

AN ABSTRACT OF THE THESIS OF

Brittany A. Beebe for the degree of Master of Science in Fisheries Science presented on September 24, 2019.

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Projected intensification of drought as a result of climate change may reduce the capacity of streams to rear fish, exacerbating the challenge of recovering ESA-listed salmon populations. Without management intervention, some stocks will likely go extinct as stream drying and fragmentation reduce juvenile survival to unsustainable levels. To offset drought-related mortality, fish rescue programs have proliferated, whereby juvenile salmonids are captured and transferred to offsite rearing facilities. However, efficacy of this potential conservation tool remains poorly understood. I developed a life cycle model to examine the implications of fish rescue on coho salmon abundance across serial life stages. The model operates under the assumption that fish rescue improves juvenile survival but may decrease smolt-to-adult return rates, either through lower marine survival or increased straying as a result of offsite rearing. The simulation model examines scenarios across various quantities of rescued fish, time in captivity, drought severity, and reduced smolt-to-

adult return rates. My results indicate that rescue increased adult returns and lowered extinction risk, particularly for fish captively reared for 1 year but decreased adult returns and increased extinction risk for fish reared only over summer when smolt-to-adult return rates were low. The findings suggest that fish rescue with long holding periods of approximately 1 year function more like a stock enhancement program than a drought adaptation tool, so its potential effects on adult returns should be evaluated with caution.

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Evaluating Fish Rescue as a Drought Adaptation Strategy for Imperiled Coho
Salmon: A Life-Cycle Modeling Approach

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Brittany A. Beebe, Author

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Introduction

Myriad studies have attempted to predict biological response to climate change (Hijmans & Graham, 2006; Cheung *et al.*, 2010; Schindler & Hilborn, 2015), yet many fail to provide tangible options to ameliorate the impacts of climate change on imperiled species (Wainwright & Weitkamp, 2013). Rising temperatures, changes in the timing and intensity of precipitation, and habitat loss can cause shifts in species distribution, life history events, population dynamics, extinction risk, and interspecific interactions (Mawdsley, O'Malley & Ojima, 2009). With the rate of climate change outpacing the ability of many species to adapt and disperse (Hoffmann & Sgrò, 2011), there is an urgent need for new tools and adaptation strategies to combat pervasive environmental changes that threaten species viability. The extent and degree of impact differs among regions (Dore, 2005; Kundzewicz *et al.*, 2008), so conservation options should be tailored to local conditions. Here, I evaluate an emerging strategy for reducing the impacts of drought on an imperiled salmonid species.

Climate adaptation strategies are classified into four types: habitat protection and management, species management, monitoring and planning, and law and policy (Mawdsley *et al.*, 2009). Current management tools use a combination of these general strategies with actions such as habitat protection and restoration, captive rearing, and assisted migration. Habitat protection and restoration often prioritize activities to conserve refugia (Beier & Brost, 2010) and reduce environmental stressors (e.g., planting trees to shade streams or removing species that transpire excessively) (Katz *et al.*, 2007). Captive rearing has been used to maintain genetic diversity (Brown & Day, 2002; Bowkett, 2009) or breed new traits (van Oppen *et al.*, 2015) and has likely saved some species from extinction (Lockwood *et al.*, 2005); however, it

can also lead to domestication selection and individuals that fare poorly in the wild (Araki, Cooper & Blouin, 2007; Tenger-Trolander *et al.*, 2019). Further, captive rearing is often an “ark” strategy that is meant to save animals from temporary threats but not necessarily an altered future (Bowkett, 2009). Lastly, assisted migration is the action of translocating organisms to areas that are predicted to have more suitable habitat in the future, but are currently inaccessible because they are fragmented or beyond the dispersal potential of the organism. Assisted migration at larger scales and beyond current species ranges is highly controversial and rarely practiced in conservation (Hewitt *et al.*, 2011). Smaller scale applications that relocate individuals (i.e., problem bears, beached whales, entrapped fishes) to more suitable areas within the local habitat matrix are common and often go largely unnoticed (Higgins & Bradford, 1996; Linnell *et al.*, 1997). For example, species may be reintroduced to portions of their native range where they have been extirpated (Sarrazin & Barbault, 1996), or introduced to portions where they have never been present but would likely fare well (Galloway *et al.*, 2016). Perhaps the most ubiquitous example of small scale species translocations is fish salvage, the act of collecting fish from areas that become fragmented or dewatered by human activities and releasing them into adjacent habitats (Nagrodski *et al.*, 2012). Salvaged fish are typically released immediately but in some instances are held in artificial rearing facilities for longer periods of time (Lopez Arriaza *et al.*, 2017). Salvage may be implemented episodically, such as with instream construction activities, or may operate on a seasonal basis, coinciding with regularly scheduled water drawdowns (KTVZ, 2017).

While fish salvage is meant to save fish from threats that last only days and assisted migration to expand species range is a response to future climatic states, there is a relative lack

of management interventions at intermediate timescales. Most stressors are seasonal, but the topic of seasonally assisted migration is not broadly recognized or assessed. In highly seasonal environments, where the largest impacts of climate change are likely to be associated with altered annual extremes rather than changes in mean conditions (Jaeger, Olden & Pelland, 2014), it is possible that relocating individuals during stressful portions of the year could allow populations to persist where they would otherwise be predicted to go extinct. However, this intermediate scale of intervention (i.e., seasonal rescue within contemporary species ranges) remains largely unexplored in the field of climate change adaptation.

Here, I explore the potential for monthly-to-annual rearing and translocations within species ranges to mitigate the effects of seasonal drying on stream-dwelling fish. Riverine ecosystems exhibit extreme seasonal variation that will likely dictate species response to climate change. For example, precipitation and runoff interact with watershed characteristics such as geomorphology and land cover to regulate the influx of water into the stream channel and dictate the temporal pattern of discharge (Poff *et al.*, 1997). Streamflow can be relatively constant (e.g., groundwater dominated streams), but generally, flow varies seasonally by several orders of magnitude (e.g., precipitation dominated streams), causing aquatic ecosystems to oscillate between contracted and expanded states (Lake, 2003; Humphries & Baldwin, 2003). The magnitude of contraction varies among regions and climatic zones, but streams with intermittent flow are common, especially in headwaters and regions with distinct wet and dry seasons (Larned *et al.*, 2010; Woelfle-Erskine, Larsen & Carlson, 2017). Reduced water input and increased water withdrawal can intensify stream contraction, resulting in severe and prolonged dryness. During the contraction process, riffle habitat sections often dry

first, transforming streams into an assortment of isolated pools (Stanley, Fisher & Grimm, 1997; Labbe & Fausch, 2000; Hwan & Carlson, 2016). In addition to reduced habitat availability, sustained drought conditions can increase extremes of physicochemical conditions, such as temperature and dissolved oxygen (Magoulick & Kobza, 2003) and even lead to seasonal pool drying. In rain-dominated watersheds of the Pacific Northwest, intermittent streams provide summer rearing habitat for culturally valued species (Everest, 1973; May & Lee, 2004; Wigington *et al.*, 2006). Projected intensification of drought conditions in the region may increase the duration and severity of stream fragmentation as summers are projected to become hotter and drier (Mote & Salathé, 2010). This will likely decrease summer minimum flow conditions throughout the region (Hamlet *et al.*, 2013), reduce the rearing capacity of many streams (Harvey, Nakamoto & White, 2006; Falke *et al.*, 2011), and exacerbate the challenge of recovering ESA-listed populations (Crozier *et al.*, 2019).

