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Beyond Isolation by Distance: Riverscape Effects on Genetic Structure of Fall-Run Chinook Salmon

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Abstract.—Habitat fragmentation, land use practices, and flow impediments modify the natural course of rivers, disrupting connectivity and subsequently affecting dispersal and gene flow in aquatic organisms. Many of the relationships between the physical river network and the genetic structure of populations are not well understood. Riverscape genetics is a developing field that uses population genetic metrics to assess genetic structure within the context of the environmental variables that drive functional connectivity in a river network. Here, we applied an effective distance network approach to characterize the effects of hydrology in shaping neutral genetic population structure of fall-run Chinook Salmon *Oncorhynchus tshawytscha* within a small, coastal Oregon catchment. We evaluated whether gene flow was limited by (1) site-specific features occurring within spawning habitat, using a dissimilarity matrix, and (2) the cumulative effect of the environment accrued while traveling en route between reaches. We found that Chinook Salmon that spawned at higher elevations (site specific effects) after traversing steeper gradients (en-route effects) were more genetically distinct from individuals that traversed gradual gradients and spawned at lower elevations. This effect (isolation by resistance) was distinguishable from isolation by distance, which was not detected among spawning groups. Our study enhanced interpretation of habitat heterogeneity in constraining gene flow and spatial genetic structure among reaches within a small, coastal catchment. Given that smaller catchments may hold life history

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variation that is important to long-term population persistence, there is need to understand these relationships that maintain genetic diversity.

Introduction

Expanding quantitative genetic research in river systems by explicitly considering habitat heterogeneity and the physical configuration of river networks could clarify the evolutionary consequences of environmental change and habitat fragmentation in rivers on population persistence. Habitat fragmentation, land use practices, and barriers modify the natural courses of rivers disrupting functional connectivity within the riverscape (Ward and Stanford 1983). These alterations have subsequent effects on species dispersal ability and gene flow (Nehlsen et al. 1991; Yoshiyama et al. 1998; Brenkman et al. 2012). The genetic response resulting from the inability of individuals to disperse may include reduced genetic and life history variation (Yoshiyama et al. 1998). The ability to observe and assess genetic changes to life history traits is necessary to understand how natural and anthropogenic changes to functional connectivity may affect fish assemblages now and in the future.

The distribution of riverine habitat is driven by hydrologic, stochastic (e.g., fires and floods), and geomorphic (e.g., erosion and deposition) processes that create and reconfigure stream habitats over time (Reeves et al. 1995). Physical habitat diversity within riverscapes is characterized by differences in bed type, channel morphology, biological communities, and physical configuration, processes that are driven by natural and anthropogenic disturbance (Frissell et al. 1986; Montgomery 1999; Fausch et al. 2002; Borrett et al. 2014). River research that considers the spatial structure of the physical network in conjunction with disturbance and geomorphic processes may use network theory and graph theoretic approaches in analyses (Ganio et al. 2005; Wipfli et al. 2007). River network structure complicates traditional spatial statistics because of the directional covariation inherent in a river system that is formed and maintained by unidirectional water, sediment, and organic material flows (Wipfli et al. 2007; Wohl et al. 2019). However, advances in geospatial tools and availability of geospatial data now facilitate evaluation of hydrologic, geomorphic, and ecological changes throughout entire river networks (Benda et al. 2007; Peterson and Ver Hoef 2014; Roux et al. 2015). The spatial structure of rivers influences functional connectivity, but many of the relationships between the physical network and genetic structure are not well understood (Frissell et al. 1986; Benda et al. 2004; Peterson et al. 2013).

Riverscape genetics (RG), a counterpart to land- and seascape genetics, is a developing field with methodology that combines spatial statistics, population genetics, and landscape ecology to understand the role of habitat heterogeneity in shaping gene flow (Kanno et al. 2011; Selkoe et al. 2016). The term "riverscape" in RG is analogous to the use of "landscape" in landscape genetics (LG) and "seascape" in seascape genetics (SG). Therefore, it is defined here as "a hierarchically structured mosaic of differentially distributed habitat within freshwater environments" (Davis et al. 2018). Collectively, LG and SG strive to develop methodologies that move beyond explaining genetic structure as a function of geographic distance (isolation by distance [IBD]) by describing how specific habitat variables such as elevation, tree canopy coverage, or oceanic currents inhibit or facilitate dispersal (McRae 2006; Selkoe et al. 2010; Liggins et al. 2013). The methods developed in LG quantify the contribution of habi-

tat variation along the path traveled en route (e.g., effective distance, path analysis; Figure 1) on spatial genetic variation among individuals and groups (Shirk et al. 2010; Zeller et al. 2012; Hall and Beissinger 2014). Similarly, seascape genetics research has adapted graph-theoretic models (Galindo et al. 2006; Riginos and Liggins 2013) to quantify relationships between hydrogeologic features and genetic distance or differences between populations (Banks et al. 2007; Selkoe et al. 2010; Johansson et al. 2015).

