the population would respond to six versions of increased rates of *en-route* survival (from the locks to the Cedar River) and prespawning survival in the river and hatchery (Tables 3 and A1). *En-route* survival and prespawning survival in the river were increased by 20%, 40%, 60%, 80%, or 100%, or set to 0.8, while rates of prespawning survival in the hatchery were increased from an average of 57% and 66% (for males and females, respectively) to 72-90% each (Table A1). For the two versions (5 and 6) with the highest *en-route* survival values, adult abundance increased over time towards 60,000 spawners (Figure 7b). For version 4, spawner abundance leveled off around 13,000 fish, whereas for versions 1-3, with lowest *en-route* survival values, spawner abundance declined slowly over time.

In Scenario 4 we explored six modifications associated with the Cedar River Sockeye Salmon hatchery (Tables 3 and A1). In each version, we added 10% to the percent of fish taken to the hatchery to be spawned for each threshold number of returning adults to the Cedar River. For example, in the observed 2000-2018 values, when < 5,000 fish returned to the river, 50% of them were taken the hatchery. In the first version of this scenario, when < 5,000 fish returned, 60% of them were taken the hatchery; in the second version 70% were taken to the hatchery, etc. These versions also resulted in very low numbers of spawners (< 5,000) that decreased over time (Figure 7c).

Scenario 5 changed input variables at multiple stages (Tables 3): fry-to-presmolt survival (increased from an average of 3% to 4%, 4.5%, and 5%), *en-route* survival (increased 20%-60%), prespawning survival in the river (increased 20%), prespawning survival in the hatchery (no change and then increased to 85%), and the percent of fish taken into the hatchery (increased by 10 or 20% for each threshold; Table A1). The first two versions resulted in stable spawning abundance values around 10,000 and 20,000 fish each and the third version showed a growing number of spawners that stabilized around 73,000 fish (Figure 6b). Under Version 4, the projected number of spawners increased rapidly to 100,000 by year 29.

Our final two scenarios (6 and 7) involved modifying fry-to-presmolt survival only of hatchery-origin Sockeye Salmon (vs. both hatchery- and natural-origin fish in Scenarios 1 and 5), as might occur if they were held in the hatchery, fed, and released later and larger than at present. There are no existing data on Cedar River fry-to-presmolt survival of such releases and we did not find such data from other systems. However, survival to adulthood of larger juvenile releases of Redfish Lake, Idaho, USA Sockeye Salmon were 3- to 10-times greater than releases of smaller fish (Kline and Flagg 2014, Johnson et al. 2020).

For Scenario 6, hatchery fry-to-presmolt survival averaged 13-65% (Table A1). These increases had greater lower range values than those in Scenarios 1 and 5. All versions of this scenario resulted in Cedar River stable or increasing spawner abundance over time, but hatchery fry-to-presmolt survival values of 55% (version 5) were required for the population to exceed 100,000 spawners by 2040 (Figure 6c).

For Scenario 7 we increased both hatchery fry-to-presmolt survival (to average values of 13-45%; the lower range values were higher than those in Scenarios 1 and 5 and similar to those in Scenario 6) and the percent of fish spawned in the hatchery by 10% for each threshold (Table

A1). For version 1, an average of 13% hatchery juvenile in-lake survival stabilized abundance at 30,000-35,000, and in version 2, a 20% average survival rate resulted in a stable trend of ~ 65,000 spawners (Figure 6d). With a 35% in-lake survival rate (version 3), abundance reached 100,000 before year 20. In version 4's 45% survival rate, 100,000 spawners were estimated by year 11.

[A] Discussion

The Cedar River Sockeye Salmon population has faced low survival rates, relative to other populations, at several (but not all) life stages over the last two decades, resulting in the population declining to precariously low levels. Our model predicted that if survival rates and other variables remain at the values seen from 2000-2018 into the future, the population is likely to continue declining rapidly to functional extinction (Wainwright and Waples 1998). The two single-life-stage changes that increased abundance of spawners were increasing fry-to-presmolt (i.e., juvenile in-lake) survival rate of either the entire population (Scenario 1) or only hatchery-reared fish (Scenario 6) and increasing adult survival in freshwater (Scenario 3). However, only changes in fry-to-presmolt survival increased the adult spawning abundance to levels supporting tribal and recreational fishing. Since changes to other single life stages did not improve spawner abundance, juvenile survival in Lake Washington, followed by adult survival in freshwater, are likely to be the bottlenecks for this population, consistent with the conclusions reached by McPherson and Woodey (2009).

Average fry-to-presmolt survival rates in recent years were much lower than those observed in other populations (e.g., Foerster 1968, Macdonald et al. 1987, Bradford 1995), and our model showed that increasing survival at this stage seems necessary if this population is to recover to fishable levels (> 100,000 spawners) or even stabilize at lower levels. Specifically, an increased average juvenile in-lake survival to 8% would stop the decline in spawning abundance over time and stabilize the population at 20,000 adults. For the population to reach a level approximating that needed to achieve maximum sustainable yield (100,000 fish spawning in the Cedar River) by ~ 2050, fry-to-presmolt survival for all fish (Scenario 1) must average 17% annually or 55% for just hatchery-reared fish (Scenario 6). These scenarios both predict the population by 2040-2050 would be comprised of 20-25% hatchery-origin adult spawners. These survival rates are, however, hypothetical rather than observed in this system, and would require one or more changes in the lake's ecology, hatchery practices, or both.

An unknown fraction of juvenile Cedar River Sockeye Salmon emigrates to the ocean in their first year of life. Limited data on this alternative life history suggest that these subyearling emigrants have poorer survival at sea compared to yearling smolts (E. Warner, Muckleshoot Tribal Fisheries Office, pers. comm.; N. Overman, WDFW, pers. comm.). Subyearling smolts would probably not be counted in the March presmolt surveys because they would be counted as fry. This life history variant would affect the apportionment between in-lake (fry-to-presmolt) and marine survival, depending on its prevalence, but would not affect the overall productivity of the population. To tease apart survival of these stages better, presmolt survival estimates should be made annually as these counts are necessary to distinguish changes in survival in Lake Washington from changes during migration to salt water, at sea, and back to the locks. Smolt seining in the Lake Washington ship canal should be continued into July to sample subyearling smolts, and examination of scales and otoliths should reveal whether this life history pattern contributes to adult returns. This information would also be helpful for annual pre-season forecasting and fisheries management strategy evaluation. Additionally, it would contribute to better understand the survival of presmolts as they emigrate from Lake Washington into Puget Sound, and whether there are specific bottlenecks in space or time (sensu Clark et al. 2016, Rechisky et al. 2019).

Survival rates of adult Sockeye Salmon in fresh water after they return from the ocean until they spawn varied more between 2000 and 2018 than survival rates at other stages (Table 2). *En-route* survival values dropped from an average of 78% from 2005-2013 to 35% between 2014 and 2018 while pre-spawning survival of fish spawned in the hatchery averaged 83% prior to 2013 and then 62% since then. Fish are counted as they enter freshwater at the locks (Figure 1) and again when they spawn in the river and at the hatchery some months later (Barnett et al. 2020), making it difficult to pinpoint where *en-route* mortality make place (i.e., in the ship canal, in Lake Washington, or near the mouth of Cedar River). Mechanisms related to survival at these stages are not fully understood, but *en-route* and pre-spawning mortality are seen in other Sockeye Salmon populations (e.g., Quinn et al. 2007, Tillotson and Quinn 2017, Atlas et al. 2021).

Scenarios involving changes at multiple life stages were also forecast to increase Cedar River Sockeye Salmon spawning abundance. First, a combination of a modest increase in fry-to-presmolt survival of all fish from an average of 3% to 5.5%, a 40% increase in adult survival in fresh water before spawning, and a higher proportion of fish spawned in the hatchery (20% more at each abundance threshold; Scenario 5) was predicted to bring the population close to fishable abundances over the next 60 years. This scenario shows that while fry-to-presmolt survival increases must be included in recovery actions for the population, when combined with other actions, the fry-to-presmolt survival increases need not be large to succeed. Second, increases in the proportion of fish spawned in the hatchery, combined with an increase in fry-to-presmolt survival of the hatchery-reared fish (to 35%; Scenario 7), resulted in a fishable population by 2040. For comparison, when the proportion of fish spawned in the hatchery was not increased, fry-to-presmolt survival of the hatchery-reared fish needed to be 55% to provide a fishable population.

