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ARTICLE

Estimating the benefits of widespread floodplain reconnection for Columbia River Chinook salmon

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Abstract: In the Pacific Northwest, widespread stream channel simplification has led to a loss of habitat area and diversity for rearing salmon. Subsequent efforts throughout the Columbia River basin (CRB) have attempted to restore habitats altered through land development to recover imperiled salmon populations. However, there is scant evidence for demographic change in salmon populations following restoration. We used a process-based approach to estimate the potential benefit of floodplain reconnection throughout the CRB to Chinook salmon (*Oncorhynchus tshawytscha*) parr. Using satellite imagery, we measured stream habitats at 2093 CRB stream reaches to construct random forest models of habitat based on geomorphic and regional characteristics. Connected floodplain width was the most important factor for determining side channel presence. We estimated a current CRB-wide decrease in side channel habitat area of 26% from historical conditions. Reconnection of historical floodplains currently used for agriculture could increase side channel habitat by 25% and spring Chinook salmon parr total rearing capacity by 9% over current estimates. Individual watersheds vary greatly in habitat factors that limit salmon recovery, and large-scale estimates of restoration potential like these are needed to make decisions about long-term restoration goals among imperiled populations.

Résumé : Dans le Pacific Northwest, la simplification répandue des chenaux de cours d'eau a entraîné une diminution de la superficie et de la diversité d'habitats d'élevage des saumons. Des efforts subséquents à la grandeur du bassin versant du fleuve Columbia (CRB) ont tenté de restaurer des habitats dégradés par l'aménagement de terrains afin de rétablir des populations de saumons en péril. Il y a toutefois peu d'indices de changements démographiques dans les populations de saumons à la suite d'efforts de restauration. Nous avons utilisé une approche basée sur les processus pour estimer les bénéfices potentiels de la reconnexion de plaines inondables à la grandeur du CRB pour les tacons de saumon chinook (*Oncorhynchus tshawytscha*). Nous avons mesuré, à l'aide d'images satellites, les habitats de cours d'eau dans 2093 tronçons dans le CRB afin de produire des modèles de forêt aléatoire des habitats basés sur des caractéristiques géomorphologiques et régionales. La largeur des plaines inondables connectées est le plus important déterminant de la présence de faux chenaux. Nous avons estimé une diminution de 26 % à l'échelle du CRB de la superficie d'habitats de faux chenal par rapport aux conditions historiques. La reconnexion d'anciennes plaines inondables aujourd'hui utilisées pour l'agriculture pourrait entraîner une augmentation de 25 % des habitats de faux chenal et de 9 % de la capacité totale d'élevage de tacons de saumon chinook par rapport aux estimations actuelles. Il existe de grandes différences entre les bassins versants en ce qui concerne les facteurs associés à l'habitat qui limitent le rétablissement des saumons, et de telles estimations à grande échelle du potentiel de la restauration sont nécessaires pour éclairer les décisions touchant aux objectifs de restauration à long terme pour les populations en péril. [Traduit par la Rédaction]

Introduction

Throughout decades of declining salmon abundance in the Pacific Northwest, managers have taken considerable mitigation actions including hatchery operation, improved fish passage, and habitat restoration. Increasingly, hatchery programs are viewed skeptically, as their record as conservation tools is mixed (Naish et al. 2008). Mainstem river dam passage survival has substantially improved in recent years (Skalski et al. 2016), but recovery of Chinook salmon (*Oncorhynchus tshawytscha*) and other freshwater dependent salmon species has remained slow or nonexistent (NOAA 2016*a*, 2016*b*), expanding the number of evolutionarily significant units (ESU; Waples 1991) listed under the United States Federal Endangered Species Act (ESA). Currently, nearly all spring-run Chinook ESUs in the Columbia River basin are listed as either threatened (Snake River, Lower Columbia River, Upper Willamette River) or endangered (Upper Columbia River).

Evidence of density dependent growth and survival of juvenile salmon in freshwater habitats, despite historically low adult abundances, has brought renewed focus on the condition of tributary habitats where spawning and primary rearing occur (Walters et al. 2013*b*; ISAB 2015; Bal et al. 2018). In addition, ESA listing recovery plans often indicate habitat degradation as a primary factor in declines in abundance, resulting in billions of dollars spent on restoration actions to date (Bernhardt et al. 2005; National Marine Fisheries Service 2018). Despite this immense investment, observed demographic responses to restoration actions are limited (Roni et al. 2008) because of inadequate monitoring, insufficient habitat actions (Roni et al. 2010), or survival limitations at other life stages.

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Recently, there has been a call for process-based approaches to stream restoration, which rely on re-establishing the appropriate functions of a stream and eventually the potential diversity of habitats and biota, given the constraints of the morphology and hydrology of the system (Beechie et al. 2010). Therefore, process-based restoration may seek to address the ultimate causes of stream degradation, rather than more proximate limitations on fish growth and survival. For example, floodplain reconnection may lead to channel and habitat complexity that is more persistent than engineered mainstem habitats.

Ecologists and fisheries resource managers have long recognized the value of habitat diversity for successive life stages of salmonids (Kiffney et al. 2006; Bisson et al. 2009). We observe ontogenetic shifts in habitat preference as the relative value of those environments changes with an individual's size, age, and physiological state (Bisson et al. 1988; Rosenfeld and Boss 2001). Further, studies have begun to demonstrate the demographic benefits of increased stream complexity for juvenile salmonids with extensive stream rearing (e.g., Chinook salmon; coho salmon, *Oncorhynchus kisutch*) (Morley et al. 2005; Rosenfeld et al. 2008; Bellmore et al. 2013). Therefore, stream habitat restoration occurs with an understanding that functioning freshwater habitats can promote increases in survival at all life stages of Chinook salmon (Quinn and Peterson 1996; Sommer et al. 2001; Ebersole et al. 2006). Implemented restoration actions vary widely in their scope, from in-stream wood placement and riparian plantings to improving seasonal access and flow, channel reorganization, or reclamation of floodplains (Roni et al. 2002; Bennett et al. 2016). However, the value of these actions for fish will depend upon the spatial scale of the restoration, the state of other components of the ecosystem, the persistence of the action, and the life history of the target population.

Although stream habitat complexity can be measured at small scales (e.g., streambed rugosity, large woody debris) or large (e.g., island braided channel networks), the hydrology and geomorphology of the system will determine the large-scale channel heterogeneity on which other attributes may further filter the rearing potential of a stream (e.g., primary productivity, predation, competition, etc.) (Beechie et al. 2006). Unfortunately, urbanization and agricultural development have resulted in simplification of stream channels by truncating floodplains, removing riparian vegetation, or moving streambeds (Sedell and Froggatt 1984). These processes restrict the ability of streams to produce their historical suite of habitats and biota (Allan 2004). In addition to a loss of multithread channel structure, mainstem channels can lose function by becoming either over-widened or incised (Kondolf et al. 2002; Beechie et al. 2006; Pollock et al. 2007; White et al. 2017). Therefore, to understand the potential value of widespread floodplain reconnection, we need estimates of the amount of existing habitat and its restoration potential. In the Columbia River basin (CRB), habitat modeling work has indicated that in areas with intact floodplains, channel pattern can be predicted from a few geomorphic and hydrological attributes (Beechie and Imaki 2014), validating the efficacy of estimating the historical state of streams in the CRB at large spatial scales with a fine resolution.

To make effective management recommendations about the relative benefit of various restoration scenarios affecting stream habitats, each resulting habitat type must be weighted by its value to the life stage of interest. Traditionally, habitats are weighted by capacity or the maximum density of individuals that can be expected to reside in the habitat at that life stage, called habitat capacity. This forms the mechanism for identifying nursery habitats (Beck et al. 2001) and has been used in a number of studies to evaluate both habitat loss and the restoration potential of salmonid habitats (Beechie et al. 1994, 2012; Bartz et al. 2006). An advantage of this approach is that it creates a snapshot capacity, or index, that can be compared among regions and restoration projects. Habitat capacity estimates may also benefit a limiting factors analysis with life-cycle models that track abundance and survival throughout the life cycle (e.g., Scheuerell et al. 2006). Unfortunately, habitat capacity estimates for CRB Chinook salmon have not been produced at a scale needed for widespread restoration planning or comparison among restoration options.

Here, we employed satellite image-based measurements and empirically derived geomorphic attributes of stream habitats throughout the CRB to estimate the contribution of side channel habitats to juvenile salmon rearing area. We then computed spring-run Chinook salmon habitat capacity for each stream reach. We chose to estimate the side channel presence and restoration potential, because floodplain habitats are extensively used by juvenile salmonids and are not well quantified by currently available GIS-based stream networks. Additionally, geomorphic controls on side channel habitat have shown their potential to be modeled at large spatial extents with a fine grain (Hall et al. 2007; Beechie and Imaki 2014). Finally, floodplain reconnection is a prominent, yet costly, restoration tool for imperiled stream-rearing salmon populations (Barnas et al. 2015), though the potential demographic benefit of widespread floodplain reconnection has not previously been estimated.

Methods

Methods overview

To estimate the parr (young-of-the-year juvenile) Chinook salmon rearing capacity of Columbia River tributaries, we used geomorphic characteristics of stream reaches to extrapolate measurements of stream habitat area and condition from a large number of sample sites to the entire river network (Beechie and Imaki 2014; Hill et al. 2017). We measured habitat widths from recent satellite imagery at each of 2093 sample sites. We then used basin-wide estimates of topography, hydrography, geology, precipitation, and land use to estimate the discharge, slope, sediment supply, sinuosity, and confinement of each stream reach. These attributes were used to predict mainstem stream habitat across the basin using a model that relates the variables driving channel planform (e.g., island-braided, meandering, etc.) to a stream's potential for providing high quality fish habitat (Beechie and Imaki 2014). Throughout habitats currently accessible to anadromous Chinook salmon, we examined alternative restoration scenarios to identify subwatersheds in which floodplain reconnection would likely create and maintain increased side channel habitats.