In response to current and projected threats, there is growing interest in developing strategies to mitigate the effects of stream drying on salmonid populations. A potentially controversial implementation of assisted movement and rearing, called *fish rescue*, has been used to combat drought-induced mortality in intermittent streams. Fish rescue differs from the more typical fish salvage operations. Instead of immediately transporting fish to other habitats, fish rescue holds fish for an extended period of time before releasing them back to the stream. The California Department of Fish and Wildlife (CDFW) has used this strategy in the Russian River Basin in central California for the past few years, rescuing thousands of stranded juvenile coho and chinook salmon and steelhead each year (CDFW, personal communication). Rescued coho salmon are transported to a hatchery for use in a broodstock program or reared until

streamflow improves. Likewise, the Carmel River Steelhead Association has also implemented fish rescue in California, collecting fish from fragmented habitat during low flows (May-Oct) and rearing them in a specialized facility until release the following winter (Lopez Arriaza *et al.*, 2017). Fish rescue programs aim to increase overall survival by circumventing life stages with low survival, but the length of time fish are held and the number of fish rescued can influence the effects of rescue. Rescue often occurs over summer months when streamflow is low, but if habitat is limited for subsequent life stages, then returning rescued fish to the stream may increase fish density beyond a sustainable threshold and decrease survival. Additionally, captively reared fish may exhibit altered phenotypes (Kihlslinger, 2006), which could additionally lower their subsequent survival compared to wild (i.e., non-rescued) counterparts. If a large percentage of fish are rescued, the effects of rescue are magnified, underscoring the need to better understand the consequences of fish rescue.

To evaluate the efficacy of fish rescue, I developed a simulation model to explore how drought-induced fragmentation and seasonal fish rescue interact to affect salmon population dynamics. Specifically, I developed a life-cycle model to examine abundance of returning adults and extinction risk across various levels of rescue intervention, drought severity, and smolt-to-adult return rates. The model is flexible enough for use in systems with a range of environmental conditions and different rescue interventions. To showcase my life-cycle model, I use it to evaluate one of the most prominent fish rescue programs in the Pacific Northwest. The program, Northwest Wild Fish Rescue (NWFR), removes tens of thousands of ESA-listed juvenile coho salmon (*Oncorhynchus kisutch*) from stream reaches that are susceptible to drying and rears them in captivity until smoltification (approximately 1 year). My life-cycle

model will enable managers to assess the trade-offs associated with fish rescue and identify the range of scenarios when intervention may be an appropriate action in a specific watershed.

Here, I compare the abundance of returning adults and extinction risk resulting from differing rescue scenarios to answer the following questions:

1. Under what ecological conditions does rescue increase adult returns and lower extinction risk compared to scenarios without fish rescue?
2. Can fish rescue effectively operate as a drought mitigation tool by maintaining adult returns across various levels of drought severity?
3. How are the results of fish rescue sensitive to model parameters that represent ecological context (survival in wild, population size, drought severity, etc.) or the costs of rescue (hatchery-like effects on post-rescue survival)?

Methods

Model Overview

Coho salmon have complex life cycles and exhibit ontogenetic habitat shifts, so survival during one life stage, such as juvenile oversummer survival, may or may not influence population productivity (Mason, 1976). Life-cycle models are widely used in salmon conservation to explore life stage-specific impacts on population dynamics (Moussalli & Hilborn, 1986; Nickelson & Lawson, 1998; Oosterhout *et al.*, 2005; Scheuerell *et al.*, 2006). I developed a life-cycle model to examine the effects of fish rescue across varying levels of intervention, drought severity, and assumptions regarding the effects of captive rearing on smolt-to-adult survival. The model operates under the assumption that fish rescue improves

juvenile survival but may decrease smolt-to-adult return rates, either through lower marine survival (Jonsson, Jonsson & Hansen, 2003; Saloniemi *et al.*, 2004; Jokikokko *et al.*, 2006) or increased straying as a result of captive rearing (Keefer & Caudill, 2014). Additionally, I assume that drought reduces summer rearing capacity, thus reducing survival of wild fry (Harvey *et al.*, 2006; Hwan *et al.*, 2018).

Case Study

Located within the Cascade Mountain foothills of the Pacific Northwest, the East Fork (EF) Lewis River, originates in the Gifford Pinchot National Forest and flows westward, emptying into the Lewis River which flows into in the Columbia River. The EF Lewis River watershed is approximately 610 km² and consists of small urban and rural communities. It is labeled as a *Tier 1, key watershed* by the President's Forest Plan because it provides, or is expected to provide, high quality fish habitat and water quality (USFS, 1995). However, land use activity throughout the watershed (e.g., agriculture, logging, and mining) has degraded habitat and increased stream temperatures in the lower EF Lewis River Basin (National Marine Fisheries Service, 2013). Juvenile coho salmon are primarily distributed throughout tributaries in the lower EF Lewis River and in side- and off-channel habitat in the main stem river. Two streams within the lower EF Lewis River sub-basin, Mason Creek and its tributary, Tsugawa Creek, are used as a case study for which the model is applied. These rain-dominated intermittent streams in southwestern Washington are dominated by the region's Mediterranean climate, which is characterized by wet, mild winters and dry, warm summers. They flow approximately 19 km in total length, exclusively through private land. Elevation of the creeks range from 5-210 m above

sea level and there are relatively few slopes >4%, with the steepest areas occurring abruptly as a result of beaver dams and log jams. By late summer, much of these streams (>50%) have become fragmented.

Northwest Wild Fish Rescue

From May through July, ~15,000-32,000 coho salmon fry, along with some steelhead and cutthroat juveniles, are collected from tributaries throughout the East Fork Lewis River (Mason Creek, Tsugawa Creek, Rock Creek, Mill Creek) and Salmon Creek sub-basins (Mill Creek). The fish are then reared for approximately 8-12 months in spring-fed raceways and released in March or April the following spring. Fish are released into 12 different tributaries within the EF Lewis River and Salmon River sub-basins, but not necessarily back into the same stream from which they were removed. In the model, I represent NWFR in one scenario of parameter combinations but also explore scenarios representing a range of conditions.

Model Application

Although I use NWFR as a case study, the model is flexible, representing a range of environmental conditions and rescue interventions that can be applied to a variety of systems and rescue programs. I explored numerous combinations of freshwater rearing capacities for summer and winter, the range of which were influenced by the study system yet are applicable to other systems exhibiting similar capacities. Likewise, the range of rescue levels (i.e., number of fish rescued) was influenced by the study program but combined with differing captive rearing durations can still be applied to a variety of rescue programs, not just NWFR. The only

parameter that is specific to the study system is the capacity for eggs (i.e., total spawning habitat, discussed in spawner to fry section below). In the simulations, spawning habitat was not a limiting factor, which supports the common assumption that only a small number of coho salmon adults are needed to fully “seed” a stream (Quinn, 2018). Consequently, model results may be less applicable to systems where spawning habitat is a constraint on production.

Coho Salmon Life Cycle

The model framework imitates a three-year coho salmon life cycle. Coho salmon in the Lower Columbia River (LCR) spawn in tributaries during late November through early January (Hirose, 1983). After incubating in the gravel over winter, fry emerge in spring and hold in slow margins or off-channel habitat until late spring to early summer when they move into thalweg habitat which serves as refuge during low flow periods (Hodges & Magoulick, 2011). During the winter, parr are thought to move back into slow, off-channel habitat which protect them from high flows (Bustard & Narver, 1975; Hartman & Brown, 1987; Nickelson *et al.*, 1992). Winter has often been cited as the factor limiting smolt production (Nickelson, 1998), though some argue that summer rearing capacity limits production (Bradford, Taylor & Allan, 1997; Grantham *et al.*, 2012). The following spring, smolt migrate downstream to the ocean. Generally, coho salmon rear in marine waters for 1.5 years before returning to spawn in their natal streams during fall or early winter (Quinn, 2018). A portion of male adult salmon are precocious males (known as jacks) that return to spawn after spending less than one year in the ocean. Spawning surveys conducted between 2002-2005 in Oregon found that jacks comprise 3-23% of all male spawners but jack proportions vary among populations within the LCR

(Suring, Brown & Moore, 2006). To reduce model complexity, all spawning coho in the model were assumed to be age 3 given that the effects of cohort dynamics on resilience was beyond the scope of the model.

