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Salmonid Habitat and Population Capacity Estimates for Steelhead Trout and Chinook Salmon Upstream of Scott Dam in the Eel River, California

Abstract

Estimating salmonid habitat capacity upstream of a barrier can inform priorities for fisheries conservation. Scott Dam in California's Eel River is an impassable barrier for anadromous salmonids. With Federal dam relicensing underway, we demonstrated recolonization potential for upper Eel River salmonid populations by estimating the potential distribution (stream-km) and habitat capacity (numbers of parr and adults) for winter steelhead trout (*Oncorhynchus mykiss*) and fall Chinook salmon (*O. tshawytscha*) upstream of Scott Dam. Removal of Scott Dam would support salmonid recovery by increasing salmonid habitat stream-kms from 2 to 465 stream-km for steelhead trout and 920 to 1,071 stream-km for Chinook salmon in the upper mainstem Eel River population boundaries, whose downstream extents begin near Scott Dam and the confluence of South Fork Eel River, respectively. Upstream of Scott Dam, estimated steelhead trout habitat included up to 463 stream-kms for spawning and 291 stream-kms for summer rearing; estimated Chinook salmon habitat included up to 151 stream-kms for both spawning and rearing. The number of returning adult estimates based on historical count data (1938 to 1975) from the South Fork Eel River produced wide ranges for steelhead trout (3,241 to 26,391) and Chinook salmon (1,057 to 10,117). An approach that first estimated juvenile habitat capacity and then used subsequent life stage survival rates yielded 1,281 (CV 56%) steelhead trout and 4,593 (CV 34%) Chinook salmon returning adults. Variability in estimated fish numbers reflects application of densities and survival rates from other populations, assumptions about salmonid productivity in response to potential spawning habitat capacity, residency and outmigration of early life-stages, summertime water quality conditions, and inter-annual hydrograph, marine, and population variability.

Keywords: Eel River, salmonid, habitat, dam

Introduction

Large flood control and hydroelectric dams have contributed to freshwater habitat degradation and fish population declines through watershed fragmentation, disruption of natural flow regimes, interference with nutrient distribution, and blockage from historical spawning and rearing habitat (Sheer and Steel 2006). Efforts to remove dams as barriers to fish passage and reconnect migratory fish to suitable stream habitat has eventually resulted in successful recolonization on several accounts (Pess et al. 2003, 2012; Brewitt 2016). Homing instincts are documented for most anadromous salmonids (Quinn 1993), but straying from the return to natal streams is also well documented (Hendry et al. 2004; Quinn 2005; Keefer et al. 2005, 2008). Straying from a natal stream is considered an ecological and evolutionary mechanism for population persistence (Cooper and Mangel 1999, Hill et al. 2002, Hilborn et al. 2003) and is hypothesized to initially increase in response to an increase in disturbance regime and habitat availability, such as from dam removal (Quinn 1984).

Located in northern California, the upper mainstem Eel River is considered the area upstream

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of its confluence with the Middle Fork Eel River, where the National Marine Fisheries Service (NMFS) identified the Northern California (NC) Steelhead trout (*Oncorhynchus mykiss)* and California Coastal (CC) Chinook salmon (*O. tshawytscha)* populations as Ecologically Significant Units (ESU) (NMFS 2016). Near the headwaters of the upper mainstem Eel River is a water storage, diversion, and hydropower facility known as the Potter Valley Project (PVP). The PVP includes two dams—Cape Horn Dam, a run-of-the-river dam with a fish ladder, and 19 river-km upstream from Cape Horn Dam is Scott Dam, a water storage dam with no fish passage. Impacts from the PVP in combination with other anthropogenic impacts in the basin have resulted in degradation of the Eel River's aquatic habitat (O'Farrell et al. 2012), and native salmonid populations have declined to an estimated 1 to 3% of their historic levels (Yoshiyama and Moyle 2010). Upper Eel River ESUs including NC steelhead trout and CC Chinook salmon have the potential to become a recolonization resource to newly opened habitat upstream of Scott Dam upon barrier removal.

Since its construction in 1922, Scott Dam of the PVP has blocked fish passage to upstream habitat historically used by anadromous salmonids, including fall-run Chinook salmon and winter-run steelhead trout (NMFS 2016). Genetic integrity and resiliency of migratory populations such as anadromous salmonids rely on access to uninterrupted spawning and rearing streams (Moyle et al. 2017). As salmonid populations throughout Pacific Coast watersheds have been listed under the Federal Endangered Species Act, fisheries management has responded with recovery strategies involving passage and habitat restoration to allow anadromous salmonids to recolonize their ancestral habitats (Pess et al. 2008, NMFS 2016). Beyond the presence and condition of nearby salmonid populations, recolonization potential upstream of Scott Dam for those ESUs also depends on habitat suitability and capacity in tune with each colonist species' life history variants (Pess et al. 2014). Consequently, salmonid passage restoration and recolonization often involves efforts to predict the suitability of potentially reopened habitat and the increase in salmonid production resulting from restored migratory access (Hanrahan et al. 2004, Winter and Crain 2008, Roni et al. 2010).

Past efforts to quantify the amount of blocked salmonid habitat in the mainstem Eel River upstream of Scott Dam and its potential population production involved various methods with coarse habitat measurements, resulting in estimates ranging from 50 to 400 km of habitat (CDFG 1979, VTN 1982, USFS and BLM 1995, Becker and Reining 2009, NMFS 2016). However, all of these studies acknowledge that fall Chinook salmon and winter steelhead trout would potentially benefit from restored access to habitat above Scott Dam. Other anadromous salmonids native to the Eel River are less likely to use habitats above Scott Dam, as evidenced by sparse observations over the past few decades of Coho salmon (*O. kisutch*), and no observations of coastal cutthroat trout (*O. clarkii*) at Cape Horn Dam's fish passage facility, Van Arsdale Fisheries Station (VAFS) (PVID 2017). This portion of the watershed extends beyond present Coho salmon and coastal cutthroat trout distribution (Xanthippe 2004).

In this study, we quantified extent of suitable habitat and its capacity for steelhead trout and Chinook salmon above Scott Dam. Field habitat sampling, habitat suitability models, and historical fish count data were used in estimating potential stream capacities for different life stages of steelhead trout and Chinook salmon. The challenge of predicting salmonid production in habitat not currently available to those species required modeling from salmonid populations in other areas. Quantifying salmonid habitat suitability and its capacity for an expected long term average population must reflect biological requirements at different life stages and stream environment conditions as they vary spatially and temporally. Linking the biology and habitat requirements of salmonids to habitat conditions and identifying limiting factors for potential salmonid production should therefore be incorporated into modeling potential stream habitat capacity in prioritized watersheds (Anlauf-Dunn et al. 2014).

Hydraulic units of suitable stream habitat change seasonally and with different biological phases of a species. Adult salmonid habitat is often measured in units of stream length with suitable spawning habitat and related to number of fish observed or expected to occur in those stream lengths to calculate fish capacity. Alternatively, because salmonids occupy different habitat type units (e.g., pools, riffles, flatwater, etc.) at certain times of year, habitat capacity can also be quantified by the availability of habitat types and the number of fish observed or expected to occur in those habitat types. For example, the distribution and proportion of habitat type units within a stream reach at summer base flows can be used to approximate the quantity of rearing habitat for summertime-rearing juvenile steelhead trout (Agrawal et al. 2005). However, quantifying salmonid habitat with habitat-typed units to then calculate its capacity must reflect the geomorphic and hydraulic conditions that change with seasonally varying discharge (Rosenfeld et al. 2011), such as during the spring hydrograph recession when juvenile Chinook rear and emigrate. Other studies estimate salmonid habitat capacity by incorporating linkages between habitat conditions and fish density, relying on variables such as habitat unit composition, substrate composition, instream shelter, discharge, and water quality (Cramer and Ackerman 2009a, USFWS 2011, Gallagher et al. 2014). Habitat capacity models should be sensitive to local conditions and interactions between nearby populations and their habitat conditions. When possible, local data on habitat conditions, nearby fish populations, and streamflow gaging should be incorporated into the described parameters for estimating potential salmonid habitat capacity.

Research Objectives

The objectives of this research were to quantify the salmonid habitat upstream of Scott Dam and estimate the potential adult and juvenile stream capacity for steelhead trout and Chinook salmon. Populations of native salmonids in the Eel River have been affected by degraded habitat conditions and these populations now legally require recovery as stated in the NMFS Coastal Multispecies Recovery Plan (2016). NMFS identified the upper Eel River as a high priority for population recovery, calling for an estimate of salmonid habitat in order to assess the benefits of restoring fish passage above Scott Dam (NMFS 2016). Initiation of the PVP Federal Energy Regulatory Commission (FERC) relicensing process in 2017 underscored the opportunity and need to quantify salmonid habitat extent and potential production capacity upstream of Scott Dam, and provided a primary impetus for this study. The information presented here will aid fisheries managers in assessing whether restoring salmonid access to the area is merited.

Methods

Study Area

Located in northern California, the upper mainstem Eel River includes its headwaters down to the confluence of the mainstem Eel and Middle Fork Eel River near Dos Rios, California. The study area includes the upper mainstem Eel River watershed upstream of Scott Dam where the Mendocino National Forest lies within the Coast Mountain Range (Figure 1). Scott Dam is located at an elevation of 554 m along the upper mainstem Eel River at river km 260. This area is characterized by a Mediterranean climate with wet winters and hot, dry summers (Cid et al. 2017). Lake Pillsbury, the reservoir formed by Scott Dam, accumulates runoff from the mainstem Eel River watershed and the watershed of major tributary known as Rice Fork, totaling a drainage area of 746 km^2 (Figure 2) (Brown and Ritter 1986). Average annual precipitation is 120 cm, falling during winter months primarily as rain with some snow (US Climate Data 2017). Land cover includes mixed conifer forests on north facing slopes and oak woodlands on drier, south facing slopes.

Methods Overview

The purpose of this research included two main goals: 1) to map and characterize potential salmonid habitat extent in the streams above Scott Dam's reservoir and 2) to estimate the juvenile and adult capacity of those streams for steelhead trout and Chinook salmon. Limits to salmonid extent were first identified using the NMFS (2016) Intrinsic Potential (IP) model, which predicts salmonid habitat in a GIS using a 10-m resolution Digital Elevation Model (DEM) to calculate stream slope, valley confinement, and drainage area as limiting factors to suitable habitat as defined by NMFS for steelhead trout and Chinook salmon. A disputed passage barrier at Bloody Rock roughs on the mainstem Eel River was assessed in the field for upstream passage of steelhead trout and Chinook salmon adults. Suitable habitat was quantified under two passage scenarios (based on passage or blockage at Bloody Rock roughs), and habitat capacity was estimated within the reaches of these two scenarios.

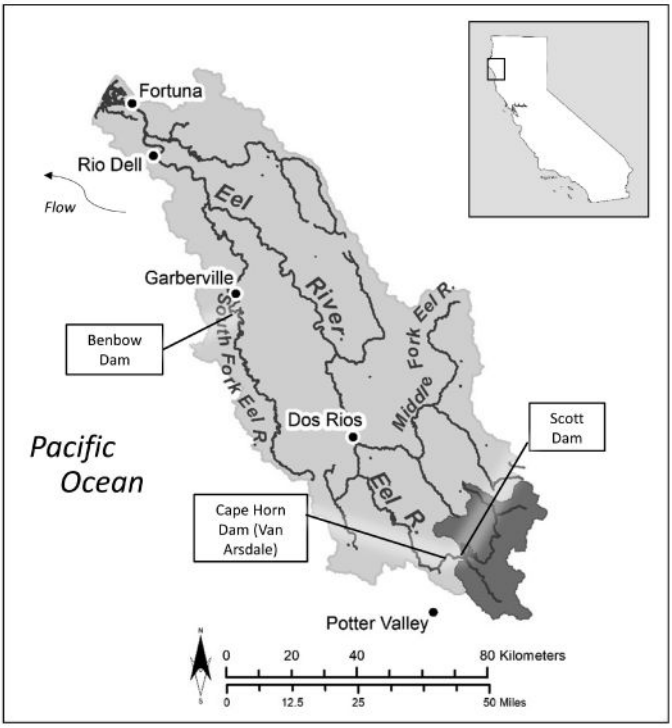


Figure 1. Located in northern California, the study area (darker shading) is in the headwaters of the mainstem Eel River upstream of Scott Dam. Points of interest pertaining to this study include the Van Arsdale fish station at Cape Horn Dam, Benbow Dam on the South Fork Eel River, and the confluence of the Middle Fork with the mainstem Eel River at Dos Rios. Spatial Reference: World Geodetic System 1984 (WGS84), Universal Transverse Mercator (UTM) Zone 10 North (USGS 2016b, ERCZO 2016).

