Deep-Seated Landslides Drive Variability in Valley Width and Increase Connectivity of Salmon Habitat in the Oregon Coast Range

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Research Impact Statement: Deep-seated landslides promote connectivity among seasonal habitat types — spawning, summer-rearing, and winter-refuge habitat — for Coho Salmon in the Oregon Coast Range.

ABSTRACT: Declines in populations of Pacific salmon have prompted extensive and costly restoration efforts, yet many populations are still in peril. An improved understanding of landscape-scale controls on salmon habitat should help focus restoration resources on areas with the greatest potential to host productive habitat. We investigate the contribution of deep-seated landslides (DSLs) to Coho Salmon habitat by comparing the quantity and connectivity of potential seasonal habitat observed in five streams with extensive DSLs to five lacking significant landsliding. Further, we measure valley width in these streams and relate it to connectivity. We show that median fractions of stream length identified as spawning, summer-rearing, winter-refuge habitat, and as having high connectivity among seasonal habitat types are greater in streams with DSLs and that distances between units of each seasonal habitat type are significantly lower in DSL terrain. The median R^2 value for the relationship between drainage area and valley width is lower in landslide terrain and we observed that high connectivity among seasonal habitat types tends to occur where valley width is variable. Our results suggest that DSLs promote connectivity among seasonal habitat types for Coho Salmon and that prioritizing restoration projects in streams in DSL terrain could improve the effectiveness of salmonid recovery programs.

(KEYWORDS: fish; geomorphology; fluvial processes; landslides; valley width; habitat connectivity; habitat proximity.)

INTRODUCTION

A well-accepted concept in biogeography is that landforms control the types and distribution of habitat (Swanson et al. 1988). Pacific salmon *Oncorhynchus* spp. are adapted to dynamic landscapes shaped by natural disturbance processes (Montgomery 2000). Habitat degradation and loss as well as overfishing and hatchery fish management have led to precipitous declines in wild-spawning salmonids in the Pacific Northwest (Nehlsen et al. 1991; Montgomery 2003). Declining populations prompted federal listing of multiple species in the 1990s, leading to extensive restoration efforts (OCSRI 1997) that rely on the identification of high-quality fish habitat and the processes that create it. Despite ongoing restoration efforts, populations remain unstable. Although salmon are intrinsically tied to place, watershed-scale landforms are rarely included alongside the many other factors that go into planning and implementing restoration projects. Here, we explore whether kilometer-scale hillslope processes can inform salmonid restoration priorities.

Applying the observation that the three primary controls on salmon habitat are streamflow, valley

constraint, and channel gradient, Burnett et al. (2007) developed species-specific intrinsic potential (IP) models of high-quality habitat for salmonids in Oregon Coast Range streams, United States. A multi-year study of Coho Salmon (*Oncorhynchus kisutch*) populations in multiple basins in the Oregon Coast Range over time showed that Coho Salmon IP scores predicted patterns of juvenile Coho Salmon occupancy over time (Flitcroft et al. 2014). This raises the question of what controls the distribution of areas with high IP, or more directly, what processes control valley constraint and channel gradient. Reach-scale variations in valley width relating to tributary confluences (Benda et al. 2004), and landslide deposits (May et al. 2013) are well documented, but regional and local controls on valley width remain poorly understood.

In soil-mantled landscapes, debris flows are thought to be the dominant hillslope-fluvial coupling process in channels with slopes >10%; these steep settings comprise approximately 80% of the network relief structure of the Oregon Coast Range (Stock and Dietrich 2003). Debris flows, initiated by shallow landsliding in colluvial hollows, are rapid, episodic events that scour and erode low-order valleys and can deposit large amounts of debris at tributary junctions (Benda 1990; Benda and Dunne 1997). Recurrence intervals for debris flows in second-order basins have been estimated to be a few hundred years, resulting in frequent deposition in higher order basins where numerous sources exist upstream (Benda and Dunne 1997; May and Gresswell 2004). The resulting deposits, known as debris flow fans, are persistent and prevalent features in the Oregon Coast Range and an important source of habitat-forming sediment and wood in streams (May and Gresswell 2004; Lancaster and Casebeer 2007; Miller and Burnett 2008; Kirkby 2013).

Evidence of deep-seated landslides (DSLs) is prevalent in 5%–25% of the Oregon Coast Range and occurs where Eocene Tyee turbidites with abundant siltstone layers have been exhumed and where the hillslope aspect coincides with the bedrock dip slope (Roering et al. 2005). DSLs are larger features with longer lasting, more stable geomorphic legacies that have the potential to create a much more substantial and persistent signature on valley and stream morphology than a single debris flow. DSLs have been observed to produce less-concave longitudinal profiles (Booth et al. 2013), knickpoints in longitudinal profiles (Korup 2006), wider valleys (Korup et al. 2006; May et al. 2013), and in the most extreme cases, full channel occlusion and landslide-dammed lakes (Baldwin 1958; Korup 2005). Still, little is known about the long-term effects of DSLs on fluvial processes (Korup et al. 2010). Possible initiation mechanisms

for DSLs include seismic activity, stream erosion through weak bedrock, and high groundwater levels and/or precipitation caused by a wetter climate (Baldwin 1958; Hammond et al. 2009). Although there is some evidence of DSL activity within the last 150 years (Burns et al. 2012), most of the DSLs in the Oregon Coast Range are of Pleistocene age (Hammond et al. 2009) and Hammond et al. (2009) postulated that the depth of erosion suggests that some landslides may be as old as the Pliocene. Despite the age of the DSLs, the large volume of these features implies that rivers in terrain with DSLs in the Oregon Coast Range are still reworking sediment delivered from these ancient slides.

In a recent study on Coho Salmon in the Oregon Coast Range, proximity of different seasonal habitat types (spawning, summer-rearing, and winter-refuge habitat) was found to be a better predictor of juvenile fish density than instream variables alone, highlighting the need to understand the processes that drive patterns of instream connectivity or proximity among habitats (Flitcroft et al. 2012). May et al. (2013) showed that anomalously wide valleys exist upstream from and adjacent to two discrete DSLs (isolated slope failures) and that these areas had high IP for Coho Salmon owing to the lack of valley constraint. We expand on the work by May et al. (2013) by investigating the geomorphic effects of extensive deep-seated landsliding, which we define as slope failure of the majority of hillslopes in a given watershed — a phenomenon that is prevalent in the Oregon Coast Range (Roering et al. 2005). We explore how the presence of extensive deep-seated landsliding affects valley floor width and the quantity and connectivity of seasonal habitat for Coho Salmon by comparing these metrics in five subbasins in the Umpqua River Basin with extensive DSLs to five subbasins in the Umpqua River Basin without deep-seated landsides. We hypothesize that DSLs promote variable valley width and hence a higher frequency of anomalously wide valleys and that this results in greater connectivity between seasonal habitat types.

STUDY AREA

The central Oregon Coast Range is an ideal place to study the effects of DSLs on Coho Salmon habitat because (1) landslides are abundant in an area with otherwise relatively uniform topography and lithology (Heller and Dickinson 1985) and (2) stream habitat survey data taken explicitly in light of Coho Salmon life cycle needs (Moore et al. 1997, 2007) are available from the Oregon Department of Fish and

Wildlife (ODFW) Aquatic Inventories Project (AIP) for numerous basins across the region.

We chose to conduct our study in the Umpqua River Basin because it is the basin most comprehensively surveyed for Coho Salmon habitat by the AIP in the Oregon Coast Range and limiting the study to one basin mitigates for interbasin variability at a broad scale. The Umpqua River Basin crosses through the Oregon Coast Range with a portion of the system draining from the Cascade Mountains. Therefore, we focused on the portion of the Umpqua River Basin contained in the Oregon Coast Range. Within this area, we selected all of the subbasins that met the following criteria: (1) available fish habitat survey data from a subset of years that have been subject to quality control testing (see Methods); (2) either extensive DSLs or uniformly steep and dissected (USD) valley-ridge topography (see Methods); and (3) available Light Detection and Ranging (lidar) data. This resulted in

five streams in DSL terrain (Halfway, Sand, Rock, Scare, and Yellow Creeks) and five streams without DSLs (Charlotte, Dean, Herb, Scholfield, and Sweden Creeks) (Figure 1 and Table 1). We excluded a small basin (Little Sand Creek) that is a subbasin of a larger one that we included (Big Sand Creek) because none of the other streams had surveyed tributaries.