The model framework reflects the basic life cycle of coho salmon and simulates abundance across five serial life stages: spawner, fry, parr, smolt, and adult (Table 1). Wild fish move sequentially through each life stage and are subjected to corresponding survival processes. I simulated fish rescue as an alternative pathway between the fry and smolt life stages and examined two captive rearing durations: short- and long-term rescue. For the short-term scenario, fish are held in captivity only during the season of wetted habitat contraction, which was considered as the summer fry-to-parr survival stage. For long-term rescue, fish are held for roughly a year through both the fry-to-parr (i.e., summer) and the parr-to-smolt (i.e., winter) stages (Figure 1).

Table 1. State variables in the life-cycle model.

State Variables	Description
Fry	Fish that hatch and survive through first spring in natal stream and are then rescued
Parr _r	Rescued fish surviving through first summer in captivity (short-term rescue only)
Parr _w	Wild fish surviving through first summer in natal stream
Smolt _r	Fish surviving rescue activities, including time in captivity, up until release as smolts
Smolt _w	Wild fish surviving through first winter in freshwater; before seaward migration
Adult	Fish surviving seaward migration and first summer in marine environment
Spawner	Rescued and wild adults surviving a full year in marine environment from end of first summer and migrating back to natal stream to spawn

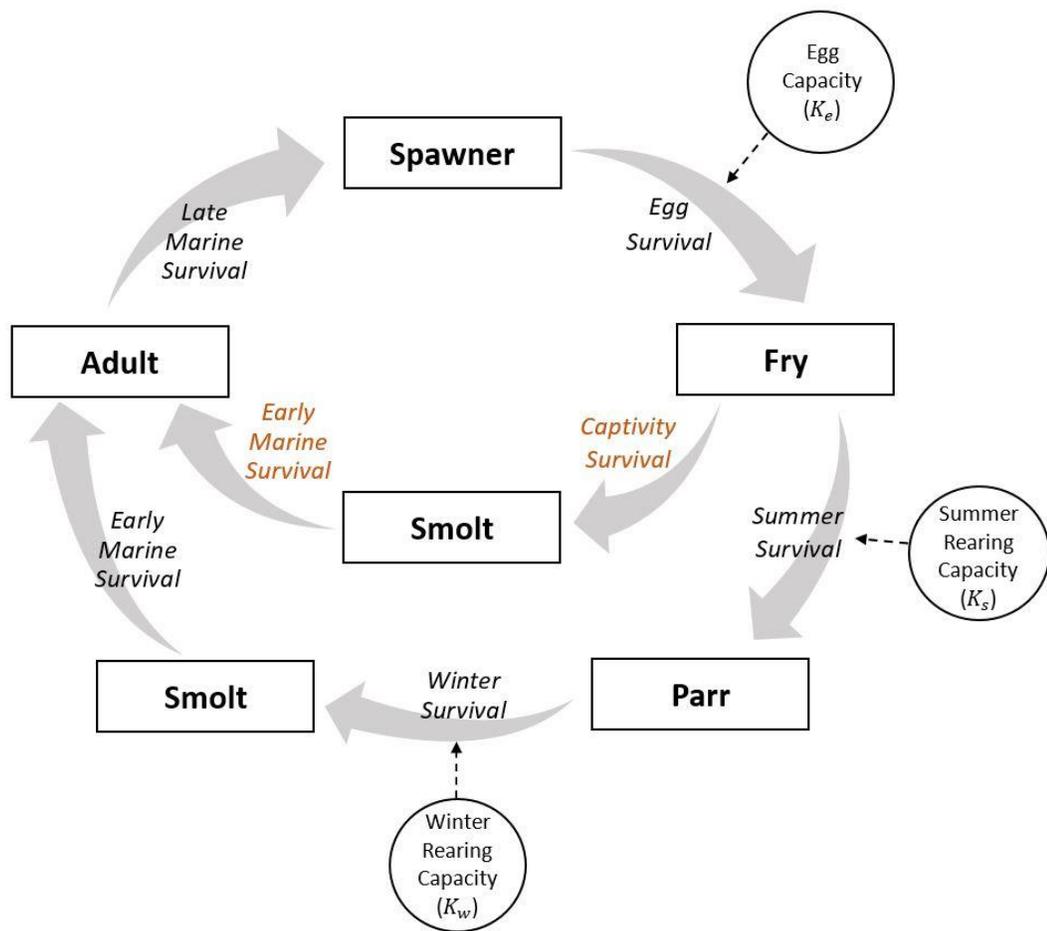


Figure 1. Box and arrow diagram of the life-cycle model with long-term rescue depicted in orange.

Model Functions

Survival was represented by the transition of individuals from one life stage to the next. The transition between the spawner and fry life stages included fecundity in addition to survival. The survival probabilities for each transition (explained below) were used in a binomial distribution to incorporate demographic stochasticity to the simulated number of individuals at the subsequent life stage (Nickelson & Lawson, 1998). Binomial distributions are expressed as

$$(1) \quad N_{s+1} \sim \text{Binom}(N_s, S_s)$$

where, S_s is the probability of surviving from life stage s to life stage $s + 1$, N_s is the number of individuals at life stage s , and N_{s+1} is the number of individuals at life stage $s + 1$.

Three general methods were used to calculate survival. The Beverton-Holt function was used for freshwater survival (Moussalli & Hilborn, 1986), a beta distribution was used for marine survival (Hill, Botsford & Hastings, 2003), and a constant parameter value was used for survival in captivity (NWFR, personal communication).

Freshwater Survival

Mean survival within the freshwater portion of the model (from spawner to smolt) was density-dependent (Jonsson, Jonsson & Hansen, 1998) and represented by sequential Beverton-Holt functions. The classic density-dependence equation is expressed as

$$(2) \quad \bar{N}_{s+1} = \frac{N_s}{\frac{1}{p_s} + \frac{N_s}{K_s}}$$

where, N_s is the number of individuals at life stage s , P_s is the productivity from life stage s to life stage $s + 1$, and K_s is the habitat capacity between life stage s to life stage $s + 1$ (Moussalli & Hilborn, 1986). With simple algebra, the equation can be rearranged and solved for survival, where X_s is the survival from life stage s to life stage $s + 1$.

$$(3) \quad X_S = \frac{\bar{N}_{S+1}}{N_S} = \frac{1}{\frac{1}{p_S} + \frac{N_S}{K_S}}$$

Marine Survival

Mean survival within the marine portion of the model (from smolt to spawner) was density-independent (Jonsson *et al.*, 1998). These state transitions used a beta distribution to produce survival probability (Hill *et al.*, 2003). Beta distributions are expressed as

$$(4) \quad X_S \sim \text{Beta}(\alpha, \beta)$$

$$(5) \quad \alpha = \left(\frac{\bar{x} * (1 - \bar{x})}{\sigma^2} - 1 \right) * \bar{x}$$

$$(6) \quad \beta = \left(\frac{\bar{x} * (1 - \bar{x})}{\sigma^2} - 1 \right) * (1 - \bar{x})$$

where, \bar{x} is the mean survival from life stage s to life stage $s + 1$ and σ is the standard deviation of the survival estimates from life stage s to life stage $s + 1$ (Johnson, Kotz & Balakrishman, 1995). Both \bar{x} and σ are calculated from gathered literature values (Table 2).

Captive Survival

The controlled captive environment eliminates mortality from starvation and predation resulting in high survival rates. Northwest Fish Rescue reports a 98% survival rate (NWFR, personal communication), which was used in the simulations. This survival level was comparable to the 95.3% mean survival rate observed in four hatcheries in Washington (WDFW, unpublished data); however, other fish rescue captive rearing facilities have had issues

with cannibalism or constraints of drought on fish rearing capacity, which may result in lower survival rates (Lopez Arriaza *et al.*, 2017).

Table 2. Model parameters, their values, and references for these values.