"Capacity" was defined as the highest number of fish at a specific life stage that a stream could support given its environmental conditions. Two approaches were used to model the capacity for steelhead trout and Chinook salmon upstream of Scott Dam, one for adult fish and the other for juvenile parr (rearing life stage preceding emigration). The adult capacity model used historical adult fish count data from the South Fork Eel River (CDFG 1975), species-specific distribution data (NMFS 2016), ground-based assessments, and spatial analysis to determine baseline extent of suitable habitat and potential densities for adult steelhead and Chinook upstream of Scott Dam. The juvenile parr capacity model characterized juvenile rearing extent and capacities using spatial analysis to quantify and characterize streams upstream of Scott Dam for creating a data collection and extrapolation framework, followed by ground-based data collection of salmonid rearing habitat. Habitat inventory data collected in the field were used as inputs into the juvenile capacity estimation model known as the Unit Characteristic Method (UCM), which relates small-scale habitat conditions to density of juvenile parr steelhead trout and Chinook salmon (Cramer and Ackerman 2009a, 2009b). The Oregon coastal watersheds that provided surrogate habitat-specific parr densities for this study are similar to the upper Eel River watershed in that they support winter steelhead trout and fall Chinook salmon populations, but contrast in hydrologic frequency, duration, and timing from differences in climate, geomorphology, and land use. Surrogate density data from local watersheds would be more appropriate for this study, but those data were not available. Parr densities were calculated at the habitat unit scale, then summed and extrapolated to the reach and watershed scales. Parr estimates were multiplied by life-stage survival rates for estimating returning adults from parr capacities. Results from both capacity modeling methods were compared to each other as well as those from historical efforts (CDFG 1939, 1975, 1979; VTN 1982; USFS and BLM 1995; Becker and Reining 2009; NMFS 2016; FOER 2017).

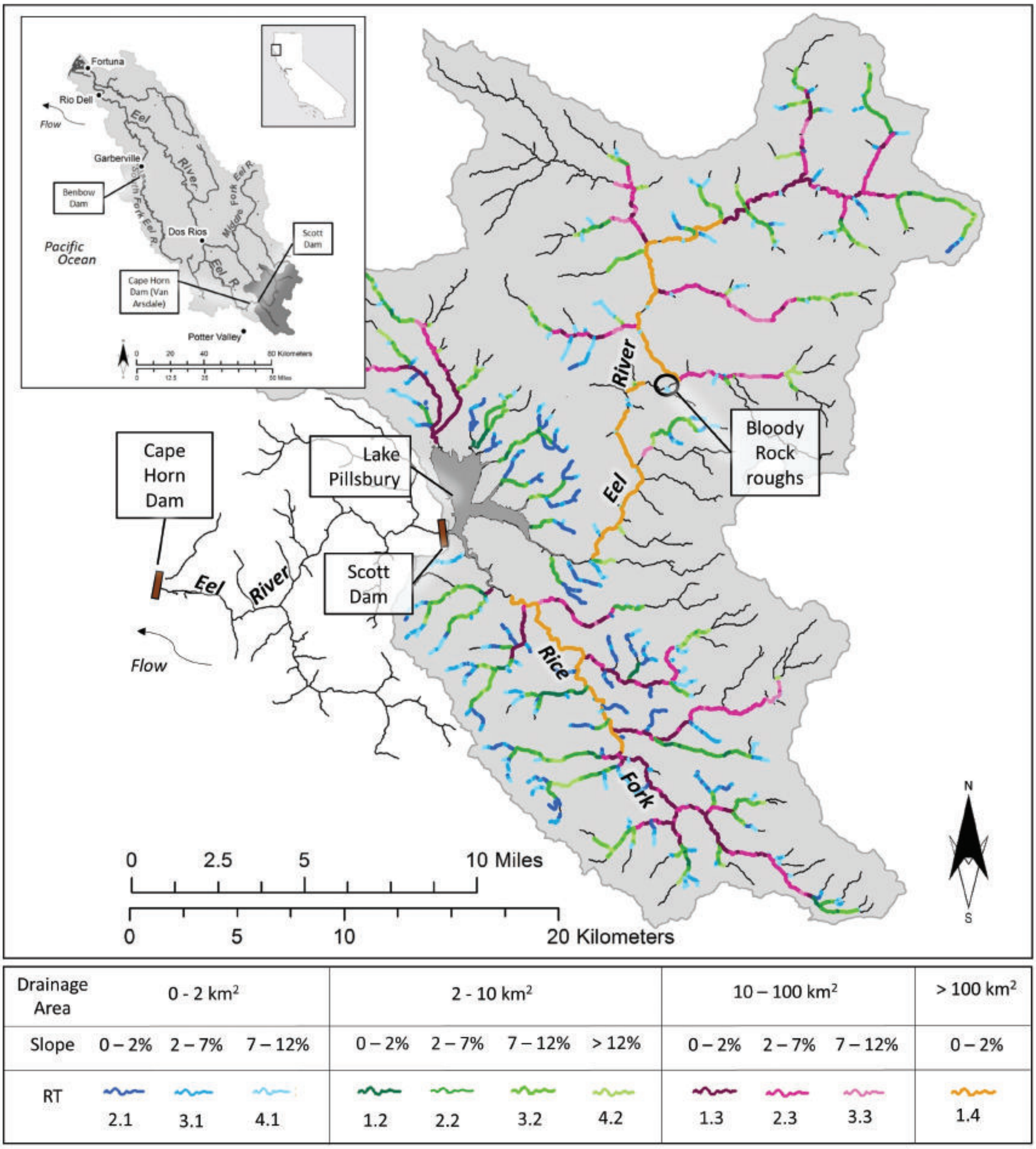


Figure 2. Study area streams were classified and coded into Reach Types (RT) by categories of drainage area (color) and slope (steeper slopes in lighter shades) for data collection and extrapolation. Bloody Rock roughs is a partial barrier and thin black streams upstream of Scott Dam are inaccessible to anadromous salmonids.

Sample Design

Potential Distribution Scenarios—Initial steps in this research required identifying limits to salmonid distribution for each species of interest within the study area. This was achieved by evaluation of existing data from past habitat assessments and geospatial analysis of data from the NMFS Intrinsic Potential (IP) model (NMFS 2016). Bloody Rock roughs (BR) is a large cascade-falls feature along the mainstem Eel River and was previously considered a complete (VTN 1982) or partial (USFS and BLM 1995, NMFS 2016) barrier for Chinook salmon and steelhead trout upstream passage, and ground-based observations of this feature in winter–spring 2016 assessed it as a barrier during extremely dry years. Therefore, we included both scenarios for passage and no passage at Bloody Rock roughs in our estimates.

Potential salmonid habitat distribution and capacity estimates upstream of Scott Dam were applied to two fish passage scenarios. The first scenario (Scott Dam removal, BR passage) considers passage restoration at Scott Dam via dam removal and does not consider Bloody Rock roughs a barrier. This "Scott Dam removal, BR passage" scenario includes stream habitat currently inundated by Lake Pillsbury, habitat along the mainstem Eel River and its tributaries both below and above Bloody Rock roughs, as well as the Rice Fork and its tributaries (Figure 2). The second scenario (Scott Dam removal, no BR passage) considers passage restoration at Scott Dam via dam removal with abnormally dry winter-spring conditions that would not allow passage upstream of the partial barrier at Bloody Rock roughs. The "Scott Dam removal, no BR passage" scenario includes stream habitat currently inundated by Lake Pillsbury, habitat along the mainstem Eel River and its tributaries up to Bloody Rock roughs, and the Rice Fork and its tributaries (Figure 2).

The National Marine Fisheries Service (NMFS 2016) designated Distinct Population Segments (DPS) for steelhead and Ecologically Significant Units (ESU) for salmon throughout the Eel River watershed and defined population boundaries for each species within the upper mainstem Eel River. This resulted in two separate population boundaries for the upper Eel River California Coastal (CC) Chinook and the upper Eel River Northern California (NC) Steelhead populations, with the CC Chinook boundary much larger than that of the NC Steelhead boundary. The upper Eel River CC Chinook population boundary downstream extent is at the mainstem's confluence with the South Fork Eel River, extending upstream into the North Fork, Middle Fork, and mainstem Eel Rivers and their tributaries. The NC Steelhead population boundary downstream extent is just below Scott Dam on the mainstem Eel River. We calculated the potential increase in suitable habitat for adult steelhead trout and Chinook salmon within the upper mainstem Eel River with the addition of maximum spatial extent this study identified upstream of Scott Dam (Figure 1).

Stream Characterization—The stream network within the study site was classified into a total of 11 types we refer to as 'Reach Types' based on categories of gradient and drainage area as they are geomorphically pertinent to salmonid habitat found in other studies (Higgins et al. 2005, Stillwater Sciences 2013, Lane and Sandoval 2014) (Figure 2). Stream gradient was included as a stratification variable due to its correlation with velocity, substrate composition, channel morphology, and habitat type composition; stream size measured in drainage area was included due to its correlation with channel morphology, habitat types, habitat stability, and discharge (Higgins et al. 2005). The frequency (stream-kms) of each Reach Type was used to assign a proportional number of habitat survey sites using stratified, equal probability Generalized Random Tesselation Stratification (GRTS) methods for a linear resource in program R version 1.0.136 (R Core Team 2017) with the spsurvey package (Kincaid et al. 2012). Reach Type classifications were used for extrapolating finer-scale habitat data collected in field surveys.

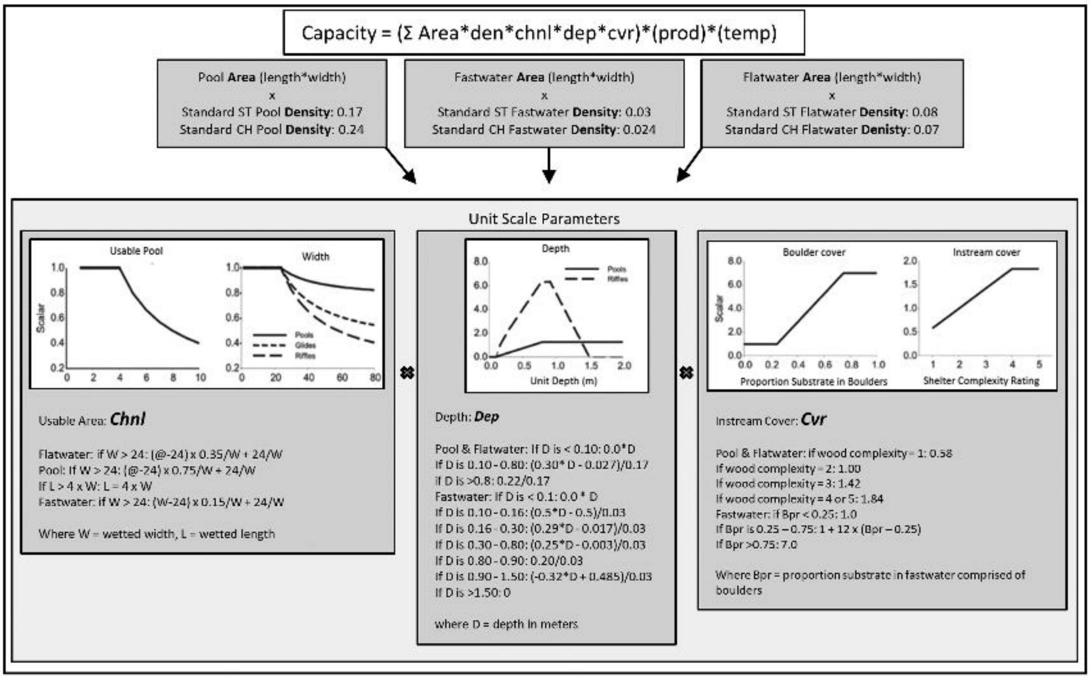
Data Collection—Once survey locations were selected throughout the watershed's stream network, field data collection was conducted during June through August 2016. The number of survey sites was proportional to the total stream length within each Reach Type, with two or more sites per Reach Type. The habitat data collected from our surveys provided a subsample intended for extrapolating habitat characteristics to streams in corresponding Reach Types that were not surveyed. The survey protocol followed methods from the California Department of Fish and Wildlife's California Salmonid Stream Habitat Restoration Manual, Part III (CDFW 2004). Working in an upstream direction, each habitat unit encountered in a survey reach was classified as a pool, riffle, cascade, flatwater, or dry unit and measured for wetted surface area. Other habitat variables related to juvenile fish density were measured including instream large woody debris, instream cover, streambed substrate composition and embeddedness, canopy cover, and water quality variables such as discharge, temperature, pH, and turbidity. See CDFW (2004) for details of how these variables were measured.

Analysis

Habitat Data—We tested how our Reach Type classes were discrete representations of fine-scale habitat-typing data. Variables including unit area, mean depth, instream cover, percent fine substrate, and proportion of pools and fastwater habitat were analyzed in a Linear Discriminant Analysis (LDA) for discriminating groups among Reach Types with program R (packages Mass, GGplot2, Scales, gridExtra, and RColorBrewer). Habitat variables between Reach Types were evaluated for combining select Reach Type classes that did not discriminate groupings of habitat data. Reach Type-classified survey data were extrapolated onto remaining unsurveyed streams in corresponding Reach Types. These reach-classified habitat data were used as inputs for modeling habitat capacity.