For streams <8 m bankfull width (BFW), we assumed that all channels are single thread, as streams below this threshold do not have sufficient discharge and sediment supply to maintain side channels (Hall et al. 2007). In these small streams, we estimated pool and riffle area based on channel slope (Beechie et al. 1994, 2001). For larger river segments (>8 m wide) we estimated bank, bar, and midchannel areas, as well as side channel area (Fig. 1). Because of the importance of side channels in providing high quality rearing habitat and their vulnerability to floodplain modification (Morley et al. 2005; Bellmore et al. 2013), we made additional estimates of side channel habitat area under estimated historical floodplain widths and a restoration scenario that improves floodplain connectivity in agricultural regions. After habitat unit areas were estimated, we applied capacity parr densities to each distinct habitat unit and then summed across all unit types to estimate reach- and basin-scale habitat capacities. Uncertainty in habitat-specific parr capacity densities led us to make three contemporary capacity estimates that each utilized independent parr density data sources with our modeled habitat area estimates.

CRB stream network

Our hydrography data set spanned the entire CRB and included reach characteristics developed by Beechie and Imaki (2014). This

Fig. 1. Flow chart of habitat capacity modeling process. Grey boxes indicate random forest models, and dotted boxes indicate steps where we applied estimates to make decisions in branch direction or used established relationships to achieve outputs. All model outputs are in boxes with solid black lines. NHD, National Hydrography Dataset; BFW, bankfull width.
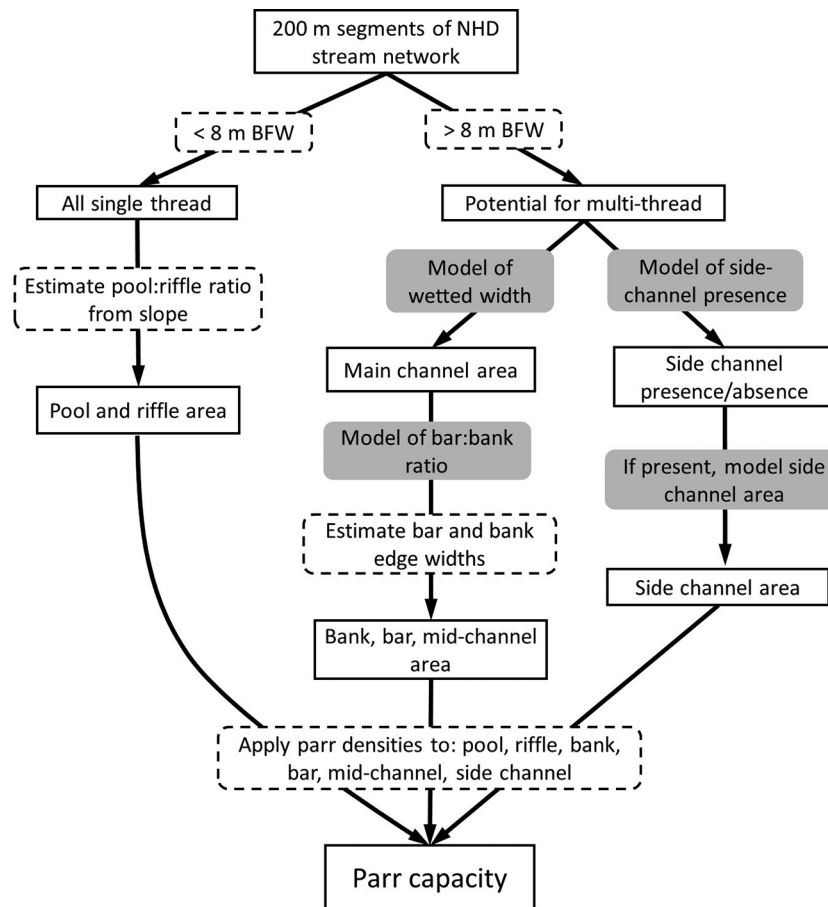
stream layer consists of two merged hydrography data sets: the National Hydrography Dataset Plus (NHDplus 2.10, mapped at 1:100 000 scale (US Geological Survey 2007–2014) for US streams and The Watershed Atlas (mapped at 1:50 000 scale) for Canadian streams (Fig. 2). The stream network is broken into 200 m segments, and each segment is designated small stream (<8 m BFW) or large river (>8 m BFW). We joined fish distribution data from the StreamNet Project (2012) to the stream layer, and reaches were designated as being accessible or inaccessible to spring Chinook salmon and whether they were utilized for rearing.

Habitat area estimates in small streams

In small streams (<8 m BFW), we estimated reach area as the product of the reach length and the estimated stream width (Beechie and Imaki 2014). We accounted for heterogeneity in rearing habitat availability among reaches by estimating a pool to riffle ratio for each 200 m stream segment as a function of slope (Beechie et al. 2001). The pool/riffle ratio was used to estimate the proportion of pool and riffle habitat areas in each reach.

Habitat area estimates in large streams

Habitat measurement site selection

We used a generalized random tessellation stratified approach (GRTS; Kincaid and Olsen 2016) to draw a spatially balanced sample of reaches from the total of 243 544 large river (>8 m BFW) segments in the CRB. We stratified by land cover (five types), channel type (five types), and stream width (three types), resulting in 75 unique strata (Table 1). Dominant land cover was assigned to each reach using a 250 m resolution continuous land cover data set for North America (Commission for Environmental Cooperation 2010; http://www.cec.org/tools-and-resources/map-files/land-cover-2010-modis-250m). We aggregated the data set's land cover types into five classes (urban, cropland, grassland, shrubland, and forest) and calculated the dominant land cover class (class with highest frequency) that occurred in a 100 m radius of the midpoint of each stream segment. Using channel patterns predicted by Beechie and Imaki (2014), we also stratified by the following channel types: straight, meandering, island-braided, braided, and confined. Finally, to ensure all stream sizes were represented we used estimated bankfull width (Beechie and Imaki 2014) to stratify by streams 8–20 m, 20–50 m, and >50 m BFW (Table 1). We sampled 50 sites from all island-braided strata, where we expected to find the most side channel habitat, and for all other strata we sampled 25 sites or as many sites as were available for rare combinations (e.g., >50 m, braided, urban), totaling a sample size of 2093 reaches (Fig. 2).

Measurement of response variables

We measured habitat area at each of 2093 stream segments using the highest quality aerial satellite available from Google and Microsoft. We used an imagery integration extension (Arc2Earth) to view this imagery in ArcMap 10.3 and to digitize habitat characteristics. Satellite images were primarily taken during summer months between June and August. Although flow conditions, and thus wetted area, may vary among images, the relationship between main channel and side channel wetted area should be well maintained over the range of stream sizes and conditions evaluated. When we encountered images with snowfall or poor image

Fig. 2. Locations of 2093 sample sites selected with a generalized random tesselation stratified (GRTS) sample design. At each site, mainstem and off channel wetted habitat widths were measured from satellite imagery.
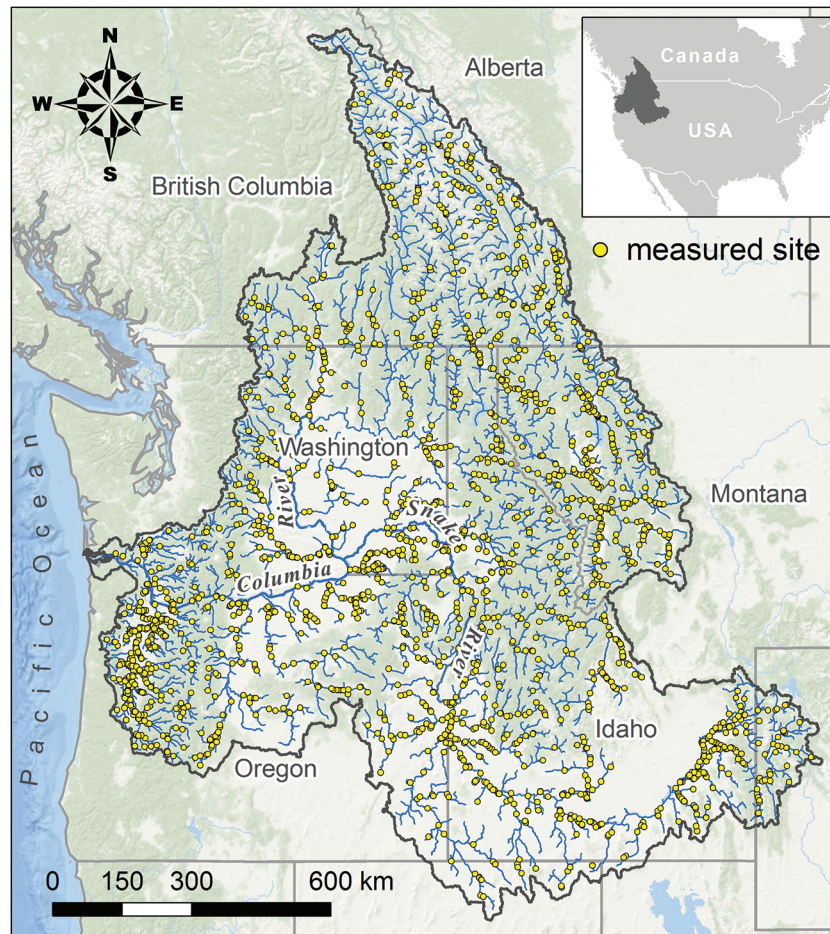
Table 1. Parameters governing the stratification of sites randomly chosen for satellite image analysis of channel habitat characteristics.