Increases in other single-stage variables, such as presmolt-to-adult return rate (i.e., marine survival; Scenario 2) and the proportion of Sockeye Salmon taken into the hatchery to be spawned (Scenario 4), are not likely to successfully increase the population's size in the next 60 years. Cedar River Sockeye Salmon experience comparatively high marine survival rates (mean = 14%, assuming no subyearling smolts) for their region, though even higher rates are seen in Alaska (e.g., Ricker 1962, Macdonald et al. 1987, Thorne and Ames 1987). Cedar River Sockeye Salmon marine survival rates have been considerably higher than those of Puget Sound Coho Salmon, *O. kisutch* (Zimmerman et al. 2015) and steelhead, *O. mykiss* (Kendall et al. 2017), to which they are comparable in body size.

Given the importance of fry-to-presmolt survival in stabilizing and recovering the Cedar River Sockeye Salmon population, management options aimed at increasing juvenile in-lake survival may be key to changing the long-term outlook for the population. Predator control, artificial light conditions around the lake, and hatchery operations are important management considerations. Reducing the abundance of Sockeye Salmon predators in Lake Washington, such as Northern Pikeminnow, *Ptychocheilus oregonensis*, and to a lesser extent Cutthroat Trout, *O. clarkii* (Clark 2017) and Smallmouth Bass, *Micropterus dolomieu*, through activities such as intensive gillnetting, could increase Sockeye Salmon in-lake survival. However, culling Cutthroat Trout, a native salmonid species that has a stable population and supports a fishery of its own may be a challenging policy to institutionalize. Culling Smallmouth Bass, an introduced exotic salmonid predator supporting a robust, lucrative fishery (Pflug 1984, Carey et al. 2011), could also be problematic.

The proliferation of artificial light at night in the area around Lake Washington and the two bridges across it has increased the visual foraging capability of salmon predators through the night and thus their predation rates on salmon (D. Beauchamp, USGS, unpublished data; Mazur and Beauchamp 2006). Measurable reductions in artificial light at night could reduce predation risk from native (Northern Pikeminnow, Cutthroat Trout, and Prickly Sculpin, *Cottus asper*) (Tabor et al. 2007b) and non-native predatory fishes (Yellow Perch, *Perca flavescens,* Smallmouth Bass, Largemouth Bass, *Micropterus salmoides*, Rock Bass, *Ambloplites rupestris*, Walleye, *Sander vitreus*, Northern Pike, *Esox lucius*, and Black Crappie, *Pomoxis nigromaculatus*) in Lake Washington.

Extending the rearing of Sockeye Salmon fry in the hatchery and releasing them at larger sizes into Lake Washington is another option to increase fry-to-presmolt survival. Since much of the in-lake predation by native and non-native predators is directed at relatively large parr (fork length > 80-160 mm; Clark 2017) in summer, fall, and spring, the hatchery program might need to release presmolts in mid to late spring, just before their seaward migration, to avoid significant in-lake predation. Monitoring of these fish to examine whether prolonged rearing increases their survival or propensity to residualize (Kaeriyama 1996, Ban 2007) would be necessary to determine how they contribute to adult returns. Johnson et al. (2020) noted that while longer hatchery rearing of Redfish Lake Sockeye Salmon increased their survival to adulthood, there was significant variation in productivity and life history trait expression among the release strategies (embryos, presmolts, or smolts). They suggested that hatchery salmon release programs monitor and evaluate survival and productivity rates to increase the likelihood of achieving the desired outcomes.

Reducing adult Sockeye Salmon mortality in freshwater (*en-route* mortality and PSM) could also be a focus of future management actions, including pumping cold water into the ship canal to reduce temperature stress on the fish, transporting fish from the locks directly to the hatchery to reduce temperature stress and exposure to conditions in the ship canal and the lake, and modifying the hatchery to decrease PSM of adults held there. The fish may succumb to disease, while *en-route* or after arriving in the river, due to travel through hot temperatures, and any future warming might only increase mortality in this stage.

As noted in the Methods section, all the empirical data used in this study are subject to some observation error and some possible bias. Additionally, as the population of Sockeye Salmon becomes smaller, the needed expansion of small counts inevitably introduces error. For example, the trap monitoring the fry leaving the Cedar River and entering Lake Washington takes a sample rather than intercepting all the migrants at any point in time, and the catches must be expanded to the entire river and extrapolated for time when the trap did not operate. Trap efficiency is regularly assessed during the season (Lisi 2019), but small catches must be expanded. Similarly, the sampling in the lake involves standard hydroacoustic methods and net-based species composition sampling, but Sockeye Salmon are now a very small fraction of the planktivorous fish community. The numbers of adults returning to the locks are assessed visually, and some fish might drop back and be counted twice or migrate through the locks rather than the ladder. In the Cedar River, adults are counted by observers from rafts, and the counts are expanded based on estimates of how long individual salmon are alive in the river. Fish counts and longevity both influence the accuracy of the method (Parsons and Skalski 2010), and though there are more sophisticated ways to analyze the data, Hilborn et al. (1999) concluded that the classic area-under-the-curve performs well. Despite these and other sources of error, and perhaps also bias as the abundance of Sockeye Salmon changes, the overall patterns revealed by the models here seem sufficiently clear that they are likely to be robust. The run has been in steep decline, is likely to continue to decline, and certain life stages show more promise for contributing to stabilization and recovery than others.

While we feel confident that our life-cycle model can provide helpful information to guide management and conservation, there are ways that it could be modified, including the addition of density-dependent interactions at juvenile and adult life stages. Such interactions are not included in our model because we believe they are unlikely to have a strong influence on the results and conclusions in this case. As discussed above, fishing on returning adults to the lake is likely to maintain the number of spawners below that expected to result in competition for spawning habitat in the large Cedar River (McPherson and Woodey 2009). The density of Sockeye Salmon adults in the Cedar River is ~ 3-10% of former densities, so the typical density-dependent effects on reproductive success seen in salmonids elsewhere (Quinn 2018) are highly unlikely. The large size of juveniles indicates that their growth is probably not density-limited during their lake rearing phase, and they are a small fraction of the limnetic fish community (Quinn et al. 2012), being far outnumbered by Longfin Smelt and Threespine Sticklebacks among the planktivorous fishes in the lake.

We suggest that future monitoring should consider the importance of understanding presmolt abundance so that fry-to-presmolt survival estimates can continue to be made. It would also be helpful to better understand smolt survival as they emigrate from Lake Washington and make their way to marine waters of Puget Sound and whether there are specific bottlenecks in space or time (sensu Clark et al. 2016, Rechisky et al. 2019), and the fraction of fish who are emigrating as subyearlings. The model could also be improved by adding additional years of data. Future data collection efforts should include presenting the data within a statistical framework (i.e., as a distribution rather than point estimates) so that the variation inherent in the input data could be translated into the model's outputs, results, and conclusions.

The Cedar River Sockeye Salmon run has decreased 84% from 2000 to 2020, when it reached the lowest level since the population was established and regularly monitored, and there is increasing concern for management actions to prevent the population's functional extinction (Wainwright and Waples 1998). Climate change likely is and will continue to contribute to the decline of Cedar River Sockeye Salmon, especially as related to adult *en-route* and prespawning mortality (Newell et al. 2007, Barnett et al. 2020), and perhaps also by decreasing egg-to-fry survival through increased scour (Lisi 2019). A climate-related decrease in marine survival (Crozier et al. 2021) would also accelerate the decline, as survival in the ocean has been among the stages with higher values, aided by low fishery interception rates. Assessing potential impacts of climate change on Cedar River Sockeye Salmon was outside the scope of our study, but it is an important topic to review and examine in the future for marine and freshwater systems.

Managers must weigh various options when working to conserve species in decline. This life-cycle model provides a framework for exploring the approach and refining expectations around Cedar River Sockeye Salmon recovery. The model estimates the timeline and likelihood for continued decline while scenarios under consideration highlight an integrated approach that utilizes complimentary actions at multiple life stages as the most promising path forward.

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Tables

Table 1. Variables used in the Cedar River Sockeye Salmon life-cycle model.