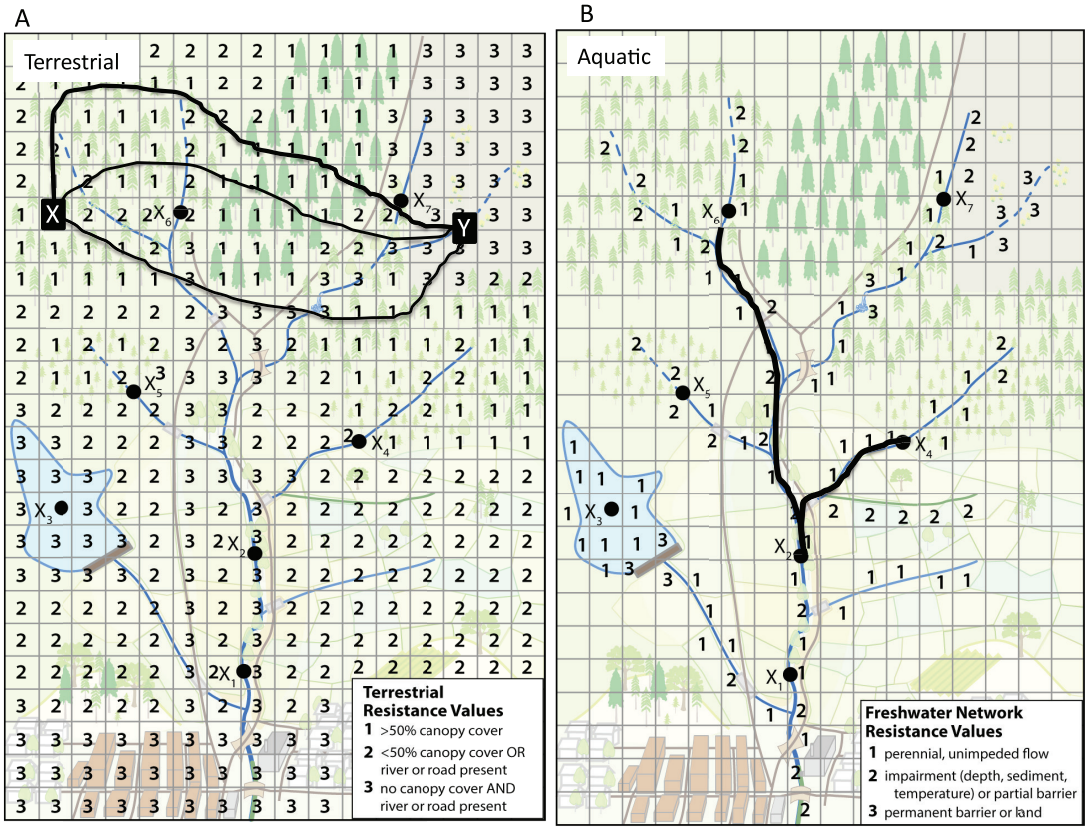

Figure 1. A hypothetical catchment has been transformed into a resistance surface that represents travel by a terrestrial organism across areas with different levels of **(A)** canopy cover and **(B)** travel by an aquatic organism through areas with varying water flow. Within each image, the origin and destination for potential dispersing aquatic and terrestrial organisms are labeled: seven reaches (black dots X_1–X_7) are labeled within the river and two sample locations (black squares X, Y) are on land. The resistance surface transforms an image into a grid of cells (raster image) that is used to test hypotheses about the influence of environmental variables on movement or gene flow. The values within each cell depict the cost of traveling caused by a covariate of interest (e.g., elevation, canopy cover, and water flow). Routes of travel between two points may be modeled (solid black lines) using least-cost path analysis, circuit theory, or other models, resulting in a calculation of effective distance. Effective distance value(s) are then used to understand how habitat complexity affects movement. However, the lack of alternative pathways within dendritic river networks poses a difficulty in the application of this landscape genetic method. Background images are modified from Davis et al. (2018).

Studies of RG have identified effects of isolation by resistance to understand the effects of climate variation and habitat heterogeneity (e.g., temperature, confluence number, discharge, and maximum stream gradient) within rivers on genetic variation of freshwater species (i.e., Olsen et al. 2010a, 2010b; Kanno et al. 2011; Galbraith et al. 2015; Pilger et al. 2015; Hand et al. 2016). The body of research in freshwater systems emphasizes the usefulness of RG approaches to explain genetic variation beyond geographic distance metrics (e.g., waterway distance). Unlike research in terrestrial and marine systems, RG has yet to incorporate the en-route effects of the heterogeneous habitat on dispersal beyond physical barriers like dams.

Linking genetic variation to riverscapes requires consideration of the functional connectivity within the network (Cote et al. 2009; Auerbach and Poff 2011; Flitcroft et al. 2014), conditions that alter functional connectivity, and the spatial configuration of the network (Ganio et al. 2005; Thorp et al. 2006; Blanchet et al. 2011; Peterson et al. 2013). Given the differences between terrestrial, marine, and freshwater habitats, Davis et al. (2018) reviewed the applicability of using LG (Figure 1) and SG (Figure 2) methods to explore the en-route effects of traversing rivers on genetic variation. The authors suggested an integrated network model where edges of the network are weighted using effective distance and nodes represent sampling areas (Figure 3). Both genetic diversity (e.g., allelic richness, heterozygosity) and genetic distance (e.g., Jost's *D*, fixation index) could be modeled as a function of the network, either as metrics of the sample site (e.g., genetic diversity as a function of reach characteristics) or difference-based metrics (genetic difference between pairs of reaches as a function of edge characteristics that link them). This approach would enable broad-scale (e.g., catchment, evolutionarily significant units [ESUs]) and fine-scale (e.g., within catchments, within reach) analysis (Figure 3).

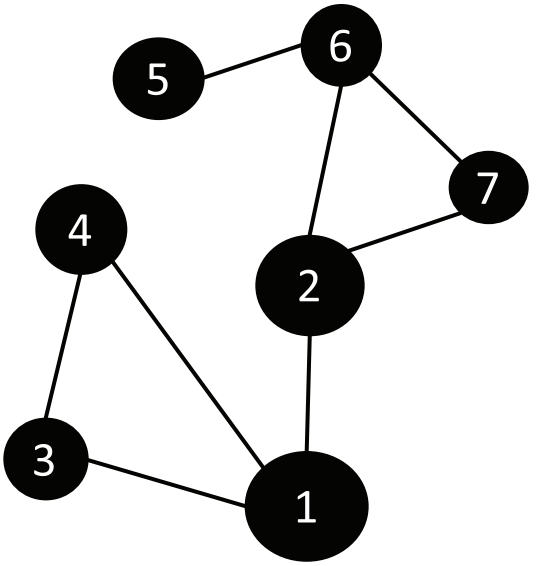

Figure 2. A hypothetical island system is modeled as a graph-theoretic network representing movement by marine organisms among islands based on the direction of ocean currents. Nodes (filled circles) represent individual islands, and differences in node size reflects genetic distance within each island population (larger nodes reflect greater genetic distance). Edges (black lines) connecting nodes reflect gene flow between island populations.

Here, we apply this concept of riverscape genetics to characterize the effects of riverscape variability in shaping the genetic structure of fall-run Chinook Salmon *Oncorhynchus tshawytscha* within a small coastal catchment. Chinook Salmon express diverse life histories that are characterized by the season of the adult return migration to spawning habitat (called a run). Life history diversity of Chinook Salmon in the Pacific Northwest is characterized by differences in return timing (O'Malley and Banks 2008; O'Malley et al. 2013), homing fidelity to natal spawning rivers (Waples 2001), and freshwater rearing strategies (Groot and Margolis 1991). Addition-

