Landscape characteristics and coho salmon (*Oncorhynchus kisutch*) distributions: explaining abundance versus occupancy

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Abstract: Distribution of fishes, both occupancy and abundance, is often correlated with landscape-scale characteristics (e.g., geology, climate, and human disturbance). Understanding these relationships is essential for effective conservation of depressed populations. We used landscape characteristics to explain the distribution of coho salmon (*Oncorhynchus kisutch*) in the Oregon Plan data set, one of the first long-term, probabilistic salmon monitoring data sets covering the full range of potential habitats. First we compared data structure and model performance between the Oregon Plan data set and two published data sets on coho salmon distribution. Most of the variation in spawner abundance occurred between reaches but much also occurred between years, limiting potential model performance. Similar suites of landscape predictors are correlated with coho salmon distribution across regions and data sets. We then modeled coho salmon spawner distribution using the Oregon Plan data set and determined that landscape characteristics could not explain presence vs. absence of spawners but that the percentage of agriculture, winter temperature range, and the intrinsic potential of the stream could explain some variation in abundance (weighted average $R^2 = 0.30$) where spawners were present. We conclude that the previous use of nonrandom monitoring data sets may have obscured understanding of species distribution, and we suggest minor modifications to large-scale monitoring programs.

Résumé : La répartition des poissons, tant en occupation qu'en abondance, est souvent corrélée à des caractéristiques à l'échelle du paysage, telles que la géologie, le climat et les perturbations anthropiques. Il est essentiel de comprendre ces relations pour une conservation efficace des populations réduites. Nous utilisons des caractéristiques du paysage pour expliquer la distribution des saumons coho (*Oncorhynchus kisutch*) dans la banque de données d'Oregon Plan, une des premières banques de données probabilistes et à long terme de surveillance des saumons qui couvre l'entière gamme des habitats potentiels. Nous comparons d'abord la structure des données et la performance des modèles dans la banque de données d'Oregon Plan avec deux ensembles de données publiées sur la répartition du saumon coho. La plus grande partie de la variation de l'abondance des reproducteurs se produit entre les sections, mais il y en a aussi beaucoup entre les années, ce qui restreint la performance potentielle du modèle. Des séries semblables de variables prédictives du paysage sont en corrélation avec la répartition des saumons coho, et cela dans toutes les régions et les ensembles de données. Nous avons ensuite modélisé la répartition des reproducteurs chez les saumons coho à partir de l'ensemble de données d'Oregon Plan; les caractéristiques du paysage ne peuvent expliquer la présence opposé à absence des reproducteurs, mais le pourcentage d'agriculture, l'étendue des températures hivernales et le potentiel intrinsèque du cours d'eau peuvent expliquer une partie de la variation (R^2 moyen pondéré = 0,30) là où les reproducteurs sont présents. Nous concluons que l'utilisation antérieure d'ensembles de données aléatoires de surveillance ont pu avoir restreint la compréhension de la répartition de l'espèce et nous suggérons des modifications mineures aux programmes de surveillance à grande échelle.

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Introduction

Correlative analyses linking landscape characteristics to the distribution and abundance of aquatic species and their habitats are used increasingly to understand how landscape structure and content drive aquatic systems (Hughes et al. 2006; Steel et al. 2010; Johnson and Host 2010). The theoretical

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framework underlying these analyses is that the local habitat conditions on which aquatic species depend are, in turn, controlled by patterns of land use, land form, climate, and geology over broad spatial extents (Frissell et al. 1986; Imhof et al. 1996; Richards et al. 1996). This landscape perspective is built on an understanding of geomorphic controls, environmental gradients, and relationships between instream habitat and biological communities (Ward 1998). While linkages among landscapes and associated physicochemical and biological characteristics of rivers have long been recognized (Gorman and Karr 1978), the development of conceptual frameworks and tools for measuring and quantifying such linkages is more recent (e.g., Allan and Johnson 1997; Fausch et al. 2002; Hughes et al. 2006). Many studies have documented the statistical associations between land use and in-stream habitat conditions or biological communities using multisite comparisons and empirical models (Allan 2004). Collectively, these studies provide strong evidence of the importance of the surrounding landscape and of human activities to a stream's ecological integrity (Durance et al. 2006; Steel et al. 2010).