Variable	Description
y	spawning brood year
n	naturally spawning or natural origin
h	spawned in the hatchery or hatchery origin
S_n	number of naturally-spawning fish
S_h	number of fish spawned in the hatchery
E_n	number of naturally-spawned eggs
E_h	number of eggs spawned in the hatchery
F_n	number of natural-origin fry
F_h	number of fry released from the hatchery
j_n	natural-origin egg-to-fry survival rates
j_h	hatchery-origin egg-to-fry survival rates
p	fry-to-presmolt survival rate (both natural- and hatchery-origin fish)
D	number of presmolts in March (both natural- and hatchery-origin fish)
SAR	smolt-to-adult return rate (both natural- and hatchery-origin fish)
A	number of adult sockeye returning to the locks (both natural- and hatchery-origin fish)
$PropOAge$	proportion of fish of ocean age (both natural- and hatchery-origin fish)
x	en-route survival of fish from the locks to Cedar River (both natural- and hatchery-origin fish)
g	fraction of adult fish taken to the hatchery for spawning
PSM_n	prespawning mortality of fish spawning naturally
PSM_h	prespawning mortality of fish spawned in the hatchery

Table 2. Estimates of survival rates and other input variables for Cedar River Sockeye Salmon from 2000-2018 along with their average values, ranges, and standard deviations across all data available during this period. Grey shaded cells represent years for which data were not available.

Spawning brood year	Proportion female	Average fecundity	Natural egg-to-fry survival	Hatchery green-egg-to-fry survival	Fry-to-presmolt survival	Presmolt-to-adult survival to locks	Proportion ocean age 1	Proportion ocean age 2	Proportion ocean age 3	*Adult return and spawning year*	En-route survival--Locks to river	Proportion taken to hatchery	Female pre-spawn survival in river	Total pre-spawn survival in hatchery	Male pre-spawn survival in hatchery	Female pre-spawn survival in hatchery
2000		3,451	0.144	0.997	0.0363	0.1886			0.161							
2001	0.540	3,568	0.140	0.968	0.0667	0.0359		0.823	0.087							
2002	0.518	3,395	0.082	0.935	0.0218	0.4301	0.0160	0.911								
2003	0.547	3,412	0.190	0.949	0.0451	0.0250	0.0009		0.076							
2004	0.500	3,276	0.197	0.937	0.0229	0.0324		0.922	0.281							
2005	0.483	3,065	0.147	0.842	0.0089	0.1186	0.0000	0.702	0.023	*2005*	0.832	0.124		0.775	0.727	0.828
2006	0.575	2,910	0.053	0.800			0.0174	0.976	0.202	*2006*		0.093		0.928	0.923	0.933
2007	0.396	3,450	0.407	1.000			0.0007	0.782	0.467	*2007*	0.823	0.046		0.803	0.719	0.909
2008	0.480	3,135	0.063	0.900			0.0155	0.409	0.129	*2008*	0.560	0.127		0.877	0.790	0.971
2009	0.508	3,540	0.557	0.976			0.1224	0.862	0.413	*2009*	0.785	0.288		0.811	0.720	0.927
2010	0.599	3,075	0.041	0.842	0.0385	0.0511	0.0066	0.533	0.168	*2010*	0.592	0.111		0.925		
2011	0.586	3,318	0.321	0.935	0.0384	0.0465	0.0480	0.810	0.182	*2011*	0.901	0.265		0.718		
2012	0.493	3,515	0.362	0.970	0.0146	0.0620	0.0160	0.784	0.187	*2012*	0.867	0.136		0.928	0.901	0.964
2013	0.544	3,362	0.148	0.944	0.0135	0.1676	0.0337	0.808	0.332	*2013*	0.900	0.045		0.700	0.659	0.821
2014	0.446	3,368	0.885	0.917		0.3732	0.0039	0.660	0.472	*2014*	0.467	0.607	0.660	0.500	0.431	0.586
2015	0.509	3,070	0.192	0.838			0.0011	0.521		*2015*	0.448	0.451	0.780	0.631	0.569	0.694
2016	0.561	3,144	0.190	0.920			0.0044			*2016*	0.304	0.555	0.700	0.645	0.606	0.681
2017	0.651	3,053	0.140	0.890						*2017*	0.304	0.120	0.654	0.691	0.711	0.654
2018	0.600	3,152	0.325	0.919						*2018*	0.244	0.476	0.672	0.618	0.540	0.672
Average	0.530	3277	0.241	0.920	0.031	0.139	0.020	0.750	0.227		0.617	0.246	0.693	0.754	0.691	0.803
Range	0.396-0.651	2910-3568	0.041-0.885	0.800-1.000	0.009-0.067	0.025-0.430	0-0.122	0.409-0.976	0.023-0.472		0.244-0.901	0.045-0.607	0.654-0.780	0.500-0.928	0.431-0.923	0.586-0.971
Std. Dev.	0.061	195	0.205	0.056	0.018	0.142	0.032	0.166	0.145		0.247	0.196	0.052	0.133	0.143	0.139

Table 3. Overview of the seven Cedar River Sockeye Salmon alternative scenarios assessed with our life-cycle model. The variable(s) modified in each scenario is/are listed along with their baseline values (range and [average]), the number of scenario versions assessed, and the range and average of the changes in each variable. Hatchery-only fry-to-presmolt survival estimates have not been made in the past; fry-to-presmolt survival have been estimated for all fish (hatchery and natural origin combined). Detailed model scenario information is available in Table A1.

Scenario		**Modified variable**	**Baseline values: range [average]**	**Number of versions**	**Range, average of changes**
1	Increase fry-to-presmolt survival	fry-to-presmolt survival	0.01-0.07 [0.03]	6	ranges from 0.03-0.4, averages from 0.04-0.22
2	Increase presmolt-to-adult survival	presmolt-to-adult survival	0.03-0.43 [0.14]	7	ranges from 0.04-0.45, averages from 0.15-0.33
3	Increase adult survival in freshwater	en-route survival	0.24-0.47 [0.35]	6	20-100% increase & increased to 0.8, averages from 0.42-0.8
		female prespawn survival in hatchery	0.59-0.69 [0.66]		no change-increased to 0.9
		male prespawn survival in hatchery	0.43-0.71 [0.57]		no change-increased to 0.9
		prespawn survival in river	0.65-0.78 [0.69]		20-40% increase, averages from 0.85-0.95
4	Increase % of fish spawned in hatchery	% of fish spawned in hatchery	0.04-0.46 [0.20]	6	10-60% increase at each threshold
5	Increase fry-to-presmolt survival, increase adult survival in freshwater, and increase % of fish spawned in hatchery	fry-to-presmolt survival	0.01-0.07 [0.03]	4	ranges from 0.03-0.07, averages from 0.04-0.05
		en-route survival	0.24-0.47 [0.35]		20-60% increase, averages from 0.42-0.57
		female prespawn survival in hatchery	0.59-0.69 [0.66]		no change-increased to 0.85
		male prespawn survival in hatchery	0.43-0.71 [0.57]		no change-increased to 0.85
		prespawn survival in river	0.65-0.78 [0.69]		20-40% increase, averages from 0.85-0.95
		% of fish spawned in hatchery	0.04-0.46 [0.20]		10-20% increase at each threshold
6	Increase hatchery only fry-to-presmolt survival	hatchery fry-to-presmolt survival		6	ranges from 0.05-0.8, averages from 0.13-0.65
7	Increase hatchery only fry-to-presmolt survival and increase % of fish spawned in hatchery	hatchery fry-to-presmolt survival		4	ranges from 0.05-0.6, averages from 0.13-0.45
		% of fish spawned in hatchery	0.04-0.46 [0.20]		10% increase at each threshold

Figure captions

Figure 1. Total numbers of adult Sockeye Salmon passing through the Chittenden Locks from 1972 to 2020 from June 12-July 31 (https://wdfw.wa.gov/fishing/reports/counts/lake-washington#sockeye-annual).

Figure 2. Map of Cedar River in the Lake Washington drainage of western Washington State.

Figure 3. Life stages included in the model of Cedar River Sockeye Salmon. Black text indicates numbers or percent at different stages and gray text indicates survival or other values used to estimate fish numbers at various stages. Presmolt and adult Sockeye Salmon illustrations courtesy of Quinn (2018) and University of Washington Press.