The selected subbasins have comparable surface geology, occurring in the extensive region underlain by the Tyee Formation, an Eocene-age, relatively undeformed sandstone and siltstone layer with minimal facies variation (Heller and Dickinson 1985). Climate is temperate maritime throughout the Oregon Coast Range, and hence can be assumed to vary minimally among subbasins. Douglas-fir forest blankets the mountains, but throughout the central Oregon Coast Range stand composition has been altered by logging and land use to a landscape dominated by younger stands (Kennedy and Spies 2004). Land use
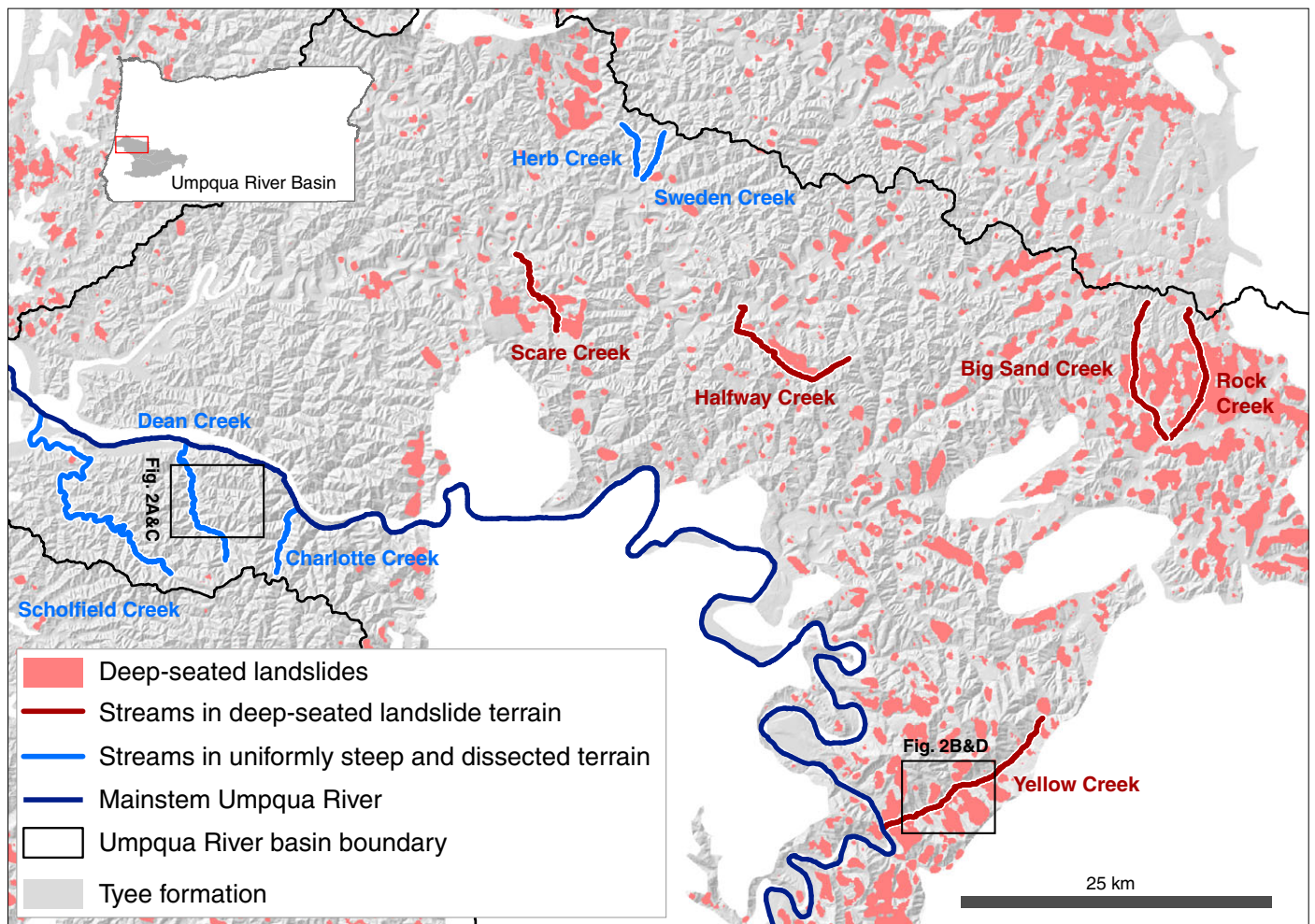

FIGURE 1. Location of the 10 streams in the Umpqua River Basin, used for an assessment of Coho Salmon habitat connectivity and the presence (or absence) of deep-seated landslides (DSLs).

TABLE 1. Study subbasins in the Umpqua River Basin.

Stream name	Drainage areas surveyed (km²)	Total drainage area in basin (km²)	Mainstem stream length surveyed (km)	Mainstem total stream length (km)	Elevation range (m)	Vegetation type	Distance to coast from outlet (km)	Mean annual precipitation (mm)	Year surveyed by AIP
Streams in USD terrain									
Charlotte Creek	0.5–9.9	9.9	5.5	5.5	1–563	Evergreen forest	28.4	2,455	1993
Dean Creek	2.5–34.4	34.4	10.9	12.1	6–1,600	Evergreen forest, Mixed forest	21.2	2,272	1994
Herb Creek	1.0–6.3	6.8	4.4	4.8	319–1,333	Evergreen forest, Mixed forest	45.0	1,814	1994
Scholfield Creek	4.9–57.8	57.8	25.3	28.4	0–537	Evergreen forest, Mixed forest, Shrub/scrub	12.2	2,008	1994
Sweden Creek	0.7–5.2	5.2	3.5	3.7	367–1,512	Evergreen forest, Mixed forest	45.5	1,779	1994
Streams in DSL terrain									
Halfway Creek	0.5–20.0	20.0	13.1	13.1	490–1,792	Evergreen forest	52.2	1,467	1994
Rock Creek	1.8–15.4	13.5	10.1	10.4	98–363	Shrub/scrub, Evergreen forest	78.5	1,255	1995
Big Sand Creek	1.1–35.3	35.3	10.8	11.3	315–1,495	Shrub/scrub, Evergreen forest	78.0	1,283	1993
Scare Creek	2.6–14.7	14.8	7.6	9.7	204–1,761	Evergreen forest, Mixed forest, Shrub/scrub	38.6	1,841	1994
Yellow Creek	0.5–50.2	52.5	15.2	15.2	245–2,458	Evergreen forest	67.3	1,220	1994

Note: AIP, Aquatic Inventories Project; USD, uniformly steep and dissected.

in the study subbasins is predominantly evergreen forest, mixed forest, and shrub/scrub (Table 1, Homer et al. 2015).

METHODS

Identifying Extensive DSLs

To locate DSLs, we used the automated algorithm developed by Roering et al. (2005) that exploits the relationship between curvature and slope that is characteristic of DSLs. We used the algorithm threshold that was shown to be consistently accurate at delineating DSL masses that were also identified using aerial photos, field observations, and topographic maps (Roering et al. 2005). Subbasins characterized as occurring in "DSL terrain" are affected by extensive deep-seated landsliding (slope failure of the majority of at least one side of the valley). These basins are less uniformly dissected by stream networks and have more irregular hillslope gradients (and broad, gentle hillslopes) than basins in the Oregon Coast Range with no DSLs (Figure 2). Subbasins chosen as controls have no slopes mapped as DSL masses and have USD valley-ridge topography. Hereafter we refer to the deep-seated

landslide terrain as DSL terrain and the control group in uniformly steep and dissected terrain as USD terrain.

