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i. **Title**

Modeling the reestablishment of coho salmon (*Oncorhynchus kisutch*) in Klamath River tributaries after dam removal

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v. **Running Title**

Coho salmon reestablishment in Klamath River tributaries

vi. **Abstract and Keywords**

The planned removal of four dams on the Klamath River (anticipated 2024) will be the largest river restoration effort ever undertaken on the planet. Dam removal will restore access to >50 km of the Klamath River mainstem for coho salmon, but mainstem habitat may not be suitable for rearing juvenile coho salmon. Instead, small tributaries may provide most rearing habitat for reestablishing coho salmon. We used four approaches to evaluate six Klamath River tributaries above existing dams to assess their potential to support juvenile coho salmon: 1) We measured summer temperature regimes and evaluated thermal suitability. 2) We applied an Intrinsic Potential (IP) model to evaluate large-scale geomorphological constraints on coho salmon habitat. 3) We used the Habitat Limiting Factors Model (HLFM) to estimate rearing capacity for juveniles given current habitat conditions. 4) We developed an occupancy model using data from reference tributaries to predict coho salmon rearing distribution. All six streams had summer temperatures cooler than the mainstem Klamath River. However, five of the streams have barriers that will restrict coho salmon to within 5 km of the confluence with the Klamath River and two were disconnected mid-summer. Despite these constraints, the tributaries will likely produce coho salmon. Most streams had high IP in their lower reaches, the HLFM model estimated a total capacity of 105,000 juvenile coho salmon, and the occupancy model predicted juvenile coho salmon will rear throughout the accessible reaches. Protection and habitat enhancement for these tributaries will be important for coho salmon reestablishment post-dam removal.

Keywords: Klamath River, Dam Removal, Coho Salmon, Occupancy, Reestablishment

## vii. Main text

### Introduction

For anadromous species, impassable dams eliminate access to habitat, decreasing the species' abundance (Ugedal et al. 2008). Dam removal has proven an effective restoration technique globally, increasing accessible habitat to Pacific and Atlantic ocean salmon stocks and other diadromous fishes. In France, the removal of the Maisons-Rouges dam (3.8 m high) on the Vienne River in 1999, allowed allis shad (*Alosa alosa*), sea lamprey (*Petromyzon marinus*), and Atlantic salmon (*Salmo salar*) to reestablish upstream within a year of decommissioning (Basilico 2019). In the United States, removing dams has led to increased abundances of anadromous fishes throughout the Pacific Northwest (McMillan et al. 2019, Allen et al. 2016, Schroeder et al. 2012). For example, dam removal and active relocation of adult hatchery coho salmon (*Oncorhynchus kisutch*) to small tributaries after the Elwha River dam removals led directly to naturally-spawned smolt production in previously inaccessible tributaries (McMillan et al. 2019). Dam removal allows rapid reestablishment of coho salmon even in the absence of re-introduction of adults: coho salmon naturally reestablished in reaches above a former dam site on the Little White Salmon River only four years after dam removal (Jezorek and Hardiman 2018) and they reestablished the Cedar River immediately after access was restored by installation of fish passage (Anderson et al. 2008).

Most dam removal projects to date have targeted small old dams (< 3 m) and have primarily occurred in North America and Europe (Ding et al. 2019). The planned removal of four large dams (height range: 8 – 53 m) on the Klamath River, anticipated in 2024, will be the largest dam removal project ever undertaken in the world (Figure 1). Klamath dam removal will restore access to spawning and rearing habitat for coho and Chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*Oncorhynchus mykiss*), and Pacific lamprey (*Entosphenus tridentatus*). Of these, only coho salmon are currently listed on the federal Endangered Species Act in the Klamath River basin. Completion of the Klamath River dam removal project will be globally significant and provide a precedent for other large dam removal projects currently underway such as the Kangaskoski dam on the Hiitolanjak River in Finland and the Vezins dam on the Sélune River in France.

**INSERT FIGURE 1**

The four impassable Klamath River dams that are scheduled for removal block access to hundreds of kilometers of historic spawning habitat for anadromous species, including major tributaries to Upper Klamath Lake in the headwaters of the basin. However, available evidence indicates that coho salmon were historically restricted to the Klamath Basin downstream of Upper Klamath Lake (Hamiltion et al. 2005). While the area downstream of Upper Klamath Lake includes only 50 km of main stem habitat, juvenile coho salmon rearing in the Klamath River generally rear in smaller tributaries due to the extreme seasonal flows and temperatures in the main stem. In this study, we assess the potential for tributaries of the Klamath River above the existing dams but within the historic distribution of coho salmon to support the production of coho salmon following dam removal

**INSERT FIGURE 2**

We assessed six Klamath River tributaries upstream of Iron Gate Dam (IGD), the current upstream limit to anadromy (Figure 2). The streams that we selected are the six largest tributaries that are above the dams and within the known historical distribution of coho salmon. We sought to answer the question: What is the potential of the six tributaries to support production of coho salmon after dam removal? We focused our research on evaluating summer rearing habitat for juvenile coho salmon as it is likely that summer habitat availability will constrain coho salmon production in these relatively warm, inland streams near the southern range limit for coho salmon (National Research Council 2004).

We used four complementary techniques to assess potential coho salmon habitat above the Klamath River dams: an assessment of summer water temperature and three physical habitat models. Evaluating water temperature was important because previous studies in the Klamath River basin have identified summer temperature as a key constraint on juvenile coho salmon summer rearing distribution (Belchick 2003, Deas et al. 2006, Chiaramonte 2016, Sutton et al. 2007, Stenhouse et al. 2012). Previous work has also shown that large-scale coho salmon smolt production can be predicted from physical habitat characteristics (Sharma and Hilborn 2001) and a large amount of literature emphasizes the importance of instream habitat structure for juvenile coho salmon (Reeves 1989, Nickelson et al. 1992, Quinn and Peterson 1996, Burnett et al. 2003, Shirvell 1990, Anlauf-Dunn et al. 2014). The three models we used to assess habitat suitability for coho salmon each had a different purpose. We used an Intrinsic Potential (IP) model to evaluate large-scale geological and hydrological constraints on coho salmon habitat (Agrawal et al. 2005), a Habitat Limiting Factors model (HLFM) to estimate rearing capacity for juveniles given current habitat conditions (Nickelson 1998), and an occupancy model using data from our reference tributaries to predict small-scale coho salmon rearing distribution in the streams after dam removal.

## Methods

### Summertime Temperature Variation

We recorded a time-series of thalweg temperature for tributaries above IGD. We installed sensors near the tributary confluence with the mainstem Klamath River. We installed additional sensors upstream to the limit to anadromy in each tributary, but for simplicity we only include the data for the location near the confluence here. Upstream sensors provided similar results within each stream but were generally cooler. We deployed sensors from mid-June 2018 to late September 2018 (Jenny, Fall, and Shovel Creeks) and mid-May 2019 to late-October 2019 (all creeks). Sensors recorded temperature at 60-minute intervals. We compare tributary temperatures to mainstem temperatures from the same time period acquired from the USGS gaging station at Keno Dam, near the Spencer Creek confluence.

There are no empirical studies of thermal physiology of Klamath River coho salmon, but there are many studies examining their habitat use in relation to temperature. Juvenile coho salmon in the Klamath River clearly avoid warm summer temperatures and congregate in cool-water refugia (Belchick 2003, Deas et al. 2006, Chiaramonte 2016, Sutton et al. 2007). Based on a literature review and field observations in the Shasta River (a major Klamath River tributary), Stenhouse et al. (2012) identify temperatures >15.6 °C as suboptimal for growth and temperatures >20.3 °C as detrimental. We used these temperatures as an initial screen for suitability. However, juvenile coho salmon can tolerate temperatures well outside the optimal range, particularly if there is consistent cooling at night (Jeffres et al. 2009) or if food is not limited (Lusardi 2020). Therefore, we treat these temperature criteria as guidelines rather than hard rules for future coho utilization.

Rather than relying on instantaneous temperatures to inform assessments, Welsh et al. (2001) suggest that integrated metrics such as Maximum Weekly Average Temperature (MWAT) are better predictors of coho salmon distribution or Maximum Weekly Maximum Temperature (MWMT). We also present the MWAT and MWMT values for our sites to facilitate comparison with other studies.

### Habitat Models

We used three models to estimate coho salmon summertime rearing potential: the IP model, the HLFM, and a single-season occupancy model. The IP model estimates the stream's "potential" to exhibit habitat features conducive to juvenile coho salmon rearing based on broad-scale landform and hydrological characteristics (Burnett et al. 2003). The HLFM approach relies on habitat unit classifications and physical habitat characteristics at the scale of individual habitat units (Nickelson et al. 1998) to predict capacity using fish density-habitat type relationships observed in stream inventories for coastal Oregon (Nickelson et al. 1992).The occupancy model uses the relationship between coho salmon presence-absence and habitat characteristics at the reference sites to estimate the probability that a given site is occupied (Mackenzie et al. 2002, Kery and Schaub 2011).

The results of these analyses provided complementary information. The IP model identifies streams which, under ideal conditions and restored habitat, could support large populations of coho salmon. The HLFM model predicts the expected capacity for coho salmon under current habitat conditions. The occupancy model predicts the distribution of coho salmon within each stream under current conditions using habitat relationships developed within the Klamath Basin and nearby systems.

*Intrinsic Potential Model*

The IP model estimates the potential for stream sections to provide suitable habitat for coho salmon using associations between fish presence or abundance and stream geomorphological characteristics (Burnett et al. 2003). Uniquely, IP models do not require direct measurements of stream habitat features. Instead, IP models use general, large-scale landscape attributes favorable to habitat formation to offer an assessment of the potential for a stream to produce suitable habitat at local or regional scales. Management authorities commonly use IP models to direct restoration funds, plan recovery efforts, and to estimate historic ranges of fishes (Agrawal et al. 2005, Busch et al. 2013, NMFS 2014). In application, the intrinsic potential of a stream reach represents its relative historical potential as pristine habitat or the current habitat potential neglecting anthropogenic disturbances (Sheer et al. 2009).

The IP model assumes that three landscape and hydrological attributes (mean annual discharge, channel gradient, and valley constraint) interact in creating channel morphology and ultimately determining salmon production (Burnett et al. 2003). We calculated IP at the scale of reaches within each stream based on Nagel et al. (2010); with reach lengths from 160-810 m depending on large-scale stream gradient (shorter reaches in steeper gradient). Annual discharge measurements were not available for all study streams and discharge in some study streams is affected by diversions. To maintain consistency across sites and estimate discharge independent of diversions, we calculated the mean annual stream discharge for study streams using a multiple linear regression developed for ungaged sites in eastern Oregon (Lorensen et al. 1994). We calculated drainage area for each reach using the United States Geological Survey (USGS) StreamStats version 4.0 online delineation tool (Ries et al. 2017). We calculated the discharge at the bottommost and uppermost points of each stream's IP length and used a linear model to calculate discharge of discrete IP reaches. We used 10-m resolution digital elevation models in a geographic information system to calculate channel gradient ($G$) and an index of valley constraint. We calculated the valley width index ($V$) as the ratio of valley-floor width to active-channel width for a given stream reach (Burnett et al. 2003) using established regression models (Burnett et al. 2003, see Ramos 2020 for details).