Figure 4. Concurrence between the numbers of Cedar River Sockeye Salmon observed and estimated by the life-cycle model during model ground-truthing at different life stages between 2000 and 2018 using estimated presmolt-to-adult survival rates for years 2006-2009: a) millions of natural-origin and hatchery-origin fry produced and b) millions of adults observed at the Chittenden Locks and in the Cedar River. The black line represents 1:1 for reference.

Figure 5. The number of Sockeye Salmon spawning in Cedar River predicted annually in each of the 1,000 baseline scenario runs (thin gray lines) 60 years into the future with the median value shown in the thick black line. Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery.

Figure 6. The median number of Sockeye Salmon spawning in Cedar River predicted 60 years into the future in each of a) seven versions of modified fry-to-presmolt survival rates (values listed by version numbers; Scenario 1); b) four versions of the combination scenario of modified fry-to-presmolt survival, returning adult survival, and proportion of fish taken into the hatchery to be spawned (Scenario 5); c) six versions of modified hatchery fish fry-to-presmolt survival

(values listed by version numbers; Scenario 6); and d) four versions of modified hatchery fish fry-to-presmolt survival (values listed by version numbers) with a constant increased proportion of fish taken into the hatchery to be spawned (Scenario 7). Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery.

Figure 7. The median number of Sockeye Salmon spawning in Cedar River predicted 60 years into the future in each of a) seven versions of modified presmolt-to-adult survival rates (values listed by version numbers; Scenario 1); b) six versions of modified returning adult survival in freshwater values (*en-route* survival and prespawning survival in the hatchery and in the river; Scenario 3; and c) six versions of modified proportion of fish taken into the hatchery to be spawned (Scenario 4). Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery.

Figures

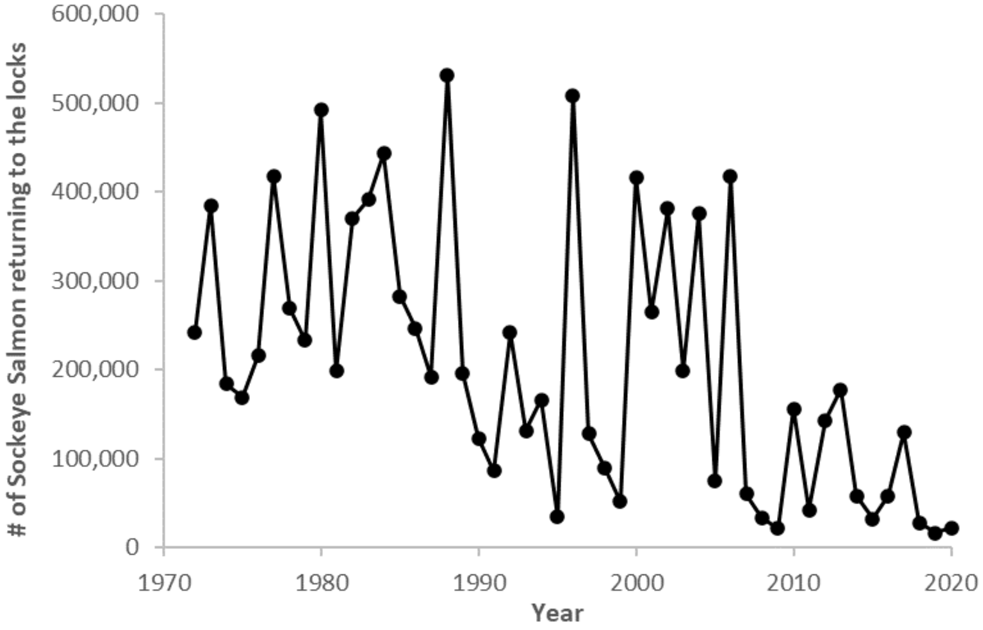

Figure 1. Total numbers of adult Sockeye Salmon passing through the Chittenden Locks from 1972 to 2020 from June 12-July 31 (https://wdfw.wa.gov/fishing/reports/counts/lake-washington#sockeye-annual).

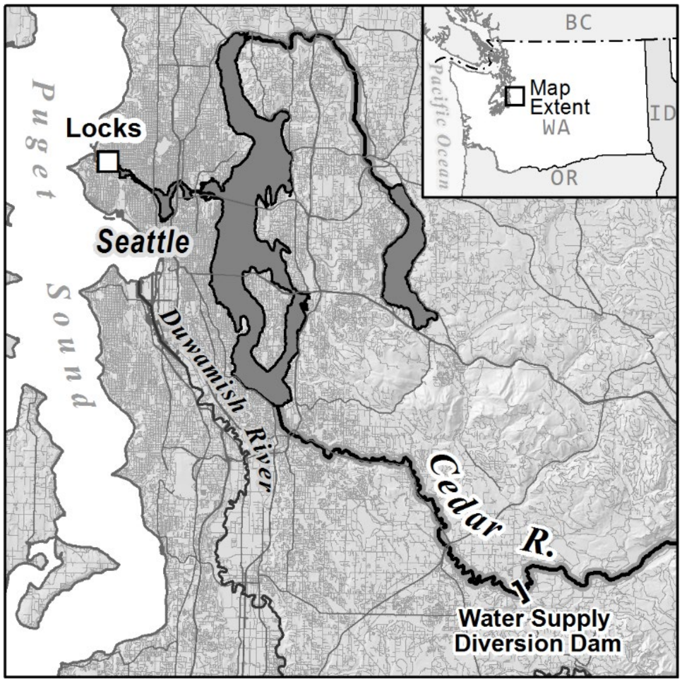

Figure 2. Map of Cedar River in the Lake Washington drainage of western Washington State.

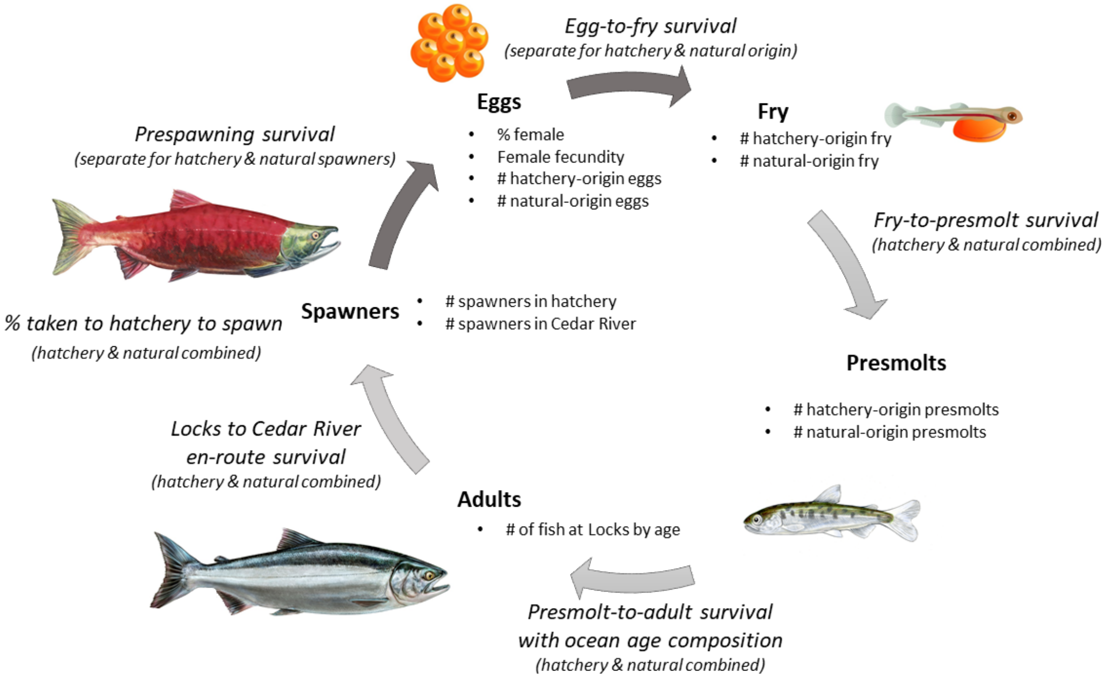

Figure 3. Life stages included in the model of Cedar River Sockeye Salmon. Black text indicates numbers or percent at different stages and gray text indicates survival or other values used to estimate fish numbers at various stages. Presmolt and adult Sockeye Salmon illustrations courtesy of Quinn (2018) and University of Washington Press.