Sample strata	
Land cover	Urban
	Cropland
	Grassland
	Shrubland
	Forest
Channel type	Straight
	Meandering
	Island-braided
	Braided
	Confined
Bankfull width	8–20 m
	20–50 m
	>50 m

quality obscuring habitats, we skipped that site and moved on the next site in our random draw of sites.

At each sample site we measured wetted habitat features along three transects. Measurement transects were drawn perpendicular to valley axis with 100 m spacing. Our validation exercises showed that measuring habitat features at three transects at this

spacing adequately characterized a 200 m reach (see online Supplementary material S1–S3[1]). Transects spanned the width of the valley floor, and wherever wetted habitat was crossed the width of the feature was digitized and stored in a geodatabase with a common reach identifier.

Our primary response variables were side channel width and mainstem wetted width, but other habitat features were also digitized including bankfull width, braids, off-channels (sloughs and backwaters), and ditches as well as historical and contemporary floodplain widths (Table 2). We defined a side channel as an unmodified or minimally modified channel connected to the main stem on two sides and separated from the main stem by a vegetated island (Beechie et al. 2017). However, we also included side channels that were disconnected from the main channel on one end because of flow levels when the imagery was taken. If the side channel was heavily altered or degraded from its natural state and not considered to be suitable salmonid habitat it was classified as a modified channel or ditch. Channels separated from the main stem by an unvegetated gravel bar were classified separately as braids (Beechie et al. 2017). Habitat feature widths were digitized along the transect axis except for bankfull width, which was measured perpendicular to the direction of flow. Aside from the bankfull width metric, which spanned the entire width of the main channel including unvegetated bars and islands, only wetted habitats were measured; if a transect crossed a dry side channel or slough the feature was not digitized.

Table 2. Descriptions of stream habitat types measured with satellite imagery at each of 2093 reaches and standardized orientation of measurements.

Name	Description	Measurement axis
Side channel	Channel regularly connected to main stem on both sides and separated from the main stem by a vegetated island	Perpendicular to valley axis
Off channel	Feature only connected to main stem on one end with little or no flow (slough, backwater)	Perpendicular to valley axis
Braid	Channel regularly connected to main stem on both sides and separated from the main stem by an unvegetated gravel bar	Perpendicular to valley axis
Modified side channel	Highly modified or degraded side channel determined to be inaccessible to fish or unsuitable for rearing	Perpendicular to valley axis
Ditch	Artificial channel determined to be inaccessible to fish or unsuitable for rearing	Perpendicular to valley axis
Wetted width	Wetted width of main channel	Perpendicular to valley axis
Bankfull width	Width of stream at bankfull flows	Perpendicular to stream flow
Historical floodplain	Width of valley bottom defined by rise in elevation >5 m above main channel elevation using DEM	Perpendicular to valley axis
Current floodplain	Width of unmodified floodplain; same as historical floodplain if no modification exists	Perpendicular to valley axis

Estimate of predictor variables

We estimated side channel and mainstem habitat area for each reach in our large river network using geomorphic reach attributes calculated by Beechie and Imaki (2014) (Table 3) and additional metrics developed for this analysis. Variables developed by Beechie and Imaki (2014) include bankfull width, bankfull depth, slope, elevation, discharge, stream segment position in a reach, and sediment supply. Slopes and elevations were derived from a basin-wide 10 m digital elevation model (DEM) that was created by merging US (NED) and Canadian (CDED) elevation data sets. Bankfull width, depth, and discharge were estimated based on DEM derived drainage area and mean annual precipitation models (PRISM, ClimateBC). We used two sediment supply surrogates that were derived from flow accumulation, drainage area in alpine terrain, and flow accumulation weighted by fine sediment source. For more detail on the calculation of these reach attributes, see Beechie and Imaki (2014). We also considered the variable "ecoregion", assigned to reaches using EPA level III ecoregion classes.

We estimated historical floodplain width perpendicular to the valley axis by filling valley-floor polygons derived from a detrended DEM to 5 m above main-channel elevation (Beechie and Imaki 2014). In many streams, however, floodplain width has effectively been reduced because of development and land modification. Therefore we developed an additional predictor variable of "contemporary" floodplain width, which was the historical floodplain truncated by "modified" land-use categories: urban, agriculture, and rangeland. Using a 30 m resolution land-cover data set and road layers (Homer et al. 2015) (LU2010 Agriculture and Agri-Food Canada, USGS National Transportation Dataset, Canada National Road Network), we mapped floodplain modification and used these modified zones to restrict the historical floodplain width assigned to each reach.

To make historical side channel habitat area predictions, we substituted the contemporary floodplain width used in model development with estimated historical floodplain widths and predicted side channel area for all stream segments. Although historical side channel area provides a useful benchmark, it is not a practical restoration target as floodplain is unlikely to be reconnected in urbanized areas, including paved roads. To estimate what salmon rearing habitat may be gained by reclaiming floodplains in less urbanized areas, we used the same procedure to estimate the side channel habitat area that could be gained by reconnection in areas where floodplains are currently restricted by rangeland, cropland, and unimproved roads.

Habitat models

Because our goal was to make accurate predictions of habitat area from the available data, rather than evaluate the statistical relationship of the factors governing or correlated with side channel habitat, we elected to use random forest prediction models instead of more traditional statistical approaches like binomial or gamma hurdle models. Random forest models work well with very large data sets that include many correlated predictors and, unlike classification and regression trees, are resistant to overfitting by constructing thousands of trees with a random subset of predictors, rather than a single large tree (Cutler et al. 2012). In addition, random forest models perform equally well for both classification (presence or absence of habitat) and regression (habitat amount). We used this approach to model four important aspects of fluvial habitats for rearing salmonids: mainstem wetted width, bank and bar edge amount, presence of side channel, and total amount of side channel (in areas with a predicted presence).

To estimate mainstem habitat area, we first modeled wetted widths for each stream segment using a random forest regression. The model included eight predictors: current floodplain width, sediment accumulation, discharge, bankfull width, bankfull depth, slope, sinuosity, and elevation. Predicted wetted widths were then multiplied by stream segment length to estimate total mainstem wetted habitat area.

To account for differences in juvenile salmonid capacity among mainstem edge habitats, we measured the bank to bar ratio of both banks at a subset of 70 sites throughout the CRB with satellite imagery. We then used a random forest model to estimate the bank to bar ratio for each 200 m stream segment. The random forest regression model included slope, historical floodplain width, current floodplain width, and sediment accumulation. The resulting bank to bar ratio was used to estimate the total stream edge length occupied by banks or bars in each reach. To estimate usable bank and bar area we used regressions of bar (eq. 1) and bank (eq. 2) width on total stream width developed from measurements of the Chehalis River in Washington State (T. Beechie, unpublished data).

$$(1) \quad B_{rw} = 0.0872 \times W_w + 2.114$$

$$(2) \quad B_{kw} = 0.0837 \times W_w + 0.328$$

where B_{rw} is the bar width, B_{kw} is the bank width, and W_w is the predicted stream segment wetted width. Mainstem habitat area

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Table 3. Predictor variables and data sources used to predict the presence of side and off channel habitat throughout the Columbia River basin.

Predictor variable	Description	Data source
Bankfull width	Stream channel width at bankfull flows estimated from drainage area and mean annual precipitation upstream of each reach	Beechie and Imaki 2014
Discharge	Two-year flood discharge estimated from drainage area and mean annual precipitation upstream of each reach	Beechie and Imaki 2014
Flow accumulation by precipitation and (or) sediment	Estimated from digital elevation model (DEM) derived drainage area. Flow accumulation weighted by precipitation and fine sediment source also included	Beechie and Imaki 2014
Slope	Reach slope estimated from digital elevation and hydrography models	Beechie and Imaki 2014
Bankfull width	Estimated bankfull width in metres	Beechie and Imaki 2014
Bankfull depth	Estimated bankfull depth in metres	Beechie and Imaki 2014
Elevation	Estimated from digital elevation and hydrography models	Beechie and Imaki 2014
Sinuosity	Shortest distance between reach endnodes divided by reach length	Beechie and Imaki 2014
Hydrologic regime	Categorical variable indicating if reach belongs to a snowmelt-dominated, rain-dominated, or transitional drainage	Beechie and Imaki 2014
Sediment supply	Sediment supply surrogates estimated from flow accumulation, fine sediment sources, and relative slope	Beechie and Imaki 2014
Position	Segment number upstream from confluence	Beechie and Imaki 2014
Historical floodplain width	Valley bottom width estimated from DEM and hydrography models	Beechie and Imaki 2014; National Hydrography Dataset (NHD), https://nhd.usgs.gov/data.html; National Land Cover Database 2011 (Homer et al. 2015), http://www.mrlc.gov/data?f%5B0%5D=category%3Aland%20cover; Agriculture and Agri-Food Canada Land Use 2010, https://open.canada.ca/data/en/dataset/9e1efe92-e5a3-4f70-b313-68fb1283eadf; USGS National Transportation Dataset, Canada National Road Network
Current floodplain width	Width of currently unmodified floodplain estimated from DEM, hydrography models, and land use data	
Restored floodplain width	Width of floodplain assuming reclamation of cropland, rangeland, and small roads	
Ecoregion	Level III Environmental Protection Agency ecoregions	EPA, https://www.epa.gov/eco-research/ecoregions

not encompassed by bank and bar area was considered to be mid-channel area, which is not preferred habitat by salmon parr and receives a unique density during fish capacity estimation.