To calculate IP for each reach, we first converted each attribute (i.e. mean annual discharge, gradient, and valley constraint) to a proportional suitability score (1=ideal habitat, 0=unsuitable) using published suitability curves for coho salmon (Agrawal et al. 2005). The reach's IP is the geometric mean of the three suitability scores. Higher intrinsic potential values indicate a greater potential to produce high quality fish habitat (Burnett et al. 2007). To represent IP at the scale of the entire tributary, we calculated the weighted IP kilometers of each stream by multiplying each reach's length by its calculated IP value and then calculating the sum of all reaches within the stream. We also report density-based spawner escapement targets based on densities of 40 individuals per IP km, which agencies use as a salmon population restoration benchmark for small watersheds assuming no anthropogenic disturbance and full restoration of geomorphological processes (NMFS 2014).

*HLFM Model*

Nickelson's (1998) HLFM estimates potential rearing capacity for coho salmon based on pre-established capacity population densities multiplied by surface area of available habitat. The approach includes different densities for each habitat type, season, and life stage. As no data are available for the Klamath River basin, the HLFM densities we used were calibrated based on maximum densities observed in Oregon coastal streams. Coho salmon in coastal streams may face different constraints from interior Klamath River tributaries that we surveyed, but we assumed that the maximum densities across different types of physical habitat would be similar. For summer rearing, the HLFM capacities for each habitat type in individuals/$m^2$ are as follows: 0.0 (cascades), 0.6 (rapids), 0.8 (plunge pools), 1.0 (trench pools), 1.2 (riffles), 1.3 (both lateral and mid-channel scour pools), 2.6 (dammed pools and beaver ponds), 2.8 (alcoves), and 5.8 (backwater pools). HLFM also estimates spawning capacity based on the area of suitable gravels assuming 830 eggs/$m^2$ of spawning gravel. To predict which life stage capacity will limit the population, HLFM projects smolt production from each life stage's capacity assuming egg to parr survival of 0.43 and parr to smolt survival of 0.70).

To obtain estimates of habitat area for the HLFM, we conducted longitudinal habitat surveys in each tributary from the confluence with the mainstem Klamath River up to the first likely barrier for adult coho salmon migration. We surveyed habitats from mid-June 2018 through mid-August 2018 for Beaver, Jenny, Fall, and Shovel creeks and from early-June 2019 through late-July 2019 for Bogus, Scotch, and Spencer creeks. We were unable to perform habitat surveys on Camp Creek due to inaccessible private property. In each tributary, we selected a randomized subset of approximately fifty percent of the available 200-m reaches selected 15 percent of available reaches on Spencer Creek due to its length. Lawrence and Quartz creek data were collected by the CDFW and were not aggregated into 200-m reaches and included only pools.

We developed a habitat survey protocol based on methods described by the USFS (Overton 1997) and CDFW (Garwood and Ricker 2013, Garwood and Ricker 2017). We modified these survey protocols to provide data required for the Habitat Limiting Factors Model (HLFM) while including methods consistent with CDFW surveys so that we could combine data sets for occupancy modeling. Survey crews walked the length of each reach and recorded the location and size of discrete habitat units defined by breaks in channel width, depth, and morphometrics (runs, riffles, pools). We classified multiple habitat units within one stream cross-section when multiple discrete habitat types described greater than one third of the channel wetted width.

We recorded channel wetted width (m), habitat unit length (m), maximum depth (cm), available spawning gravel ($m^2$), and instream cover area ($m^2$) for each non-riffle type habitat unit and a subset of riffle-type habitat units (every second or third). We visually estimated instream cover (area of the habitat unit occupied by cover suitable for fish refuge) to the nearest 0.25 $m^2$. Instream cover included but was not limited to: bank undercutting, woody debris, boulder undercutting, root wads, aquatic and overhanging terrestrial vegetation., including all features >0.25 $m^2$ within the wetted channel or <1.0 m above the water's surface.

*Estimation of Occupancy*

We used an occupancy model based on actual observations of habitat use in our reference streams to predict the small-scale distribution of coho salmon in the study streams. We selected four reference sites to supply this data, two Klamath River tributaries below the existing dams (Beaver and Bogus creeks, we conducted these surveys) and two in other river basins with similar climate and flow regimes (Lawrence and Quartz creeks, these surveys were conducted by CDFW cooperators; Figure 3). The occupancy model extends the spatial scale of our analysis to finer resolution and, unlike the IP and HLFM models, is parameterized with observations of coho salmon habitat associations within the Klamath River basin.

**INSERT FIGURE 3**

We determined occupancy at the scale of individual habitat units using snorkel surveys. During HLFM habitat surveys on reference streams we flagged every other unit of each habitat type for subsequent snorkeling. CDFW data from Lawrence and Quartz creeks only included pool-type habitat units that fit characteristics defined in their field protocol (Garwood and Ricker 2013). In each selected habitat unit, we performed two-pass snorkel surveys. On each pass, a snorkeler would enter the unit at the downstream end and move slowly upstream, systematically searching for fish. Each individual fish was identified to species and recorded on a cuff. After a 5-10 minute interval, a second snorkeler would repeat the protocol. Snorkelers did not communicate regarding fish counts or species during surveys to maintain independence.

Traditional species distribution modeling ignores detection probability, resulting in estimates of "apparent species distribution" rather than real species distribution (Mackenzie et al. 2002, Kery and Schaub 2011). Using the independent observations of the same unit, occupancy models estimate the probability of occupancy and address issues of imperfect detection (Kery and Schaub 2011). The ecological component of an occupancy model corresponds to the probability that a site is occupied; the observational component corresponds to the probability of detecting the target species at a site on a given survey given its presence (Kery and Schaub 2011). The structure of occupancy models allows assessment of the effects of measured covariates on both occupancy and detection.

We selected a subset of habitat characteristics to include as potential predictors in the occupancy model based on a priori hypotheses. We hypothesized that detection depth might affect detection probability (Albanese et al. 2011). We hypothesized that occupancy of juvenile coho salmon at the habitat-unit scale might vary with: percent instream cover, surface area, HLFM capacity multiplier, and a categorical effect for the presence of a hatchery in the watershed. Cover might affect occupancy because juvenile coho salmon use instream cover structures such as large woody debris jams, boulder, and undercuts to minimize energy expenditures while maintaining advantageous drift feeding position (Mundie 1969, Fausch 1993). Larger surface area logically provides more opportunity for juvenile coho salmon occurrence. We included the HLFM capacity multiplier for each habitat unit as a continuous proxy for habitat type (i.e. HLFM capacities differ for pool, riffle, run) as coho might be more likely to occur in habitat units with higher habitat capacity. We included a categorical term for the presence of a hatchery to account for the effect of the hatchery on Bogus Creek. Streams in close proximity to hatcheries exhibit an exponential decay relationship with abundance of hatchery salmonids with distance from hatchery (Brenner et al. 2012).

Temperature strongly affects the summer distribution of juvenile coho salmon. However, temperature did not vary much between individual habitat units within tributaries. Further, we did not have temperature data available for the CDFW reference streams. For the Klamath Basin reference sites, examination of potential temperature effects was confounded by a large effect of proximity to the Iron Gate Fish Hatchery: Bogus Creek, adjacent to the hatchery, had consistently warmer water temperatures than other streams. We therefore did not include temperature as a predictor of small-scale distribution in the occupancy model.

We fit the occupancy model using program PRESENCE version 12.39. Coho salmon presence or absence on each snorkel pass was the response and habitat characteristics were included as potential predictors of coho salmon occupancy and detection probability. We tested all potential covariates for collinearity using the variance inflation factor method. No collinearity issues existed. We standardized covariates using the z-score method prior to model fitting for scaling.

We used Akaike's Information Criterion (AIC) for model selection. We performed the model selection in two phases, first for the detection component and second for the occupancy component. During model selection for the detection component, we used the null model for the occupancy component. During model selection for the occupancy component, we kept the detection component fixed at the detection model with the lowest AIC. We did not include any interactions among the potential predictors. We selected the simplest model within 2 AIC units of the top model.

Once we selected a model, we performed a cross validation analysis to test the utility of the model for predicting coho salmon distribution at sites that are not included in the model input. For model validation, we removed Lawrence and Quartz creeks from the dataset and re-ran the occupancy analysis using the covariates from the "best" model and the input data for Beaver and Bogus creeks. We used the model results to predict coho salmon distribution in Lawrence and Quartz creeks and assigned each occupancy prediction to "correct" or "incorrect". Model predictions were classified as correct if the model predicted occupancy probability of $> 0.5$ and the unit was occupied or if the model predicted occupancy probability of $< 0.5$ and the unit was unoccupied. We used similar cross validation using Lawrence and Quartz creeks as input to predict occupancy in Beaver and Bogus creeks. However, for this analysis, we evaluated the accuracy of model predictions separately for Beaver and Bogus, because the input data set did not contain a categorical predictor category representing the hatchery effect in Bogus Creek.

**Results**

All study streams except for Spencer Creek had substantial natural barriers within 5 km of the confluence with the Klamath River. These barriers will prevent anadromous adults from accessing most of the watershed. Jenny, Fall, and Shovel creeks had additional, smaller anthropogenic and natural barriers closer to the confluence that could prevent establishment of the stream by non-natal juvenile coho salmon that are dispersing in search of summer rearing habitat.

The two smallest tributaries, Scotch and Camp creeks, were reduced to a few disconnected pools by late summer, but we still summarize the results from these streams as they could provide at least seasonal rearing habitat and may provide continuous habitat in wetter years. Below, we present the results for the summer water temperature variance analysis, the HLFM predictions, the overall occupancy model, followed by detailed results for all data types organized by stream, and finally a summary and comparison of results across the study streams.

Water Temperature

All of the streams provided summer temperatures cooler than the main stem Klamath River. Fall and Shovel Creek in particular had cool, stable temperature regimes, likely heavily influenced by groundwater inputs and heavy riparian shading. Jenny Creek had similarly stable temperatures, but less groundwater influence so temperatures were warmer overall. Spencer Creek was warmer and had more temporal variation in temperature, likely associated with more open riparian zone, water diversions, and less groundwater influence. The temperature regimes we measured in Scotch and Camp creeks were affected by drying and disconnection, with temperature measurements reflecting intermittent periods of temperature probes immersion in stagnant exposed pools, small groundwater seeps, and exposure to air as water levels declined, Temperature regimes in Fall and Shovel produced MWAT and MWMT in ranges associated with summer coho salmon use in the Mattole River (Table 1; Welsh et al. 2001).

**INSERT FIGURE 4**

**INSERT TABLE 1**

Intrinsic Potential

The average of the IP suitability scores for each tributary ranged from a low of 0.38 in Jenny Creek to a high of 0.72 in Camp Creek (1=ideal habitat, 0=unsuitable; Figure 5). Extrapolating the IP scores over the length of the IP reaches combined for a total of 20.6 IP km (Figure 5). The density-based spawner escapement targets (Williams et al. 2008) based on 40 adults per IP km combined for a total of 823 adult coho salmon.