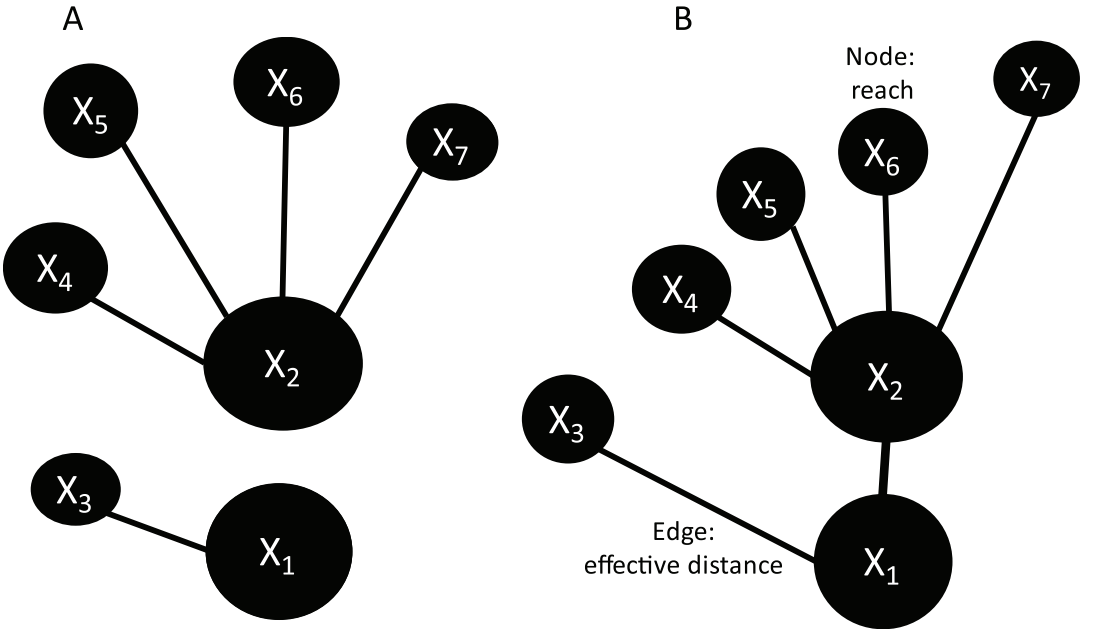

Figure 3. A riverscape genetics approach to evaluate the effects of environmental resistance on gene flow based on the hypothetical river system in Figure 1B. The number within each node corresponds to its location in Figure 1B, site X_3 is upstream of a permanent barrier (e.g., dam) and site X_7 is upstream of a semipermanent barrier (e.g., waterfall). Each node (circle) represents genetic distance within each reach (e.g., D_{est}, F_{ST}). Edges (black lines) reflect **(A)** geographic distance and **(B)** effective distance measured as the cumulative effect of a covariate of interest (e.g., gradient) on dispersal. Evaluating genetic distance between pairs of reaches as a function of (A) distance may result in no relationship. However, by evaluating genetic variation or genetic distance as a function of (B) riverscape characteristics that link them, the effects of the riverscape on genetic diversity at sites X_3 and X_7 become clearer.

ally, changes in genetic structure that reflect restricted gene flow resulting from decreased functional connectivity among essential habitat have been well documented among the Salmonidae (Dionne et al. 2008; Fraser et al. 2011; Kanno et al. 2011; Bradbury et al. 2014; Benavente et al. 2015). Identifying features of the riverscape that facilitate or impede dispersal would provide an ecological context for understanding how Chinook Salmon populations are genetically structured and may help prevent further decline in population abundances or extinctions (Manel et al. 2003).

Chinook Salmon have specific requirements for spawning habitat that are characterized by streamflow, water depth, gradient, and other variables (Reiser and White 1988; Bjornn and Reiser 1991; DeVries 1997; Geist and Dauble 1998; Moir and Pasternack 2010). Geomorphic processes that affect spawning habitat are constrained by the hierarchical properties of nested catchments within drainage basins (Miller et al. 2008). Therefore, site-specific variation is associated with the position of habitat in the network and may be a predictor for genetic structure at the reach scale. However, salmonids may undergo different costs that occur en route when traveling within the network (e.g., between spawning and overwintering habitat, or dur-

ing upstream migration). The cumulative effect of riverscape variables, both site specific and en-route, should be considered in assessments of spatial genetic structure.

Fall-run Chinook Salmon are a genetically distinct phenotype that spawn in river main stems and tributaries, returning from September to December and spawning from late October through January (Moran et al. 2013; Clemento et al. 2014; Davis et al. 2017). The primary objective of this study was to assess whether riverscape indicators (e.g., gradient, elevation, stream width, or stream depth) influenced observed genetic structure in fall-run Chinook Salmon, after accounting for the influence of geographic distance and network structure. The different drivers of within-run genetic structure were assessed by first testing if the geographic distance among tributaries predicted spatial genetic structure. Then, the effect of riverscape features on genetic structure was assessed using both site-based and en-route or effective distance to characterize differences. To our knowledge, this is the first time that an en-route or effective distance approach has been applied to a riverscapes genetics study.

Methods

Study Area

The Siletz River is 120 river kilometers long, with headwaters located in the Central Oregon Coast Range. Its catchment area is 523 km^2 with average annual discharge of 1,500 m^3/s (https://waterdata.usgs.gov/nwis/inventory?). The river drains principally volcanic lithology and is located in a Mediterranean climate where water flow is sourced by winter rains. Six anadromous salmon populations spawn in the Siletz River: spring and fall Chinook Salmon, summer and winter steelhead *Oncorhynchus mykiss*, Coho Salmon *O. kisutch*, and Coastal Cutthroat Trout *O. clarkii clarkii* (Davis et al. 2017). In addition to natural disturbances, historic logging and damming have made substantial and long-lasting alterations to water, sediment and wood flows, and habitat availability throughout the catchment (Miller 2010).

Environmental Layers

Combined utilities in ArcGIS 9.3, ArcMap, and NetMap were used to develop a synthetic stream layer with modeled environmental data layers in vector format of the Siletz River. NetMap is a community-supported geographic analysis platform containing standardized digital catchment data that are commonly used for analysis of freshwater systems (Benda et al. 2007). Relevant riverscape variables were selected for analysis based on review of the ecological literature, knowledge of habitat characteristics most likely to affect gene flow, and dispersal of fall-run Chinook Salmon. After assessing collinearity among variables, four riverscape variables (elevation, gradient, channel depth, and channel width), and two geographic distance variables (the path of the river between sampled reaches [waterway distance] and distance to mouth) were selected for analysis.

Dispersal requires sufficient water velocities and depths during migration to pass obstacles (e.g., waterfalls, log jams). Streamflow velocity and stream depth are two important factors that also influence formation of suitable spawning habitat for Chinook Salmon (Isaak et al. 2007; Hamann et al. 2014). However, because only one flow gauge exists on the Siletz River, this variable was not used for analysis. Channel depth (m) and channel width (m) were modeled as a power function of mean annual flow, drainage area, or precipitation (Benda et al. 2007). Gradient (m/m) was calculated from 10 m digital elevation models (DEMs). Spatial resolution used in NetMap was at a finer resolution than the spatial scale used during genetic sampling. The reach-scale descriptors of physical habi-

tat conditions, stream depth, stream width, and elevation were averaged within each genetically sampled reach for site-based analyses. To facilitate modeling of riverscape resistance (see below), stream gradient (m/m) was first standardized by dividing by the smallest observed gradient and then converted into degree (hereafter, "standardized gradient"), resulting in the lowest gradient having a value of 1.

