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An invader in salmonid rearing habitat: current and future distributions of smallmouth bass (*Micropterus dolomieu*) in the Columbia River Basin

Erika S. Rubenson[1*]
Julian D. Olden[1#]

[1] School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat Street, Seattle, Washington 98195, USA.

[*]E-mail: esuther@uw.edu
[*]Phone: 206-685-9582
[#]E-mail: olden@uw.edu

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Abstract:

Invasive species and climate change are leading threats to freshwater ecosystems. In the Columbia River Basin (CRB), nonnative fishes are a critical consideration in salmon recovery, yet managers lament a lack of distribution information. Combining a species distribution model (SDM) with environmental DNA (eDNA), we locate range boundary regions of nonnative smallmouth bass (*Micropterus dolomieu*) and evaluate its overlap with native salmonids. A combination of thermal, hydrological, and geomorphic variables predict that smallmouth bass is distributed across approximately 18 000 river kilometers and overlaps with 3-62% of rearing habitat of salmonids (species dependent) in the CRB. Under a moderate climate change scenario, smallmouth bass is predicted to expand its range by two-thirds (totaling ca. 30 000 river kilometers) by 2080. Basin-wide models were sufficiently accurate to identify upstream invasion extents to within 15 km of the eDNA-based boundary, and including eDNA data improved model performance at critical range boundary regions without sacrificing broad-scale model performance. Our study highlights how eDNA approaches can supplement large geospatial datasets to result in more accurate SDM predictions, guiding nonnative species management.

Freshwater ecosystems remain extremely vulnerable to the combined threats of multiple stressors (Craig et al. 2017). Climate-induced stream warming is causing widespread changes to species assemblages, promoting the secondary spread of nonnative, and often invasive, species (Comte et al. 2013). Consequently, understanding current and projected future distributions of nonnative species is fundamental to strategic conservation planning for freshwater ecosystems (Bush et al. 2014). Modeling efforts, however, are challenged by the simultaneous need to be both generalizable to capture a species' broad distribution while also being adequately specific to inform local scale management and conservation practices (Dormann et al. 2012). Although myriad methods to improve model performance exist, data availability remains limited, prompting the continued use of correlative species distribution models that utilize only species occurrence and spatial environmental data. Advancements in the performance of correlative models, however, are possible by integrating diverse datasets that span different spatial scales and sources (Ibáñez et al. 2014). Although this does not necessarily capture processes that set range constraints, spatially diverse datasets may improve model accuracy at critical range boundaries where management relevance is the greatest.

The Columbia River Basin (CRB) once supported large populations of ecologically, culturally, and socioeconomically important native salmonids (salmon, trout, and char), but habitat alteration, nonnative species proliferation, and ongoing climate change have contributed to dramatic declines in many parts of their range (Rieman et al. 2015; Hand et al. 2018). Recovery efforts are complicated by the broad expanse and diverse ecology of the CRB, which spans portions of seven states (Washington, Oregon, Idaho, Montana, Nevada, Utah, and Wyoming), two countries (United States and Canada), and countless management agencies that operate at different spatial scales. Although $300 million is spent annually on salmonid recovery in the CRB, a disproportionate focus on habitat restoration has been highlighted as insufficient to produce meaningful benefits (Naiman et al. 2012; Rieman et al. 2015; Hand et al. 2018). By contrast, landscape scale assessments and factors that impact food webs, such as presence of nonnative species, are cited as critically overlooked components in salmon recovery efforts (Naiman et al. 2012; Rieman et al. 2015).

Smallmouth bass (*Micropterus dolomieu*) is a prevalent nonnative recreational fish in the CRB, and has been highlighted as a critical management priority to achieve salmon recovery goals (Sanderson et al. 2009; Carey et al. 2011). A high trophic-level predator, smallmouth bass is capable of consuming large proportions of salmon runs (up to 35%) when co-occurring with small salmonids in water sufficiently warm for activity (Fritts and Pearsons 2004; Sanderson et al. 2009; Carey et al. 2011). Smallmouth bass was first introduced into the Willamette and Yakima Rivers in the 1920s (Lampman 1946). Secondary introductions, such as the introduction into the John Day River in 1971 (Shrader and Gray 1999), have occurred throughout the region since that time, to include extensive stocking efforts by multiple state agencies (Carey et al. 2011). Today, substantial local abundances (up to 2 300 fish per river kilometer) and voracious consumption rates (up to 0.623 salmonids per smallmouth bass per day) have been found in parts of the CRB (Erhardt et al. 2018), making smallmouth bass one of the most frequent predators of juvenile salmonids in the CRB (Carey et al. 2011). These estimates are derived from mainstem rivers or reservoirs where the predominant threat for salmonids occurs during outmigration events. Recent evidence suggests that smallmouth bass is also capable of colonizing some portions of sensitive salmonid spawning and rearing habitat in Columbia River tributaries in spite of having warmer thermal preferences (Lawrence et al. 2014; Rubenson and Olden 2017). This portends a year-round predation and competition threat during a sensitive life-history stage for salmonids. Despite this, very little information is available on current or predicted future distributions of smallmouth bass and its potential overlap with native salmonid species' spawning and rearing habitat in the CRB.

Upstream range boundaries of smallmouth bass constitute the regions of most probable overlap with spawning and rearing salmonids, and thus offer powerful management opportunities. For instance, the high threat to salmon confined to relatively isolated locations may assist in gaining support to prevent further upstream invasions (Rahel 2013) or for localized efforts to control (Loppnow et al. 2013). In addition, upstream range boundaries represent regions where physiological stress, habitat suitability, and/or dispersal barriers present potentially exploitable constraints on expanding populations (Sexton et al. 2009; Lawrence et al. 2012). These factors make range boundaries critical battlegrounds for invasive species management. Determining the location of range boundaries, however, often requires extensive sampling or accurate species distribution models developed from large datasets, both of which may be prohibitively costly (Urban et al. 2016). Environmental DNA (eDNA), however, may present a new opportunity to supplement correlative modeling efforts at critical boundary regions by providing fine-scale distributional resolution at relatively low costs. Moreover, eDNA samples may be combined with existing data sources, potentially enhancing model performance both range wide and at range boundaries.

In this study we explore the efficacy of developing a correlative species distribution model from existing smallmouth bass records to guide eDNA survey design at range boundaries. By leveraging multiple sources of data, the resulting models can identify management-relevant range boundary regions in individual streams as well as contribute to more accurate basin-wide distribution predictions for smallmouth bass. Our objectives were to 1) develop and validate a species distribution model for smallmouth bass in the CRB, 2) use eDNA to refine the location of and improve model performance at predicted upstream range boundaries, 3) predict future distributions of smallmouth bass in the CRB under future climate change scenarios, and 4) quantify the degree of spatial overlap of smallmouth bass with critical habitat and designated refugia for CRB salmonid species.

Methods

Smallmouth bass occurrence

We collated smallmouth bass distribution data from a diversified set of databases and individual biologists across Washington, Oregon, Montana, Idaho, and Canada. We refer to this as the "initial" dataset, whereas the dataset that also includes the additional eDNA-derived records is referred to as the "final" dataset. Although distribution data was provided for Canada, the Canadian portion of the CRB was not included due to the lack of compatible environmental predictor variables (i.e., current and future mean August water temperature, Variable Infiltration Capacity (VIC) hydrologic models for spring flow, and waterfall distributions). Distribution in Canada, however, is currently limited and concentrated along the border with the United States.

Data were provided by Washington Department of Fish and Wildlife (WDFW), Idaho Department of Fish and Game (IDFG), Idaho Department of Environmental Quality (IDEQ), Oregon Department of Fish and Wildlife (ODFW), Yakima Nation Fisheries, Confederated Salish and Kootenai Tribes, and the Nez Perce Tribe. Responses to data requests that contained location, confirmed presence or absence of smallmouth bass, and sampling dates between 1981 and 2016 were included in our database. In addition, we included data from the EPA and Regional Environmental Monitoring and Assessment Program (EMAP and REMAP), the EPA

National Rivers and Streams Assessment (NRSA), the USGS National Water Quality Assessment Program (NAWQA), the USGS Nonindigenous Aquatic Species Database (https://nas.er.usgs.gov), Montana Fish, Wildlife, and Parks MFish database (http://fwp.mt.gov/fish), and the published literature (Table S1). Database entries were limited to those that were sampled between 1981 and 2016 and labeled as confirmed, established, accurate, and confined to flowing water environments. Different survey techniques were used by the various agencies and sources (i.e., electrofishing, snorkeling, weir trapping, and seining), thus we recognize issues related to differing sampling efficiency and detection probabilities.

