

Current landscapes and legacies of land-use past: understanding the distribution of juvenile coho salmon (*Oncorhynchus kisutch*) and their habitats along the Oregon Coast, USA

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Abstract: The Oregon Coast landscape displays strong spatial patterns in air temperature, precipitation, and geology, which can confound our ability to detect relationships among land management, instream conditions, and fish at broad spatial scales. Despite this structure, we found that a suite of immutable or intrinsic attributes (e.g., reach gradient, drainage area, elevation, and percent weak rock geology of the catchments draining to each of our 423 study reaches) could explain much of the variation in pool surface area across the landscape and could contribute to an estimate of how many juvenile coho salmon (*Oncorhynchus kisutch*) one might expect to find in those pools. Further, we found evidence of differences in pool surface area across land ownership categories that reflect differing management histories. Our results also suggest that historical land and river management activities, in particular splash dams that occurred at least 50 years ago, continue to influence the distribution of juvenile coho salmon and their habitats today.

Résumé : Le paysage du littoral de l'Oregon présente un degré de structure spatiale élevé en ce qui concerne des caractéristiques du paysage comme la température de l'air, les précipitations et la géologie. Malgré cette structure sous-jacente, nous avons constaté qu'une série d'attributs immuables ou intrinsèques comme, par exemple, le gradient des tronçons, la superficie drainée, l'élévation moyenne du bassin versant et le pourcentage de la géologie constitué de roches peu résistantes des réseaux hydrographiques se déversant dans chacun des 423 tronçons étudiés, pourrait expliquer une bonne partie des variations de la superficie des fosses à l'échelle du paysage et pourrait aider à estimer le nombre de saumons cohos (*Oncorhynchus kisutch*) juvéniles possiblement présents dans ces fosses. Nous avons également trouvé des indices de variation de la superficie des fosses selon la catégorie de propriété terrienne qui reflètent différents historiques de gestion. Nos résultats donnent à penser que les activités passées de gestion des terres et des rivières, en particulier le flottage de billots il y a au moins 50 ans, continuent à ce jour d'influencer la répartition des saumons cohos juvéniles et leurs habitats. [Traduit par la Rédaction]

Introduction

Understanding the distribution of instream habitats and the density of fish within those habitats is essential for effective watershed management and conservation of depressed fish populations. For wide-ranging species with a complex life history, such as Pacific salmon, untangling these relationships is particularly challenging. Field data describing instream habitats are generally only available over a small fraction of a species' range; occupied habitat types may differ by life stage; and, even within a particular habitat type, suitability and capacity rarely remain constant over time. Landscape-scale studies, based on the conceptual model that natural attributes and human impacts across watersheds drive instream habitat conditions, which in turn regulate, at least to some degree, salmon distribution and productivity, have been relatively successful at predicting adult spawners for coho salmon (*Oncorhynchus kisutch*) (Steel et al. 2012; Pess et al. 2002), Chinook salmon (*Oncorhynchus tshawytscha*) (Feist et al. 2003), and steelhead (i.e., sea-run *Oncorhynchus mykiss*) (Steel et al. 2004). Juve-

nile salmonids and their habitats have rarely been evaluated at the landscape scale; however, there are likely important changes to juvenile salmon rearing habitats across the region. In one set of examples, Beechie et al. (1994, 2001) quantified substantial losses of juvenile coho salmon rearing habitat in the Skagit River basin as well as losses linked to landscape evolution and human land use across the Skagit River and Stillaguamish River basins using mapping and inventorying approaches.

Processes driving the distribution of juveniles and their habitats cannot be inferred from studies of spawning habitats or adults (Flitcroft et al. 2012; Gresswell et al. 2006), as juveniles do not simply rear in the same habitats in which they emerged from the spawning gravel. Juvenile salmonids often move over fairly long distances to occupy separate habitat niches that are likely driven by different suites of natural conditions and that are uniquely impacted by human activities. A better understanding of the location and condition of juvenile coho salmon habitats and of juvenile coho salmon density within freshwater streams can

Received 19 December 2015. Accepted 12 July 2016.

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contribute to improved restoration and conservation planning as well as a more holistic and detailed conceptual model of the relationship among landscape drivers, instream conditions, and coho salmon during the freshwater phases of their life cycle.

Listed as threatened under the Endangered Species Act (ESA) (Federal Register 2008), coho salmon along the Oregon Coast inhabit at least two distinct freshwater habitat types over their 3-year lifespan. Adults spawn in riffles and runs within low-gradient, gravel-bed rivers; juvenile coho salmon rear in deep pool habitats during summer and may redistribute into pools in more off-channel habitats with the onset of the fall rains (Sandercock 1991; Rosenfeld et al. 2000). When adult escapement is adequate, the availability of high-quality winter pool habitat for juveniles is thought to limit coho salmon smolt production along the Oregon Coast (Nickelson et al. 1992; Solazzi et al. 2000). Landscape-scale studies have provided evidence that the habitat characteristics associated with high-quality juvenile habitat can be influenced by human activities such as tree harvesting and road building across watersheds. Pool density and large wood volume, for example, were strongly influenced by these land management descriptors in the Oregon Coast after accounting for natural landscape attributes such as gradient and geology (Anlauf et al. 2011).

River landscape analyses have been proliferating, effectively describing useful patterns and making predictions about where on the landscape particular species or habitats are likely to be found (Allan 2004; Steel et al. 2010; Johnson and Host 2010). Yet, untangling anthropogenic impacts from the intrinsic suitability of river reaches to support high-quality coho salmon habitat as defined by natural landscape attributes is daunting. Across the Oregon Coast, a high level of covariation among natural landscape gradients (e.g., land form, climate, and geology) and human activities (e.g., forest management, agriculture, and urban development) hinders the interpretation of statistical models and our ability to establish causal linkages between landscape-scale variables and fish (Lucero et al. 2011). In evaluating landscapes, we need to be able to differentiate between the potential of a site given those factors that humans cannot reasonably change (intrinsic or immutable factors) and the impact of human actions, both locally and across the watershed. One approach has been to develop an index or summary metric that describes a stream's ability to provide high-quality habitat in the absence of human impacts. Burnett et al. (2007) developed such an index of intrinsic potential (IP) for juvenile coho salmon on the Oregon Coast based on three immutable factors: stream flow, valley constraint, and stream gradient. By separating, mapping, and exploring immutable landscape attributes versus measures of human impacts, we can begin to identify those streams that naturally do not support high-quality juvenile habitat or large densities of juvenile coho salmon versus streams that are likely to support production of juvenile coho salmon in the absence of human disturbance. This approach can theoretically identify streams that do not reach their potential in supporting high-quality habitat or high densities of juvenile fish because of human modifications of the natural landscape. The efficacy of this IP has yet to be tested on empirical observations over large spatial extents.

We are also interested in understanding the role of past land management on instream conditions and on fish response to those conditions across the Oregon Coast. In New England and in Puerto Rico, for example, researchers have identified persistent impacts of past land and aquatic management activities (Zimmerman et al. 1995; Harding et al. 1998; Thompson et al. 2002). A better understanding of linkages between site history and current conditions can improve our understanding of the structure and function of current ecological systems as well as improve land management policies for the future (Foster et al. 2003).

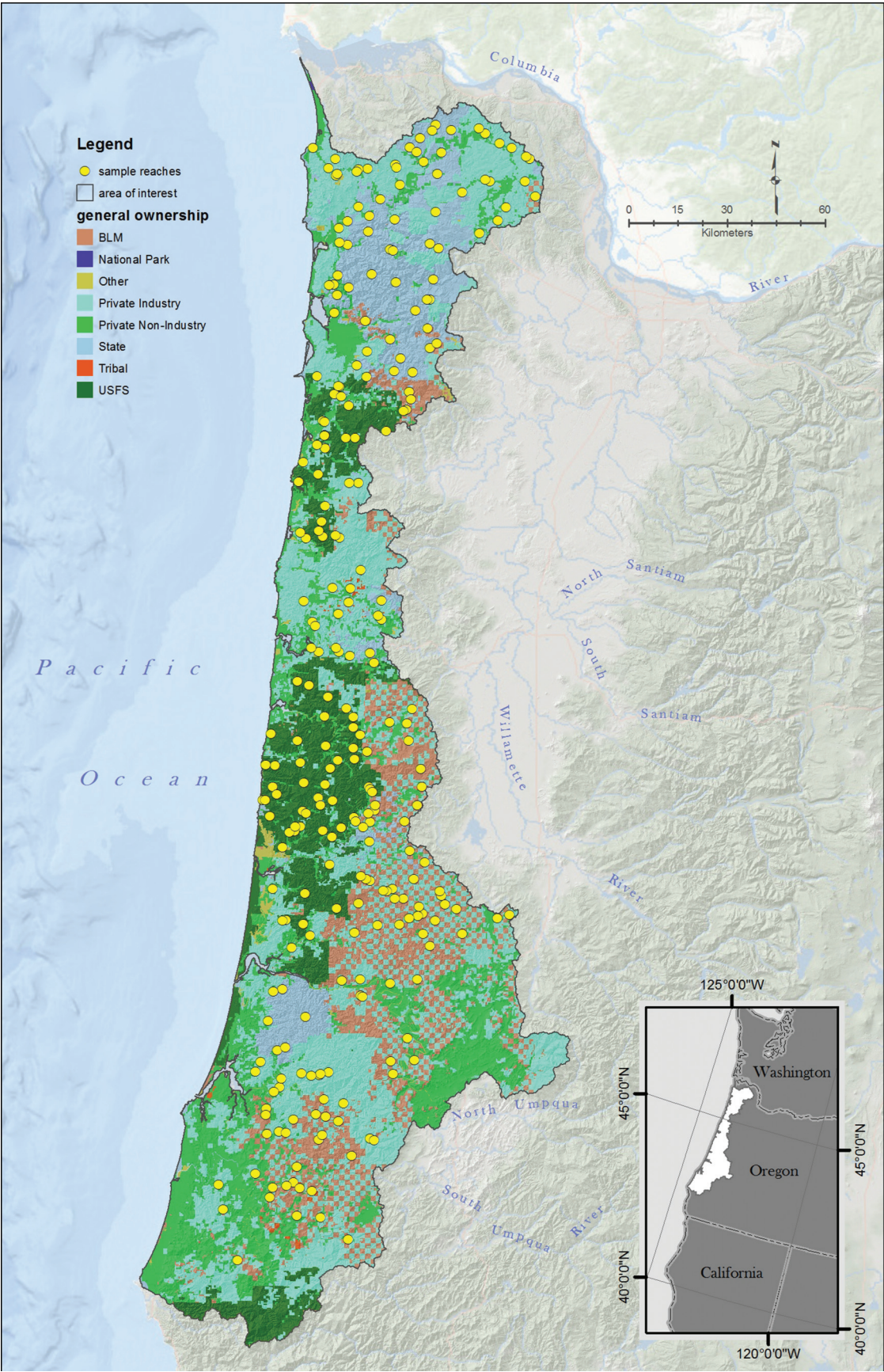
Within our landscape, land ownership can be used as an indicator of complex site histories, including road-building, human recreational activities, grazing and agricultural usage, aquatic