All of the study streams had reaches with the highest IP concentrated near the confluence with the Klamath River with the exception of Fall Creek (additional high IP reaches adjacent to the Fall Creek hatchery) and Spencer Creek (patches of high IP throughout).

**INSERT FIGURE 5**

Habitat Limiting Factors

We conducted surveys on 13.4 km of stream habitat and detailed habitat measurements in 740 total habitat units. The average HLFM capacity multiplier weighted by accessible habitat surface area for summertime juvenile coho salmon rearing density ranged from a low of 0.3 individuals/$m^2$ (a habitat type between a cascade and a rapid) in Fall Creek to 1.0 individuals/$m^2$ in Scotch Creek (roughly equivalent to a trench pool) (Figure 6). Although the average HLFM multipliers are low, they are averages and all five tributary streams contained habitat units of higher HLFM multiplier value (pools and slow-water habitats). The HLFM predicted maximum summer rearing capacities ranging from 2,600 to 66,300 summer juvenile coho salmon across the study tributaries (Figure 6) for a total capacity of approximately 105,000 individuals. Summertime rearing habitat capacity was much lower than the HLFM predicted coho salmon parr production based on available spawning gravels in Scotch, Jenny, Fall, Shovel, and Spencer creeks (219,600, 54,600, 97,500, 24,600, and 19,278,200 individuals respectively), indicating that summer rearing habitat is more likely to limit these populations than spawning habitat.

**INSERT FIGURE 6**

Occupancy Model

We conducted habitat surveys and snorkel counts of fish abundance in 81 habitat units in reference streams, with 94 additional units from CDFW surveys. Naive occupancy rates varied across streams; coho salmon were observed by at least one snokeler in 46% of habitat units in Beaver Creek, 83% in Bogus Creek, 38% in Lawrence Creek, and 60% in Quartz Creek. The two snorkelers agreed on observations of coho salmon presence or absence in 83% of pools.

*Model selection*

In initial model selection for the detection probability component, the model that incorporated depth as a coefficient for detection probability performed significantly better than the "null" model based on AIC (Table 2). For the occupancy component, two models that we fit resulted in similar AIC scores: Ψ(Hatchery + SA + Cover), p(Depth) with an AIC of 362.78 and Ψ(Hatchery + SA + Cover + HLFM), p(Depth) with an AIC of 363.57 (SA indicates Surface Area). We selected the Ψ(Hatchery + SA + Cover), p(Depth) as the final model as it is the simplest model within 2 AIC units of the model with lowest AIC (Table 2). The final model's depth coefficient was positively correlated to detection probability (Figure 7). An increase in surface area and percent instream cover increased occupancy probability in the final model (Figure 7). Hatchery presence also increased occupancy probability (Figure 7).

**INSERT TABLE 2**

**INSERT FIGURE 7**

*Occupancy model validation*

The final model refit using solely Bogus and Beaver creek data correctly predicted coho occupancy in Quartz and Lawrence creeks 70% of the time. The final model refit using solely Quartz and Lawrence creek data correctly predicted coho occupancy in Beaver Creek 66% of the time. When predicting occupancy probability in Bogus Creek (hatchery influenced) the streams predicted correct occupancy assignments 25% of the time. Many units that the model predicted would be unoccupied were occupied in Bogus Creek, likely due to the much higher overall densities of coho salmon in Bogus Creek associated with the presence of the hatchery.

*Predictions for Sites above IGD*

We fit the final occupancy model to discrete habitat unit data collected on streams above the IGD. We included the "null" hatchery effect, assuming no hatcheries in the vicinity of the streams. Occupancy probability varied widely within and between tributary streams (Figure 8). Spencer Creek had the highest median occupancy probability (0.54) and Shovel Creek had the lowest median occupancy probability (0.33) (Figure 8). Some streams, although low in median occupancy probability, contained clusters of discrete habitats of high occupancy probability (exceeding 0.7) such as Scotch Creek (five habitat units in the lower 900 m), Jenny Creek (five habitat units in the lower 1600 m,) and Shovel Creek (five habitat units in the lower 3100 m) (Figure 8). Based on the predicted distribution in each stream, we estimate juvenile coho salmon will occupy approximately 96,000 $m^2$ of tributary habitat by surface area, or 48,000-96,000 summer parr at typical rearing densities of 0.5-1 fish per square meter in occupied habitat.

**INSERT FIGURE 8**

Summary by Stream

Both Scotch and Camp Creeks became disconnected in late summer low flows during our study years, although they may be perennial in wetter years. Scotch Creek is steeper and more confined than Camp Creek, leading to lower IP. However, even in our dry survey years, there were large, perennial bedrock-formed pools in Scotch Creek. Based on our measurements, these two small streams may contribute cool water refuge (Figure 4) and access to high IP habitat (Camp) or pool habitat (Scotch) when they are wetted (Table 3).

Jenny Creek is a relatively high-gradient, confined system, leading to low IP. However, a very large median substrate size led to a substantial number of boulder-formed pools that contributed to HLFM capacity in Jenny Creek. Low water temperature suitability (Figure 4, Table 1), high HLFM capacity estimates, low IP, and moderate occupancy probability in Jenny Creek indicates low-moderate suitability for summertime rearing of juvenile coho salmon (Table 3).

Despite very high water temperature suitability (Figure 4, Table 1), the accessible length of Fall Creek is short and habitat is limited by high gradient and valley constraint (Table 3). However, there are patches of suitable habitat near the confluence, including a large beaver colony. These areas could prove valuable for non-natal coho salmon. Further, Fall Creek is the planned location of a coho salmon conservation hatchery operation to facilitate reestablishment of coho salmon, which may lead to increased use of this tributary.

Shovel Creek also has high temperature suitability (Figure 4, Table 1), but has more accessible length than tributaries downstream and lower gradient, and less valley constraint than Fall Creek (Table 3). While anthropogenic habitat alteration, including floodplain disconnection and small barriers, likely limit its current capacity for coho salmon, Shovel Creek has potential to be an important spawning and rearing stream.

Spencer Creek represents the vast majority of the coho salmon rearing habitat from our study tributaries (Table 3). Despite Spencer Creek's low-moderate water temperature suitability (Figure 4, Table 1), the stream has a much larger accessible area, relatively low gradient and low valley constraint, and very abundant spawning gravel. Spencer Creek is by far the largest potential producer of coho salmon among our study streams (Table 3).

**INSERT TABLE 3**

## Discussion

We gained valuable insights into the potential for coho salmon to reestablish in tributaries to the Klamath River after dam decommissioning. Our surveys were the first comprehensive measurements of the available habitat in the six largest, currently inaccessible tributaries of the Klamath River within the historic range of coho salmon. Summing the stream length in each tributary below the anadromy barriers, we found that coho salmon will gain access to at least 33 km of tributary habitat within Scotch, Camp, Jenny, Fall, Shovel, and Spencer creeks in addition to approximately 50 km of mainstem habitat after the dam removal project.

Coho salmon in the Klamath River face a distinct set of challenges compared to coastal populations. Extreme seasonal temperatures are more likely to be a constraint in these arid, interior basins than in coastal systems. Summer temperatures in four of the study streams are in a range that Klamath River coho salmon avoid in summer (Belchick 2003, Deas et al. 2006, Chiaramonte 2016, Sutton et al. 2007). While not immediately lethal, some previous studies suggest that these warmer temperatures are detrimental to growth and potentially survival of juvenile coho salmon (Stenhouse et al. 2012). However, Klamath River coho salmon can survive and grow rapidly at warmer temperatures (e.g. MWAT 18.6°C, MWMT 20.6°C in Lusardi et al. 2020). We suspect that coho salmon reestablishing the study area will exhibit habitat selection and seasonal redistribution strategies similar to extant populations in the Shasta, Scott, and other tributaries below the dams, moving to find cool water at seeps, springs, and tributaries as temperatures increase in summer (Belchik 2003, Deas et al. 2006, Chiaramonte 2016, Sutton et al. 2007). This behavior can lead to very high densities of juvenile coho salmon at cool water sites, emphasizing the potential constraint of summer habitat on production.

Our focus on summer habitat and cool-water sources does not imply that the warmer tributaries and the main stem Klamath River are not valuable habitats. Although coho salmon use of warmer areas in summer may be constrained, warmer locations may be very productive in cooler seasons (Armstrong et al. 2021). Further, even in summer, salmon may be able to capitalize on abundant food resources in warm habitats by exploiting locations near cool water inputs (Brewitt et al. 2017). Whether reestablishing coho salmon can express behavioral strategies and flexible juvenile life histories that allow them to take advantage of the complex habitat and temperature mosaic in the upper Klamath River is a critical area for future research following dam removal.

The three habitat models that we applied converged on similar estimates of potential habitat capacity or abundance. The IP model spawner abundance target for all tributaries combined was 823 adult coho salmon. The juvenile capacity estimate from the HLFM model was 105,000. Translating from summer juveniles to adults requires estimates of parr-smolt survival and smolt-adult survival. While we do not have these estimates for Klamath River coho salmon, as a very rough approximation, applying the parr-smolt survival from the HLFM model (0.7) and smolt-adult survival of 0.01 (Cochran et al. 2019), the juvenile capacity translates to 735 adults. This is less than the IP model target, suggesting that the current habitat conditions do not exhibit the full potential of the watersheds. Extrapolating juvenile abundance from the occupancy model yields an estimate of 48,000-96,000 or up to 672 adults. As expected, this extrapolation of actual abundance from the occupancy model is lower than the capacity estimate from HLFM. Overall, these models suggest potential production on the order of hundreds of adult coho salmon spawners from the study tributaries following dam removal.

Despite the convergence across the approaches, there is considerable uncertainty in the output of our habitat models. The IP is a generic model developed to explain large-scale patterns across the range of coho salmon, not variation within a watershed. The HLFM model is parameterized based on coastal coho salmon streams, not interior tributaries of a large watershed. The occupancy model sample size for tributaries in the Klamath is small and based only on a snapshot of late summer distribution. Further, none of these models account for interactions with other species, food availability, or potentially unique attributes of Klamath River coho salmon. Research to evaluate these biotic determinants of habitat capacity as coho salmon reestablish their historic habitats will be very valuable for informing further Klamath River conservation efforts and other reintroduction and reestablishment programs for coho salmon.

The capacities and spawning targets that we report are not predictions of average future production after dam removal. Actual capacity in any given year will be a function of the interaction between annual seasonal flow conditions and physical habitat. Across years, the long-term expected abundance of coho salmon will depend on both the density-dependent processes that determine habitat capacity as well as density-independent processes that determine productivity for all life stages including marine survival of adults (Mobrand et al. 1997). These factors will lead to annual abundance that varies widely and may yield average abundance well below these estimates based on potential productivity.