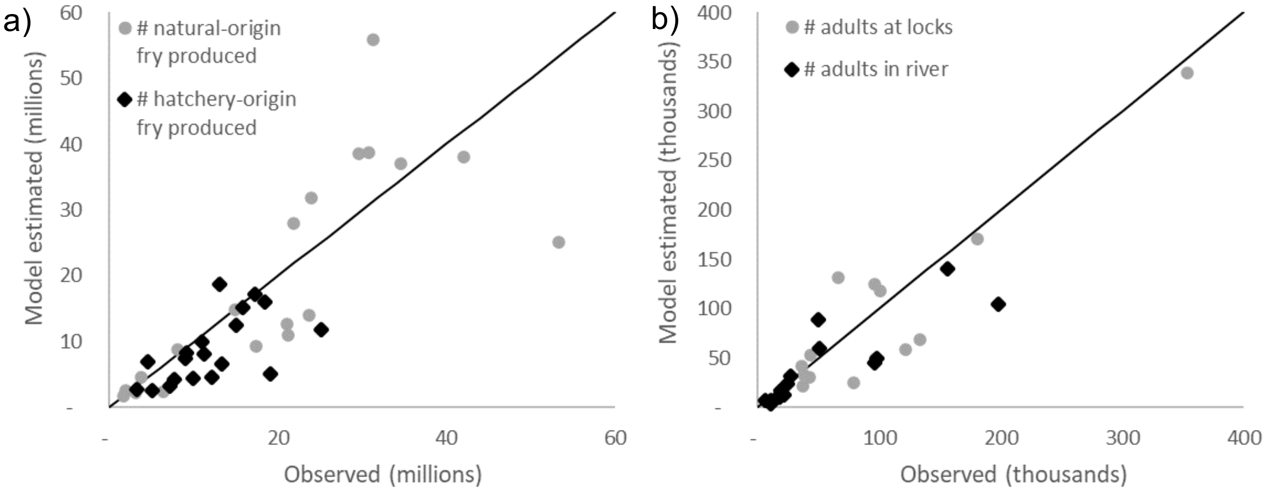

Figure 4. Concurrence between the numbers of Cedar River Sockeye Salmon observed and estimated by the life-cycle model during model ground-truthing at different life stages between 2000 and 2018 using estimated presmolt-to-adult survival rates for years 2006-2009: a) millions of natural-origin and hatchery-origin fry produced and b) millions of adults observed at the Chittenden Locks and in the Cedar River. The black line represents 1:1 for reference.

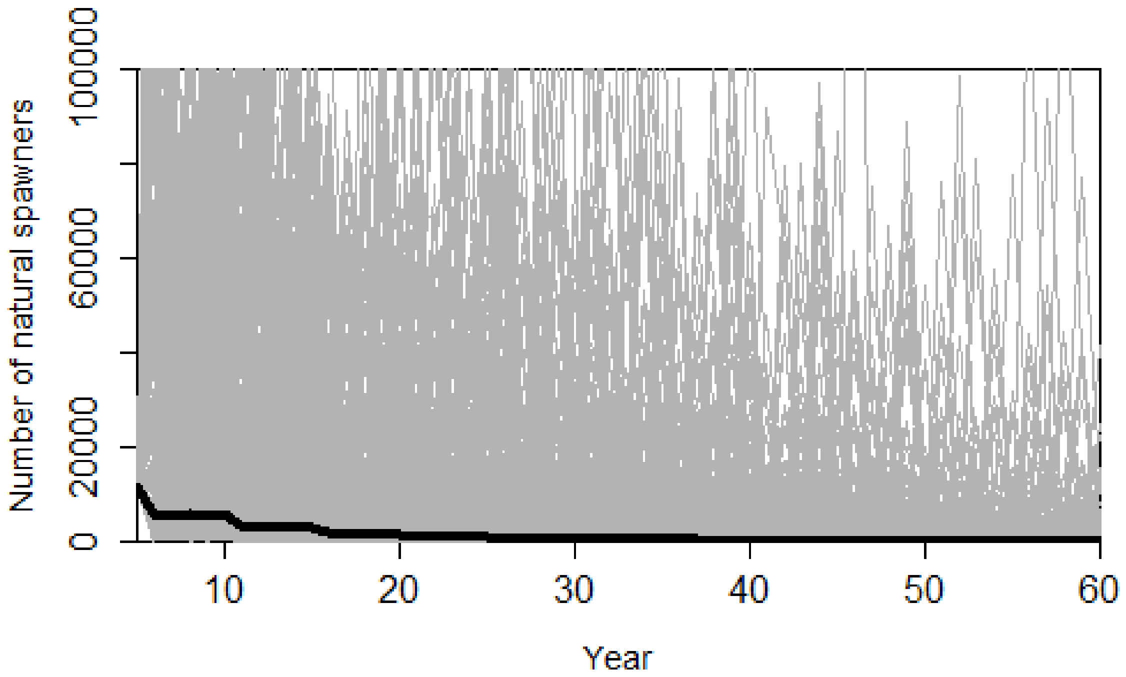

Figure 5. The number of Sockeye Salmon spawning in Cedar River predicted annually in each of the 1,000 baseline scenario runs (thin gray lines) 60 years into the future with the median value shown in the thick black line. Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery.

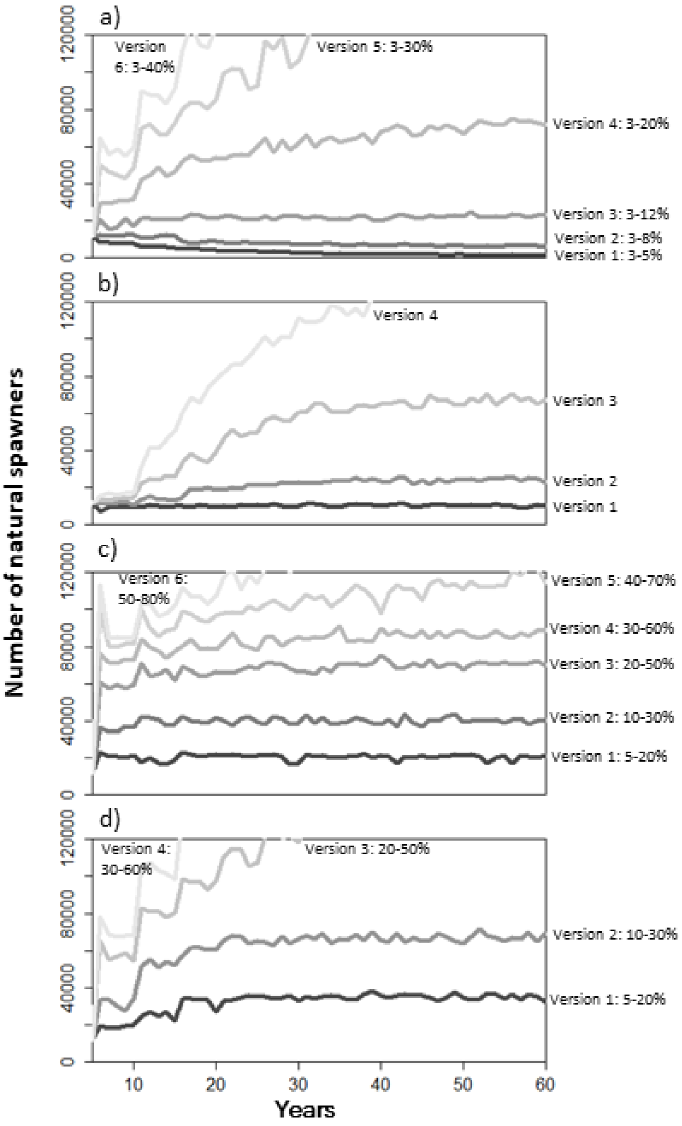

Figure 6. The median number of Sockeye Salmon spawning in Cedar River predicted 60 years into the future in each of a) seven versions of modified fry-to-presmolt survival rates (values listed by version numbers; Scenario 1); b) four versions of the combination scenario of modified fry-to-presmolt survival, returning adult survival, and proportion of fish taken into the hatchery to be spawned (Scenario 5); c) six versions of modified hatchery fish fry-to-presmolt survival (values listed by version numbers; Scenario 6); and d) four versions of modified hatchery fish fry-to-presmolt survival (values listed by version numbers) with a constant increased proportion

of fish taken into the hatchery to be spawned (Scenario 7). Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery.