The National Hydrography Database (www.usgs.gov/core-science-systems/ngp/national-hydrography) stream layer at 1:100,000 scale was clipped to Hydrologic Unit Code 8: 17100204, representing the Siletz and Yaquina catchments. Using the Network Analyst extension in ArcMap, waterway distance was calculated using the downstream boundary for each reach. This measure of distance follows the path of the river and is a more biologically meaningful measure than straight-line Euclidean distance for freshwater organisms.

Spawning Surveys and Genetic Data Collection

Tissue samples were removed from carcasses of fall-run Chinook Salmon by the Oregon Department of Fish and Wildlife Coastal Chinook Research and Monitoring Program (CCRMP) during yearly spawning surveys in 2011 and 2012. The long-term CCRMP survey consisted of 34 adjacent reaches that were distributed throughout the Siletz River and identified by upstream and downstream Global Positioning System coordinates. Although all reaches were sampled, tissue samples were successfully collected from carcasses within only 23 reaches. Furthermore, reaches that had low sample sizes ($N < 9$) were combined with samples from an adjacent reach where appropriate, but samples were not combined if the adjacent reach spanned a confluence. Therefore, a total of 17 reaches were used in the final analysis (Figure 4). Tissue samples were assigned to a reach according to the downstream boundary of the reach where each carcass was collected. Spatial locations for combined reaches were assigned the downstream reach boundary of the upstream reach, representing an approximate midpoint (shared middle boundary) of the two adjacent reaches (Figure 4).

Genetic Analysis and Population Structure

Genotyping and genetic differentiation of Chinook Salmon in the Siletz River was previously described using 11 neutral microsatellite markers (Davis et al. 2017). Neutral microsatellite markers are not known to be associated with phenotypic expression and are considered to be selectively neutral. Therefore, they may be used to infer demographic processes that have shaped population structure (Holderegger et al. 2006; Kirk and Freeland 2011). This riverscape genetics analysis was conducted using the neutral microsatellite marker genotype data set of fall-run Chinook Salmon from Davis et al. (2017) containing 540 fall-run Chinook Salmon.

Characterization of genetic diversity among loci was evaluated using allelic richness (A_r), a measure of allelic number that corrects for unequal sample sizes using a rarefaction method with HP_RARE (Kalinowski 2005). Observed (H_o) and expected (H_e) heterozygosity were calculated in GenAlEx (Peakall and Smouse 2012).

Population structure is popularly estimated using the fixation index (F_{ST}). Interpretation of the index becomes difficult because it is calculated from estimates of heterozygosity (Weir and Cockerham 1984). Therefore, maximum values are strongly constrained to near zero when the number of alleles per locus is high (Meirmans and Hedrick 2011). Several alternate models have been proposed, including Jost's D (D_{est}), that do not rely on heterozygosity (for details see Gerlach et al.

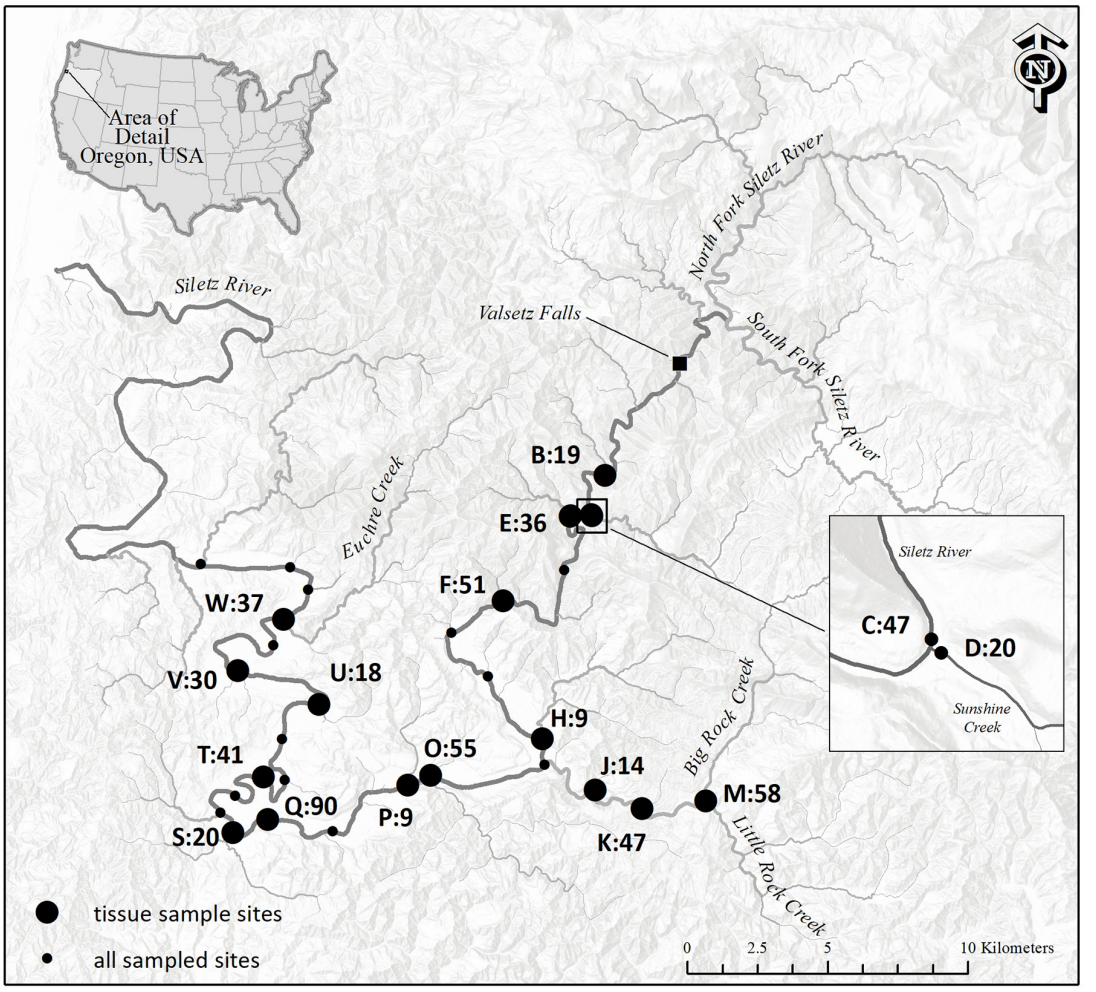

Figure 4. Map of the Siletz River and study reach locations, Oregon. Gray lines represent the main stem and tributaries, black dots represent the downstream boundary of each reach, and numbers represent sample size.