Our study focused on potential production from the six largest, currently inaccessible tributaries within the documented historic range of coho salmon in the Klamath River. We did not consider potential production from tributaries higher in the Klamath River watershed (i.e. above Upper Klamath Lake). This decision was based on historical analysis of reported coho salmon distribution (Hamilton et al. 2005) and general information on coho salmon migration distance, but the records may be incomplete, and the habitat has changed considerably since dams were built and a few coho salmon populations do undertake longer migrations (Sandercock 1991). If coho salmon are able to reestablish the tributaries above Upper Klamath Lake, their potential production will be much larger than estimated here. Abundant low-gradient, cool-water habitat in spring streams above Upper Klamath Lake (Wood and Williamson rivers) could support much larger coho salmon production.

The removal of Klamath River dams could contribute to recovery of coho salmon beyond the production arising from fish rearing in newly accessible habitat above the dams. For example, disease is a major source of mortality for coho salmon moving through the main stem Klamath River below the existing dams during juvenile redistribution and smolt outmigration (Som et al. 2019). The primary pathogen, *Ceratonova shasta*, has a complex life cycle including upstream transport in spawning adult salmon and benthic annelids as an intermediate host. Removing the dam should reduce crowding of infected adults below the dam and near the hatchery and may alter the river's flow regime, temperatures, and sediment transport in ways detrimental to the annelid host (Alexander et al. 2014). Reduced disease mortality for juveniles and smolts will increase overall coho salmon abundance in the Klamath River and increase the likelihood that populations reestablish tributaries above the existing dams.

**Conclusions**

This study contributes to the growing body of knowledge of baseline upstream habitat conditions before globally unprecedented, large scale dam decommissioning and to what constitutes suitable summertime rearing habitat for the SONCC coho salmon ESU in warm, inland streams. In tributary streams to the Klamath River within the Klamath Hydroelectric Project area, we found that coho salmon habitat is widely variable. We documented prolific cool water sources that will likely play an important role in supporting reestablishing coho salmon and we identified potential rearing areas, particularly in Spencer Creek, that merit attention for habitat protection and restoration. We hypothesize that newly accessible habitat in the study tributaries will provide substantial rearing and spawning habitat for coho salmon after dam removal.

viii. Acknowledgements

We thank Dr. Bret Harvey and Dr. Mark Henderson with Cal Poly Humboldt for their review, advice and support throughout the project. Thanks to Morgan Knechtle at CDFW, hopefully you will still venture up Jenny Creek with us when the dams come out; Mark Hereford and William Tinniswood at ODFW for their dedication to the upper Klamath; Tommy Williams at NOAA Fisheries for his continued guidance, support, and knowledge of anadromous fishes in the Klamath Basin; and Demian Ebert of PacifiCorp for his help throughout the project. Two anonymous reviewers provided valuable comments. This project could not have been completed without financial support from NOAA Fisheries through the Cooperative Institute for Marine, Earth, and Atmospheric Systems, the Marin Rod and Gun Club, the Sequoia Park Zoo, and Granite Bay Flycasters.

ix. Data Availability Statement

Data available upon request.

x. References

Agrawal, A., R.S. Schick, E.P. Bjorkstedt, R.G. Szerlong, M.N. Goslin, B.C. Spence, T.H. Williams, K.M. Burnett. (2005) Predicting the Potential for Historical Coho, Chinook, and Steelhead Habitat in Northern California. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFSC-379.

Albanese, B., K. A. Owers, D. A. Weiler, W. Pruitt. (2011) Estimating Occupancy of Rare Fishes using Visual Surveys, with a Comparison to Backpack Electrofishing. Southeastern Naturalist. 10(3): 423–442.

doi:10.1656/058.010.0304

Alexander, J. D., S.L. Hallett, R.W. Stocking, L. Xue, J.L. Bartholomew. (2014). Host and parasite populations after a ten year flood: *Manayunkia speciosa* and *Ceratonova (syn Ceratomyxa) shasta* in the Klamath River. Northwest Science, *88*(3), 219-233.

doi:10.3955/046.088.0305

Allen, M. B., R. O. Engle, J. S. Zendt, F. C. Shrier, J. T. Wilson, P. J. Connolly. (2016) Salmon and Steelhead in the White Salmon River after the Removal of Condit Dam–Planning Efforts and Recolonization Results. Fisheries. 41(4): 190–203.

doi:10.1080/03632415.2016.1150839

Anderson, J. H., P. M. Kiffney, G. R. Pess, T. P. Quinn. (2008). Summer distribution and growth of juvenile coho salmon during colonization of newly accessible habitat. Transactions of the American Fisheries Society, 137(3). 772-781.

Anlauf-Dunn, K.J., E.J. Ward, M. Strickland, K. Jones. (2014) Habitat connectivity, complexity, and quality: predicting adult coho salmon occupancy and abundance. Canadian Journal of Fisheries and Aquatic Sciences. 71(12): 1864-1876.

doi:10.1139/cjfas-2014-0162

Armstrong, J.B., A.H. Fullerton, C.E. Jordan, J.L. Ebersole, J.R. Bellmore, I. Arismendi, B.E. Penaluna, and G.H. Reeves. (2021) The importance of warm habitat to the growth regime of cold-water fishes. Nature Climate Change. 11(4):354-361.

doi:10.1038/s41558-021-00994-y

Basilico, L. (2019) Meetings: Dam Removal, The Sélune River free to run. AFB, 5 square Félix-Nadar, 94300 Vincennes, France.

Belchik, M.R. (2003) Use of thermal refugial areas on the Klamath River by juvenile salmonids; Summer 1998. Yurok Tribal Fisheries Program Technical Report. 1-36.

Brenner, R.E., S.D. Moffitt, W.S. Grant. (2012) Straying of hatchery salmon in Prince William Sound, Alaska. Environmental Biology of Fishes. 94:179–195

doi:10.1007/s10641-012-9975-7

Brewitt, K.S., E. M. Danner, J. W. Moore. (2017) Hot eats and cool creeks: juvenile Pacific salmonids use mainstem prey while in thermal refuges. Canadian Journal of Fisheries and Aquatic Sciences. 74(10): 1588–1602.

doi:10.1139/cjfas-2016-0395

Burnett, K.M., G.H. Reeves, D. Miller, S. Clarke, K. Christiansen, K. Vance-Borland. (2003) A First Step Toward Broad-Scale Identification of Freshwater Protected Areas for Pacific Salmon and Trout in Oregon, USA. Proceedings of the World Congress on Aquatic Protected Areas, Cairns, Australia, August 2002.

Busch, D.S., M. Sheer, K. Burnett, P. McElhany, T. Cooney. (2013) Landscape-Level Model to Predict Spawning Habitat for Lower Columbia River Fall Chinook Salmon (Oncorhynchus tshawytscha): Intrinsic Potential Model for Spawning Fall Chinook. River Research and Applications. 29(3): 297–312.

doi:10.1002/rra. 1597

Chiaramonte, L.V., R. A. Ray, R. A. Corum, T. Soto, S. L. Hallett. (2016) Klamath River Thermal Refuge Provides Juvenile Salmon Reduced Exposure to the Parasite Ceratonova shasta. Transactions of the American Fisheries Society. 145(4): 810-820.

doi:10.1080/00028487.2016.1159612

Cochran, S. M., S. Ricker, C, Anderson, S.P. Gallagher, D.M. Ward. (2019). Comparing abundance-based and tag-based estimates of coho salmon marine survival. Fisheries Management and Ecology. 26(2), 165-171.

doi:10.1111/fme.12339

Deas, M.L., S.K. Tanaka, J.C. Vaughn. (2006) Klamath River Thermal Refugia Study: Flow and Temperature Characterization. Final Project Report. Report of Watercourse Engineering, Inc. to the US Bureau of Reclamation, Klamath Area Office, Klamath Falls, OR.

Ding, L., L. Chen, C. Ding. (2019). Global Trends in Dam Removal and Related Research: A Systematic Review Based on Associated Datasets and Bibliometric Analysis. Chinese Geographical Science. 29: 1-12.

https://doi.org/10.1007/s11769-018-1009-8

Fausch, K.D. (1993) Experimental analysis of microhabitat selection by juvenile steelhead (Oncorhynchus mykiss) and coho salmon (Oncorhynchus kisutch) in a British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences. 50: 1198–1207.

doi:10.1139/f93-136

Garwood, J., S. Ricker. (2013) Juvenile Coho Salmon Summer Spatial Structure Monitoring Survey Protocol. California Department of Fish and Wildlife. Coastal Salmonid Monitoring Program.

Garwood, J., S. Ricker. (2017) Salmonid Spatial Structure Monitoring Survey Protocol: Summer Snorkel Survey Methods. California Department of Fish and Wildlife. Coastal Salmonid Monitoring Program.

Hamilton, J.B., G.L. Curtis , S.M. Snedaker, D.K. White. (2005) Distribution of Anadromous Fishes in the Upper Klamath River Watershed Prior to Hydropower Dams—A Synthesis of the Historical Evidence, Fisheries, 30(4): 10-20

doi: 10.1577/1548-8446(2005)30[10:DOAFIT]2.0.CO

Jeffres, C. A., R.A. Dahlgren, M.L. Deas, J.D. Kiernan, A.M. King, R.A. Lusardi, J.M. Mount, P.B. Moyle, A.L. Nichols, S.E. Null, S.K. Tanaka, A.D. Willis. (2009). Baseline Assessment of Physical and Biological Conditions Within Waterways on Big Springs Ranch, Siskiyou County, California. Report prepared for: California State Water Resources Control Board.

Jezorek, I.G., and Hardiman, J.M., 2018, Juvenile salmonid monitoring following removal of Condit Dam in the White Salmon River watershed, Washington, 2017: U.S. Geological Survey Open-File Report 2018-1106, 31 p.

doi: 10.3133/ofr20181106

Kery, M., M. Schaub. (2011) Bayesian Population Analysis Using WinBUGS : A Hierarchical Perspective. Elsevier Science and Technology.

doi:10.1016/C2010-0-68368-4

Lorensen, T., C. Andrus, J. Runyon (1994). The Oregon Forest Practices Act water protection rules: scientific and policy considerations. Forest Practices Policy Unit, Oregon Department of Forestry.

Lusardi, R.A., B.G. Hammock, C.A. Jeffres, R.A. Dahlgren, J.D. Kiernan. (2020) Oversummer growth and survival of juvenile coho salmon (Oncorhynchus kisutch) across a natural gradient of stream water temperature and prey availability: an in situ enclosure experiment. Canadian Journal of Fisheries and Aquatic Sciences. 77(2): 413-424.

doi:10.1139/cjfas-2018-0484

Mackenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, C. A. Langtimm, (2002). Estimating Site Occupancy Rates when Detection Probabilities are Less than One. 83(8): 8.

doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

McMillan, J., R. Peters, M. McHenry, S. Brenkman, S. Morley, G. Pess, J. Anderson, T. Quinn, M. Foley, K. Denton, M. Moser, R. Paradis, P. Crain, H. Hugunin, J. Geffre, A. Geffre. (2019) The Elwha River: What Have We Learned Since Dam Removal? The Osprey. 93: 14-17

Mobrand, L.E., J.A. Lichatowich, L.C. Lestelle, T.S. Vogel (1997) An approach to describing ecosystem performance "through the eyes of salmon." Canadian Journal of Fisheries and Aquatic Sciences. 54: 2964–2973.

doi: 10.1139/f97-189

Mundie, J.H. (1969) Ecological implications of the diet of juvenile coho in streams. In Symposium on Salmon and Trout in Streams. Edited by T.G. Northcote. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C. pp. 135–152.