Following measurement of satellite imagery for side and off channel area at the 2093 sample sites, side channels were present in 35% of sites, while off channel habitats were found at 2% of sites. Low rates of the presence of any side or off channel habitat indicated that a hurdle model approach would be the most effective at estimating habitat areas (Potts and Elith 2006). A hurdle model is used for count data, where separate processes may govern the presence and magnitude of the response and where the zeros cannot be effectively modeled with standard probability distributions (Martin et al. 2005). Therefore, the presence and (or) absence is modeled first, and sites where the presence of habitat is predicted are placed into a second model to estimate the magnitude.

To construct predictive models, we created a binary classification of side and off channel habitats, 0 where no habitat was present, and 1 where any side or off channel was measured. Therefore, all of the 2093 sites were used to construct the classification model. We randomly selected 80% of sites to be included in training the model, with the remaining 20% reserved for testing model accuracy. To train the random forest model we included 12 predictors: current floodplain width, historical floodplain width, discharge, flow by precipitation, sediment, sediment accumulation, average elevation, watershed position, flow accumulation, ecoregion, slope, and hydrologic regime (Table 3). We constructed models with the randomForest and caret packages in the R statistical software platform version 3.2.3 (R Development Core Team 2011). During the training phase we used 10-fold cross-validation and tuned two parameters: the number of trees constructed and the number of variables randomly drawn to include

at each tree node. We used the kappa tuning metric and evaluated the final model for balanced accuracy. Our final model included 2000 trees and two variables at each node. A second regression random forest model was constructed with only the 874 sites that had side channels present, using the same suite of predictors used in the side channel presence classification model. We used the same training procedure employed in the classification model but tuned the regression model by maximizing the receiver operating characteristic.

Once both models were sufficiently tuned, we used the classification model to predict the presence or absence of side channel habitat for all CRB stream segments. For all sites with a predicted side channel presence, the regression model was used to predict side channel area. The effect of floodplain width on side channel presence and area in our models allows for the prediction of side channels with a novel floodplain width. Therefore, to estimate historical side channel area and floodplain restoration potential, we made new predictions with both models where floodplain width was updated to historical or restoration width values.

Fish capacity estimation

A key uncertainty in translating habitat area to habitat capacity lies in choosing appropriate fish densities to populate each stream segment. Problems can arise with differences in scale between habitat estimates and fish density data that misrepresent capacity. Additionally, much of the empirical fish density data available has been collected at historically low abundances and may only characterize capacity at the smallest spatial scales. In light of these difficulties, we chose to apply three independent data sources of spring Chinook parr density to our modeled habitat areas at scales appropriate for each data source, effectively producing three separate capacity estimates.

Table 4. Densities of Chinook parr used to estimate capacity with habitat expansion approach (from T. Beechie and J.N. Thompson, unpublished review).

| Habitat	Chinook parr·hectare⁻¹
Mainstem bank	8884
Mainstem bar	4720
Mainstem midchannel	100
Side channel	6000
Small stream pool	452
Small stream riffle	4

1. A habitat expansion based on the total area of each habitat type multiplied by habitat-specific fish densities for small and large streams (Table 4).
2. A coarser expansion based on reach-level habitat characteristics, total wetted area of each large stream reach, and a quantile regression of observed reach-level fish densities in the CRB.
3. A single, empirically derived parr capacity estimate based on observed average fish densities from midsummer snorkel surveys in the Salmon River and total habitat area estimates for large stream reaches (Thorson et al. 2014).

We used densities from review and re-analysis of published and unpublished habitat specific capacities spring Chinook parr (T. Beechie and J.N. Thompson, unpublished data; Table 4). These data were derived primarily from repeated beach seining or electrofishing specific habitat types over a range of stream flows and spawner abundances in the Skagit River, the most abundant Chinook salmon population in the ESA listed Puget Sound ESU. Skagit River Chinook densities have been used in previous habitat capacity studies (Beechie et al. 2015) because of an abundance of habitat-specific juvenile densities derived from extensive monitoring in that system (Beechie et al. 2005a; Zimmerman et al. 2015). The average maximum observed parr density was applied to each habitat type: side channel, mainstem bank, mainstem bar, mainstem midchannel, small stream pool, and small stream riffle.

The quantile regression approach is also an expansion approach, but the fish density data were for entire stream reaches and not separated by habitat type. Therefore, a single abundance and wetted area were used to calculate density. The Integrated Status and Effectiveness Monitoring Program (ISEMP) has been electrofishing stream reaches previously sampled by the Columbia River Habitat Monitoring Program (CHaMP) for several years. The ISEMP data have the advantage of being measured over a range of spawner abundances. However, the observed fish density at a given site may vary from zero to several fish per square metre over the period of record. Therefore, a mean or median density may not accurately reflect capacity. To account for these differences we used a quantile random forest procedure, which allows for the modeling of any percentile of fish density (Cade and Noon 2003). We indexed the ISEMP sample densities for spring Chinook to the sites used in our habitat model construction and used the same suite of predictors to model fish capacity. We created and tuned quantile random forest models with the R package quantreg-Forest using similar tuning procedures to the habitat estimation. After tuning, we predicted the 90th percentile fish density for each stream segment and multiplied those densities by the sum of mainstem and side channel habitat for that reach.

Finally, we employed the spring Chinook capacity estimated from a hierarchical stock–recruit model of spawner and midsummer parr densities in the Salmon River (Thorson et al. 2014). Thorson et al. (2014) used decades of snorkel survey data to estimate an average capacity of 5200 parr·hectare⁻¹. To estimate capacity we multiplied the total habitat area (mainstem bars,

Fig. 3. A comparison of wetted width measurements from satellite imagery (x axis) and predicted wetted width from a random forest model. Solid line indicates a 1:1 relationship.
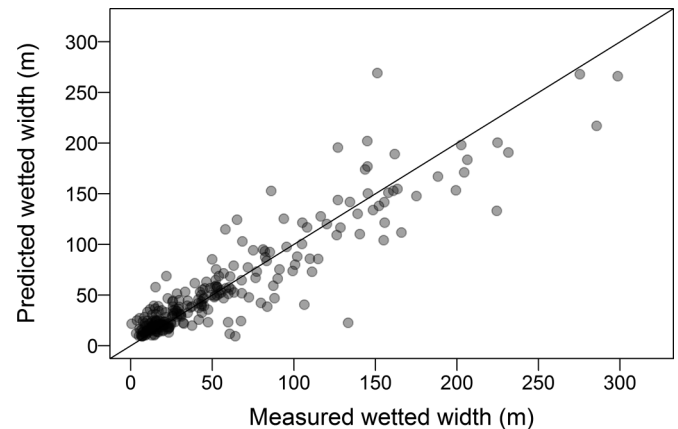
Fig. 4. The relative importance of each input variable included in the random forest model predicting the wetted width of mainstem stream segments. Importance is estimated from the gini impurity criterion based on the number of nodes that a given variable is included in the model. "Flow by precip." indicates accumulated flow by precipitation source. "Curr. floodplain" indicates the current floodplain width.
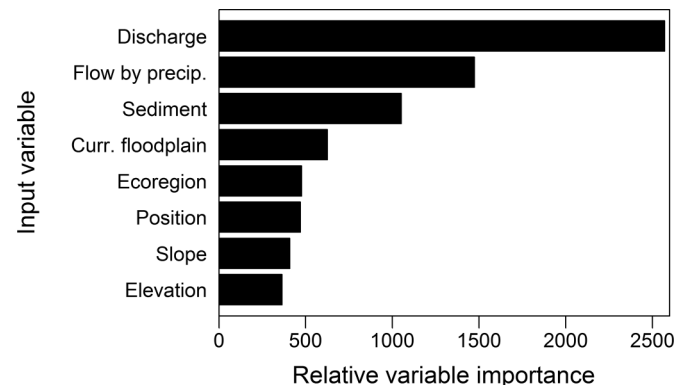
mainstem banks, side channel) in hectares by 5200, regardless of reach characteristics or habitat types. Because of data limitations, both quantile regression and snorkel estimated capacities were made for streams greater than 8 m BFW only, and small streams were characterized by the pool and riffle specific fish densities.
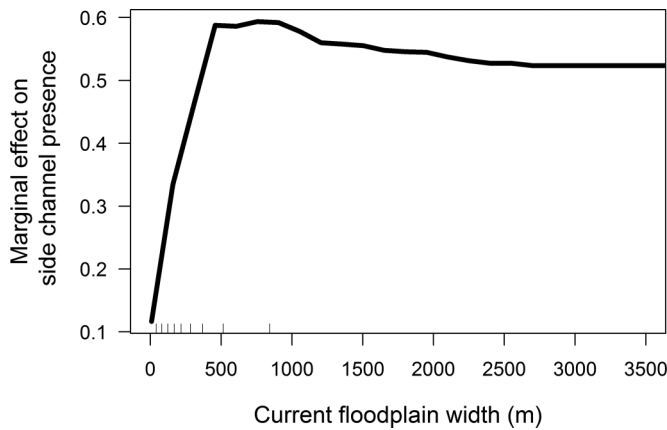
Results

Habitat area prediction

We estimated large river (>8 m BFW) mainstem habitat areas with two random forest models, one for wetted width of the main channel and one for bank to bar edge habitat ratios. Regression of predicted versus measured wetted widths indicated that the wetted width model performed well, with slope near one and intercept near zero, and an R^2 of 0.86 ($n = 419$; Fig. 3). Estimated stream discharge was the most important variable in the model predicting wetted width (Fig. 4). Bank to bar ratios were also relatively accurately estimated (regression slope and intercept near one and zero, respectively), but with lower precision ($R^2 = 0.58$, $n = 70$).