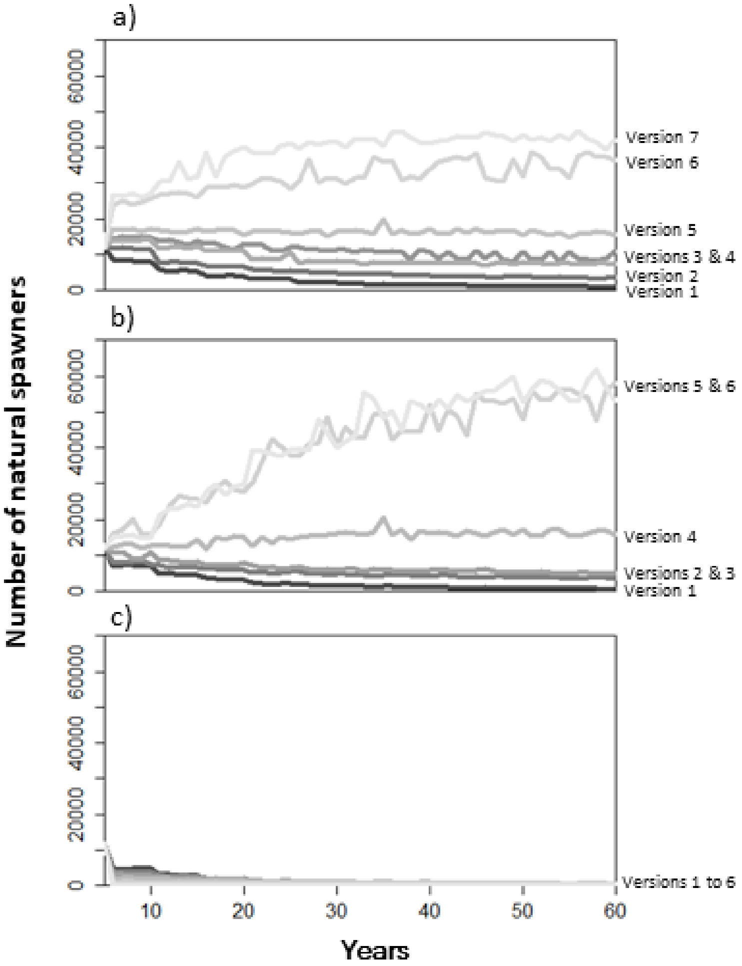

Figure 7. The median number of Sockeye Salmon spawning in Cedar River predicted 60 years into the future in each of a) seven versions of modified presmolt-to-adult survival rates (values listed by version numbers; Scenario 1); b) six versions of modified returning adult survival in freshwater values (*en-route* survival and prespawning survival in the hatchery and in the river; Scenario 3; and c) six versions of modified proportion of fish taken into the hatchery to be spawned (Scenario 4). Numbers of fish shown here will subsequently be reduced by prespawning mortality and do not include fish spawned in the hatchery

Appendix

Table A1. Detailed information about the seven Cedar River Sockeye Salmon alternative scenarios assessed with our life-cycle model. The versions of the scenario are listed along with the variable(s) modified, the baseline values (range and [average]), the years from which the baseline was taken, and the modified values (range and [average]).

Scenario and version		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
1.1	Increase fry-to-presmolt survival	fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.05 [0.04]	increase
1.2		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.08 [0.055]	increase
1.3		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.12 [0.075]	increase
1.4		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.2 [0.12]	increase
1.5		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.3 [0.17]	increase
1.6		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.4 [0.22]	increase
2.1	Increase presmolt-to-adult survival	presmolt-to-adult survival	0.025-0.43 [0.14]	0.04-0.25 [0.15]	increase
2.2		presmolt-to-adult survival	0.025-0.43 [0.14]	0.05-0.3 [0.18]	increase
2.3		presmolt-to-adult survival	0.025-0.43 [0.14]	0.05-0.4 [0.22]	increase
2.4		presmolt-to-adult survival	0.025-0.43 [0.14]	0.1-0.3 [0.2]	increase
2.5		presmolt-to-adult survival	0.025-0.43 [0.14]	0.1-0.4 [0.25]	increase
2.6		presmolt-to-adult survival	0.025-0.43 [0.14]	0.2-0.4 [0.3]	increase
2.7		presmolt-to-adult survival	0.025-0.43 [0.14]	0.2-0.45 [0.33]	increase
3.1	Increase adult survival in freshwater	en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	increased by 20%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
3.2		en-route survival	0.24-0.47 [0.35]	0.34-0.65 [0.49]	increased by 40%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
3.3		en-route survival	0.24-0.47 [0.35]	0.39-0.75 [0.57]	increased by 60%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%
3.4		en-route survival	0.24-0.47 [0.35]	0.44-0.84 [0.64]	increased by 80%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69	0.92-0.99 [0.95]	increased by 40%
3.5		en-route survival	0.24-0.47 [0.35]	0.49-0.93 [0.71]	increased by 100%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.74-0.86 [0.8]	increased by 25%
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.54-0.89 [0.72]	increased by 25%
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%
3.6		en-route survival	0.24-0.47 [0.35]	0.8	increased to 0.8
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.9	increased to 0.9
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.9	increased to 0.9
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%

Scenario		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
baseline		*% of fish spawned in hatchery*	*if <5000 fish to river, 50% to hatchery; if <15000 fish, 40%; if <25000 fish, 30%; if <40000 fish, 20%; if <50000 fish, 10%; if >50000 fish to river, 5%*		
4.1	Increase % of fish spawned in hatchery	% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
4.2		% of fish spawned in hatchery		if <5000 fish to river, 70% to hatchery; if <15000 fish, 60%; if <25000 fish, 50%; if <40000 fish, 40%; if <50000 fish, 30%; if >50000 fish, 20%	increased 20% at each threshold
4.3		% of fish spawned in hatchery		if <5000 fish to river, 80% to hatchery; if <15000 fish, 70%; if <25000 fish, 60%; if <40000 fish, 50%; if <50000 fish, 40%; if >50000 fish, 30%	increased 30% at each threshold
4.4		% of fish spawned in hatchery		if <5000 fish to river, 90% to hatchery; if <15000 fish, 80%; if <25000 fish, 70%; if <40000 fish, 60%; if <50000 fish, 50%; if >50000 fish, 40%	increased 40% at each threshold
4.5		% of fish spawned in hatchery		if <5000 fish to river, 100% to hatchery; if <15000 fish, 90%; if <25000 fish, 80%; if <40000 fish, 70%; if <50000 fish, 60%; if >50000 fish, 50%	increased 50% at each threshold
4.6		% of fish spawned in hatchery		if <5000 fish to river, 100% to hatchery; if <15000 fish, 100%; if <25000 fish, 90%; if <40000 fish, 80%; if <50000 fish, 70%; if >50000 fish, 60%	increased 60% at each threshold
5.1	Increase fry-to-presmolt survival, increase adult survival in freshwater, increase % of fish spawned in hatchery	fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.05 [0.04]	increase
		en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	increased by 20%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
5.2		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.06 [0.045]	increase
		en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	(same as prior version)
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	(same as prior version)
5.3		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.07 [0.05]	increase
		en-route survival	0.24-0.47 [0.35]	0.34-0.65 [0.49]	increased by 40%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	(same as prior version)
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	(same as prior version)
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	(same as prior version)
5.4		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.07 [0.05]	(same as prior version)
		en-route survival	0.24-0.47 [0.35]	0.39-0.75 [0.57]	increased by 60%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	(same as prior version)
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	(same as prior version)
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 70% to hatchery; if <15000 fish, 60%; if <25000 fish, 50%; if <40000 fish, 40%; if <50000 fish, 30%; if >50000 fish, 20%	increased 20% at each threshold

Scenario		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
6.1	Increase hatchery only fry-to-presmolt survival	hatchery fry-to-presmolt survival		0.05-0.2 [0.13]	increase
6.2		hatchery fry-to-presmolt survival		0.1-0.3 [0.2]	increase
6.3		hatchery fry-to-presmolt survival		0.2-0.5 [0.35]	increase
6.4		hatchery fry-to-presmolt survival		0.3-0.6 [0.45]	increase
6.5		hatchery fry-to-presmolt survival		0.4-0.7 [0.55]	increase
6.6		hatchery fry-to-presmolt survival		0.5-0.8 [0.65]	increase
7.1	Increase hatchery only fry-to-presmolt survival and increase % of fish spawned in hatchery	hatchery fry-to-presmolt survival		0.05-0.2 [0.13]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.2		hatchery fry-to-presmolt survival		0.1-0.3 [0.2]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.3		hatchery fry-to-presmolt survival		0.2-0.5 [0.35]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.4		hatchery fry-to-presmolt survival		0.3-0.6 [0.45]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold

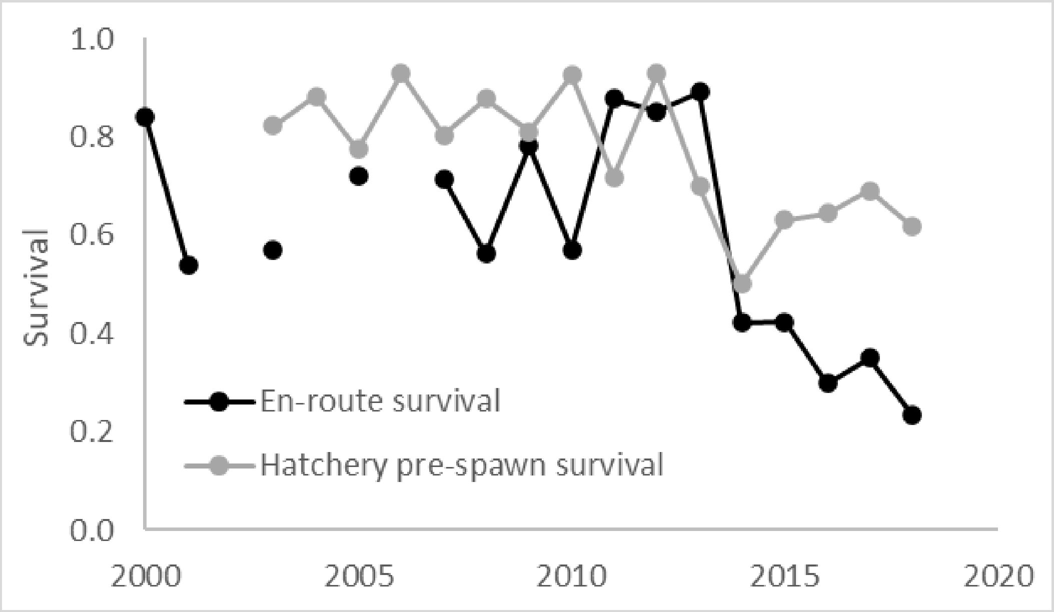

Figure A1. *En-route* survival and prespawning survival of fish spawned in the hatchery for Cedar River Sockeye Salmon from 2000-2018.

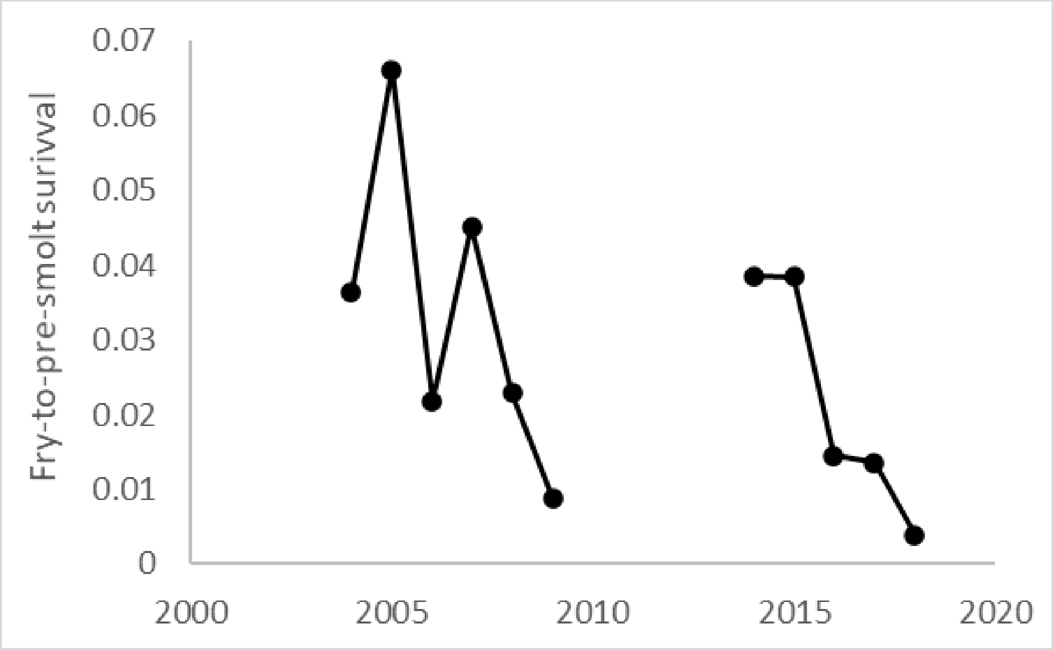

Figure A2. Fry-to-presmolt survival of Cedar River Sockeye Salmon from 2000-2018.

Life-cycle model reveals sensitive life stages and evaluates recovery options for a dwindling Pacific salmon population

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Appendix

Table A1. Detailed information about the seven Cedar River Sockeye Salmon alternative scenarios assessed with our life-cycle model. The versions of the scenario are listed along with the variable(s) modified, the baseline values (range and [average]), the years from which the baseline was taken, and the modified values (range and [average]).

Scenario and version		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
1.1	Increase fry-to-presmolt survival	fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.05 [0.04]	increase
1.2		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.08 [0.055]	increase
1.3		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.12 [0.075]	increase
1.4		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.2 [0.12]	increase
1.5		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.3 [0.17]	increase
1.6		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.4 [0.22]	increase
2.1	Increase presmolt-to-adult survival	presmolt-to-adult survival	0.025-0.43 [0.14]	0.04-0.25 [0.15]	increase
2.2		presmolt-to-adult survival	0.025-0.43 [0.14]	0.05-0.3 [0.18]	increase
2.3		presmolt-to-adult survival	0.025-0.43 [0.14]	0.05-0.4 [0.22]	increase
2.4		presmolt-to-adult survival	0.025-0.43 [0.14]	0.1-0.3 [0.2]	increase
2.5		presmolt-to-adult survival	0.025-0.43 [0.14]	0.1-0.4 [0.25]	increase
2.6		presmolt-to-adult survival	0.025-0.43 [0.14]	0.2-0.4 [0.3]	increase
2.7		presmolt-to-adult survival	0.025-0.43 [0.14]	0.2-0.45 [0.33]	increase
3.1	Increase adult survival in freshwater	en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	increased by 20%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
3.2		en-route survival	0.24-0.47 [0.35]	0.34-0.65 [0.49]	increased by 40%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
3.3		en-route survival	0.24-0.47 [0.35]	0.39-0.75 [0.57]	increased by 60%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%
3.4		en-route survival	0.24-0.47 [0.35]	0.44-0.84 [0.64]	increased by 80%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69	0.92-0.99 [0.95]	increased by 40%
3.5		en-route survival	0.24-0.47 [0.35]	0.49-0.93 [0.71]	increased by 100%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.74-0.86 [0.8]	increased by 25%
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.54-0.89 [0.72]	increased by 25%
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%
3.6		en-route survival	0.24-0.47 [0.35]	0.8	increased to 0.8
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.9	increased to 0.9
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.9	increased to 0.9
		pre-spawn survival in river	0.65-0.78 [0.69]	0.92-0.99 [0.95]	increased by 40%