Pacific salmonids have been a focus of landscape riverine analyses because these fish inhabit a large range, migrate over long distances, and are a target of conservation efforts (e.g., Pess et al. 2002; Feist et al. 2003; Steel et al. 2004). A better understanding of salmonid abundance and spatial structure during their freshwater life stages is needed for managing declining populations. Information about how abundance and structure are impacted by landscape conditions and large-scale human activities can support decisions about the location of conservation and restoration actions, monitoring plan designs, or mitigation of the impacts of future human development.

Although landscape predictor variables are widely available (Johnson and Gage 1997; Mertes 2002), the collection of biological response data over landscape scales remains a major challenge. Much of the research on correlations between salmon and landscapes (e.g., Pess et al. 2002; Isaak et al. 2003; Steel et al. 2004) has been hampered by dependence on existing biological data, small data sets, and nonrandom sample-reach selection. Data are often from index reaches, which are usually handpicked to monitor areas of high fish production. Trends in coho salmon (*Oncorhynchus kisutch*) stocks along the coast of Oregon, USA, for example, have been estimated from spawning fish surveys conducted in index reaches annually since 1950 (Cooney and Jacobs 1995). While such data may have a long history, they are not sufficient for salmonid population management (Jacobs et al. 2002). Population estimates based on data from index reaches are often biased (Jacobs et al. 2002; Isaak et al. 2003; Courbois et al. 2008).

The monitoring strategy of the Oregon Plan for Salmon and Watersheds (http://nrimp.dfw.state.or.us/OregonPlan/) (hereafter referenced as the Oregon Plan) was developed in response to the need for accurate estimates of salmon population abundance, trend, and spatial structure over large areas. It implements a probabilistic sampling of river reaches and thus improves collection of salmon abundance and distribution data. The sampling strategy provides a system for collecting data on salmon population performance using a spatially balanced, random sample that produces unbiased es-

timates of population abundance over time with associated estimates of precision (Stevens 2002). A further advantage of probabilistically sampled data is that the explicit sampling frame provides a clear domain over which inference can be drawn and over which models based on that data can be applied. Observations cover a wide range of stream reaches, adding types of reaches often excluded by opportunistic or selective sampling schemes. Including a wide range of reaches, for example, those where salmon only occasionally spawn, allows one to differentiate between landscape characteristics driving fish abundance and productivity and those correlated with occupancy or spatial structure. However, such a sampling approach is likely to yield a data set with numerous observations of zero. These zeros might result from multiple processes such as observer error, absence of fish even where reach conditions are suitable, and unsuitable conditions (Martin et al. 2005). Although potentially providing new information on salmon distribution and occupancy, a data set with numerous zeros also presents statistical challenges.

In this paper, we take advantage of probabilistically sampled data, collected under the Oregon Plan, to expand our understanding of coho salmon spawner distribution and to quantify relationships between landscape characteristics and both occupancy and abundance of spawning coho salmon. The specific objectives of our study are (*i*) to quantify and compare variance in spawner counts over space and time, (*ii*) to identify those landscape features most strongly correlated with occupancy and abundance, (*iii*) to compare models of occupancy versus abundance, and (*iv*) to compare models built from the Oregon Plan data set to models based on data collected using more ad hoc sampling schemes. The two previously published data sets, each from a nonrandom selection of index reaches, are the Firman et al. (2011) data set on coho salmon within the same Oregon Coast region and the Pess et al. (2002) data set describing coho salmon distribution in the Snohomish River basin. Our analysis goes beyond previous riverine landscape studies because of the probabilistically sampled biological response data and the large sample size (9 years of data from 95 stream reaches). We synthesize how data collected using a random sampling design has changed our understanding of the impacts of landscape characteristics on salmon populations, and we outline the implications of our analyses for designing large-scale aquatic monitoring programs.

Materials and methods

Study area

All Oregon Plan survey reaches in our analysis are within the Oregon Coastal Province (Fig. 1; 20 305 km^2). The region is dominated by mountains and 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 is below 700 m and in areas of lower gradients (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 following winter rainstorms and rain-on-snow events.