Off channel habitats were too rare in our data set to make useful landscape level predictions. Although the model had a high sensitivity (true positive rate, 99%), the specificity (true negative rate, 81%) led to vast overestimates of off channel habitat. While we measured only 46 sites with off channel habitat, our model predicted 407 sites with off channel habitat. In contrast, our model

Fig. 5. The importance of predictors in side channel presence. The *x* axis indicates scaled mean decrease in classification accuracy when each variable is permuted over all random forest trees. "Curr. Floodplain" indicates the current floodplain width. "Hist. Floodplain" indicates the historical unrestricted floodplain width. "Flow acc." indicates total flow accumulation. "Flow by sed." indicates flow accumulation by sediment source.
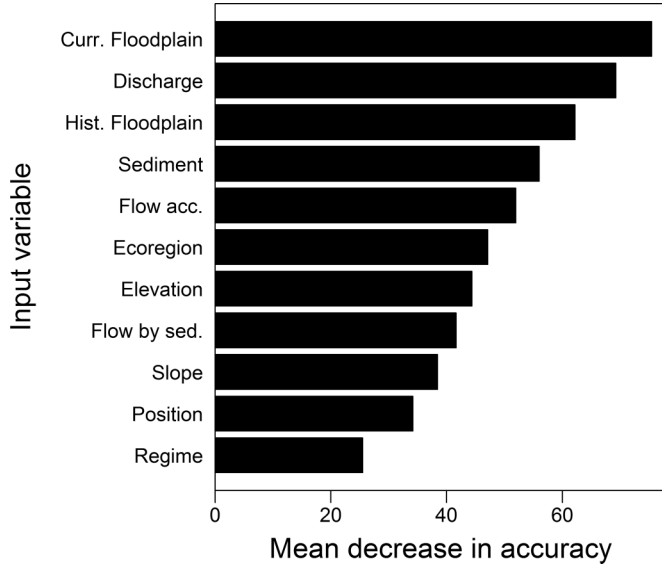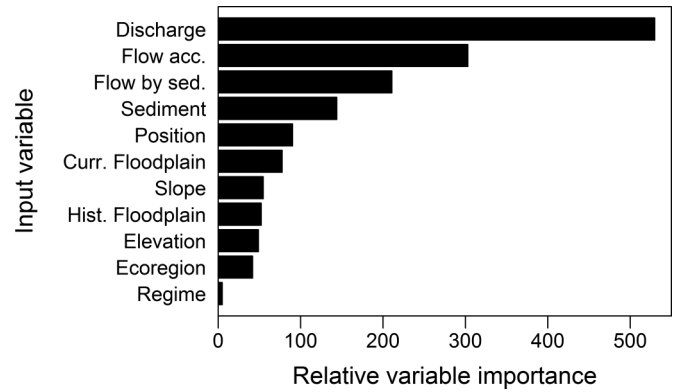

Fig. 6. Vote influence of floodplain width on predictions of the presence of side channel habitat. Increasingly positive values of vote influence predict the presence of side channel habitat more strongly. Similarly, decreasing vote influence values indicate a stronger prediction of no side channel. Small ticks on the *x* axis indicate deciles of floodplain width for all measured reaches.

Fig. 7. The relative importance of each input variable in predicting the average side channel width (m) at each reach where side channels were present. Importance is estimated from the gini impurity criterion based on the number of nodes that a given variable is included in the model.

Fig. 8. Partial dependence plot of the marginal effect of floodplain width on side channel width prediction. The influence of floodplain width becomes saturated at ~2000 m floodplain width. Small ticks on the *x* axis indicate deciles of floodplain width for all measured stream segments.
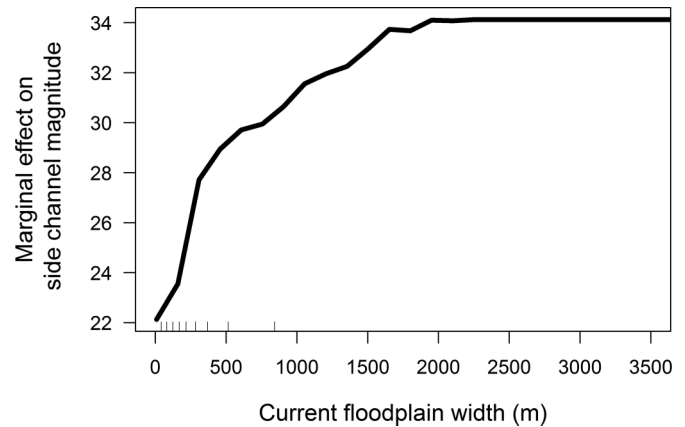

predicting the presence of any side channel had a balanced accuracy (correct positive and negative detections) of 75% when tested on the 20% of sites withheld from model development, although there was some bias between specificity (true negative rate, 86%) and sensitivity (true positive rate, 60%) of the classification. Overall, the model tended to underpredict side channel presence; 640 of 2093 reaches were predicted to have side channels, fewer than the 732 we measured.

Floodplain width was the most important predictor in determining side channel presence (Fig. 5) with the prevalence of side channels increasing rapidly as floodplain width increased from 0 to 500 m, then remaining relatively flat with increasing floodplain width (Fig. 6). The most important predictor in the side channel area model was river discharge (Fig. 7). While floodplain
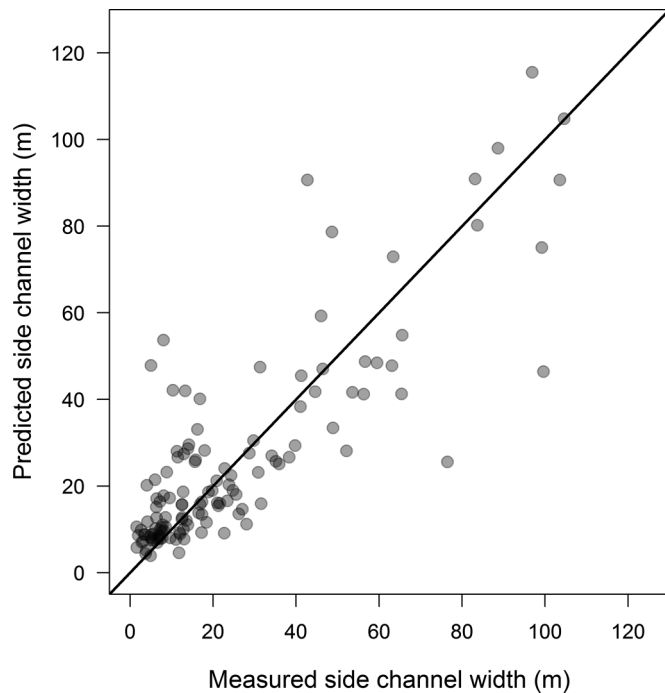
width was less important in the model, side channel area increases with increasing floodplain width up to floodplain width of about 2 km (Fig. 8). However, the largest effect of floodplain width on side channel area occurs in the first 250 m of floodplain width. A regression of predicted on measured total side channel area had an R^2 of 0.52, when predicting sites not included in model development (Fig. 9).

Across all HUC-8 watersheds (US Geological Survey level 8 hydrologic unit) containing spring Chinook (Table 5) we estimated approximately 45 270 hectares of contemporary juvenile rearing habitat. Contemporary side channel habitat comprises 13.6% of the total wetted habitat area. However, contemporary side channels comprise over 42% of the high value juvenile rearing habitat (i.e., all habitat excluding midchannel area). Across the CRB, the contemporary area of side channel habitat was 26% lower than historical estimates, although individual HUC-8's range from 0% to 78% loss in side channel area. Our model predicted that restoration of floodplain connectivity in rangeland, cropland, and areas currently restricted by small roads could increase side channel habitat by as much as 25% across the CRB, although individual HUC-8's could see increases of none to as much as 333% above current side channel area.

Fig. 9. A comparison of measured side channel width (*x* axis) and predicted side channel width (*y* axis) from the random forest regression model for 128 novel sites that were not included in model development. Solid line indicates 1:1 correspondence between measurements and model output.

Discussion

Currently, multiple CRB Chinook salmon population trends suggest density dependent processes may be limiting freshwater growth and survival despite historically low population abundances, indicating that habitat quality or quantity may be limiting recovery (Walters et al. 2013b; ISAB 2015). One important constraint to population recovery may be loss of side channels that often provide high quality rearing habitat for juvenile salmon and other stream fishes. However, despite widespread urbanization and agricultural development, loss of floodplain habitat has not been ubiquitous in the CRB. Our analysis demonstrates that watersheds vary widely in historical, contemporary, and restoration potential of side channel habitats. In many watersheds, side channels were likely never prominent habitats, as valley confinement has limited their creation or maintenance, restricting their potential for floodplain habitat restoration. For example, tributaries of the upper Columbia River and Clearwater River have few areas where widespread floodplain reconnection would provide additional side channel habitat because those streams are naturally confined (Fig. 12). However, we note that areas with little floodplain restoration potential should not be viewed as without other restoration opportunities. Naturally confined stream channels operate as collectors of allocthonous material that increases the productivity and diversity of more complex habitats downstream (Bellmore and Baxter 2014). In these areas, other process-based restoration options are available to restore stream complexity and function (e.g., natural flow patterns, wood delivery, or riparian function, Beechie et al. 2010). Additionally, the importance of discharge in our models indicates that sufficient stream flow is needed to create or maintain side channels regardless of floodplain width. Although we did not distinguish between flow-regulated and flow-unregulated river reaches, deviations form a natural flow regime in many watersheds may reduce the connection and ecological function of floodplain habitats, which would limit their restoration value (Galat et al. 1998).