Identifying Potential Seasonal Habitat and Calculating Habitat Connectivity

Seasonal habitat data were acquired from the ODFW AIP. The AIP provides quantitative data on stream habitat conditions for Oregon streams. The survey methods employed by the AIP involve systematically identifying and measuring stream geomorphic features in the field as the surveyors walk upstream. Different habitat units are identified (i.e., pool, riffle, glide) and characteristics of substrate are estimated while modal depth is measured. Channel width and unit length were measured every 10th habitat unit providing a means to calibrate all estimated lengths. Geomorphic features and measurements are georeferenced, allowing for distance downstream and habitat unit lengths to be calculated in a geographic information system (GIS) (Moore et al. 1997, 2007). A robust literature using AIP field survey data has demonstrated the relevance and utility of this methodology to explain patterns of Coho Salmon occupancy (Steel et al. 2012; Flitcroft et al. 2014), to describe relationships between instream habitat and landscape conditions (Anlauf et al. 2011),
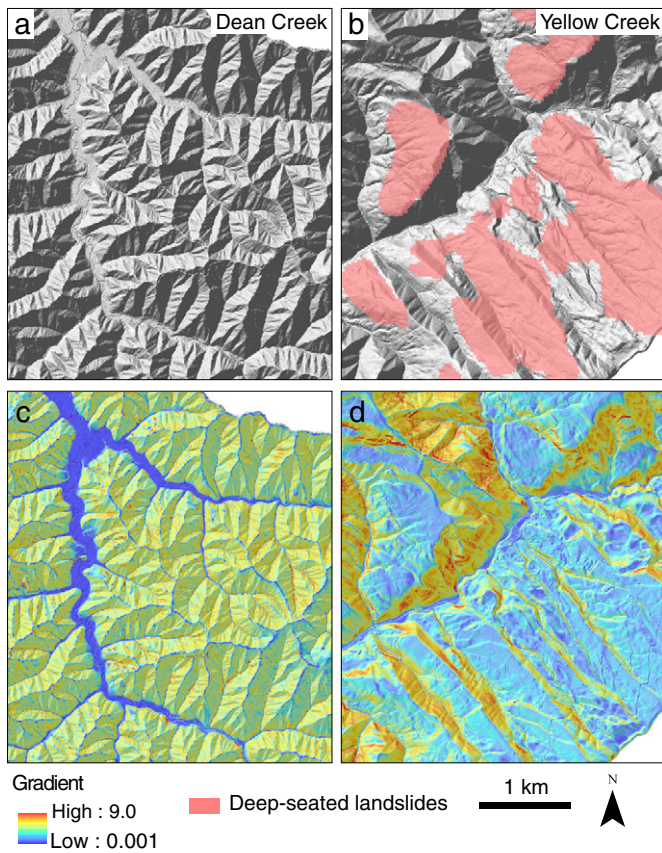
FIGURE 2. Examples of USD terrain (a, c) and terrain shaped by DSLs (b, d). (a) Hillshade of Dean Creek. (b) Hillshade of Yellow Creek with DSLs shown in light red. (c) Gradient of Dean Creek with USD hillslopes. (d) Gradient of Yellow Creek with irregular and overall low hillslope gradients. See extent indicators in Figure 1 for locations.

TABLE 2. Criteria used for characterizing habitat units as potential Coho Salmon seasonal habitat types from the Oregon Department of Fish and Wildlife AIP stream survey data.

Potential habitat type	Criteria
Spawning habitat	Riffles with ≥50% gravel and ≤8% silt/organics
Summer-rearing habitat	Pools with residual pool depth (depth minus pool tail crest depth):
	≥0.5 m deep in streams <7 m wetted width
	≥0.6 for streams 7–15 m wetted width
	≥1 m deep in streams >15 m wetted width
Winter-refuge habitat	Habitats identified peripheral to, or off the mainstem that become slower water-refuge habitats during high-flow events: backwaters, alcoves, and isolated pools

survey training occurs annually, there is always some level of uncertainty among survey professionals. Performance of the AIP survey methodology compares similarly with respect to other habitat survey programs for repeatability and accuracy of measurements (Roper et al. 2010). Concern regarding inconsistency of field measurements in field habitat surveys has been presented in the literature generally, and regarding sediment (Olsen et al. 2005; Faustini and Kaufmann 2007) and habitat typing in particular (Poole et al. 1997). For the purposes of our research, the evidence that the AIP surveys are generally strong at identification of habitat types (Roper et al. 2010), and that pool depth was a measured attribute, made this dataset adequate to the main purpose of our effort (Table 2). Development of stream habitat survey methods with high repeatability and consistency are being developed with remotely sensed tools (i.e., green lidar), but are not currently available.

Coho Salmon use different habitats seasonally in response to life-stage needs (Groot and Margolis 1991; Nickelson et al. 1992). In the autumn, spawning Coho Salmon lay their eggs in riffles in the interstitial spaces in gravel. After they hatch, Coho Salmon fry migrate to slow water to feed, grow, and seek thermal refuge during the summer. In the winter, off-channel habitat provides refuge from high-flow events. Based on these life cycle needs (Groot and Margolis 1991), adequate potential habitat for Coho Salmon for spawning, summer-rearing, and winter-refuge can be identified by querying the stream survey data for specific criteria. We identified habitat variables known to be biologically relevant for different life stages (sensu Flitcroft et al. 2014; Flitcroft et al. 2016). Coho Salmon are known to need gravel for spawning (Groot and Margolis 1991; Bilby and Bisson 1998). Fine-grained sediment is known to decrease juvenile survival to emergence (Bryce et al. 2008, 2010) and off-channel habitat has been identified as important refuge for juveniles to survive

and to understand patterns of juvenile Coho Salmon habitat use (Steel et al. 2016).

In this study, we utilize AIP instream habitat data on habitat units, residual pool depth (maximum pool depth minus pool tail crest, e.g., Hilton and Lisle 1993), and percent cover of silt/organics. Comprehensive, census-style stream habitat survey data that captures stream conditions during a similar window of time across a basin are rare. We were able to acquire survey data for this study that were collected during mid-summer (July–August) 1993–1995. Ideally, we would have used field data collected synchronously with available lidar imagery used in the geomorphic assessment of valley width. While there is a gap between the time of the field survey and lidar data acquisition, the geomorphic features captured by lidar are likely to be semipermanent geomorphic features with respect to instream habitat. Therefore, the "snapshot" of stream conditions collected by the field survey is still relevant to explore relationships between geomorphic conditions and fish habitat. Although stream survey methods are systematic and

winter storm events (Nickelson et al. 1992). Evaluation of the AIP field survey dataset allowed us to identify habitat characteristics that would generally represent these life-stage habitat needs (Table 2). The percent cover of silt/organics is assessed visually and, given the low threshold needed for a unit to qualify as potential spawning habitat (Table 2), is therefore a source of uncertainty in our analysis. To address this uncertainty, we include a secondary analysis using a threshold of 16% silt/organics to identify potential spawning habitat.

Connectivity between seasonal habitats is as important as habitat quality for individual life stages of Coho Salmon (Flitcroft et al. 2012). Therefore, we calculated the distance from each surveyed habitat unit to each of the nearest types of seasonal habitat. Because each habitat unit is a unique length, we included the length of the unit in question (Figure 3) such that the resulting distance represents the maximum distance a fish would have to travel between habitat units. Although the actual distance a fish might travel could be shorter, especially in the case of long habitat units, this approach reduces the potential to overestimate connectivity. This approach does not capture interannual variation of water depth or chemistry that have the potential to alter connectivity among sites (i.e., shallow water limiting passage).

We based our assessment of habitat proximity on the maximum recorded distance of 234 m traveled by juvenile Coho Salmon in the summer (Kahler et al. 2001). Therefore, we identified potential spawning habitat and potential summer-rearing habitat that were less than 250 m apart and classified habitat units between them as part of a high-connectivity reach (Figure 3). Juvenile Coho Salmon are observed to exhibit high fidelity to winter-refuge habitat (Bell et al. 2001; Ebersole et al. 2006). However, in other portions of their range, juvenile Coho Salmon are

known to move extensive distances for feeding coincident with available food sources and thermal conditions (Armstrong and Schindler 2013). In the Oregon Coast Range, Flitcroft et al. (2012) observed that juvenile fish abundances in summer were substantially higher at sample sites that were within 500 m from spawning, summer, or winter habitat. Thus, we classified units of a high-connectivity reach that also had potential winter-refuge habitat within 250 m, as well as the units connecting the high-connectivity reach with the winter habitat, as part of a "comprehensive patch" (Figure 3). The choice of 250 m in these calculations results in comprehensive patch distances between potential summer-rearing and potential winter-refuge habitat below 500 m, thus within the threshold observed by Flitcroft et al. (2012). To determine whether our results were dependent on the distances chosen for the analysis, we performed the same calculations with half the original distances (125 and 250 m) and twice the original distances (500 m and 1 km) (see Supporting Information). The algorithm used to calculate minimum distances to each type of potential seasonal habitat and resulting connectivity among habitat types is available as Supporting Information.