Potential Adult Returns—Steelhead trout and Chinook salmon adult count data from other sources in the Eel River were used to develop a baseline for potential adult densities in the habitat upstream of Scott Dam. While Van Arsdale Fisheries Station provided historical count data from the upper mainstem Eel River, those data were not used due to the impacts of Scott Dam on downstream salmonid habitat since its construction in 1922. The adult salmon and steelhead monitoring station operated at Benbow Dam on the South Fork Eel River (Figure 1) from 1938 to 1975 provided a relevant data set that was used to estimate the adult capacity in the upper mainstem Eel River. Both the South Fork Eel and upper mainstem Eel River include geologic Franciscan assemblages (Lisle 1990) and experience similar hydrologic cycles from their Mediterranean climates. We assumed that the number of adults produced per unit stream length in the South Fork Eel would be similar to the number of adults produced by the mainstem Eel watershed above Scott Dam, in a straight ratio. While this estimate does rely on unquantified assumptions, not least of which was the equivalence of habitat densities in each of the watersheds, we believe this approach nevertheless provided a reasonable approximation of adult production capacity in a region where historical empirical data do not exist. Other factors may render this estimate conservative. For example, the Benbow counts may not include all actual adult salmonid migrants due to varying time spent monitoring fish passage (CDFG 1939 to 1941, 1970 to 1971), count accuracy, or impassable conditions that occurred at the Benbow Dam Fisheries Station ladder throughout a run season. Maximum-recorded values from the Benbow Dam count data were used as an index for potential maximum long-term production of adults per salmonid stream length upstream of Benbow Dam. Calculations provided fish$\cdot$km^{-1} densities for both Chinook salmon and steelhead trout that were then multiplied by stream-kms in the study area upstream of Scott Dam for two passage scenarios. Similarly, mean values of fish counts from trends over time in Benbow data were converted to fish$\cdot$km^{-1} for a representation of potential average spawner density in the streams above Scott Dam.

Juvenile Parr Capacity Modeling—This study also utilized a stream capacity modeling application for summertime salmonid juvenile rearing developed by Cramer and Ackerman (2009a) known as the Unit Characteristic Method (UCM). The UCM incorporates habitat suitability indices into its functions (Figures 3a, 3b). The model multiplies a baseline surrogate fish density ("den" in units of fish$\cdot$m^{-2}) by a measured wetted habitat unit area ("area" in units of m^2); the density values are then adjusted by scalar values of habitat parameters specific to stream-rearing juveniles. The scalar values for each parameter are expressed as suitability curves whose equations are defined in Figures 3a and 3b. Juvenile parr capacity estimates used habitat parameters at the unit-scale (i.e., usable area "chnl", depth "dep", and instream cover "cov") (Equation 1), and reach-scale (i.e., turbidity, fine substrate, pH, and temperature)



Capacity = (Σ Area*den*chnl*dep*cvr)*(prod)*(temp)

Pool **Area** (length*width)
x
Standard ST Pool **Density**: 0.17
Standard CH Pool **Density**: 0.24

Fastwater **Area** (length*width)
x
Standard ST Fastwater **Density**: 0.03
Standard CH Fastwater **Density**: 0.024

Flatwater **Area** (length*width)
x
Standard ST Flatwater **Density**: 0.08
Standard CH Flatwater **Denisty**: 0.07

Usable Area: ***Chnl***

Flatwater: if W > 24: (@-24) x 0.35/W + 24/W
Pool: If W > 24: (@-24) x 0.75/W + 24/W
If L > 4 x W: L = 4 x W
Fastwater: if W > 24: (W-24) x 0.15/W + 24/W

Where W = wetted width, L = wetted length

Depth: ***Dep***

Pool & Flatwater: If D is < 0.10: 0.0*D
If D is 0.10 - 0.80: (0.30* D - 0.027)/0.17
if D is >0.8: 0.22/0.17
Fastwater: If D is < 0.1: 0.0 * D
If D is 0.10 - 0.16: (0.5*D - 0.5)/0.03
If D is 0.16 - 0.30: (0.29*D - 0.017)/0.03
If D is 0.30 - 0.80: (0.25*D - 0.003)/0.03
If D is 0.80 - 0.90: 0.20/0.03
If D is 0.90 - 1.50: (-0.32*D + 0.485)/0.03
If D is >1.50: 0

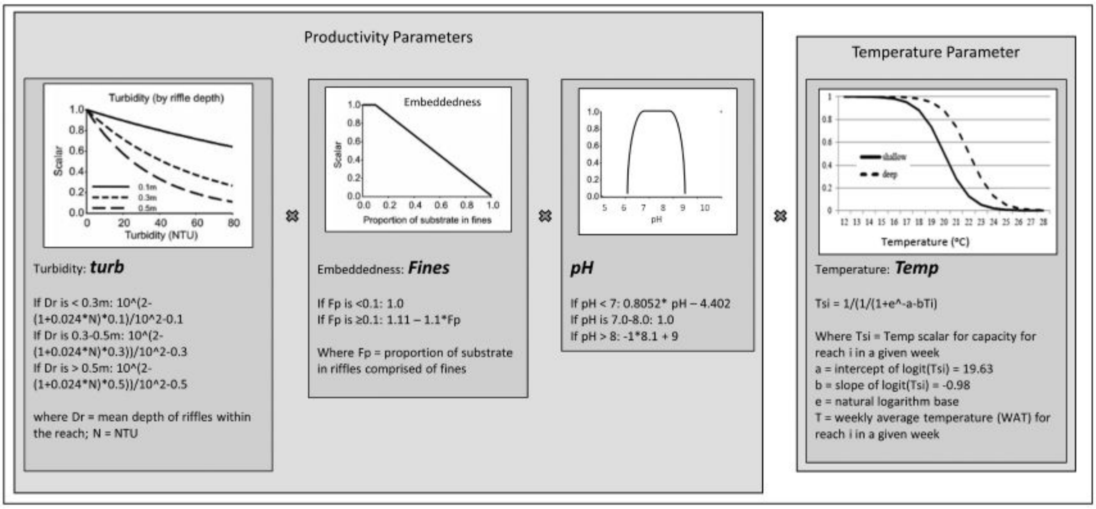
where D = depth in meters

Instream Cover: ***Cvr***

Pool & Flatwater: if wood complexity = 1: 0.58
If wood complexity = 2: 1.00
If wood complexity = 3: 1.42
If wood complexity = 4 or 5: 1.84
Fastwater: if Bpr < 0.25: 1.0
If Bpr is 0.25 – 0.75: 1 + 12 x (Bpr – 0.25)
If Bpr >0.75: 7.0

Where Bpr = proportion substrate in fastwater comprised of boulders

Figure 3a. Model flowchart for stream capacity modeling for juvenile salmonid rearing using the Unit Characteristic Method (UCM), with baseline parameters (Area of habitat unit [e.g., pool, fastwater, flatwater], Den = density) for steelhead trout (ST) and Chinook salmon (CH) as well as unit parameters (Chnl = channel, Dep = depth, Cvr = instream cover) for adjusting capacity with rearing suitability curves. Each curve is presented with its respective equation, and each parameter in bold font within its respective box (adapted from Cramer and Ackerman 2009a, 2009b; Cramer et al. 2012).



Turbidity: ***turb***

If Dr is < 0.3m: 10^(2-(1+0.024*N)*0.1)/10^2-0.1
If Dr is 0.3-0.5m: 10^(2-(1+0.024*N)*0.3))/10^2-0.3
If Dr is > 0.5m: 10^(2-(1+0.024*N)*0.5))/10^2-0.5

where Dr = mean depth of riffles within the reach; N = NTU

Embeddedness: ***Fines***

If Fp is <0.1: 1.0
If Fp is ≥0.1: 1.11 – 1.1*Fp

Where Fp = proportion of substrate in riffles comprised of fines

pH

If pH < 7: 0.8052* pH – 4.402
If pH is 7.0-8.0: 1.0
If pH > 8: -1*8.1 + 9

Temperature: ***Temp***

Tsi = 1/(1/(1+e^-a-bTi)

Where Tsi = Temp scalar for capacity for reach i in a given week
a = intercept of logit(Tsi) = 19.63
b = slope of logit(Tsi) = -0.98
e = natural logarithm base
T = weekly average temperature (WAT) for reach i in a given week

Figure 3b. Model flowchart for stream capacity modeling for juvenile salmonid rearing using the Unit Characteristic Method (UCM), with reach-scale productivity parameters (turb = Turbidity, Fines = Fine Sediment, pH) and temperature parameter (Temp), for adjusting capacity with rearing suitability curves. Each curve is presented with its respective equation, and each parameter in bold font within its respective box (adapted from Cramer and Ackerman 2009a, 2009b; Cramer et al. 2012).

(Equations 2 and 3) in the UCM derived from proxy habitat suitability indices (Figures 3a, 3b) (adapted from Cramer and Ackerman 2009b). The scalar values can be greater than one depending on the suitability curve of the habitat parameter, and a value of one reflects the assumed average condition within a suitability curve. The suitability curves are assumed the same for both Chinook salmon and steelhead trout, but not all scalars are applied to each species (e.g., temperature scalar is not applied to spring-rearing Chinook).

(Eqn 1)

$$\text{Parr Capacity}_i = (\sum \text{area}_k \times \text{den}_j \times \text{chnl}_{jk} \times \text{dep}_{jk} \times \text{cvr}_{jk}) \times \text{prod}_i \times T_{si}$$

Where

i = stream reach. “Reach” is a sequence of channel units that compose a geomorphically homogenous segment (Reach Type) of the stream network,

j = habitat unit type (i.e., pool, fastwater (riffle or cascade), flatwater, or dry),

k = individual habitat unit,

area = wetted area (m^2) of habitat unit k,

den = standard fish density (fish m^{-2}) for a given species in unit type j,

chnl = discount scalar for unproductive portions of large channels,

dep = depth scalar,

cvr = instream cover scalar,

prod = productivity scalar for the reach. This scalar combines the separate effects from three additional factors defined in Equation 2, and

T_{si} = temperature scalar for capacity for reach in a given week (defined in Equation 3)

(Eqn 2)

$$\text{prod}_i = \text{turb}_i \times \text{fines}_i \times \text{pH}_i$$

Where

prod_i = productivity scalar for the reach i is a product of:

turb = turbidity scalar during summer low flow (measured in (measured in Nephelometric Turbidity Units [NTU])

fines = percentage of substrate in riffles composed by fines, and

pH = pH scalar during summer low flow;

(Eqn 3)

$$T_{si} = \frac{1}{1+e^{-a-bT}}$$

Where

T_{si} = Temperature scalar for capacity for reach i in a given week, based on:

e = natural logarithm base

a = intercept of logit(Tsi) = 19.63;

b = slope of logit(Tsi) = –0.98;

T = average maximum temperature for reach i.

Under the assumption of identifying a capacity-limiting life stage for each species of interest, subsequent life stages from the estimated population may then theoretically be calculated based on survival rates between each life stage derived from surrogate fish data in streams with similar fish-habitat relationships. Studies have shown that summer and fall conditions are typically most limiting for juvenile salmonids in regions with hot, dry summers due to rising water temperatures and lowered oxygen levels (Keleher and Rahel 1996), loss of habitat connectivity (Isaak et al. 2007), and an increasing demand for territory size as habitat area diminishes (Cramer and Ackerman 2009a, Ayllon et al. 2012). There was little evidence of availability of low-flow refugia for rearing juveniles upstream of Scott Dam, so our study applied the UCM to evaluate habitat for the steelhead juvenile parr life stage at summertime as most limiting to production. Fall-run Chinook salmon can be limited during upstream migration and spawning when flow conditions are low or when water temperatures are too high, and juveniles may also be limited by winter and spring rearing or emigration conditions (Bartholow and Henriksen 2006, Cramer et al. 2012). Therefore, habitat conditions for both parr and adult life stages of Chinook salmon were analyzed to identify limiting stream conditions for population production in our study area.

The UCM functions were applied to each habitat survey dataset, and estimated density values were averaged among survey reaches within the same Reach Type. Average wetted area per habitat unit type in a Reach Type was extrapolated to unsurveyed streams in corresponding Reach Types for calculating fish density per wetted area. Estimated density values were extrapolated onto remaining unsurveyed streams of corresponding Reach Types for a watershed-scale estimate of potential capacity for juvenile steelhead trout and Chinook salmon. The standard deviation of the average of those varying densities within a grouped Reach Type provided a measure of variability, ultimately expressed as a coefficient of variation (CV). The average density was multiplied by the total area of usable habitat to get the parr capacity (number of fish), and the standard deviation of each Reach Type density was used for expressing variability as CV in the capacity calculations. Despite inherent assumptions from using surrogate density values ("den" in Eqn 1; shown in top three boxes in Figure 3a) derived from six salmonid-bearing watersheds in Oregon (Cramer and Ackerman 2009a, 2009b), the UCM incorporates local habitat conditions by using stream survey data as model inputs, which then adjust a given density value. The UCM also assumes median environmental conditions that typically vary annually, but capturing that variation was beyond the scope of this study. Nonetheless, the UCM provided a tool for estimating capacity based on common field methods for habitat typing salmonid streams.

