frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 11 September 2026
DOI 10.3389/fevo.2026.1924685

Check for updates

OPEN ACCESS

EDITED BY
Nicholas A. Som,
California Polytechnic University,
United States

REVIEWED BY
Tinyiko Cavin Shivambu,
University of South Africa, South Africa
Carlos Polivka,
Forest Service (USDA), United States

*CORRESPONDENCE
Tobias J. Kock
tkock@usgs.gov

RECEIVED 30 June 2026
REVISED 04 August 2026
ACCEPTED 24 August 2026
PUBLISHED 11 September 2026

CITATION
Hatten JR, Hardiman JM, Daw DA, Couch CE and Kock TJ (2026) Estimating habitat availability for Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) to inform reintroduction planning in the middle Snake River basin, USA. *Front. Ecol. Evol.* 14:1924685. doi: 10.3389/fevo.2026.1924685

COPYRIGHT
This work is authored by James R. Hatten, Jill M. Hardiman, Claire E. Couch, Tobias J. Kock on behalf of the U.S. Government and as regards Dr. Hatten, Dr. Hardiman, Dr. Couch, Dr. Kock and the U.S. Government, is not subject to copyright protection in the United States. Foreign and other copyrights may apply. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

Estimating habitat availability for Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) to inform reintroduction planning in the middle Snake River basin, USA

James R. Hatten[1], Jill M. Hardiman[1], Dennis A. Daw[2], Claire E. Couch[3] and Tobias J. Kock[1]*

[1]U.S. Geological Survey, Western Fisheries Research Center, Cook, WA, United States, [2]Upper Snake River Tribes Foundation, Boise, ID, United States, [3]U.S. Geological Survey, Western Fisheries Research Center, Corvallis, OR, United States

Anadromous fishes have been blocked from the middle Snake River basin since the construction of flood control, irrigation, and hydroelectric projects during the 19th and 20th centuries, culminating with the construction of Hells Canyon Dam (river kilometer [rkm] 398) in 1967. Seven large watersheds in the blocked area of the basin are under consideration for Pacific salmon reintroduction. The primary objective of this study was to identify and characterize potential reintroduction sites with high-quality rearing and spawning habitat for Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) upstream of the Hells Canyon Complex in Idaho, Oregon, and Nevada, USA. We created and tested habitat models to predict rearing presence/absence, rearing abundance, and spawning presence/absence using channel morphology, hydrology, and stream temperature variables obtained from regional peer-reviewed datasets. Habitat models were trained with salmonid presence and abundance records collected in the lower Snake River basin (downstream of Hells Canyon Dam), where anadromous fish can currently access, from 1993 to 2011. Model performance was tested with set-aside data comprised of randomly selected reaches and independent environmental DNA data. An index model was created in the middle Snake River basin for each species by combining results from the habitat models. Modeling covariates differed by species and life stage and included different combinations of August stream temperature, summer flow, channel slope, and quadratic terms for temperature and slope. The habitat models predicted high versus low Chinook salmon and steelhead probability and abundance with 66% to 85% accuracy depending on species and life stage. The index models predicted a total of 2,887 km of Chinook salmon habitat and 2,434 km of steelhead habitat in the blocked area. The three basins in the blocked area with the greatest amount of predicted habitat were the Powder River, South Fork Payette River, and North Fork Payette River for Chinook salmon, and the Powder River, South Fork Boise River,

and South Fork Payette River for steelhead. The modeling approach presented here is complementary to other planning efforts for Chinook salmon and steelhead reintroduction in the blocked area of the Snake River basin, and similar approaches may be useful for reintroduction planning in other systems.

KEYWORDS

rearing habitat, reintroduction, salmon, spawning habitat, steelhead

1 Introduction

Habitat loss is a leading cause of declining biodiversity and species abundance worldwide, and anadromous fish species are particularly vulnerable given their unique life histories (Sheer and Steel, 2006; Joppa et al., 2016; Connor et al., 2019; Hogue and Breon, 2022). These fish have critical life stages (migration, spawning, incubation and rearing) that occur in freshwater habitats adversely affected by human disturbances such as dam construction, mining, logging, water withdrawal and power generation (Dauble et al., 2003; Williams et al., 2005; Waldman and Quinn, 2022). In western North America, large impassable dams have drastically reduced access to historical habitats of Pacific salmon (*Oncorhynchus* spp.), contributing to the loss or decline of many populations (NPPC, 1986; Nehlsen et al., 1991; Dauble et al., 2003; McClure et al., 2008). For example, Chinook salmon (*O. tshawytscha*) are currently restricted from accessing 50–80% of their historical habitat in the Columbia and Snake River basins and in California's Central Valley (Yoshiyama et al., 2001; Dauble et al., 2003; Baldwin et al., 2022). Pacific salmon are economically, culturally, and ecologically important, and therefore are the focus of recovery efforts throughout much of their historical range (Gende et al., 2002; Johnsen, 2009; Galbreath et al., 2014; Noakes, 2014; Baldwin et al., 2022; Waldman and Quinn, 2022).

Salmon recovery efforts are not only critical for biodiversity but also for preserving the heritage and well-being of local Indigenous peoples who have long depended on salmon for cultural, spiritual, and subsistence purposes (Galbreath et al., 2014; U.S. Columbia Basin Tribes and Canadian First Nations, 2015; Polissar et al., 2016). The loss of salmon has disrupted traditional fishing practices, ceremonies, and diets, resulting in cultural and economic hardships for many Tribal communities (Blanchet et al., 2022). Thus, in numerous locations, Tribal entities have initiated salmon reintroductions to restore viable populations in historically important areas where they have been absent for decades (Galbreath et al., 2014; Matala et al., 2019; Baldwin et al., 2022; O'Sullivan and Alex, 2024). However, salmon remain absent from large swaths of their historical habitat. For example, in the Snake River basin, dams constructed during 1892–1967 eliminated access for Chinook salmon to an estimated 8,249 river kilometers (rkm) of high-quality stream habitat (Parametrix, 2023). This loss adversely affected numerous Tribes including, but not limited to, the Burns Paiute, Fort McDermitt Paiute-Shoshone, Shoshone-Bannock Tribes of the Fort Hall Reservation, and Shoshone-Paiute Tribes of the Duck Valley Reservation (hereafter "Upper Snake River Tribes" [USRT]) who have been forced to exist without salmon for decades (USRT, 2015, 2018; Parametrix, 2023). In recent years, USRT has initiated efforts to examine salmon reintroduction opportunities throughout the basin, which have focused on assessing historical losses as well as habitat quantity and quality in the blocked area (USRT, 2018; Parametrix, 2023). Because recent information on Pacific salmon distribution and abundance is often lacking in areas where these species have been extirpated, habitat assessments based on environmental variables can be valuable for identifying currently unoccupied reaches with the potential to support reintroduction. Habitat assessments have often been the first step in other salmon reintroductions, as they provide necessary information to inform decisions regarding reintroduction site selection, hatchery fish production, and collection and transport programs to move fish around impassable dams (Anderson et al., 2014; UCUT, 2019, 2022; USRT, 2018; Kock et al., 2021).

Field assessments of salmon habitat across large riverscapes are time-intensive, costly, and often impractical, therefore habitat modeling approaches using Geographic Information Systems (GIS) are commonly used as a first step to broadly identify and characterize potential habitat in the reintroduction area (Osborne and Seddon, 2012; Isaak et al., 2017a). For example, Intrinsic Potential (IP) models have been widely applied across the Pacific Northwest (USA) to assess salmon habitat availability. IP models integrate expert opinion and published literature on species-habitat relationships with geomorphic, climatic, and hydrologic variables from existing spatial datasets to identify and classify stream reaches based on physical habitat potential (e.g., poor, fair, good) (Burnett et al., 2007; Sheer et al., 2009; Parametrix, 2023). Alternatives to IP models include predictions based on empirically derived statistical relationships between habitat variables and species presence or abundance. These relationships can be derived from field sampling datasets (e.g., spawner surveys, beach seines, or electrofishing) and existing habitat data (Tiffan et al., 2002; Hatten et al., 2009; Isaak et al., 2017a). Whereas IP models produce nominal outcomes, empirical models produce continuous probabilities (e.g., 70% probability of salmonid habitat) that are more flexible and information rich. Decisions related to which approach should be used largely depend on the underlying datasets from which models are derived. IP models are a good choice when training datasets are sparsely populated or absent altogether, while empirical models are well suited for large, robust training datasets that allow for statistical analysis and verification. Importantly, the actual distribution and abundance of a species depend on numerous factors beyond the set of attributes often included in habitat models, which are often limited. For example, species distribution and abundance may be affected by unmeasured habitat variables (Geist and Dauble, 1998), prey availability (Rosenfeld and Ptolemy, 2012), inter-and intra-specific interactions (Taylor, 1991; Bugert and Bjornn, 1991; Elvidge

et al., 2016), or the overall abundance of the species in question (Hedger et al., 2005). When species abundance is low, areas that are predicted as "good" habitat may remain unoccupied, even given robust training datasets and high model accuracy (e.g., White et al., 2026). Despite these limitations, habitat models based on empirical data can provide valuable baseline information on habitat quality in currently unoccupied areas.

In this study we developed statistical relationships between habitat variables and empirical data on spring Chinook salmon and summer steelhead (*O. mykiss*) in the lower Snake River basin, the in-basin region currently accessible to anadromous fish, and projected those relationships to the middle Snake River basin to quantify suitable habitat for these species that are being considered for reintroduction (USRT, 2018; Parametrix, 2023). Our objectives were to (1) identify habitat suitable for two life stages (juvenile rearing and adult spawning) of Chinook salmon and steelhead in the blocked area of the Snake River basin, and (2) develop a management-relevant habitat index using peer-reviewed, publicly available datasets. While this approach was developed to address specific needs related to potential reintroduction in the Snake River basin, these methods provide a useful framework for assessing habitat quantity across large spatial areas of interest where field sampling may be unfeasible.

2 Methods

2.1 Project area

The Snake River basin is the largest sub-basin of the Columbia River (in Canada and the United States (U.S.)) and spans six U.S. states including Wyoming, Idaho, Utah, Nevada, Oregon, and Washington (Figure 1; Mahler, 2019). The Snake River originates in the Rocky Mountains and flows ~1,674 km downstream to its confluence with the Columbia River near Pasco, Washington (Mahler, 2019). The watershed covers approximately 280,000 km^2 and comprises approximately 41% of the total Columbia River basin (Kammerer, 1987). The climate of the basin ranges from semi-arid to alpine and is heavily influenced by the rain shadow of the Cascade Range. Precipitation is highly variable, ranging from 15–25 cm in desert areas, such as the Snake River Plain in southern Idaho and the lower Snake River in southeastern Washington, to over 241 cm in high mountain headwaters such as the Teton Range (Hoekema and Sridhar, 2011; Mahler, 2019). Air temperature extremes range from approximately -18 °C in winter to over 38 °C in summer, and high-elevation areas serve as critical cold-water refuges for sensitive fish species as low altitudes warm. Approximately 30% of the watershed is farmland; the Snake River Plain is a global leader in irrigated agriculture with over 3.8 million acres of crops including potatoes, sugar beets, and wheat (Idaho State University, 2026). Roughly 50% of the basin consists of semi-arid shrubland and rangeland used primarily for livestock grazing and another 15% is forested (largely managed by the U.S. Forest Service); urban and industrial areas account for only about 1% of the land use, despite housing major cities like Boise and Idaho Falls (Benke and Cushing, 2005).