Distribution data were assigned to stream segments according to hydrographic flow lines obtained from the National Hydrography Dataset Plus, Version 2 (NHDPlusV2; McKay et al. 2012) (http://www.horizon-systems.com/NHDPlus). Stream segments classified as intermittent hydrology and those not containing all climate and habitat data metrics were removed, resulting in 118 708 total segments, equating to approximately 204 700 river kilometers. After excluding distribution records from the same location (river segment), we identified 240 presence records (Fig. 1). Visual investigation revealed no evidence of spatial sampling bias in the presence data, however there was a disproportionate number of absence points in certain regions, including the Willamette River basin. Consequently, to ensure equal representation of all available habitat types across the CRB, absence points were spatially rarefied, resulting in the initial database containing a total of 177 absence records (Fig. 1).

We used the predictions from our model based on the initial database to inform the collection location of eDNA samples along the predicted upstream range boundary in 14 major rivers of the CRB (Fig. 1). These rivers encompass a subsample of the diverse environmental contexts and disparate invasion histories of smallmouth bass in the CRB (Carey et al. 2011). All samples were collected during the late summer (last 2 weeks of July 2016) to ensure congruence with the stream temperature predictor variable used in the model (described below). We defined the predicted range boundary regions as sections of rivers where the probability of presence exhibited a visible decline from > 0.9 towards probabilities < 0.5. In each tributary, 25-75 km stretches of river that bracketed the predicted range boundary of smallmouth bass were targeted for sampling. We attempted to collect samples every 5-7 km, but were often constrained by accessibility to the river. For the Salmon River, sampling locations were informed by conversations with local fishery biologists, guiding us to our sampling location. At each sampling location, 5-L of water was filtered through a 1.5 µm pore-sized fiberglass filter using the equipment and protocol of the Rocky Mountain Research Station (Carim et al. 2016b). When possible, we prioritized sampling locations just downstream of pools where flow increased and the channel-width narrowed. We chose these locations because smallmouth bass are known to prefer slower-water habitat, and sampling at knick-points increased the probability that water from both banks of large rivers would be sampled. Smallmouth bass presence was assessed by extracting and amplifying eDNA from the filters using an assay specifically developed to detect smallmouth bass (Franklin et al. 2018). Marker and assay development as well as extraction and amplification were completed by the Rocky Mountain Research Station (U.S. Forest Service) following the methods in Carim et al. (2016a). Finally, to test the accuracy of eDNA detection in these contexts, we conducted snorkel surveys (when flow and visibility allowed) immediately following eDNA collection. Here, two snorkelers swam 100 m upstream from where water samples were collected on opposite banks of the river. Both snorkelers then floated down the thalweg, noting presence or absence of smallmouth bass.

Environmental determinants of smallmouth bass occurrence

Referencing the extensive knowledge of smallmouth bass ecology (e.g., Peterson and Kwak 1999; Sharma and Jackson 2008; Lawrence et al. 2015), we selected seven predictor variables that represent thermal, hydrologic and geomorphic attributes known to influence fish distributions (Table 1, S2). Climate and habitat data were georeferenced at the stream segment scale. We provide summary statistics for the entire network (Table 1) in addition to statistics at presence and absence sites (Table S2).

Thermal variables were selected to incorporate conditions that are known to physiologically support smallmouth bass. Specifically, evidence suggests that mean summer daily temperatures near 20-22°C constrain the upstream range boundary of smallmouth bass populations in Columbia River tributaries (Rubenson and Olden 2017) and that winter severity limits the establishment of colonizing populations (Lawrence et al. 2015; Rubenson and Olden 2017). As such, we included mean August water temperature (WaterT) and the mean monthly air temperature between October 1 and March 31 (WinterAirT). Historical summer water temperature data were developed by the NorWeST stream temperature project based upon data from 1993-2011, and air temperatures were developed by the University of Washington Climate Impacts Group based upon data from 1916-2006 (Table 1). Because water temperature data was developed for NHDPlusV1, we first spatially joined these data to the NHDPlusV2 layer before conducting our analyses. In addition, reservoir temperatures were not modeled in the baseline water temperature dataset, so river segments in mainstem reservoirs were linearly interpolated between the nearest upstream and downstream riverine segment adjacent to the reservoir.

Hydrologic variables were selected based upon smallmouth bass flow affinities. Generally, smallmouth bass thrive in high-order streams and is preferentially found in perennial pools or glides (Dauwalter et al. 2007). We included mean annual flow (MAFlow) to represent stream size and the slope of each river segment (Slope) to capture localized velocities and habitat structure associated with reach morphology. Slope was extracted from the NHDPlusV2 dataset (Table 1). In addition, smallmouth bass show varied responses to spring hydrologic conditions, specifically related to movement patterns, spawn timing, and spawning success (Rubenson and Olden 2017). We thus included the magnitude of flow during the spring (April-May) standardized by mean annual flow (SpringFlow) to enable comparisons between small headwater streams and large mainstem rivers. All flow metrics were extracted from the Western U.S. Stream Flow Metrics dataset, and were based upon data from 1916-2006 (Table 1).

Geomorphic variables were included to represent zones of high-velocity flow or barriers such as waterfalls, cascades, or dams that can deter or prevent smallmouth bass upstream dispersal. Geomorphic variables included slope (described above), the density of dams in the watershed (DamDensity) as published by StreamCat (Hill et al. 2016), and a categorical variable accounting for whether or not the stream segment was located above a waterfall or cascade (as defined in the Fish Passage Barriers dataset from StreamNet.org) (Waterfall) (Table 1). Recognizing that smallmouth bass stocking has occurred above some major barriers in the CRB in the past, we considered barriers in the waterfall dataset functionally absent in the model (i.e., permeable) in sections of river with a known stocking history. By contrast, although some mainstem dams have fish passage structures, the ability of non-salmonids to utilize these opportunities for upstream movement remains uncertain, so these barriers were retained.

Baseline thermal and hydrological metrics (i.e., WaterT, WinterAirT, MAFlow, SpringFlow) were paired with their associated predictions for 2080 according to an ensemble mean of 10 or more global climate models (GCM) for A1B emission scenarios for 2080 (IPCC 2007). The A1B emission scenario is considered a moderate estimate for future carbon emission scenarios, and is similar to the 2010 Representative Concentration Pathway 6.0. Although updated emission scenarios are available from the IPCC 2013, only the A1B scenario was consistently modeled for all our metrics for the same time period (i.e., 2080). For mean August water temperature (WaterT2080), the NorWeST stream temperature scenario 32 was used for the 2080 predictions, which incorporates both modeled mean August air temperatures and stream discharge changes for 2080 (specifics in Wenger et al. 2010 and Hamlet et al. 2013). These data also account for differential sensitivity among streams to climate warming (Luce et al. 2014). Predicted air temperatures for winter (WinterAirT2080) were derived by the University of Washington Climate Impacts Group using the ensemble mean from 19 GCMs associated with the A1B emission scenario (specifics in Littell et al. 2011). Predictions for both flow metrics (MAFlow2080 and SpringFlow2080) were developed using the Variable Infiltration Capacity (VIC) macroscale hydrologic model developed by the University of Washington Climate Impacts Group for the stream segments in the western U.S. (specifics in Wenger et al. 2010).

Species distribution model

We used multivariate adaptive regression spline (MARS) models to estimate smallmouth bass probability of occurrence at the reach scale. We used the initial dataset to predict current distribution for identifying eDNA survey locations and the final (i.e., initial and eDNA records) dataset to predict current and future distribution and overlap with salmon habitat. We selected MARS models because they allow for easy interpretation of complex relationships between the response and predictor variables and have been widely shown to be one of the top performing techniques for species distribution modeling (Muñoz and Felicísimo 2004). MARS models describe non-linear species-environment relationships using a series of piecewise linear segments (Leathwick et al. 2005). MARS models, however, are built assuming normal data, and thus needed to be adapted to accommodate the binomial error structure of our presence-absence data. As such, we fit generalized linear models (GLM) to the extracted basis functions from the MARS model following the methods of Leathwick et al. (2005) and Elith and Leathwick (2007). We used source code from Elith and Leathwick (2007) to run the models in R (R Foundation for Statistical Computing, Vienna). This code fits the initial models using the 'mda' package (Hastie and Tibshirani 1996), extracts the set of linear segments that best describe the nonlinear relationships between the response and explanatory variables (i.e., basis functions), and relates species occurrences to these functions by fitting a GLM with a binomial error distribution to the data. The functions extracted during the MARS/GLM modeling process were applied to each stream segment's unique set of predictor variables to determine the probability of species occurrence at that location for both current and future (i.e., 2080) conditions. In addition, response curves (i.e., the basis functions used during the MARS modeling process) were examined to evaluate the primary influences of each predictor variable on species occurrence probability in the model. Multicollinearity between variables was examined using Variance Inflation Factor (VIF); high multicollinearity is evident when individual VIFs are ≥ 10 or the mean VIF across variables is ≥ 5. No indications of multicollinearity were discovered between any of the predictor variables (all individual VIF < 2.6; mean VIF = 1.8), thus all variables were included in the model. Although VIF was low, we did reveal moderate levels of correlation (r = 0.5-0.6) between WaterT, WinterAirT, and Slope, as well as between WinterAirT and SpringFlow (Table S2).