The study area is dominated by coniferous forests. Western red cedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyl-*

Fig. 1. Study area in Oregon, USA, with watersheds draining to each survey reach identified. Legend denotes coho salmon spawners per kilometre in the study reach within each watershed.
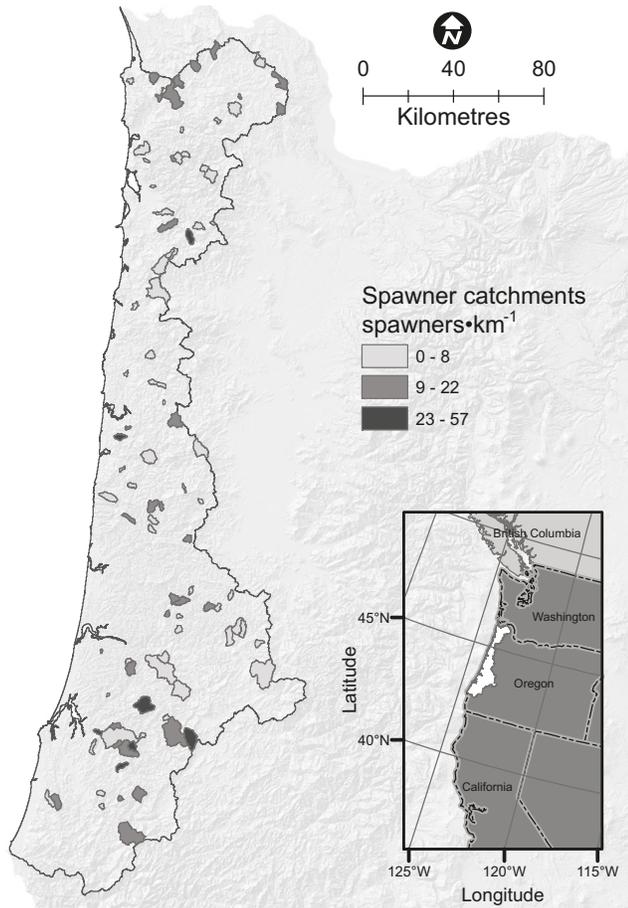
lum) are found in riparian areas. Approximately 50% of the riparian areas adjacent to streams with the highest potential to provide habitat for coho salmon is either nonforested or has been recently logged (Burnett et al. 2007). Upland forest disturbance regimes have been driven by timber harvest and recent fire suppression as well as by past infrequent but intense wild fires and windstorms (Franklin and Dyrness 1988). Most of the current forestland is relatively young, and the larger river valleys have been cleared for agriculture (Ohmann and Gregory 2002). The majority of the land is privately owned; about a third of the land is publicly managed (Spies et al. 2007). In addition to coho salmon, four other salmonid species reside in the study area: coastal cutthroat trout (*Oncorhynchus clarkii*), Chinook salmon (*Oncorhynchus tschawytscha*), chum salmon (*Oncorhynchus keta*), and steelhead (*Oncorhynchus mykiss*).

Coho salmon data

Coho salmon in the study region belong to the Oregon Coastal Coho Evolutionarily Significant Unit (ESU) (Weitkamp et al. 1995), which is listed as threatened under the US Endangered Species Act of 1973. To monitor abundances of coho salmon spawners under the Oregon Plan, the Oregon Department of Fish and Wildlife first divided the river network in the ESU into reaches about 1.6 km long; reach breaks were aligned with natural features whenever possible.

They selected reaches for monitoring according to a probabilistic survey design (Stevens 2002). Reaches were visited every 7–10 days from mid-October until late January to estimate total spawners. Coho salmon abundance over an entire spawning season in each sampled reach was estimated from the spawning survey counts using the area-under-the-curve (AUC) method (e.g., an approximation to the integral of the curve that describes fish counts over time; Beidler and Nickelson 1980; Hilborn et al. 1999) and standardized as spawners per kilometre. During each survey, surveyors walked upstream counting all live and dead coho salmon. Counts of jacks (≤50 cm fork length) were kept separate from counts of adults; counts of marked fish were kept separate from unmarked fish; and counts of new carcasses were kept separate from counts of previously handled carcasses, which were marked by removing the tail. Counts were included in AUC estimates only when water visibility was good enough to see to the bottom of riffles. If fish were still spawning in a reach at the end of the season, surveys of that reach generally continued until a zero count was obtained. The average coho salmon is assumed to stay alive on the spawning grounds for 11.3 days (Willis 1954; Beidler and Nickelson 1980; Perrin and Irvine 1990). Thus, the probability of detection, if fish were present, was very high, and the probability of detecting an effective spawning situation (two fish present at the same time) was even higher.

Oregon Plan monitoring surveys feature a rotating panel design with rotations every 1, 3, and 9 years to coincide with the 3-year life cycle of coho salmon. Under the Oregon Plan, an additional set of sites are surveyed only once. These sites are not used in our analysis. The Oregon Plan sampling 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).