2010; Jost 2008; Meirmans and Hedrick 2011; Whitlock 2011). D_{est} is calculated from the effective number of alleles (Jost 2008), thus allowing a slightly different interpretation of genetic distance. The use of F_{ST} and D_{est} together in this study provides measures of genetic distance that are based on different components of genetic diversity at the spatial resolution of a stream reach. Pairwise genetic distance values were calculated in the program GenAlEx with 1,000 permutations to determine if the values differed significantly from zero, an indication that populations may be genetically distinct (Peakall and Smouse 2012).

Riverscape Genetics of Chinook Salmon

Characterization of genetic diversity was completed in a prior study of Chinook Salmon population genetics in the Siletz River (Davis et al. 2017). The authors found no deviations from Hardy–Weinberg equilibrium, null alleles, or allelic dropout, and further descriptions of microsatellite markers are detailed

in that publication. Therefore, we evaluated two hypotheses to explore the relationship between spatial genetic structure and habitat heterogeneity. Each hypothesis evaluated if correlations were best explained through geographic distance or riverscape variation.

Hypothesis 1: isolation by distance.—Within the IBD framework, we predicted that genetic distance would increase with increased waterway distance between reaches, similar to relationships found in larger catchments (Dionne et al. 2008; Petrou et al. 2014). Significance was assessed by Mantel tests (Guillot and Rousset 2013) and multiple regression on distance matrices (MRDM; Lichstein 2006; Oksanen et al. 2015) using the 'ecodist' package in R (Goslee and Urban 2007; R Core Team 2016). Multiple regression on distance matrices was applied with 10,000 permutations to test for significant relationships between a dependent matrix (F_{ST} and D_{est}) and one or multiple predictor matrices (Lichstein 2006). To identify the contribution of each explanatory variable to the overall fit of the model, each dependent matrix was unfolded into vectors that represented pairwise waterway distances. A regression was performed between the response variable and each predictor. Statistical significance was interpreted through permutations. Mantel tests also have been used to compare distance matrices but have received criticism in landscape genetics literature because of elevated risk of type-1 error (Castellano and Balletto 2002; Legendre and Fortin 2010; Diniz-Filho et al. 2013; Guillot and Rousset 2013). Mantel tests were used to provide a comparison among analytical methods, but because results of partial Mantel tests showed similar relationships among models, only MRDM results are presented.

Hypothesis 2: isolation by resistance.—The hypothesis that gene flow is limited by reach-specific spawning habitat conditions was evaluated by examining the differences among reaches in elevation, stream width, and stream depth. Dissimilarity matrices were calculated as the difference between measurements, $x_i - x_j$, where x represents an environmental predictor variable (e.g., stream depth) and sample reaches were represented by i and j. The relationship of genetic distance (i.e., F_{ST} and D_{est}) with waterway distance between reaches was quantified using pairwise measures of genetic distance calculated as linearized (index * [1 – index]–1) values. The correlation between genetic distance and each riverscape variable was quantified individually in three univariate models. Significance among models was assessed as described above. Next, the model with the largest significant R^2 (MRDM) was re-evaluated for significance after accounting for waterway distance between reaches to further evaluate the effect of the predictor while holding waterway distance constant.

In addition to spawning reach conditions, a riverscape genetic approach was used to evaluate the costs associated with traveling between reaches because these costs may also be functionally important components of genetic structure. To do so, we used an integrated network model where edges between reaches represented effective distance (Figure 3). Our approach adapts the effective distance approach from landscape genetics (Figure 1) but is also informed by considerations of current flow in graph theoretic networks as applied in seascape genetics (Figure 2). Increased travel costs were hypothesized to be associated with steeper gradients because steeper gradients maintain faster flows and therefore require more energy to navigate than a river distance with gradual gradients. Model optimization techniques were employed that were similar to approaches used in landscape genetics analysis (Epps et al. 2007; Castillo et al. 2014; Bowlby et al. 2016). The appropriate biologically relevant range or cut-off values for individual variables were determined by

testing a wide range of parameters for each model against genetic structure. Therefore, five candidate models were developed to evaluate the hypotheses that steeper or gradual gradients increased resistance to dispersal. A power function modeled as x^y, where x = standardized gradient and y = 0.001, 0.01, 0.1, 1.0, 1.5, was used to produce transformations of gradient. Transformations included a linear increase, an exponentially increasing relationship between resistance and gradient, and a steep initial increase in resistance with increasing gradient followed by a plateau. Transformed gradients were multiplied by the length of a stream unit as it occurs in NetMap and summed along the shortest path to quantify effective distance (Shirk et al. 2010). The shortest path was identified from a river network designed using the Network Analysis and Visualization library and package 'igraph' (R Core Team 2016; Csardi and Nepusz 2006). A pairwise matrix representing cumulative gradient along the shortest path between reaches was compared against pairwise genetic distance. Significance among models was assessed as described above. Univariate tests identified which of the five gradient models were the best predictors of genetic distance. Models were re-evaluated to identify if correlations changed after accounting for the waterway distance between reaches, as described above.

Results

Genetic Analysis

Allelic richness had a mean value of 7.5 that ranged from 7.3 (site J) to 7.8 (site H; Figure 4). Allelic richness was not influenced by distance from the river mouth (Figure 5). Observed heterozygosity had a mean value of 0.85 and ranged between 0.83 (site J) and 0.87 (sites Q and F) but was not significantly influenced by distance from mouth (Figure 5). Pairwise comparisons of genetic distance for both indices ranged between <0.01 and 0.02 ($p < 0.05$; Table 1).

Isolation by Distance and Resistance

Genetic structure was not influenced by waterway distance between reaches (Table 2). However, genetic distance was influenced by elevation (Figure 6). Differences in elevations of sampling locations were correlated with greater genetic differentiation as measured by D_{est} ($R^2 = 0.11$, $P < 0.01$) but not linearized F_{ST} ($R^2 < 0.001$, $P = 0.90$), both as a univariate model and after controlling for waterway distance in a bivariate model (Table 2).

Path-based measures of river characteristics also influenced genetic distance as assessed through a riverscape genetics approach (Figure 7). Model optimization by MRDM showed that for univariate models, steeper channel gradients were more resistant to gene flow as measured by D_{est} ($grad^{1.0}$, $R^2 = 0.11$, $P < 0.001$; $grad^{1.5}$, $R^2 = 0.13$, $P < 0.001$; Table 3). When the gradient model was re-evaluated for correlation with genetic distance after accounting for waterway distance, the multivariate model including $grad^{1.5}$ still displayed significant correlation ($R^2 = 0.14$, $P < 0.01$), indicating that the relationship with gradient was not an artifact of distance. As with results from reach-specific comparisons, linearized F_{ST} did not show significant relationships in any model.