management, and forest harvest. The majority of the land on the Oregon Coast is privately owned, with about a third of the land in public ownership (Spies et al. 2007); there are two large federal land owners: the US Forest Service (USFS) and the Bureau of Land Management (BLM). The State of Oregon also owns land within the study area (Fig. 1). USFS lands have been managed for a combination of goals, including timber harvest, old growth forest conservation, wildlife habitat, fish habitat, water quality, and recreation (USDA Forest Service 1990). Management of BLM lands is intended to balance a variety of uses from energy development and livestock grazing to recreation, timber harvest, and protection of natural, cultural, and historical resources (http://www.blm.gov/wo/st/en/info/About_BLM.html). Private industrial forest lands, on the other hand, are presumably managed for timber production and have likely been harvested multiple times. Private nonindustrial forest lands include multiple management objectives across diverse ownerships. These private nonindustrial forest lands, while nearly half forested, also include a large amount of agricultural land use, residential development, and even a small amount of urban development. Although public and private lands share some aspects of site history, forest management on public and private lands diverged about 30 years ago (FEMAT 1993).

Legacies of logging history on aquatic systems of the Pacific Northwest are of particular interest. The long logging history includes not only forest clearing but also transporting of logs down river channels and using log drives and splash dams to build up adequate water supply (Maser and Sedell 1994). Splash damming and log drives were common across western Oregon from the 1880s through the 1950s (Miller 2010). Scouring from these activities has led to widespread stream simplification across the Pacific Northwest, and evidence suggests that physical conditions in splash-dammed streams have yet to recover (Miller 2010; Lichatowich 1999; Dolloff 1996; Sedell and Duval 1985). Though no consistent record was kept of splash dams or log drives at the time, Miller (2010) used a combination of archival, historical aerial photographs and field searches to develop a geo-database of all known splash-dam sites and log drives in western Oregon. This comprehensive resource enables investigation of the legacies of these particular logging activities on streams across the Oregon Coast.

In this analysis, we quantify the ability of immutable attributes of the landscape to explain the observed distribution of pool habitats, on which juvenile coho salmon depend, and to explain the observed density of juvenile coho salmon within those pools. We also evaluate the explanatory capacity of the summary index of IP (Burnett et al. 2007) by adding it to and comparing it with our base immutable models. Further, we test whether we can detect effects of site history, via land ownership or records of splash dams and log drives, on the distribution of pool surface area or on the density of juvenile coho salmon within those pools after accounting for immutable landscape attributes. We initiate our analysis with a detailed exploration of the spatial distribution of climate, geology, site history indicators, and IP throughout the region. Our work is novel in the explicit presentation of exploratory versus confirmatory analysis, the incorporation of a priori knowledge and streamlining of hypothesis testing, the access to a multiyear empirical data set over a vast spatial extent, and the consideration of site history both as reflected by current land ownership and by legacies of specific past logging activities. Our results enable (i) a comparison of relationships between landscape attributes and pool surface area versus relationships between landscape attributes and juvenile coho salmon density in pools; (ii) an evaluation of the summary index of IP to describe the current distribution of pool surface area and of juvenile coho salmon within these pools; and (iii) tests of the degree to which indices of site history are correlated with pool surface area and with the density of juvenile salmon in these habitats.

Fig. 1. Map of the Oregon Coast, USA, with study reaches identified by yellow points. Underlying colors denote land ownership based on Oregon Department of Forestry (2004) (Table 1).



Methods

Study area

All survey reaches in our analysis are within the Oregon Coastal Province (Fig. 1; 20 305 km²). This mountainous region is underlain primarily by marine sandstones and shales or by basaltic volcanic rocks. Elevations range from 0 to 1250 m, though most coho salmon habitat occurs in areas of lower gradients and below 700 m (Burnett et al. 2007). The temperate, maritime climate provides mild, wet winters and dry summers. Base flows predominate in late summer; peak flows occur in the fall and early winter following storm events.

Coho salmon in the study region belong to the Oregon Coastal Coho Evolutionarily Significant Unit (ESU) (Weitkamp et al. 1995). In addition to coho salmon, four other salmonid species reside in the study area: coastal cutthroat trout (*Oncorhynchus clarkii*), Chinook salmon, chum salmon (*Oncorhynchus keta*), and steelhead.

The upland portion of the study area is dominated by coniferous forests composed primarily of Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with Sitka spruce (*Picea sitchensis*) along the coast. Within riparian areas, western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*) are common. Natural disturbances that potentially continue to influence upslope and riparian habitats include infrequent but intense wildfires and storms (Franklin and Dyrness 1988). Fire has had a strong impact on the Oregon Coast landscape, particularly along the north coast where a series of fires from 1933 to 1951 burned 1400 km² of mostly primary forest. Our study area also periodically experiences strong storms that cause major flooding and severe landslides. For example, particularly large storms in 1964, 1996, and 2007 altered channel conditions across many watersheds (Danehy et al. 2011; Johnson et al. 2000). Most of the current forestland is relatively young, and the larger river valleys have been cleared for agriculture (Ohmann and Gregory 2002).

Pool and coho salmon data

The Oregon Plan for Salmon and Watersheds (<http://nrimp.dfw.state.or.us/OregonPlan/>) defines the State of Oregon's system for monitoring instream habitat and coho salmon, including both the juvenile and adult life stages, through a probabilistic sampling design of available stream reaches (generalized random tessellation stratified design (GRTS); Stevens 2002). Using the 1:24 000 scale high-resolution US Geological Survey National Hydrography Dataset (USGS NHD; <http://nhd.usgs.gov/>) drainage network, streams and rivers have been attributed according to the current and known distribution of coho salmon and steelhead trout; a random sample of these reaches was chosen for monitoring. A portion of sites are visited annually, while the majority are resurveyed based on a rotating panel design of 3 and 9 years, meant to coincide with the 3-year life cycle of coho salmon. The design is intended to balance the need to estimate population abundance in each year (for which precision improves by sampling more reaches within a year) and the need to detect trends over time (for which power improves by revisiting the same reaches year after year) (Larsen et al. 2001, 2004).

Our data set included two response variables: pool surface area within a reach and density of juvenile coho salmon within pools. We used all available data for first through fourth-order streams within the distribution of coho salmon except for three reaches in catchments dominated by Siltcoos, Tahkenitch, and Tenmile lakes. These reaches are quite different from the rest of the Oregon Coast and were also excluded from similar landscape analyses (Steel et al. 2012; Anlauf et al. 2011). Our final data set contained 1118 site-year observations collected over 16 years (1998 through 2013) at 423 reaches within 324 seventh field hydrologic units (HUs), referred to as "catchments" for modeling purposes. Individual reaches ranged in length from 130 to 1462 m, with the majority

between 600 and 1200 m. Each was visited between one and 16 times. Eleven reaches were visited in all 16 years; 193 reaches were visited for two to 15 repeat surveys; and 219 reaches were visited only once.

Pools within each reach were enumerated and measured to provide an estimate of total pool surface area within each reach. All pools with maximum depth of ≥ 20 cm and surface area ≥ 6 m² were snorkeled to identify and enumerate juvenile coho salmon. Snorkel surveys consisted of a single pass conducted during base flows in August–September. Juvenile coho salmon are known to move least in summer (Nickelson et al. 1992; Kahler et al. 2001), making the snorkel survey a "snapshot" of the abundance and distribution of fishes in the surveyed reach. Pools were assessed for water clarity or quality, receiving a rating based on visibility. To ensure data quality, only counts of juvenile coho salmon from pools receiving the higher visibility ratings (85%–92% of all pools) were included in this analysis.

Landscape data

Landscape variables were used in exploratory and confirmatory analysis. We summarized landscape characteristics across catchments, defined as the seventh field HU draining to or surrounding each reach. Drainage area was defined as the area draining to the downstream end of the reach. To quantify landscape predictor variables, we calculated the proportion of the catchment in each category for categorical variables (i.e., geology, land ownership). We calculated the area-weighted mean to provide an indication of average conditions over the entire catchment for continuous variables (e.g., air temperature range) (Table 1).