For each stream, we summed stream length for each potential seasonal habitat resulting in three datasets. Additionally, we summed stream length characterized as a high-connectivity reach (linking potential spawning and summer-rearing habitat), or as a comprehensive patch (connectivity among all three seasonal habitats). We then calculated the fraction of total stream length for each of these, resulting in two more datasets. We grouped streams as occurring in DSL terrain or USD terrain and observed that the grouped fractions of stream length were not normally distributed. We tested for equal variances using a Brown–Forsythe test and used a Mann–Whitney–Wilcoxon test on datasets with equal variance to determine whether differences between groups were statistically significant ($\alpha = 0.05$). The Mann–Whitney–Wilcoxon test is a nonparametric statistical test that does not assume normal distribution but does assume equal variance. The Mann–Whitney–Wilcoxon also assumes independence, an assumption that may be violated by spatial autocorrelation given the proximity between some sample streams. Given that we selected all subbasins that met the criteria presented above, eliminating streams based on proximity to other study subbasins would have severely limited the number of samples in each group. We report and compare the median and the median absolute deviation (MAD) for each group of streams for each category assessed.

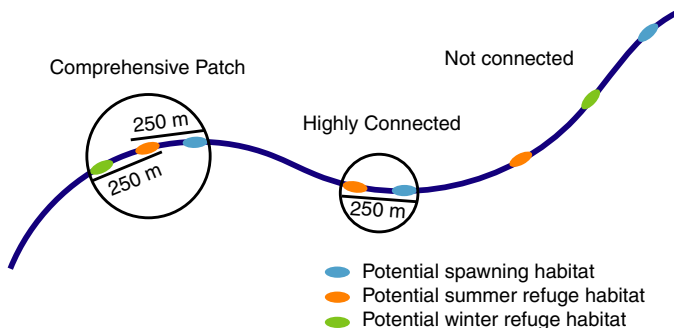To explore how the distribution of potential seasonal habitat types differs between groups, we

FIGURE 3. Characterization of potential seasonal habitat connectivity. Habitat units connecting potential spawning habitat with potential summer habitat were characterized as having high connectivity if the spawning and summer habitats were within 250 m of each other. If potential winter-refuge habitats were within 250 m of any of the high-connectivity units, all the connected habitat units were characterized as a "comprehensive patch."

compared the distances to the nearest type of each potential seasonal habitat. For all habitat units in each stream, we calculated the distance to the nearest potential spawning, summer-rearing, and winter-refuge habitats. We combined all the minimum distances for each group for each seasonal habitat type such that each group (USD and DSL) had three datasets of minimum distances. Although these six datasets were not normally distributed, the sample sets were large enough ($n = 1{,}083$ and $2{,}902$ for USD and DSL streams, respectively) such that a two-sample unpaired t-test was appropriate to determine if the minimum distances differed significantly ($\alpha = 0.05$) between groups for each seasonal habitat type. We used a Welch's t-test, an alternative to the Student's t-test that does not assume equal variances. We report the mean with the results of the t-test as well as the median and MAD.

Measuring Valley Floor Width

We used 1-m resolution airborne data (lidar), acquired from the Oregon Department of Geology and Mineral Industries, to measure valley floor width in a GIS. We first used a 15×15 m moving window algorithm to smooth the lidar and calculate gradient from a fitted second-order polynomial (Wood 1996) (Figure 2c, 2d). Smoothing resulted in less variability in slope such that the valley–hillslope transition was easily defined by a break in slope (Figure 2c, 2d). Using a combination of the gradient layers and hillshades derived from the lidar in a GIS, we manually measured the valley widths along the mainstem every 100 m in all subbasins at cross sections perpendicular to the valley walls. We used an eight-direction model to route flow on unsmoothed lidar in order to calculate drainage area at each point. In all study subbasins except Scholfield Creek, we measured valley widths from a drainage area of 1 km^2 to the same downstream drainage area as AIP survey data, which in all basins starts at the stream's confluence with a larger river (generally either the mainstem Umpqua or the North Fork Smith). In Scholfield Creek, we measured valley widths only above the head of tide to avoid conflating hillslope processes with coastal processes.

Valley widening may occur at tributary junctions from the accumulation of flood or debris flow deposits (Benda et al. 2004). Because extensive DSLs can influence the number and location of confluences, to avoid conflating landslide effects on confluences with landslide effects on valley width, we excluded all points where valleys were wider at confluences as well as points upstream or downstream that fell where valleys remained anomalously wide. Thus, our valley width measurements only reflect the direct effect of DSLs on the width of the primary valley. Large confluences resulted in more skipped points and small confluences resulted in a negligible number of excluded points. To understand how the exclusion of these data may have influenced our results, we documented the fraction of stream length where valley width measurements were bypassed because of confluences and tested whether the fractions differed significantly between groups with a Mann–Whitney–Wilcoxon test ($\alpha = 0.05$). Further, we characterized high-connectivity reaches and comprehensive patches as being associated with a confluence if the reach/patch began at a measurement that was excluded because of confluence effects and did not extend more than 200 m upstream or downstream of the confluence.

Using the same groupings of streams as were used for the analysis of potential seasonal habitat (streams in USD terrain vs. those with DSLs), we assessed whether the relationships between valley floor width and drainage area differed between the two groups. First, we fit power functions to the relationships between valley floor width and drainage area for each stream. Because measurements were made along mainstems, the R^2 value of the best-fit power function reflects longitudinal variability in valley width and the exponent of the best-fit power function reflects how rapidly valley width changes as drainage area increases or decreases. The distributions of valley width-drainage area R^2 values and valley width-drainage area exponents are both non-normal. We tested for equal variance using the Brown–Forsythe test and, because variances were not significantly different (see Results), we used a Mann–Whitney–Wilcoxon test to determine if values were significantly different between groups ($\alpha = 0.05$).

At each valley width measurement, we recorded whether a high-connectivity reach or a comprehensive patch crosses the point in question and whether valleys are wider than the best-fit power function for drainage area-valley width predicts. To investigate the parameters that influence connectivity, we plotted the relationships between the fractions of stream length characterized as high-connectivity reaches and comprehensive patches and the R^2 values of the best-fit power functions, the exponents of the best-fit power functions, and the median minimum distances to potential spawning, summer-rearing, and winter-refuge habitat.

Lastly, to explore whether basin size influenced our results, we used a Brown–Forsythe test for equal variance and, because variances did not differ significantly between groups (see Results), a Mann–Whitney–Wilcoxon test to determine if the selected basins differed significantly ($\alpha = 0.05$) in size
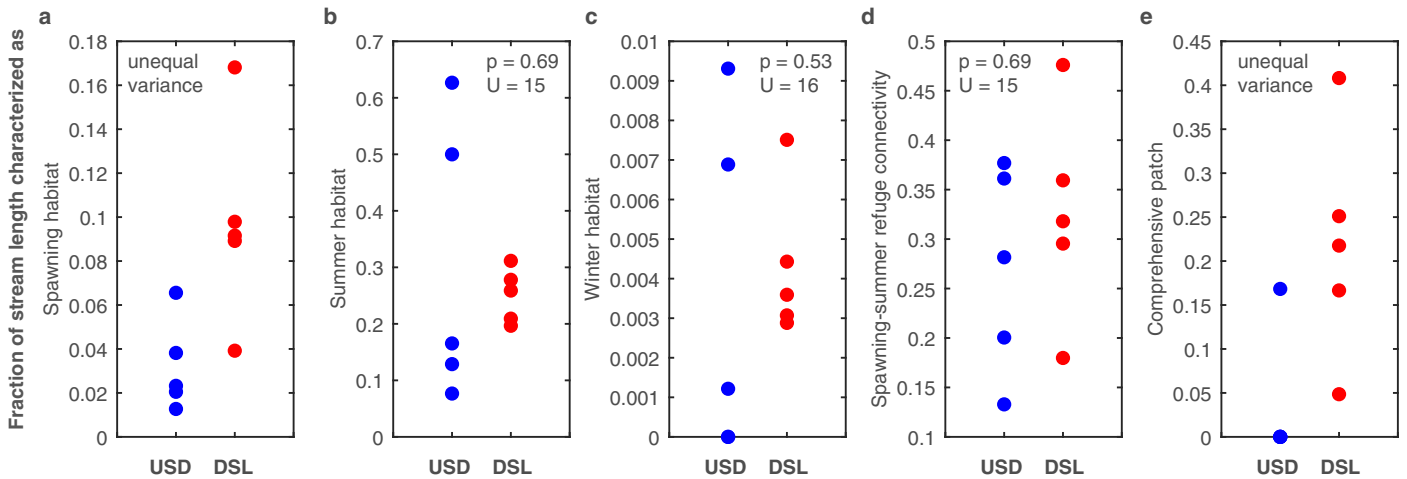
FIGURE 4. Comparisons of habitat data from streams in USD terrain with streams in DSL terrain. Fractions of stream length characterized as potential spawning habitat (a), potential summer-rearing habitat (b), or potential winter-refuge habitat (c). (d) Fraction of stream length characterized as a high-connectivity reach with both potential spawning and potential summer-rearing habitat within 250 m. (e) Fraction of stream length characterized as a comprehensive patch where potential spawning, potential summer-refuge habitat, and potential winter-refuge habitat all occur within 500 m. Red markers represent streams in DSL terrain and blue markers represent streams in USD terrain. See Table S1 for values for specific streams.