To estimate potential capacity during spring rearing, hydraulic stream conditions (e.g., velocity, wetted width, and depth) collected during summer low flows were translated to hydraulic conditions for juvenile stream rearing Chinook, which most often rear at highest abundances during May and emigrate during the first two weeks in June. Two studies conducted by Rosenfeld et al. (2007, 2011) compared rates of change in hydraulic conditions at low flows compared to high flows. These hydraulic conditions distinguished individual habitat units at lower flows; however, at higher flows—increasing velocity, wetted width, and depth caused habitat units to be less distinguishable and to contribute less hydraulic control. These rates of change in hydraulic conditions were then quantified specific to habitat unit type (Rosenfeld et al. 2007). Because there are no stream gauges upstream of Scott Dam, USGS stream gauge data collected near the mouth of the Middle Fork Eel (MF Eel) River (USGS 11473900) were used as surrogate streamflow data for our study site. The MF Eel River's watershed characteristics are similar to the upper mainstem Eel River. Mean daily flow data from the Middle Fork gauge were ranked to create a flow exceedance curve by typical peak month of Chinook salmon rearing. Exceedance values were then converted by drainage area to stream sites in the study area. Because this study's stream measurements lacked a temporal resolution representative of spring to summer flow variation, Rosenfeld et al. (2007) rates of hydraulic change specific to habitat unit types were applied to model seasonal flow variability. Assuming 50% exceedance flows for springtime Chinook and steelhead rearing, basic relations for hydraulic geometry from Rosenfeld et al. (2007) and described in Cramer et al. (2012) were applied to predict differences in width and depth at higher flows in the upper mainstem Eel watershed specific to habitat units. Applying these methods with greater exceedance values (lower streamflows) would decrease the converted habitat capacity.

Estimates from the UCM for capacity of steelhead trout and Chinook salmon juveniles were converted from parr to smolts and smolts to adults based on different survival rates, life history variation, juvenile fork length, and the two passage scenarios at Bloody Rock roughs. For Chinook salmon, a survival rate of 76% from parr to smolt was used and a range of smolt to adult survival rates including 1.5%, 3%, and 4% were used to estimate adult returns from juvenile capacity estimates (Lister and Walker 1966, Johnson et al. 1993, Quinn 2005, Klein et al. 2008, Rawding et al. 2010, Cramer et al. 2012). A survival rate of 28% for steelhead trout parr to smolt was used and a range of smolt to adult

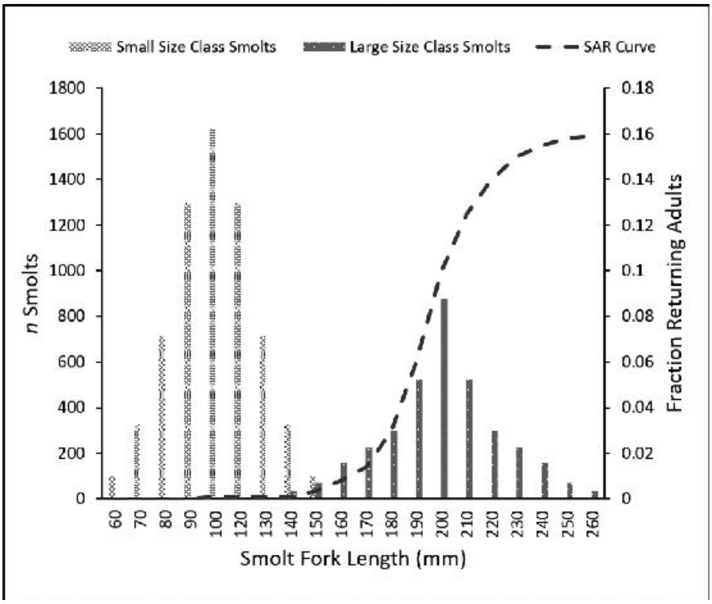


Figure 4. Size class distribution and smolt-to-adult survival rate (SAR) curve used for age 1+ steelhead smolt emigrants modeled from Unit Characteristic Method (UCM) parr estimates in the upper mainstem Eel watershed upstream of Scott Dam. The size distribution shifted to the right (greater number of large smolts) as the proportion of the cohort emigrated at older ages.

survival rates from the literature including 1.5%, 13%, and 20% were used to estimate adult returns from juvenile capacity estimates (Johnson and Cooper 1995, Cramer and Beamesderfer 2002, Quinn 2005, Cramer et al. 2012, Anderson and Ward 2016). In addition to applying static life stage specific survival rates from juvenile to adult, a bimodal fork length frequency distribution among summertime rearing juvenile salmonids that is commonly observed in coastal California watersheds (Zedonis 1992, Engle 2005, SHG 2006, Klein et al. 2008, Mitchell 2010) was imposed on the UCM-estimated steelhead juvenile cohort in our study area above Scott Dam. After the modeled juvenile population was manipulated into reflecting a distribution of size classes, a relationship between smolt-to-adult return and size frequency distribution (Shapovalov and Taft 1954, Klein et al. 2008) was used to calculate an estimate for number of returning steelhead adults in the two passage scenarios upstream of Scott Dam (Figure 4). Greater proportions of the smolt population increasingly occurred within the larger size class of the bimodal distribution. Small to large size distributions were iterated from 65% to 35%, 55% to 45%, 50% to 50%, and 40% to 60%, respectively. The percentage of the cohort emigrating as smolts at different sizes was based on averages of smolt populations in California (Busby et al. 1996) and measures of juvenile emigrants from the upper South Fork Eel River (Connor 1996) and the Van Arsdale Fisheries Station (VAFS) (Day 1962).

Model Comparison and Validation—Historical fish count data from the South Fork Eel River and upper mainstem Eel River were additionally used in an approach to validate the conversion of parr estimates to number of returning adults with life stage specific survival rates suggested by the UCM. In the first step of this analysis, UCM smolt to adult conversion methods (Cramer et al. 2012) were applied to historical juvenile emigrant data at Benbow Dam (CDFG 1939) and historical juvenile emigrant abundance estimates at VAFS reported by CDFG (Day 1962) to estimate a potential number of returning adults, which was then compared to actual number of adults observed migrating up the fish ladder at Benbow Dam and VAFS. Adult counts from three years following emigrant observations were considered potential recruitment years based on North Coast Steelhead population age structure observations (NMFS 2016), although we realize the adult age composition contributes some uncertainty in this consideration for smolt to adult recruitment since steelhead can spend more than three years in the marine stage before returning to streams as adults. The observed adult counts were expected to be higher than the estimated adults due to smolt to adult survival rates changing in response to varied timing of downstream movement among juvenile

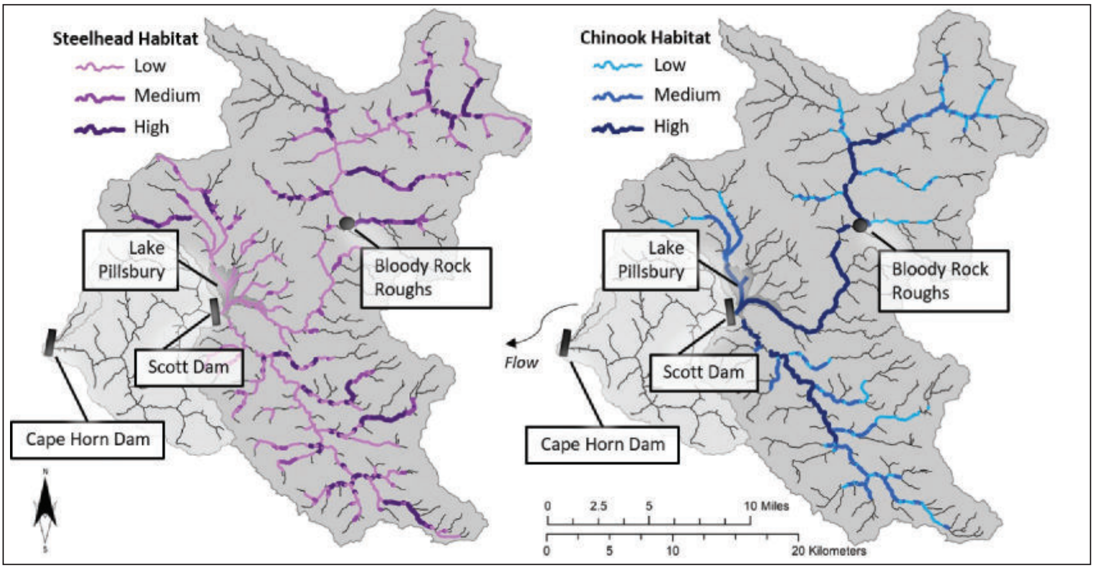


Figure 5. Potential extent of suitable habitat categories for steelhead trout (left) and Chinook salmon (right) upstream of Scott Dam in the Eel River, CA. Darker, thicker habitat streams represent higher suitable habitat relative to field measurements. Habitat upstream of Bloody Rock Roughs was not included in a distribution scenario where the roughs become impassable for upstream migration during very dry years. (NMFS 2016, USGS 2016a). Spatial reference: WGS 84, UTM Zone 10 North.

steelhead (Scheuerell et al. 2009, Tattam et al. 2013), growth during juvenile emigration (Bond et al. 2008), and juvenile size distribution (Tipping et al. 1995, Klein et al. 2008) observed among steelhead trout. Historical juvenile populations observed from streams above Benbow Dam and Van Arsdale were available from some years; those juvenile counts were also converted to density per stream length and compared to densities calculated from modeled juvenile populations in steelhead streams above Scott Dam.

Results

Potential Spawning and Rearing Distribution

Geospatial and ground-based analysis estimated potential spawning and rearing distribution for steelhead trout and Chinook salmon under two fish passage scenarios. Among both fish passage scenarios, potential spawner habitat distribution ranged between 318 and 463 stream-kms for steelhead trout and between 100 and 151 stream-kms for Chinook salmon, depending on passage at Bloody Rock roughs (Figure 5). Using the IP Model (NMFS 2016), we calculated 27 km of stream habitat for steelhead and 16 km for Chinook currently inundated by Lake Pillsbury. In the event the Bloody Rock roughs is a barrier during dry years, 318 km of stream habitat is accessible for steelhead trout and 100 km for Chinook salmon. Reach Types with smaller drainage areas (typically < 2 km^2) that were observed without any summertime surface flow during the field survey season were deemed unsuitable for steelhead summertime rearing. Consequently, stream drainage areas less than 2 km^2 were excluded from potential summertime steelhead rearing habitat and density estimations, erring on the conservative side. This resulted in 178 to 291 stream-kms of summertime rearing habitat for steelhead, depending on adult passage at Bloody Rock roughs. Because Chinook salmon rearing takes place in larger, lower channels earlier in the water year, the amount of rearing habitat is not susceptible to receding headwater habitat. Therefore, the distribution of Chinook salmon rearing habitat was determined to be the same as Chinook adult distribution.

Using NMFS (2016) upper mainstem Eel River population boundaries delineated for CC Chinook and NC steelhead, we estimated the increase in adult population habitat with restored access to the habitat we identified upstream of Scott Dam. The upper mainstem Eel River CC Chinook population boundary is much larger than that of the NC Steelhead population boundary. Restored access upstream of Scott Dam would increase habitat for CC Chinook by up to 16.5% from the currently available 920 stream-kms, but the habitat above Scott Dam compared to habitat in other areas of the CC Chinook upper mainstem Eel boundary is of higher Intrinsic Potential (NMFS 2016). The upper mainstem Eel River NC Steelhead population was estimated to historically occur almost entirely upstream of Scott Dam, so restored access above Scott Dam would add 463 stream-kms habitat to the currently available 2 stream-kms downstream of the dam.

Stream Characterization, Data Collection, and Habitat Data

Out of 31 selected sites, 20 wetted stream reaches totaling 13.2 stream-km were habitat typed and 11 completely dry stream reaches totaling 6.3 stream-km were encountered in the field. Dry stream reaches were not measured for rearing habitat. Surveys included 4.2% and 6.0% of total habitat within potential steelhead trout and Chinook salmon distribution, respectively. Data collected during stream habitat surveys were evaluated by Reach Type with habitat unit composition as well as all other measured variables (Table 1). Linear Discriminant Analysis grouped multiple variables of habitat data from 11 original Reach Types into five Reach Type categories for habitat data extrapolation: 1) small to medium drainage area, high to very high gradient (2–10 km^2 and 10–100 km^2, 7–12% and > 12%); 2) large drainage area, low gradient (> 100km^2, 0–2%); 3) small drainage area, medium to high gradient (2–10km^2, 2–7% and 7–12%); 4) medium drainage area, medium gradient (10–100 km^2, 2–7%); and 5) medium drainage area, low gradient (10–100 km^2, 0–2%,). We chose a linear discriminant model with unit area, unit mean depth, unit instream cover, reach-scale percentage fine substrate, and proportion of habitat unit types as a multivariate explanation for distinguishing Reach Types because this model explained the most variability while capturing the habitat data we collected. The first two discriminant functions explained 89% of the variability in group discrimination, with an overall accuracy of 80% where Reach Types were accurately assigned to discrete groupings of habitat variables (see Supplemental Figure S1, available online). Habitat data extrapolation resulted in relative species-specific habitat suitability symbolized in a map where greater habitat suitability for steelhead trout occurred (Figure 5).