Discussion

This study highlights the importance of a comprehensive RG approach to understand the effects of the environment on genetic variation. Using a more typical analytical framework of differences among reaches, we found that genetic variation was influenced by differences in spawning habitat elevation. However, by incorporating continuous-path analysis in RG, we were able to further identify effects of resistance resulting from the

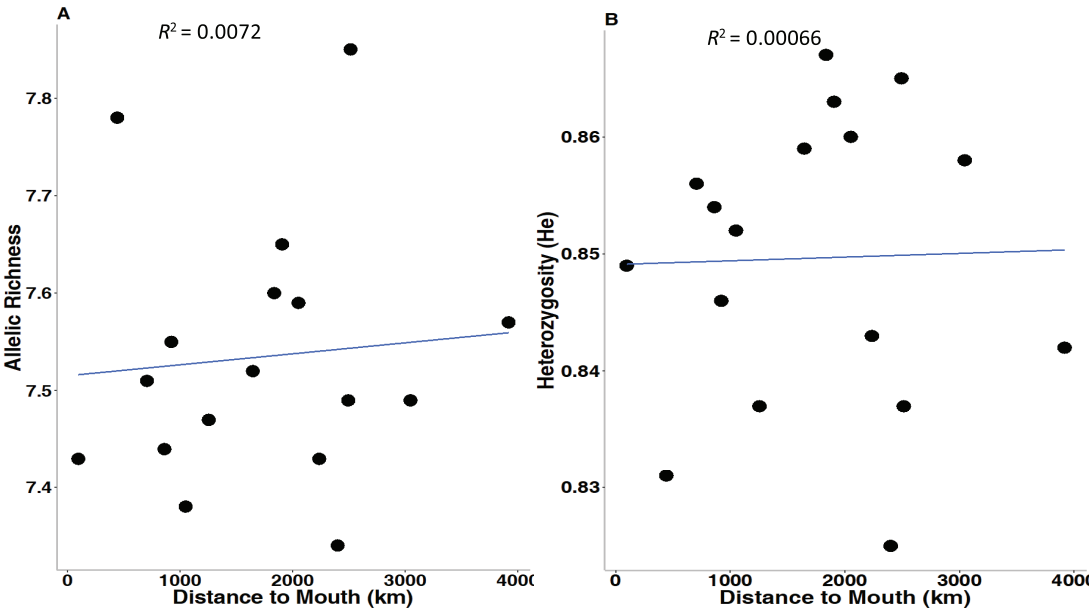

Figure 5. **(A)** Allelic richness and **(B)** expected heterozygosity (H_e) versus distance from Siletz River mouth for each reach.

cumulative effect of gradient incurred en route to spawning habitat. Salmon that traveled through habitat with steeper gradients to spawn in reaches that were at higher elevations were more genetically distinct from those individuals spawning at lower-elevation reaches that required traveling through lower-gradient areas.

Our approach calculated an effective distance based on changes in gradient, and to our knowledge, this is one of the few studies that has begun to explore the contributions of resistance (beyond barriers) on genetic distance that are accrued during upstream migration. However, challenges remain in RG because of the limited statistical tools available for evaluating relationships that capture river flow direction in analyses.

It is worth noting that the interpretation of spatial genetic variation differed between the two indices of genetic diversity that we evaluated. F_{ST} did not resolve spatial genetic variation in fall-run Chinook Salmon, but D_{est} did identify significance resulting from riverscape features. There was an abundance of low D_{est} values that approached zero, which may have affected the interpretation and inference of spatial genetic relationships from a statistical perspective. However, given the simplicity of the Siletz catchment and the connectivity among spawning groups, it is expected that low values would result. Indeed, our approach highlights the power of the RG approach, even when genetic structure is weak. These metrics (F_{ST} and D_{est}) are not interchangeable and describe different components of genetic diversity, highlighting the importance of evaluating the underlying genetic relationships that are used to calculate each index given the hypotheses being tested within each study.

On the Use of Isolation of Distance and Isolation by Resistance Models in Riverscape Genetics

Previous studies that have assessed spatial genetic structure of salmonids within and among catchments using the classical IBD

Table 1. Pairwise genetic distance between fall-run Chinook Salmon sampling locations. Pairwise estimates of linearized Jost's *D* (D_{est}; above diagonal) and linearized fixation index (F_{ST}; below diagonal) for all population pairs. Significant ($p < 0.05$) D_{est} values are in bold.

	B	C	D	E	F	H	J	K	M	O	P	Q	S	T	U	V	W
B		0.020	<0.001	<0.001	0.001	<0.001	<0.001	<0.001	0.007	<0.001	<0.001	<0.001	<0.001	0.019	0.007	<0.001	<0.001
C	0.011		**0.030**	**0.021**	**0.018**	<0.001	<0.001	0.009	**0.025**	0.007	0.018	**0.019**	0.018	**0.029**	0.005	0.011	**0.018**
D	0.012	0.012		<0.001	<0.001	<0.001	0.013	<0.001	<0.001	0.014	<0.001	0.005	0.000	0.008	0.012	<0.001	0.013
E	0.010	0.008	0.009		0.012	<0.001	<0.001	<0.001	0.010	0.003	<0.001	0.009	0.018	0.030	0.000	0.003	0.004
F	0.009	0.007	0.009	0.007		<0.001	0.006	<0.001	0.004	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.008
H	0.018	0.016	0.016	0.015	0.012		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
J	0.014	0.010	0.016	0.011	0.012	0.020		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
K	0.009	0.006	0.009	0.006	0.004	0.014	0.009		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
M	0.009	0.007	0.008	0.007	0.005	0.013	0.011	0.005		0.012	<0.001	0.011	<0.001	0.006	<0.001	<0.001	0.017
O	0.008	0.006	0.010	0.006	0.005	0.013	0.008	0.004	0.006		<0.001	0.001	<0.001	<0.001	<0.001	<0.001	<0.001
P	0.018	0.019	0.019	0.016	0.015	0.019	0.020	0.015	0.016	0.014		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Q	0.007	0.006	0.008	0.006	0.004	0.014	0.009	0.003	0.005	0.004	0.012		0.001	<0.001	0.000	<0.001	<0.001
S	0.012	0.010	0.011	0.011	0.009	0.016	0.014	0.009	0.008	0.008	0.018	0.008		<0.001	0.006	<0.001	0.002
T	0.012	0.008	0.010	0.009	0.005	0.015	0.011	0.005	0.006	0.005	0.015	0.004	0.008		0.004	<0.001	0.004
U	0.014	0.010	0.014	0.009	0.009	0.018	0.013	0.010	0.009	0.008	0.017	0.009	0.014	0.011		<0.001	<0.001
V	0.010	0.008	0.010	0.008	0.005	0.014	0.010	0.005	0.006	0.005	0.015	0.005	0.008	0.006	0.011		<0.001
W	0.010	0.008	0.011	0.007	0.007	0.014	0.011	0.006	0.007	0.005	0.015	0.005	0.010	0.007	0.009	0.007	

Table 2. Models of pairwise genetic distance (linearized D_{est} and F_{ST}) as a function of pairwise difference between riverscape variables measured at each reach using multiple regression on distance matrix. Riverscape variables: WD = waterway distance between reaches, elev = elevation, width = stream width, and depth = stream depth. Asterisk (*) represents significant values.