For exploratory analysis, we calculated a set of immutable landscape attributes identified as important predictors of the distribution of coho salmon and their habitats in previous analyses of this region (Firman et al. 2011; Anlauf et al. 2011; Steel et al. 2012) and of the Snohomish River in Washington State (Pess et al. 2002), for example, air temperature range (Fig. 2; Table 1). To better understand potential and observed differences across land ownership categories, we identified descriptors of the age of dominant and codominate trees and the proportion of each catchment dominated by large conifers (Table 1). To account for immutable landscape attributes expected to be correlated with the distribution of pool habitat and the density of juvenile coho salmon within those pools, we used predictors found to be important in Anlauf et al. (2011) to build base models, which we then used to test a small set of specific hypotheses.

For each surveyed reach, we calculated the length-weighted mean of IP scores for coho salmon within the study reach (MeanIP; Table 1) (Burnett et al. 2007). To quantify total amount of high-quality habitat available to juvenile coho salmon within the catchment associated with each reach, we also calculated total length of stream with IP > 0.75 (LengthHighIP). This variable was missing for three reaches, and so the three reaches were excluded from models testing for the statistical significance of LengthHighIP. Inputs used to calculate coho salmon IP were previously estimated from field data and 10 m digital elevation models (Clarke et al. 2008). For each surveyed reach, we used the geo-database of Miller (2010) (Table 1) containing 232 potential splash-dam sites and 213 log drives in western Oregon to summarize the counts of historical splash dams and length of historical log drives in the catchment.

Habitat data

Habitat data to further explore observed relationships between ownership and juvenile coho salmon and their habitats were available because they were collected as part of the coast-wide, integrated monitoring described above. In this analysis, we explored mean values (1998 through 2013) of three habitat variables: percent gravel, wood volume (m³), and percent channel shade. These three habitat characteristics, surveyed mid-June to late September, were included because they are both important to

Table 1. Geospatial data layers and variables extracted for use in exploratory analysis, base models, and hypothesis testing.

Geospatial datalayer	Map scale; gridcell size	Variable
Modeled air temperature: ambient air temperatures (1961–1990) expressed as means over the subtypes described in Precipitation Elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994); variables are calculated as an area-weighted mean across grid cells within the catchment area.	NA; 4000 m	TempRange: annual temperature range (°C)
Modeled precipitation: cumulative mean annual precipitation (1961–1990), from PRISM (Daly et al. 1994); calculated as area-weighted mean across grid cells within the catchment area.	NA; 500 m	Precip: mean annual precipitation (mm)
Geology: classification of geologic map units according to major lithology (Walker et al. 2003).	1:500 000; NA	Landslide: proportion of watershed with an estimated delivery weighted landslide density above 2.3 landslides-km ⁻² ; Sedimentary: proportion of watershed classified as sedimentary geology
Land ownership: land ownership classification (Oregon Department of Forestry 2004).	1:24 000; NA	BLM: proportion of watershed owned by US Bureau of Land Management; USFS: proportion of watershed owned by USDA Forest Service; Public: BLM + USFS + proportion of watershed owned by State of Oregon; PrivateInd: proportion of watershed that is private industrial forest and all other private lands; PrivateNI: proportion of watershed that is private nonindustrial forest
Forest age: predictive mapping of forest structure using direct gradient analysis and nearest neighbor imputation (Bell et al. 2015 ; Davis et al. 2015).	NA; 30 m	Age: basal area weighted stand age based on field-recorded or modeled ages of dominant and codominant trees (AGE_DOM in original data layer, available from http://lemma.forestry.oregonstate.edu/data/structure-maps ; accessed March 2016)
Tree size and type: predictive mapping of forest composition using direct gradient analysis and nearest-neighbor imputation (Ohmann and Gregory 2002).	NA; 25 m	BigTrees: proportion of catchment estimated to be in the following classes: conifers (50–75 cm) + very large conifers (>75 cm) + large mixed (50–75 cm) + very large mixed (>75 cm)
Digital elevation model (DEM): USGS 10 m DEM.	NA; 10 m	DrainageArea: total area upslope of the downstream end of any given index reach; gGenerated from a USGS 10 m DEM (m ²); Gradient: change in elevation (upstream elevation minus downstream elevation) divided by length of the reach (%); Elevation: elevation of downstream terminus of reach, as measured from 10 m DEM (m)
Intrinsic potential: predicted total area of instream rearing habitat for juvenile coho salmon (<i>O. kisutch</i>) based on the geometric mean of normalized values for flow, gradient, and valley constraint (Burnett et al. 2007 ; Clarke et al. 2008).	1:24 000; NA	MeanIP: length-weighted mean value of intrinsic potential for the reach (unitless); LengthHighIP: total length of stream with intrinsic potential >0.75 in catchment (unitless)
Historical stream disturbances: archives were used to create a geodatabase of historical splash dam and log-drive sites in western Oregon (Miller 2010).	1:24 000; NA	SplashDams: presence of historical splash dams within the catchment are (0/1); LogDrive: length of historical log drives within the catchment area (m)

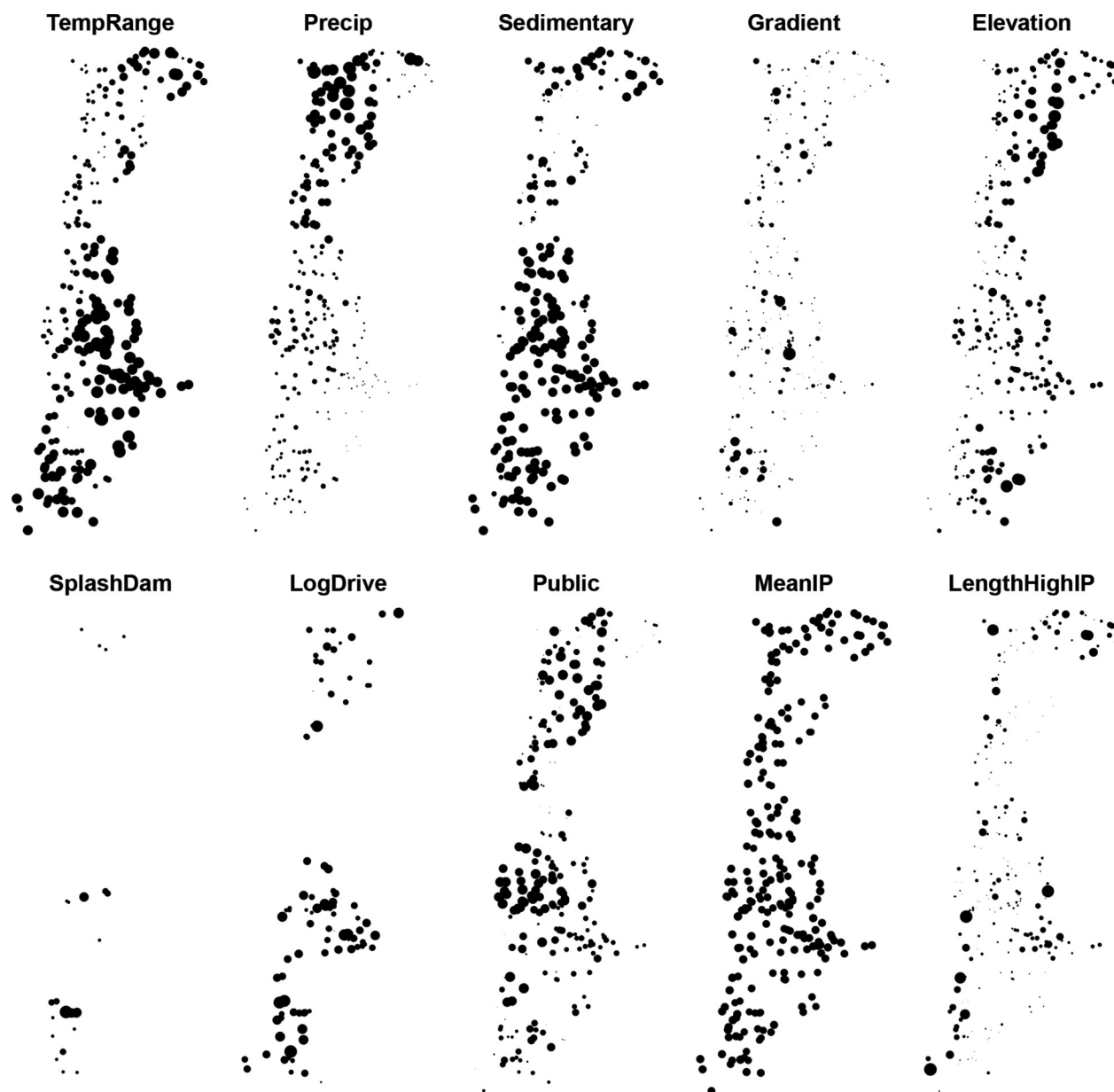
juvenile coho salmon habitat and were found to be particularly sensitive to land management ([Anlauf et al. 2011](#)). Gravel is the estimated proportion of the stream-bed area that is classified as gravel (2–64 mm). Wood volume is the volume of instream wood per 100 m of reach length (m³ per 100 m); it includes all pieces of wood that are within the active channel and are ≥0.15 m in diameter and ≥3 m in length. Percent channel shade is the percentage of the stream channel that is shaded. It is measured with a clinometer by recording the angle from the horizon to open sky on both the left and right sides of the stream and using these measurements to estimate the percentage of open sky covered by vegetation. All three habitat variables were collected by habitat unit

(e.g., riffle, pool) and summarized by reach. For further field details, see [Moore et al. \(2007\)](#).