The Snake River basin supports 35 native fish species including Chinook salmon, sockeye salmon (*O. nerka*), and steelhead (Maret and Mebane, 2005). These fish undertake an inland journey of over 1,400 km, and the basin comprises approximately 50% of all available cold-water habitat for west coast Pacific salmon (NOAA, 2026). Shoshone Falls (rkm 990), formed about 14,000 years ago, marks the historical upper limit of fish migration in the Snake River. Hells Canyon Dam (rkm 398) was completed in 1967 (BOR, 2024) and is owned and operated by Idaho Power. Although Hells Canyon Dam is the most downstream barrier to anadromy on the Snake River, a series of dams constructed by the Bureau of Reclamation in the early 1900s blocked access to major tributaries, including the Boise, Burnt, Malheur, Owyhee, Powder and Payette rivers (BOR, 2024). Throughout this work, "lower basin" refers to the Snake River basin from Hells Canyon Dam downstream to the confluence with the Columbia River, and "middle basin" refers to the Snake River from Shoshone Falls to Hells Canyon Dam (Figure 1). Almost half of the middle basin is latitudinally similar to the lower basin, between 44 and 45.5 degrees north latitude. The Owyhee and Bruneau basins are further south than the Payette, Boise, and Malheur basins and do not overlap latitudinally with the lower basin. The middle basin includes 12 damsheds (defined by the watershed area upstream of a major dam) that range in size from 803 km^2 (Unity) to 28,156 km^2 (Owhyee) (Parametrix, 2023). At the HUC-8 scale, there are 29 basins that range in size from 750 km^2 (Middle Snake-Payette) to 8,735 km^2 (Bruneau). These two spatial scales overlap, such that some damsheds contain multiple HUC-8 basins and some HUC-8 basins include multiple damsheds.

2.2 Data acquisition

We integrated six datasets for habitat modeling: (1) the National Hydrography Database Plus (NHDPlus, 100 km resolution, https://www.epa.gov/waterdata/nhdplus-national-hydrography-dataset-plus) depicted stream networks (McKay et al., 2012); (2) the NorWeST database (https://research.fs.usda.gov/rmrs/projects/norwest) provided estimated August stream temperatures (Isaak et al., 2017b); (3) the Variable Infiltration Capacity dataset (VIC, https://research.fs.usda.gov/rmrs/products/dataandtools/archived-western-streamflow-metrics-interior-columbia-river-basin) provided mean summer flow estimates (Liang et al., 1994; Wenger et al., 2010); (4) a dataset stored in Dryad (https://datadryad.org/dataset/doi:10.5061/dryad.d0s7k) contained georeferenced occurrence and rearing abundance records for Chinook salmon and *O. mykiss* (steelhead are anadromous *O. mykiss*) throughout the lower Snake River basin (Isaak et al., 2017a); (5) an environmental DNA (eDNA) dataset (https://www.fs.usda.gov/rds/archive/Catalog/RDS-2018-0010) contained presence-absence surveys for both species (Young et al., 2018), and (6) StreamNet, a geospatial dataset (https://www.streamnet.org/) provided information about spring Chinook salmon and steelhead spawning locations in the lower Snake River basin (Figure 2) (StreamNet, 2025). StreamNet contained spawning data for Chinook salmon in 11,526 NHDPlus reaches (3,164 presence, 8,362 absence) and spawning data for steelhead in 25,092 reaches (10,734 presence, 14,358 absence).

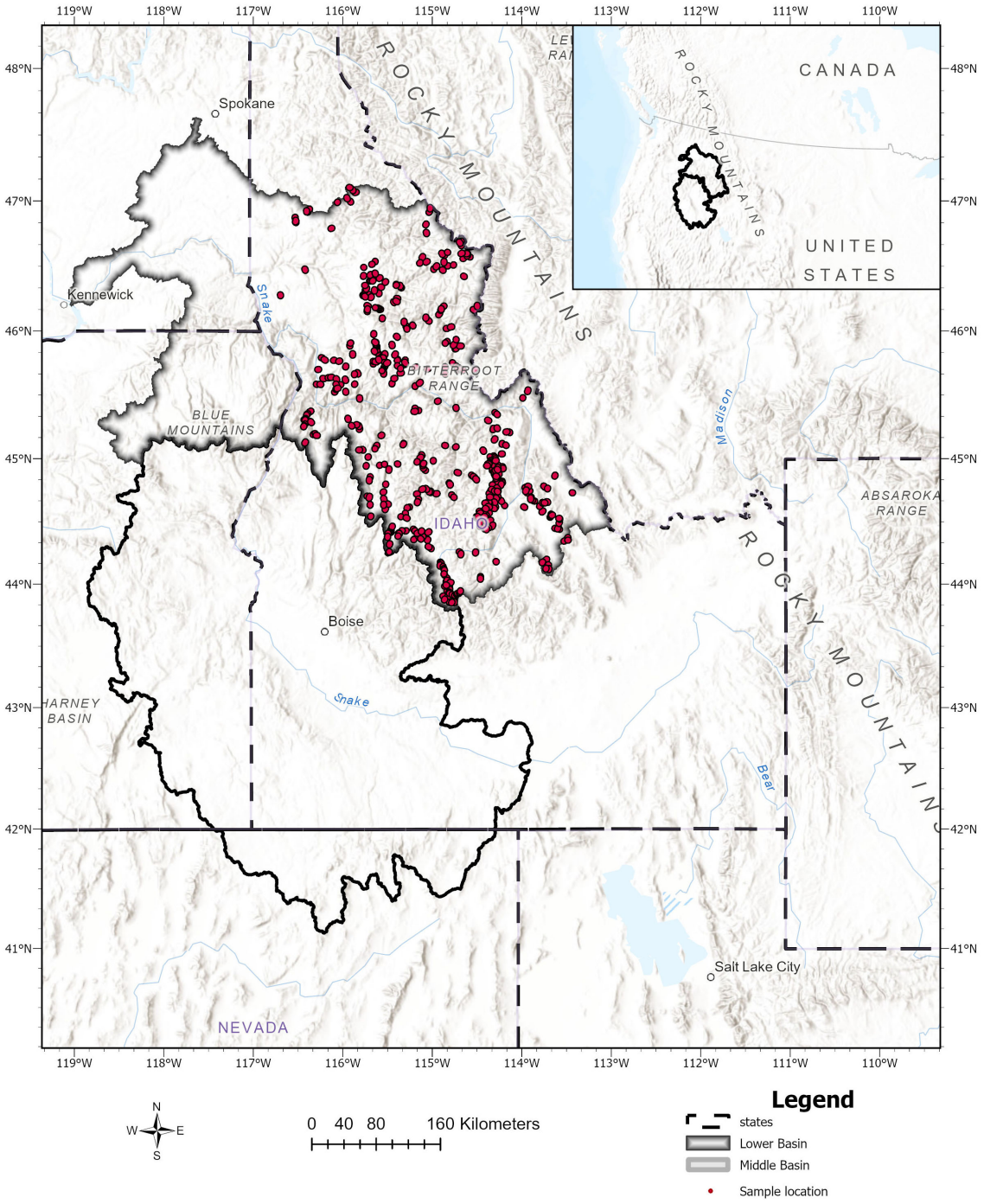


FIGURE 1
Map of the lower Snake River basin downstream (north) of Hells Canyon Dam, and the middle Snake River basin upstream (south) of Hells Canyon Dam. Red points indicate the locations of Chinook salmon and steelhead rearing data used for model training and testing.

To identify potential Chinook salmon and steelhead habitat in the blocked area, habitat models were developed and tested in the lower basin and projected to the middle basin. The lower basin contained ~ 57,000 NHDPlus reaches, of which ~33% (18,735) were second-order or larger perennial streams (Strahler, 1957). The middle basin contained ~67,000 NHDPlus reaches, of which ~21% (13,782) were second-order or larger perennial streams. A comparison of physical attributes of perennial second-order or larger streams revealed lower basin streams were steeper on average and had cooler August stream temperatures than middle basin streams, but summer flow and Strahler stream order were similar (Figure 3). Approximately 80% of intermittent streams in the lower basin were first order compared to ~74% in the middle basin.

The Dryad fish survey data were compiled from multiple organizations and included snorkeling and backpack electrofishing records from perennial streams with summer flows <32 m^3/sec (Isaak et al., 2017a). The range of flows included in the dataset resulted in exclusion of mainstem reaches from rearing habitat

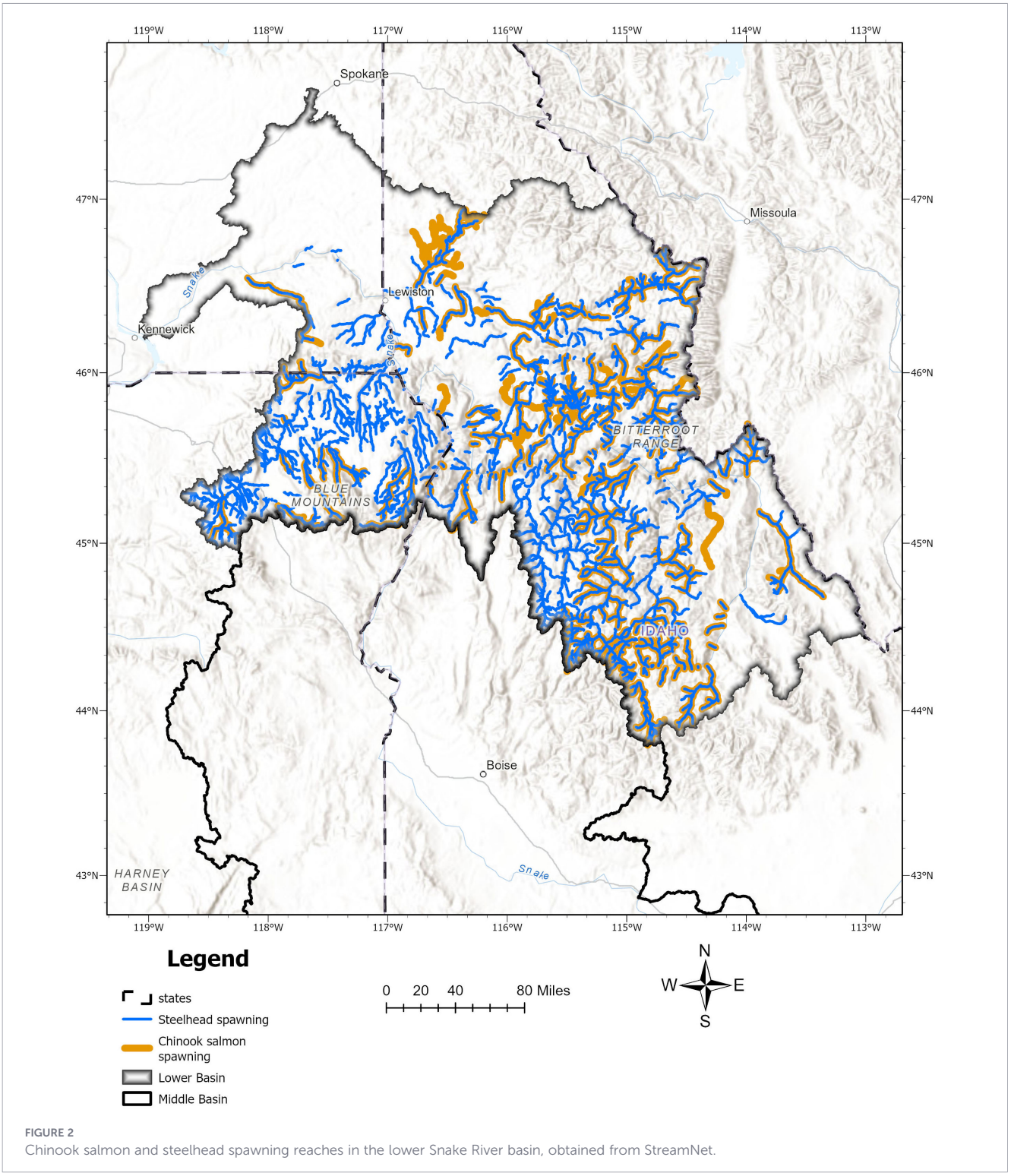


FIGURE 2
Chinook salmon and steelhead spawning reaches in the lower Snake River basin, obtained from StreamNet.