	D_{est}				F_{st}			
	Coefficient	*P*-value	R^2	*P*-value	Coefficient	*P*-value	R^2	*P*-value
Index ~ WD	2.41E-08	0.6514	<0.01	0.6514	<0.00001	0.60	<0.01	0.60
Index ~ depth	3.28E-03	0.3537	<0.01	0.3537	<0.001	0.99	<0.01	0.99
Index ~ width	4.96E-05	0.5833	<0.01	0.5833	−1.04E-07	1.00	<0.01	1.00
Index ~ elev	5.28E-05	<0.01	0.11	<.01*	<0.001	0.90	<0.01	0.90
Index ~ elev(WD)			0.12*	<.01*			0.004	0.90
Int	0.001	0.93			0.009	0.71		
elev	6.10E-05	<0.01			−8.3E-07	0.95		
WD	−5.23E-08	0.3			<0.001	0.62		

framework have established waterway distance as a consistent predictor for observed genetic isolation with genetic distance measured primarily by F_{ST} (Gomez-Uchida et al. 2009; Meeuwig et al. 2010; Petrou et al. 2014; Harris et al. 2015). However, these relationships are commonly identified among groups at spatial extents that spanned thousands of kilometers and included multiple catchments (Castric et al. 2001; Ozerov et al. 2012; Bowlby et al. 2016). Olsen et al. (2010) determined that differences in spatial genetic structure as measured by F_{ST} for Chinook Salmon in the Yukon, Kuskowim, and Nortin River watersheds was influenced by the number of major drainages and flow velocity. The authors also

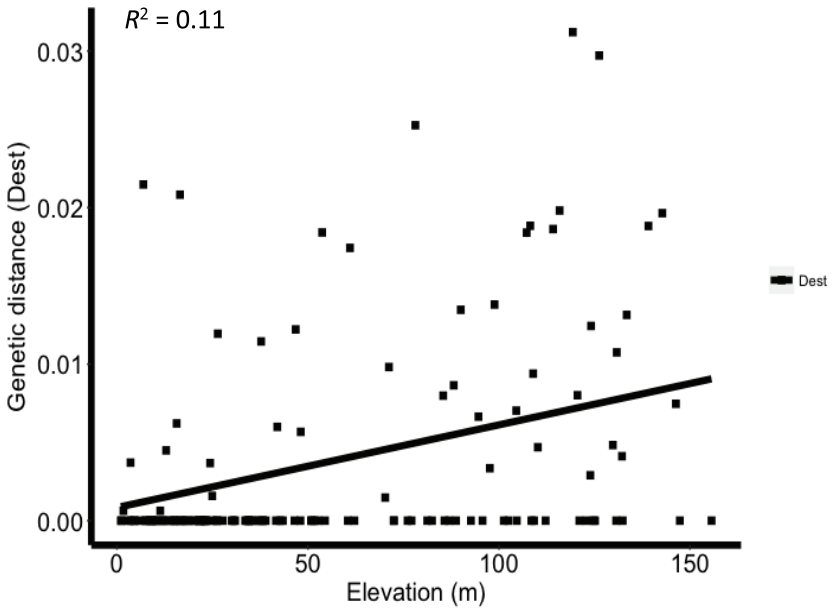

Figure 6. Elevation versus genetic distance between all possible pairs of reaches.

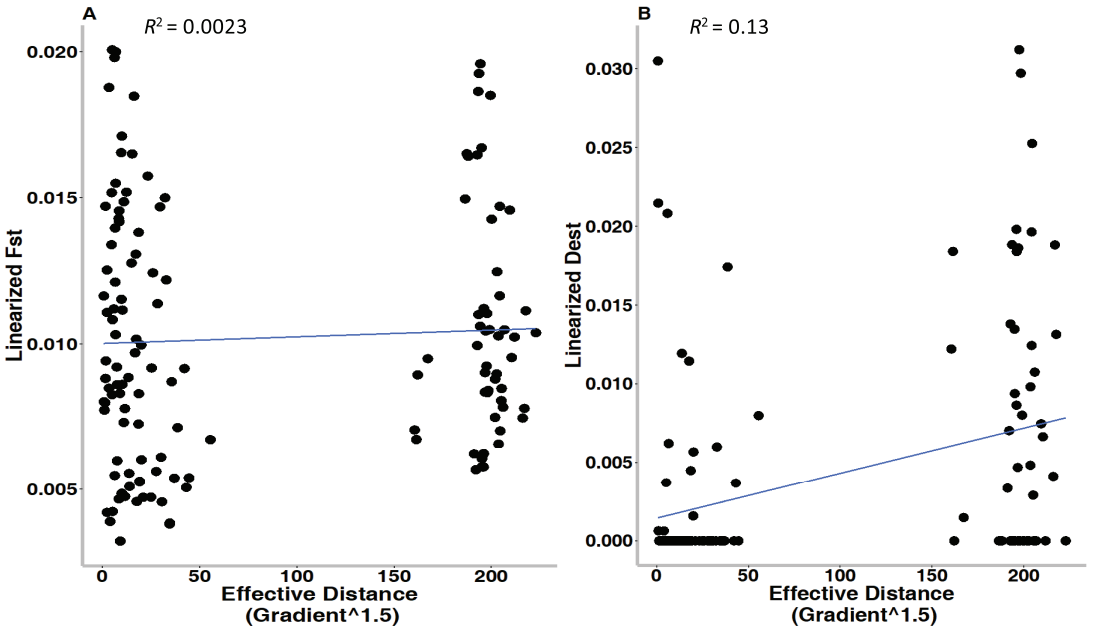

Figure 7. Genetic distances (**[A]** linearized F_{ST}; **[B]** D_{est}) versus effective distances estimated between all possible pairs of reaches. Effective distance, in this case, is a power function transformation of standardized gradient multiplied by the length of stream segment and summed along the shortest path. The gap within each figure results from data transformation where effective distances are not present within the river. Results indicate that effective distance for F_{ST} is relatively flat, whereas effective distance increases for D_{est}.

found that relationships were not maintained at intermediate spatial extents and riverscape indicators did not explain genetic structure better than geographic distance (Olsen et al. 2010). Likewise, similar patterns between isolation by resistance (IBR) and IBD have been identified at large and small spatial extents among Rocky Mountain Sculpin *Cottus* sp. populations in Alberta, Canada. Ruppert et al. (2017) described genetic structure among drainages within the species' eastern range using F_{ST}. The authors found significant IBD was identified across multiple catchments, but at a small spatial extent (i.e., within Lee Creek or St. Mary River). The difference in elevation among sites (IBR) was also a predictor of spatial genetic variation in some, but not all, catchments (Ruppert et al. 2017). The complexity of interactions between IBD and IBR highlights the need for continued investigation of specific riverscape features on spatial genetic variation at multiple spatiotemporal scales and extents. Tools and methods being developed for riverscape genetics analysis will help identify how riverscapes facilitate or impede genetic exchange and resolve patterns of genetic structure (Landguth et al. 2012; Davis et al. 2018).