Statistical methods

Data analysis was completed in five steps. (1) We first conducted extensive exploratory and mapping analyses to understand and display the spatial distribution of landscape attributes of interest as well as of each potential predictor and of the two response variables: pool surface area and density of juvenile coho salmon within pools. (2) We developed a base model of pool surface area as a function of immutable landscape attributes found to be important for predicting pool habitat in previous work. At this stage,

Fig. 2. Spatial distribution of a set of landscape descriptors across the Oregon Coast study area. The first row describes both exploratory variables of interest from other studies (e.g., TempRange) as well as predictor variables used in the base models for pool surface area and coho salmon density (based on Anlauf et al. 2011). The bottom row describes key variables of interest, including descriptors of site history and metrics of intrinsic potential. Point size is linearly scaled to the value of the variable at a particular reach. For variable definitions and data sources, see Table 1.



we did not conduct statistical tests to select a best model but built it from previously published relationships for this study area. (3) We built a similar base model of juvenile coho salmon density within pool habitats. Because juvenile coho salmon were only counted in pools, this model included an offset describing the total pool habitat within a reach; therefore, although the modeled response variable was a count of juvenile coho salmon, the model effectively describes counts of juvenile coho salmon per pool habitat (m^2), otherwise understood as density of juvenile coho salmon. With these two base models, we examine how well a previously published suite of immutable landscape variables explains observed spatial variation in pool surface area or in juvenile coho salmon density. (4) We used these two base models as the foundation for formal statistical hypothesis testing to (a) understand intrinsic potential (IP) and (b) detect the influence of site history either as reflected in land ownership or as described by past splash dams and log drives on both

pool surface area and density of juvenile coho salmon within pools. (5) In the final step of our analysis, we introduce habitat data from Anlauf et al. (2011) and additional landscape-scale data in an exploratory analysis to consider whether or not we can see other differences in instream habitat conditions across land ownership categories or differences in forest cover across land ownership categories that might contribute to an understanding of observed relationships between land ownership and pool surface area.

(1) **Landscape patterns:** To best understand landscape structure, we conducted extensive exploratory analyses including correlation tables, spatial maps, and boxplots comparing the distribution of predictor variables across categories of, for example, land ownership. Given the challenges of conducting analyses over large extents without true replication or control, the goal of these exploratory analyses was to understand the underlying relationships that might cloud our ability to interpret statistical models.

(2) **Base model for pool surface area:** A linear mixed model was built using the natural logarithm of pool surface area (m^2) as the response variable and survey year, catchment, reach, and the catchment by year interaction as random effects. Catchment was included as a random effect because, in some cases, there were two to four reaches within one catchment.

We based our model of pool surface area on [Anlauf et al. \(2011\)](#). They described pools per 100 m using five immutable variables: reach gradient, drainage area, mean elevation of the catchment, flow (cubic feet per second, cfs; $1 \text{ foot}^3 = 28.317 \text{ dm}^3$), and percent weak rock geology in the catchment. We wanted to account for these relationships with immutable variables before testing our key variables of interest related to IP and history. As explained above, we eliminated mean annual flow from our pool surface area model because it is generally estimated from drainage area; therefore, these variables are highly correlated. As in [Anlauf et al. \(2011\)](#), there appeared to be a linear relationship between the natural log of pool surface area and the natural log of drainage area as well as between the natural log of pool surface area and stream gradient. We used an updated geology layer and substituted percent sedimentary rock for the percent weak rock geology layer used in previous analyses. In our data set, survey lengths varied considerably both across and, somewhat surprisingly, within reaches across years. Intuitively, pool surface area should depend on the survey length, and so survey length was included in the model.

Our base model of $\ln(\text{pool surface area})$ contained gradient (%), elevation (m), $\ln(\text{drainage area})$, percent sedimentary rock in the catchment, and survey length as fixed effects. Residuals were checked for temporal and spatial autocorrelation using autocorrelation function plots and semivariograms, respectively. Overall model fit was assessed using marginal pseudo- R^2 ([Nakagawa and Schielzeth 2013](#)).

(3) **Base model for juvenile coho salmon:** Juvenile coho salmon count data were analyzed with a generalized linear mixed model using a Poisson distribution with a natural logarithm link. Because the amount of pool habitat varied by reach and year, the natural logarithm of total pool surface area (m^2) was used as an offset. We emphasize that this model, with a response of juvenile coho counts and pool surface area as an offset, implicitly describes fish density. Statistical research on best methods for managing ratio data, observations with a random denominator, suggests that our approach of using the denominator as an offset is best when modeling data on fish in pools ([Liermann et al. 2004](#)). Survey year, catchment, reach, and the catchment by year interaction were included in the model as random effects. To account for overdispersion (extra-Poisson variation), the observation-level random effect represented by the reach by year interaction was also included as a random effect.

Our base model of juvenile coho salmon counts was built from the suite of variables in the best habitat models in [Anlauf et al. \(2011\)](#) and contained precipitation, gradient (%), gradient², percent sedimentary rock in the catchment, elevation (m), and drainage area as fixed effects. We explored quadratic as well as linear relationships for all predictors; gradient² was included in the model based on graphical evidence of a quadratic relationship in which juvenile coho salmon per pool are highest at intermediate values of stream gradient. Residuals were checked for temporal and spatial autocorrelation using autocorrelation function plots and semivariograms, respectively. Overall model fit was assessed using marginal pseudo- R^2 ([Nakagawa and Schielzeth 2013](#)).

(4) **Statistical tests for IP and site history:** Statistical tests were used only on a suite of key variables describing IP and site history. IP indices describe the potential for excellent local habitat conditions (MeanIP) and the potential quality of nearby habitats, potential for outmigration to cooler upstream habitats, and potential for downstream fluxes of material as food sources (LengthHighIP; [Table 1](#)). Indices of site history describe the proportion public

ownership in the catchment (Public); the proportion private ownership used for industrial forestry (PrivateInd); the proportion private ownership not used for industrial forestry (PrivateNI); the historical presence of splash dams (SplashDams); and the length of historical log drives (LogDrives) in the catchment ([Table 1](#)).

To test for a relationship with either pool surface area or juvenile coho salmon density, the above variables were added one-by-one to the base model. All test results are for each variable when added alone to the base model. The one exception was mean IP. Because IP is a summary index that includes gradient, it was tested against the full immutable model including gradient as well as against the immutable model without gradient. Tests of coefficients when key variables were added to the base pool surface area model were conditional F tests using the Kenward–Roger degrees of freedom correction ([Kenward and Roger 1997](#)). Tests of coefficients when key variables were added to the base juvenile coho salmon model were 1 degree of freedom χ^2 likelihood ratio tests. Reported confidence intervals of coefficients are 95% profile likelihood confidence intervals. Effect sizes are presented as the change in $\ln(\text{pool surface area})$ or in the density of juvenile coho salmon for a change of approximately 10% of the observed range in each variable.

(5) **Exploratory analyses to understand observed relationships with land ownership:** To better understand the characteristics of different land ownership categories, we overlaid the ownership classification with an existing land-use data layer ([Burnett et al. 2007](#)) and summarized land use by ownership category. We also overlaid land ownership with two descriptors of forest condition: proportion of catchment with big trees (>50 cm) and an estimate of stand age based on dominant and codominant trees ([Table 1](#)). We graphically observed patterns across four land ownership categories. To observe possible differences in other instream conditions across land ownership categories, we graphically compared the distribution of instream habitat variables, percent gravel, percent shade, and large wood volume, across these same land ownership categories.