projections (see section 3.4 below). Some reaches were sampled multiple times per year, or once per year over many years, while other reaches were only sampled once. We eliminated pseudo-replication by grouping fish records by NHDPlus reach, assigned an occurrence value of 1 to a reach if there was an occurrence record during the sampling period and a zero otherwise, and averaged fish abundance records across all sampling occasions within a reach. Abundance summaries were based on 6,189 juvenile Chinook salmon survey records obtained from 455 unique NHDPlus reaches, and 5,182 juvenile steelhead records obtained from 478 NHDPlus reaches (Figure 1). Juvenile Chinook salmon average abundances ranged from 0 to 707 per NHDPlus reach (mean of 31.5) and juvenile steelhead average abundances ranged from 0 to 691 per NHDPlus reach (mean of 53.2). Eighty-six percent of Chinook salmon sample reaches and 84% of steelhead sample reaches were sampled more than once.

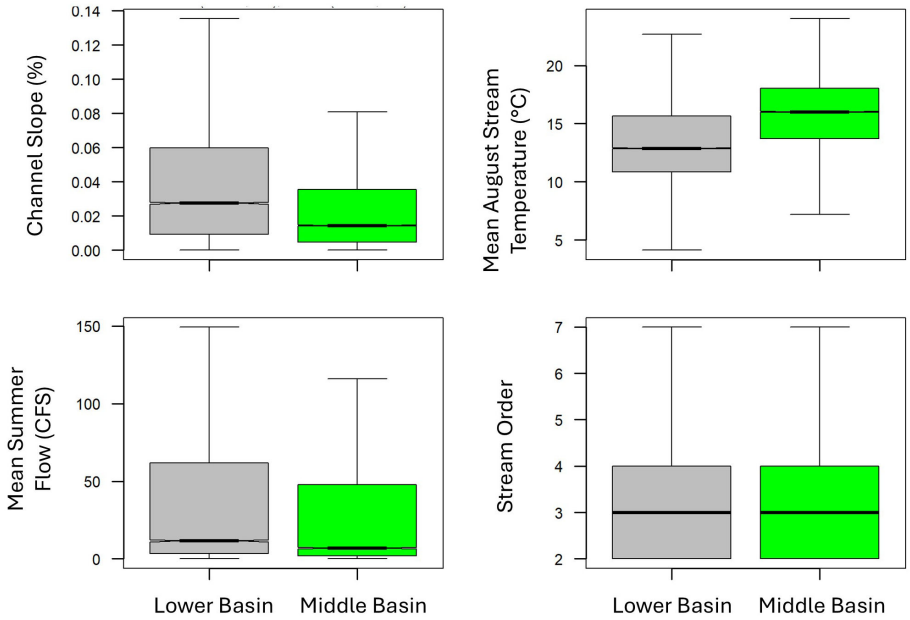


FIGURE 3
Comparison of physical stream attributes in the lower versus middle Snake River basins (outliers not shown).

We used eDNA data to independently verify the rearing presence-absence habitat models (Young et al., 2018). The eDNA data were collected by staff representing numerous agencies that have partnered with the National Genomics Center for Wildlife and Fish Conservation (NGC) to create the eDNA Atlas database with coverage throughout the United States. We grouped eDNA records by NHDPlus reach, assigned an occurrence value of 1 to a reach if there was an occurrence record during the sampling period and a 0 otherwise. This resulted in a total of 393 NHDPlus reaches for Chinook salmon and 576 reaches for *O. mykiss*. Importantly, eDNA sampling was conducted separately from the fish sampling that comprised the Dryad database and thus provided independent verification of the presence-absence models.

The six datasets described here were linked by reach using NHDPlus composite outlet ID after excluding firstorder, intermittent reaches to ensure conservative and reliable habitat estimates (Isaak et al., 2017a, 2025). A GIS database was then constructed containing summer flow from June through September [FLOW], August stream temperature [S1], channel slope [SLOPE], fish presence-absence, rearing abundance, spawning presence/absence, and eDNA sampling results. Importantly, VIC and NorWeST modeled datasets contained 1993 to 2011 average summer flow and August stream temperatures that corresponded with decades when the fish survey information was collected (Isaak et al., 2017a; StreamNet, 2025).

2.3 Habitat model development

We developed three separate generalized linear models (GLMs) for each species, with spawning (presence/absence), rearing (presence/absence), or rearing abundance (average counts per reach) as response variables. Model selection resulted in a total of six GLMs, which were assembled into a single habitat index model. All analyses, model training, and verification were conducted in the R statistical environment, version 4.5.1 (R Core Team, 2024) and ArcGIS Pro Version 3.7 (Esri Inc, 2022). The GLMs were constructed (trained) with a 70% randomized draw of NHDPlus reaches that contained data for focal species and life stage. The remaining 30% of reaches were set aside and used to test the predictive performance of the models constructed with the training data.

Binomial logistic regression was used to model spawning and rearing presence-absence for each species (Hosmer and Lemeshow, 2000) and zero inflated negative binomial regression was used to model rearing abundance (Yau et al., 2003). We tested nine alternative combinations of explanatory variables for each of the six models (Table 1) and used Akaike's information criterion (AIC) to identify the combination of variables that best explained each response variable (Burnham and Anderson, 2002). The full model included SLOPE, S1, log-transformed flow (lnFLOW) to account

TABLE 1 Alternative combinations of explanatory variables that were compared for Chinook salmon and steelhead spawning and rearing models.

Model	Explanatory variables
1	lnFLOW, SLOPE, S1
2	lnFLOW, SLOPE
3	S1, $S1^2$
4	lnFLOW, S1
5	lnFLOW, SLOPE, $SLOPE^2$, S1, $S1^2$
6	lnFLOW, S1, $S1^2$
7	S1
8	lnFLOW
9	SLOPE

for differential responses across the range of FLOW values, and quadratic terms for SLOPE and S1, as explanatory variables. Quadratic terms for SLOPE and S1 were evaluated to identify potential nonlinear relationships with habitat. A pseudo R-squared statistic (Nagelkerke, 1991) was generated for each alternative model to quantify explained variability, and leave-one-out cross-validation (LOOCV), which captures absolute error associated with a prediction (Molinaro et al., 2005), was conducted to confirm model selection results.

2.4 Habitat model verification

The best performing logistic models for rearing and spawning were verified using receiver operating characteristic (ROC) curves to evaluate overall model accuracy based on true positive and true negative rates across a range of probability thresholds (Egan, 1975). ROC curves were constructed using the 30% randomized set-aside of NHDPlus reaches from the Dryad dataset, which included 136 set-aside reaches for Chinook salmon rearing, 169 for steelhead rearing, 3,640 for Chinook salmon spawning, and 8,364 for steelhead spawning. For the logistic rearing models, a second ROC curve was generated using the eDNA dataset, which included presence/absence data for Chinook salmon in 393 NHDPlus reaches and presence/absence data for *O. mykiss* in 576 NHDPlus reaches. The area under the curve (AUC) was calculated based on the ROC curves to summarize and compare overall classification performance for each of the logistic models. The predictive accuracy of each logistic model was evaluated by identifying a probability threshold that balanced sensitivity and specificity of the model projections based on the set-aside data (i.e., omission and commission errors) and then calculating the mean of model sensitivity and specificity [(sensitivity + specificity)/2] at the given probability threshold. The rearing abundance models were verified by calculating Pearson's correlation coefficient (r) between predicted and observed rearing abundances in 30% set-aside reaches. Additionally, the predictive accuracy of each abundance model was tested based on its ability to predict abundances above versus below the median observed abundance values in the set-aside reaches. Similar to the logistic models, predictive accuracy for the abundance models was evaluated using ROC curves and the mean of model sensitivity and specificity.

2.5 Index model

Following model development and verification, spawning and rearing models were projected into the blocked middle basin to identify potential habitat. To make the habitat predictions as accurate as possible, we removed all areas known to have natural blockages to anadromy from the habitat projections (NOAA, 2025). For each species, we used GLM results to create three binary habitat prediction maps (spawning presence-absence, rearing presence-absence, and rearing abundance) in the middle basin. For the presence-absence models, we converted the predicted probability output for each reach into binary format by selecting a probability threshold that balanced sensitivity and specificity (Story and Congalton, 1986). Predicted values above the threshold were assigned a 1 and predicted values below the cut-point were assigned to 0. For the rearing density models, we converted the predicted densities into binary format by assigning a 1 to any values above the median observed density and a 0 to any values below the median observed density from the training datasets. We then overlaid the three resulting binary outputs to create a habitat index value from 0 to 3 for each focal species. An index value of 0 indicated that a NHDPlus reach did not contain predicted habitat based on any of the models, whereas a value of 3 indicated that all three binary models predicted habitat in an NHDPlus reach. Intermediate index values (1 or 2) indicated that predicted habitat existed in an NHDPlus reach but was not supported by all three models. Following examination of the index model projections, probability and abundance thresholds for the rearing and spawning models were re-evaluated and adjusted if needed, based on historical information about fish distribution in the middle basin. We summarized predicted index-3 habitat quantity (stream length) in the middle basin at two spatial scales: (1) damshed, and (2) HUC-8 hydrological units, which represent large subbasins inside the project area (Figure 4).

3 Results

3.1 Habitat model development

The final structure of the best performing models varied by species, life stage, and presence/absence versus abundance models (Table 2). In general, the alternative model with the lowest AIC value was selected. The single exception was the Chinook salmon rearing abundance model where the AIC ranking conflicted with LOOCV results. In this case, the simpler model with slightly higher AIC (delta = 7.2) had lower LOOCV, therefore it was selected in lieu of the more complex model. For steelhead rearing presence, the best performing model had only slightly lower AIC (delta = 0.8), but this model was also simpler than the closest competing model and was therefore selected. For the Chinook salmon rearing abundance model and the steelhead rearing presence model, AUC was calculated for the top two competing models. Chinook salmon and steelhead spawning and rearing presence were negatively associated with SLOPE and positively associated with S1 and lnFLOW (Table 3; Supplementary Figure 1). Quadratic terms in the final presence/absence models indicated nonlinear effects of SLOPE and S1 on Chinook salmon rearing and spawning presence and steelhead spawning presence. For the rearing abundance models, the coefficients in the zero-inflation component predicted the probability that fish were absent from the reach, and the coefficients in the count component predicted the abundance at sites where fish were predicted to be present. Chinook salmon rearing abundance at occupied sites was primarily driven by SLOPE, which had a strong negative effect on abundance. Steelhead rearing abundance at occupied sites was positively associated with FLOW and S1 and exhibited unimodal relationships with SLOPE and S1 (Supplementary Figure 1).