In watersheds with more extensive historical floodplains, our model suggests that there are widespread floodplain restoration opportunities. While reconnecting entire floodplains is impractical in many areas, our analysis demonstrates that in many streams a modest increase in active channel width is likely to substantially increase the amount of side channel. On average, the greatest improvement in side channel presence and area was found with a floodplain width increase of ~250 m (Figs. 6 and 8).

Where feasible, large-scale floodplain restoration activities can lead to increases in productivity (Bellmore et al. 2017), and Chinook salmon populations experiencing density dependence at contemporary spawner numbers may benefit from increases in rearing habitat (Walters et al. 2013b). Floodplains are known to contain a variety of prominent rearing habitats for salmon parr (Beechie et al. 1994; Morley et al. 2005; Bellmore et al. 2013). Within floodplains, side channels can provide increased growth opportunities (Sommer et al. 2001; Giannico and Hinch 2003; Jeffres et al. 2008) as well as refuge from predation, because shallower side channels are generally unoccupied by larger piscivorous species (Bellmore et al. 2013). While we found no studies that empirically evaluated the benefit of constructed or reconnected side channels for Chinook salmon, studies of natural systems showed that densities of Chinook salmon during winter were an order of magnitude higher than in the adjacent main stem or nearby tributaries (Martens and Connolly 2014). Moreover, seasonally inundated floodplain habitats have demonstrated higher growth and survival of juvenile Chinook salmon (Sommer et al. 2001), indicating a potential value to salmon beyond habitat capacity.

Mainstem habitats comprise the majority of wetted habitat in our model, and their value for rearing fish cannot be understated. However, there are several potential improvements in the estimation

Fish capacity estimates

Estimates of contemporary Chinook parr capacity using the habitat expansion method varied substantially among watersheds, totaling 96.6 million parr across the entire currently accessible portion of the CRB (Table 5; Fig. 10). As a percentage of total reach production, contemporary side channel habitat accounted for 40% of total parr capacity, although the percentage varied widely among watersheds, from 0%–59% (Fig. 11). The quantile random forest method of assigning capacity to each stream segment predicted fewer fish in most watersheds, but many more at a few sites (e.g., Middle and Upper Willamette). In total, the quantile regression method estimates a higher Chinook parr capacity than habitat expansion (105.8 million parr; Table 5). Chinook parr capacity estimated from applying 5200 fish per hectare to the total wetted area for each reach produced a lower total capacity than either expansion or quantile random forests (76 million parr across all watersheds). However, the Upper Willamette HUC-8 watershed alone accounted for much of the difference between the methods, with over 16 million parr predicted using quantile random forest, compared to 7.4 million and 5.8 million for habitat expansion and 5200 per hectare, respectively. For many watersheds, the estimates were very similar among methods; the coefficient of variation among was less than 20% for 27 of 57 watersheds. There was a small but significant ($R^2 = 0.11$, $F_{[1,56]} = 6.82$, $p = 0.011$) increase in CV with increasing proportion of side channel area, but no increase in CV with increasing total habitat area ($R^2 = 0.01$, $F_{[1,56]} = 0.39$, $p = 0.53$).

Using the habitat expansion approach, we estimated potential changes in Chinook parr capacity due to restoration by increasing the current floodplain width to include rangeland and cropland. This scenario increased CRB-wide capacity by 9.4% over contemporary estimates, although there were a few watersheds with increases of 50% or more, notably the Lemhi R. (81%), and Upper Grande Ronde (70%; Table 5; Fig. 12).

Table 5. Spring Chinook parr habitat area and rearing capacity by HUC-8 subbasin.

HUC-6	HUC-8	Habitat area (hectares)						Chinook parr capacity (individuals)					
		Main	Current side channel	Historical side channel	Restoration side channel	Side channel loss from historical (%)	Side channel increase from current with restoration (%)	Current >8 m BFW streams	Restoration >8 m BFW streams	Increase with side channel restoration (%)	Quantile regression >8 m BFW	5200 parr per hectare, >8 m BFW	Current <8 m BFW streams
Lower Columbia	Lewis	141.5	12.5	19.0	14.0	−34.3	12.2	285 931	295 087	3.2	319 336	218 374	28 771
	Lower Columbia–Clatskanie	254.8	17.8	20.1	17.8	−11.7	0.0	495 212	495 212	0.0	467 483	364 884	43 193
	Lower Columbia–Sandy	580.7	66.2	73.7	67.6	−10.1	2.0	1 266 072	1 269 993	0.3	1 102 423	976 322	33 101
	Lower Cowlitz	454.7	57.7	85.7	67.6	−32.7	17.2	978 276	1 037 951	6.1	1 177 151	743 042	33 168
	Upper Cowlitz	678.6	169.0	192.3	185.5	−12.1	9.8	1 974 635	2 073 544	5.0	1 792 603	1 574 004	10 663
Willamette	Clackamas	890.6	124.6	140.6	131.7	−11.3	5.7	2 086 128	2 128 863	2.0	2 477 358	1 611 201	21 188
	Coast Fork Willamette	278.7	47.1	120.3	90.3	−60.8	91.5	713 440	971 851	36.2	1 245 196	557 368	2310
	Lower Willamette	29.3	0.3	1.0	0.3	−69.4	0.0	41 485	41 485	0.0	41 686	29 328	23 475
	McKenzie	1 444.4	507.8	574.6	559.1	−11.6	10.1	5 207 995	5 503 421	5.7	5 443 837	4 199 754	127 283
	Middle Fork Willamette	976.9	259.3	295.9	283.9	−12.4	9.5	3 085 220	3 230 568	4.7	3 009 425	2 470 267	131 771
	Middle Willamette	2 113.8	471.0	659.0	615.2	−28.5	30.6	5 708 246	6 573 509	15.2	9 112 475	4 480 042	65 055
	Molalla-Pudding	797.3	63.4	97.3	105.1	−34.8	65.7	1 671 132	1 911 317	14.4	2 532 000	1 273 057	31 219
	North Santiam	1082.2	321.0	385.8	361.2	−16.8	12.5	3 499 640	3 737 892	6.8	4 922 581	2 801 469	47 428
	South Santiam	885.7	173.2	253.3	240.7	−31.6	38.9	2 412 919	2 817 661	16.8	4 017 124	1 907 205	26 642
	Upper Willamette	2 253.5	695.8	1 173.3	1 065.8	−40.7	53.2	7 399 446	9 618 055	30.0	16 479 084	5 894 195	41 321
Deschutes	Lower Crooked	321.2	17.6	75.8	67.3	−76.8	282.4	605 335	903 662	49.3	800 183	461 405	NA
	Lower Deschutes	1 740.3	114.0	152.0	136.4	−25.0	19.7	3 203 425	3 337 836	4.2	2 537 810	2 456 100	14 817
	Trout	0.4	0.1	0.2	0.1	−29.3	0.0	1534	1534	0.0	494	1286	NA
	Upper Deschutes	203.1	10.4	14.6	13.3	−28.9	28.0	406 081	423 505	4.3	458 014	317 094	2739
John Day	Lower John Day	2 077.5	338.6	367.7	361.0	−7.9	6.6	4 952 420	5 085 956	2.7	4 815 557	3 870 168	45
	Middle Fork John Day	243.7	19.4	25.4	25.3	−23.9	30.5	548 997	584 463	6.5	245 816	436 931	94 416
	North Fork John Day	724.6	43.2	59.3	55.3	−27.1	27.8	1 435 191	1 507 341	5.0	1 560 261	1 097 226	88 239
	Upper John Day	491.7	96.2	138.1	121.7	−30.4	26.5	1 429 236	1 578 939	10.5	1 930 852	1 176 785	32 296
Middle Columbia	Klickitat	620.0	92.3	103.4	93.0	−10.7	0.7	1 483 469	1 487 247	0.3	1 460 173	1 158 633	7745
	Middle Columbia–Hood	409.9	67.1	72.0	69.2	−6.8	3.2	1 064 312	1 077 158	1.2	918 031	839 490	106 043
	Umatilla	552.9	92.1	226.1	195.7	−59.3	112.5	1 444 628	2 066 039	43.0	1 203 297	1 159 626	38 983
	Walla Walla	162.8	4.8	21.0	11.0	−77.0	128.0	342 033	379 040	10.8	364 072	274 270	21 345
Yakima	Lower Yakima, Washington	1 880.6	585.1	647.8	597.8	−9.7	2.2	6 078 184	6 129 889	0.9	6 807 410	4 935 626	50 341
	Naches	444.3	105.4	115.4	107.8	−8.6	2.2	1 341 240	1 352 140	0.8	737 197	1 084 655	40 522
	Upper Yakima	1 221.8	282.6	345.6	301.5	−18.2	6.7	3 499 068	3 610 038	3.2	1 801 625	2 817 275	37 807
Upper Columbia	Chief Joseph	1.6	0.0	0.0	0.0	NA	NA	3 619	3 619	0.0	2 348	3119	169
	Methow	1 267.4	225.8	251.4	232.0	−10.2	2.7	3 198 422	3 233 536	1.1	1 443 710	2 605 905	21 557
	Upper Columbia–Entiat	175.1	27.6	38.8	31.4	−28.9	13.9	443 959	465 883	4.9	139 736	359 595	9498
	Wenatchee	1 115.7	203.4	263.0	218.6	−22.7	7.4	2 862 676	2 950 188	3.1	1 215 227	2 294 165	40 374
Lower Snake	Hells Canyon	22.9	0.0	0.0	0.0	NA	NA	34 690	34 690	0.0	29 995	25 875	40 291
	Imnaha	448.9	17.1	19.2	19.2	−10.9	12.2	885 426	897 954	1.4	513 132	687 420	62 733
	Lower Grande Ronde	510.8	15.6	15.6	15.6	0.0	0.0	869 559	869 559	0.0	629 576	650 744	70 300
	Lower Snake–Tucannon	99.4	6.3	9.1	8.6	−31.1	36.9	217 884	231 740	6.4	197 826	170 438	8420
	Upper Grande Ronde	709.1	52.5	240.5	227.2	−78.2	332.5	1 503 877	2 551 121	69.6	2 176 811	1 160 457	86 611
	Wallowa	595.7	41.9	91.5	81.3	−54.3	94.2	1 262 398	1 499 071	18.7	1 153 676	966 512	35 964
Clearwater	Clearwater	1 482.6	92.5	111.0	102.0	−16.7	10.3	2 778 192	2 829 467	1.8	1 486 872	2 146 813	277 559
	Lochsa	1 009.8	29.5	35.3	30.5	−16.4	3.5	1 761 151	1 767 298	0.3	1 591 429	1 304 017	165 793
	Lower North Fork Clearwater	22.5	2.5	2.7	2.5	−7.7	0.3	46 199	46 237	0.1	21 859	36 123	NA
	Lower Selway	769.3	12.5	12.5	12.5	0.0	0.0	1 274 586	1 274 586	0.0	801 184	944 119	98 923
	Middle Fork Clearwater	484.8	37.8	25.7	39.4	47.2	4.4	884 637	894 521	1.1	376 147	684 528	56 743
	South Fork Clearwater	667.2	26.1	33.9	31.2	−23.1	19.6	1 240 573	1 271 289	2.5	858 797	927 369	254 070
	Upper Selway	547.0	17.8	17.8	18.2	0.0	2.1	1 026 048	1 028 315	0.2	819 270	765 741	190 910