Model validation was conducted using both threshold-independent and threshold-dependent model statistics. For the threshold-independent test, 10-fold cross-validation (i.e., 90% of the data were used to train the model, and the remaining 10% were withheld for testing) was conducted and model accuracy assessed by calculating the area under the receiver operating characteristics (ROC) curve (AUC) (Olden and Jackson 2002). AUC measures the ability of a model to discriminate between presence and absence sites. A score of 0.5 implies no better than a random guess whereas a score of 1.0 indicates perfect accuracy; intermediate scores are ranked poor (< 0.7), good (0.7-0.9), and excellent (> 0.9) (Olden and Jackson 2002). By contrast, threshold-dependent model statistics were calculated to facilitate comparisons with the distributions of salmonid species. We used the maximum sensitivity plus specificity to determine the threshold value by which species were considered present (Liu et al. 2013). Confusion matrices were then constructed, from which sensitivity (correctly predicted presence), specificity (correctly predicted absence), true skill statistic (TSS) (average of net prediction success), Cohen's Kappa (extent to which the agreement between observed and expected are better than chance alone), and model accuracy (overall probability that either presence or absence were correctly predicted) were calculated. We then calculated the proportion of total river kilometers predicted to be occupied by smallmouth bass and the predicted percent change by 2080 for each of the 9 HUC-4 sub-basins of the CRB.

We used model predictions using the initial dataset to guide our eDNA collection efforts and to determine the effect that combining datasets had on model performance. Predictive performance of the SDMs built using the initial versus final distribution datasets were compared to assess whether model performance was improved with the addition of targeted samples at range boundaries. Model performance was separately evaluated at the range boundaries, comparing initial and final model performance at the eDNA data locations only. To assess the accuracy of our initial model for guiding sampling locations at range boundaries, we calculated the approximate watercourse distance (in river kilometers) between the most upstream presence point and the location where probability of occurrence dropped below the pre-determined threshold value. Finally, we compared eDNA detection with our detection during paired snorkel surveys.

Smallmouth bass overlap with critical salmonid habitat and cold-water refugia

We assessed the amount of spatial overlap between the predicted current distribution of smallmouth bass and the location of critical (i.e., spawning and rearing) salmonid habitat and cold-water refugia. Critical habitats of salmonids were delineated using publically available species distributions for the 5 anadromous species of Pacific salmon that spawn and rear in the CRB and the 4 resident trout species (StreamNet GIS Data 2003). These salmonid distributions were developed by StreamNet.org using data collected by agencies in Oregon, Washington, Idaho, and Montana and represent the best professional judgment of local fish biologists in the Pacific Northwest region. These distributions contained species locations classified by habitat-type (i.e., year-round residence, migration, rearing, and/or spawning), and Pacific salmon distributions organized by "runs" of individual species (i.e., spring, summer, or fall) when appropriate. To determine critical habitat, we excluded segments marked as migration-only, thus including only rearing, spawning, and year-round habitat. We then used ArcGIS 10.2 to quantify the percentage of total critical habitat (% total river kilometers) of each salmonid species predicted to be sympatric with current smallmouth bass occurrence (i.e., probability greater than the determined occurrence probability threshold). The salmonid species distributions were not projected into the future, so we could not calculate the predicted change in overlap with smallmouth bass under future climate conditions.

In addition to the above salmonid distributions, we compared smallmouth bass distributions to cold-water refugia as delineated by the U.S. Forest Service (USFS) Climate

Shield project (Isaak et al. 2015). Isaak et al. (2015) identified specific cold water habitat associated with juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) (www.fs.fed.us/rm/boise/AWAE/projects/ClimateShield.html) – both species of conservation concern that have cold thermal niches relative to other salmonids in the CRB (Isaak et al. 2015). These cold-water refugia represent only a subset of the entire ranges of these species, but are considered priorities for conservation and cold enough to prevent encroachment by nonnative species. Because the probability of smallmouth bass occurrence in these regions was always less than the pre-determined occurrence threshold, we calculated the summary statistics of predicted probabilities in each cold-water refuge under current and future climate conditions instead of number of river kilometers likely inhabited by smallmouth bass.

Results

We show that nonnative smallmouth bass is widely distributed throughout the CRB, with established populations spanning most of the Columbia River mainstem and its major tributaries (Fig. 1). Smallmouth bass is predominantly (79%) located in high-order streams (i.e., stream orders 5-9 which represent all mainstem habitats and major tributaries of the CRB), as well as some low-order streams (i.e., stream orders 1-4); this suggests that smallmouth bass occupy a diverse spectrum of habitats (Table S3). Although smallmouth bass occurrence was predicted across all stream orders, we do note that the low-order streams that had presence points were all located adjacent to high-order streams (Fig. 2a). The eDNA survey included 87 stream locations, resulting in 30 presence records and 57 absence records. At 74 of the sample locations, paired snorkel surveys were also conducted. Smallmouth bass were observed in 18 surveys, and not observed in 56 surveys. We had positive eDNA detection in all 18 sites where smallmouth bass were also observed as well as 8 positive eDNA detections where no smallmouth bass were observed. There were no smallmouth bass visually detected (n = 48 surveys) at any of the eDNA absence locations. All eDNA data were located in high-order, major CRB tributaries. These 87 records were subsequently combined with the initial database, and the model was parameterized again.

In concordance with the final distribution dataset, our model predicted a present-day distribution of smallmouth bass that spans a diversity of climates, geomorphology, and hydrography across the CRB (AUC = 0.90, Table 2, Fig. 2a). Geospatial data containing smallmouth bass occurrences and model predictions are available at: https://databasin.org/datasets/eafa4c3d466a41e790843fb73573437e. Although distributed across a large geographic space, smallmouth bass occurrence is predominantly limited to larger, high-order streams or adjacent low-order streams (Fig. 2a). Using the maximum sensitivity plus specificity as a threshold for probability of presence (0.5), we found that approximately 17 660 river kilometers of the CRB were predicted as occupied by smallmouth bass under current environmental conditions (Kappa = 0.62, TSS = 0.62; Table 2). The Middle Snake, Middle Columbia, Upper Columbia, and Yakima sub-basins had the highest proportion of total river kilometers predicted to be occupied by smallmouth bass (16%, 13%, 12% and 12% respectively), whereas the Lower Snake, Kootenai-Pend Oreille-Spokane and Lower Columbia had the lowest proportion of occupied riverine habitat (5%, 5%, and 7% respectively; Fig. S1). The model built using the final dataset demonstrated similar performance to a SDM constructed using just the initial database of past survey efforts (Table 2).

The primary environmental drivers contributing to model performance included a combination of thermal, hydrological, and geomorphic variables. Mean August water temperature, spring flow, and slope were the most influential with respect to the amount of total deviance explained (Δ Deviance = 80.3, 29.0, 27.4; respectively), followed by mean annual flow and the presence of barriers (Δ Deviance = 11.3, 3.7; respectively) (Fig. 3). Dam density and winter air temperature did not contribute to model accuracy (Δ Deviance = 0.0). Habitat suitability was generally negatively associated with slope and spring flow and positively associated with water temperatures and large rivers, suggesting that smallmouth bass benefitted from shallow gradients, large rivers, moderate magnitude spring flows, and warm water temperatures (Fig. 3). In addition, the presence of hydrologic barriers was associated with reductions in the probability of smallmouth bass occurrence.

Although our model responses generally matched what is known about smallmouth bass habitat suitability, a number of interesting results emerged. First, we expected increasingly steep gradients to have a negative association with smallmouth bass occurrence probability. Instead, we found that shallow gradients had a positive effect on smallmouth bass occurrence probability, whereas steeper gradients had no effect (Fig 3). However, the model response curve shows that smallmouth bass rarely occur in regions where reach slopes exceed 3% (i.e., Slope = 0.03), suggesting that high gradient reaches are not suitable for smallmouth bass. Second, rivers with the most stable flow regimes (i.e., low values of spring flow) were associated with lower probabilities of smallmouth bass occurrence. These more stable flow regimes were predominantly isolated to the coastal regions of the CRB. There was a threshold response to spring flow, however, such that moderate levels of spring flow had a positive impact on smallmouth bass occurrence probability, but as spring flows continued to increase, the relationship changed to a steep, negative association. Third, there was a nonlinear relationship between water temperature and smallmouth bass occurrence probability. A positive association with smallmouth bass occurrence was only evident when mean August water temperatures exceeded 17°C, and this association slightly weakened when temperatures exceeded 20°C.