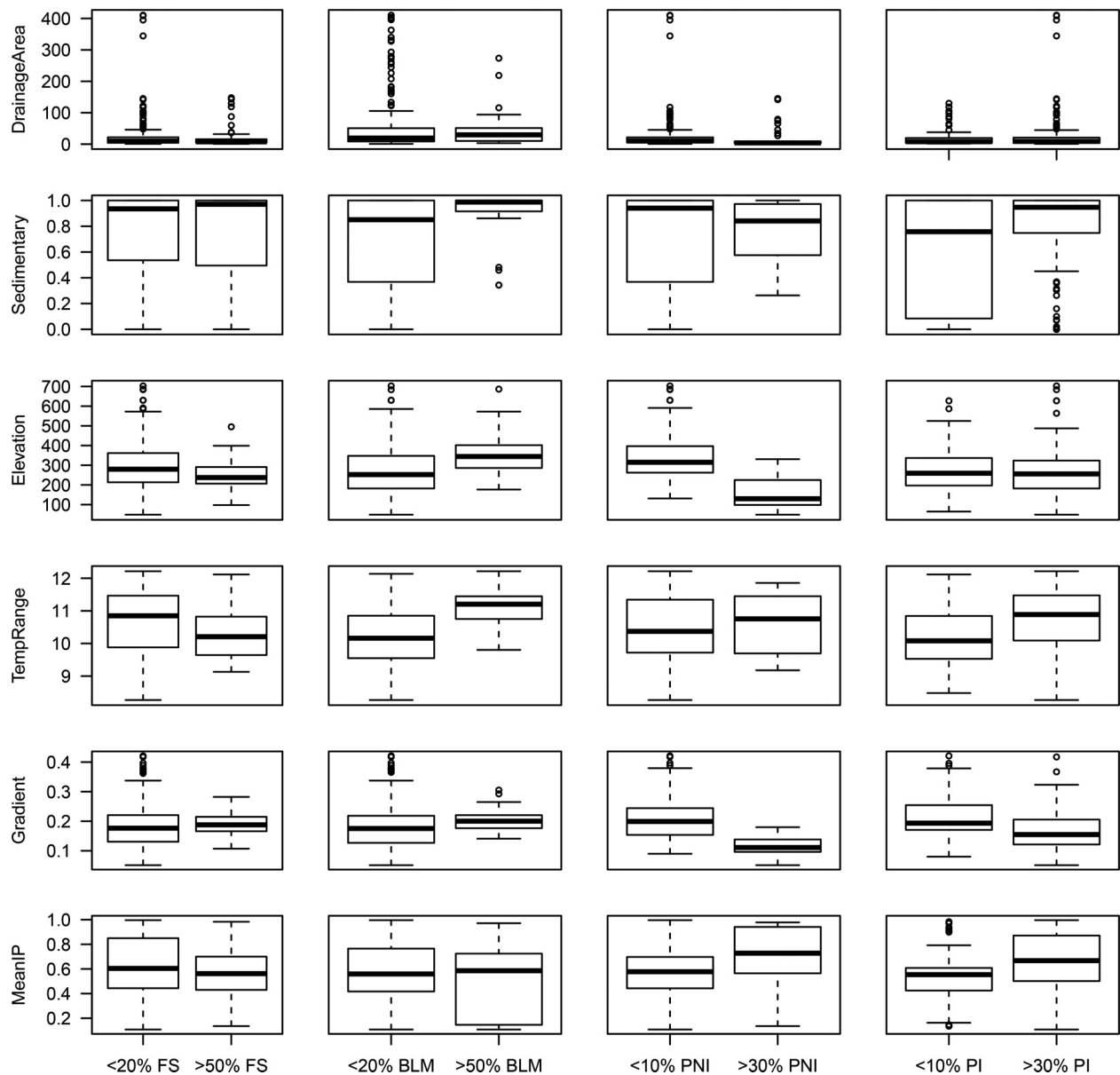
Results

Landscape pattern

Spatial pattern is evident for most descriptors of the study area, including potential predictors of pool surface area and juvenile coho salmon density ([Fig. 2](#)). For example, study reaches draining catchments with large annual ranges in air temperature (TempRange) are in the southeastern parts of the study area, and those with high mean annual precipitation (Precip) are in the northwestern portion of the study area. Study reaches draining catchments with high proportions of sedimentary geology (Sedimentary) are more prevalent in the southern parts of the study area and the northern tip. Log drives (LogDrive) and splash dams (SplashDams) appear to have occurred predominantly in the southern portions of the study landscape. Values for variables describing IP (MeanIP and LengthHighIP) are mildly clustered but distributed across the entire study area. Land ownership is not distributed evenly ([Figs. 1 and 2](#)), with public lands scattered throughout as well as clustered in the central and northern areas.

The uneven distribution of land ownership is reflected in different distributions of immutable landscape variables for areas with relatively high versus relatively low ownership in each of four ownership categories: BLM, USFS, private non-industrial (PrivateNI), and private industrial (PrivateInd) ([Fig. 3](#)). For example, the elevation range is wider for catchments with low proportions of land managed by the USFS. Areas with more land in private nonindustrial (PrivateNI) ownership are generally at lower elevations, have lower stream gradients, and higher MeanIP scores. In summary, we observe

Fig. 3. Comparison of landscape attributes for sites that have relatively more of a particular ownership classification versus relatively less. The cutoffs differ between the two private and the two public ownership categories in order to provide reasonable sample sizes. FS = USDA Forest Service; BLM = Bureau of Land Management; PI = private industrial; PNI = private nonindustrial.



that the lands under different ownership categories differ with respect to several immutable variables.

Pool surface area

Marginal pseudo- R^2 for this linear base model, including $\ln(\text{total pool surface area})$ gradient, elevation, $\ln(\text{drainage area})$, survey length, and sedimentary geology, is 0.632 (Table 2). The majority of the variance is at the reach level (0.429), with a smaller amount of variance at the catchment level (0.141). Graphical assessment of residuals did not indicate serious problems with temporal or spatial autocorrelation; however, there is some spatial autocorrelation primarily in the east–west direction. Such anisotropic spatial autocorrelation may be difficult to eliminate as rivers in this area run from the Coast Range to the Pacific Ocean in a more or less east to west orientation. As might be expected, there is very little overall annual variation in pool surface area (0.021). Unexplained catchment by year and reach by year (residual) variability are relatively high (0.203 and 0.106, respectively).

Table 2. Linear model estimating $\ln(\text{pool surface area})$ using immutable variables from Anlauf et al. (2011).

Predictor variable	Unit*	Coefficient†	Lower 95% CI	Upper 95% CI
Gradient	0.016	−0.251	−0.322	−0.181
Elevation	65.427	0.062	0.014	0.110
$\ln(\text{drainage area})$	0.558	0.412	0.358	0.465
Survey length	133.200	0.196	0.143	0.250
Sedimentary	0.100	−0.010	−0.038	0.018

Note: Variables and their units are provided in Table 1. Marginal pseudo- R^2 for this linear model was 0.632. CI = confidence interval.

*The unit column describes approximately 1/10 of the observed range of the predictor variable.

†The coefficients describe the effect of a one-unit change in the predictor variable on the log-scale response.

Fig. 4. Effect sizes for key variables when entered in either (A) the pool surface area model or (B) the juvenile coho salmon density model. In each case, the unit of the effect is approximately 1/10 of the observed range of that variable within our data (see Table 4). Note that mean intrinsic potential is tested in two ways: once on the full immutable model (MeanIP) and once on the immutable without gradient (MeanIPng). Splash dams were not included because there was no equivalent effect of 1/10 of the observed range of the data for presence-absence of splash dams.

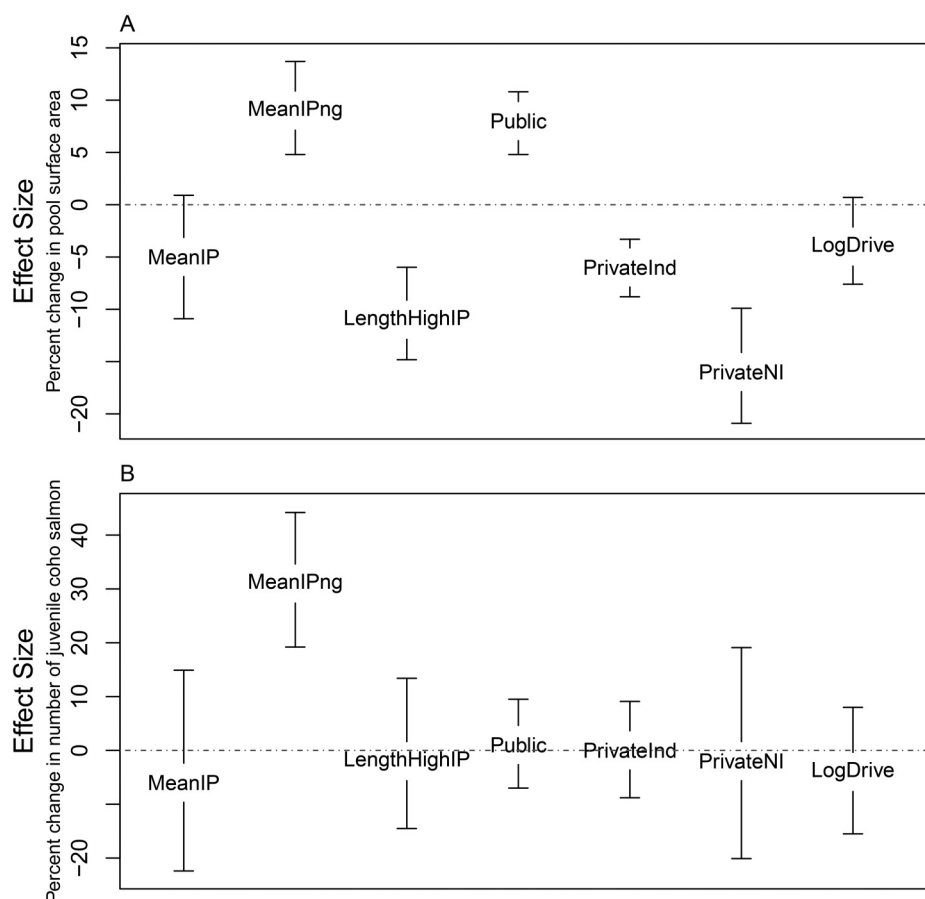


Table 3. The Poisson model (log link) for juvenile coho salmon density using immutable variables from Anlauf et al. (2011).

Predictor variable	Unit*	Coefficient†	Lower 95% CI	Upper 95% CI
Precipitation	292.553	-0.114	-0.257	0.029
Sedimentary	0.100	0.091	-0.005	0.186
Gradient	0.016	-0.211	-0.399	-0.023
Gradient ²	0.016	-0.074	-0.147	-0.001
Elevation	65.427	0.011	-0.122	0.143
Drainage area	16.919	-0.382	-0.545	-0.218

Note: Variables and their units are provided in Table 1. Marginal pseudo- R^2 for this linear model was 0.338. CI = confidence interval.

*The unit column describes approximately 1/10 of the observed range of the predictor variable.

†The coefficients describe the effect of a one-unit change in the predictor variable on the log-scale response.

Juvenile coho salmon

The marginal pseudo- R^2 for this Poisson model with a log link including precipitation, sedimentary geology, gradient, gradient², elevation, and drainage area is 0.338 (Table 3). Graphical assessment of residuals indicates no problems with temporal or spatial autocorrelation. A relatively large amount of the variance (2.665) is distribution-specific (on the link scale) owing to the relationship between the mean and variance for the Poisson distribution; a Poisson GLMM will have this distribution-specific variance, and so it is important to remember that the pseudo- R^2 can

never be 1 (Nakagawa and Schielzeth 2013). There was a large amount of unexplained variance at the catchment scale (2.437) and at the reach scale (1.497). The overall year-to-year variance was relatively less (0.443). There was also unexplained variability for catchment by year (1.409) and reach by year (residual) (0.225).