Nagel, D., J., M. Buffington, D. Isaak (2010). Estimating Stream Gradient Using NHD Stream Lines and DEM Data. ESRI International User Conference, July. 2010.

National Research Council. 2004. *Endangered and Threatened Fishes in the Klamath River Basin: Causes of Decline and Strategies for Recovery*. Washington, DC: The National Academies Press. https://doi.org/10.17226/10838.

Nickelson, T.E., M.F. Solazzi, S.L. Johnson, J.D. Rodgers. (1992) An approach to determining stream carrying capacity and limiting habitat for coho salmon (*Oncorhynchus kisutch*). In Proceedings of the coho workshop. Edited by L. Berg and P.W. Delaney. Nanaimo, B.C., May 26-28, 1992. pp. 251-260.

Nickelson, T.E. (1998) A Habitat-Based Assessment of Coho Salmon Production Potential and Spawner Escapement Needs for Oregon Coastal Streams. ODFW. Information Reports Number 98-4.

NMFS (National Marine Fisheries Service). (2013) Klamath Dam Removal Overview Report for the Secretary of the Interior. U.S. Department of the Interior, U.S. Department of Commerce, National Marine Fisheries Service.

NMFS (National Marine Fisheries Service). (2014) Final Recovery Plan for the Southern Oregon/ Northern California Coast Evolutionarily Significant Unit of Coho Salmon (Oncorhynchus kisutch). U.S. Department of the Interior, U.S. Department of Commerce, National Marine Fisheries Service.

Overton, C. K., S.P. Wollrab, B.C. Roberts, M.A. Radko. (1997) R1/R4 (Northern/Intermountain Regions) Fish and Fish Habitat Standard Inventory Procedures Handbook. USDA. United States Forest Service General Technical Report INT-GTR-346.

doi:10.2737/INT-GTR-346

Perry, R.W., J.C. Risley, S.J. Brewer, E.C. Jones, D.W. Rondorf. (2011) Simulating Water Temperature of the Klamath River under Dam Removal and Climate Change Scenarios. USGS. Open-File Report 2011-1243.

doi:10.3133/ofr20111243

Petts G.E., A.M Gurnell. (2005) Dams and geomorphology: Research progress and future directions. Geomorphology. 71: 27–47.

doi:10.1016/j.geomorph.2004.02.015

Quinn, T.P., N.P. Peterson. (1996) The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (Oncorhynchus kisutch) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences. 53(7): 1555-1564.

doi:10.1139/f96-092

Quinn, T.P., N.P. Peterson (1996). The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Canadian Journal of Fisheries and Aquatic Sciences. 53: 1555-1564.

doi: 10.1139/f96-092

Quinn, T.P. (2005). The Behavior and Ecology of Pacific Salmon and Trout. 1st edition. University of Washington Press.

Ramos, M.M. (2020). Recolonization potential for Coho salmon (*Oncorhynchus kisutch*) in tributaries to the Klamath River after dam removal. Cal Poly Humboldt theses and projects. 445. https://digitalcommons.humboldt.edu/etd/445

Rebenack, J.J., S. Ricker, C. Anderson, M. Wallace, D.M. Ward. (2015) Early Emigration of Juvenile Coho Salmon: Implications for Population Monitoring. Transactions of the American Fisheries Society. 144: 163-172.

doi:10.1080/00028487.2014.982258

Reeves, G. H., F. H. Everest, T. E. Nickelson. (1989) Identification of physical habitats limiting the production of coho salmon in western Oregon and Washington. General Technical Report PNW-GTR-245. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

doi:10.2737/PNW-GTR-245

Ries, K.G., J.K. Newson, M.J. Smith, J.D. Guthrie, P.A. Steeves, T.L. Haluska, K.R. Kolb, R.F. Thompson, R.D. Santoro, H.W. Vraga. (2017) StreamStats, version 4: U.S. Geological Survey Fact 2017–3046, 4 p.

doi:10.3133/fs20173046

Sandercock, F.K. (2019) Life history of coho salmon (*Oncorhynchus kisutch*) pp 396-445 *in* C. Groot and L. Margolis eds, *Pacific Salmon Life Histories*. UBC Press, Vancouver, BC.

Schroeder, K., B. Cannon, L. Whitman, M. Walker. (2012) Sandy River Basin Spring Chinook USDASalmon Spawning Surveys – 2012. Oregon Department of Fish and Wildlife 4034 Fairview Industrial Drive SE Salem, Oregon 97302. 73.

Sharma, R., R. Hilborn. (2001) Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences. 58: 1453-1463.

doi:10.1139/f01-091

Sheer, M.B., D.S. Busch, E. Gilbert, J.M. Bayer, S. Lanigan, J.L. Schei, K. Burnett, D. Miller. (2009) Development and Management of Fish Intrinsic Potential Data and Methodologies: State of the IP 2008 Summary Report. Pacific Northwest Aquatic Monitoring Partnership Series. 2009-004: 56.

doi:10.13140/RG.2.1.3548.2960

Shirvell, C.S. (1990) Role of Instream Rootwads as Juvenile Coho Salmon (*Oncorhynchus kisutch)* and Steelhead Trout (*O. mykiss*) Cover Habitat Under Varying Streamflows. Canadian Journal of Fisheries and Aquatic Sciences. 47(5): 852-861.

doi:10.1139/f90-098

Som, N. A., N.J. Hetrick, R. Perry, J.D. Alexander. (2019). Estimating annual *Ceratonova shasta* mortality rates in juvenile Scott and Shasta River Coho Salmon that enter the Klamath River mainstem (No. TR 2019-38). US Fish and Wildlife Service.

Stenhouse, S.A., C. Bean, W. R. Chesney, M. S. Pisano. (2012) Water temperature thresholds for coho salmon in a spring-fed river, Siskiyou County, California. California Fish and Game 98:19-37.

Sutton, R.J., M.L. Deas, S.K. Tanaka, T. Soto, R.A. Corum. (2007) Salmonid observations at a Klamath River thermal refuge under various hydrological and meteorological conditions. River Research and Applications. 23: 775-785.

doi:10.1002/rra.1026

Ugedal, O., T. F. Næsje, E. B. Thorstad, T. Forseth, L. M. Saksgård, T. G. Heggberget. (2008) Twenty years of hydropower regulation in the River Alta: Long-term changes in abundance of juvenile and adult Atlantic salmon. Hydrobiologia. 609(1): 9–23.

doi:10.1007/s10750-008-9404-2

Welsh, H. H., G. R. Hodgson, B. C. Harvey. (2001) Distribution of Juvenile Coho Salmon in Relation to Water Temperaturs in Tributaries of the Mattole River, CA. North American Journal of Fisheries Management. 21: 464-470.

doi:10.1577/1548-8675(2001)021<0464:DOJCSI>2.0.CO;2

Williams, T. H., B. C. Spence, W. Duffy, D. Hillemeier, G. Kautsky, T. E. Lisle, M. McCain, T. E. Nickelson, E. Mora, T. Pearson. (2008) Framework for Assessing Viability of Threatened Coho Salmon in the Southern Oregon/Northern California Coast Evolutionarily Significant Unit. NOAA-TM-NMFS-SWFSC-432. U.S. Department of Commerce, National Marine Fisheries Service, Southwest Fisheries Science Center.

## xi. Figure Legends

Figure 1. Overview of the geographic location of the Klamath River on the west coast of the United States of America. **A)** Location of the Klamath River in relation to the world (circle with crosshairs is the Klamath River). **B)** The Klamath River originates in southern Oregon and flows southwesterly through California to the Pacific Ocean (gray stars indicate dams to be removed; white stars indicate dams to be retained with volitional fish passage). **C)** A close-up of the

Klamath Hydroelectric reach and tributaries in relation to the Klamath River Basin (gray stars indicate dams to be removed).

Figure 2. Study tributaries in the Klamath Hydroelectric Project reach that will be accessible after dam removal. Watersheds are differentiated by fill pattern (black dots for Scotch Creek; diagonal lines for Camp Creek; staggered notch marks for Jenny Creek; cross hatched for Fall Creek; “v” shapes for Shovel Creek; “x” shapes for Spencer Creek).

Figure 3 Reference tributaries below the IGD. Bogus and Beaver creeks are tributaries to the Klamath River, while Lawrence Creek is a tributary to the Van Duzen River and Quartz Creek is a tributary to the Smith River. Reference stream watershed boundaries are shown by the dotted fill.

Figure 4. Temperature time series for the mainstem and all study tributaries, arranged from downstream to upstream. The colored band is the range of daily temperatures and the heavy line is the daily average. Red is 2018, blue is 2019. Horizontal lines indicate reference temperatures from Stenhouse et al. (2012); they define temperatures >15.6 C (dotted line) as suboptimal for juvenile coho salmon growth and temperatures >20.3 C (solid line) as detrimental to juvenile coho salmon growth.