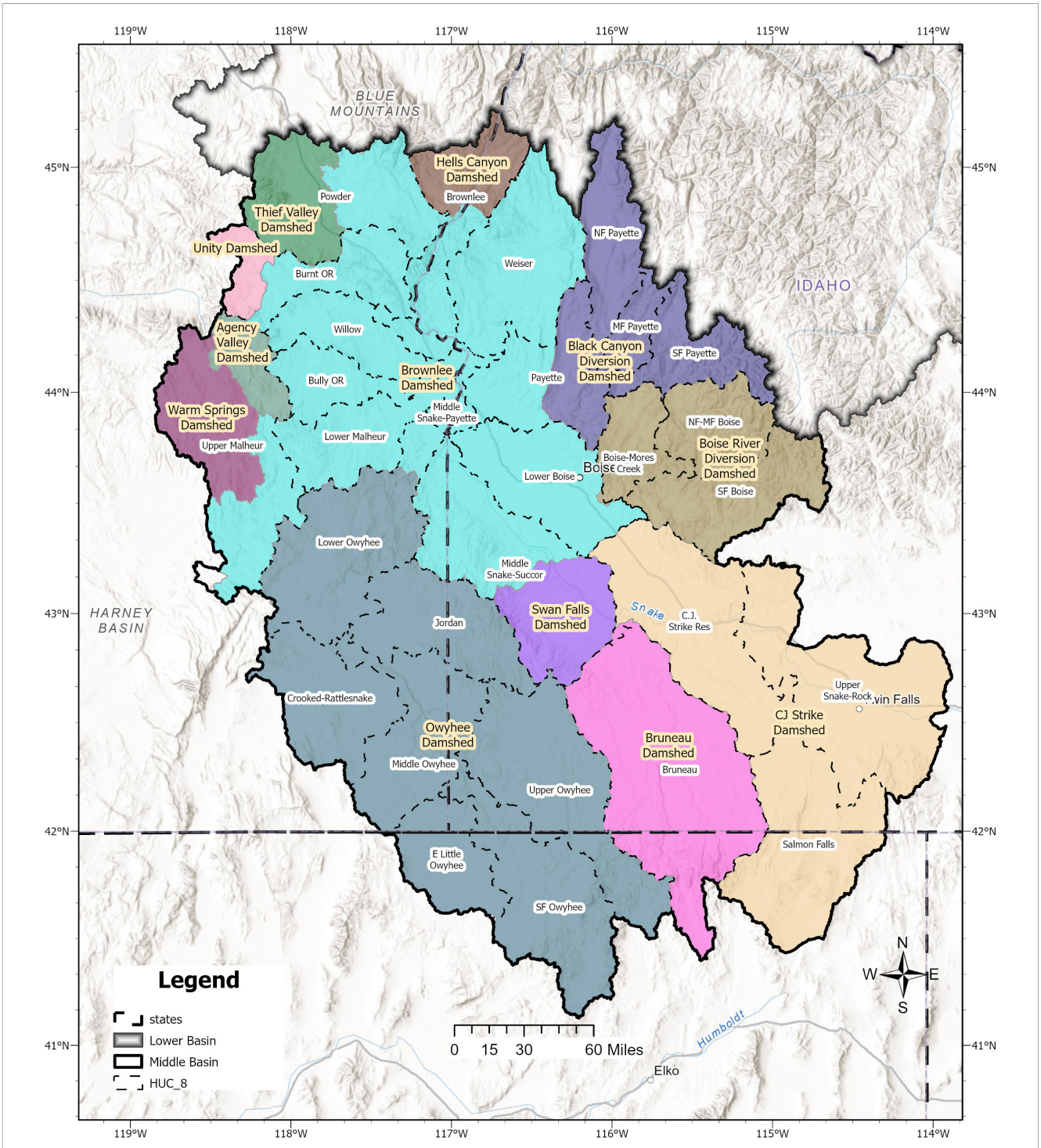


FIGURE 4
The two spatial scales used to summarize predicted habitat for Chinook salmon and steelhead in the middle Snake River basin: (1) damshed (gray labels), and (2) HUC8 (white labels).

3.2 Habitat model verification

The Chinook salmon and steelhead rearing presence/absence models produced high AUC values (0.922 and 0.928) and predictive accuracy (0.859 and 0.851) on the 30% set-aside reaches (Chinook salmon N = 136; steelhead N = 169) using 0.50 and 0.70 probability thresholds, respectively (Table 2). The rearing presence/absence models achieved predictive accuracies of 0.731 (Chinook salmon, 0.35 probability threshold) and 0.702 (steelhead, 0.35 probability threshold) with the independent eDNA dataset. Predictions from the Chinook salmon rearing abundance model in the set-aside reaches were moderately correlated with observed values (r = 0.436), and observed values above versus below the median were predicted with AUC of 0.941 and accuracy of 0.841. Predictions from the steelhead rearing abundance model were also moderately correlated with observed values in the set-aside reaches (r = 0.385),

10.3389/fevo.2026.1924685

TABLE 2 Model selection criteria and performance metrics for the models for Chinook salmon and steelhead rearing presence/absence, rearing abundance, and spawning presence/absence.

Chinook salmon rearing (presence/absence)						
Model	ΔAIC	R^2	LOOCV	AUC	Threshold	Accuracy
*5**	*0*	*0.692*	*0.104*	*0.922*	*0.5*	*0.859*
1	8.9	0.665	0.105			
2	10.6	0.657	0.107			
6	29.5	0.620	0.119			
4	37.8	0.597	0.119			
8	43.2	0.579	0.125			
9	76.1	0.497	0.144			
3	104.3	0.425	0.169			
7	115.7	0.386	0.170			
Steelhead rearing (presence/absence)						
Model	ΔAIC	R2	LOOCV	AUC	Threshold	Accuracy
*1**	*0*	*0.660*	*0.097*	*0.928*	*0.70*	*0.851*
4	0.8	0.653	0.097	0.926		
6	2.6	0.653	0.098			
5	3.8	0.660	0.099			
2	28.1	0.585	0.114			
8	32.9	0.567	0.116			
7	60.7	0.491	0.136			
3	62.6	0.491	0.137			
9	90.7	0.399	0.153			
Chinook salmon rearing (abundance)						
Model	ΔAIC	R2	LOOCV	AUC	Threshold	Accuracy
5	0	0.603	4387.572	0.938		
*1**	*7.2*	*0.584*	*4331.377*	*0.941*	*2*	*0.814*
2	14.8	0.568	4353.705			
6	78.9	0.478	4927.045			
4	79.0	0.472	4958.561			
8	87.6	0.450	4923.418			
9	93.2	0.441	4454.841			
3	159.3	0.320	5130.909			
7	266.7	0.050	5931.058			
Steelhead rearing (abundance)						
Model	ΔAIC	R2	LOOCV	AUC	Threshold	Accuracy
*5**	*0*	*0.566*	*6400.592*	*0.846*	*13*	*0.702*
6	6.3	0.546	6441.224			
4	13.4	0.529	7034.149			
1	15.0	0.533	7071.667			
2	52.5	0.470	6932.647			
8	54.0	0.456	6898.454			
3	78.4	0.419	6565.397			
7	86.6	0.395	7028.945			
9	135.0	0.293	7267.927			

(Continued)

TABLE 2 Continued

Chinook salmon spawning (presence/absence)						
Model	ΔAIC	R2	LOOCV	AUC	Threshold	Accuracy
*5**	*0*	*0.219*	*0.167*	*0.763*	*0.27*	*0.714*
1	74.2	0.207	0.169			
6	166.2	0.193	0.171			
2	232.6	0.182	0.173			
4	254.0	0.178	0.174			
8	331.1	0.165	0.176			
9	669.3	0.109	0.184			
3	1148.4	0.026	0.196			
7	1250.7	0.007	0.198			
Steelhead spawning (presence/absence)						
Model	ΔAIC	R2	LOOCV	AUC	Threshold	Accuracy
*5**	*0*	*0.171*	*0.213*	*0.717*	*0.40*	*0.660*
6	83.5	0.165	0.214			
4	940.9	0.103	0.225			
1	941.8	0.103	0.225			
2	1047.2	0.095	0.226			
8	1070.0	0.093	0.226			
3	1951.5	0.026	0.240			
9	2077.3	0.016	0.242			
7	2269.5	0.001	0.245			

The top models are indicated with an asterisk. Models were selected based on AIC and LOOCV. If AIC scores were equivalent (<2 point difference) or if AIC results conflicted with LOOCV results, then the simpler model was used for habitat projections. Area under the curve (AUC) was calculated based on receiver operating curves for the best performing models. Thresholds were defined by selecting a value that balanced model sensitivity and specificity for the presence/absence models, and by selecting the median observed value for the abundance models. Accuracy indicates the mean of model sensitivity and specificity [(sensitivity + specificity)/2] at the given threshold value.

with values above versus below the median predicted with AUC of 0.846 and accuracy of 0.702 (Table 2, Figure 5). The Chinook salmon and steelhead spawning presence/absence models had somewhat lower AUC values (0.763 and 0.717) and predictive accuracy (0.714 and 0.660) on the set-aside reaches (Chinook salmon N = 3,640, steelhead N = 7,886) at 0.27 and 0.40 probability thresholds, respectively.

3.3 Habitat model projections

Model projections in the middle basin produced distinct patterns for each species and life stage (Supplementary Figures 2, 3). The Chinook salmon rearing presence/absence model produced higher presence probabilities in large tributaries with low channel gradients. The steelhead rearing presence/absence model produced higher model probabilities throughout much of the basin, except for the smallest tributaries at higher elevations. Projected rearing abundance patterns in the middle basin also differed between the two focal species. Chinook salmon rearing densities were predicted to be high in some large and intermediate sized tributaries, but not in smaller tributaries. Steelhead rearing densities were predicted to be high in a wider range of large, intermediate, and small tributaries, but in general, upper elevation tributaries on the eastern edge had low predicted abundance, consistent with the rearing presence/absence projections. Predicted spawning habitat for Chinook salmon generally included large and intermediate tributaries, but smaller tributaries in the northern and eastern portions of the basin also had high predicted probabilities. Predicted steelhead spawning habitat was widespread, but the highest predicted probabilities were in small to intermediate sized tributaries at relatively high elevations.

3.4 Index models and habitat summaries

Based on the initial probability and abundance thresholds for each of the presence and abundance models (Table 2), predictions for index-3 habitat values totaled 1,185 km for Chinook salmon (9.1% of perennial, >1st order streams in the basin), and 5,197 km for steelhead (39% of perennial, >1st order streams in the basin). For Chinook salmon, projected index-3 habitat based on initial threshold values did not include habitat in the upper Malheur and Bruneau river basins. These basins historically produced Chinook salmon, and there is no evidence that habitat capable of supporting Chinook salmon has disappeared. Because the index was highly sensitive to small changes in the threshold value for Chinook salmon rearing presence/absence, the threshold for this model was adjusted from 0.50 to 0.35 to generate the index. This adjustment resulted in 2,887 km of predicted Chinook salmon habitat (<32 m^3/sec; 22% of the stream network) and included all major basins that historically produced Chinook salmon (Figure 6).