between groups. We then tested the relationships between basin size and (1) the R^2 value of the drainage area-valley width best-fit power function, (2) the exponent of the drainage area-valley width best-fit power function, (3) the fraction of stream length characterized as a high-connectivity reach, and (4) the fraction of stream length characterized as a comprehensive patch.

RESULTS

Potential Coho Salmon Habitat and Hillslope Processes

We calculated the percent stream length characterized as potential spawning, summer-rearing, winter-refuge habitat, high connectivity between spawning and summer-rearing habitat, and comprehensive patches for each stream and compare these between the group of streams in USD terrain and the group of streams in DSL terrain. For all five of these categories, the median percent stream length is higher in DSL terrain and the median absolute deviation is lower (Figure 4 and Table 3). Using the Brown–Forsythe test for equal variances, we determined that variances are unequal for percent stream length of potential spawning habitat and for percent stream length of comprehensive patches ($p = 0.03$ for both), thus no statistical test could be done to determine if the differences between groups for these categories are statistically significant. Equal variance between groups for percent

stream length of potential summer-rearing, winter-refuge and comprehensive patches ($p = 0.69$, 0.71, 0.43, respectively, Brown–Forsythe test for equal variance) indicates valid use of a Mann–Whitney–Wilcoxon test. Results from the Mann–Whitney–Wilcoxon test for percent stream length of potential summer-rearing, winter-refuge, and high connectivity between spawning and summer-rearing show the differences between groups are not statistically significant ($p = 0.69$, 0.53, 0.69, respectively). Two streams in USD terrain have no potential winter habitat and, across both terrain types, where potential winter habitat exists, it comprises <1% stream length.

Using half the original distances (125 and 250 m), the medians are similar between groups for percent of stream length characterized as high-connectivity reaches but MAD is lower in DSL terrain (Figure S1, Tables S2 and S3). For percent stream length characterized as comprehensive patches, both the median percent stream length and the MAD is higher in DSL terrain (Figure S1, Tables S2 and S3). Variance is not significantly different between groups for either high-connectivity reaches or comprehensive patches (Brown–Forsythe, $p = 0.19$ and 0.06, respectively), so we were able to use the Mann–Whitney–Wilcoxon test to show that differences between groups are only significant for percent stream length characterized as a comprehensive patch ($p = 0.55$ and 0.02, respectively).

Using twice the original distances (500 m and 1 km), both the median percent stream length characterized as high-connectivity reaches and the MAD is higher in USD terrain but the median and MAD for percent stream length characterized as comprehensive

TABLE 3. Summary of results for seasonal habitat/connectivity analysis and valley width/connectivity analysis.

	Percent stream length spawning	Percent stream length summer	Percent stream length winter	Percent stream length HC	Percent stream length CP	Minimum distance to spawning (m)	Minimum distance to summer (m)	Minimum distance to winter (m)	DA-VW R^2	DA-VW exp	Percent HC with wide VW	Percent CP with wide VW	Percent stream length excluded by confluences	Percent HC influenced by confluences	Percent CP influenced by confluences
Median (MAD) USD	2.32 (1.05)	16.53 (8.87)	0.12 (0.12)	28.16 (8.11)	0.00 (0.00)	338 (247)	52 (29)	3,161 (2,291)	0.51 (0.12)	0.62 (0.25)	47 (10)	50 (0)	18 (2)	0 (0)	0 (0)
Median (MAD) DSL	9.16 (0.63)	25.89 (4.97)	0.36 (0.07)	31.80 (4.14)	21.76 (5.10)	118 (101)	40 (23)	475 (351)	0.41 (0.29)	0.60 (0.25)	58 (17)	61 (9)	11 (1)	13 (1)	0 (0)

Notes: MAD, median absolute deviation; DA, drainage area; HC, high connectivity; CP, comprehensive patches; VW, valley width. Values for each subbasin are reported in Table S1. *Percent HC with wide VW* refers to the percent of valley width measurements with high connectivity between spawning and summer-rearing habitat that had valley width measurements that exceeded the width predicted by the best-fit power function. *Percent CP with wide VW* is the analogous measurement but with comprehensive patches.

patches is higher in DSL terrain (Figure S2, Tables S2 and S3). Variance is not significantly different between groups for percent stream length of high-connectivity reaches but it is significantly different for percent stream length of comprehensive patches (Brown–Forsythe, $p = 0.08$ and 0.01, respectively). Thus, no statistical test was performed on percent stream length characterized as comprehensive patches and the difference between groups for high-connectivity reaches is not significantly different between groups ($p = 0.10$; Mann–Whitney–Wilcoxon test).

To explore how the distribution of seasonal habitat types differed between terrain types, we compared the minimum distances to potential spawning, summer-rearing, and winter-refuge habitat between groups such that each category contains values from all habitat units in all five basins within that group (Figure 5). The differences between groups are significant for all three categories — potential spawning, summer-rearing, and winter-refuge habitat ($p < 0.001$; Welch's two-sample unpaired t-test) (Figure 5). Mean minimum distance to spawning habitat is 444 m in DSL terrain compared with 615 m in USD terrain, mean minimum distance to summer-rearing habitat is 60 m in DSL terrain compared with 77 m in USD terrain, and the mean minimum distance to winter-refuge habitat is 1,366 m in DSL terrain compared with 3,471 m in USD terrain. The median minimum distances and the MAD are also lower in DSL terrain for all three types of potential habitat (Table 3).

In all the above analyses, potential spawning habitat was defined as riffles with ≥50% gravel and ≤8% silt/organics. Because the percent cover of silt/organics is visually assessed according to the AIP protocol and thus potentially subject to high levels of uncertainty, we conducted the same analyses with spawning habitat defined as riffles with ≥50% gravel but ≤16% silt/organics. The difference in the threshold used for silt/organics did not change the results (Figure S3, Tables S4 and S5).