Parameter	Description	Value	Reference(s)
f	Fecundity	2500	
s	Sex ratio	0.5	
p_e, p_s, p_w	Egg, summer, and winter maximum productivity	0.429, 0.26, 0.9	Nickelson, 1998; Bradford <i>et al.</i> , 2000
K_e, K_s, K_w	Egg, summer, and winter capacity	902,500; 5,000-45,000; 5,000-45,000	See text (spawner to fry; fry to parr; parr to smolt)
\bar{x}_c	Mean captivity survival	0.98	NWFR, personal communication
\bar{x}_{we}	Mean wild early marine survival	0.098	Bradford 1995
\bar{x}_{re}	Mean rescued early marine survival	0.0196, 0.0392, 0.0588, 0.0784, 0.0980	See text (rescued fish)
\bar{x}_l	Mean late marine survival (all fish)	0.15	
σ_{re}	Rescued early marine survival standard deviation	0.01	
σ_{we}	Wild early marine survival standard deviation	0.01	
σ_l	Late marine survival standard deviation (all fish)	0.01	
E	Encounter probability at low fry density	0.4	

Spawner to Fry

Simulations were initialized using an arbitrary spawner abundance of 500 based loosely on the number of coho salmon spawners that would be expected in a stream the size of Mason and Tsugawa Creeks. To calculate egg abundance, the spawner abundance in each generation

was multiplied by the sex ratio (0.5 proportion of females) and fecundity (2500 eggs/female). This egg abundance was then used in the Beverton-Holt equation as the N_s value and used to calculate the number surviving to fry. The egg capacity (K_e) used in the Beverton-Holt equation is calculated by multiplying stream length for the focal system (19 km) by a regional estimate for maximum spawner density (19 female/km; Bradford, Myers & Irvine, 2000) and fecundity (2500 eggs/female). This value remained unchanged throughout the simulations. Thus, the quantity of spawning habitat, (i.e., capacity for egg-to-fry rearing) was representative of a subcomponent of a catchment consisting of small tributary streams.

Fry to Parr

Simulated fry that were not diverted to the rescue pathway reared over summer in the natural environment. I explored a range of parameters that represent different levels of rearing capacity due to either different levels of drought or intrinsic differences among streams in their summer habitat and hydrology. Mean summer rearing capacities (K_s), ranging from 5000 to 45000 in increments of 5000, were used in the simulations and represented severe to minimal constraints of habitat contraction on survival, respectively (Table 2). The range of values were consistent with those observed in Mason and Tsugawa Creeks during the summer of 2017 (WDFW, unpublished data).

Parr to Smolt

Parr reared over winter to reach the smolt life stage. To make direct comparisons between summer and winter limitations, winter rearing capacity (K_w) used the same range of

values ($K_w = 5000$ to 45000) that were used for summer rearing capacity. A winter rearing capacity was randomly chosen from this range and used in the model for each simulation.

Smolt to Adult

Early marine survival of wild fish (\bar{x}_{we}) encompassed the time of downstream migration through the first summer in the ocean. For this transition, I drew survival probabilities from a beta distribution (eq. 4-6) with mean early marine survival of 9.8% (Bradford, 1995) for each time step.

Adult to Spawner

The state transition between adult and spawner encompassed the second year in the marine environment, from the end of the first summer through upstream migration to spawn. A single late marine survival (\bar{x}_l) was drawn from a beta distribution with a mean of 15% for each time step and applied to all fish, rescued and wild.

Rescued Fish

Fish rescue removed fish from the stream at the fry life stage. At this point, rescued fry move to the parr life stage via short-term captivity survival or directly into the smolt life stage via long-term captivity survival. The short-term rescue scenario replaces the summer survival applied to wild fish, and the long-term rescue scenario circumvents both the summer and winter survival applied to wild fish (Figure 1). While captivity survival is much higher than either summer or winter survival experienced by wild counterparts, rearing in artificial conditions

(such as hatcheries) has been shown to alter fish behavior (Nickelson, 1986; Berejikian *et al.*, 1995) and survival (Leider *et al.*, 1990) in subsequent life stages once returned to the natural environment. Although not bred in captivity, rescued fish spend much of their freshwater life stages in artificial conditions, and I assumed this could negatively affect smolt-to-adult return rates. Since it is unknown how rescuing fish impacts later life stages, I explored a range of survival penalties based on empirical estimates of how marine survival differs between hatchery and wild fish. Reported estimates of marine survival of hatchery fish compared to wild fish range from ~37-100% (Jonsson *et al.*, 2003; Kallio-Nyberg *et al.*, 2004; Jokikokko *et al.*, 2006; Hyvärinen & Rodewald, 2013). The highest comparative survival (i.e., 100%) occurred for captively reared fish released as parr (Jokikokko *et al.*, 2006), while the lowest comparative survival was associated with fish released as 1 year-olds smolts (Jonsson *et al.*, 2003). Saloniemi *et al.* (2004) reported that wild smolts had 4.5 times higher survival than hatchery-reared counterparts, and considering the wild marine survival rate of 0.098, this represents ~22% comparative marine survival for hatchery fish. Lower values could represent the combined effects of post-release mortality, reduced marine survival and reduced homing. In the model, early marine survival of rescued fish was calculated by multiplying early marine survival of wild fish by a penalty value. I explored penalties of 0.2, 0.4, 0.6, 0.8 and 1, where 0.2 was the most severe penalty and 1 represented no penalty. Though it is possible that the magnitude of penalty increases with the duration of rescue, I did not explore this potential relationship.

Rescue Level

The attempted rescue level remained constant for every generation of a given simulation, ranging from 5000 to 35000 in increments of 10000. Since fry abundance may fall below the attempted rescue level, I used a functional response to model the realized rescue level as a function of fry abundance. I used a capped linear (i.e., “hockey-stick”) functional response, in which 40% of the total fry are captured, up to the attempted rescue level (i.e., the capacity for captive rearing). In other words, when fry abundance was less than the captive rearing capacity, 40% of the available fry were rescued. This avoids rescuing an unrealistic percentage of available fry.

Model Output

Two main response metrics were used to explore the impact of fish rescue on coho salmon population dynamics: spawner abundance and extinction risk. These metrics are commonly used for various salmonid life-cycle models within the Columbia River Basin (Zabel *et al.*, 2013). Spawner abundance was calculated by taking the geometric mean of spawner abundance across all generations of a given simulation. Recruitment variability tends to be log-normal as a result of the multiplicative survival framework, so geometric mean is commonly used in life cycle models to avoid placing undue weight on outliers and to better explain the central tendency of the dataset (Zabel *et al.*, 2013). Extinction risk was calculated as the percentage of generations within a simulation in which spawner abundance falls below an extinction threshold. Following the standards set by Zabel *et al.* (2013), the extinction threshold was set at 50 spawners.

Scenarios Modeled

The effects of fish rescue were examined by varying rearing duration (i.e., short, long) and limiting season (i.e., the degree to which production is limited by summer or winter rearing capacity). For each scenario (outlined in table 3), rescue level and drought condition were allowed to vary. Rescue levels were set to 0, 5000, 15000, 25000, and 35000. No rescue simulations (rescue level = 0) served as a baseline to which the other four rescue simulations were compared. Drought conditions were explored by adjusting the summer rearing capacity (K_s). For low drought conditions, the capacity was higher, and for more severe drought, the capacity was lower.

Table 3. Five sets of parameter combinations are run for each rescue level (none, 5000, 15000, 25000, 35000). Rearing duration refers to length of time in captivity, short-term or long-term, and limiting season is the season that exhibits the least amount of available habitat. Note that for no rescue simulations, rearing duration does not apply because no fish are rescued.

Scenario	Rearing Duration	Limiting Season
1	short	winter
2	short	summer
3	long	winter
4	long	summer

Each complete life cycle followed one generation through the three-year lifespan. Simulations spanned 33 generations (99 years), and 10,000 replicate simulations were run for each rescue level. Other life-cycle models in the Columbia River Basin project simulations for 100 years (Zabel *et al.*, 2013), and I aimed for a similarly long projection timeframe. This allows for comparison among results from the different models, which is particularly helpful for

comparing extinction risks. Since several parameters were chosen at random from statistical distributions, 10,000 simulations per rescue level ensured that a sufficient number of simulations were run for each combination of parameter values to accurately summarize the central tendency of stochastic processes and explore parameter space. All modeling was done using Program R (R Core Team, 2017).