TABLE 3 Intercepts and coefficients for top models of Chinook salmon and steelhead rearing (presence/absence and abundance) and spawning (presence/absence).

Rearing presence/absence models
(1) Chinook salmon presence = -12.55 + (0.097 * lnFLOW) – (80.97 * SLOPE) + (404.09 * $SLOPE^2$) + (1.86 * S1) – (0.07 * $S1^2$)
(2) Steelhead: Presence = -6.37 + (0.99 * lnFLOW) – (11.41 * SLOPE) + (0.50 * S1)
Rearing abundance models
(3a) Chinook salmon count model = 6.28 + (0.07 * lnFLOW) - (62.70 * SLOPE) - (0.14 * S1)
(3b) Chinook salmon zero inflation model = 5.89 – (1.72 * lnFLOW) + (51.44 * SLOPE) – (0.32 * S1)
(4a) Steelhead count model = -5.22 + (0.22 * lnFLOW) + (35.23 * SLOPE) – (464.73 * $SLOPE^2$) + (1.16 * S1) - (0.04 * $S1^2$)
(4b) Steelhead zero inflation model = -1.43 – (1.35 * lnFLOW) + (13.2 * SLOPE) – (56.06 * $SLOPE^2$) + (1.18 * S1) – (0.08 * $S1^2$)
Spawning presence/absence models
(5) Chinook: -3.09 + (0.45 * lnFLOW) - (16.31 * SLOPE) + (38.30 * $SLOPE^2$) + (0.41 * S1) – (0.02 * $S1^2$)
(6) Steelhead: = -5.84 + (0.32 * lnFLOW) – (1.45 * SLOPE) + (10.07 * $SLOPE^2$) + (0.94 * S1) – (0.04 * $S1^2$)

lnFLOW is the log of summer flow (average June – September, 1993 - 2011) of each NHDPlus reach.
S1 is average August water temperature (1993 – 2011) of each NHDPlus reach.
SLOPE is average channel slope (%) of NHDPlus reach.

Projected index-3 habitat for steelhead initially included more than half of the middle basin, but these relatively indiscriminate results were minimally informative for reintroduction planning. The steelhead index was highly sensitive to the spawning habitat probability threshold; therefore, we increased the threshold from 0.40 to 0.55, resulting in 2,434 km of predicted habitat (Figure 7; 18% of the stream network).

The two habitat index models produced similar patterns for each focal species by damshed, with the most abundant predicted Chinook salmon and steelhead habitat in the Black Canyon diversion, Brownlee, and Boise River diversion damsheds and least abundant habitat in the Unity, Warm Springs, and Agency Valley damsheds (Figure 8; Table 4). Predicted habitat by HUC-8 differed slightly between the two focal species. For Chinook salmon, the Powder, South Fork Payette, and North Fork Payette basins contained the most predicted habitat, whereas for steelhead, the Powder, South Fork Boise, and South Fork Payette river basins contained the largest amounts of predicted habitat (Figure 8; Table 5).

Mainstem reaches with mean summer flows that exceeded 32 m^3/sec were excluded from the habitat index projections because these flow rates fell outside the calibration range of the rearing models. However, these flows were within the calibration range of the spawning habitat model that was built with StreamNet data, and therefore spawning habitat projections could be made for the 1,381 km of mainstem habitat that exceeded 32 m^3/sec. Projections from spawning models in these mainstem reaches identified 494 km of predicted Chinook salmon spawning habitat and 138 km of predicted steelhead spawning habitat. Adding predicted mainstem spawning habitat (FLOW >32 m^3/sec) to the index-3 habitat predictions increased estimates to 3,381 km of predicted Chinook salmon habitat and 2,572 km of predicted steelhead habitat.

4 Discussion

In this study, a rich set of publicly available datasets, combined with a simple, flexible modeling framework were used to evaluate habitat availability for critical freshwater life stages of Chinook salmon and steelhead in the blocked area of the Snake River basin. The goal of this effort was to generate information useful for advancing salmon reintroduction efforts aimed at ecological and cultural restoration in the basin. Our results indicate that a large amount of habitat is currently available within the blocked area to support juvenile and adult life stages of Chinook salmon and steelhead. Model estimates suggest that at least 2,887 rkm of suitable habitat exists for Chinook salmon and 2,434 rkm of habitat exists for steelhead. The largest habitat quantities were identified in the Powder River, North Fork Payette River, and South Fork Payette River damsheds for Chinook salmon and in the Powder River, South Fork Boise River, and North Fork Payette River damsheds for steelhead. The predicted probability and abundance thresholds used

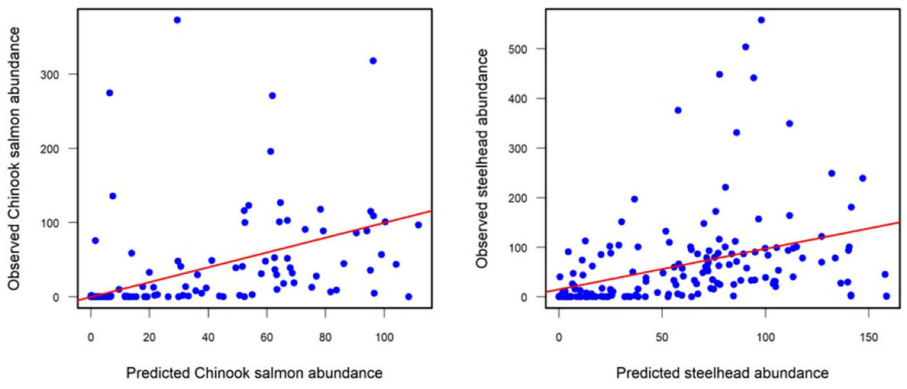


FIGURE 5
Observed versus predicted rearing densities for Chinook salmon and steelhead. The model was trained on 70% of randomly selected reaches in the lower Snake River basin. Observed and predicted values shown here are for 30% set-aside datasets from the same basin.

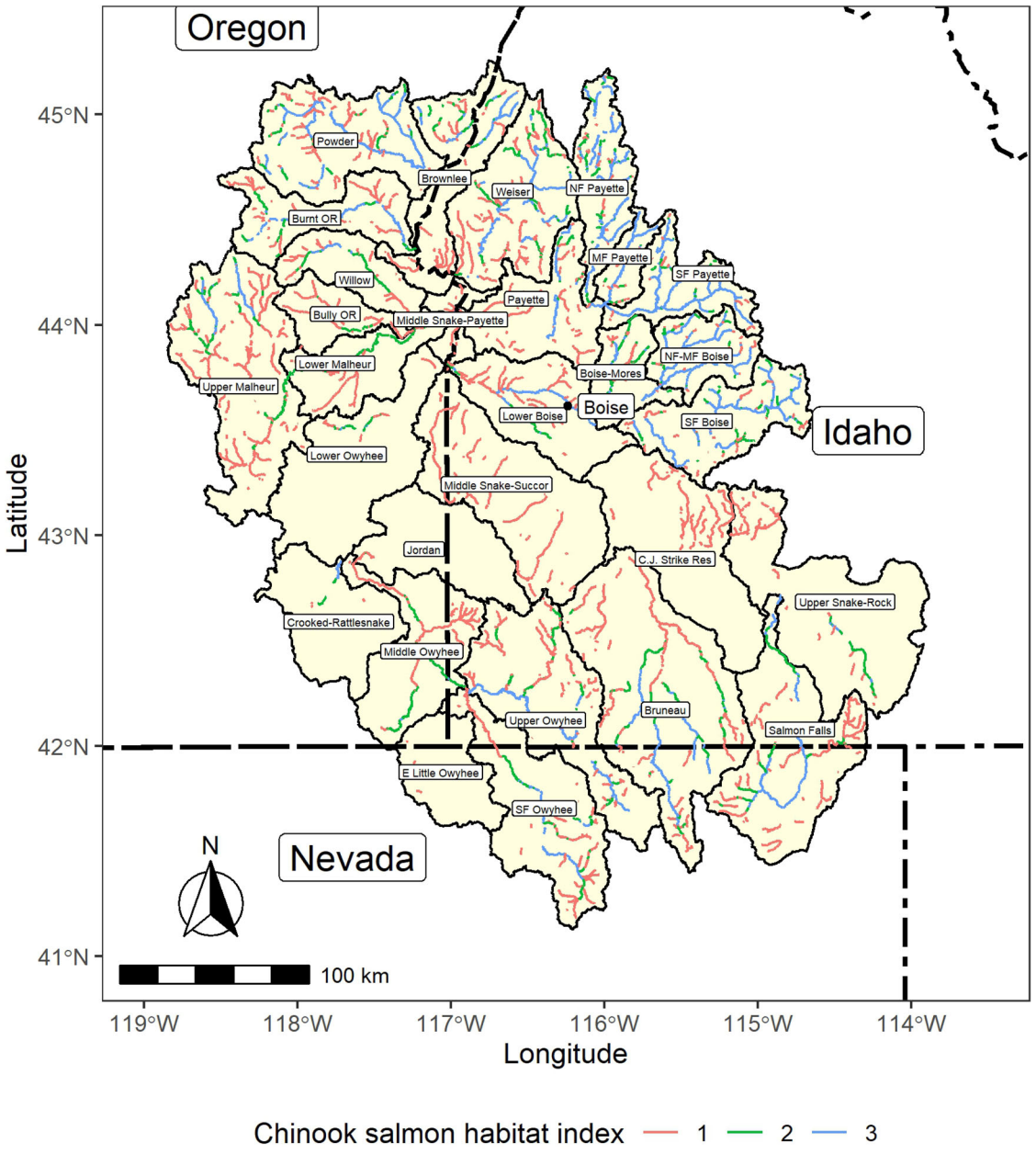


FIGURE 6
Chinook salmon habitat index values for HUC-8 basins in the middle Snake River basin. A habitat index value of one indicates only one habitat model predicted suitable habitat in a given reach, whereas a value of three indicates that all three habitat models predicted suitable habitat. Reaches with a habitat index of zero (no models indicate suitable habitat) are not shown. Reaches with mean summer flows > 32 m^3/sec were excluded as they fell outside the calibration range of the model.

to generate these habitat estimates can be adjusted to be more or less conservative depending on the needs of managers and could be used in conjunction with other assessments (e.g., IP modeling, field surveys) to provide additional lines of evidence for habitat availability. Moreover, the framework provided here demonstrates the utility of publicly available data for evaluating habitat availability for Pacific salmon and other anadromous species in areas that are currently inaccessible.