Predicted changes to future (i.e., 2080) flow and temperature resulted in dramatic increases to smallmouth bass distribution throughout most of the CRB (Fig. 2b). Specifically, smallmouth bass are predicted to gain over 12 000 kilometers of river by 2080, representing a 69% increase from predicted current occupied habitat (Table 2). In addition, some small headwater tributaries that are currently predicted to be inhospitable to resident smallmouth bass appear vulnerable to invasion under warmer water conditions (Fig. 2b). This was most apparent in the Middle Snake, Middle Columbia, and Yakima sub-basins of the CRB, where smallmouth bass are predicted to spread through an additional 10% of the available riverine habitat in each sub-basin (Fig. S1). All other sub-basins are predicted to see gains of 4-6%, with the exception of the Lower Columbia, where there is no predicted change to the distribution of smallmouth bass (Fig. S1).

We found our model based on the initial collation of existing data useful in guiding our localized eDNA sampling efforts. In 10 of 14 sampled rivers, we located a transition from eDNA presence to absence points near the location where the model predicted a range boundary (Fig. 5, S2). According to the initial SDM, the watercourse distance between the most upstream eDNA presence point and the model predicted upstream extent (considered the first location where the model probability of occurrence fell below 0.5) averaged 15 kilometers (range = 0 - 40 km) (Fig. 5). In the Yakima, Payette, Kootenai, and Salmon Rivers, no smallmouth bass were detected using eDNA. When comparing model performance at these range boundary regions, we note a marked improvement of the model built using the final database that incorporated eDNA data (Table 2, Fig. S2). The final model demonstrated overall greater performance (as indicated by

Kappa, TSS and Accuracy indices) and was twice as successful in correctly predicting species absence (specificity = 0.61 vs. 0.30) at the range boundaries while demonstrating comparable sensitivity (Table 2).

We found various amounts of overlap between the predicted current-day smallmouth bass distributions and critical habitat for all CRB salmonids except Chum salmon (Table 3). Percentages of critical habitat overlap across these species ranged from 3-62% (mean = 20%) (Table 3). Fall Chinook and Sockeye salmon, in particular, had relatively high percentages of overlapping habitat (i.e., 62% and 39% respectively) (Table 3). By contrast, there was little to no predicted overlap between designated cold-water refugia for either bull trout or cutthroat trout. Instead, we see very low (albeit non-zero) probabilities of smallmouth bass presence for both current day (mean = 0.06 for both species) and future climate (mean = 0.06 for both species) predictions (Fig. 4).

Discussion

By combining phenomenological distribution modeling with enhanced species detectability at range edges using eDNA, we provide new insight into the present and forecasted future invasion of smallmouth bass in the Columbia River Basin. Models performed well at predicting smallmouth bass distribution at the basin scale (Table 2), including a strong ability to determine the approximate upstream range boundary locations at the channel segment (Fig. 2a, Fig. 5). Species detection using eDNA sampling proved useful to improve model predictions from correlative models at the range boundaries without sacrificing model performance at the broader spatial extent, and successfully refined the location of the leading-edge invasion to within management-relevant regions of multiple rivers (Fig. 5, Fig. S2).

Empirical data and model predictions depict a broad invasion of smallmouth bass across diverse climates, hydrological conditions, and geomorphologic contexts that define the rivers of the CRB. Combinations of shallow gradients, large rivers that display moderate-magnitude spring flows, and warm water were associated with increased probability of smallmouth bass occurrence. According to these habitat correlates, nearly 18 000 river kilometers are suitable to, or currently, support smallmouth bass populations under current environmental conditions (Fig. 2a, Table 2). Although the distribution of smallmouth bass is spread broadly across geographic space, we show that smallmouth bass is still relatively confined to warmer, low-gradient rivers in the CRB (Fig. 2a). This, however, is not unique to cool-water smallmouth bass. Isaak et al. (2017) demonstrate that across 11 fish species, including several cold-water salmonids, only small proportions of total stream habitat (measured only in Idaho) are accessible or suitable to fish. If a majority of the CRB network is not accessible or suitable to fish, the basin-wide occupancy of smallmouth bass may be much more significant than our results depict.

Although our model depicts a propensity for smallmouth bass to inhabit large, higher-order streams, it also portrays suitable habitat throughout a number of smaller headwater tributaries (Fig. 2). As a result, we found that there was spatial overlap ranging from 3-62% with critical spawning and rearing habitat for native salmonids across the CRB (Table 3). This observation denotes a potential challenge for salmon conservation where the invasion of smallmouth bass is rarely considered in large-scale conservation and restoration efforts (Carey et al. 2011; Naiman et al. 2012). For anadromous species, in particular, our estimates of habitat overlap provide a conservative estimate of potential impact given that this only depicts the potential threat of year-round co-occurrence, excluding interactions that may occur during outmigration. Furthermore, forecasted changes to flow and temperature regimes predicted a two-third increase in suitable habitat, equating to over 10 000 more river kilometers of potentially suitable habitat to smallmouth bass in 2080 (Fig. 2b, Table 2). Despite this striking pattern, there remains only scant research evaluating the predator and competitive impacts of smallmouth bass on juvenile salmonids in critical spawning and rearing habitats. Instead, most literature is focused either on predation on outmigrating salmonids (e.g., Fritts and Pearsons 2004) or effects of habitat degradation and loss, dams and impoundments, harvest, and hatcheries (e.g., Naiman et al. 2012). This exposes a potentially important overlooked impact to Pacific salmonids.

We show that the critical spawning and rearing habitat of most salmonids, especially fall Chinook and Sockeye salmon, overlap with established year-round smallmouth bass populations (Table 3) and that much of the CRB will see an increase in suitable smallmouth bass conditions in the future (Fig. 2b, Fig. S1). The Middle Snake, Middle Columbia, and Yakima sub-basins, in particular, show high percentages of occupancy by smallmouth bass under current climate conditions, which encompass much of the critical habitat for fall Chinook and Sockeye salmon. These same sub-basins show the greatest projected increase in habitat suitability under future climate conditions (Fig. S1). Smallmouth bass is predicted to increase by 4-6% in the Willamette, Lower and Upper Snake, Kootenai-Pend O’reille-Spokane, and Upper Columbia. Many of these sub-basins include forested mountain streams that currently support native trout species, including both cutthroat trout and bull trout. A positive implication of our study is that refugia for cutthroat and bull trout (Isaak et al. 2015) appear safe from major encroachment by smallmouth bass both in present day and forecasted futures (Fig. 4). Protecting these refugia and focusing efforts on the early detection and prevention of secondary spread, where possible, may prove a cost-effective strategy to minimize future impacts of smallmouth bass on salmonid species in these sub-basins. This will require continued investigation of the spatiotemporal patterns of fish movement at the leading-edge of the invasion (Rubenson and Olden 2017).

Little change to the projected distribution of smallmouth bass was observed in the Lower Columbia basin. This sub-basin appears relatively buffered to climate-induced temperature changes observed in other sub-basins, with only a small proportion of the sub-basin warming above the model-identified breakpoint of 17°C. Interestingly, further analysis reveals that many of the segments predicted to warm do not see large increases to the probability of smallmouth bass occurrence. Here, non-temperature related drivers, such as hydrologic conditions or slope, are likely important for determining the future of smallmouth bass in this basin. For instance, many of the stream segments predicted to warm also have steep slopes. This suggests that steep slopes may prevent smallmouth bass from moving upstream in response to warming temperatures or that the physical habitat characteristics often associated with steep stream reaches are unsuitable for smallmouth bass colonization. This is supported by our regional database that has very few ($n = 4$) presence points in stream reaches with slopes > 3% (Table S3), and the model response curve that shows that smallmouth bass rarely occur in stream reaches with slopes > 3% (Fig. 3). Gibson-Reinemer et al. (2017) demonstrated that high channel slopes likely limit the ability of fish to track climate change. Additional research is required to determine what slope constitutes a barrier for movement to smallmouth bass, but our data suggest that the physical habitat characteristics associated with streams that have reach slopes > 3% are rarely suitable for smallmouth bass. Knowing where smallmouth bass are unlikely to expand even if climate change increases habitat suitability may help target management funds to regions where secondary spread is more likely.