Statistical tests for intrinsic potential (IP) and site history

Intrinsic potential (IP)

Mean IP provides only minor additional explanatory power beyond that of gradient for pool surface area and no additional explanatory power for juvenile coho salmon density in pools. There is a large and positive statistically significant effect of MeanIP when gradient is not included in the model (Table 4; Fig. 4). The length of high IP habitat (LengthHighIP) has a statistically significant relationship with pool surface area but not with juvenile coho salmon density (Table 4; Fig. 4). We caution that although the coefficient describing the effect of total length of high IP is negative (suggesting that study reaches in catchments with longer lengths of river estimated as high IP have lower pool surface areas), it is difficult or impossible to untangle the effect of one predictor variable entered in a model that already contains so many similar and potentially collinear variables. This problem is potentially greater for LengthHighIP than for other variables because it may be a descriptor of catchment position in the landscape.

Land ownership

There is a statistically significant positive effect of public ownership on pool surface area (Table 4; Fig. 4). In other words, after

Table 4. Hypothesis tests for key variables of interest in which p values describe one degree of freedom χ^2 tests (generalized linear mixed model) or Kenward–Roger F tests (linear mixed model) for the addition of a key variable of interest to a model that already contains immutable variables (see Table 2 for base pool model and Table 3 for base juvenile coho salmon model).

Variable	Unit*	Pool surface area			Juvenile coho salmon		
		p	Effect†	95% CI	p	Effect†	95% CI
MeanIP (full model)	0.1	0.093	−5.2%	(−10.9, 0.9)	0.567	−5.6%	(−22.4, 14.9)
MeanIP (without gradient)	0.1	<0.0001	9.2%	(4.8, 13.7)	<0.0001	30.7%	(19.2, 44.2)
LengthHighIP (m)	2641	<0.0001	−10.5%	(−14.8, −6.0)	0.828	−1.5%	(−14.5, 13.4)
Public	0.1	<0.0001	7.7%	(4.8, 10.8)	0.827	0.9%	(−7, 9.5)
PrivateInd	0.1	<0.0001††	−6.1%	(−8.8, −3.3)	0.972††	−0.2%	(−8.8, 9.1)
PrivateNI	0.1	<0.0001††	−15.6%	(−20.9, −9.9)	0.972††	−2.4%	(−20.1, 19.1)
SplashDams	+§	0.514	11.4%	(−19.2, 53.5)	0.049	139.5%	(0.4, 474.9)
LogDrive (m)	0.0001	0.109	−3.5%	(−7.6, 0.7)	0.466	−4.4%	(−15.5, 8.0)

Note: CI = confidence interval.

*The unit column describes approximately 1/10 of the observed range of the predictor variable.

†The effect sizes (Effect) are for a one-unit change in the predictor variable. A positive number indicates the percent increase, and a negative number indicates a percent reduction.

††Tests for private ownership were conducted by adding private industrial (PrivateInd) and private nonindustrial (PrivateNI) to the immutable model simultaneously. The two p values therefore reflect a χ^2 test with two degrees of freedom.

§The plus symbol for the unit size of splash dams indicates that this effect is for presence versus absence of any splash dams in the catchment draining to the study reach.

accounting for geology, elevation, gradient, and drainage area, reaches with a higher percentage of the catchment in public ownership have a larger pool surface area. Conversely, reaches with a higher proportion of private ownership and, in particular, private ownership that was classified as not industrial forest (PrivateNI) have smaller pool surface areas. There is no statistical relationship between land ownership and density of juvenile coho salmon within pools (Table 4; Fig. 4).

Log drives and splash dams

The density of reaches with historical log drives (LogDrive) in the catchment is not statistically significant in either model, though there are indications that log drive length may have a negative effect on pool surface area. We do see a statistically significant effect of splash dam presence versus absence in the catchment of the study reach on juvenile coho salmon density. The effect of splash dam presence on juvenile coho salmon density is potentially fairly large; one splash dam is estimated to increase juvenile coho salmon density by 139.5%; however, there is also a large amount of associated uncertainty (95% confidence interval equals 0.4% to 474.9%) reflecting the relatively small number of sites ($n = 24$) with splash dams present (Table 4).

Exploratory analyses to understand observed relationships with land ownership

Comparing land use (Burnett et al. 2007) across ownership categories, private industrial lands (PrivateInd) are composed of just over 98% forest lands. Private nonindustrial lands (PrivateNI) represent a combination of urban (5.4%), residential (14.4%), agricultural (29.7%), forest (46.3%), and other uses (4.1%).

The distribution of forest age classes by ownership (Fig. 5) reveals several clear patterns, in particular between lands under public and private ownership. This analysis confirms that nonindustrial private land has considerably more non-forest land than the other ownership categories (Fig. 5a); however, when those are removed, the age distribution of forests on the nonindustrial privately owned forest lands is very similar to that of the private industrial forest lands (Fig. 5b), suggesting a similar overall management history for private forested lands. There are substantially older trees on public than on private lands, with the vast majority of very old forests on public lands (Fig. 5). We can also observe the divergence of forest management across public and private lands in recent years. The <30-year-old age classes comprise 10% of the federal forest lands and 40% of private forests (Fig. 5b). Reaches whose catchments drained areas with high proportions of public land are also those whose catchments drained areas with high

proportions of very large conifers (Fig. 6). Across the study area, the mean proportion of a catchment in large trees is 16.7%. More than 40% of the study reaches drain catchments with less than 10% of the area in big trees; only 2% of the study reaches drain catchments with more than 50% of the area in big trees.

There is little qualitative difference in shade or gravel across land ownership categories (Fig. 6). The sites with the lowest distribution of instream wood volume tend to be those with greater than 30% private industrial (PrivateInd) or private nonindustrial (PrivateNI) ownership.

Discussion

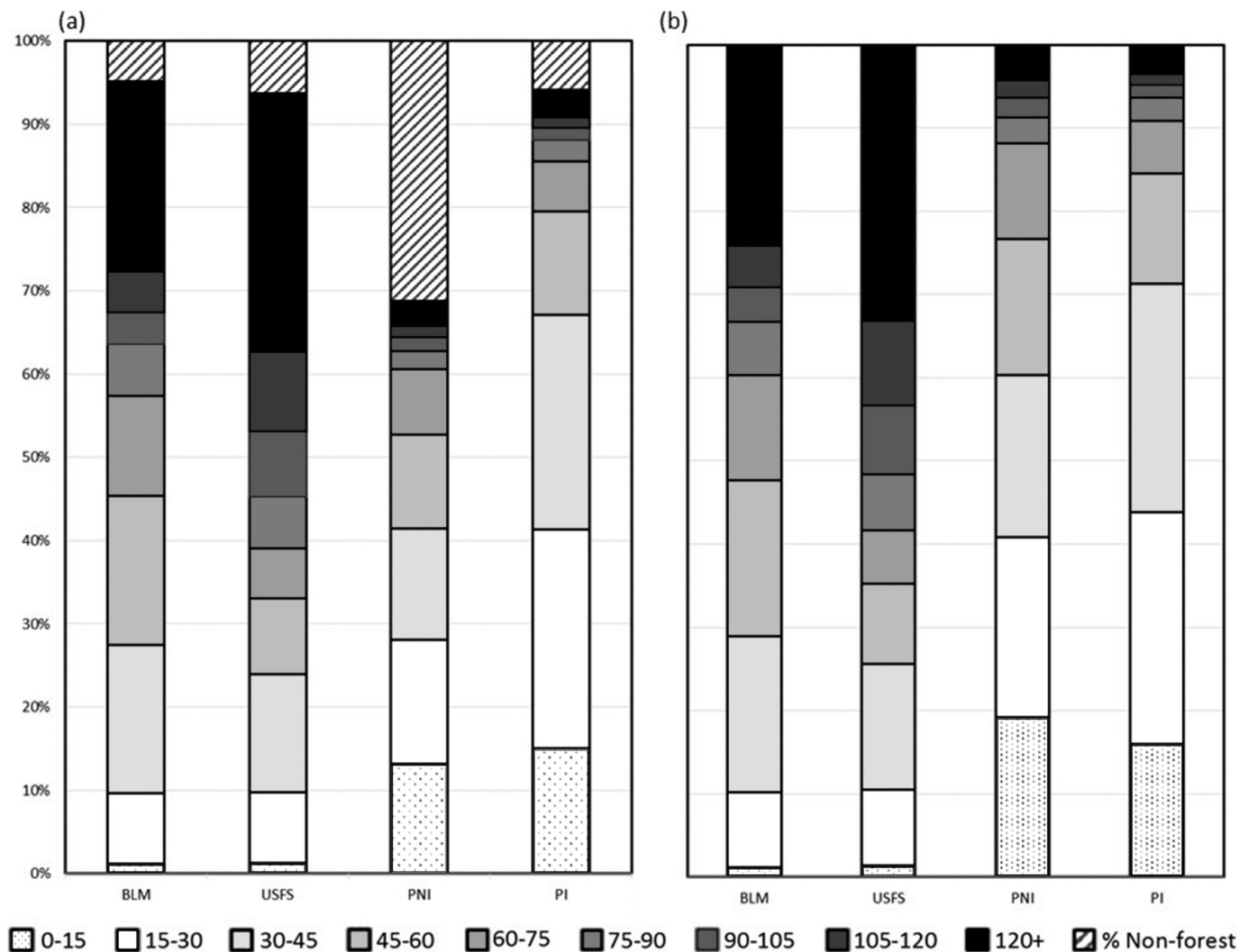
Given the high level of spatial structure in landscape attributes on the Oregon Coast, untangling relationships among landscape attributes, instream habitat conditions, and aquatic biota is particularly important for effective management of aquatic resources. We found that pool surface area, an essential element of coho salmon habitat, is well described by relatively immutable landform attributes: drainage area, elevation, geology, and gradient. A similar set of immutable landform attributes also plays a role, albeit a smaller role, in explaining juvenile coho salmon density within pools. Building on these landscape models, we corroborated the management relevance of the concept of “intrinsic potential”, quantified an association between reduced pool habitat and private land ownership, and observed that splash dams may continue to play a role in determining patterns of juvenile coho salmon and their habitats across the landscape.