We analyzed Oregon Plan data from reaches that were surveyed annually from 1998 to 2006 and used log-transformed coho salmon densities (spawners per kilometre) to help meet normality assumptions. For all analyses, we excluded four reaches in basins dominated by lakes (Siltcoos Lake, Tahkenitch Lake, and Tenmile Lake) and reaches that were shorter than 0.6 km. In addition, we excluded all reaches with fewer than seven surveys in the period 1998–2006 and two reaches that were never observed to have spawners and were therefore considered not to reflect potential spawning habitat. Our total sample size was 95 reaches, with 53 reaches surveyed in all 9 years, 28 reaches surveyed in 8 years, and 14 reaches surveyed in only 7 years.

Landscape data

Our predictor variables for modeling coho salmon were created from geospatial data layers describing climate, geology, land form, and land use. These predictors are similar to those used in other riverine landscape studies on other salmonid species or life stages (e.g., Van Sickle et al. 2004; Steel et al. 2004; Burnett et al. 2006). We focused on those landscape characteristics thought to influence the distribution and abundance of coho salmon in the Oregon Coastal Province (Table 1). We included stream gradient, precipitation, and mean annual flow because coho salmon spawn in small, low-

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Table 1. Geospatial variables used in analysis and source data layers with associated scale.

Geospatial data layer	Map scale	Gridcell size	Description
Modeled air temperature	NA	4000 m	Ambient air temperatures (1961–1990) expressed as means over the subtypes described, from Precipitation Elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 1997); calculated as an area-weighted mean • Maximum annual temperature • Minimum annual temperature • Annual temperature range (AnnualRange) • Summer temperature range • Winter temperature range (WinTRange)
Modeled precipitation	NA	4000 m	Cumulative mean annual precipitation (1961–1990) from PRISM (Daly et al. 1997); calculated as an area-weighted mean (Precip)
Geology A	1:500 000	NA	Classification of geologic map units according to major lithology (Walker et al. 2003) • Alluvium • Landslide (Landslide) • Mafic (Mafic) • Sedimentary (Sedimentary)
Geology B	1:500 000	NA	Classification of geologic map units according to major lithology as generalized from the Quaternary geologic map of Oregon (Walker and MacLeod 1991) • Resistant rock (Resistant) • Intermediate rock • Weak (erosive) rock (Weak) • Unconsolidated deposits (Unconsol)
Land ownership	1:24 000	NA	Land ownership classification from the Oregon Department of Forestry and aggregated into classes (Burnett et al. 2007) • US Bureau of Land Management (BLM) • USDA Forest Service • Public lands = BLM + USDA Forest Service + State of Oregon (Public) • Private industrial forests and all other private lands (PrivateInd) • Private nonindustrial forest (PrivateNI)
Tree size and type	1:24 000 – 1:500 000	NA	Predictive mapping of forest composition using direct gradient analysis and nearest neighbor imputation. Thirty-four original vegetation types were generalized to five (Ohmann and Gregory 2002). • Large conifers (>50 cm diameter) • Medium trees (25–50 cm diameter) • Small trees (SmallTrees, <25 cm diameter) • Remnant (Remnant) • Hardwood (Hardwoods)
Timber harvest	NA	25 m	Timber harvest occurrence (Lennartz 2005) • Not harvested before or during spawner survey • Harvested prior to 1998 (Cut) • Nonforested land (NonForest)

Land use	NA	25 m	A combination of forest cover, human development, and zoning (Burnett et al. 2007)
			• Agricultural (Ag)
			• Rural
			  a. Rural residential
			  b. Low density rural residential

Roads	1:24 000	10 m	Road density expressed as linear km of road per unit area of corresponding area of influence (Roads)
Cow density	NA	30 m	Density of cows per unit area of grazeable land on grazing allotments, by county; based on the 1997 Agricultural Census and the National Land Cover Data (NLCD) (National Atlas of the United States 1997) (CowDensity)
Gradient	1:24 000	10 m	Calculated from USGS 1:24 000, 10 m digital elevation model (DEM); defined as rise (upstream elevation minus downstream elevation of index reach) over run (river kilometre length of index reach) multiplied by 100
Elevation	1:24 000	10 m	Elevation of downstream terminus of reach, as measured from 10 m DEM (Elevation)
Stream flow	1:24 000	NA	Modeled mean annual (1961–1990) stream discharge ($m^3 \cdot s^{-1}$, Clarke et al. 2008)
Intrinsic potential	1:24 000	10 m	Predicted total area of instream rearing habitat for juvenile coho salmon (*O. kisutch*) (Burnett et al. 2007) (IntPotential)