Correlative associations manifested in the distributional model may facilitate targeted management strategies to prioritize locations for early detection monitoring and prevention of secondary spread of smallmouth bass (Vander Zanden and Olden 2008). Here, we highlight potential mechanisms that may be exploited for management purposes at range boundaries. Warmer water temperatures increased the probability of smallmouth bass occurrence in the CRB (Fig. 3). The positive influence of warmer water temperatures on smallmouth bass corresponds to current understanding of this species' physiology and aligns with results from previous modeling efforts (e.g., Peterson and Kwak 1999; Sharma and Jackson 2008). Although this clear and strong relationship presents a challenge under likely climate futures, it also highlights a management opportunity that can both benefit native fishes while deterring smallmouth bass (and other cool or warm-water nonnatives). The model-identified breakpoints of 17°C and 20°C may represent water-quality targets and decision points for management action to potentially prevent or dissuade the upstream secondary spread of smallmouth bass.

Restoring riparian vegetation remains a powerful approach to offset climate-induced losses in suitable salmonid spawning and rearing habitat while concurrently reducing the upstream expansion of smallmouth bass. By using downscaled regional climate-change forecasts of air temperature and streamflow with a fine-scale stream temperature model, Lawrence et al. (2014) showed that complete riparian restoration was effective at reducing temperatures in a major tributary of the CRB by up to 2.5°C (7-day average-daily mean water temperatures). Smallmouth bass were projected to occupy the entire Middle Fork John Day River (Oregon, USA) in late summer by 2080, but simulations of 50% riparian restoration restricted smallmouth bass from invading most of the upper 30+ km of river where spring Chinook salmon rearing-habitat persisted. Other management efforts, such as the creation of deeper pools, reconnecting sites to cold water sources, and even the construction of temporary shade structures and selective seasonal releases of colder water from dams (Kurylyk et al. 2015) near or at range boundaries are also potentially viable solutions to reduce water temperature, but require additional investigation.

Although efforts to reduce local stream warming reveals encouraging opportunities, the broad-scale increase of habitat suitability throughout the CRB necessitates a diversity of management approaches. Our model suggests that smallmouth bass occurrence is driven by both temperature and flow, and research shows that manipulating releases downstream from dams may prove useful in the deterrence of secondary spread (Carey et al. 2011). Interestingly, we found a positive relationship between smallmouth bass occurrence probability and moderate spring flows. This association may be related to a mismatch in timing of high discharge events and the initiation of smallmouth bass upstream movement and spawning. For instance, smallmouth bass typically commence spawning as water temperatures warm above 15°C (Rubenson and Olden 2017) and large spring discharge events in much of the CRB are a result of snowmelt and are thus associated with cold water temperatures. Careful consideration of the timing of dam releases is required to effectively deter spawning or upstream movement. In addition, tactics such as nest destruction and targeted adult removals (Loppnow et al. 2013) may also prove feasible, especially at range boundaries where population abundances are generally lower. The high-resolution predictions from our study can inform monitoring efforts (potentially using eDNA) in key locations to allow for early detection of smallmouth bass presence. Once present, targeted removal or suppression efforts by state agencies could be instituted sufficiently early in the invasion to reduce or prevent negative impacts. Similarly, outreach to incentivize anglers to actively target and remove smallmouth bass from regions critical to salmonid conservation may be an option.

In addition to the aforementioned management options, intentional fragmentation using natural or artificial barriers to upstream movement may provide opportunities to protect currently uninvaded habitat for native salmonids (Rahel 2013). Here, the assumption would be that selective barriers could be designed to impede movements of smallmouth bass (or other nonnative fishes), but still allow salmonid passage; an undoubtedly large challenge. Intentional fragmentation is successfully used in South Africa, where gabion dams have been constructed to prevent recolonization of nonnative black basses after their removal from streams (Weyl et al. 2014). In our model, the probability of occurrence was negatively associated with the location of barrier features such as waterfalls or cascades. Designating areas upstream of these features as refugia and instituting regulations, monitoring, and education programs to restrict the human-aided transport of species above these barriers may provide cost-effective safeguards to ensure these areas remain free from nonnative predators. In short, the notion that barriers may be useful to prevent secondary spread of invasive fishes requires careful consideration of current efforts to reconnect currently fragmented upstream habitat (Swan and Brown 2017). Before restoration projects to defragment streams occur (e.g., fish passage at road culverts), it would be wise to determine the risk of a predator invasion (Rahel 2013). If invasion risk is high, the benefits of increasing habitat connectivity for target native species may be overridden by new predation and competition threats.

Environmental DNA enabled rapid local-scale assessments of multiple rivers across a large geographical area, confirming the location of management-relevant range boundary regions in individual streams. We found it encouraging that basin-wide models were sufficiently accurate to identify upstream invasion extents to within 15 km of the field-based boundary (Fig. 5). Furthermore, including the eDNA presence and absence data in the final model improved model performance at critical range boundary regions (Table 2, Fig. 5, Fig. S2). We show that including supplemental eDNA from targeted regions can improve the fine-scale distributional resolution of correlative models at relatively low costs without sacrificing broad-scale model performance.

There were some exceptions to identifying approximate range boundaries using eDNA technology. In the Salmon, Kootenai, and Payette Rivers, sampling occurred upstream of where the initial model predicted the range boundary (Fig. S2), therefore the series of absences was expected. In the Yakima River, presence data from our initial distribution database overlaps with the lower 3 eDNA samples that showed absences, suggesting the range boundary was sampled, but that smallmouth bass was not detected by eDNA. Similarly, eDNA results suggest that the range boundary was located in the Clark Fork, but the initial model depicts that smallmouth bass have a high probability of occurrence hundreds of kilometers farther upstream (Fig. S2); calling into question either eDNA detection accuracy or model performance. Little research currently exists on eDNA detection in large rivers such as the Yakima and Clark Fork, and conditions such as low visibility, swift currents, and deep and wide channels make testing the accuracy of eDNA sampling difficult. Both eDNA detection and factors that influence invasion expansion rates in large rivers are ripe areas for additional research. We do note, however, that the final model improved upon the initial model in all of the aforementioned examples (Fig. 5).

One key limitation to our study is that eDNA research in waterbodies caution that spatial inferences made on eDNA could vary dramatically between systems based upon local transport processes (Jane et al. 2014; Perez et al. 2017). We specifically targeted rivers with diverse habitat conditions, to include different sizes, sediment load, and velocities. These factors alter DNA concentrations, the detection probability of eDNA, and the distance from an eDNA source at which detection occurs (Pilliod et al. 2013; Goldberg et al. 2016). Although we concede that there is certain to be variability in the precise river kilometer relative to a positive detection from eDNA that defines the range boundary across these systems, we argue that the precision and insight gained relative to the effort exerted far exceeds other capabilities currently available to managers. In addition, we visually located smallmouth bass at 18 of the 30 eDNA detections and had an absence point upstream of the most upstream presence point in all rivers, further narrowing the potential location of the range boundary (Fig. 5). Thus, although there are uncertainties in the range at which a positive eDNA detection might occur, our study illustrates the ability to rapidly narrow our knowledge of an invasion extent to within kilometers in multiple rivers across the diverse and vast CRB in a matter of days using only a correlative species distribution model and eDNA.

Conclusion

Conservation and recovery of endangered salmonid species in the CRB are inextricably intertwined with the management of nonnative species. Successful management, however, is contingent on accurate information about species' distributions – especially at range boundary regions. Here, we show how combining new eDNA technology with broad-scale phenomenological modeling was effective in elucidating the current and potential future distribution of invasive smallmouth bass in the CRB and identified range boundary regions to a management-relevant scale. Furthermore, the flexibility, accuracy, and rapidity of these methods are not unique to smallmouth bass, but can also be applied to nearly two dozen other nonnative predators currently established in the CRB, thus providing essential information to managers tasked with ensuring the long-term future sustainability of salmonids.

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Table 1: List of predictor variables used in the smallmouth bass distribution model, as well as summary statistics.