Potential Adult Returns

Amount of stream habitat (km) and number of adults from historical data were compared with those generated from the UCM. Assessments in the past estimated stream habitat kms (Figure 6) and potential abundance (Figure 7) upstream of Scott Dam for Chinook salmon and steelhead trout adults based on spawner data from other areas of the Eel River (CDFG 1979, VTN 1982, USFS and BLM 1995, Becker and Reining 2009, Higgins 2010, NMFS 2016). Annual runs of steelhead trout counted at Benbow Dam Fisheries Station (BDFS) on the South Fork Eel River from years 1938 to 1975 resulted in a median (50th percentile) of 12,664 adults per year and exceeded 14,457 adults per year toward the upper limits of recorded number of fish (90th percentile). Chinook salmon runs at Benbow from years 1938 to 1975 reached a median of 5,016 adults per year and exceeded 14,480 adults (90th percentile) toward the upper limits of recorded number of fish per year. Declining trends in annual runs among datasets from both stations at Benbow Dam and Van Arsdale occurred after water years (October 1 through the next September) 1955 and 1964, presumably in response to the extremely large floods in 1955 and 1964, and greatly increased logging activity (Yoshiyama and Moyle 2010). Periodic trends in adult count data from water years 1955 through 1963 and from 1964 through 1975 were compared to UCM-modeled estimates (Figure 7). Steelhead trout densities from Benbow Dam annual counts were 57 adults$\cdot$km^{-1} among historic highs, 24 adults$\cdot$km^{-1} in water years 1955 through 1963, and 7 adults$\cdot$km^{-1} in water years 1964 through 1975. Chinook salmon densities were 67 adults$\cdot$km^{-1}

TABLE 1. Habitat variables measured in stream surveys conducted for the upper mainstem Eel River watershed upstream of Scott Dam during June to August 2016. Length, width, and depths were measured in meters and averaged at the unit and reach scales (SD in parentheses), ND = no data available.

	Reach Type							
Drainage area	2–10 km^2				10–100 km^2			> 100 km^2
Slope	0–2%	2–7%	7–12%	> 12%	0–2%	2–7%	7–12%	0–2%
Reach Type code	1.2	2.2	3.2	4.2	1.3	2.3	3.3	1.4
No. of surveys	1	3	2	1	4	4	1	4
Habitat variables								
Total reach length (m)	187	1552	902	623	3,615	2545	528	3060
Avg. unit wetted width (m)	2.26 (1.29)	2.67 (0.8)	2.70 (1.06)	1.93 (0.94)	3.60 (2.0)	4.15 (1.58)	3.60 (1.58)	8.67 (3.2)
Avg. unit mean depth (m)	0.18 (0.08)	0.25 (0.11)	0.27 (0.14)	0.20 (0.14)	0.23 (0.15)	0.34 (0.19)	0.32 (0.16)	0.45 (0.28)
Pool max depth (m)	0.38 (0.09)	0.54 (0.22)	0.60 (0.21)	0.48 (0.17)	0.59 (0.22)	0.70 (0.36)	0.59 (0.22)	1.03 (0.55)
Instream shelter (% cover)	37 (27)	48 (25)	29 (14)	31 (20)	36 (23)	22 (21)	63 (25)	54 (19)
Boulder cover (%)	0	21 (18)	16 (10)	24 (16)	14 (12)	14 (14)	41 (23)	23 (19)
Canopy cover (%)	48 (34)	62 (21)	74 (23)	77 (25)	49 (33)	40 (38)	42 (26)	25 (23)
pH	6.5	7.5 (0.5)	6.5	6.5	7.4 (0.5)	7.3 (0.5)	8.2	7.7 (0.6)
Turbidity (NTU)	0.7	0.6 (0.3)	ND	0.71	0.3 (0.1)	0.7 (0.5)	1.2	2.4 (3.3)
Discharge (cfs)	0.15	1.54 (0.71)	0.04 (0.02)	0.05	2.65 (3.78)	2.92 (1.06)	0.63	6.25 (1.82)
Temperature °C	21.4 (1.4)	16.2 (1.2)	14.5 (0.6)	14.9 (1.3)	17.9 (3.3)	15.1 (1.2)	18.2 (1.3)	20.2 (2.8)

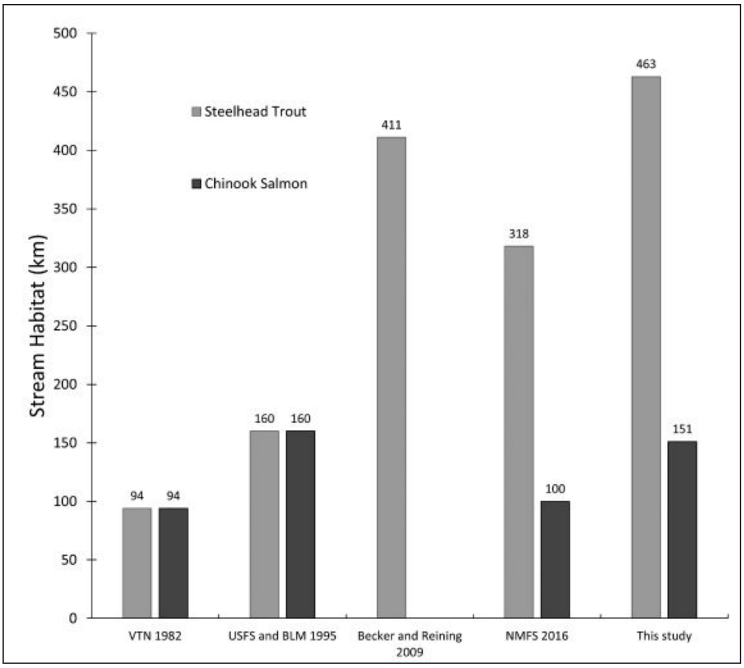


Figure 6. Quantified stream habitat (km) for steelhead trout and Chinook salmon upstream of Scott Dam from four other sources and this study (Cooper et al.).

among historic highs, 7 adults·km^{-1} in water years 1955 through 1963, and 14 adults·km^{-1} in water years 1964 through 1975. Densities calculated from those periods of historical data were applied to the 463 steelhead spawner stream-kms and 151 Chinook spawner stream-kms upstream of Scott Dam (including channels submerged by Lake Pillsbury and access upstream of Bloody Rock roughs), resulting in ranges of 3,241 to 26,391 steelhead trout adults and 1,057 to 10,117 Chinook salmon adults (Figure 7, Tables 2, 3).

Juvenile Capacity Modeling

The UCM resulted in steelhead trout and Chinook salmon parr estimates using surrogate densities adjusted by local habitat parameters measured at unit and reach scales. Density estimates ranged from 0.02 to 0.07 fish·m^{-2} for steelhead trout parr and 0.13 to 0.23 fish·m^{-2} for Chinook salmon parr (Figure 8, Tables 4, 5). After extrapolating estimated densities to corresponding Reach Types at the watershed scale, parr capacity estimates resulted in up to 57,374 (CV 55.9%) steelhead trout (Table 4) and 201,426 (CV 33.5%) Chinook salmon (Table 5) in the area upstream of Scott Dam.

Streams suitable for steelhead trout and Chinook salmon juveniles occurred in different areas. Modeled parr densities were a direct representation of habitat suitability since the densities were calculated based on the suitability curves for each habitat parameter. For steelhead trout parr capacity, the highest estimates were calculated from surveys in tributaries of the mainstem Eel River mostly upstream of Bloody Rock roughs (such as Cold Creek) and along tributaries of the Rice Fork (including upper Bear Creek) (Figure 5). These streams fell into the Reach Type class characterized by medium-sized drainage area (10–100 km^2) and moderate gradient (2–7%) where riffle-pool ratios were high with ample summer base streamflow and maximum temperatures observed below 17 °C. Conversely, relatively high predicted densities (and therefore greater habitat suitability) for Chinook salmon occurred along the mainstem Eel and lower, larger drainage area reaches of the Rice Fork, which are typical-sized reaches for Chinook salmon spawner use and parr occupancy (Quinn 2005) (Figure 5). The spatial distribution of species-specific suitable rearing streams affected capacity estimates between distribution scenarios. Parr capacity estimates in the passage scenario with Scott Dam removal and passage at Bloody Rock roughs were two times higher for steelhead trout and three times higher for Chinook salmon compared to parr capacity estimates in the scenario with Scott Dam removal but no passage at Bloody Rock roughs (Tables 4, 5).

Parr estimates were converted to number of returning adults with ranges depending on various

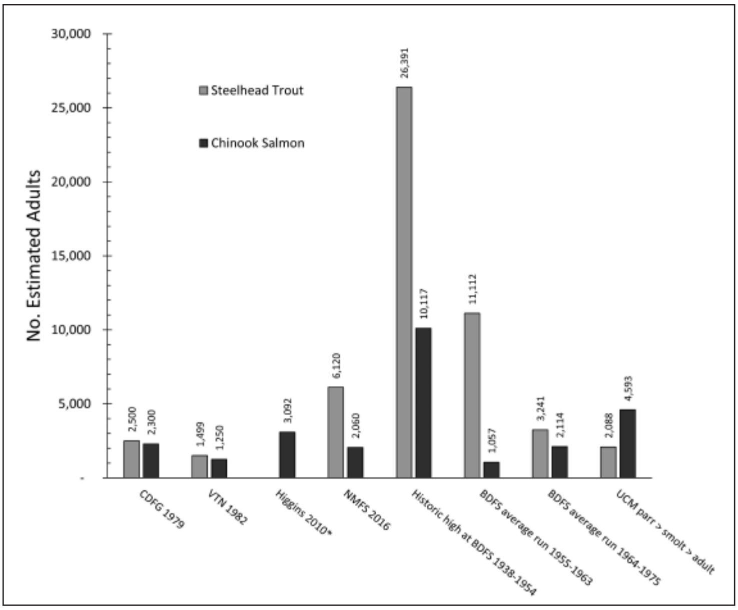


Figure 7. Estimates of potential number of steelhead trout and Chinook salmon adult populations in streams above Scott Dam in the upper mainstem Eel River watershed, CA. First four estimates are from other sources (CDFG 1979, VTN 1982, Higgins 2010, NMFS 2016); the last four were calculated in this study—surrogate adult data at Benbow Dam Fisheries Station (BDFS) on South Fork Eel River during three data periods over time; and modeled estimates for "UCM parr > smolt > adult" = recruited adults calculated from Unit Characteristic Method (UCM) parr capacity of 57,374 steelhead parr × 28% parr to smolt survival rate × 13% ocean survival rate and 201,426 Chinook parr × 76% parr to smolt survival rate × 3% ocean survival rate). *Higgins 2010 reflects estimates of the mainstem Eel River adult Chinook population in streams above Van Arsdale and below Scott Dam.

smolt to adult survival rates (Tables 2, 3). Adult estimates from UCM parr capacities ranged from 1,014 to 2,088 steelhead trout and 1,487 to 4,593 Chinook salmon for the two passage scenarios in the study area. Adults recruited from UCM steelhead juvenile estimates using smolt to adult return curves in relation to smolt size frequency distribution (Figure 4) resulted in up to 1,281 (CV 56%) steelhead trout adults depending on passage scenario and proportion of cohort size distribution frequency (Table 4).

Model Comparison and Validation

Historical steelhead trout emigrant count data from Benbow Dam on the South Fork Eel River in 1939 (CDFG 1939) recorded observations of 23,430 juveniles migrating downstream from April through August. Steelhead trout stream lengths above Benbow Dam were calculated at 443 river-kms (CDFW 2017), resulting in estimates of 52.9 steelhead juveniles per stream-km upstream of Benbow Dam from emigrant count observations. Adult steelhead trout converted from Benbow Dam's 1939 emigrant population resulted in a range of 269, 3046, and 4686 adults calculated with the respective 1.15% (Cramer et al. 2012), 13% (Quinn 2005, Anderson and Ward 2016), and 20% (Moore et al. 2014) smolt to adult survival rates. Observed upstream migrating adults at BDFS from potential steelhead trout adult recruitment years (1940 to 1943) averaged 21,035 adults, which was much greater than the number of adults estimated with surrogate survival rates. CDFG estimated a steelhead trout emigrant population at VAFS from years 1961 to 1962 totaling 47,671 juveniles (Day 1962), converting to a density of 547 juveniles per 87.1 steelhead trout stream-km (6.3 fish km^{-1}) upstream of Van Arsdale and downstream of Scott Dam. Adults recruited from the Van Arsdale emigrant population from 1961 to 1962 resulted in a range of 548, 6197, and 9534 adults calculated with the respective 1.15%, 13%, and 20% smolt to adult survival rates. Observed upstream migrating adults from potential steelhead trout spawner recruitment years at VAFS (1963 to 1966) ranged 423 to 846 adults, which is similar to the recruited adult estimate with a low smolt to adult survival rate. The highest estimate for steelhead trout juveniles modeled with the UCM upstream of Scott Dam was a population of 57,374 parr. These parr converted to 16,065 smolts with a 28% parr to smolt survival rate. Throughout 291

TABLE 2. Potential steelhead trout stream habitat and abundance estimates from historical studies compared to those from this study in the upper mainstem Eel River watershed upstream of Scott Dam. ND denotes no data available.

Steelhead trout Habitat in Stream-km	Steelhead trout Adult Abundance	Source
-	2,500	CDFG 1979, unpublished
94	1,499	VTN 1982
160	ND	USFS and BLM 1995
411	ND	Becker and Reining 2009
318	6,120	NMFS 2016
463	26,391	This study via conversion of historic high adult count data from BDFS in SF Eel
463	11,112	This study via conversion of post-1955 flood adult count data from BDFS in SF Eel
463	3,241	This study via conversion of post-1964 flood adult count data from BDFS in SF Eel
318–463	1,014–2,088	This study via UCM parr capacity[1]

[1] Includes estimates of adults recruited from capacity estimate of 57,374 parr converted with a 28% parr to smolt survival rate and 13% ocean survival rate. Ranges were due to two passage distribution scenarios.