Results

Relative Changes in Abundance

My model explored how the positive effects of fish rescue propagated through the coho salmon life-cycle under alternative scenarios of seasonal habitat capacity and the effects of captive rearing on marine survival. I found that increasing freshwater survival through fish rescue translated into higher adult returns across most of the parameter space I explored (Figure 2). In the small watershed my simulation represented, the median adult coho salmon returns without fish rescue was 62 fish (range = 0-152). In contrast, at an intermediate rescue level (collecting 15,000 fry) and intermediate penalty value (40% reduction in marine survival), I observed the following results. For short-term rescue in summer-limited simulations, the median of adult returns among simulations was 132 fish (range = 45-198), representing a 112.9% increase in abundance compared to no-rescue simulations in the respective modeling scenario. The median adult returns for short-term rescue in winter-limited simulations was 87 fish (range = 24-190), an 86% increase. For long-term rescue in summer-limited simulations, the median adult return was 225 (range = 154-327) a 262.9% increase. Long-term rescue in winter-limited simulations produced a median of 227 fish (range= 160-329), a 266.1% increase. While

fish rescue increased adult returns in most contexts explored, I also found that it could have a negative effect on returns if rescue was short-term (i.e., only for summer) and the penalty on subsequent adult survival was substantial (i.e., captive reared fish had one-fifth the marine survival of wild fish) (Figure 3).

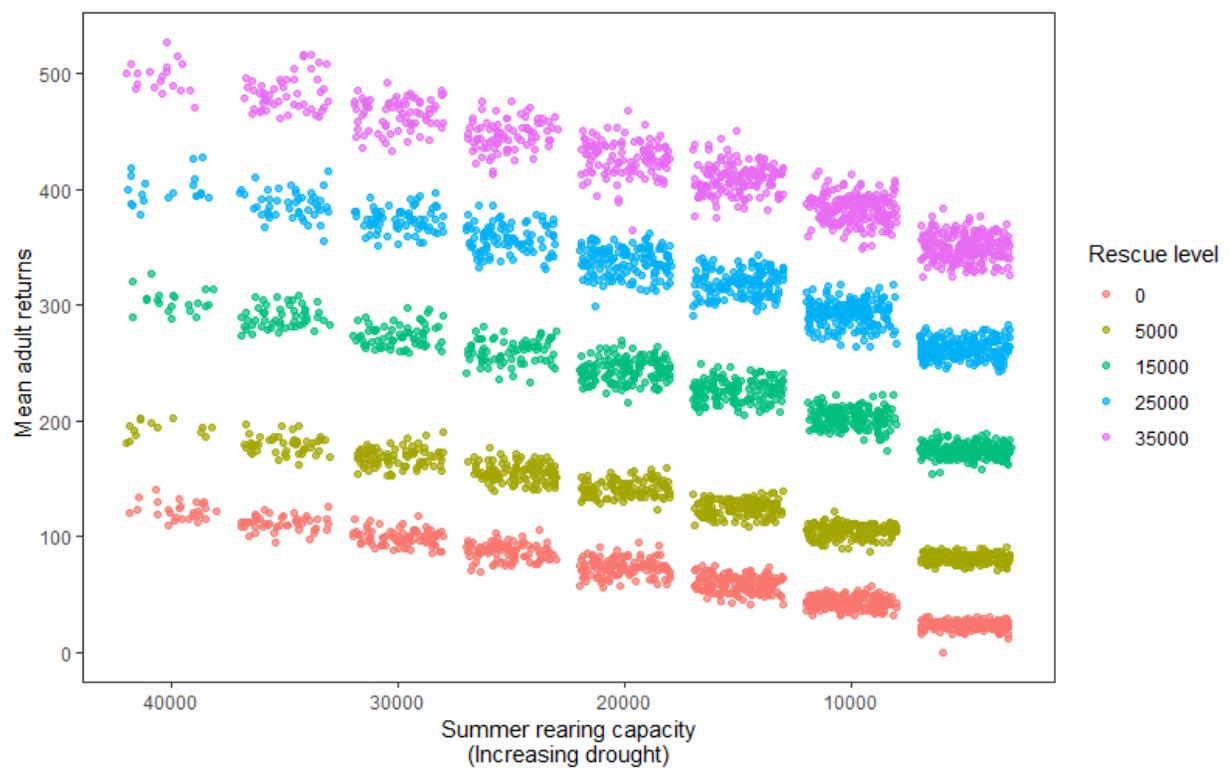


Figure 2. Geometric mean adult returns across increasing drought severity and rescue level for long-term rescue with summer-limited rearing capacity and intermediate penalty (i.e., 0.6).

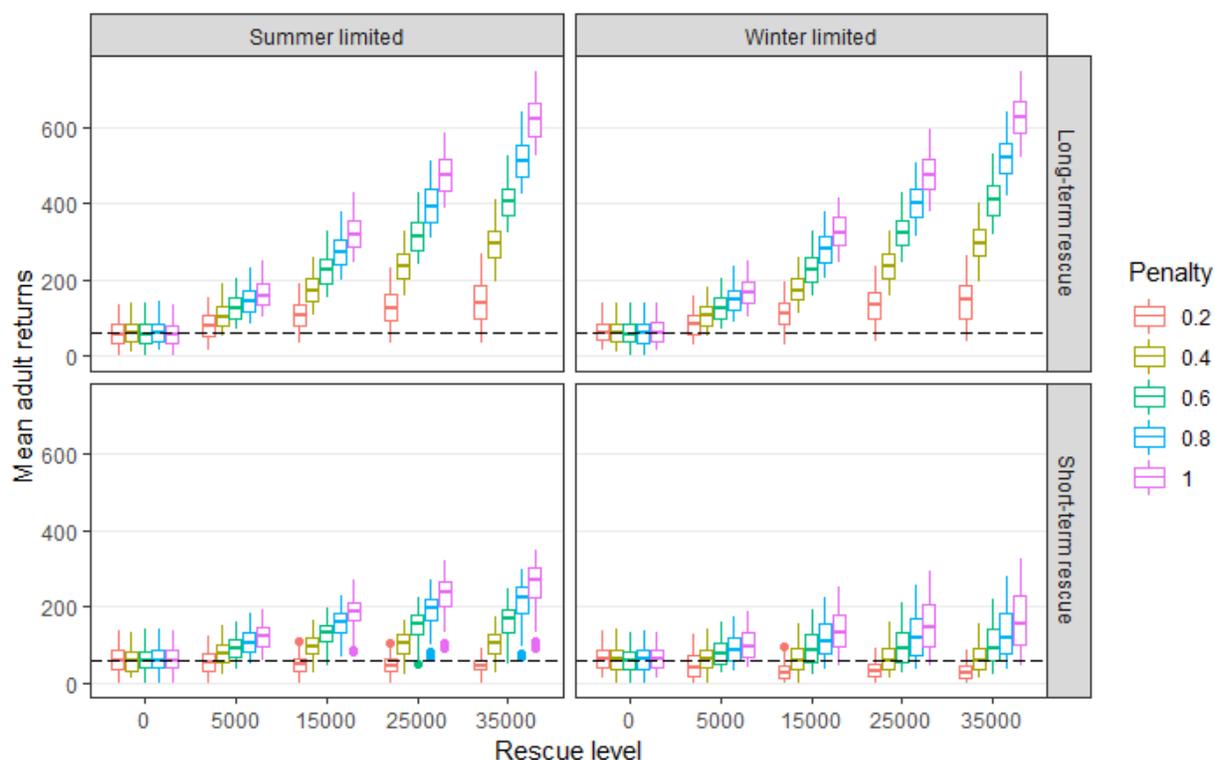


Figure 3. Geometric mean adult returns across rescue level and colored by penalty (0.2 is most severe penalty) for each of four scenarios: long-term rescue with summer limitation, long-term rescue with winter limitation, short-term rescue with summer limitation, and short-term rescue with winter limitation. The median value of no rescue simulations is represented by a dashed line.