Scenario		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
baseline		*% of fish spawned in hatchery*	*if <5000 fish to river, 50% to hatchery; if <15000 fish, 40%; if <25000 fish, 30%; if <40000 fish, 20%; if <50000 fish, 10%; if >50000 fish to river, 5%*		
4.1	Increase % of fish spawned in hatchery	% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
4.2		% of fish spawned in hatchery		if <5000 fish to river, 70% to hatchery; if <15000 fish, 60%; if <25000 fish, 50%; if <40000 fish, 40%; if <50000 fish, 30%; if >50000 fish, 20%	increased 20% at each threshold
4.3		% of fish spawned in hatchery		if <5000 fish to river, 80% to hatchery; if <15000 fish, 70%; if <25000 fish, 60%; if <40000 fish, 50%; if <50000 fish, 40%; if >50000 fish, 30%	increased 30% at each threshold
4.4		% of fish spawned in hatchery		if <5000 fish to river, 90% to hatchery; if <15000 fish, 80%; if <25000 fish, 70%; if <40000 fish, 60%; if <50000 fish, 50%; if >50000 fish, 40%	increased 40% at each threshold
4.5		% of fish spawned in hatchery		if <5000 fish to river, 100% to hatchery; if <15000 fish, 90%; if <25000 fish, 80%; if <40000 fish, 70%; if <50000 fish, 60%; if >50000 fish, 50%	increased 50% at each threshold
4.6		% of fish spawned in hatchery		if <5000 fish to river, 100% to hatchery; if <15000 fish, 100%; if <25000 fish, 90%; if <40000 fish, 80%; if <50000 fish, 70%; if >50000 fish, 60%	increased 60% at each threshold
5.1	Increase fry-to-presmolt survival, increase adult survival in freshwater, increase % of fish spawned in hatchery	fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.05 [0.04]	increase
		en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	increased by 20%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.59-0.69 [0.66]	no change
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.43-0.71 [0.57]	no change
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	increased by 20%
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
5.2		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.06 [0.045]	increase
		en-route survival	0.24-0.47 [0.35]	0.29-0.56 [0.42]	(same as prior version)
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	increased to 0.85
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	increased to 0.85
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	(same as prior version)
5.3		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.07 [0.05]	increase
		en-route survival	0.24-0.47 [0.35]	0.34-0.65 [0.49]	increased by 40%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	(same as prior version)
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	(same as prior version)
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	(same as prior version)
5.4		fry-to-presmolt survival	0.01-0.07 [0.03]	0.03-0.07 [0.05]	(same as prior version)
		en-route survival	0.24-0.47 [0.35]	0.39-0.75 [0.57]	increased by 60%
		female pre-spawn survival in hatchery	0.59-0.69 [0.66]	0.85	(same as prior version)
		male pre-spawn survival in hatchery	0.43-0.71 [0.57]	0.85	(same as prior version)
		pre-spawn survival in river	0.65-0.78 [0.69]	0.76-0.94 [0.85]	(same as prior version)
		% of fish spawned in hatchery		if <5000 fish to river, 70% to hatchery; if <15000 fish, 60%; if <25000 fish, 50%; if <40000 fish, 40%; if <50000 fish, 30%; if >50000 fish, 20%	increased 20% at each threshold

Scenario		Modified variable	Baseline values: range [average]	Modified values: range [average]	Modification
6.1	Increase hatchery only fry-to-presmolt survival	hatchery fry-to-presmolt survival		0.05-0.2 [0.13]	increase
6.2		hatchery fry-to-presmolt survival		0.1-0.3 [0.2]	increase
6.3		hatchery fry-to-presmolt survival		0.2-0.5 [0.35]	increase
6.4		hatchery fry-to-presmolt survival		0.3-0.6 [0.45]	increase
6.5		hatchery fry-to-presmolt survival		0.4-0.7 [0.55]	increase
6.6		hatchery fry-to-presmolt survival		0.5-0.8 [0.65]	increase
7.1	Increase hatchery only fry-to-presmolt survival and increase % of fish spawned in hatchery	hatchery fry-to-presmolt survival		0.05-0.2 [0.13]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.2		hatchery fry-to-presmolt survival		0.1-0.3 [0.2]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.3		hatchery fry-to-presmolt survival		0.2-0.5 [0.35]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold
7.4		hatchery fry-to-presmolt survival		0.3-0.6 [0.45]	increase
		% of fish spawned in hatchery		if <5000 fish to river, 60% to hatchery; if <15000 fish, 50%; if <25000 fish, 40%; if <40000 fish, 30%; if <50000 fish, 20%; if >50000 fish, 10%	increased 10% at each threshold

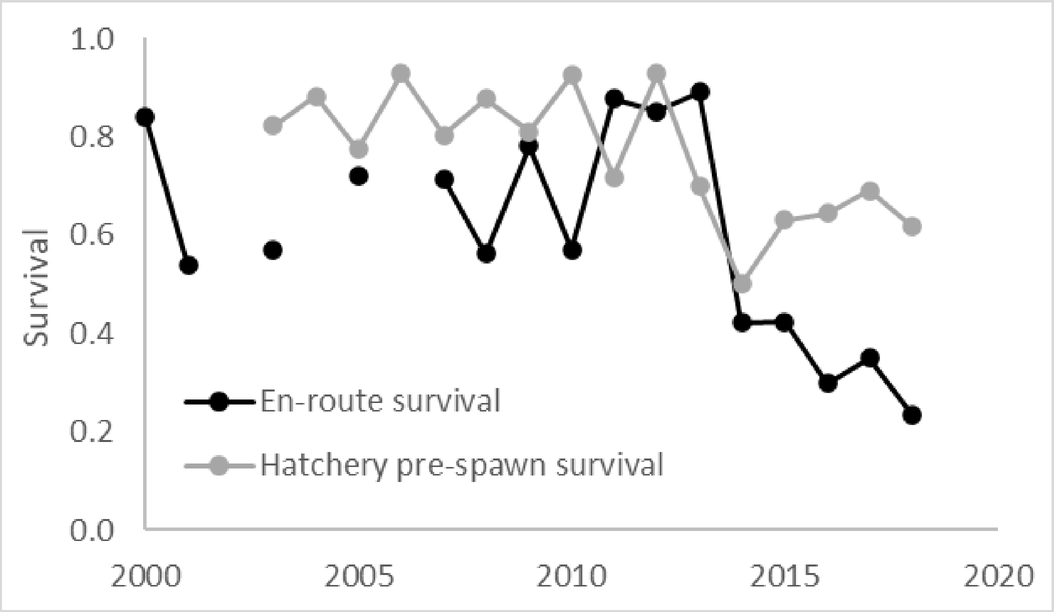

Figure A1. *En-route* survival and prespawning survival of fish spawned in the hatchery for Cedar River Sockeye Salmon from 2000-2018.

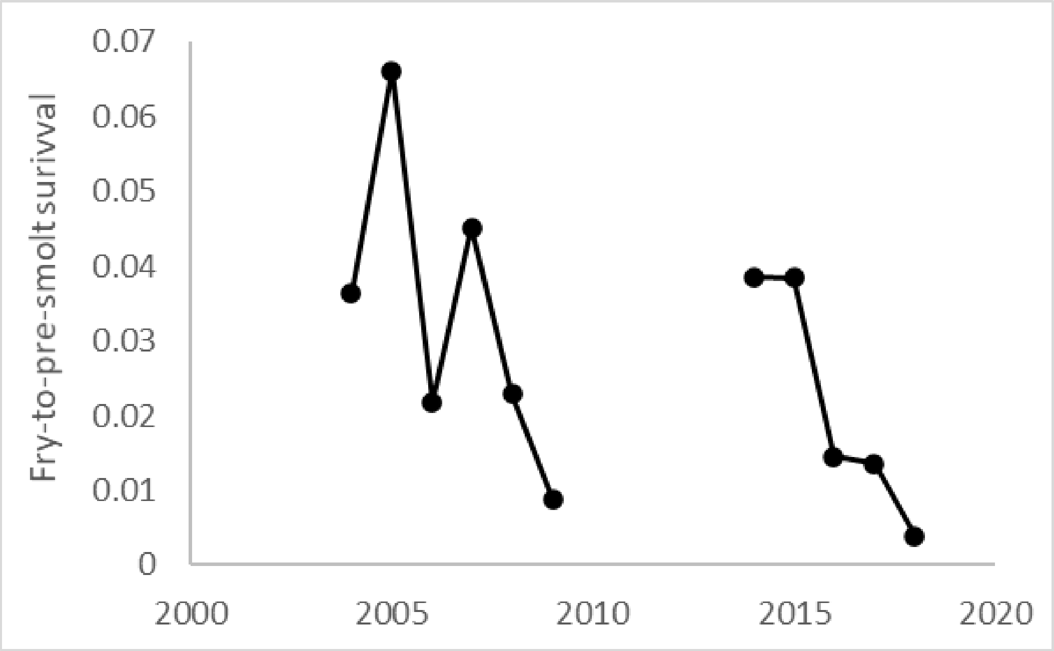

Figure A2. Fry-to-presmolt survival of Cedar River Sockeye Salmon from 2000-2018.