TABLE 3. Potential Chinook salmon stream habitat and abundance estimates from historical studies compared to those from this study in the upper mainstem Eel River Drainage Area upstream of Scott Dam; ND denotes no data available.

Chinook Salmon Habitat in Stream-km	Chinook Salmon Adult Abundance	Source
ND	2,300	CDFG 1979
94	1,250	VTN 1982
160	ND	USFS and BLM 1995
ND	3,092	Higgins 2010[1]
100	2,060	NMFS 2016
151	10,117	This research via conversion of historic high adult count data from BDFS in SF Eel
151	1,057	This research via conversion of post-1955 flood adult count data from BDFS in SF Eel
151	2,114	This research via conversion of post-1964 flood adult count data from BDFS in SF Eel
100–151	1,487–4,593	This research via UCM parr capacity[2]

[1] Includes estimates of adult abundance in streams below Scott Dam and above Cape Horn Dam.

[2] Includes estimates of spawners recruited from capacity estimate of 201,426 parr converted with a 76% parr to smolt survival rate and 3% ocean survival rate. Ranges were due to two passage distribution scenarios.

stream-kms, a density of 55.2 juveniles km^{-1} was estimated for streams above Scott Dam.

Discussion

Summary of Findings

This study estimated habitat for steelhead trout and Chinook salmon upstream of Scott Dam in the upper mainstem Eel River. The National Marine Fisheries Service delineated separate population boundaries for fall-run Coastal California (CC) Chinook and winter-run North Coast (NC) Steelhead in the upper mainstem Eel River (NMFS 2016). Restoring access to the habitat above Scott Dam would increase habitat availability for the upper mainstem Eel River NC steelhead population

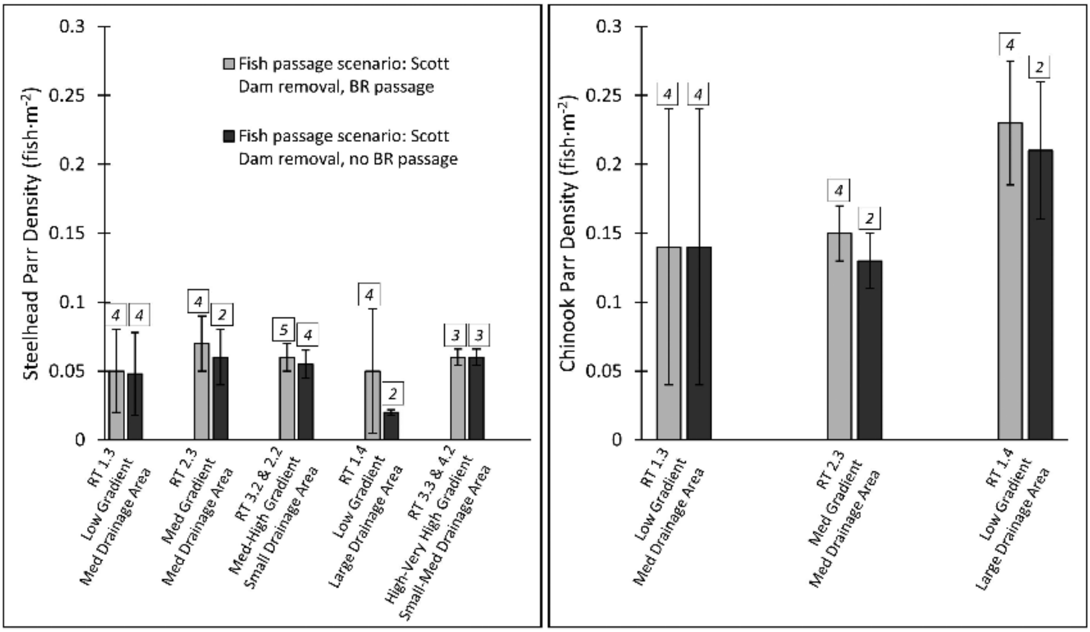


Figure 8. Predicted mean density values for steelhead parr (left) and Chinook parr (right) organized by Reach Type (RT) and estimated with the Unit Characteristic Method (UCM). Light shaded bars represent a distribution scenario with Scott Dam removal, Bloody Rock (BR) roughs passage; dark shaded bars represent a scenario with Scott Dam removal, no BR passage. Error bars represent 1 standard deviation of the mean reach-scale density for surveys within a RT, and number of surveys within each distribution scenario denoted in boxes (note: all surveys did not fall within each species estimated extent and passage scenarios, resulting in varying survey sample sizes in some cases).

by up to 463 stream-kms (from 2 stream-kms currently available), and for the upper mainstem Eel River CC Chinook population by 16.5% (by adding 151 stream-kms to the currently available 920 stream-kms). Because the CC Chinook population boundary is so much larger (1,071 total stream-kms) than the NC Steelhead population boundary (465 total stream-kms), the potential increases with restored access to habitat above Scott Dam are quite different. It is notable, however, that the Intrinsic Potential quantified by NMFS for both species is high, especially for Chinook when compared to other reaches within the CC Chinook population boundary. Those higher IP values are indicative of more suitable, or better quality potential habitat that would support greater fish densities. The salmonid habitat quantified upstream of Scott Dam was applied to different modeling approaches to evaluate potential steelhead trout and Chinook salmon capacity. One approach used historical fish observation data from the upper mainstem Eel River and the South Fork Eel River, resulting in wide ranges of estimated returning adults (Figure 7) for steelhead trout (3,241 to 26,391) and Chinook salmon (1,057 to 10,117). Another approach modeled potential capacity with juvenile habitat conditions limiting fish density that also yielded highly variable estimates for returning adults of 2,088 (CV 55.9%) for steelhead trout and 4,593 (CV 33.5%) for Chinook salmon, depending on various scenarios. The results from these approaches were evaluated to determine potential salmonid habitat capacity with spatial fish distribution scenarios and temporal distribution strategies, and those results were further compared to historical estimates (CDFG 1979, VTN 1982, USFS and BLM 1995, Becker and Reining 2009, Higgins 2010, NMFS 2016) (Figure 7).

Our study identified potential habitat capacity for steelhead trout and Chinook salmon upstream of Scott Dam. Further research is needed on the status of the upper mainstem Eel River popula-

TABLE 4. Steelhead trout parr stratified mean densities (fish/m^2) for the upper mainstem Eel River watershed upstream of Scott Dam. Densities were generated by the Unit Characteristic Method (UCM), along with length of habitat by Reach Type (drainage area, slope; n = number of surveys) streams that fall within steelhead trout parr habitat. Steelhead trout parr capacity is shown in mean stratified density (coefficient of variation in parentheses) and returning adults reflect watershed-scale estimate for each scenario.

	Steelhead Trout Passage Scenario			
	Scott Dam Removal, BR Passage		Scott Dam Removal, No BR Passage	
Reach Type	Mean Density (fish m^{-2})	Stream Habitat (km)	Mean Density (fish m^{-2})	Stream Habitat (km)
RT 1.3 (10–100 km^2, 0–2%; n = 4)	0.05	48.9	0.05	36.8
RT 2.3 (10–100 km^2, 2–7%; n = 4)	0.07	51.6	0.06	27.5
RT 3.2 and 2.2 (2–10 km^2, 2–12%; n = 5)	0.06	97.1	0.06	72.8
RT 1.4 (> 100 km^2, 0–2%; n = 4)	0.05	61.9	0.02	22.9
RT 3.3 and 4.2 (2–100 km^2, > 7%; n = 2)	0.06	31.7	0.06	18.6
Total Stream-km		291.2		178.4
Parr Capacity	57,374 (55.9%)		27,848 (35.8%)	
Returning adults from parr capacity with SAR[1] curve	1,281		622	

[1] SAR= Smolt to Adult Return based on outmigrant size class

TABLE 5. Chinook salmon parr mean densities for the upper mainstem Eel River watershed upstream of Scott Dam. Densities were generated by the Unit Characteristic Method (UCM) and length of habitat by Reach Type (drainage area, slope; n = number of surveys) streams that fall within Chinook salmon parr habitat. Chinook salmon parr capacity is shown in mean stratified density (coefficient of variation in parentheses) and returning adults reflect watershed-scale estimate for each scenario.

	Chinook Salmon Passage Scenario			
	Scott Dam Removal, BR Passage		Scott Dam Removal, No BR Passage	
Reach Type	Mean Density (fish m^{-2})	Stream Habitat (km)	Mean Density (fish m^{-2})	Stream Habitat (km)
RT 1.3 (10–100 km^2, 0–2%; n = 4)	0.14	51.6	0.14	26.0
RT 2.3 (10–100 km^2, 2–7%; n = 4)	0.15	48.9	0.13	35.1
RT 1.4 (> 100 km^2, 0–2%; n = 4)	0.23	50.9	0.21	38.9
Total Stream-km		151.4		100.0
Parr Capacity	201,426 (33.5%)		65,200 (29.0%)	
Returning adults from parr capacity with 76% parr to smolt survival and 3% marine survival rates	4,593		1,487	

tions that currently persist downstream of Scott Dam to determine the overall potential increase in population production upon recolonization of streams above the dam, potential downstream source populations for recolonization, as well as potential downstream impacts on watershed processes upon removal of Scott Dam. A long-term, watershed-scale approach with local fish-habitat relationships including biotic and abiotc factors would aid in better determining changes in population production and salmonid recovery from removal of Scott Dam.

Evaluation of Estimates with Reference to Historical Data

Modeled estimates of adult steelhead and Chinook salmon returns to the upper Eel River were compared with surrogate historical estimates from the Benbow Dam Fisheries Station from 1938 to 1975. This provided a comparison for identifying limiting life stages for both species in the habitat above Scott Dam, which presumably is limited by summertime rearing. Estimated adult returns for steelhead trout converted from UCM parr capacities were 16% to 92% less than historical estimates; yet Chinook salmon estimates converted from UCM parr capacities were 0.49 to 3.27 times the historical estimates, except for the BDFS 1938 to 1954 counts, where the UCM estimate for Chinook was 55% less than the historic high (Figure 7).

Evaluation of the UCM

The spatial distribution of predicted parr densities varied between steelhead trout and Chinook salmon. Based on relative modeled densities, the most suitable rearing habitat (Table 4,) for steelhead occurred in medium sized, medium gradient (10–100 km^2, 2–7%; RT 2.3) tributaries, and for Chinook salmon occurred in larger, lower gradient (> 100 km^2, 0–2%; RT 1.4) reaches (Table 5). The lack of spatial overlap for habitat use combined with varying temporal habitat use between steelhead and Chinook juveniles implies the importance of varying reaches throughout the upper Eel watershed for the benefit of both species.

While the UCM provided useful estimates of salmonid stream rearing capacity in our study area, we identified some assumptions, sensitivities, and uncertainties that impacted the model's utility for this study. The range of predicted parr densities within Reach Types (Figure 8) directly reflects the range of habitat conditions measured within Reach Types. Reach Types with low gradient and medium-large drainage areas were the most sensitive to temperature and fine sediment parameters. More surveys among stratified Reach Types over several survey seasons would capture more variation within and between Reach Types, thus better representing the salmonid habitat and potential parr capacity. Additionally, the conversion of UCM parr estimates to adults was highly sensitive to life stage-specific survival rates as well as size of outmigrants, which were derived from various literature sources (Johnson et al. 1993, Quinn 2005, Klein et al. 2008, Rawding et al. 2010, Cramer et al. 2012). Steelhead trout have over 30 anadromous life history strategies (Moore et al. 2014). Our estimates used a subset of freshwater rearing life histories typical for coastal California steelhead trout juveniles (Busby et al. 1996) for calculating conversions from estimated steelhead trout parr to adults. However, a more locally specified representation of the freshwater rearing strategies (including rainbow trout taking up residence) as well as size distribution among juveniles leaving the upper Eel River and among juveniles entering the ocean would result in different estimates for subsequent adult steelhead trout numbers. Chinook salmon parr estimates are also subject to uncertainty with the assumption that spring rearing conditions are at median flows. Adding to the UCM a range of habitat availability in response to flow variation from yearly hydrographs would affect rearing capacity estimates. Survival rates in response to juvenile size distribution and outmigration growth are also needed for Chinook salmon in the Eel River to better represent potential adult returns.

Model Comparison, Validation, and Effects of Underlying Assumptions

The disparity between adults observed in historical data versus those converted from UCM parr capacity is likely explained by some underlying model assumptions. There were substantially higher steelhead adults observed at BDFS and VAFS versus steelhead adults converted from UCM-generated smolts (Figure 7). One underlying assumption for calculating number of adults from UCM parr capacity is that rearing habitat limits population production and adults are recruited only from natal-rearing juveniles. Adult estimates from historical data however, potentially include adult recruitment either from natal and non-natal rearing juveniles or from returning adults greater in number than capacity of habitat. Consequently, model assumptions infer substantial population contribution from non-natal rearing habitat, therefore suggesting density dependent juvenile movement and growth downstream of the study area.

The assumption for a uniform size and therefore uniform survival rate across all parr or smolts modeled from the UCM compared to using a smolt to adult return rate curve greatly impacted estimates of returning adults. A range of parr to smolt and smolt to adult survival rates from the literature were used in an effort to capture some variability. While larger salmonid juveniles typically have higher marine survival and adult return rates than smaller juveniles (Tipping 1997, FERC 2000, Zabel and Achord 2004, Bond et al. 2008, Klein et al. 2008), there is also mortality associated with every year spent in freshwater (Quinn 2005, Cramer et al. 2012). Although steelhead juveniles residing in freshwater longer may not grow as much as their first year of freshwater rearing, Klein et al. (2008) estimated an exponential increase in number of returning adults with increasing smolt size > 140 mm based on smolt and adult return data (Kabel and German 1967) from the Cedar Creek Experimental Hatchery in the South Fork Eel River.