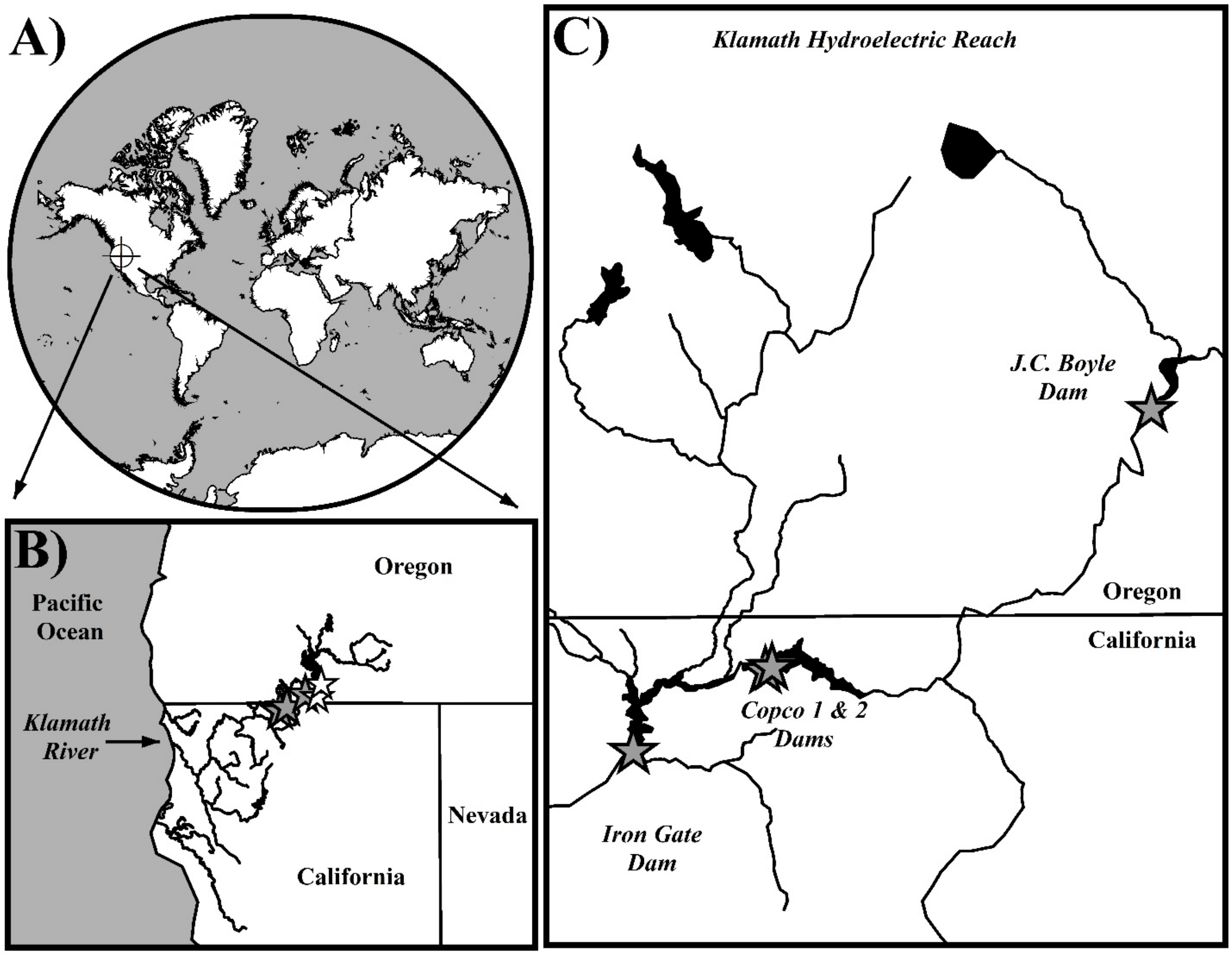
Figure 5. A summary of the HLFM model results for the six tributary streams in the project reach. Total summertime juvenile coho salmon capacities (number of individuals) are represented by the “grey bars” for each stream and the primary y-axis (left). The average HLFM habitat type multiplier, standardized by surface area, for accessible summertime habitat of each tributary stream is represented by the “black circles” and the secondary y-axis (right).

Figure 6. A summary of the IP model results for the six tributary streams in the project reach. IP kilometers are represented by the “grey bars” for each stream and the primary y-axis (left). The average juvenile coho salmon IP value for accessible summertime habitat of each tributary stream is represented by the “black circles” and the secondary y-axis (right).

Figure 7. A) Effect of standardized percent instream cover on occupancy probability for the final model structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval. B) Effect of standardized square meters of surface area on occupancy probability for the final model structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval. C) Effect of hatchery presence on occupancy probability for the final model structure (left) and observed proportions of habitat units occupied (right). The vertical lines with ticks indicate the 95% confidence interval. D) Effect of standardized depth on detection probability for the “best” model

structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval.

Figure 8. A box and whisker plot of occupancy probabilities of study tributaries. The boxes identify the interquartile range. The upper box bound delineates the 75th percentile and lower box bound delineates the 25th percentile while the solid line through the middle indicates the median. The “whiskers” identify the maximum and minimum occupancy probability for each tributary and the “solid black circles” show potential outliers.

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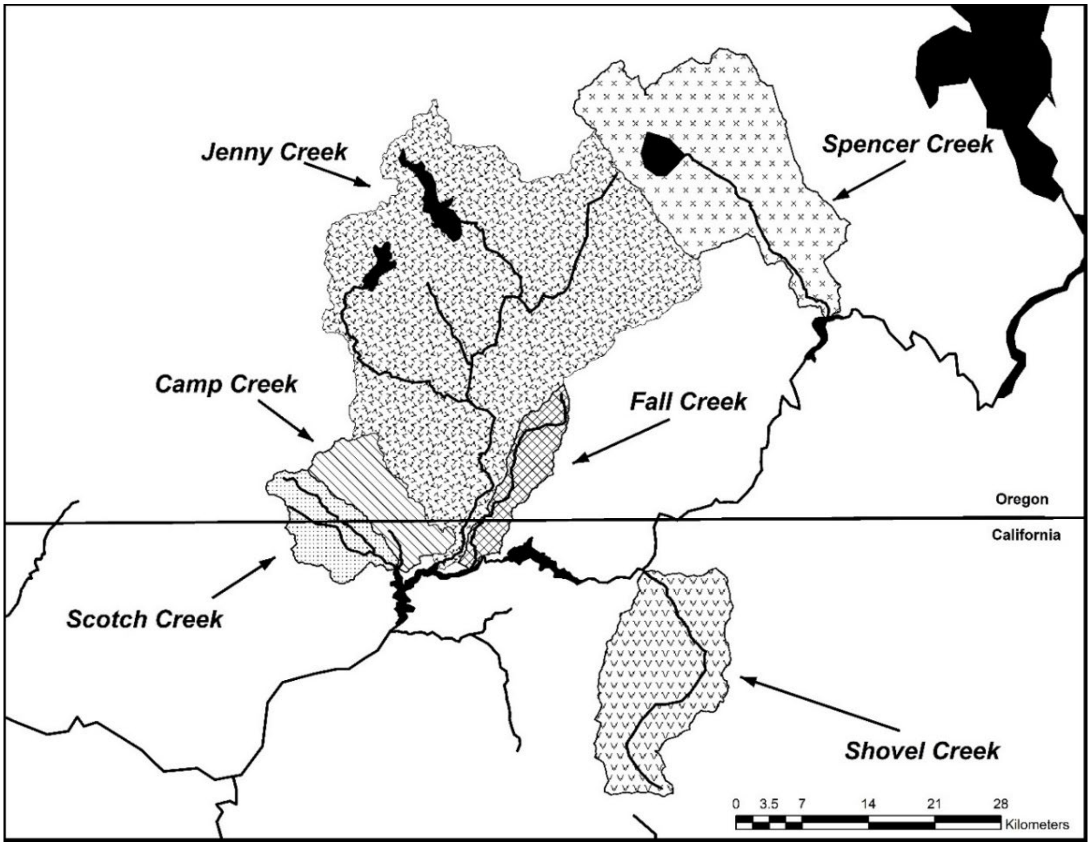


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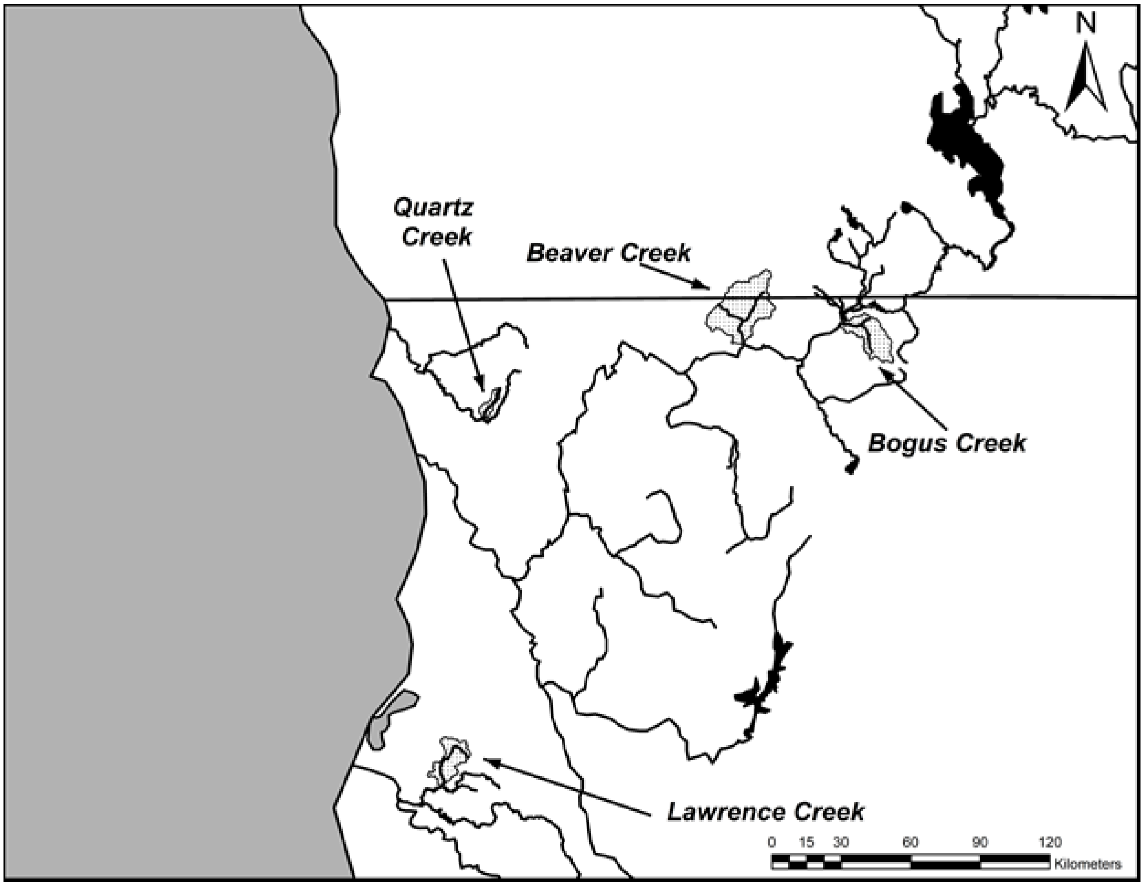


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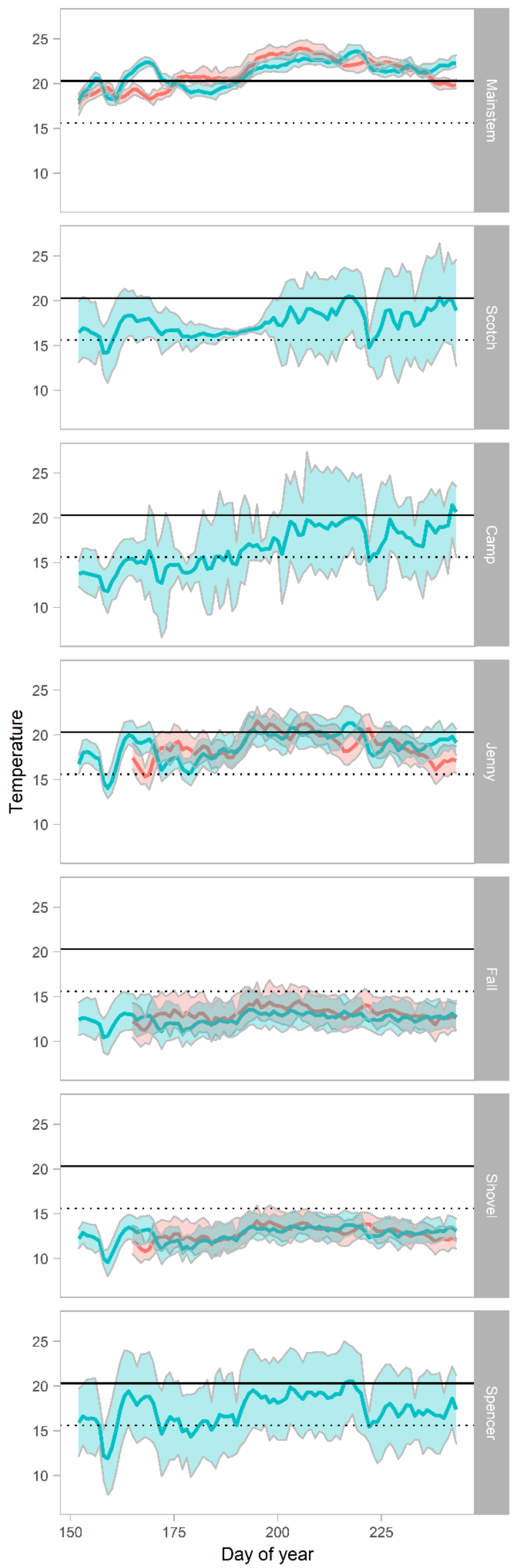

Temperature
25
20
15
10
Mainstem
Scotch
Camp
Jenny
Fall
Shovel
Spencer
150
175
200
225
Day of year

Figure 4. Temperature time series for the mainstem and all study tributaries, arranged from downstream to upstream. The colored band is the range of daily temperatures and the heavy line is the daily average. Red is 2018, blue is 2019. Horizontal lines indicate reference temperatures from Stenhouse et al. (2012); they define temperatures >15.6 C (dotted line) as suboptimal for juvenile coho salmon growth and temperatures >20.3 C (solid line) as detrimental to juvenile coho salmon growth.