The blocked area of the Snake River basin represents a vast expanse of ancestral salmon habitat—once biologically rich, culturally vital, and ecologically dynamic (USRT, 2018). Restoring access to the blocked area of the Snake River basin, which contains a large amount of the existing coldwater habitat in the Columbia River basin (NOAA, 2026), has the potential to significantly benefit salmon and steelhead recovery efforts in the region by providing opportunities to increase abundance, productivity, spatial structure, and diversity, the four characteristics that influence the biological viability of salmon populations (Anderson et al., 2014). For USRT, this region is not only a homeland but a place shaped by and deeply connected to anadromous salmonids (USRT, 2018). The long-

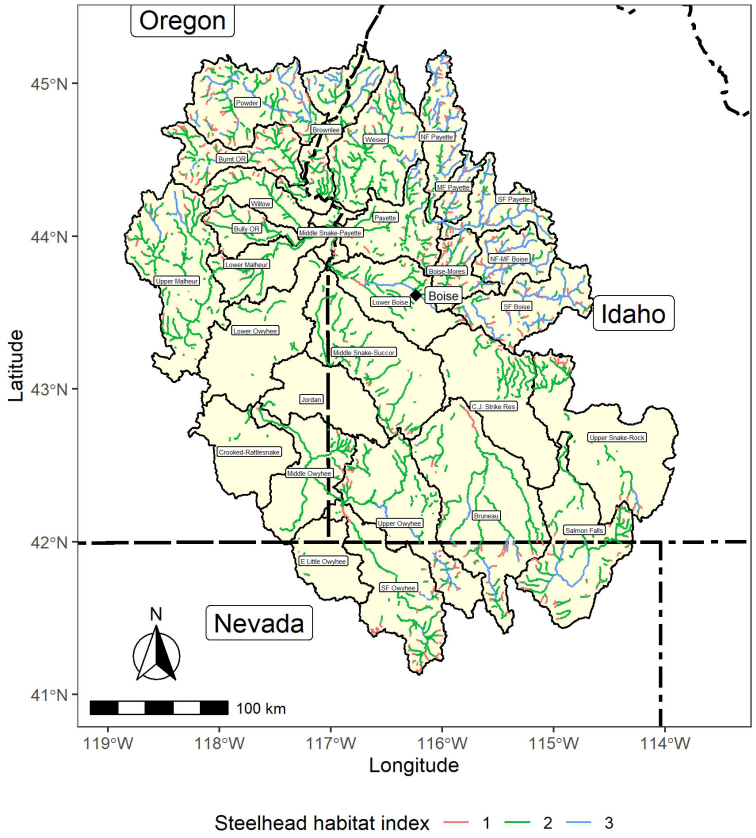


FIGURE 7
Steelhead habitat index values for HUC-8 basins in the middle Snake River basin. A habitat index value of one indicates only one habitat model predicted suitable habitat in a given reach, whereas a value of three indicates that all three habitat models predicted suitable habitat. Reaches with a habitat index of zero (no models indicate suitable habitat) are not shown. Reaches with mean summer flows > 32 m^3/sec were excluded as they fell outside the calibration range of the model.

standing loss of salmon and steelhead due to dam construction, habitat degradation, and disconnection from the ocean has had profound ecological, cultural, and economic consequences (Gresh et al., 2000; Noakes, 2014; Lamb et al., 2023). As momentum grows around reintroducing salmon into historical habitats blocked by dams, habitat modeling provides a foundational tool that can be used to guide restoration efforts and support the sovereign rights, health, and heritage of Tribes and other key stakeholders (Giorgi, 2018; Baldwin et al., 2022; Chan et al., 2025).

Our estimates of habitat availability for Chinook salmon (2,287 km) are notably lower (~72% reduction) than those produced during an earlier study (8,249 km; Parametrix, 2023). For that study, an IP modeling approach was used to estimate historical habitat losses under the assumption that all habitat in the basin was pristine prior to European colonization and development. The IP model incorporated generic parameters that included bankfull channel width, channel gradient, and valley-width-ratio (Parametrix, 2023). For our approach, we included several elements that were intended to refine habitat prediction so the differences in habitat quantity estimates between the two studies are not surprising. Notably, we omitted intermittent, 1st-order streams, and stream reaches located upstream of impassable fish barriers to eliminate habitat that would not have been historically accessible to anadromous fish species. We also explicitly evaluated parameters that are biologically important for Pacific salmon species including summer streamflow, summer water temperature, and channel slope. Additionally, our index estimates are based on empirically derived probability and abundance thresholds for salmon that may be more stringent than the criteria used for previous IP modeling efforts. Although there are notable differences between results from the two studies, they collectively demonstrate the existence of substantial habitat suitable for supporting Chinook salmon and steelhead in the blocked area of the Snake River basin. It is important to note that numerous ecological factors influence how Chinook salmon and steelhead distribute within available habitat (Geist and Dauble, 1998; Rosenfeld and Ptolemy, 2012; Taylor, 1991; Bugert and Bjornn, 1991; Elvidge et al., 2016). Thus, all reaches that were identified as suitable may not actually be used by salmon and steelhead if reintroduction is implemented in the blocked area. Once salmon and steelhead are present within specific watersheds, additional research and monitoring would be required to identify priority areas based on realized habitat use patterns.

The modeling approach presented here may be applicable for quantifying habitat availability in other systems that currently lack

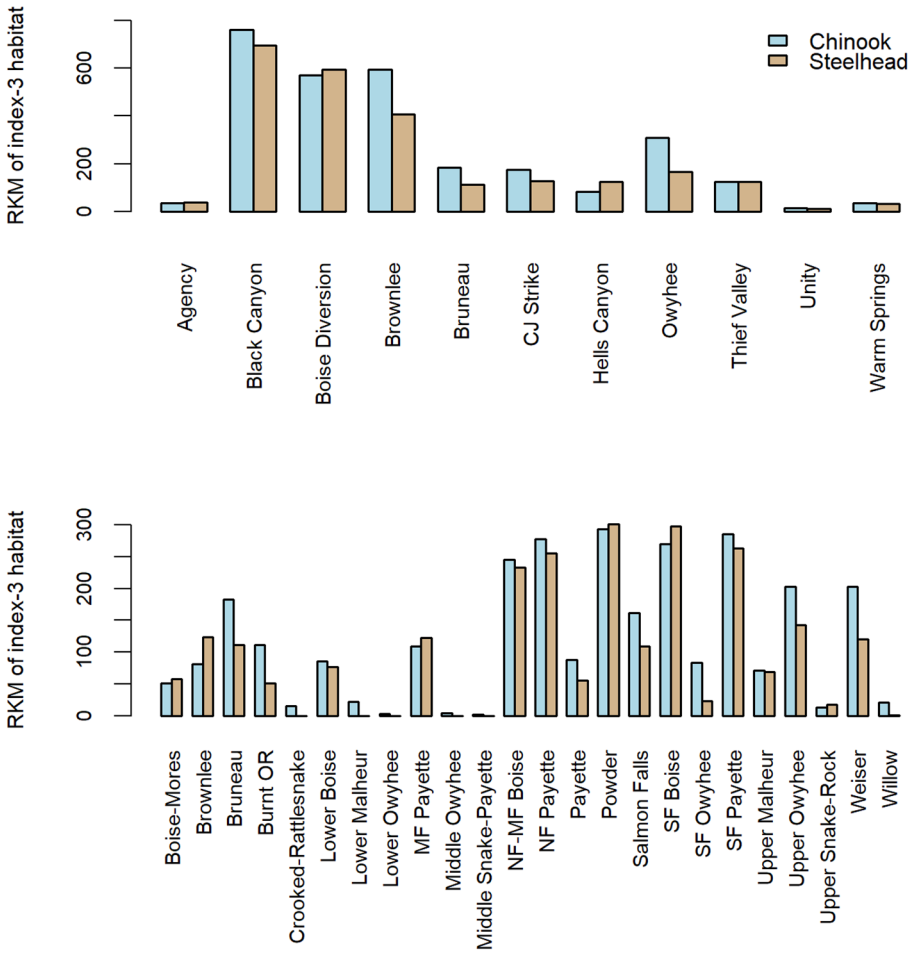


FIGURE 8
Predicted quantity of index-3 habitat (in river kilometers [RKM]) for Chinook salmon and steelhead in the middle Snake River basin at the damshed (top) and HUC-8 basin (bottom) scale. Index-3 habitat indicates that a reach has a high probability of supporting salmon rearing and spawning according to three separate models.

anadromous fish, particularly in spatially expansive areas where comprehensive field surveys may be impractical. This approach effectively identified priority habitats for two anadromous fish species based on habitat variables important for both juvenile and adult life stages in a study area that spanned multiple states and included 29 basins that individually ranged in size from 750 to 8,735 km^2. Results generated from this modeling effort provided overall estimates of habitat availability within the study area and identified (to the reach level) potential habitat for both adult spawning and juvenile rearing (Figures 6, 7). This establishes a critical baseline that will benefit future studies by eliminating a large amount of unsuitable habitat from consideration in an expansive area of interest, thereby allowing efforts to focus on high priority reaches that are most likely to support anadromous fish populations.

A key challenge for assessing habitat availability in currently unoccupied areas is the lack of contemporary occurrence data. Our framework addresses this challenge by (1) developing and validating models based on salmon presence and abundance records in a geographical area that is adjacent and latitudinally similar to the focal area and that lies within the same basin, and (2) projecting probability and abundance estimates into the unoccupied focal area. The present study benefitted from robust fish presence, abundance, and eDNA datasets in the lower Snake River basin, publicly available information on physical stream attributes, and apparent similarities between the lower basin and middle basin based on several habitat parameters (Figure 3). Combining the results of three complementary model outputs (rearing presence/absence, rearing abundance, and spawning presence/absence) strengthens inference and may be particularly valuable to managers, as it identifies habitat that is suitable for multiple life stages. However, we also identified several limitations of this approach. For example, our analysis relied on modeled temperature and flow data produced during 1993-2011, and current and future climate conditions may shift the distribution and abundance of suitable habitat in the focal area. Additionally, this modeling framework assumes that fish in the lower basin are biologically representative of fish that were historically present in the middle basin. Additionally, the index model outputs provided here are sensitive to the selection of thresholds that were used to convert continuous probability and abundance predictions into binary habitat maps. Ultimately,

10.3389/fevo.2026.1924685

TABLE 4 River kilometers (RKM) of index-3 Chinook salmon and steelhead habitat at the damshed scale in the middle Snake River basin.

DSpecies	Damshed	DRKM of index-3 habitat
Chinook salmon	Agency Valley	36.1
	Black Canyon Diversion	**761.6**
	Boise River Diversion	**572.3**
	Brownlee	**594.7**
	Bruneau	183.2
	CJ Strike	174.8
	Hells Canyon	81.4
	Owyhee	307.8
	Thief Valley	125.3
	Unity	14.1
	Warm Springs	35.5
	Total =	2886.8
Steelhead	Agency Valley	38.4
	Black Canyon Diversion	**697.7**
	Boise River Diversion	**594.3**
	Brownlee	**408.7**
	Bruneau	111.9
	CJ Strike	127.3
	Hells Canyon	123.2
	Owyhee	166.3
	Thief Valley	124.1
	Unity	11.5
	Warm Springs	30.7
	Total =	2434.1

Bold text identifies the three damsheds (per species) with the largest amount of predicted habitat.

TABLE 5 River kilometers (RKM) of index-3 Chinook salmon and steelhead habitat at the HUC-8 basin scale in the middle Snake River basin.