Observations of more adults returning from a juvenile cohort than expected may reflect annual variability but may also be explained by density-dependent movement of juveniles to non-natal parts of the watershed downstream of the Scott Dam location. Upon recolonization of salmonids, the habitat upstream of Scott Dam could reach spawning capacity, subsequently allowing a saturation of the seedbank for egg recruits. Although modeled rearing habitat capacity suggests that rearing conditions in the study site are more limited for salmonid production than spawning conditions, a proportion of the recruits from a highly seeded spawning population could seek available habitat elsewhere, migrating downstream. Such juvenile movement in response to instream rearing conditions was observed among Chinook salmon in the Shasta River, CA (Roddam and Ward 2015). Furthermore, studies have shown benefits for juvenile salmonids that utilize estuarine habitats whose productive environments are conducive to high growth rates for rearing juveniles (Zedonis 1992, Bond et al. 2008, Daly et al. 2014). Successful downstream migration and growth in turn produces larger smolts entering the ocean with greater chances of survival and higher numbers of returning adults (Reimers 1971, Ward and Slaney 1988, Ward et al. 1989, Koenings et al. 1993, Hayes et al. 2011).

Observed steelhead trout emigrant estimates from VAFS in the early 1960s (Day 1962) were much higher than UCM-generated juvenile estimates (547.0 fish km^{-1} above VAFS and below Scott Dam vs 55.1 fish km^{-1} modeled above Scott Dam). The lower density of subsequent returning adults from observations in years 1963 to 1966, may in part be attributed to disturbances from the 1964 flood and therefore potentially misrepresentative of return rates for modeling purposes. Those historically observed juvenile density data are useful in that they suggest the streams above Scott Dam may be able to support higher juvenile capacities than what was estimated with the UCM. In addition to historical data, modern fish abundance data in the upper Eel River are needed for model validation.

Further efforts for improving models should compare habitat above Scott Dam to accessible, colonized habitat below the dam or in nearby Black Butte River of the Middle Fork Eel. This would reduce uncertainties in extrapolating habitat data to reach type classifications. Salmonid monitoring in those streams would also allow fish density-habitat relationships to be developed for a localized representation of habitat-density suitability relationships in the upper Eel River. Curves developed by locally observed fish density-habitat relationships could in turn be applied to salmonid habitat capacity models in streams above Scott Dam. Finally, quantification of return and stray rates among upper Eel River DPS and ESU populations of steelhead trout and Chinook salmon would provide a better understanding of recolonization potential on a metapopulation scale, as assessed by Pess et al. (2014).

Study Improvements with a Holistic Approach

There is room for improvement in understanding salmonid recolonization response not only upstream of Scott Dam, but also to responses downstream of the dam in the event of dam removal, modified passage, or adaptive flow management. Passage restoration via means other than dam removal (e.g., via ladder, or trap and haul techniques), must also quantify reservoir impacts on inundation of spawning and rearing habitat, migration conditions, water quality, and non-native invasive Sacramento pike-minnow (*Ptychocheilus grandis*) predation on juvenile salmonids. Furthermore, alternatives to dam removal such as trap and haul, although widely implemented, have been ineffective for wild salmonid recovery and are not recommended for California rivers (Lusardi and Moyle 2017). Recolonization of steelhead and salmon to habitat upstream of Scott Dam would likely aid in population recovery, and managers who strive for salmonid recovery in the Eel River should prioritize the most effective restoration strategy for long-term population production.

Another consideration is that the habitat above Scott Dam may be of higher quality compared to other areas of the Eel River watershed and reconnecting this habitat to downstream waters could facilitate habitat changes on a larger, watershed scale. Mesohabitat studies show the importance of preserving the connection of headwater streams to lower areas of a watershed for transport and duration of water and sediment supply (Alexander et al. 2007, Meyer et al. 2007). Furthermore, connection to headwater streams affects the timing and spatial transport of nutrient cycling which in turn affects primary and secondary production and ultimately fish food supply (Meyer et al. 2007). Throughout a stream network, headwater streams are most abundant, smaller in size, and steeper in gradient, thereby increasing interaction between flowing water and surrounding land area (Likens and Bormann 1974, Polis et al. 1997). Such nutrient cycling and land-water interaction as with allochthonous energy inputs from confined, denser riparian canopies in headwater streams is demonstrated in the river continuum concept (Vannote et al. 1980). In addition to headwater streams functioning and interacting differently than larger drainages, headwater streams provide high habitat diversity which in turn promotes niches for biodiversity (Lowe and Likens 2005). This study identified high-elevation headwater tributaries in federally protected lands draining Hull and Snow Mountains, which can provide cold water habitat important for summertime salmonid rearing. Restoring the watershed-scale roles of the mainstem Eel River headwaters to downstream areas by removing Scott Dam has potential for improving salmonid habitat capacity both up- and down-stream of the barrier.

Conclusion

Potential distribution of Chinook salmon and steelhead trout in the waterways upstream of Scott Dam was mapped, and potential production under two distribution scenarios was estimated. We reviewed past and current methods for estimating potential salmonid habitat and production in the upper mainstem Eel River watershed along with ground-based surveys. The habitat in the upper mainstem Eel River watershed provides cold-water refugia in tributaries over summertime for steelhead trout as well as ample spawning grounds for Chinook salmon and steelhead trout. The UCM provided a useful interpretation of habitat conditions and how they relate to potential salmonid capacity, as well as allowing spatial identification of the quantity and quality of potential stream rearing habitat upstream of Scott Dam. Despite limited modern data in the upper Eel River, historical adult count data from Benbow Dam and Van Arsdale in the Eel River provided a useful comparison to the UCM approach.

NMFS (2016) found that habitat historically used by the upper mainstem Eel River steelhead population was almost entirely comprised of habitat upstream of Scott Dam. Thus restoring access to the habitat we identified upstream of the dam for steelhead would greatly aid in the recovery of that population. Restoring upper Eel River Chinook access to the habitat upstream of Scott Dam would increase habitat availability by 16.5%, much of which is considered high quality habitat compared to other reaches within that population's boundary. Habitat upstream of Scott Dam includes exposure to conditions that support localized adaptations and life history plasticity important to long-term persistence of Pacific salmonids (Spence et al. 2008). Evidence from counts at Van Arsdale Fisheries Station over the past 20 years shows declining trends in annual salmon and steelhead runs (FOER 2017). Increasing overall salmonid production such as with colonization of reopened streams above Scott Dam would likely increase average annual production upstream of VAFS substantially. Despite discrepancies in efforts to quantify potential number of fish that may recolonize streams above Scott Dam, this study found that restoring access to the habitat above Scott Dam with dam removal would provide habitat suitable for aiding recovery of upper mainstem Eel River salmonid populations.

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Literature Cited

Agrawal, A., R. S. Schick, E. P. Bjorkstedt, R. G. Szerlong, M. N. Goslin, B. C. Spence, T. H. Williams, and K. M. Burnett. 2005. Predicting the potential for historical coho, Chinook salmon, and steelhead trout habitat in northern California. US Dept of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-379. National Marine Fisheries Service, Santa Cruz, CA.

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

Alexander, R. B., E. W. Boyer, R. A. Smith, G. E. Schwarz, and R. B. Moore. 2007. The role of headwater streams in downstream water quality. Journal of American Water Resources Association 43:41-59.

Anderson, C. W., and D. Ward. 2016. Results of Freshwater Creek salmonid life cycle monitoring station 2015–2016. Humboldt State University Department of Fisheries Biology, Arcata, CA.

Asarian, E. 2016. Long-term trends in streamflow and precipitation in northwest California and southwest Oregon. Journal of American Water Resources Association 52:241-261.

Ayllon, D., A. Almodovar, G. G. Nicola, I. Parra, and B. Elvira. 2012. Modelling carrying capacity dynamics for the conservation and management of territorial salmonids. Fisheries Research 136:95-103.

Bartholow, J. M., and J. A. Henriksen. 2006. Assessment of factors limiting Klamath River fall Chinook salmon production potential using historical flows and temperatures. US Geological Survey Open File Report 2006-1249, in cooperation with the US Fish and Wildlife Service. US Department of Interior, Reston, VA.

Becker, G. S., and I. J. Reining. 2009. Steelhead trout/rainbow trout (*Oncorhynchus mykiss*) resources of the Eel River watershed, California. Cartography by D. A. Asbury. Center for Ecosystem Management and Restoration, Oakland, CA.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242-2252.

Brewitt, P. K. 2016. Do the fish return? A qualitative assessment of anadromous Pacific salmonids' upstream movement after dam removal. Northwest Science 90:433-449.

Brown, W. M., and R. J. Ritter. 1971. Sediment transport and turbidity in the Eel River basin, California. Geological Survey Water-Supply Paper 1986. US Government Printing Office, Washington, DC.

Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27. US Dept of Commerce, Springfield, VA.

[CDFG] California Department of Fish and Game. 1938. Stream survey reports for the Eel River and tributaries upstream of Lake Pillsbury in 1938. California Department of Fish and Game, Region III, Yountville.

[CDFG] California Department of Fish and Game. 1939. Benbow Dam stream steelhead downstream fish taken in trap in south fishway. California Department of Fish and Game, Arcata.

[CDFG] California Department of Fish and Game. 1975. Stream survey reports for the Eel River and tributaries upstream of Lake Pillsbury. California Department of Fish and Game, Region III, Yountville.

[CDFG] California Department of Fish and Game. 1939–1941, 1970–1971. Benbow Dam fish station monitoring diaries. California Department of Fish and Game, Arcata.

[CDFG] California Department of Fish and Game. 1979. Potter valley project, FERC 77: relicensing recommendations of the California Department of Fish and Game. Presented at Potter Valley Project Settlement Conference on May 24, 1979. FERC, San Francisco, CA.

[CDFW] California Department of Fish and Wildlife. 2004. California Salmonid Stream Habitat Restoration Manual, Part III. California Department of Fish and Wildlife, Water Resources Division, Sacramento.

[CDFW] California Department of Fish and Wildlife. 2017. Steelhead trout distribution GIS stream layer. Unpublished data available online at https://www.calfish.org/ProgramsData/Species/AnadromousFishDistribution.aspx (accessed June 2017).

Cid, N., N. Bonada, S. Carlson, and V. Resh. 2017. High variability is a defining component of Mediterranean-climate rivers and their biota. Water 9:52-76.

Connor, E. J. III. 1996. Comparative evaluation of Pacific giant salamander and steelhead trout populations among streams in old-growth and second-growth forests of Northwest California. Ph.D. Dissertation, University of California, Berkeley.

Cooper, A. B., and M. Mangel 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fishery Bulletin 97:213-226.

Cramer, S. P., and R. C. P. Beamesderfer. 2002. Population dynamics, habitat capacity, and a life history simulation model for steelhead in the Deschutes River, Oregon. Prepared for Portland General Electric, 121 SW Salmon Street, Portland, Oregon.

Cramer, S. P., and N. K. Ackerman. 2009a. Linking stream carrying capacity for salmonids to habitat features. *In* E. E. Knudsen and J. H. Michael Jr. (editors), American Fisheries Society Symposium 71, American Fisheries Society, Bethesda, MD. Pp. 225-254.

Cramer, S. P., and N. K. Ackerman. 2009b. Prediction of stream carrying capacity for steelhead trout: the Unit Characteristic Method. *In* E. E. Knudsen and J. H. Michael Jr. (editors), American Fisheries Society Symposium 71, American Fisheries Society, Bethesda, MD. Pp. 255-288.

Cramer, S. P., J. Vaughan, M. Teply, and S. Duery. 2012. Potential gains in anadromous salmonid production from restoration of Beaver Creek (Sandy River Basin, Oregon). Unpublished report on file at US Army Corps of Engineers, Portland, OR.

Day, J. S. 1962. A study of downstream migration of fish past Cape Horn Dam on the upper Eel River, Mendocino County, as related to the Pacific Gas and Electric Company's Van Arsdale Diversion. Marine Resources Administrative Report No. 68-4. California Department of Fish and Game, Arcata.

Daly, E. A., J. A. Scheurer, R. D. Brodeur, L. A. Weitkamp, B. R. Beckman, and J. A. Miller. 2014. Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 6:62-80.

Engle, R. O. 2005. Distribution and summer survival of juvenile steelhead trout (*Oncorhyncus mykiss*) in two streams within the King Range National Conservation Area, California. M.S. Thesis, Humboldt State University, Arcata, CA.

[ERCZO] Eel River Critical Zone Observatory. 2016. Eel River GIS data hub. Available online at http://criticalzone.org/eel/ (accessed April 2016).

[FERC] Federal Energy Regulatory Commission. 2000. Proposed changes in minimum flow requirements at the Potter Valley Project, Final Environmental Impact Statement, FERC Project No. 77–110, California. FERC-EIS-0119F. Federal Energy Regulatory Commission, Washington, DC.