Note: Variable names are identified and underlined for those variables that were identified in a logistic model (Table 3), ended up in the final set of mixed models (Tables 4 and 5), or were included in the large-scale models in Firman et al. (2011) (Table 5). NA, not applicable.

gradient tributaries (Nickelson et al. 1992; Montgomery et al. 1999; Lawson et al. 2004). Land management, such as forest harvest and agriculture, also clearly affects the abundance of deep, shaded pools (Bisson and Sedell 1984) that are important for juvenile rearing (e.g., Hartman 1965; Narver 1978; Scrivener and Andersen 1984). We specifically included attributes identified as important predictors of coho salmon distribution in previous analyses of index-reach data for this same region (Firman et al. 2011) and of index-reach data for the Snohomish River in Washington State (Pess et al. 2002).

The area of influence (AOI) over which we summarized landscape characteristics relevant to each survey reach included all seventh-field hydrologic units (Clarke and Burnett 2003) adjacent to that reach. Hydrologic units are nested watersheds as designated by the US Geological Survey. The AOI in our analysis usually encompassed all lands draining directly into the reach from the sides (for larger reaches) and all lands draining into the reach from both the sides and above (for smaller reaches). To quantify landscape predictor variables within each AOI, we calculated the fraction of total AOI for categorical variables (i.e., geology, land cover). For continuous variables (i.e., air temperature or road density), we calculated the area-weighted mean to provide an indication of average conditions over the entire AOI. For each surveyed reach, we also calculated the length-weighted average of intrinsic potential for coho salmon. Intrinsic potential evaluates species-specific suitability in the absence of anthropogenic impacts by indexing and combining stream gradient, stream constraint, and mean annual stream flow (Burnett et al. 2007). Inputs used to calculate coho salmon intrinsic potential were previously estimated from field data and 10 m digital elevation models (DEMs) (Clarke et al. 2008).

Statistical methods

We applied a series of three independent statistical analyses. (*i*) We used variance partitioning to better understand the sources of variation in our coho salmon spawner data. (*ii*) We built the best possible model to explain the distribution of coho salmon in the Oregon Plan data set from landscape characteristics. Because of the large number of zeros in the data, we modeled occupancy and abundance of coho salmon spawners separately using a two-step modeling process akin to a hurdle model. Hurdle models have been successfully used on a wide range of problems (e.g., Shonkwiler and Shaw 1996; Potts and Elith 2006). In the first step, we built a logistic regression model to explain presence vs. absence patterns or occupancy. In the second step, we modeled annual abundance patterns within occupied reaches. (*iii*) We compared variance partitioning results and significant landscape predictors between the Oregon Plan data set and the Firman et al. (2011) and Pess et al. (2002) data sets.

Understanding and comparing the structure of the data: variance partitioning

Variance partitioning allows us to estimate the proportion of total variation in coho salmon spawner abundance data that we could account for if our landscape models were perfect. Accounting for all of the variation in the data is an unrealistic expectation if a part of that variation comes from unmodeled sources. In our case, we are modeling consistent reach-to-reach differences not temporal variation. We fit ran-

dom effects models to explain this reach-to-reach variation only. Our modeling approach accounted for differences in mean abundance for each year but did not explain differences in mean abundance across years. The residual variation in our final models includes measurement error, lack of fit, and year-to-year variation. We calculated the ratio of reach-to-reach variance over residual variance as a relative measure of precision that indicates the potential for finding a relationship between variables (Kaufmann et al. 1999). The ratio of reach-to-reach to residual variation is a measure akin to a signal-to-noise ratio. It explains how much of the variation in the data occurs between reaches (the signal) versus how much variation remains unexplainable even after considering year-to-year variation (the noise).

From the variance components, we estimated the ratio of reach-to-reach variance over residual variance ($\sigma^2_{reach}/\sigma^2_{residual}$) and, from that, the maximum R^2 value that could be achieved given the observed residual variance and a perfect correlation between coho salmon density (spawners per kilometre) at a particular reach and landscape characteristics. We explored the magnitude of year-to-year variance as compared with reach-to-reach variance, but we did not include the year-to-year variance in the residual variance because our models accounted for some of the differences in mean abundance each year. The estimated maximum R^2 is simply an indication of what might be considered a good model fit. The exact value of the maximum model fit will depend on the type of model used.