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Table 5 (concluded).

HUC-6	HUC-8	Habitat area (hectares)						Chinook parr capacity (individuals)					
		Main	Current side channel	Historical side channel	Restoration side channel	Side channel loss from historical (%)	Side channel increase from current with restoration (%)	Current >8 m BFW streams	Restoration >8 m BFW streams	Increase with side channel restoration (%)	Quantile regression >8 m BFW	5200 parr per hectare, >8 m BFW	Current <8 m BFW streams
Salmon	Lemhi	210.9	31.9	120.9	108.9	−73.6	241.6	570 307	1 032 635	81.1	156 898	458 452	43 315
	Little Salmon	234.2	9.7	11.9	10.7	−18.0	10.2	458 438	464 389	1.3	541 245	351 697	33 937
	Lower Middle Fork Salmon	795.7	19.8	20.8	21.0	−4.9	5.9	1 392 105	1 399 065	0.5	1 735 069	1 014 904	268 377
	Lower Salmon	150.1	2.4	3.0	3.1	−17.3	25.9	285 715	289 523	1.3	222 679	216 448	81 506
	Middle Salmon–Chamberlain	235.6	7.3	7.3	7.3	0.0	0.0	467 715	467 715	0.0	414 904	353 698	194 336
	Middle Salmon–Panther	704.4	137.0	161.4	153.8	−15.1	12.3	1 921 854	2 018 837	5.0	2 490 330	1 518 733	209 370
	Pahsimeroi	85.8	32.1	37.8	37.3	−14.9	16.2	349 497	380 686	8.9	184 292	289 469	NA
	South Fork Salmon	889.5	39.8	42.0	41.9	−5.3	5.2	1 679 670	1 692 004	0.7	2 044 231	1 263 941	253 775
	Upper Middle Fork Salmon	555.2	87.9	90.9	90.7	−3.3	3.2	1 516 197	1 533 195	1.1	1 742 764	1 209 109	380 324
	Upper Salmon	1 328.5	160.3	235.0	216.8	−31.8	35.3	3 060 223	3 392 352	10.9	3 118 350	2 402 031	572 012
Total		39 077	6 193	8 355	7 724	−25.9	24.7	96 656 545	105 750 668	9.4	105 888 913	75 998 501	4 658 794

Note: Main indicates bank, bar, midchannel area. Current side channel indicates contemporary side channel area. Historical side channel indicates side channel area with unrestricted floodplains. Restoration side channel indicates side channel area for floodplain reconnection in agricultural lands and areas with small roads. Current >8 m bankful width (BFW) streams indicates the expansion method sum of bank, bar, midchannel, and contemporary side channel capacity. Restoration >8 m BFW streams indicates the sum of mainstem and restored side channel capacity. Quantile regression >8 m BFW indicates estimates from quantile random forest model (90th percentile) of Integrated Status and Effectiveness Monitoring Program (ISEMP) fish survey data and habitat area. Both historical and contemporary estimates are limited to habitats defined as rearing habitat by StreamNet.

of mainstem habitat area that could be made. First, we were not able to measure the width of favorable flow and depth from satellite imagery, so our estimates rely on measurements of bar and bank edge widths from the Chehalis River in coastal Washington State. Bank and bar forming processes are likely similar in the Chehalis River and CRB, but measuring bar and bank widths at various locations in the CRB would increase confidence in the model estimates of edge habitat area. Second, we were unable to address other habitat types such as hydromodified banks and backwaters, which decrease and increase rearing capacity, respectively (Beamer and Henderson 1998; Beechie et al. 2005a). Measurement of these features may improve model accuracy, although total capacities of these habitat types at the watershed and larger spatial scale are likely very small relative to the capacity of natural banks and bars.

Although we estimated the potential for increases in rearing habitat resulting from floodplain reconnection, the benefits of floodplain reconnection extend beyond the creation and maintenance of side channels. Floodplain habitats tend to increase the overall heterogeneity of riverine habitats through periodic inundation (Ward et al. 1999; Tockner and Stanford 2002), which produces a diverse and productive link between aquatic and terrestrial ecosystems (Junk et al. 1989). Therefore, where geomorphologically appropriate, allowing floodplain reconnection will directly benefit riverine vertebrates and invertebrates through increased growth and survival (Galat et al. 1998; Tockner et al. 2010). However, successful floodplain reconnection requires that appropriate flow, sediment supply, and wood delivery, along with intact riparian habitat in the reconnected area to allow the diversity of biotic and abiotic function needed for their long-term viability. Unfortunately, in many parts of the CRB impoundments or water diversions may sufficiently restrict flow and sediment such that the dynamism of stream channels might continue to be reduced, despite floodplain reconnection.

Our habitat capacity estimates result from several separate habitat models and sources of parr density data. Therefore, multiple sources and scales of uncertainty exist in our modeling process. At the smallest spatial scale, previous work has shown a high degree of accuracy (e.g., $R^2 = 0.98$; Beechie et al. 2005b) measuring stream widths from aerial photography of similar resolution to our satellite imagery. A larger source of error is the variation in image collection dates, as stream widths and side channel inundation will vary with seasonal flows. Although varying image dates add error in our analysis, a time series of images over a range of discharges will eventually lead to better estimates of bank slopes and edge habitat. We also chose to measure wetted habitat along three evenly spaced transects perpendicular to each reach, rather than digitizing all habitats in each sample reach reach. This faster method classified habitats well (see online Supplementary material S1–S3[1]), although very small side channels may have been missed. The benefit of this streamlined approach is that it allowed us to measure 2093 sites stratified across the entire CRB. Although there is uncertainty in our predictions of mainstem and side channel habitats in unmeasured reaches, there appears to be little bias in our estimates (Figs. 3 and 9). Ultimately we were not able to propagate the error from all of these sources to create a confidence interval for our aggregated estimates, but the goal of our approach was large-scale estimates of habitat capacity, not reach specific estimates that would be better served by on the ground site visits. Our watershed scale estimates would benefit from validation with independent measures of habitat area that are currently unavailable at comparable scales.