Spatial structure of the Oregon Coast landscape

Landscape-scale approaches have been useful in informing management of freshwater fishes and their habitats across a wide range of ecoregions (Steel et al. 2010), and yet the spatial structure of landscape-scale data poses continuous challenges. To address these challenges, Lucero et al. (2011) suggest that landscape-scale studies, focusing on river systems, which by nature are highly structured landscapes, follow a few principles: expect multicollinearity and interpret any one particular landscape attribute with caution; conduct thorough exploratory analyses, including mapping of potential predictors; resist mechanistic or causal interpretations from correlative work; and resist extrapolation across regions. Limiting analysis to a subset of variables with known or very likely relationships to the response of interest (e.g., Beechie and Imaki 2014) can also limit spurious results.

In our exploratory analysis, we found, as expected, that neither immutable landscape attributes nor site histories are distributed randomly across the Oregon Coast landscape. Some spatial pat-

Fig. 5. Age distribution forest age classes by ownership (A) including and (B) without including non-forest lands. Forest age is estimated in this figure as the basal area weighted stand age based on field-recorded or modeled ages of dominant and codominant trees (Age). PI = private industrial; PNI = private nonindustrial. Age and ownership are as described in Table 1.



terms were as simple as “the annual range in air temperature tends to be higher at higher elevations” (Fig. 2). There are likely also complex histories and relationships that are difficult to deduce from present day conditions. Lucero et al. (2011) found results similar to ours across the Oregon Coast. Of course, the Oregon Coast is not the only region with considerable landscape structure. Looking at 261 small watersheds across Idaho, Montana, Oregon, and Washington, Kershner et al. (2004) noted that watersheds containing reference streams tended to be found at higher elevations, receive more precipitation, and have a slightly higher percentage of federally managed lands than did managed watersheds.

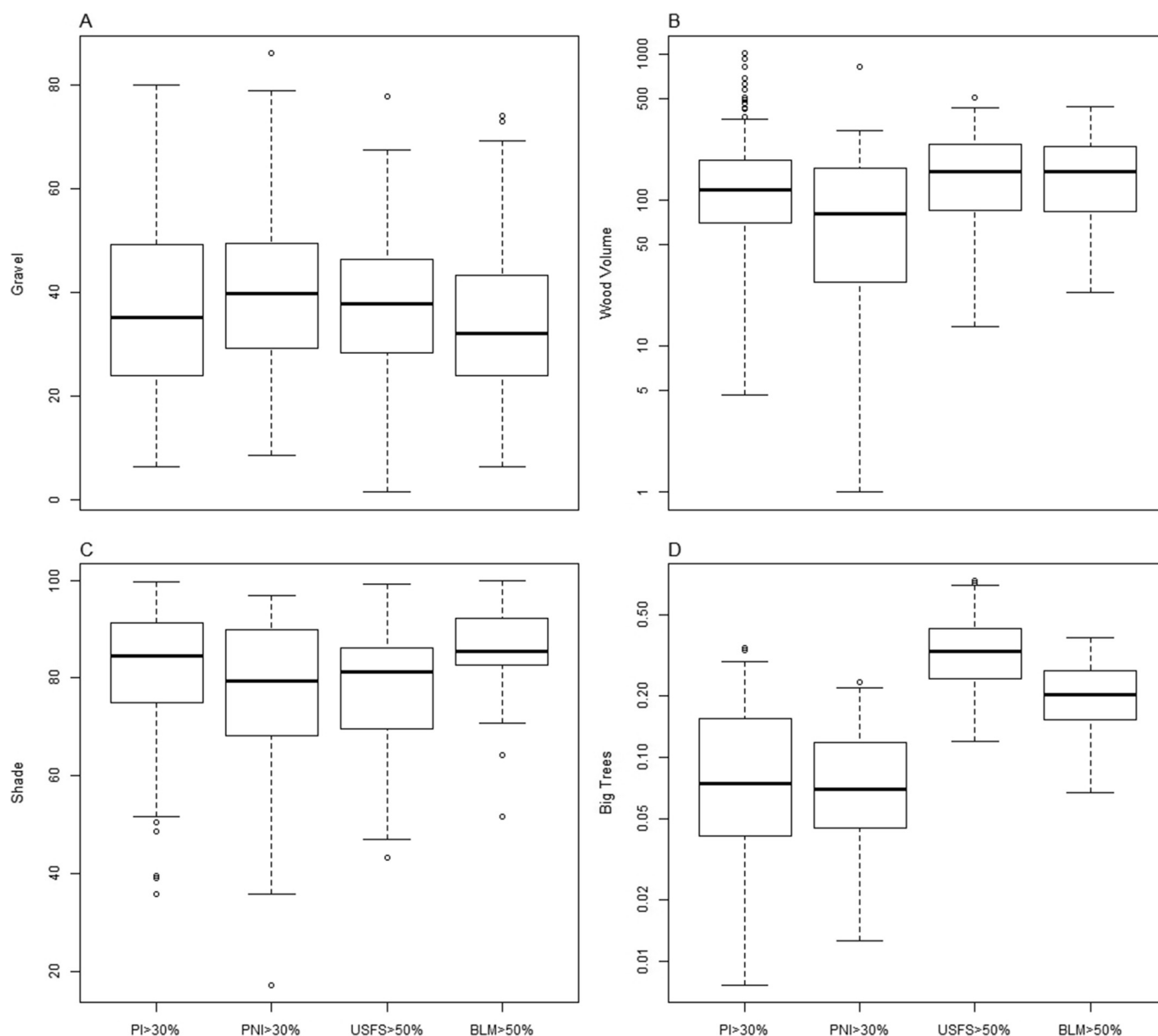
We identified a few patterns across the Oregon Coast of particular importance for model-building and interpretation. First, there is a clear north–south gradient in terms of precipitation and geology. River basins in the southern parts of our study area have less rainfall and more sedimentary rock (Fig. 2). Models that include these two variables may also include information about other, unmeasured variables that vary longitudinally, such as air temperature or landslide susceptibility. Second, there is an east–west gradient from areas of higher elevation with smaller streams that have steeper gradients to areas of lower elevation, lower gradient, and wider streams that drain to the ocean. These sets of variables covary in predictable ways, and in fact, we were not able

to eliminate all spatial covariance along this east–west gradient in our base model of pool surface area. When any one of these variables is used in a model, information about the others is also included by default. Third, land ownership is not distributed evenly across the study landscape. Therefore, statistical tests to explore relationships between site history and instream response need first to account for landscape context.

Landscape-scale predictors are better at explaining the distribution of pool habitat than at explaining the density of fish in pools

The distribution of pools across the landscape can be relatively well-modeled with landscape-scale predictors. Summer pool surface area varied across reaches but was relatively stable over time within a particular reach; there was little correspondence in pool surface area for reaches within the same catchment; and the base model of pool surface area, using only immutable landscape-scale variables, was able to explain over 60% of the variability in pool surface area. Previous correlative research in this and in other regions also identified relationships between similar landscape attributes and the distribution of pool habitats (Burnett et al. 2006; Hicks and Hall 2003). Our model includes variables that indicate stream power (e.g., elevation and drainage area) and erod-

Fig. 6. The distribution of (A–C) instream habitat variables associated with high-quality juvenile coho habitat as a function of land ownership and (D) percentage of the catchment with big trees (Table 1). Gravel is the proportion of the streambed area that is classified as gravel (2–64 mm). Wood volume is the volume of instream wood per 100 m of reach length (m^3 per 100 m). Note that the y axis for wood volume uses a log-scale. Percent shade is the percentage of the stream channel that is shaded. PI = private industrial; PNI = private nonindustrial; USFS = USDA Forest Service; BLM = Bureau of Land Management.



ibility of underlying geology (e.g., sedimentary rock) and so have a well-understood mechanistic interpretation. Pools are formed by scour around obstructions as well as where relatively soft substrates are eroded by streams with adequate stream power (Hicks and Hall 2003; Buffington et al. 2002; Montgomery et al. 1999; Wohl et al. 1993; Frissell et al. 1986).

Landscape-scale predictors explain less variation in the density of juvenile coho salmon within pools than in pool surface area. Juvenile coho salmon density varied greatly among years, and this interannual variability confounded identification of consistent relationships between fish density and landscape attributes. Landscape-scale predictors that varied annually were unavailable for use in modeling; thus, our model of juvenile coho salmon estimates the mean density over time and explains less of the observed variation in the data than our model of pool surface

area. We chose to model pool habitat and juvenile coho salmon independently to untangle how intrinsic attributes of the landscape drive these two responses and to test specific hypotheses about human impacts.

Future efforts to model juvenile coho density may benefit from exploring time-varying predictors, such as annual flow, descriptors of other life-cycle stages (e.g., counts of spawning adults), and incorporation of spatial patterns on stream networks. Observed relationships between juvenile coho salmon and landscape conditions may depend on population dynamics; when marine survival is low, adult returns are few, and the number of resulting juveniles can be very low. In years when few adults return, we might expect juvenile coho salmon to inhabit only core habitats (Flitcroft 2007), and in years with greater adult returns, we might expect juvenile coho salmon to expand into more marginal areas

(Flitcroft et al. 2014). Additionally, the proximity of adult and juvenile habitats or the network distances between suitable seasonal habitats may influence juvenile coho salmon distribution (Flitcroft et al. 2012). The most successful habitats are likely to be where there is both suitable habitat for adults to spawn and juvenile coho salmon to rear and overwinter (Anlauf-Dunn et al. 2014).