Two-step modeling: occupancy and then abundance where present

We assumed that most zeros in the Oregon Plan data set represent true absences of coho salmon spawners, as reaches were revisited on up to 10 occasions in a spawning season; therefore, we did not chose a zero-inflated model to account for incomplete detection (e.g., Wenger and Freeman 2008). Instead, we lumped zeros together and applied a modified hurdle model addressing two processes: one generating the zeros (occupancy) and one generating the positive values (abundance given occupancy). The approach begins by modeling the data as presence vs. absence. For observations in which the "hurdle" of presence is achieved, an independent model of the nonzero values is built. The use of a hurdle model allows for the possibility that the process driving occupancy (zeros) differs from the process driving abundance given that the location is occupied (positive values).

We developed logistic regression models with landscape predictor variables to explain presence vs. absence of coho salmon spawners across reaches in each year. Where spawners were present, we modeled density (spawners per kilometre) using linear mixed effects models as implemented in Proc Mixed in SAS (Littell et al. 1996). The response data were annual time series of coho salmon density (spawners per kilometre), including only observations greater than zero. Data were log-transformed to meet normality assumptions. We used a repeated measures design, with the landscape variables measured across reaches only and the density estimates measured within reaches. The correlation among density estimates at a particular reach was modeled using an ARMA (1,1) correlation structure, and reaches were assumed to be independent; thus, the unscaled covariance matrix is block di-

agonal with ARMA(1,1) blocks corresponding to each reach (Littell et al. 1996). Akaike's information criterion (AIC) was used to select the best fitting correlation structure. In addition, we assumed that the mean density in each year was randomly distributed around the mean over all years, so we included a random intercept. All models in this step were fit with maximum likelihood procedures.

The model selection procedure was a modified all-subsets procedure used in similar published analyses (Steel et al. 2004; Firman et al. 2011). We considered a maximum model size of three variables, ruling out models based on AIC values, high collinearity, or low stability (e.g., model fit is strongly influenced by only one observation with high leverage). We fit the null model (intercept only), all one-variable models, and all two-variable models including a quadratic term as a second covariate. To save computer time, we fit three-variable models by adding all potential predictors only to two-variable models with an AIC less than that of the null model. We then calculated the difference in AIC values between each model of any size and the lowest AIC among all models (ΔAIC). We retained all models with a ΔAIC less than four. This relatively conservative cut-off (Burnham and Anderson 2002) was applied to reduce the list of candidate models.

We further refined the set of best models using two criteria. The condition index (Belsley et al. 1980) identifies models in which predictor variables are correlated with one another. Models with a condition index > 10 have moderate collinearity and were rejected. Cook's D was calculated to identify unstable models due to data points with high leverage; models with data points for which $D > 1.00$ were eliminated. To identify the final set of best models, we ranked the remaining models by ascending AIC and calculated AIC weights (Burnham and Anderson 2002). The final set of best models were those for which the AIC weight of the next model was less than 0.05 or the AIC weight of the next model was less than 0.10 and the sum of the AIC weights for the current set of models was greater than 0.50. To manage for uncertainty in model selection, we present a set of best models.

Comparison with previous analyses

We compared our data structure and model results with two other previously published data sets, each from a nonrandom selection of index reaches. The Firman data set contains observations of adult coho salmon densities (spawners per kilometre) from 44 index reaches over 17 years in the study region covered by the Oregon Plan data set (Firman et al. 2011). The Pess data set contains observations of fish days (sum, over observation period, of live fish observed on each survey date multiplied by the number of days between surveys) from 54 index reaches over 15 years in the Snohomish River basin, Washington (Pess et al. 2002). We estimated the reach-to-reach, the year-to-year, the residual, and the ratio of reach-to-reach to residual variation for both of these additional data sets.

To compare our landscape modeling results with those of Firman et al. (2011), we attempted to fit a mixed model to the full Oregon Plan data set (zeros and positive values). To compare our results with that of Pess et al. (2002), we fit hierarchical linear models following their methods. Model selection considered all subsets up to three landscape variables, including a quadratic term.