Relative Changes in Extinction Risk

The positive effect of fish rescue on freshwater survival almost always translated to decreased extinction risk and only increased this risk in short-term rescue simulations (Figure 4). In the small tributary I simulated, extinction risk without fish rescue ranged from 0-100% with a median of 18.2% and mean of 38.0% for winter-limited simulations and a median of 21.2% and mean of 39.8% for summer-limited simulations. For long-term simulations, all combinations of rescue levels and penalty values had a 0% median extinction risks. For short-term simulations, increased extinction risk occurred for all rescue levels with penalty of 0.2. For

summer-limited, short-term rescue with penalty of 0.2, median extinction risk was 36.4% for rescue level of 5000 and 57.6% for rescue levels of 15000, 25000, and 35000. For winter-limited, short-term rescue with penalty of 0.2, median extinction risk was 69.7%, 90.9%, 87.9%, and 93.9% for rescue levels of 5000, 15000, 25000, and 35000, respectively. A higher median extinction risk compared to no rescue simulations also occurred for winter-limited, short-term simulations when the penalty was 0.4 and rescue level was 15000 and 25000. Extinction risk in these scenarios was 27.3% and 19.7%, respectively.

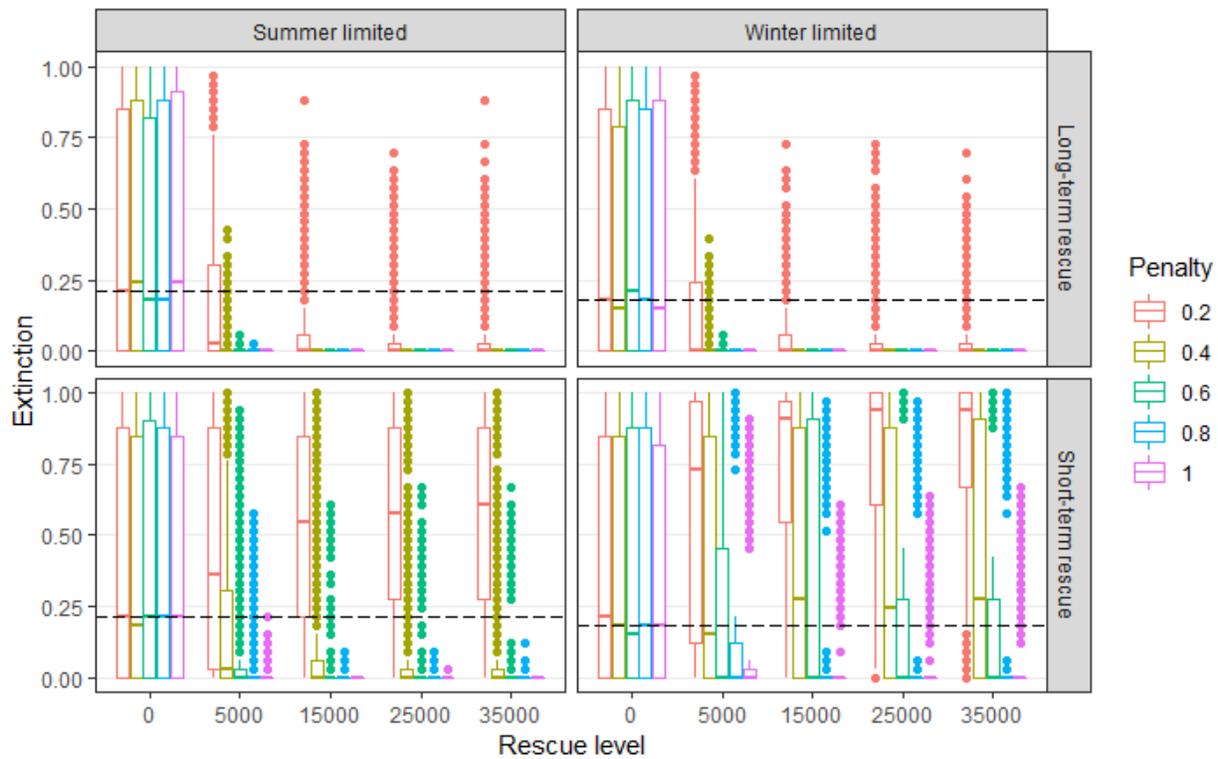


Figure 4. Median extinction risk across rescue level and colored by penalty for each of four scenarios: long-term rescue with summer limitation, long-term rescue with winter limitation, short-term rescue with summer limitation, and short-term rescue with winter limitation. The median value of no rescue simulations is represented by a dashed line.

Long-term rescue scenarios exhibited extinction risk >50% for 1.1% of summer-limited simulations and 0.9% for winter-limited systems. For short-term rescue scenarios, extinction risk >50% occurred for 10.1% and 27.2% of summer- and winter-limited simulations, respectively. Comparatively, no rescue scenarios exhibited extinction risk >50% for 40.3% of summer-limited simulations and 37.6% of winter-limited simulations.

Effect of Rescue Penalty

Rescue penalty, when expressed as the marine survival rate of rescued fish relative to that of wild fish, had a near linear effect on adult returns (Figure 5). The slope of this relationship was larger for long-term rescue (regardless of the season of habitat limitation) and less positive for short-term rescue (within this scenario it was least positive for winter-limited simulations). Short-term rescue scenarios resulted in fewer adult returns compared to long-term rescue scenarios, and simulations with high penalty (i.e., 0.2 and 0.4) resulted in negative effects on adult returns (Figure 3). Thus, the effect size of the penalty was strongest in the long-term rearing scenario, but the effects were most important in the short-term rearing scenario because it reduced abundance below that of no rescued scenarios (i.e., fish rescue can have a net negative effect).