[FOER] Friends of the Eel River. 2017. Van Arsdale Fisheries Station upstream migrant counts. Unpublished data available online at https://eelriver.org/wp-content/uploads/2020/02/Fish_Counts_PVP_1933-2018.pdf (accessed March 2017).

Gallagher, S. P., J. Ferreira, E. Lang, W. Holloway, and D. W. Wright. 2014. Investigation of the relationship between physical habitat and salmonid abundance in two coastal northern California streams. California Fish and Game 100:683-702.

Hanrahan, T. P., D. D. Dauble, and D. R. Geist. 2004. An estimate of Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat and redd capacity upstream of a migration barrier in the upper Columbia River. Canadian Journal of Fisheries and Aquatic Science 61:21-33.

Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, R. B. MacFarlane. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Canadian Journal of Fisheries and Aquatic Science 68:1341-1350.

Hendry A. P., V. Castric, M. T. Kinnison, T. P. Quinn. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. *In* A. P. Hendry and S. C. Stearns (editors), Evolution Illuminated: Salmon and Their Relatives, Oxford University Press, Oxford. Pp. 52-91.

Higgins, J. V., M. T. Bryer, M. L. Khoury, and T. W. Fitzhugh. 2005. A freshwater classification approach for biodiversity conservation planning. Conservation Biology 19: 432-445.

Higgins, P. 2010. Final Eel River fall Chinook monitoring 2010 report. Friends of the Eel River, Arcata, CA.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences (US) 100:6564-6568.

Hill, M. F., A. Hastings, and L. W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. American Naturalist 160:389-402.

Isaak, D. J., R. F. Thurrow, B. E. Rieman, and J. B. Dunham. 2007. Chinook salmon use of spawning patches: relative roles of habitat quality, size, and connectivity. Ecological Applications 17:352-364.

Johnson, S. L., M. F. Solazzi, and J. D. Rodgers. 1993. Development and evaluation of techniques to rehabilitate Oregon's wild salmonids. Annual Progress Report, Fish Research Project F-125-R-5. Oregon Department of Fish and Wildlife, Portland.

Johnson, S. L., M. F. Solazzi, and J. D. Rodgers. 1993. Development and evaluation of techniques to rehabilitate Oregon's wild salmonids. Annual Progress Report, Fish Research Project F-125-R-5. Oregon Department of Fish and Wildlife, Portland.

Kabel, C. S., and E. R. German. 1967. Some aspects of stocking hatchery-reared steelhead and silver salmon. Marine Resources Administrative Report No. 67-3. California Department of Fish and Game, Sacramento.

Keefer, M. L., C. C. Caudill, C. A. Peery, and S. R. Lee. 2008. Transporting juvenile salmonids around dams impairs adult migration. Ecological Applications 18:1888-1900.

Keefer, M. L., C. A. Peery, J. Firehammer, and M. L. Moser. 2005. Straying rates of known-origin adult Chinook salmon and steelhead within the Columbia River basin, 2000–2003. Idaho Cooperative Fish and Wildlife Research Unit Technical Report 2005-5. US Army Corps of Engineers, Portland, OR.

Keleher, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the rocky mountain region and potential habitat loss due to global warming: A geographic information systems (GIS) approach. Transactions of the American Fisheries Society 125:1-13.

Kincaid, T., T. Olsen, and M. T. Kincaid. 2012. Package 'spsurvey'. Available online at http://cran.univ-paris1.fr/web/packages/spsurvey/spsurvey.pdf (accessed 15 November 2016).

Klein, R., W. Trush, and M. Buffleben. 2008. Watershed condition, turbidity, and implications for anadromous salmonids in north coastal California streams. Unpublished report on file, California North Coast Regional Water Quality Control Board, Santa Rosa.

Koenings, J. P., H. J. Geiger, and J. J. Hasbrouck. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effect of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50:600-611.

Lane, B. A., and S. Sandoval-Solis. 2014. A regional hydrologic classification of unregulated rivers: towards the development of natural flow regime characterization and environmental flows in California. M.S. Thesis, University of California, Davis.

Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. BioScience. 24:447-456.

Lister, D. B., and C. E. Walker. 1996. The effect of flow control on freshwater survival of chum, Coho, and Chinook salmon in the Big Qualicum River. The Canadian Fish Culturalist 37:3-25.

Lisle, T. E. 1990. The Eel River, Northwestern California: high sediment yields from a dynamic landscape. *In* M. G. Wolman and H. C. Riggs (editors), Surface water hydrology 0-1: The geology of North America. Geological Society of North America, Boulder, CO. US Forest Service, Pacific Southwest Station. Pp. 311-314. Available online at https://www.fs.fed.us/psw/publications/lisle/lisleGSA90.pdf (accessed 18 January 2016).

Lowe, W. H., and G. E. Likens. 2005. Moving headwater streams to the head of the class. BioScience 55:196-197.

Lusardi, R. A., and P. B. Moyle. 2017. Two-way trap and haul as a conservation strategy for anadromous salmonids. Fisheries 42:478-487.

Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association 43:86-103.

Mitchell, W. T. 2010. Age, growth, and life history of steelhead rainbow trout (*Oncorhynchus mykiss*) in the lower Yuba River, California. Unpublished report on file, ICF International, Sacramento, CA.

Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life history diversity and its importance to population stability and persistence of a migratory fish: steelhead trout in two large North American watersheds. Journal of Animal Ecology 83:1035-1046.

Moyle, P. B., R. A. Lusardi, P. J. Samuel, and J. V. E. Katz. 2017. State of the salmonids: status of California's emblematic fishes. A report commissioned by California Trout. Center for Watershed Sciences, University of California, Davis.

[NMFS] National Marine Fisheries Service. 2016. Final Coastal Multispecies Recovery Plan for California Coastal Chinook Salmon, Northern California Steelhead and Central California Coast Steelhead. US Dept of Commerce, National Oceanic Atmospheric Administration, National Marine Fisheries Service, Santa Rosa, CA.

O'Farrell, M., W. H. Satterthwaite, B. C. Spence. 2012. California Coastal Chinook salmon: Status, data, and feasibility of alternative fishery management strategies. US Dept of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-494. National Marine Fisheries Service, Santa Cruz, CA.

Pess G. R., T. J. Beechie, J. E. Williams, D. R. Whitall, J. I. Lange, and J. R. Klochak. 2003. Watershed assessment techniques and the success of aquatic restoration activities. *In* R. C. Wissmar and P. A. Bisson (editors), Strategies for Restoring River Ecosystems: Sources of Variability and Uncertainty in Natural and Managed Systems, American Fisheries Society, Bethesda, MD. Pp. 185-201.

Pess G. R., R. Hilborn, K. Kloehn, and T. P. Quinn. 2012. The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Science 69:970-982.

Pess, G. R., M. L. McHenry, T. J. Beechie, and J. Davies. 2008. Biological impacts of the Elwha River dams and potential salmonid responses to dam removal. Northwest Science. 82(sp1):72-90.

Pess, G. R., T. P. Quinn, S. R. Gephard, and R. Saunders. 2014. Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal. Reviews in Fish Biology and Fisheries 24:881-900.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:298-316.

[PVID] Potter Valley Irrigation District. 2017. Van Arsdale Fish Counts. Potter Valley Irrigation District, Potter Valley, CA. Available online at http://www.pottervalleywater.org/van_arsdale_fish_counts.html (accessed 15 June 2017).

Quinn, T. P. 1984. Homing and straying in Pacific salmon. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill (editors), Mechanisms of Migration in Fishes, Plenum Publishing Corporation, NY. Pp. 357-362.

Quinn, T. P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fisheries Research 18:29-44.

Quinn, T. P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. University of Washington Press, Seattle.

R Core Team. 2017. R: a language and environment for statistical computing. R. Foundation for Statistical Computing, Vienna, Austria. Available online at http://www.r-project.org/index.html (accessed February 2017).

Rawding, D., T. Cooney, and C. Sharpe. 2010. Life history of Tule fall Chinook salmon in lower Columbia River tributaries with estimates of juvenile survival, intrinsic productivity, and capacity from life cycle studies. Washington Department of Fish and Wildlife, Olympia.

Reimers, P. E. 1971. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Ph.D. Dissertation. Oregon State University, Corvallis.

Roddam, M., and D. Ward. 2015. Life-history differences of juvenile Chinook salmon *Oncoryhnchus tshawytscha* across rearing locations in the Shasta River, California. Ecology of Freshwater Fish 26:150-159.

Roni, P., G. Pess, T. Beechie, and S. Morley. 2010. Estimating changes in coho salmon and steelhead abundance from watershed restoration: how much restoration is needed to measurably increase smolt production? North American Journal of Fisheries Management 30:1469-1484.

Rosenfeld, J. S., K. Campbell, E. S. Leung, J. Bernhardt, and J. Post. 2011. Habitat effects on depth and velocity frequency distributions: implications for modeling hydraulic variation and fish habitat suitability in streams. Geomorphology 130:127-135.

Rosenfeld, J. S., J. Post, G. Robins, and T. Hatfield. 2007. Hydraulic geometry as a physical template for the River Continuum: application to optimal flows and longitudinal trends in salmonid habitat. Canadian Journal of Fisheries and Aquatic Science 64:755-767.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhychus* spp.). Journal of Applied Ecology 46:983-990.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. Fish Bulletin 98. California Department of Fish and Game, Sacramento.

Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia River basins. Transactions of American Fisheries Society 135:1654-1659.

[SHG] Swanson Hydrology and Geomorphology. 2006. Arroyo Grande Creek steelhead distribution and abundance survey. Unpublished report on file at Central Coast Salmon Enhancement, Arroyo Grande, CA.

Spence, B. C., E. P. Bjorkstedt, J. C. Garza, J. J. Smith, D. G. Hankin, D. Fuller, W. E. Jones, R. Macedo, T. H. Williams, and E. Mora. 2008. A framework for assessing the viability of threatened and endangered salmon and steelhead trout in the north-central California coast recovery domain. US Dept of Commerce, NOAA Technical Memorandum NMFS-SWFSC-423. National Marine Fisheries Service, Santa Cruz, CA.

Stillwater Sciences. 2013. Modeling habitat capacity and population productivity for spring-run Chinook Salmon and steelhead trout in the Upper Yuba River watershed. Revised Technical Report. National Marine Fisheries Service, Santa Rosa, CA.

Tattam, I. A., J. R. Ruzycki, H. W. Li, and G. R. Giannico. 2013. Body size and growth rate influence emigration timing of *Oncorhynchus mykiss*. Transactions of American Fisheries Society 142:1406-1414.

Tipping, J. M. 1997. Effect of smolt length at release on adult returns of hatchery-reared winter steelhead. The Progressive Fish-Culturalist 59:310-311.

Tipping, J. M., R. V. Cooper, J. B. Byrne, and T. H. Johnson. 1995. Communications: length and condition factor of migrating and nonmigrating hatchery-reared winter steelhead smolts. The Progressive Fish-Culturalist 57:120-123.

US Climate Data. 2017. Climate Potter Valley, California. Available online at https://www.usclimatedata.com/climate/potter-valley/california/united-states/usca0899 (accessed November 2017).

[USFS and BLM] US Forest Service and Bureau of Land Management. 1995. Watershed analysis report for the Eel River watershed. USDA Forest Service and USDI Bureau of Land Management. Unpublished document on file at Mendocino National Forest, Willows, CA.

[USFWS] US Fish and Wildlife Service. 2011. Flow-habitat relationships for fall-run Chinook salmon and steelhead trout/rainbow trout spawning in Clear Creek between Clear Creek Road and the Sacramento River. USFWS Sacramento Fish and Wildlife Office, Sacramento, CA.

[USGS] US Geological Survey. 2016a. The National Map data download and visualization services. Available online at https://www.usgs.gov/core-science-systems/ngp/tnm-delivery (accessed October 2016).

[USGS] U. S. Geological Survey. 2016b. National Hydrography Dataset (ver. USGS National Hydrography Dataset Best Resolution [NHD] for Hydrologic Unit [HU] 8 – 18010103 [published 20161007]). Available online at https://www.usgs.gov/core-science-systems/ngp/national-hydrography. (accessed October 2016).

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130-137.

[VTN] Venture Tech Network. 1982. Potter Valley Project (FERC Project Number 77-110) Fisheries Study. Final report volumes I and II. Unpublished report on file at Pacific Gas and Electric Company, San Ramon, CA.

Ward, B. R., and P. A. Slaney. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 45:1110-1122.

Ward, B. R., P. A. Slaney, A. Facchin, and R. Land. 1989. Size-based survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts and the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853-1858.

Winter, B. D., and P. Crain. 2008. Making the case for ecosystem restoration by dam removal in the Elwha River, Washington. Northwest Science 82(sp1):13-28.

Xanthippe, A. 2004. Atlas of Pacific salmon: The first map-based status assessment of salmon in the North Pacific. Cartographica: The International Journal for Geographic Information and Geovisualization 41:95-96.

Yoshiyama, R. M., and P. B. Moyle. 2010. Historical review of Eel River anadromous salmonids, with emphasis on Chinook salmon and steelhead. Unpublished report on file, Center for Watershed Sciences, University of California, Davis.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795-806.

Zedonis, P. A. 1992. The biology of the juvenile steelhead (*Oncorhynchus mykiss*) in the Mattole River estuary/lagoon, California. M.S. Thesis, Humboldt State University, Arcata, CA.

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