Valley Floor Width, Hillslope Processes, and Habitat Connectivity

The strength of the relationship between valley floor width and drainage area reflects longitudinal variability in valley width because measurements were made along mainstems and drainage area changes monotonically with stream length. Three out of five basins in DSL terrain exhibit weaker relationships (lower R^2 values) between valley floor width and drainage area when compared to basins in USD terrain without DSLs (Figure 6), but R^2 values are not significantly different between the group of streams in DSL terrain and the group of streams in
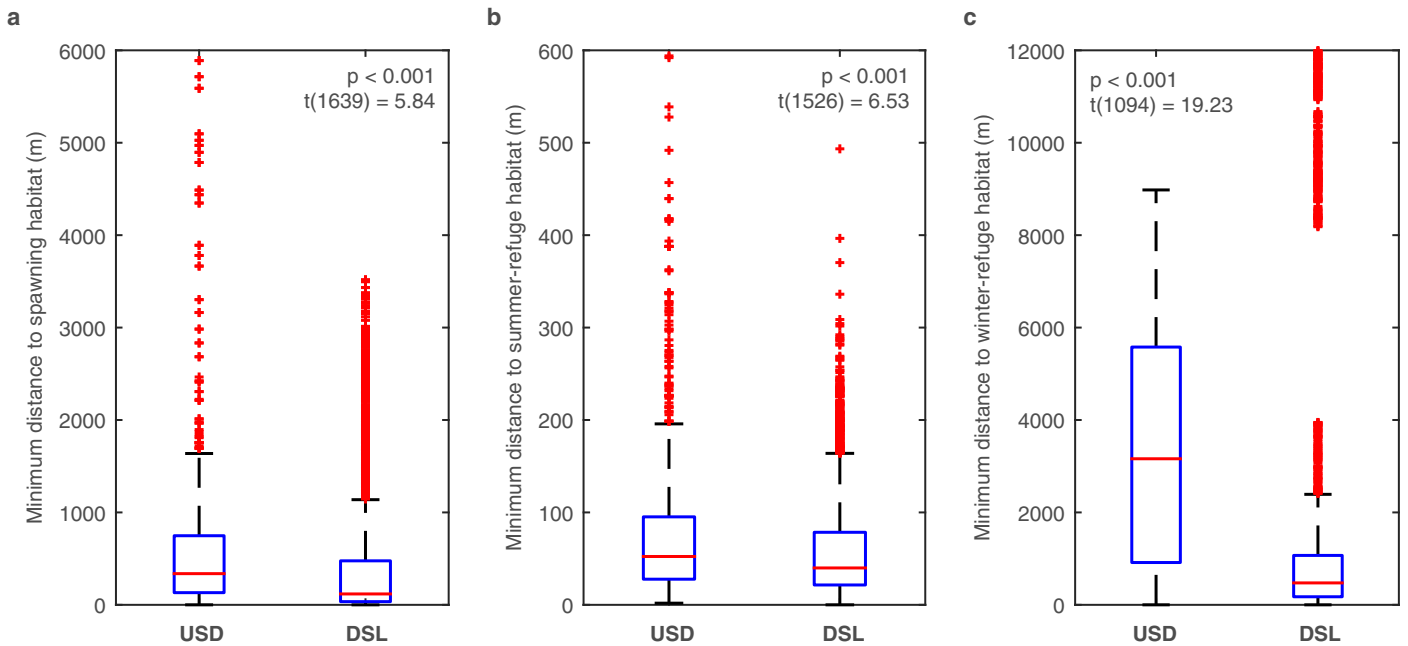
FIGURE 5. Comparisons of minimum distances to potential spawning (a), summer-rearing (b), and winter-refuge habitat (c) between streams in USD terrain and streams in DSL terrain. The central red line indicates the median; the bottom and top of the box indicates the 25th and 75th quartiles, respectively; the whiskers indicate the most extreme values; and the red plus markers indicate outliers, which are any values more than 1.5 times the interquartile range away from the top or bottom of the box. See Table 3 for summary values by group and Table S1 for summary values by stream.

USD terrain ($p = 0.29$, Brown–Forsythe test for equal variance; $p = 0.8$, Mann–Whitney–Wilcoxon test). The median R^2 value for the relationships between valley floor width and drainage area is lower in DSL terrain compared with USD terrain (0.41 vs. 0.51, respectively) and the MAD in R^2 values is higher in DSL terrain compared with USD terrain (0.29 vs. 0.12, respectively) (Table 3).

The exponent in the drainage area-valley width power function reflects the rate at which valley width changes with drainage area. The larger basins in DSL terrain have smaller exponents of the best-fit power functions than basins of comparable size in USD terrain (Figure 6), but again the difference between groups is not statistically significant ($p = 0.16$, Brown–Forsythe test for equal variance; $p = 0.3$, Mann–Whitney–Wilcoxon test). The median exponents are similar between groups (0.62 vs. 0.60) as are the MADs (0.25 for both). The two basins with the smallest exponents (Scare and Yellow Creeks) have valley widths similar to other sample creeks at low drainage area but more narrow valleys at large drainage areas (Figure 6).

The percent of stream length excluded from our valley width measurements because of widening at confluences did not differ significantly between DSL and USD terrain ($p = 0.12$, Brown–Forsythe test for equal variances; $p = 0.2$, Mann–Whitney–Wilcoxon test). However, the percent of stream length excluded is higher in USD terrain, with a median of 18%

excluded in USD terrain compared with 11% excluded in DSL terrain (Table 3). The MAD in the percent of stream length excluded is only slightly higher in USD terrain — 2% compared with 1% in DSL terrain. Few streams have high-connectivity reaches associated with confluences and/or comprehensive patches associated with confluences (Table S1) such that no valid statistical test for differences between groups could be performed. Although the majority of high-connectivity reaches and comprehensive patches were not deemed as associated with confluences in either terrain type, many high-connectivity reaches and comprehensive patches cross small confluences and continue upstream and/or downstream much more than 200 m.

Across both terrain types, 56% of reaches characterized as having high connectivity between potential spawning and summer-rearing habitat and 57% of reaches characterized as comprehensive patches occur in areas with valleys wider than predicted by the best-fit power function (Figure 6 and Table S1). Both types of high-connectivity categories, but comprehensive patches in particular, appear to occur in locations where valley width changes rapidly either upstream or downstream (Figure 6). The two basins with the highest fraction of stream length characterized with high connectivity were Halfway Creek and Yellow Creek, both in terrain dominated by extensive deep-seated landsliding (Figure 6 and Table 3).

USD terrain   **DSL terrain**

— High connectivity between spawning and summer-refuge habitat
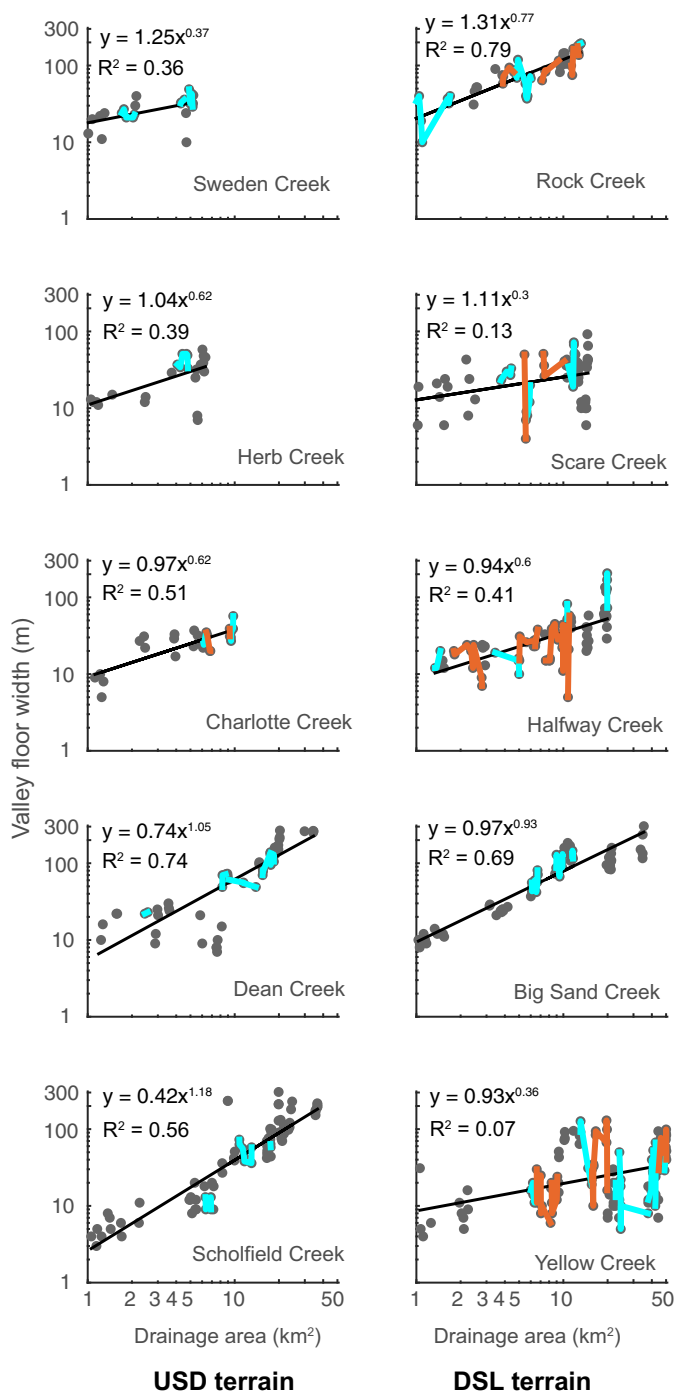— Comprehensive patches

FIGURE 6. Valley width measurements and best-fit power function relationships for the 10 study subbasins in the Umpqua River Basin (see Table 1 for detailed description of each subbasin). Basins are ranked by size in each column/group.