Fig. 2. Mean coho salmon density (spawners per kilometre) when spawners were present between 1998 and 2006 at each reach from the Oregon Plan monitoring data (y axis) organized by the number of years in which no spawners were observed at that reach (x axis). The negative slope is to be expected, but the surprising result is the relatively high density of spawners observed at reaches with 2, 3, and even 4 years in which spawners were completely absent.
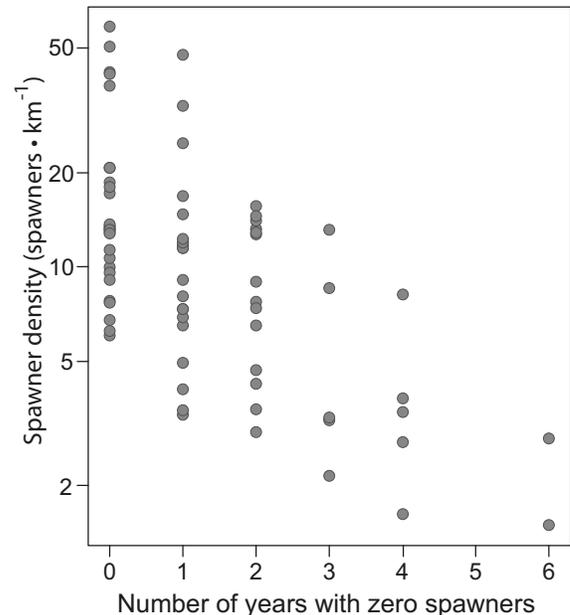
Results

Understanding the structure of the data: variance partitioning

The Oregon Plan data set contains a large number of zeros, not all of which represent poor habitat. The Oregon Plan data set included 97 annual observations of zero spawners, approximately 13% of the data. Only 27 of the 95 reaches had fish in every year surveyed; about half of the reaches (48) had no spawners in at least 2 years. While the mean spawner density when spawners were present appears related to the number of years in which spawners were absent (Fig. 2), this pattern was not as strong as might be expected. Even reaches with a relatively high mean spawner density (when spawners were present) sometimes had 2, 3, and even 4 years of observations in which not a single fish was detected.

Much variation in spawner density within the Oregon Plan data set occurs between reaches, though substantial variation also occurs between years (Table 2). The ratio of reach-to-reach variation and residual variation is only 1.2, suggesting that highly precise landscape models are not feasible. The estimated maximum R^2 we can expect for this Oregon Plan data set is 0.55 given a perfect correlation between landscape characteristics and reach-level coho salmon spawner densities in a given year.

Two-step modeling: occupancy and then abundance where present

Although coho salmon spawners were present in all surveyed reaches during 2003, in other years, up to 29 reaches were observed with zero spawners (Table 3). The annual logistic models were quite variable in their ability to predict

these observations of zero spawners (specificity; Table 3). On average, landscape models correctly classified 37% of the reaches observed with zero spawners. The proportion of these reaches correctly classified ranged from 0.10 to 0.75, depending on the year, with the highest accuracy in a year when only four reaches were without spawners. We also note that the set of landscape predictors in the best logistic model differed every year (Table 3).

Mixed models using only nonzero observations explained about 30% of the among-reach variation in spawner density (Table 4). Our set of best models included four models. Key landscape predictors in these models were percent agriculture, winter temperature range, and intrinsic potential.

Comparison with previous analyses

Variance partitioning results and the estimated maximum R^2 values were comparable for all three data sets: the Oregon Plan, the Firman et al. (2011) data set, and the Pess et al. (2002) data set (Table 2). Because all possible spawning locations were included in the sampling frame, the Oregon Plan data set contains more observations with zero fish counts than the data sets based on index reaches. The percentage of the variance attributable to year-to-year variation (σ_{year}^2) is also largest for the Oregon Plan data set, though estimated maximum R^2 was similar across all three data sets (Table 2).

Similar suites of landscape characteristics were correlated with coho salmon distribution across all three data sets (Table 5). However, geology variables were included as landscape predictors in models for the index data sets but not for the probabilistically sampled Oregon Plan data set. With the Oregon Plan data set, neither the mixed model approach from Firman et al. (2011) nor the hierarchical modeling approach from Pess et al. (2002) yielded useful models. Models built using these methods had R^2 values less than 0.10 and no statistically significant landscape predictors.