Species	HUC-8	RKM of index-3 habitat
Chinook salmon	Boise-Mores	51.6
	Brownlee	81.4
	Bruneau	183.2
	Burnt OR	111.5
	Crooked-Rattlesnake	15.0
	Lower Boise	85.4
	Lower Malheur	22.1
	Lower Owyhee	3.0
	MF Payette	109.8
	Middle Owyhee	3.6
	Middle Snake-Payette	2.1
	NF-MF Boise	246.1
	NF Payette	**278.4**
	Payette	87.5
	Powder	**293.7**
	Salmon Falls	161.5
	SF Boise	270.0
	SF Owyhee	83.1
	SF Payette	**285.9**
	Upper Malheur	71.5
	Upper Owyhee	203.1
	Upper Snake-Rock	13.2
	Weiser	202.9
	Willow	21.1
	Total =	2886.8
Steelhead	Boise-Mores	57.6
	Brownlee	123.2
	Bruneau	111.9
	Burnt OR	50.5
	Lower Boise	76.4
	MF Payette	123.1
	NF-MF Boise	233.6
	NF Payette	255.8
	Payette	55.4
	Powder	**301.6**
	Salmon Falls	109.5
	SF Boise	**298.4**
	SF Owyhee	23.1

(Continued)

threshold choices require judgement based on biological and historical knowledge of the region and the species of interest.

5 Conclusion

In summary, this study provides new information on the quantity of suitable habitat for juvenile and adult life stages of Chinook salmon and steelhead in the blocked area of the Snake River basin while also creating a template that can be useful in other large systems where ecological restoration is of interest. Given the scale of the basin and the complexities associated with reintroducing salmon across this vast, fragmented landscape,

TABLE 5 Continued

Species	HUC-8	RKM of index-3 habitat
	SF Payette	**263.4**
	Upper Malheur	69.1
	Upper Owyhee	143.2
	Upper Snake-Rock	17.8
	Weiser	120.1
	Willow	0.233
	Total =	2434.1

Bold text identifies the three HUC-8 units (per species) with the largest amount of predicted habitat.

prioritization will likely be an essential part of the planning process. Results from this study can be used to support ranking processes focused on prioritizing watersheds or stream segments based on ecological potential, restoration needs, cultural significance, and logistic feasibility. This prioritization can be used to help identify areas where probability of success is greatest for early reintroduction efforts, pilot studies, cultural programs and habitat investments. It also creates a transparent, data-driven approach that can be used to allocate funding and effort toward areas where ecological and cultural returns on investment are highest. These efficiencies and project transparencies will be critical for effective stakeholder buy-in and long-term success.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: Multiple sources, described and cited in the text.

Author contributions

JRH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. JMH: Writing – original draft, Writing – review & editing. DD: Funding acquisition, Writing – review & editing. CC: Formal analysis, Methodology, Visualization, Writing – review & editing. TK: Supervision, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. The author(s) declare that financial support was received for this work and/or its publication. Funding for this project was from a grant provided by the Upper Snake River Tribes via a grant, contract number A20AV00822, provided byfrom the U.S. Department of Indian Affairs Hydro-Compliance Program. (Contract Number A20AV00822).

Acknowledgments

The authors would like to thank the following contributors: Dan Isaak and Aimee Fullerton for their input into modeling approaches; Scott Hauser for his insights into salmon and steelhead habitat in the Snake River basin; Steve Waste for supporting the project and coordinating meetings to discuss research and modeling approaches; James White for reviewing the draft manuscript and providing additional insights regarding habitat modeling approaches; Two reviewers whose efforts improved the final document; Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2026.1924685/full#supplementary-material

References

Anderson, J. H., Pess, G. R., Carmichael, R. W., Ford, M. J., Cooney, T. D., Baldwin, C. M., et al. (2014). Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North Am. J. Fish. Manage.* 34, 72–93. doi: 10.1080/02755947.2013.847875

Baldwin, C., Giorgi, C., and Biladeau, T. (2022). Cultural and educational releases of salmon in areas blocked by major hydroelectric projects on the Columbia River. *Aquat. Ecosystem Health Manage.* 25, 16–26. doi: 10.14321/aehm.025.01.16

Benke, A. C., and Cushing, C. E. (2005). *Rivers of North America* (London: Elsevier Academic Press).

Blanchet, R., Willows, N., and Johnson, S. (2022). Enhancing cultural food security among the Syilx Okanagan adults with the reintroduction of Okanagan sockeye salmon. *Appl. Physiol. Nutr. Metab.* 47, 124–133. doi: 10.1139/apnm-2021-0321

BOR (Bureau of Reclamation) (2024). *Dams, Projects and Powerplants*. Available online at: https://www.usbr.gov/pn/snakeriver/dams/index.html (Accessed June 2026).

Bugert, R. M., and Bjornn, T. C. (1991). Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. *Trans. Am. Fish. Soc* 120, 486–493. doi: 10.1577/1548-8659(1991)120%3C0486:HUBSAC%3E2.3.CO;2

Burnett, K. M., Reeves, G. H., Miller, D. J., Clarke, S., Vance-Borland, K., and Christiansen, K. (2007). Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. *Ecol. Appl.* 17, 66–80. doi: 10.1890/1051-0761(2007)017[0066:DOSPRT]2.0.CO;2

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach. 2nd Ed* (New York: Springer), 488. doi: 10.1007/b97636

Chan, S. F., Liu, M., Rubenstein, D. R., Chung, Y. A., Lin, W. R., Liao, L. Y., et al. (2025). Assessment across life stages reveals superior habitat suitability in reintroduced historical habitats for an endangered salmon species. *J. Appl. Ecol.* 62, 1378–1391. doi: 10.1111/1365-2664.70067

Connor, W. P., Tiffan, K. F., Chandler, J. A., Rondorf, D. W., Arnsberg, B. D., and Anderson, K. C. (2019). Upstream migration and spawning success of Chinook salmon in a highly developed, seasonally warm river system. *Rev. Fisheries Sci. Aquaculture* 27, 1–50. doi: 10.1080/23308249.2018.1477736

Dauble, D. D., Hanrahan, T. P., Geist, D. R., and Parsley, M. J. (2003). Impacts of the Columbia River hydroelectric system on main-stem habitats of fall Chinook salmon. *North Am. J. Fish. Manage.* 23, 641–659. doi: 10.1577/M02-013

Egan, J. P. (1975). *Signal Detection Theory and ROC Analysis* (New York: Academic Press), 277. doi: 10.1007/BF02294103

Elvidge, C. K., Cooke, E. L. L., Cunjak, R. A., and Cook, S. J. (2016). Social cues may advertise habitat quality to refuge-seeking conspecifics. *Can. J. Zool.* 95, 1–5. doi: 10.1139/cjz-2016-0144

Esri Inc (2022). *Arcgis Pro (Version 3.7)* (Redlands, California, USA: Esri Inc). Available online at: https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview (Accessed December 15, 2025).

Galbreath, P. F., Bisbee, J. M., Dompier, D. W., Kamphaus, C. M., and Newsome, T. H. (2014). Extirpation and tribal reintroduction of coho salmon to the interior Columbia River basin. *Fisheries* 39, 77–87. doi: 10.1080/03632415.2013.874526

Geist, D. R., and Dauble, D. D. (1998). The importance of geomorphic features in large rivers. *Environ. Manage.* 22, 655–659. doi: 10.1007/s002679900137

Gende, S. M., Edwards, R. T., Willson, M. F., and Wipfli, M. S. (2002). Pacific salmon in aquatic and terrestrial ecosystems: Pacific salmon subsidize freshwater and terrestrial ecosystems through several pathways, which generates unique management and conservation issues but also provides valuable research opportunities. *BioScience* 52, 917–928. doi: 10.1641/0006-3568(2002)052[0917:Psiaat]2.0.Co;2

Giorgi, C. (2018). *Identification of Potential Habitats for Blocked Area Reintroduction*. Available online at: https://ucut.org/wp-content/uploads/2025/05/Giorgi-2018-Potential-Habitats-for-Reintroduction.pdf (Accessed September 3, 2025).

Gresh, T., Lichatowich, J., and Schoonmaker, P. (2000). An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: Evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* 25, 15–21. doi: 10.1577/1548-8446(2000)025%3C0015:AEOHAC%3E2.0.CO;2

Hatten, J. R., Tiffan, K. F., Anglin, D. R., Haeseker, S. L., Skalicky, J. J., and Schaller, H. (2009). A spatial model to assess the effects of hydropower operations on Columbia River fall Chinook salmon spawning habitat. *North Am. J. Fish. Manage.* 29, 1379–1405. doi: 10.1577/M08-053.1

Hedger, R. D., Dodson, J. J., Bergeron, N. E., and Caron, F. (2005). Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance. *J. Fish Biol.* 67, 1054–1071. doi: 10.1111/j.0022-1112.2005.00808.x

Hoekema, D. J., and Sridhar, V. (2011). Relating climatic attributes and water resources allocation: A study using surface water supply and soil moisture indices in the Snake River basin, Idaho. *Water Resour. Res.* 47. doi: 10.1029/2010WR009697

Hogue, A. S., and Breon, K. (2022). The greatest threats to species. *Conserv. Sci. Pract.* 4, e12670. doi: 10.1111/csp2.12670

Hosmer, D. W., and Lemeshow, S. (2000). *Applied Logistic Regression* (New York, New York, USA: John Wiley & Sons). doi: 10.1002/0471722146

Idaho State University (2026). *Snake River Plain Aquifer*. Available online at: https://www.isu.edu/digitalgeologyidaho/srp-aquifer/ (Accessed July 2026).

Isaak, D. J., Horan, D. L., and Nagel, D. E. (2025). The importance of trimming National Hydrography Dataset streamline networks when delineating potential habitats and species distributions for fish and amphibians in broad geographical applications. *North Am. J. Fish. Manage.* 45, 349–359. doi: 10.1093/najfmt/vqaf014

Isaak, D. J., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Nagel, D. E., Luce, C. H., et al. (2017b). The NorWeST summer stream temperature model and scenarios for the western U.S.: A crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resour. Res.* 53, 9181–9205. doi: 10.1002/2017wr020969

Isaak, D. J., Wenger, S. J., and Young, M. K. (2017a). Big biology meets microclimatology: defining thermal niches of ectotherms at landscape scales for conservation planning. *Ecol. Appl.* 27, 977–999. doi: 10.1002/eap.1501

Johnsen, D. B. (2009). Salmon, science, and reciprocity on the Northwest Coast. *Ecol. Soc* 14, 43. Available online at: https://www.jstor.org/stable/26268325.

Joppa, L., O'Connor, B., Visconti, P., Smith, C., Geldmann, J., Hoffmann, M., et al. (2016). Filling in biodiversity threat gaps. *Science* 352, 416–418. doi: 10.1126/science.aaf3565

Kammerer, J. (1987). *Largest rivers in the United States (water fact sheet) series 87-242* (Reston, Virginia: U.S. Geological Survey). doi: 10.3133/ofr87242

Kock, T. J., Fergusons, J. W., Keefer, M. L., and Schreck, C. B. (2021). Review of trap-and-haul for managing Pacific salmonids (Oncorhynchus spp.) in impounded river systems. *Rev. Fish Biol. Fish.* 31, 53–94. doi: 10.1007/s11160-020-09627-7

Lamb, C. T., Willson, R., Menzies, A. K., Owens-Beek, N., Price, M., McNay, S., et al. (2023). Braiding Indigenous rights and endangered species law. *Science* 380, 694–696. doi: 10.1126/science.adg9830

Liang, X., Lettenmaier, D. P., Wood, E. F., and Burges, S. J. (1994). A simple hydrologically based model of land surface water and energy fluxes for general circulation models. *J. Geophys. Res.* 99, 14415–14428. doi: 10.1029/94JD00483

Mahler, R. L. (2019). The impact of agriculture on the waters of the Idaho portion of the Snake River Basin, USA. *Int. J. Sustain. Dev. Plann.* 14, 93–104. doi: 10.2495/SDP-V14-N2-93-104

Maret, T., and Mebane, C. (2005).Historical and current perspectives on fish assemblages of the Snake River, Idaho and Wyoming: American Fisheries Society Symposium. Available online at: https://pubs.usgs.gov/publication/70027320 (Accessed December 19, 2025).