Variable name	Description	Time Period	Source	Unit	Mean (Min, Max)
WaterT	Mean August water temperature	1993-2011	NorWeST stream temperature[1]	°C	13.2 (0, 29.8)
WaterT2080	Future mean August water temperature	2070-2099	NorWeST stream temperature[1]	°C	15.4 (0, 30.4)
WinterAirT	Mean monthly air temperature October 1-March 31	1916-2006	Climate Impacts Group[2]	°C	0.6 (-8.1, 8.3)
WinterAirT2080	Future mean monthly air temperature October 1-March 31	2070-2099	Climate Impacts Group[2]	°C	3.2 (-4.6, 10.3)
SpringFlow	Mean daily flow between April 1 and May 31	1915-2006	Western U.S. Stream Flow Metrics[3]	cms·cms^{-1}	1.0 (0.2, 3.1)
SpringFlow2080	Future mean daily flow between April 1 and May 31	2070-2099	Western U.S. Stream Flow Metrics[3]	cms·cms^{-1}	0.7 (0.1, 3.4)
MAFlow	Mean of the yearly cumulative discharge	1915-2006	Western U.S. Stream Flow Metrics[3]	cms	35.3 (1.6 x 10^{-6}, 7 627)
MAFlow2080	Future mean of the yearly cumulative discharge	2070-2099	Western U.S. Stream Flow Metrics[3]	cms	39.0 (1.7 x 10^{-6}, 8 282)
Slope	Maximum-minimum elevation / length of the NHD Flowline	NA	NHDPlusV2[4]	km·km^{-1}	0.06 (1.0 x 10^{-5}, 0.7)
DamDensity	Density of georeferenced dams within the upstream watershed	NA	StreamCat[5]	dams·km^{-2}	0.003 (0, 23)
Waterfall	Categorical. River segments upstream of a waterfall or cascade in the Fish Passage Barriers dataset by StreamNet assigned value of 1.	NA	StreamNet[6]	NA	NA

1. www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html
2. http://regclim.coas.oregonstate.edu/index.html
3. https://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml
4. http://www.horizon-systems.com/NHDPlus/NHDPlusV2_home.php
5. https://www.epa.gov/national-aquatic-resource-surveys/streamcat
6. http://www.streamnet.org/online-data/GISData.html

Table 2: Comparison of basin-wide and range boundary test statistics using 10-fold cross-validation (AUC) and confusion matrices for the model with ("Final") and without ("Initial") supplemental eDNA data. The range boundary statistics measure model performance at the eDNA sample locations only.

	Basin-wide		Range Boundary	
Test Statistic	Final	Initial	Final	Initial
AUC	0.90	0.93	0.91	0.78
Sensitivity	0.83	0.88	0.93	1.00
Specificity	0.80	0.81	0.61	0.30
TSS	0.62	0.69	0.55	0.30
Kappa	0.62	0.69	0.47	0.23
Accuracy	0.81	0.85	0.72	0.54
Current distribution (km)	17 660	22 209	NA	NA
Future distribution (km)	29 818	33 068	NA	NA

Note: Threshold value (0.5) was determined by maximizing the sum of sensitivity and specificity. Estimated distribution is the total river kilometers occupied by smallmouth bass based upon predicted probabilities of occurrence exceeding the threshold value for both current (1981-2016) and projected future (2080).

Table 3: Percentage of the spawning, rearing, and/or year-round habitat of each Columbia River Basin salmonid species predicted to overlap with smallmouth bass and total river kilometers (RKM) of predicted overlap.

Species	Run	% of Habitat	RKM
Chinook salmon	Fall	62	2 125
	Spring	22	3 359
	Summer	9	140
Chum salmon	NA	0	0
Coho salmon	NA	19	1 174
Sockeye salmon	NA	39	116
Steelhead	Summer	11	2 606
Steelhead	Winter	15	1 272
Bull Trout	NA	6	1 160
Redband Trout	NA	14	2 810
Westslope Cutthroat Trout	NA	3	1 361
Yellowstone Cutthroat Trout	NA	4	172

Figure Captions

Fig. 1. The Columbia River Basin and the presence (filled circles) and absence (open circles) of smallmouth bass from the assembled regional database and eDNA presence (filled diamonds) and absence (open diamonds) data. The Canadian portion of the Columbia River Basin was not included in the model although smallmouth bass occurs along the United States border. Stream order 1 not depicted. Map data sources: Esri, DeLorme, HERE, MapmyIndia.

Fig. 2. Modeled distribution of smallmouth bass for a) current day (1981-2016) and b) projected future (2080). Stream order 1 not depicted. Map data sources: Esri, DeLorme, HERE, MapmyIndia.

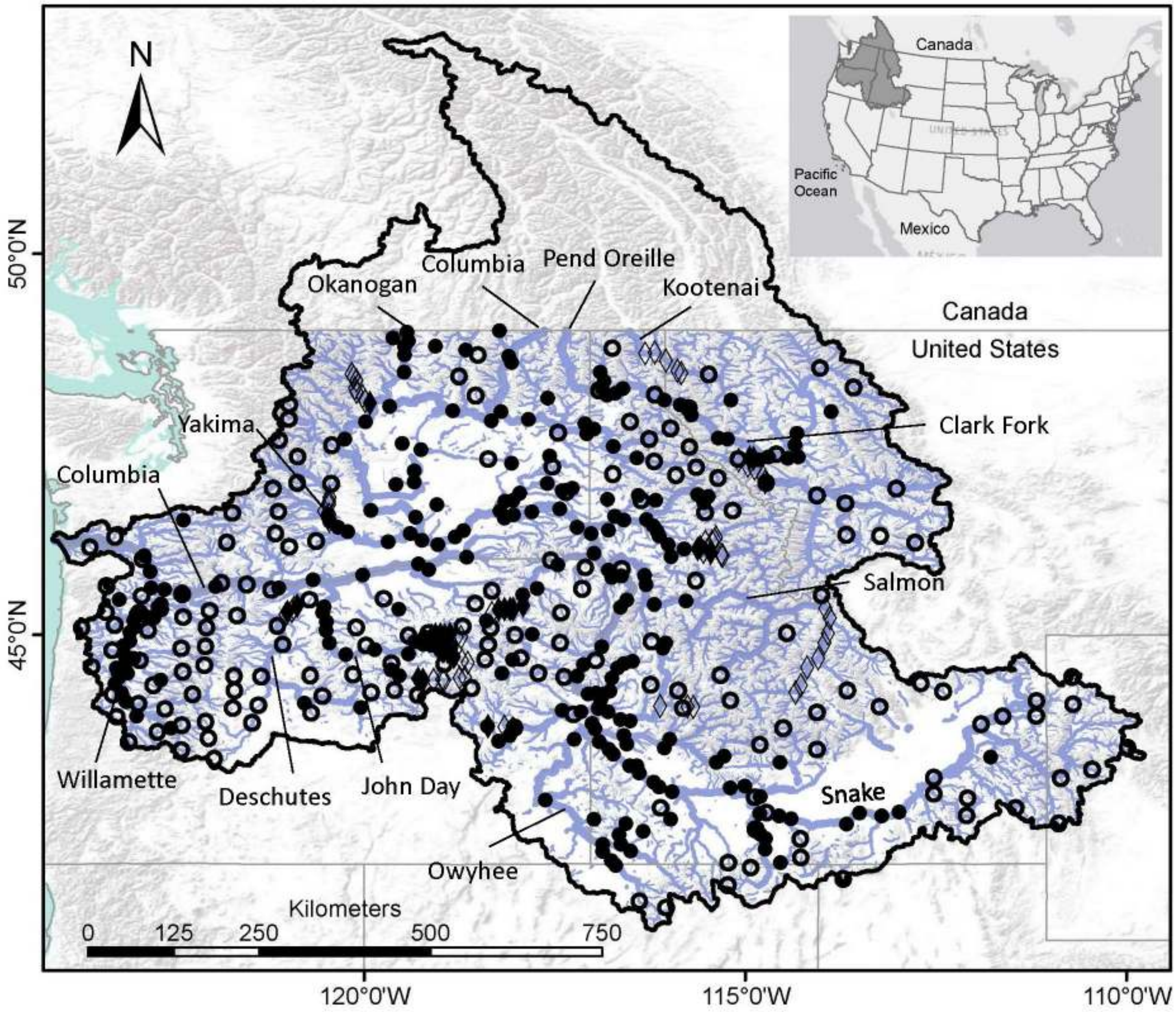
Fig. 3. Response curves for environmental variables included in the species distribution model (only those with significant contributions to the model are shown). The x-axes represent the range of predicted values for each environmental variable. The y-axes represent each variable's standardized effect on the model response.

Fig. 4. The probability of smallmouth bass occurrences in designated climate refugia for bull trout and cutthroat trout under current (1981-2016) and future (2080) climate scenarios. The lines at the top, middle and bottom of each box represent the 75th percentile, median and 25th percentile of the values, respectively, vertical bars (whiskers) represent 95% confidence interval, and points represent all observations outside the confidence interval.