A larger source of uncertainty in habitat capacity analyses likely arises from variation in available fish density data. Although a review of published and unpublished fish density data by T. Beechie and J.N. Thompson resulted in habitat-specific (i.e., bank, bar, midchannel, side channel) capacity estimates, these data were primarily collected outside of the CRB, in Puget Sound

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Fig. 10. Contemporary summer parr rearing capacity of spring Chinook within the domain currently accessible to anadromous fishes as determined by the habitat expansion approach of estimating mainstem and side channel habitat and assigning fish densities to each habitat at the 200 m stream segment scale. For graphical purposes, estimates are aggregated at the HUC-10 watershed boundary spatial scale. Black lines indicate regional HUC-6 watershed boundaries.
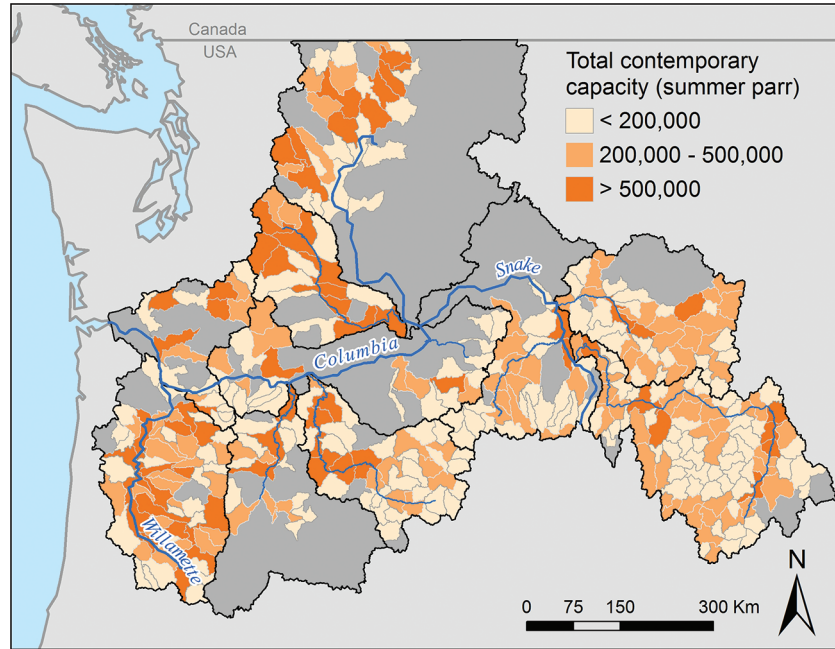

Fig. 11. Contemporary percentage of total estimated spring Chinook parr rearing capacity attributed to side channel habitat. Estimates were made with the habitat expansion approach and aggregated at the HUC-10 watershed spatial scale.
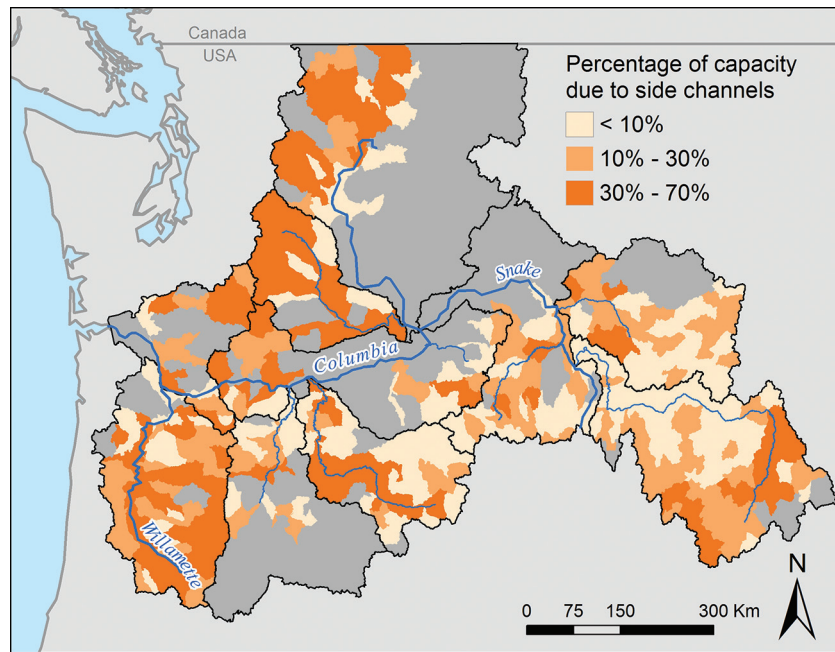
rivers that may not be representative of CRB habitats. The most extensive CRB spring Chinook fish density data come from ISEMP and were included in our quantile random forest approach to applying parr densities to each reach. Although these data include electrofishing densities from hundreds of sites throughout the CRB, even the 90th percentile of data may not represent capacity in populations that are far below their historical spawner density. Additionally, ISEMP densities are aggregated at the reach scale, and separate densities for habitats within a reach are not avail-

able. Average parr capacity of 5200 parr per hectare from Thorson et al.'s (2014) hierarchical model of several decades of snorkel based fish counts in Idaho streams provided another independently derived parr capacity. However, their model selection indicated a population specific capacity was warranted, possibly owing to differences in habitat quality among streams. The mild increase in CV we observed among capacity estimates with increasing proportion of side channel habitat is likely a factor of the higher value placed on side channel habitats in habitat expansion

Fig. 12. Estimated increase in spring Chinook parr capacity from contemporary conditions resulting from floodplain reconnection in historical floodplain currently occupied by rangeland, cropland, and small unimproved roads. Estimates were made with the habitat expansion approach and aggregated at the HUC-10 watershed spatial scale.
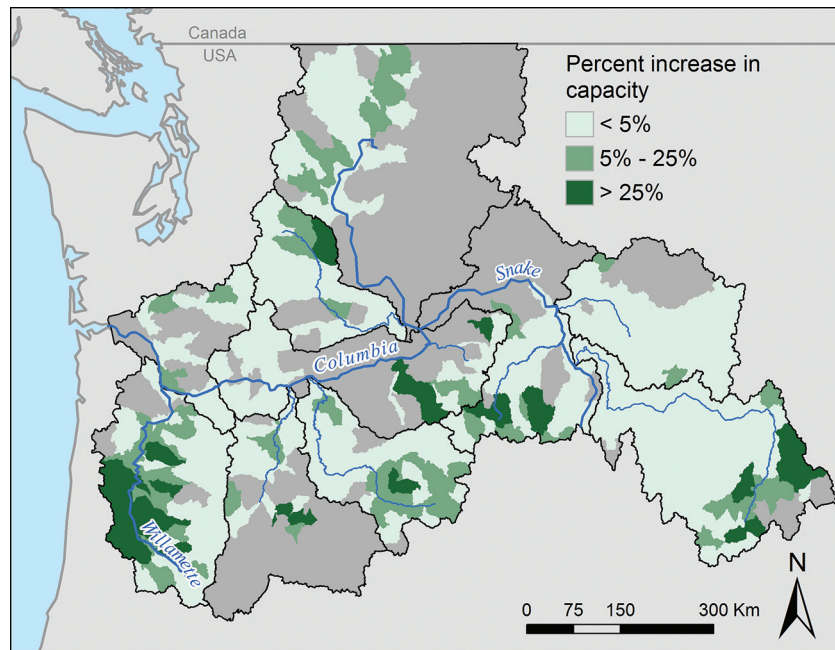
compared to the single value applied to all habitats in a reach with quantile regression and fixed density approaches.

One important assumption of the habitat capacity approach is that all habitats are at a fully seeded capacity, a state that is unlikely to occur in the wild at larger spatial scales but provides a useful index for comparisons. In this sense habitat capacity is distinct from population capacity, which is an asymptotic or long-term average capacity, derived from fitting demographic data to models that assume density dependence (Ricker 1954; Beverton and Holt 1957; Barrowman and Myers 2000). This important difference between habitat and population capacity makes validation of habitat capacity estimates from monitoring data impractical, as observations of abundance at the population level are a composite of fully seeded and underseeded habitats and density dependent processes therein. It is our expectation, therefore, that habitat capacity estimates exceed population capacity estimates in most circumstances. That said, comparisons between habitat capacity and population capacity could inform us whether limitations on the population are occurring at the spawning or pre-parr stage (population capacity ≪ habitat capacity) or at the overwintering, smolt, or marine survival stage (population capacity ~ habitat capacity). Estimation of habitat capacity, and the change in habitat capacity that may result from management or restoration actions, allows for a direct comparison of the benefit of various options independent of contemporary population dynamics (Walters et al. 2013a).

Often, individual restoration projects may be too small to detect a beneficial response, or other limiting factors in the watershed constrain their benefits (Roni et al. 2002; Beechie et al. 2008). Recently, monitoring and modeling efforts have been used to quantitatively evaluate the potential benefits of habitat restoration at larger spatial scales (e.g., Bartz et al. 2006; Wall et al. 2016; Justice et al. 2017; Wheaton et al. 2018). Similarly, our estimates of floodplain restoration potential are a first step in providing managers with guidance for focusing floodplain restoration efforts on areas with the greatest potential for increasing salmon abundance and survival. These results can be further combined with life-cycle models to demonstrate the potential benefits of restoration for increases in adult salmon abundance (Bartz et al. 2006;

Scheuerell et al. 2006), as well as to identify target reaches of high floodplain restoration potential within watersheds. Both types of studies are underway in the CRB, and the combination of our results with those of other studies should increase the cost-effectiveness of restoration efforts.

We recognize that reconnecting side channels and other floodplain habitats is only one of many habitat restoration actions that are needed for salmon recovery. A thorough body of work has related increased abundance of wood in streams to higher habitat quality for salmonids (Montgomery et al. 2003; Whiteway et al. 2010; Roni et al. 2015). Additional studies highlight the importance of riparian restoration for decreasing summer stream temperatures and ameliorating climate change effects on stream temperature (Beechie et al. 2000, 2013). While these types of actions are important for realizing the full benefits of side channel restoration, these actions without floodplain restoration will likely achieve a more limited benefit and provide less resilience to future climate change effects (Beechie et al. 2013; Bellmore et al. 2017).

In addition to ecosystem needs, restoration project selection relies on available funding, feasibility, and level of interest by practitioners. Funding for habitat restoration in Pacific Northwest streams is generally top-down, originating with a handful of Federal agencies; yet decision-making about habitat actions is often bottom-up and decentralized, with projects chosen by local entities at scales smaller than ESUs. This piecemeal project selection process has resulted in a lack of coordination and planning for restoration at population scales, resulting in potential mismatch between ecological need and funded projects (Beechie et al. 2008; Barnas et al. 2015). Further studies estimating the restoration potential and resulting potential demographic response for other restoration types throughout the CRB are needed. This approach would allow for a more formal analysis of the relative or synergistic effects of each restoration option and a cost–benefit analysis to focus restoration funds toward more effective projects.

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