However, many locations with highly variable valley width exist without comprehensive patches or high-connectivity reaches. Consequently, there are no discernible relationships between drainage area-valley width R^2 values and either fraction of stream length characterized with high connectivity ($R^2 = 0.03$) or fraction of stream length characterized as a comprehensive patch ($R^2 = 0.05$) (Figure 7). There are also no relationships between drainage area-valley width exponents and either fraction of stream length characterized as high-connectivity reaches ($R^2 = 0.07$) or fraction of stream length characterized as a comprehensive patch ($R^2 = 0.14$) (Figure 7).

The relationships between fraction of stream length characterized as comprehensive patches and median minimum distances were of somewhat similar strength, with the strongest being the relationship to median minimum distance to potential winter habitat ($R^2 = 0.51$), the next strongest being the relationship to median minimum distance to potential spawning habitat ($R^2 = 0.49$), and the weakest being the relationship to median minimum distance to potential summer-rearing habitat ($R^2 = 0.32$) (Figure 7). In contrast, the relationship between fraction of stream length characterized as high-connectivity reaches and median minimum distance to potential spawning habitat was much stronger ($R^2 = 0.44$) than the relationship with median minimum distance to potential summer-rearing habitat ($R^2 = 0.12$). As expected, there is no relationship between percent stream length of high-connectivity reaches and potential winter-refuge habitat ($R^2 = 0.02$).

The sizes of basins selected did not differ significantly between groups ($p = 0.69$, Brown–Forsythe test for equal variances; $p = 0.4$, Mann–Whitney–Wilcoxon test) and basin size did not seem to influence our results. There are no relationships between basin size and fractions of stream length characterized as high-connectivity reaches or comprehensive patches ($R^2 = 0.09$ and 0.01, respectively) or between basin size and drainage area-valley width R^2 values ($R^2 < 0.001$) and there is a weak relationship between basin size and drainage area-valley width exponents ($R^2 = 0.24$).

DISCUSSION

The clustering of populations of salmonids over time into similar locations within the stream network has been observed by Flitcroft et al. (2014), Isaak and Thurow (2006), and Gresswell et al. (2006), supporting the importance of understanding habitat patch dynamics. The Network Dynamics Hypothesis offered by Benda et al. (2004) identifies tributary junctions as "hot spots" for habitat and species diversity because they are the depositional zones for debris-flow material entering larger channels from tributaries. However, unlike many disturbance processes, such as floods and debris flows, the influence
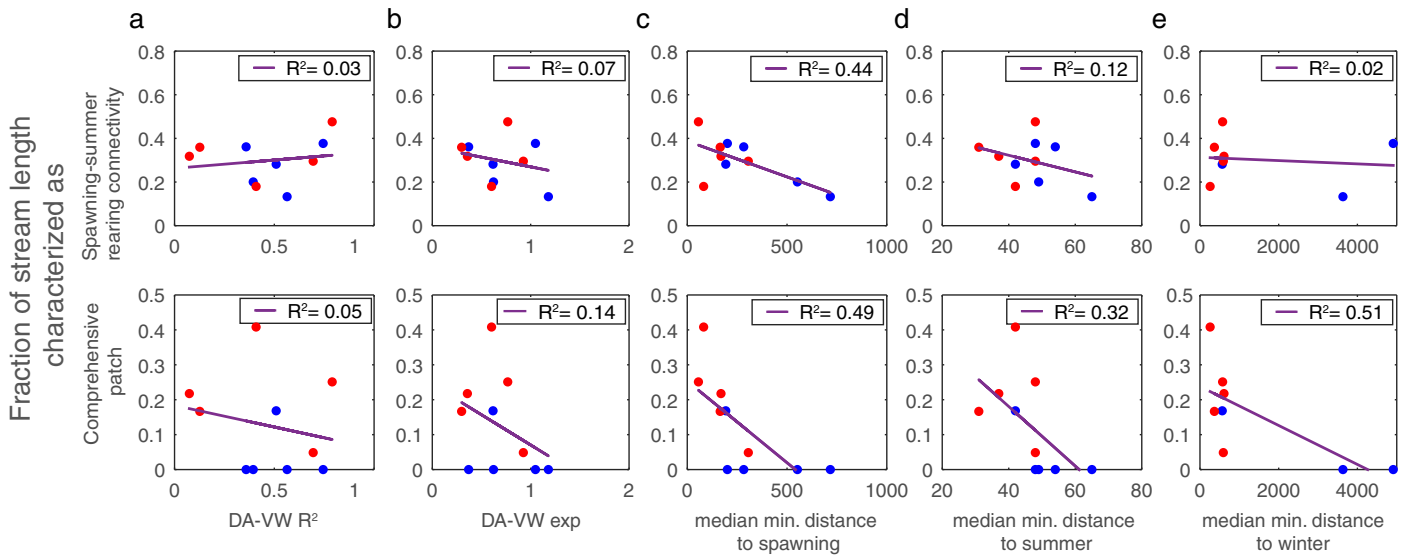
FIGURE 7. Fraction of stream length characterized as spawning-summer-rearing connectivity (top row) and comprehensive patch (bottom row) plotted against the R^2 value for the drainage area-valley width relationships (a), the exponent in the best-fit power function for each drainage area-valley width relationship (b), median minimum distance to potential spawning habitat (c), median minimum distance to potential summer-rearing habitat (d), and median minimum distance to potential winter-refuge habitat (e). Red markers represent streams in DSL terrain and blue markers represent streams in USD terrain.

of DSLs is not confined to channels and thus not concentrated at tributary junctions. DSLs are therefore likely to influence habitat formation throughout the network, potentially resulting in a more substantial influence and a more mixed distribution of habitat types than results from disturbance processes that are confined to tributaries.

In line with our hypothesis that DSLs influence the quantity and connectivity of seasonal Coho Salmon habitat, we found that the median fractions of stream length identified as each type of potential seasonal habitat and both high-connectivity reaches (spawning-summer-rearing connectivity) and comprehensive patches are higher and the MAD is lower in DSL terrain than in USD terrain (Table 3). However, the differences between groups are either not statistically testable owing to unequal variances or are not statistically significant for any of the three types of seasonal habitat or two types of connectivity (Figure 4). The distribution of minimum distances to potential spawning, summer-rearing, and winter-refuge habitat are significantly different in streams in DSL terrain compared with USD terrain and the medians of minimum distances are lower for all three types of potential habitat types as are the MADs in minimum distances (Figure 5 and Table 3). Shorter distances to potential spawning, summer, and winter habitat is partly a result of the higher fraction of all three types in DSL terrain and also likely reflects a difference in their distribution such that habitat is less clustered in DSL terrain.

By testing both smaller and larger distances to calculate connectivity, we demonstrate that increasing the chosen distance results in increased fractions of streams with high connectivity between potential habitat types. In USD terrain, the increase is primarily seen in high-connectivity reaches as potential winter habitat is more limited in streams in USD terrain. In DSL terrain, where potential winter habitat is more prevalent, the increase in distances chosen to define connectivity is reflected in an increased fraction of stream length characterized as comprehensive patches. These results highlight the importance of even small amounts of winter habitat. Corroborating this finding, the fraction of stream length identified as a comprehensive patch is correlated with median minimum distances to all seasonal habitat types, and we observe a slightly stronger relationship with median minimum distance to potential winter habitat, indicating potential winter habitat is the limiting factor for comprehensive patches.

Winter-refuge habitat has been identified as a potential limiting factor for juvenile Coho Salmon survival in coastal Oregon (Nickelson et al. 1992). Because streams in DSL terrain are more likely to have higher connectivity between spawning and summer-rearing habitat and naturally support more winter-refuge habitat and lower minimum distances to winter-refuge habitat, restoration of winter-refuge habitat in these areas might have a larger effect on connectivity among seasonal habitat types than restoration of winter-refuge habitat in streams in USD terrain.