Incorporating Network and Spatial Extent in Riverscape Genetics

Although the spatial structure of riverine systems influences connectivity and consequently affects dispersal, many of the relationships between the physical network, population distribution, and genetic structure are not well understood (Le Pichon et al. 2006; Leps et al. 2015). Thinking about the riverscape as a branched network of interconnected tributaries is an advancement in riverine ecology

Table 3. Models of pairwise genetic distance (linearized D_{est} and F_{ST}) as a function of cumulative gradient using multiple regression on distance matrix. WD = waterway distance between reaches; grad. = gradient. Asterisk (*) represents significant values.

	D_{est}				F_{st}			
	Coefficient	*P*-value	R^2	*P*-value	Coefficient	*P*-value	R^2	*P*-value
Index ~ grad$^{0.001}$			0.03	0.12			0.01	0.51
Integer	1.70E-03	0.93			0.01	0.26		
gradient	1.03E-07	0.12			<0.001	0.51		
Index ~ grad$^{0.01}$			0.03	0.12			0.01	0.5
Integer	1.73E-03	0.92			0.01	0.26		
gradient	1.02E-07	0.12			<0.001	0.5		
Index ~ grad$^{0.1}$			0.04	0.09			0.01	0.53
Integer	1.57E-03	0.94			0.01	0.27		
gradient	8.52E-08	0.09			<0.001	0.53		
Index ~ grad$^{1.0}$			0.11*	<0.001*			<0.001	0.98
Integer	8.53E-04	0.99			0.01	0.52		
gradient	5.22E-09	< 0.01			<0.001	0.98		
Index ~ grad$^{1.5}$			0.13*	<0.001*			<0.01	0.79
Integer	1.44E-03	0.99			0.01	0.62		
gradient	2.88E-10	<0.01			<0.001	0.79		
Index ~ grad$^{1.5}$ + WD			0.14*	< 0.01*				
Integer	2.50E-03	0.78						
Pwr1.5	3.13E-10	<0.001						
WD	–5.50E-08	0.35						

that is becoming increasingly incorporated into analyses (Wiens 1989; Thorp et al. 2006; Campbell Grant et al. 2007; Altermatt 2013; Borrett et al. 2014). Theoretical literature discussing connectivity in freshwater river systems has provided models and frameworks through which this scale of analysis may be accomplished (Frissell et al. 1986; Montgomery 1999; Benda et al. 2004; Campbell Grant et al. 2007; Wipfli et al. 2007; Borrett et al. 2014).

We demonstrated that IBR is detectable within a high-gene-flow population of fall-run Chinook Salmon in a relatively small catchment. We also showed that incorporating effective distance in a riverscape genetics framework helped expand interpretation of IBR by considering resistance along the path that is traveled to reach spawning habitat. Although genetic variation is weak within fall-run Chinook Salmon at the spatial extent of our analyses, the methods employed in this study highlight the usefulness of incorporating effective distance analysis into riverine research.

Research Gaps

Several options are available for calculating genetic distance. Convention and the need to make comparisons across catchments or among taxa dictate whether one or several metrics are employed. However, agreement on the best choice has not been reached (Jost 2008; Gerlach et al. 2010; Meirmans and Hedrick 2011; Whitlock 2011). Given our results, we recommend ensuring that at least F_{ST} and D_{est} are considered and compared.

There is potential for RG to provide information that would enhance our ability to identify specific catchment and riverscape features that are directly associated with population persistence. Expansion of RG methods to interpret how the environment affects genetic structure throughout the lifetime of individuals (e.g., return migration, spawning, rearing, smolting, and out-migration) would greatly improve our ability to enhance population-scale survival in freshwater habitats.

Differences between terrestrial, marine, and freshwater systems need to be explicitly considered when applying the various analytical methods available (Selkoe et al. 2016). For example, directional water flow is an important component of riverine habitats, whereas in terrestrial systems, there is no force that has a similar effect on flora and fauna (Davis et al. 2018). Directionality has yet to be integrated into existing LG and SG methods, and although it was considered in our study (results not shown), we were unable to identify any relationships. There is great potential for continued growth in the field as these challenges and others are addressed.

Geographic distance was not a predictor of genetic distance within our study, although in larger systems (i.e., greater than 1,000 km), distance is a consistent predictor of spatial variation. Given that smaller catchments may hold life history variation that is important to long-term population persistence, there is a need to understand the relationships that maintain this diversity. One component of maintaining genetic diversity is to protect the components of the watershed that contribute to gene flow. The combined context of reach-specific and effective distance variables indicated the value of a RG approach to better understand relationships among groups within the river. Continued investigation using RG at small spatial extents and incorporating network relationships are needed to reveal a better understanding of the effects of dispersal on population structure. Both are important for the conservation and management of highly migratory species.

Management Implications

Habitat fragmentation and flow changes that alter functional connectivity within riverscapes have caused increased resistance to dispersal and loss of access to suitable spawning habitat. For Pacific salmon, such physical changes have contributed to population decreases, restructuring of source-sink dynamics (Schick and Lindley 2007), and reduced range distributions (Yoshiyama et al. 1998). To combat these effects at state levels, entities like the Pacific Fishery Management Council have developed Pacific Coast Salmon Fishery Management Plans (PFMC 2016). Those plans list management objectives for Endangered Species Act-listed species, escapement goals, and catch limits and describe essential fish habitat for the management of commercial and recreational salmon fisheries. However, management at this spatial extent is based upon the status of larger, regional management units (e.g., the North Oregon Coast Chinook Salmon ESU). The ESUs are combinations of unique spawning groups from multiple, smaller river basins and do not account for finer-scale life history, genetic, and phenotypic variability that is likely present within smaller catchments (Schindler et al. 2010; Davis et al. 2017). Effective management should incorporate such diversity considerations.

Within riverscapes, geographic and hydrologic characteristics are often correlated, and identifying how each or both affect genetic structure is difficult at best. Nonetheless, the ability of conservation and management to ensure long-term viability of salmon populations or establish effective recovery strategies for any threatened species is depen-

dent on understanding how these processes affect dispersal and subsequent gene flow. Riverscape genetics methods that include network relationships would enable more informed interpretation of these fine-scale relationships, thereby ensuring the design of effective recovery strategies for Pacific salmonids in local catchments and contributing to their stability and conservation.

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