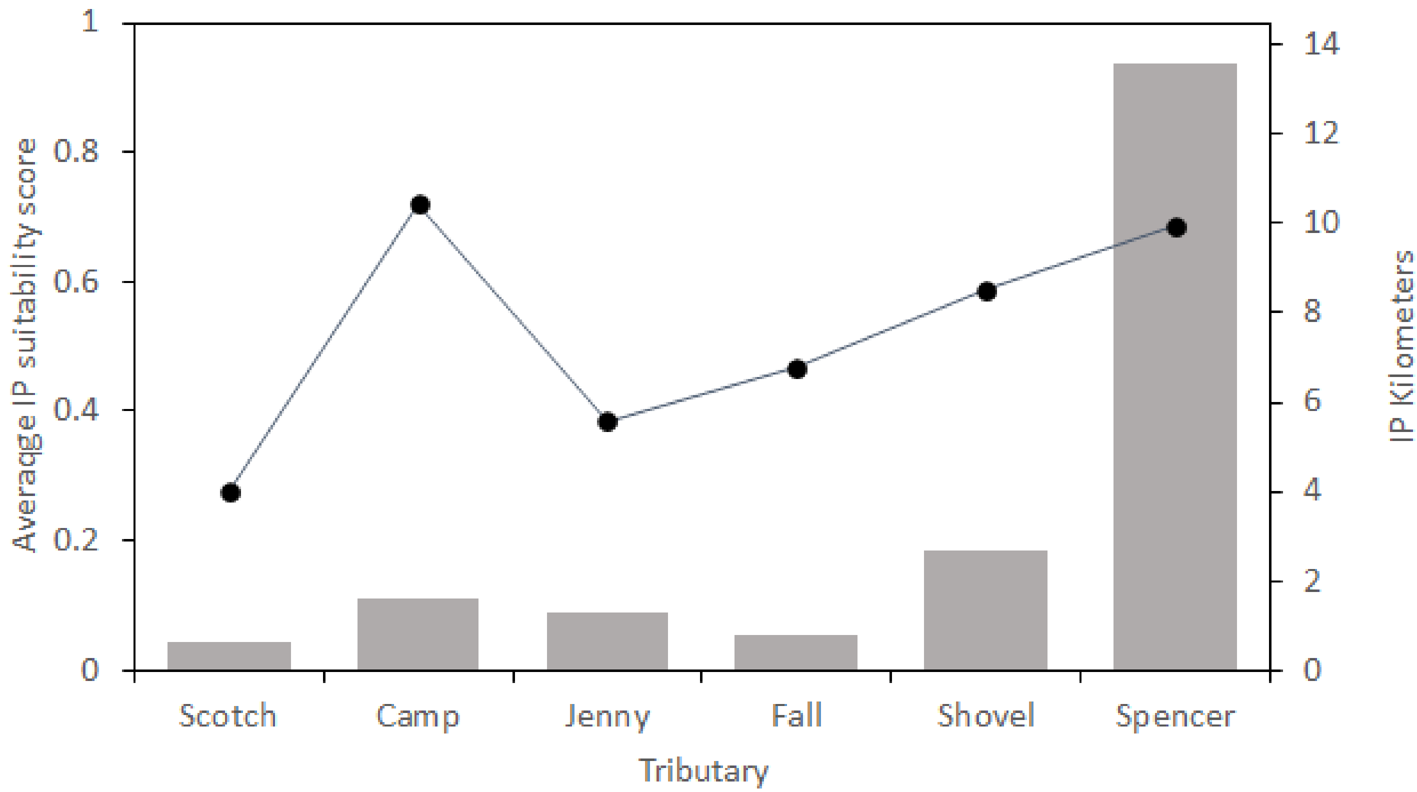


Figure 5. A summary of the HLFM model results for the six tributary streams in the project reach. Total summertime juvenile coho salmon capacities (number of individuals) are represented by the “grey bars” for each stream and the primary y-axis (left). The average HLFM habitat type multiplier, standardized by surface area, for accessible summertime habitat of each tributary stream is represented by the “black circles” and the secondary y-axis (right).

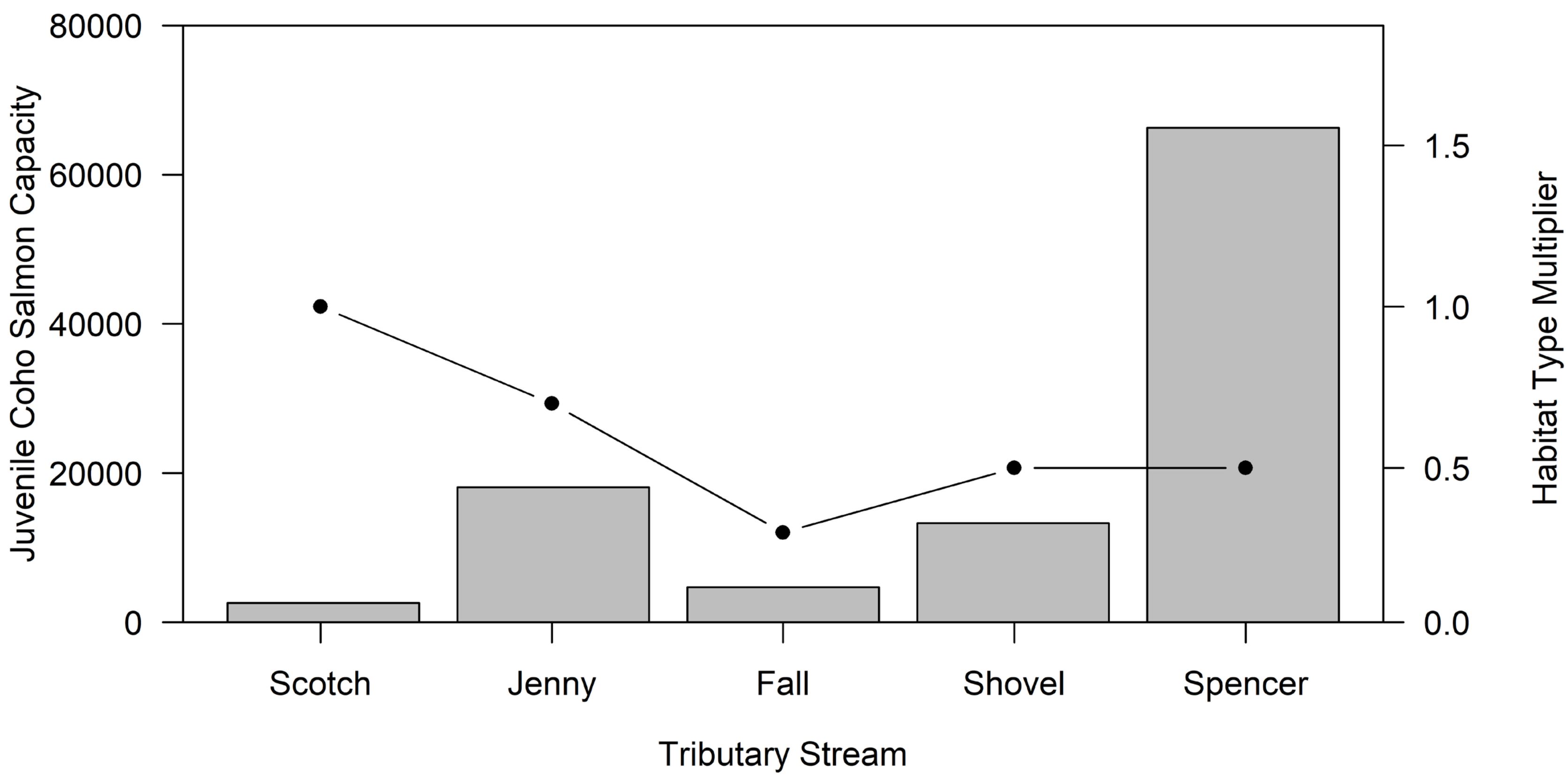


Figure 6. A summary of the IP model results for the six tributary streams in the project reach. IP kilometers are represented by the "grey bars" for each stream and the primary y-axis (left). The average juvenile coho salmon IP value for accessible summertime habitat of each tributary stream is represented by the "black circles" and the secondary y-axis (right).