Intrinsic attributes of a site are useful for explaining pool surface area

The concept behind a site's IP is that some areas are naturally, or intrinsically, more suitable as fish habitat. Burnett et al. (2007) defined the IP of a site for juvenile coho salmon as the geometric mean of normalized variables describing gradient, mean annual stream flow, and valley constraint. In the absence of human impacts, sites with a high IP are capable of supporting a larger number of fish than sites with low IP. Length-weighted mean IP was used successfully to estimate where on the landscape one might expect to find juvenile coho salmon habitat across streams in coastal Oregon, the Willamette River valley, and a part of the lower Columbia River basin when actual habitat conditions and juvenile coho salmon distribution were unknown (Burnett et al. 2007). Flitcroft et al. (2014) found that the IP of stream reaches was useful in understanding distributional patterns of juvenile coho salmon.

Using 16 years of observed pool surface area from randomly selected sites across the Oregon Coast, we found that a similar suite of variables to those for calculating IP (Burnett et al. 2007) could describe this defining characteristic of juvenile coho salmon habitat in summer (Nickelson et al. 1992): pool surface area. Like IP, our base model was strongly influenced by stream gradient. We lacked access to localized flow observations, but our model included drainage area, which is highly correlated with mean annual flow in most regions. Our model also included gradient and sedimentary geology, which in this region describes a concept very similar to valley confinement. Our results provide further evidence that IP can be a useful management tool for coho salmon across the Oregon Coast.

Indices similar to IP have been used successfully for predicting the distribution of key habitat characteristics for other salmonid species, other life stages, and in other regions. Busch et al. (2013) combined valley confinement, stream width, and gradient to successfully identify potential Chinook salmon spawning habitat in the nearby lower Columbia River basin. Bidlack et al. (2014) used mean annual flow, gradient, and glacial influence to identify probable habitat for juvenile Chinook salmon across the vast Copper River watershed, Alaska. These indices may, in fact, be useful for a wide range of fishes across a wide range of geographies. Using 1548 pan-European sample sites, Logez et al. (2012) modeled the distribution of 21 common fish species and found that stream power, a function of gradient and stream flow, was the only variable retained in the best model for all 21 species.

IP (Burnett et al. 2007) can also be used to estimate the quantity of available habitat that is potentially highly suitable. In our data set, and in most situations, field data describing instream habitat conditions are only available for a subset of a basin or for a particular reach of interest. Therefore, the total length of highly suitable habitat available to migratory species cannot be calculated or estimated from on-the-ground observations. In our models, the quantity of available habitat that is potentially highly suitable, total length of reaches within the catchment that have a high IP, improved our models of pool surface area even for a model that already included a suite of landscape variables similar to those in the primary IP index. The additional information provided by this metric was expected to estimate the total amount of high-quality habitat potentially available to fish, regardless of basin size. Given the high level of spatial correlation in variables associated with IP,

the total length of high IP habitat upstream of a reach may also serve simply as an index of landscape context for a given reach.

Land ownership is correlated with the distribution of pool habitat

Looking at the relative contributions of public, private industrial, and private nonindustrial ownership to our model, we see that pool surface area was higher in areas with higher proportions of public ownership and lower in areas with higher proportions of private ownership. Furthermore, this negative effect was stronger for private lands not used for industrial forestry than areas with high proportions of private industrial forestry. Similar results have been observed elsewhere. Examining over 200 watersheds distributed across the Columbia River Basin, Kershner et al. (2004) found that pools in unmanaged watersheds tended to be deeper and to have fewer fine sediments in the pool tails as compared with managed watersheds. As with most of our potential predictors, ownership did not have a statistically significant effect on juvenile coho salmon density within pools.

Our explanation of these results is that differences in aquatic conditions across land ownerships reflect site histories, including terrestrial and aquatic land management. In the nearby Puget Sound region, trends in adult coho salmon over time were correlated with trends in forest cover and inversely correlated with urbanization (Bilby and Mollot 2008). Across 156 watersheds on Vancouver Island, Canada, just a bit further north, a legacy of current and historical forest management, indicated by forest fragmentation, no-forest cover, and early successional forests, was the one landscape characteristic that had a generally negative relationship with anadromous salmon populations across species (Andrew and Wulder 2011).

Interpreting our results with respect to land management requires caution and further investigation. The first consideration is the underlying correlation between land ownership and topography; for example, high-elevation lands are much more likely to be managed by the USFS than to be in nonindustrial private ownership. The history of ownership across natural landscape gradients has led to the highly structured nature of the Oregon Coast landscape as described above. Testing for the effect of ownership only after incorporating the effects of various immutable landscape attributes can account for some of the unbalanced and covarying spatial patterns but cannot eliminate the issue. As such, our analysis cannot be interpreted as a causal relationship between ownership and pool habitat. Rather, our results show that surface area of pool habitat for a given reach, after accounting for immutable attributes of the landscape surrounding the reach, differs by ownership.

Legacies of past human activities persist

Although the practice of log drives and splash-damming streams and rivers ended over 50 years ago, we observed an effect on current stream habitat conditions. The length of stream affected by log drives was loosely associated with a reduction in pool area even after accounting for landscape configuration, and there is a potentially large effect of splash-damming on juvenile coho salmon density observed within pool habitat. Across the few reaches where splash dams were present, we observed an over 100% increase in juvenile coho salmon density. The evidence is not particularly strong owing to a small sample size and variable data, but the potential effect size is large (Table 4). Although our landscape-scale models were unable to detect an effect of splash dams on pool surface area, Miller (2010), by isolating the effects of splash dams through upstream–downstream comparisons, found fewer deep pools and more exposed bedrock in reaches affected by splash dams. In combination, the evidence suggests that log drives and splash dams reduce pool surface area, leaving juvenile coho salmon to be present at much higher densities than might otherwise be expected in the remaining pool habitat. Current and

future fish habitat assessments will benefit from knowledge of these and other disturbance legacies and can contribute to a refined understanding of these potential effects.

Land ownership and current habitat conditions

Ignoring the spatial structure of the data and simply comparing the distribution of various immutable variables across areas with high and low (relatively) proportions of various ownership categories, we can again see that underlying landscape attributes differ by ownership (Fig. 3). Areas with high proportions of private nonindustrial lands are at lower elevations, have lower stream gradients and somewhat larger drainage areas, and therefore somewhat higher mean IP. These streams are in downstream coastal areas that should have large amounts of pool habitat. After accounting for immutable variables to the best of our ability, we observed that reaches draining catchments with higher amounts of private nonindustrial lands, in fact, have lower pool surface areas (Table 4; Fig. 4).

In follow-up exploratory analyses, we did not find major differences in other attributes of instream habitat across land ownership other than a potential reduction in wood volume for sites in private nonindustrial ownership. We did observe large differences between public and private ownerships in the proportion of a catchment with large trees (Fig. 6). Few sites in private ownership maintained more than 30% of the catchment in big trees. Public forests are also relatively young, with approximately 30% of the forested lands estimated as older than 120 years (Fig. 5). These patterns suggest potential additional legacies of site history across the landscape.

We confirmed that public and private lands have fairly different histories of terrestrial forest management, with the most visible differences likely reflecting shifts in timber harvest practices on federal lands that began approximately 30 years ago (FEMAT 1993) (Fig. 5). Forests harvested between 30 and 90 years ago were likely harvested without riparian buffers, and similar percentages of forested land within each ownership category were harvested during this period (Fig. 5). While harvest approaches changed in the late 20th century to varying degrees on all ownerships, the disturbance legacy remains. With respect to, for example, wood recruitment, it is likely to be 200–300 years postharvest before riparian forest function approaches preloggings levels (Beechie et al. 2000).

There are plausible mechanistic interpretations of our findings. The influence of forest harvest on instream habitats and, in particular, on pool distribution are well-studied. For example, clearcutting without riparian buffers has been associated with reduced pool areas in Alaskan streams (Heifetz et al. 1986). A meta-analysis of effects of riparian harvest across many published studies found reductions in pool size across a wide variety of stream sizes and stream gradients (Mellina and Hinch 2009). It is important to also consider how other aspects of site history might vary systematically across land ownership and how these might also be influencing riverine ecosystems. Such differences reflect non-timber resource extraction, road building, cattle grazing, agriculture, water extraction, streambank stabilization practices, and human development.

Management implications

Although there is a high degree of spatial structure across the Oregon Coast landscape, we were able to identify immutable or intrinsic landscape attributes that provide a good estimate of the distribution of pool surface area and that can contribute to an understanding of juvenile coho salmon density within pools. Where on-the-ground observations are lacking, estimates based on immutable attributes or IP provide managers with useful information for identifying and prioritizing restoration and conservation opportunities. Comparisons between empirical observations and estimates based on these immutable landscape attributes can suggest where streams are not reaching their potential in supporting high-quality

habitat or high densities of juveniles, building a foundation on which to quantify and understand human effects on the landscape. Developing such a mechanistic understanding of how anthropogenic actions, across catchments and within reaches, influence aquatic ecosystems is particularly important because effects are likely long-lived. We found fairly strong evidence of differences in pool surface area across lands with varying current ownership and therefore varying site histories. Further, we found evidence that historical land and river management activities, in particular splash dams that occurred at least 50 years ago, may continue to influence the distribution of juvenile coho salmon and their habitats today.

Acknowledgements

We thank Kelly Christiansen for extensive help with spatial databases and the creation of Fig. 1. We also thank Dana Infante, Michigan State University, for a particularly helpful manuscript review and two anonymous reviewers whose ideas enriched and clarified our paper. This work was supported by the National Council for Air and Stream Improvement and the Pacific Northwest Research Station of the USDA Forest Service.

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