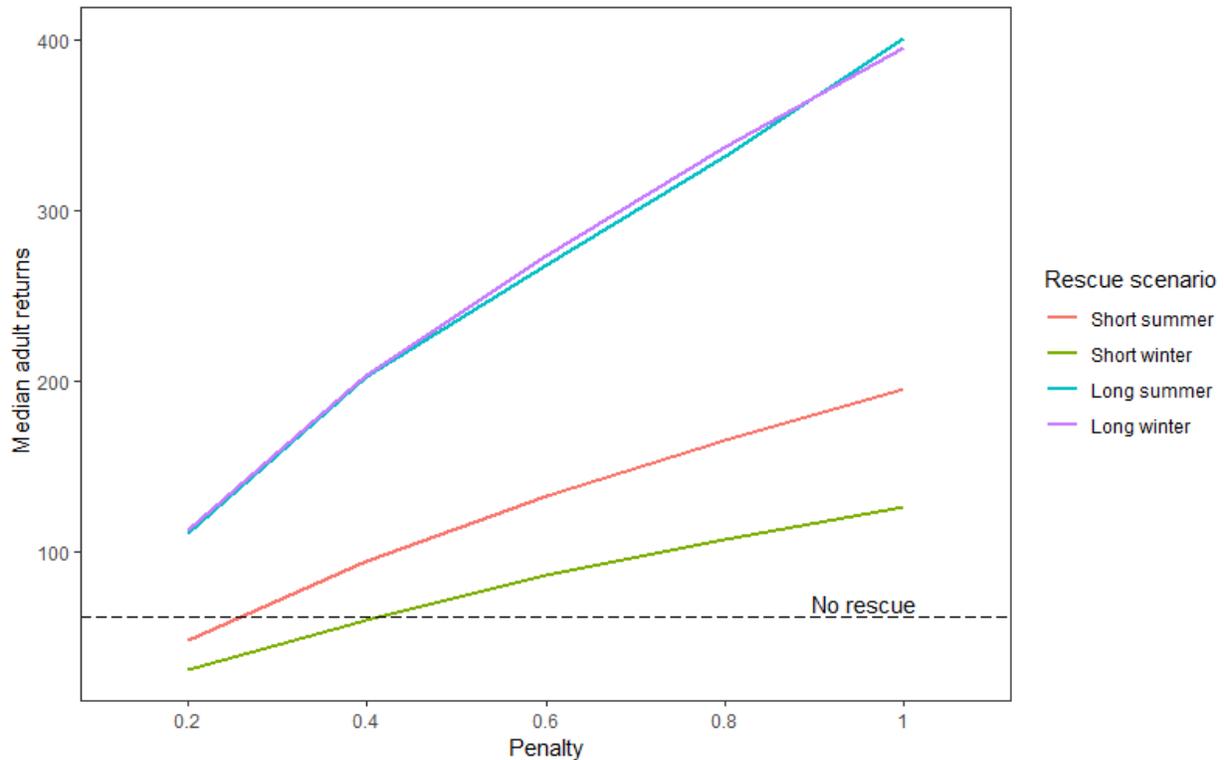


Figure 5: Median adult returns across penalty level and colored by rescue scenarios. Dashed horizontal line is median adult returns for all no rescue simulations.

Effect of Rescue Level

Rescue level (i.e., captive rearing capacity assuming a 40% collection efficiency) interacted with the duration of rescue and penalty level to affect abundance. For long-term rescue, rescue level had a positive effect on adult returns that were strongly dampened by increased penalty. For short-term rescue, the positive effect of rescue level was weaker and became negative when penalty was high (i.e., 0.2). For short-term rescue in winter-limited systems, the effect of rescue level was only positive when penalty was low (>0.6).

Discussion

Water overallocation and climate change are exacerbating the duration and severity of stream fragmentation, threatening the productivity and viability of salmonid populations. In basins where water scarcity issues are unlikely to be resolved, there is an urgent need for management interventions that ameliorate the effects of drought on fish survival. I developed a simulation model to explore how seasonally assisted movement to captive rearing facilities could function as a drought adaptation tool. My findings indicate that fish rescue could have strong positive effects on adult returns and population viability, yet they also identify potential risks (i.e., for short-term rescue if rescue strongly reduces subsequent marine survival). Further, due to the manner by which fish rescue affects adult returns in relation to drought severity, I question whether fish rescue actually functions as a climate adaptation tool or whether it would more accurately be described as stock enhancement, which is already ubiquitous for salmon stocks across the Pacific rim (Mahnken *et al.*, 1998). I would expect a climate adaptation tool to lessen the negative effect of drought on fish abundance, making the slope of this relationship less negative. However, the primary effect of fish rescue was on the intercept of this relationship, meaning fish rescue boosted returns across all drought levels (including no drought) and did not do so in proportion to the severity of drought (Figure 2). Fish rescue functioned most closely to a drought adaptation tool when summer capacity was limiting, and fish were held for summer only. This short-term rescue could produce negative effects on fish returns and population viability if winter capacity was limiting and the effects of captive rearing on marine survival were strongly negative (Figure 6). This worst-case scenario is not implausible; there is rarely data to confirm that drought-impacted streams are actually limited

by summer rather than winter rearing habitat and the negative effects of captive rearing on fitness may be stronger than I anticipated due to mechanisms beyond the scope of my model, such as intergenerational effects of captive rearing (Araki et al. 2007). The strongest positive effect of fish rescue occurred when fish were held long-term, over both summer and winter, in systems where summer capacity was limiting. Captive rearing over two seasons increases survival so strongly compared to that of the wild that it offset even the harshest scenarios of marine survival penalty that were considered. In summary, fish rescue could be an effective way to maintain higher returns of salmon in the face of exacerbated stream drying, but its effect on population dynamics more closely resembles that of hatchery supplementation rather than drought mitigation and could have negative effects in certain contexts that are difficult to rule out.

Model results reflect the particularly strong effect size of captive rearing on freshwater survival. In the wild, freshwater survival is density dependent and can be rather low due to high mortality during the post-emergence transition to feeding (Armstrong & Nislow, 2006), during periods of summer base flow (Hwan et al. 2018), and during periods of winter food limitation (Biro et al. 2005) or flooding (Bell, Duffy & Roelofs, 2001). Survival in the wild varies, but recent work found summer survival rates of ~25% for coho salmon in drought-fragmented streams (Hwan et al. 2018) and a variety of winter studies report survival rates ranging from ~5-60% (Quinn & Peterson, 1996; Solazzi *et al.*, 2000; Ebersole *et al.*, 2006, 2009; Wigington *et al.*, 2006). Thus fish rescue likely generates a ~4-fold increase in survival for summer-only programs, and potentially a > 10-fold increase in cumulative survival for year-round rescue programs. The extent to which this dramatic increase in freshwater survival translates into

increased adult returns depended on three interacting factors: (1) the penalty of rescue on survival at subsequent life stages (2) the captive rearing duration (i.e., summer only vs. summer and winter), and (3) the season that limited rearing capacity (i.e., summer vs, winter-limited).

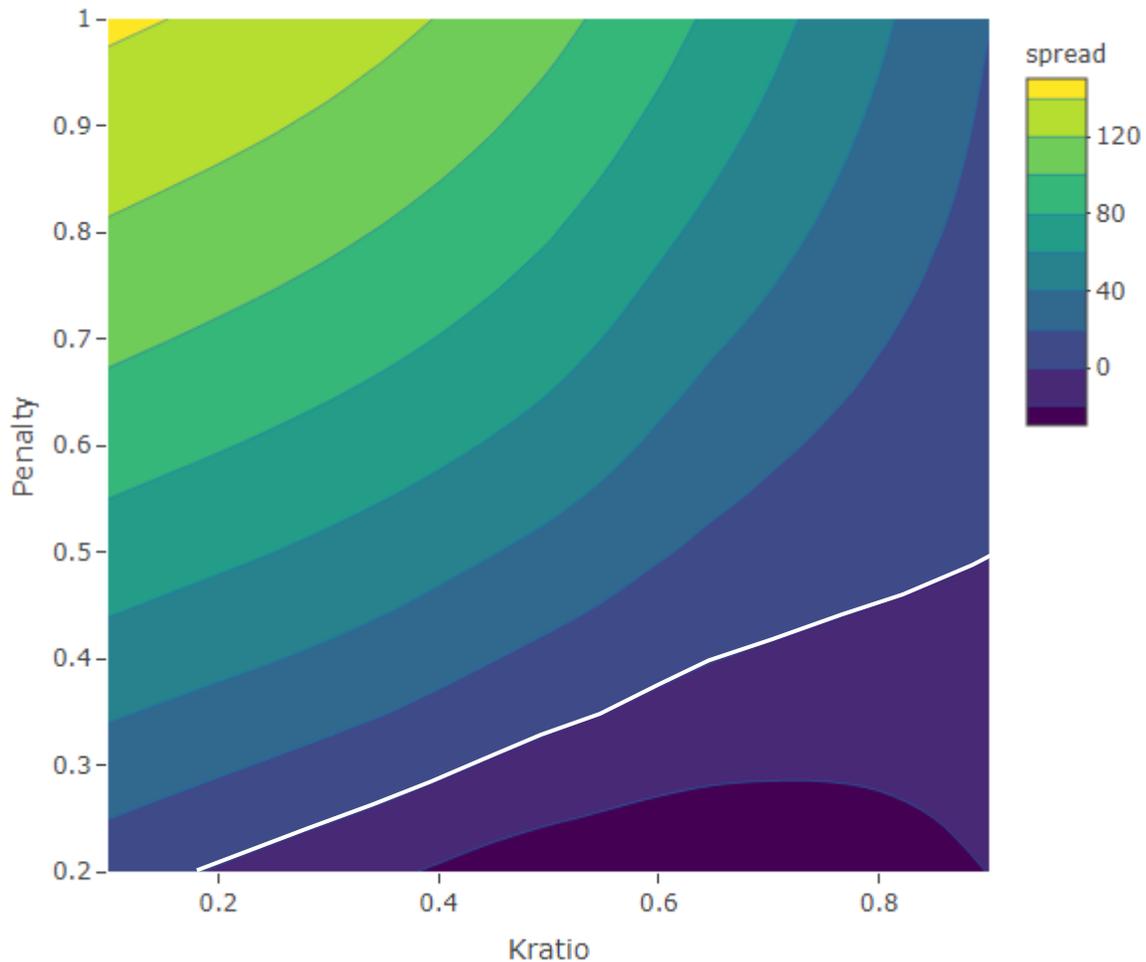


Figure 6. The difference in adult returns for short-term, moderate rescue (15,000 fish) and no rescue simulations. Kratio represents seasonal limitations, where values <0.5 indicate a summer-limited system, and values >0.5 indicate a winter-limited system. Penalty refers to the reduction in marine survival as a consequence of rescue. The only negative effect of rescue (darkest two colors below the white line) occurred for the most severe penalties ($\sim 0.4-0.2$) where adult returns for rescue simulations were less than those for no rescue.