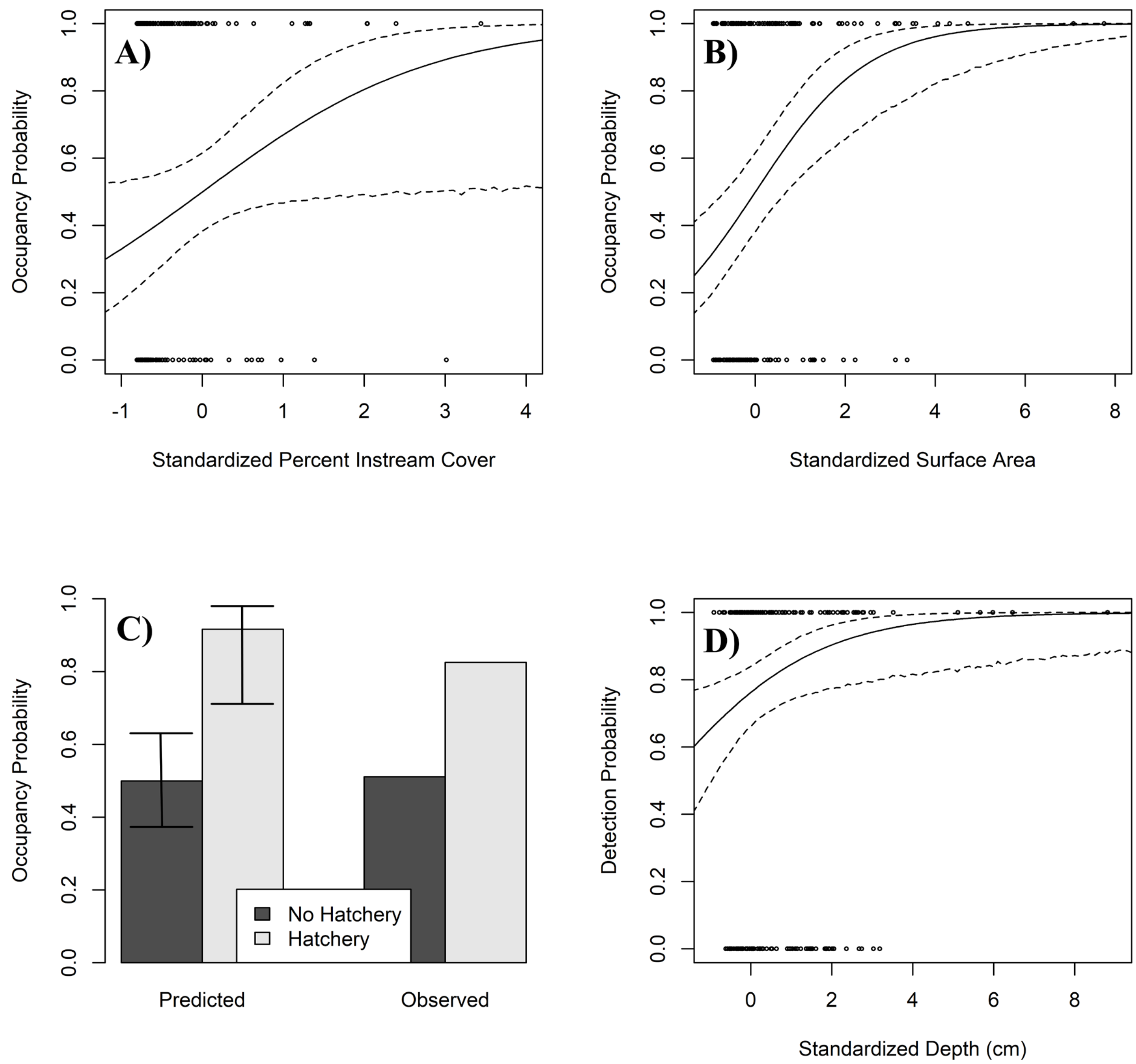


Figure 7. A) Effect of standardized percent instream cover on occupancy probability for the final model structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval. B) Effect of standardized square meters of surface area on occupancy probability for the final model structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval. C)  Effect of hatchery presence on occupancy probability for the final model structure (left) and observed proportions of habitat units occupied (right). The vertical lines with ticks indicate the 95% confidence interval. D) Effect of standardized depth on detection probability for the "best" model

structure. The solid back line indicates the covariate coefficient estimate, the open circles indicate observed data, and the dashed lines indicate the 95% confidence interval.

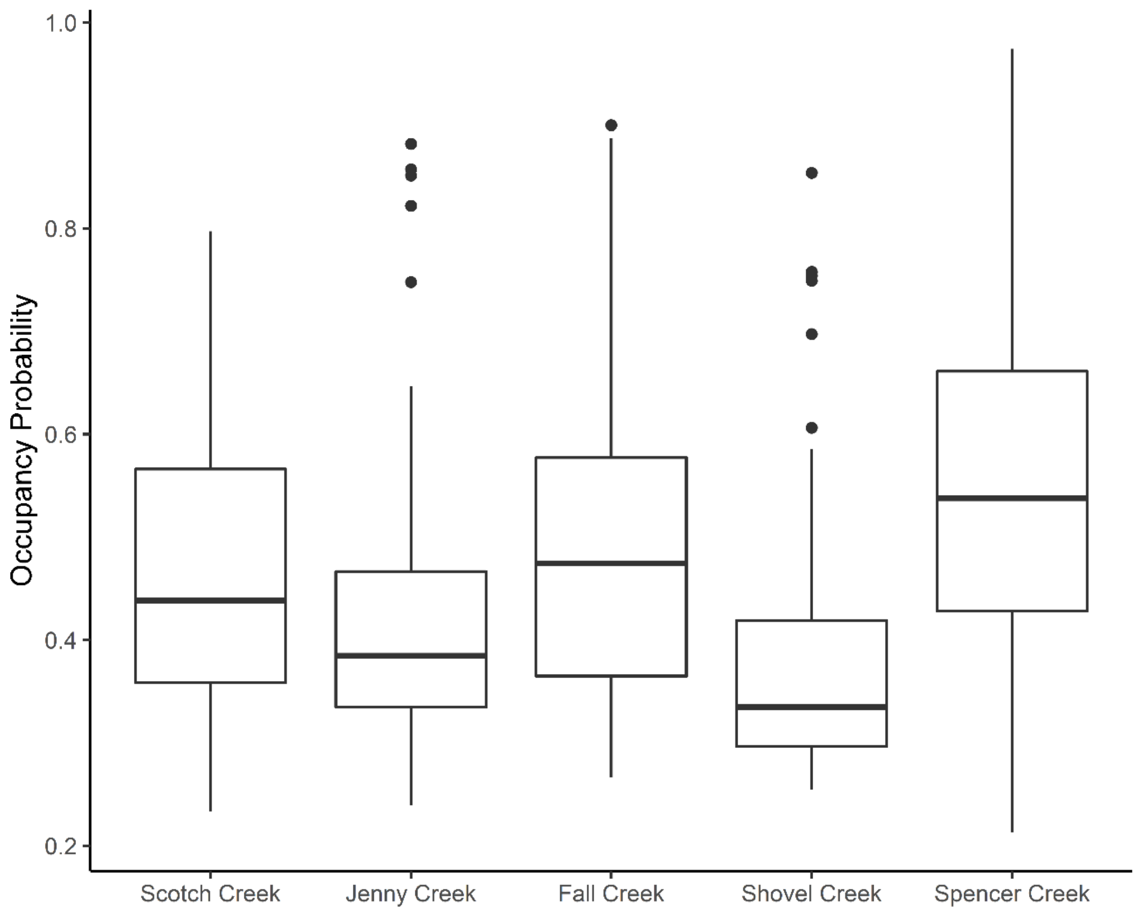


Figure 8. A box and whisker plot of occupancy probabilities of study tributaries. The boxes identify the interquartile range. The upper box bound delineates the 75th percentile and lower box bound delineates the 25th percentile while the solid line through the middle indicates the median. The “whiskers” identify the maximum and minimum occupancy probability for each tributary and the “solid black circles” show potential outliers.

Table 1. Maximum weekly average temperature (MWAT) and mean weekly maximum temperature (MWMT) for each stream. Values within the range associated with coho salmon presence in Welsh et al. (2001) are in bold (MWAT <16.7°C and MWMT <18.0°C).

| Stream | MWAT | MWMT |
|---|---|---|
| Scotch | 19.7 | 24.9 |
| Camp | 19.7 | 25.6 |
| Jenny | 21.0 | 22.6 |
| Fall | **14.2** | **16.2** |
| Shovel | **13.6** | **15.5** |
| Spencer | 19.8 | 24.2 |

Table 2 Comparison of candidate occupancy models.

| Model | AIC | ΔAIC | AICw | Number of Parameters |
|---|---|---|---|---|
| **Ψ(Hatchery + SA + Cover), p(Depth)** | **362.78** | **0.00** | **0.49** | **6** |
| Ψ(Hatchery + SA + Cover + HLFM), p(Depth) | 363.57 | 0.79 | 0.33 | 7 |
| - - - | - - - | - - - | - - - | - - - |
| Ψ(Hatchery + SA + HLFM), p(Depth) | 365.76 | 2.98 | 0.11 | 6 |
| Ψ(Hatchery + SA), p(Depth) | 366.72 | 3.94 | 0.07 | 5 |
| Ψ(Hatchery + Cover + HLFM), p(Depth) | 382.70 | 19.92 | 0.00 | 6 |
| Ψ(Hatchery + HLFM), p(Depth) | 382.75 | 19.97 | 0.00 | 5 |
| Ψ(SA + Cover), p(Depth) | 384.26 | 21.48 | 0.00 | 5 |
| Ψ(Hatchery + Cover), p(Depth) | 385.44 | 22.66 | 0.00 | 5 |
| Ψ(Hatchery), p(Depth) | 387.36 | 24.58 | 0.00 | 4 |
| Ψ(SA), p(Depth) | 388.05 | 25.27 | 0.00 | 4 |
| Ψ(SA + HLFM), p(Depth) | 389.02 | 26.24 | 0.00 | 5 |
| Ψ(Cover), p(Depth) | 397.74 | 34.94 | 0.00 | 4 |
| ψ(.), p(Depth) | 399.73 | 36.95 | 0.00 | 3 |
| Ψ(HLFM), p(Depth) | 401.72 | 38.94 | 0.00 | 4 |
| ψ(.), p(.) | 406.95 | 44.17 | 0.00 | 2 |

Note:

1. **Bold** indicates the final model selected;
2. "---" indicates the delta AIC = 2.0 cutoff;
3. "Ψ" and "p" indicate the occupancy and detection probability components of the model, respectively;
4. "Hatchery" is the hatchery categorical effect (accounting for Bogus Creek);
5. "SA" is the standardized surface area numerical effect;
6. "HLFM" is the standardized HLFM value numerical effect;
7. "Cover" is the standardized instream cover effect;
8. "." Indicates a null model or no variable effect.

Table 3 Overall summary of results for streams above IGD.

| | Scotch Creek | Camp Creek | Jenny Creek | Fall Creek | Shovel Creek | Spencer Creek |
|---|---|---|---|---|---|---|
| Total accessible habitat (km) | 1.0[1] | 2.2[1,2] | 3.3[3] | 1.6[3] | 4.7[3] | 20.5 |
| % of total IP km | 3.1% | 7.8% | 6.3% | 3.9% | 13.0% | 66.1% |
| % of total HLFM capacity | 2.5% | NA | 17.2% | 4.5% | 12.7% | 63.2% |
| % of summer habitat predicted to be occupied | 37% | NA | 47% | 53% | 37% | 70% |

Note: % total columns (% of total IP km, % of total HLFM capacity, and % of summer habitat predicted to be occupied) show the proportions of the cumulative total each tributary account for. The percent of summer habitat predicted to be occupied was calculated using habitat units with greater than 0.50 occupancy probability from our final occupancy model output.

[1]. We estimate that habitat in Camp and Scotch creeks will extend approximately 1.8 km further after reservoir drawdown (not included in total accessible habitat).

[2]. Camp Creek was not assessed for potential barriers, and accessible habitat limit is an approximation based on large boulder features apparent in aerial photography;

[3]. Accessible habitat estimate includes area above natural and anthropogenic barriers that could limit non-natal colonization