Fig. 5. The predicted probability of smallmouth bass occurrence (color gradient) in 14 major tributaries of the Columbia River Basin, as well as observed presence (closed circles) and absence (open circles) locations according to eDNA sampling. The x-axis is a measure of relative distance, where 0 indicates the most downstream and 200 the most upstream portions of

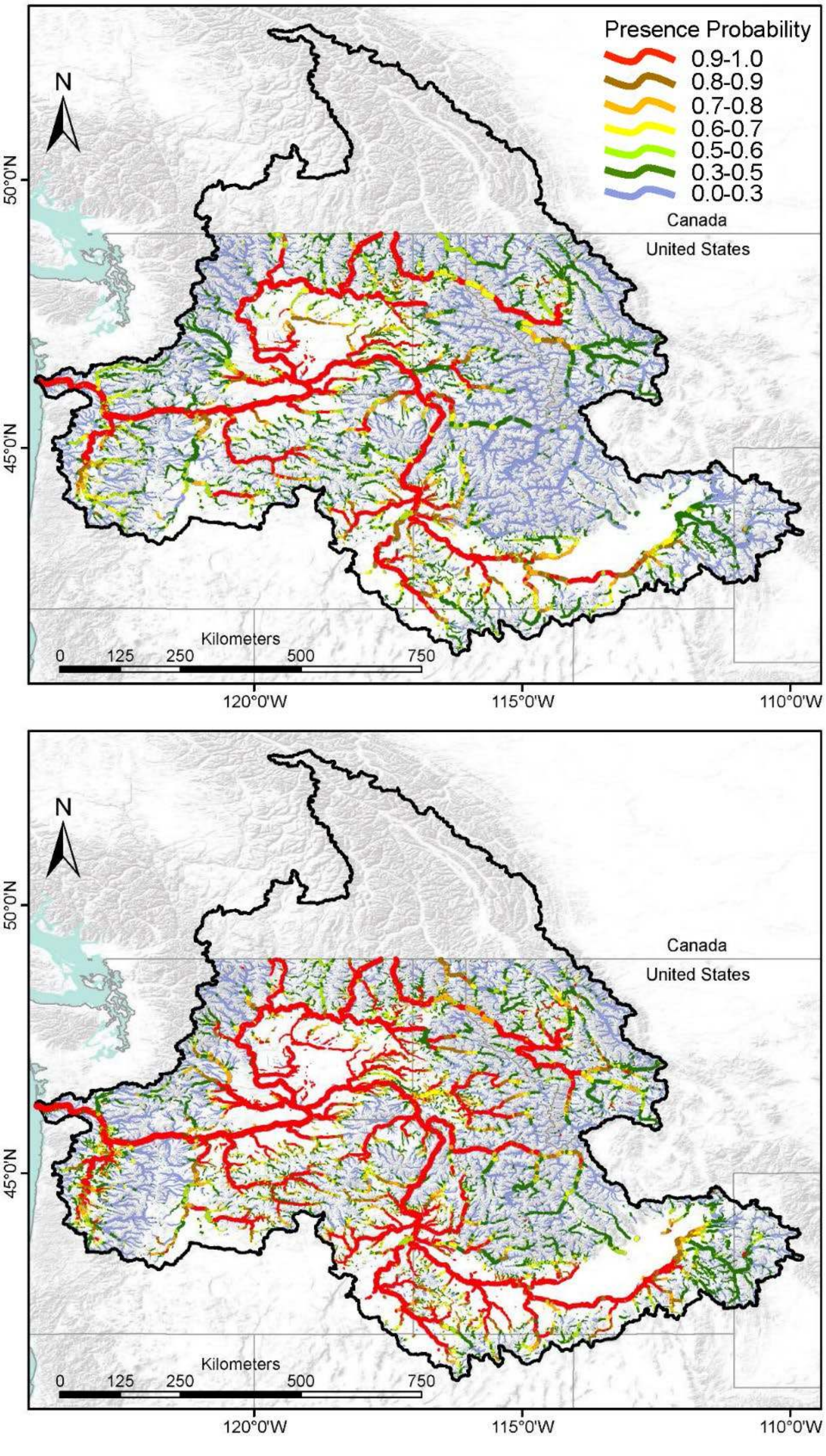
the sampled rivers. Known waterfalls or cascades thought to be barriers to upstream dispersal are indicated with an ‘X’. SF, MF and NF refer to South, Middle and North Fork, respectively.

Figure 1



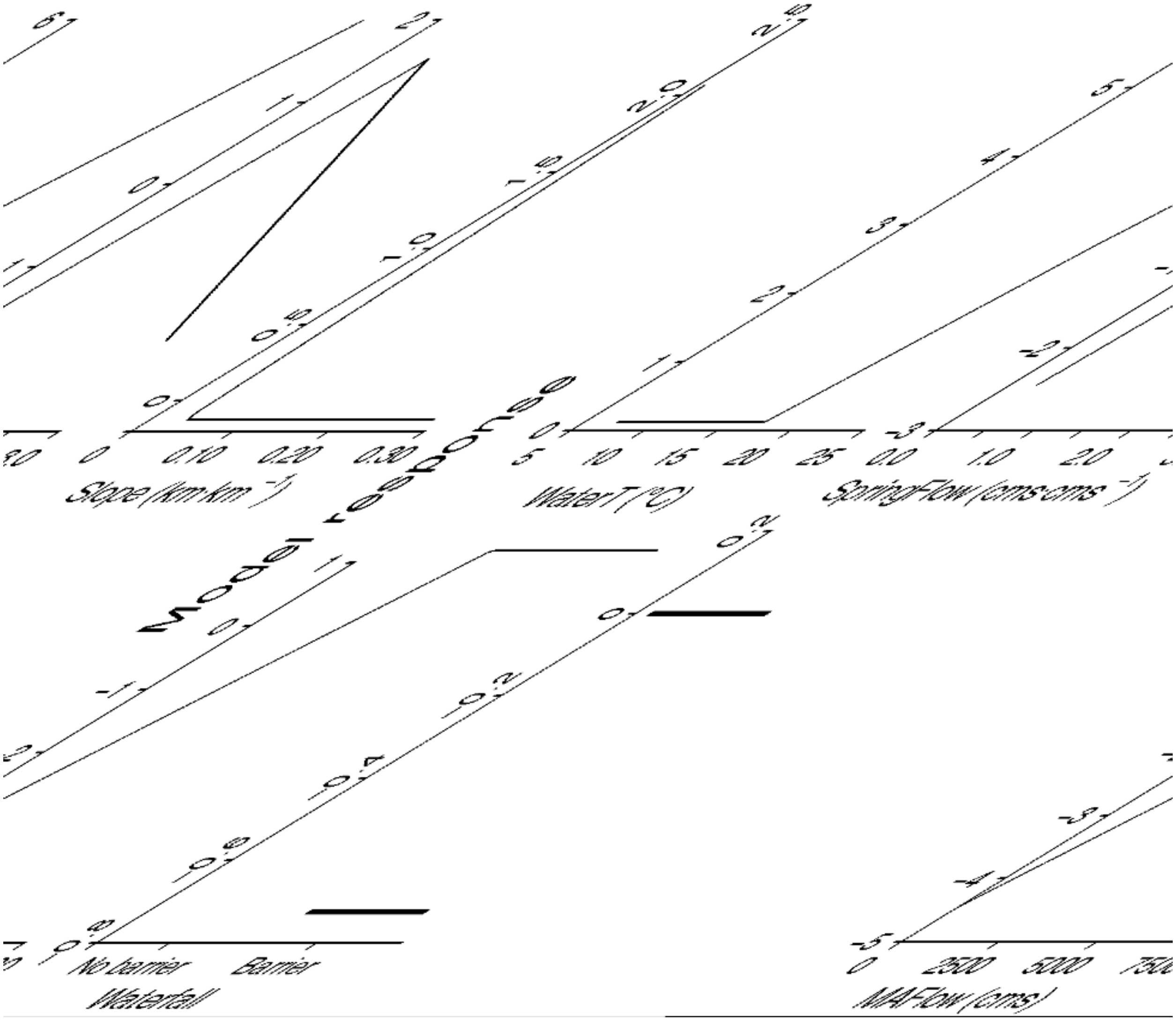
The Columbia River Basin and the presence (filled circles) and absence (open circles) of smallmouth bass from the assembled regional database and eDNA presence (filled diamonds) and absence (open diamonds) data. The Canadian portion of the Columbia River Basin was not included in the model although smallmouth bass occurs along the United States border. Stream order 1 not depicted. Map data sources: Esri, DeLorme, HERE, MapmyIndia.