Fish rescue had the strongest effect when fish were held for summer and winter (i.e., one year). This was not only because survival rates were elevated across an additional life stage, but also because the captive reared fish were released after the density dependent portion of the life cycle. Releasing fish after summer rearing in captivity causes them to compete with wild fish during the winter. This can reduce population productivity if the rescued fish have substantially lower survival as adults, particularly if overwinter habitat is limiting, in which case summer rescue increases the overabundance of fish headed into the winter survival bottleneck and effectively replaces wild fish with captive reared individuals that have lower fitness as adults. It is plausible that a stream could exhibit conspicuous summer fragmentation yet also have poor overwinter habitat that is the actual bottleneck to production. Indeed the survival rates reported by Hwan *et al.* (2018) for drought years in fragmented streams exceed many published values for winter survival. The negative effects of fish rescue that we observed would likely be stronger if overwinter survival was size-dependent, as is often reported (Quinn & Peterson, 1996; Ebersole *et al.*, 2006; Pess *et al.*, 2011). Fish have the physiological capacity to feed at much higher levels than they achieve in the wild (Armstrong & Schindler, 2011), so captive rearing with *ad libitum* feeding can dramatically increase growth and condition. It is possible that summer rescue results in large individuals that outcompete wild fish during winter, but I did not consider such scenarios because I know of no studies measuring how seasonal captivity affects size-dependent winter survival.

While there is strong debate over the role of hatcheries in salmon conservation, fish rescue programs have not attracted similar controversy, partly because of their small scale, but likely also because they are putatively drought-adaptation programs rather than tools for

fisheries enhancement. However, the plot of adult returns as a function of drought severity and rescue level (Figure 2) suggests that the quantitative effects of fish rescue are not consistent with drought adaptation. For example, in the case of long-term rescue in a summer-limited system (i.e., the scenario that Northwest Fish Rescue may represent), rescuing fish always increases returns, but it does not reduce the negative effect of drought on returns. This is because fish rescue creates a novel life-cycle pathway that is insensitive to the constraints of freshwater rearing but does not improve conditions for fish in the natural life-cycle pathway. Even at rescue levels lower than those currently in practice by existing rescue programs such as NWFR, captive survival dominates the life-cycle pathway and captive-reared individuals become a greater proportion of the population, such that the threat of drought to wild fish makes a small reduction in total fish abundance. Thus, fish rescue would more accurately be described as a form of hatchery enhancement to fish production, rather than a drought mitigation tool. In the mid-Columbia River Basin, hatchery programs are categorized as either integrated conservation programs, safety-net programs, or harvest augmentation programs (Hillman *et al.*, 2013). I argue that fish rescue emulates the integrated conservation type program as it increases production and more closely aligns with this hatchery-type program than a drought mitigation tool.

The severity of drought impacts varies among locations and through time, and managers will likely weigh the costs and benefits of rescue differently depending on their local context. When fish become stranded or isolated in poor quality habitat, simply relocating fish to adjacent continuous habitat may be a low cost and low risk option. This approach is appealing because it minimizes fish handling and reduces any known or unknown consequences of

captive rearing. However, it may not be effective if summer rearing capacity is limiting because moving fish into already occupied areas will increase density and could reduce growth and survival if these areas are density dependent. However, this method could be effective if fry spatial distributions are strongly limited by dispersal and there are underutilized habitats that translocation could help fill to capacity. Intermittent streams contain crucial rearing habitat for juvenile salmonids (Wigington *et al.*, 2006) and pockets of fragmented habitat may retain sufficient size and quality (Hwan *et al.*, 2018), in which case, intervention may not be needed. More research on the fate of fish in fragmented habitats and the ability of fish to disperse across networks prior to stream drying would help elucidate the potential benefits of in-stream translocations.

If continuous, non-fragmented habitat is not readily available, captively rearing fish during the summer low flow conditions could be the only rescue option. This strategy is intuitively attractive because it reduces time in captivity, but it could also exacerbate density dependence if winter rearing capacity is limiting, which is often difficult to determine. There is uncertainty over how rescued fish interact with wild fish, though there is some indication that captively reared fish may exhibit greater size, aggression, and dominance that outweighs any prior resident advantage of naturally-reared fish (Rhodes & Quinn, 1998). However, a study with Atlantic salmon suggests that naturally-reared wild fish may dominate over wild fish that have been hatchery-reared (Metcalfe, Valdimarsson & Morgan, 2003). The extent of domestication on dominance behavior depends on the captive rearing environment (Ruzzante, 1994). Additionally, minimizing hatchery time may reduce behavioral differences between wild

and hatchery-reared fish (Jackson & Brown, 2011), and captive rearing duration may influence the magnitude of rescue effects.

Alternatively, holding fish for both summer and winter may be an option when both summer and winter rearing capacity are low due to water overallocation and habitat degradation. This strategy effectively acts as a low and high flow rescue program and had the highest numerical response in adult returns. However, long-term rescue may increase survival and capacity far above natural levels, and may lead to multiple generations affected by captive rearing. Araki *et al.* (2007) found that fish raised for one generation in a hatchery had 62.5% of the fitness of wild fish, dropping 37.5% per captive-reared generation. If similar trends exist for rescued fish, then continually rescuing the offspring of previously rescued fish could magnify the negative effects of rescue. This may manifest in lower antipredator response (Jackson & Brown, 2011), increased stray rates (Schroeder, Lindsay & Kenaston, 2001), and lower reproductive success (Thériault *et al.*, 2011). Rescue of high fractions of the population could also inhibit natural selection for phenotypes that increase survival in the wild during drought (e.g., by migrating to different summer habitats) (Everest, 1973), but rescue may keep a population viable until conservation efforts can resolve the underlying limitation to natural production.

Fish rescue is a tempting strategy for managers responsible for dwindling salmonid populations threatened by ecological drought. The sight of ESA-listed fish dying *en masse* as fragmented pools dry up makes inaction seem irresponsible. However, this history of conservation is filled with decisions that seemed urgently needed at the time, but ultimately proved ineffective and often difficult to reverse. I hope that the model results illustrate the

potential benefits and risks of fish rescue to managers considering this intervention and help them interpret the results of existing programs. Managers should expect that fish rescue can increase adult returns, supporting the claims made by groups such as Northwest Fish rescue. However, as Lopez Arriaza *et al.* (2017) found, rescue can lead to the majority of individuals being captively reared and poses risks to the wild populations if captively reared fish have reduced fitness and compete with wild fish. Fish rescue for multiple seasons functions more like a hatchery enhancement program than a drought adaptation tool, so its potential effects on adult returns should be evaluated with caution. However, as ecological drought intensifies due to climate change, some stocks will likely go extinct without management intervention and forms of fish rescue may be the only way to method available for maintaining the viability and genetic diversity of these populations.

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