Fraction of stream length identified as high-connectivity reaches is correlated with median minimum distance to potential spawning habitat, whereas it is not correlated with median minimum distance to summer-rearing (Figure 7), indicating spawning habitat is the limiting factor for high connectivity between potential summer-rearing and spawning habitat. Although the identification of potential spawning habitat is subject to uncertainty resulting from visual estimation of percent cover of silt/organics, we found that doubling this threshold did not impact our results. Thus, we can assume that our identification of potential spawning habitat is robust and that our finding that spawning habitat is a limiting factor for connectivity is valid.

The interpretation that spawning habitat is more limited than summer-rearing habitat may be flawed if sediment flux and thus bed cover differ significantly between streams in DSL terrain and those in USD terrain. Deep pools formed in thick layers of alluvial gravel are observed to go dry in summer, resulting in substantial mortality of Coho Salmon (May and Lee 2004). Streams in DSL terrain may have higher sediment flux and thus pools may be more likely to be formed in alluvium when compared with streams in USD terrain. The AIP data used in this study were taken in late summer, leaving 2–3 months before the rainy season in which pools formed in alluvium could potentially dry out. If more pools in DSL terrain dry out than in USD terrain, summer habitat may actually be the limiting factor in connectivity rather than spawning habitat. Future research could investigate how sediment flux and bed cover differ in streams in DSL terrain and whether pools in these streams are more likely to become dry.

Another potential problem stemming from differences in sediment flux is the degree of bed armoring. In armored beds, the surface grain size is not an indicator of subsurface grain size, which is the critical zone for spawning (Dietrich et al. 1989). If armoring differs systematically between terrain types, the identification of potential spawning habitat made using AIP data on surface grain size might differ systematically and could have biased the characterization of connectivity among potential seasonal habitat types.

The median R^2 value for the relationship between drainage area and valley width is higher in USD terrain than DSL terrain and the MAD in R^2 values is lower, suggesting that valleys in USD terrain are less likely to have variable valley width than streams in DSL terrain. Although no statistically significant difference exists in R^2 values between the group of streams in DSL terrain compared with the group of streams in USD terrain, the result is potentially confounded by a lack of statistical independence in each of the two groups of streams owing to spatial autocorrelation. The three streams that had weaker relationships than basins of comparable size in USD terrain — Scare, Halfway, and Yellow Creeks — are not in close proximity, whereas the two streams that had stronger relationships between drainage area and valley width, Rock Creek and Big Sand Creek, are in close proximity. Because Scare, Halfway, and Yellow Creeks are not in close proximity, they are likely not spatially autocorrelated. Thus, statistical independence is a reasonable assumption for these creeks and the variability in valley width observed in these streams is most likely attributable to extensive deep-seated landsliding rather than a local effect. However, because Rock and Big Sand Creeks are in close proximity, they may be spatially autocorrelated. Thus, statistical independence is a poor assumption for these creeks and the lack of variability may be attributable to a process local to these basins that is unrelated to the effects of DSLs. Spatial autocorrelation and thus lack of statistical independence is also an issue in the group of streams in USD terrain. However, our result that basins in USD terrain tend to have stronger relationships between drainage area and valley width is largely a confirmation of previously published results (May et al. 2013).

Reaches with high connectivity between spawning and summer-rearing habitat and comprehensive patches in particular appear to occur where valley width changes rapidly upstream or downstream, but the lack of relationships between fractions of stream length characterized with either type of connectivity and either drainage area-valley width R^2 values or exponents suggests that variability in valley width alone does not promote connectivity between seasonal habitat types. The same percentage of both high-connectivity reaches and comprehensive patches occur in valleys wider than predicted by the best-fit power function as occur in valleys narrower than predicted. Therefore, the existence of anomalously wide valleys also seems to not be a primary driver of connectivity between seasonal habitat types.

The exclusion of valley width measurements at confluences did not seem to influence our results as there is no significant difference between groups in the fraction of stream length excluded. Too few streams have high-connectivity reaches or comprehensive patches that were deemed to be associated with confluences to determine if the differences are significant between groups. The large majority of high-connectivity reaches and comprehensive patches occur independent of confluences, thus we can infer that the indirect influence DSLs have on stream network structure and the number/location of confluences is not driving the observed differences in habitat connectivity.

Regardless of the driving mechanism, the quantity and connectivity of seasonal habitat types are greater in streams in DSL terrain than in streams in USD terrain. Connectivity among seasonal habitats has been shown to affect juvenile Coho Salmon occupancy patterns over time (Flitcroft et al. 2012), thus our results demonstrate that the presence of DSLs may be an important geomorphic characteristic in the production of quality Coho Salmon habitat in the Oregon Coast Range. Further, our results suggest that terrain shaped by extensive DSLs may be more likely to have greater variability in valley width and hence more likely to have wide valleys. Wide valleys correspond to a lack of valley constraint, which is currently used by models for intrinsic habitat potential (Burnett et al. 2007). As with IP (Burnett et al. 2007), the identification of DSL terrain as potentially conducive to proximity among habitats provides a possible template for prioritization of habitat restoration at a landscape scale. Extensive DSLs can be visually identified with 10-m terrain data, thus, incorporating DSL presence as an additional variable in the process of restoration prioritization is accessible at regional scales.

Pacific salmon evolved in a dynamic landscape where floods and debris flows temporarily wiped out populations but left habitat complexity that later served as refugia from smaller floods (Montgomery 2003; Waples et al. 2008). However, severe population declines have left numerous species of Pacific salmon at risk, including the Oregon Coastal Coho Salmon and steelhead trout (*Oncorhynchus mykiss*) (Nehlsen et al. 1991). Wide valleys in DSL terrain are often upstream of narrow valleys making them less accessible to humans than in USD terrain where wide valleys are typically less isolated. The isolation of wide valleys suggests the potential for streams in landslide terrain to host productive habitat that may be naturally protected from development and agriculture due to their location in otherwise steep terrain. Wide valleys have the potential to host side channels, floodplains, and persistent wood jams that could create habitat complexity (Wohl 2011; Wohl et al. 2012). Further research on the potential biogeographic implications of DSLs on stream habitat, including effects on sediment flux, floodplain productivity, food webs, and wood storage, could expand our current understanding of salmon metapopulation dynamics.

availability and distribution of habitat for Coho Salmon in the portion of the Umpqua River that drains the Oregon Coast Range. We compared the quantity and connectivity of potential seasonal habitat for Coho Salmon between five subbasins with extensive DSLs and five subbasins with no evidence of DSLs in the Umpqua River Basin. Further, we analyzed valley width in these subbasins to explore how DSLs affect geomorphic variables that are key to aquatic habitat. We found that streams in terrain with DSLs have higher median fractions of stream length identified as potential spawning, summer-rearing, and winter-refuge habitat, as well as higher median fractions of stream length characterized as having (1) high connectivity between spawning and summer-rearing habitat, and (2) high connectivity between all three types of seasonal habitat. Distances between units of each seasonal habitat type are significantly lower in DSL terrain for all three types of seasonal habitat, suggesting that not only is the quantity of habitat greater in DSL terrain but that habitat is also less clustered in DSL terrain. High connectivity among seasonal habitat types tends to occur in areas with variable valley width, although variability in valley width alone did not predict high connectivity. The median R^2 value for the relationship between drainage area and valley width is lower in DSL terrain, suggesting that DSL terrain tends to have more variable valley width, though the difference between terrain types is not statistically significant. Our results show that DSLs leave persistent signatures on potential Coho Salmon habitat and valley floor width that are distinct from processes occurring in comparable watersheds without DSLs. These insights complement existing broad-scale geomorphic predictors of salmon habitat assessments such as IP (Burnett et al. 2007) by expanding the scope to include a disturbance process that operates over larger spatial scales and has a longer legacy than disturbance processes such as wildfire, floods, or debris flows. Restoration practitioners should consider prioritizing projects in watersheds with DSLs as streams in that terrain are more likely to have relatively high connectivity among seasonal habitat types or have conditions conducive to naturally support close seasonal habitat proximity. Because DSLs are easily identifiable using freely available remotely sensed terrain data, this could potentially increase the efficacy of restoration efforts.

CONCLUSION

Geomorphic processes are reflected by instream habitat patterns at different scales of organization. We describe a kilometer-scale process that affects the

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: Figures and tables for the habitat

connectivity analysis completed for additional distances; figures and tables for the habitat connectivity analysis completed using a different threshold of percent cover of silt/organics for defining spawning habitat; and code for calculating minimum distances and connectivity.

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