Matala, A. P., Narum, S. R., Saluskin, B. P., Johnston, M. V., Newell, J. E., Fast, D. E., et al. (2019). Early observations from monitoring a reintroduction program: Return of Sockeye Salmon to a nursery lake of historical importance. *Trans. Am. Fish. Soc* 148, 271–288. doi: 10.1002/tafs.10133

McClure, M. M., Carlson, S. M., Beechie, T. J., Pess, G. R., Jorgensen, J. C., Sogard, S. M., et al. (2008). Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evol. Appl.* 1, 300–318. doi: 10.1111/j.1752-4571.2008.00030.x

McKay, L., Bondelid, T., Dewald, T., Johnston, J., Moore, R., and Rea, A. (2012).NHDPlus version 2: user guide. Available online at: https://www.epa.gov/waterdata/get-nhdplus-national-hydrography-dataset-plus-data#Download (Accessed January 11, 2026).

Molinaro, A. M., Simon, R., and Pfeiffer, R. M. (2005). Prediction error estimation: a comparison of resampling methods. *Bioinformatics* 21, 3301–3307. doi: 10.1093/bioinformatics/bti499

Nagelkerke, N. J. D. (1991). A note on general definition of the coefficient of determination. *Biometrika* 78, 691–692. doi: 10.1093/biomet/78.3.691

National Oceanic Atmospheric Administration (NOAA) (2025). *Historical Stream Layer Depicting Historical Anadromy in the Middle and Upper Snake River Basin*, Unpublished dataset provided by Damon Holzer (damon.holzer@noaa.gov).

Nehlsen, W., Williams, J. E., and Lichatowich, J. A. (1991). Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. *Fisheries* 16, 4–21. doi: 10.1577/1548-8446(1991)016%3C0004:PSATCS%3E2.0.CO;2

NOAA (National Oceanic and Atmospheric Administration) (2026). *Restoring Cold-Water Pathways for Idaho's Salmon and Steelhead*. (Washington, DC). Available online at: https://www.fisheries.noaa.gov/feature-story/restoring-cold-water-pathways-idahos-salmon-and-steelhead (Accessed June 2026).

Noakes, D. J. (2014). "Overview of salmon and their ecological and economic importance Salmon," in *Biology, Ecological Impacts and Economic Importance* (NOVA Publishers, New York), 1. Available online at: https://www.researchgate.net/profile/Daniel-Lopez-Angulo/publication/285763291_Possible_use_of_waste_products_from_the_Salmon_industry_Properties_of_Salmon_gelatin/links/57430b2d08aea45ee84a7c9c/Possible-use-of-waste-products-from-the-Salmon-industry-Properties-of-Salmon-gelatin.pdf#page=11 (Accessed December 20, 2025).

Northwest Power Planning Council (NPPC) (1986). *Compilation of Information on Salmon and Steelhead Losses in the Columbia River Basin* (Portland, Oregon: Northwest Power Planning Council). Available online at: https://catalog.hathitrust.org/Record/100954324 (Accessed December 11, 2025).

O'Sullivan, A. M., and Alex, K. I. (2024). Establishing present-day Sockeye Salmon (Oncorhynchus nerka| sćwin) spawning capacity in the highly impacted sq,awsitk^{w}| Okanagan River to guide population conservation and restoration. *River Res. Appl.* 40, 1195–1204. doi: 10.1002/rra.4293

Osborne, P. E., and Seddon, P. J. (2012). "Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modelling," in *Reintroduction Biology: Integrating Science and Management*, (Oxford) 73–104. doi: 10.1002/9781444355833

Parametrix (2023). *Final Work Plan for Assessment of Fish Habitat Losses in the Middle and Upper Snake River Basins* (Tech Memo). Available online at: https://uppersnakerivertribes.org/wp-content/uploads/2024/03/Loss_Assessment_of_Upper_Snake_Basin.pdf (Accessed August 8, 2025).

Polissar, N. L., Salisbury, A., Ridolfi, C., Callahan, K., Neradilek, M., Hippe, D. S., et al. (2016). *Heritage Fish Consumption Rates of the Shoshone-Bannock Tribes Final Report*. Available online at: https://www.epa.gov/sites/default/files/2017-01/documents/heritage-fish-consumption-rates-shoshone-bannock-dec2016.pdf (Accessed February 20, 2025). EPA Contract EP W14 020 Task Order10 and Contract EP W09 011 Task Order 125 with SRA International.

R Core Team (2024). *R: A Language and Environment for Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing). Available online at: https://www.R-project.org/ (Accessed January 26, 2026).

Rosenfeld, J. S., and Ptolemy, R. (2012). Modelling available habitat versus available energy flux: do PHABSIM applications that neglect prey abundance underestimate oprimal flows for juvenile salmonids? *Can. J. Fish. Aquat.Sci.* 69, 1920–1934. doi: 10.1139/f2012-115

Sheer, M. B., Busch, D. S., Gilbert, E., Bayer, J. M., Lanigan, S., Schei, J. L., et al. (2009). *Development and management of fish intrinsic potential data and methods: state of the IP 2008 summary report* (Bethesda, Maryland: Pacific Northwest Aquatic Monitoring Partnership Series 2009-004). doi: 10.13140/RG.2.1.3548.2960

Sheer, M. B., and Steel, E. A. (2006). Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia River basins. *Trans. Am. Fish. Soc* 135, 1654–1669. doi: 10.1577/T05-221.1

Story, M., and Congalton, R. G. (1986). Accuracy assessment: a user's perspective. *Photogramm. Eng. Remote Sens.* 52, 397–399. Available online at: http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=8656698.

Strahler, A. N. (1957). Quantitative analysis of watershed geomorphology. *Trans. Am. Geophysical Union* 38, 913–920. doi: 10.1029/TR038i006p00913

StreamNet (2025). *A Fisheries Data Project of the Pacific States Marine Fisheries Commission* (Portland, OR: Pacific States Marine Fisheries Commission). Available online at: https://www.streamnet.org (Accessed February 1, 2026).

Taylor, E. B. (1991). Behavioural interaction and habitat use in juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kissutch*, salmon. *Anim. Behav.* 42, 729–744. doi: 10.1016/S0003-3472(05)80119-8

Tiffan, K. F., Garland, R. D., and Rondorf, D. W. (2002). Quantifying flow-dependent changes in subyearling fall chinook salmon rearing habitat using two-dimensional spatially explicit modeling. *North Am. J. Fish. Manage.* 22, 713–726. doi: 10.1577/1548-8675(2002)022%3C0713:QFDCIS%3E2.0.CO;2

UCUT (2022). *The Phase 2 Implementation Plan: Testing Feasibility of Reintroduced Salmon in the Upper Columbia River Basin*. Available online at: https://ucut.org/wp-content/uploads/2025/05/UCUT-Phase-2-Implementation-Plan-Version-4Aug2022-1.pdf (Accessed July 19, 2023).

Upper Columbia United Tribes (UCUT) (2019). *Fish Passage and Reintroduction Phase 1 Report: Investigations Upstream of Chief Joseph and Grand Coulee Dams*. Available online at: https://ucut.org/wp-content/uploads/2025/05/Fish-Passage-and-Reintroduction-Phase-1-Report-2.pdf (Accessed July 19, 2023).

Upper Snake River Tribes Foundation (USRT) (2015). *The Policy of the Upper Snake River Tribes Foundation for Management of Columbia and Snake River Basin Resources*. Available online at: https://uppersnakerivertribes.org/wp-content/uploads/2019/02/USRTCSRP_Approved-Final-1.pdf (Accessed June 15, 2026).

Upper Snake River Tribes Foundation (USRT) (2018). *Hells Canyon Complex Fisheries Resource Management Plan* (Boise, Idaho). Available online at: https://uppersnakerivertribes.org/projects/hells-canyon-complex-fisheries-resource-management-plan/ (Accessed March 11, 2025).

U.S. Columbia Basin Tribes and Canadian First Nations (2015). *Fish Passage and Reintroduction Into the U.s. And Canadian Upper Columbia Basin: Joint Paper of the U.s. Columbia Basin Tribes and Canadian First Nations*. Available online at: https://www.friendsoftoppenishcreek.org/cabinet/data/CRT%20Fish_Passage_and_Reintroduction_into_the_US_And_Canadian_Upper_Columbia_River3.pdf (Accessed February 20, 2025).

Waldman, J. R., and Quinn, T. P. (2022). North American diadromous fishes: Drivers of decline and potential for recovery in the Anthropocene. *Sci. Adv.* 8, eabl5486. doi: 10.1126/sciadv.abl5486

Wenger, S. J., Luce, C., Hamlet, A. F., Isaak, D. J., and Neville, H. M. (2010). Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resour. Res.* 46, W09513. doi: 10.1029/2009WR008839

White, J. S., Bartelt, K. M., Kock, T. J., Overstreet, B. O., Hansen, G., and Wallick, R. (2026). Quantifying Chinook salmon habitat across flow regimes: high resolution modeling in Oregon's Willamette river basin. *Front. Ecol. Evol.* 14, 1828470. doi: 10.3389/fevo.2026.1828470

Williams, J. G., Smith, S. G., Zabel, R. W., Muir, W. D., Scheuerell, M. D., Sandford, B. D., et al. (2005). "Effects of the Federal Columbia River Power System on salmonid populations," in *Noaa Technical Memorandum Nmfs-Nwfsc-63*. (Washington, DC). Available online at: https://www.researchgate.net/publication/268435736_Effects_of_the_Federal_Columbia_River_Power_System_on_Salmon_Populations (Accessed December 5, 2025).

Yau, K. K., Wang, K., and Lee, A. H. (2003). Zero-inflated negative binomial mixed regression modeling of over-dispersed count data with extra zeros. *Biometrical Journal: J. Math. Methods Biosci.* 45, 437–452. doi: 10.1002/bimj.200390024

Yoshiyama, R. M., Gerstung, E. R., Fisher, F. W., and Moyle, P. B. (2001). "Historical and present distribution of chinook salmon in the central valley drainage of California," in *Contributions to the Biology of Central Valley Salmonids. Volumes 1 & 2. Fish Bulletin 179*. Ed. R. L. Brown (Davis, CA: University of California, Davis). Available online at: https://escholarship.org/content/qt6sd4z5b2/qt6sd4z5b2.pdf#page=94 (Accessed December 11, 2025).

Young, M. K., Isaak, D. J., Schwartz, M., McKelvey, K., Nagel, D., Franklin, T., et al. (2018). *Species occurrence data from the aquatic eDNAtlas database* (Fort Collins, CO: Forest Service Research Data Archive). doi: 10.2737/RDS-2018-0010