Figure 2



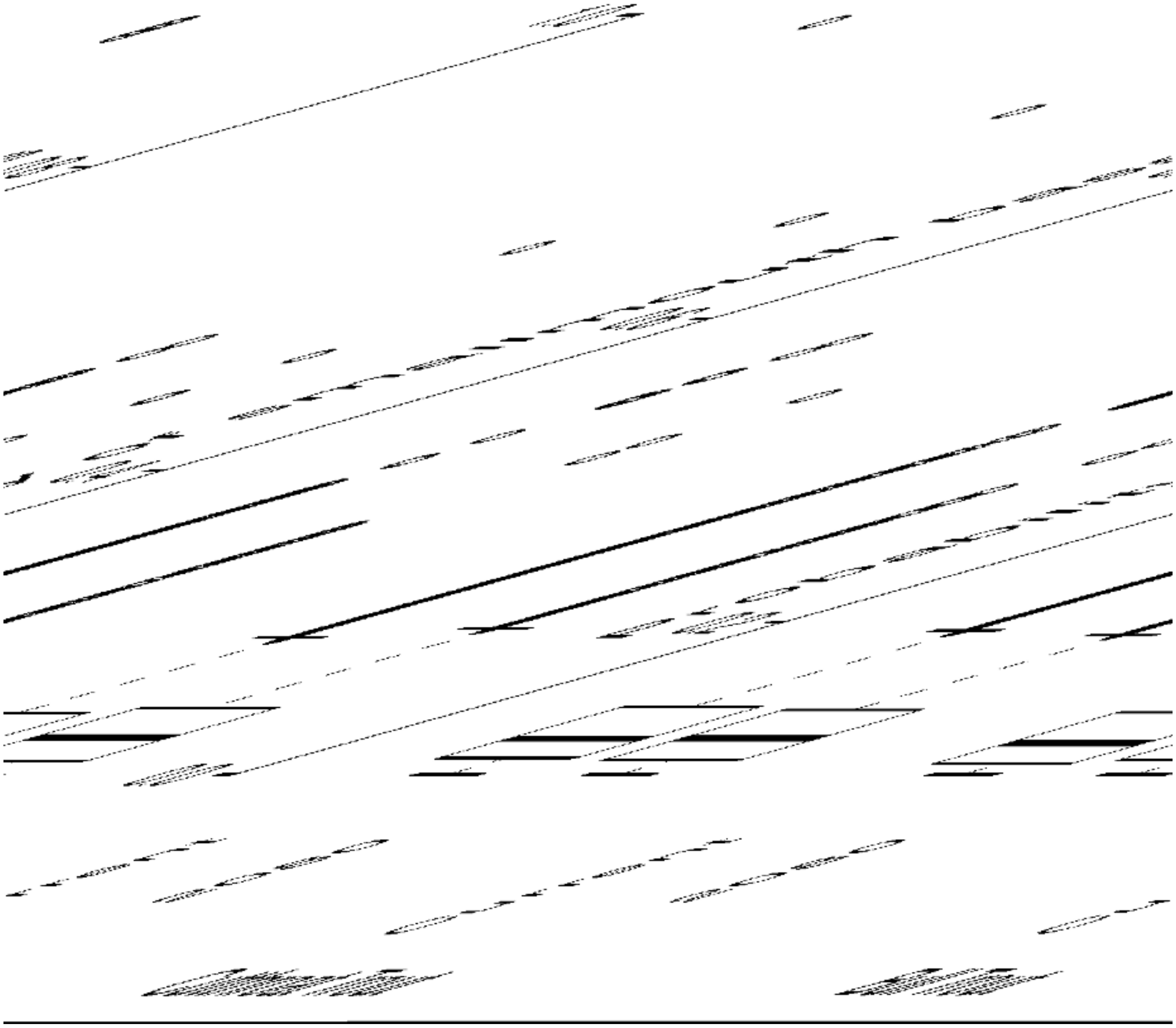
Modeled distribution of smallmouth bass for a) current day (1981-2016) and b) projected future (2080). Stream order 1 not depicted. Map data sources: Esri, DeLorme, HERE, MapmyIndia.

Figure 3



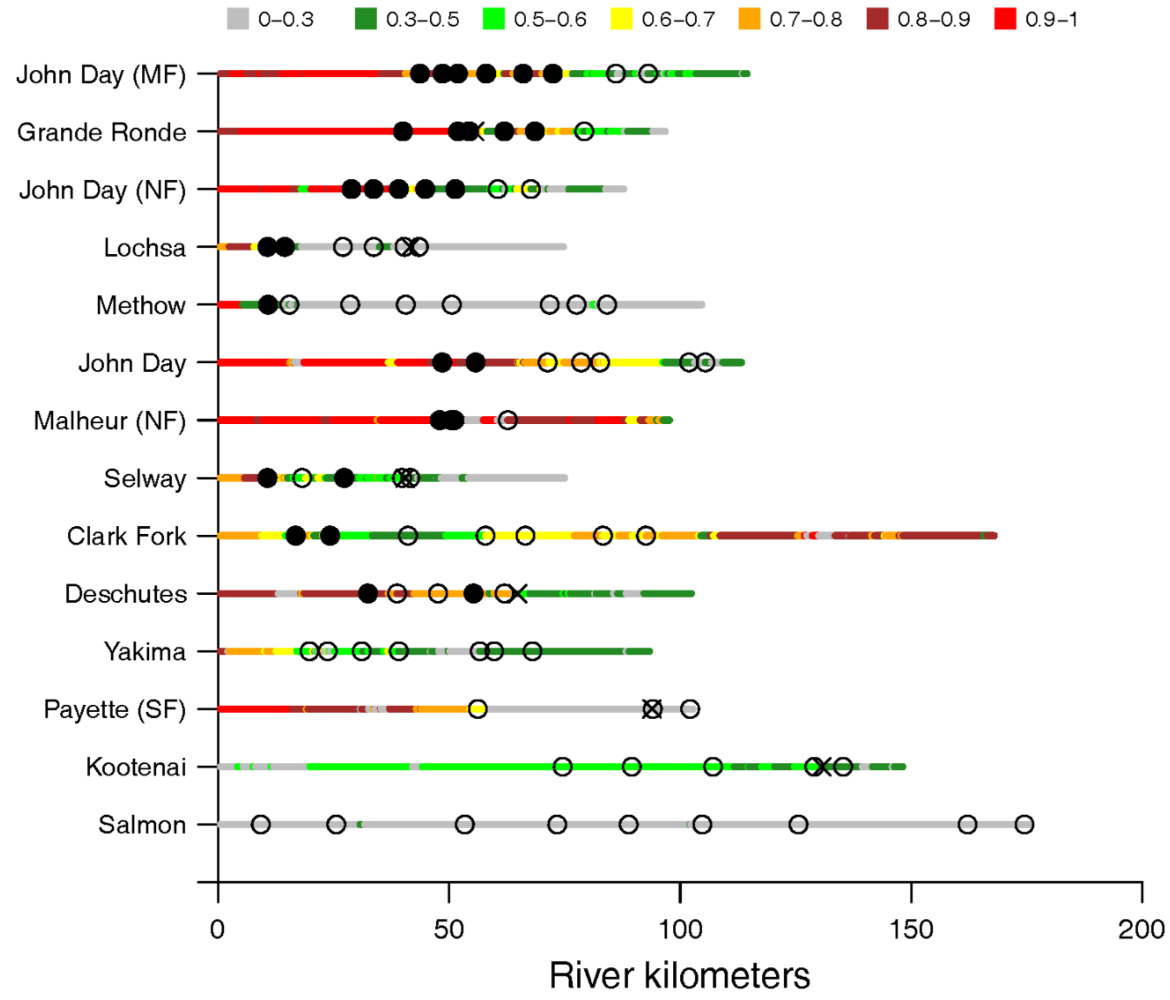
Response curves for environmental variables included in the species distribution model (only those with significant contributions to the model are shown). The x-axes represent the range of predicted values for each environmental variable. The y-axes represent each variable's standardized effect on the model response.

Figure 4



The probability of smallmouth bass occurrences in designated climate refugia for bull trout and cutthroat trout under current (1981-2016) and future (2080) climate scenarios. The lines at the top, middle and bottom of each box represent the 75th percentile, median and 25th percentile of the values, respectively, vertical bars (whiskers) represent 95% confidence interval, and points represent all observations outside the confidence interval.

Figure 5



The predicted probability of smallmouth bass occurrence (color gradient) in 14 major tributaries of the Columbia River Basin, as well as observed presence (closed circles) and absence (open circles) locations according to eDNA sampling. The x-axis is a measure of relative distance, where 0 indicates the most downstream and 200 the most upstream portions of the sampled rivers. Known waterfalls or cascades thought to be barriers to upstream dispersal are indicated with an ‘X’. SF, MF and NF refer to South, Middle and North Fork, respectively.