Discussion

We found that coho salmon spawner abundance along the Oregon Coast is linked to landscape characteristics such as land ownership, percent agriculture, and the intrinsic potential of the streams to support coho salmon. No combination of landscape predictors was, however, able to consistently explain reach occupancy of coho salmon spawners. Our models for explaining coho salmon abundance were comparable to those of previous studies using data from index reaches (Pess et al. 2002; Firman et al. 2011); however, model performance was not as strong in our study as in these previous studies. We suggest a revised conceptual model in which (i) the presence vs. absence of spawners is driven by currently unexplained factors and (ii) the abundance of spawners where present is controlled to some degree by landscape conditions. We encourage probabilistic sampling schemes in other regions and for other species to determine whether this conceptual model is unique to Oregon coastal coho salmon.

Understanding coho salmon abundance

Observed correlations between landscape characteristics and coho salmon abundance are consistent with our understanding of how underlying physical attributes can influence fish habitat. Geology and climate dictate the range of physical and morphological characteristics that a stream reach can exhibit and partially determine the physical and biological characteristics of fish habitat within the reach (Montgomery et al. 1999). Human land-use impacts such as grazing, agriculture, and forestry can further affect in-stream habitat quality and salmon population performance (Beechie et al. 1994; Bradford and Irvine 2000). Bilby and Mollot (2008), for example, found that abundance of coho salmon populations decreased in areas where urbanization increased.

Looking across modeling results from the Oregon Plan data set and the two index data sets, we find that a combination of geology, climate, and land-use variables can explain a significant proportion of the variance in spawner abundance, especially given the year-to-year and residual variance in the data. The set of predictors for our abundance model (models fit to the nonzero data) included winter temperature range, intrinsic potential, percent agriculture, percent private nonindustrial forests, and percent nonforested area. Many of these same landscape predictors occurred in the best models from the index reach data reported in Firman et al. (2011). Parallel findings may arise because the index-reach model describes only hand-picked reaches that are unlikely to have observations of zero spawners. By focusing on consistent patterns of coho salmon abundance across occupied sites, we are able to identify some of the dynamics controlling the freshwater portion of the salmonid lifecycle.

Our models built with the Oregon Plan data set are the first landscape-scale models to explore the correlation between intrinsic potential, as defined by Burnett et al. (2007), and coho salmon abundance. The concept of intrinsic potential is based on an assumption that there is a range of stream gradient, stream constraint, and mean annual flow that are ideal for supporting coho salmon. These features are often easy to calculate or estimate from remotely sensed data, and so determining how well this combination of variables can predict fish abundance is of great interest. Intrinsic potential was a significant predictor in every model in the best set of abundance models, and we therefore conclude that it is useful for helping identify those reaches that, if fish are present, are likely to support a large number of fish.

While some ecologists and statisticians have focused on the year-to-year variation in spawner abundance, our variance partitioning results for the Oregon Plan data set as well as for the Firman et al. (2011) and Pess et al. (2002) data sets suggest that a larger component of the variation in spawner abundance occurs between reaches than between years. That year-to-year variance appears highest in the shortest data set supports the conclusion of Wiley et al. (1997), who determined that very long time series may be required (~10 generations for trout in Michigan streams) to stabilize the variance estimates of mean fish density. Differences in year-to-year variance across studies may also result from differences in fish behavior, the metric recorded, and the range of years surveyed. The year-to-year variation is driven by changing ocean conditions, population cycles, and changes in feeding opportunities. Of course, landscape characteristics are not the sole means by which we hope to explain all coho salmon population performance. However, our results, especially in combination with previous studies (Pess et al. 2002; Steel et al. 2010; Firman et al. 2011), indicate that landscape charac-

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Table 2. Comparison of variance across the three adult coho salmon data sets.

Data set	Location	Reach selection	Sample size	Years	σ^2_{reach}	σ^2_{year}	$\sigma^2_{residual}$	$\sigma^2_{reach}/\sigma^2_{residual}$	Estimated max. R^2
Oregon Plan	Oregon Coast, Ore.	Randomly selected	$N_{reaches} = 95$ $N_{years} = 9$	1998–2006	0.91	0.61	0.75	1.2	0.55
Firman et al. 2011	Oregon Coast, Ore.	Index	$N_{reaches} = 44$ $N_{years} = 17$	1981–1997	0.42	0.10	0.53	0.79	0.44
Pess et al. 2002	Snohomish River, Wash.	Index	$N_{reaches} = 54$ $N_{years} = 15$	1984–1998	2.0	0.4	2.4	0.84	0.46

Note: Reach variance (σ^2_{reach}) describes the amount of variance between reaches, and σ^2_{year} describes variation between years. Maximum R^2 (Kauffmann et al. 1999) is an estimate of maximum model strength for a simple regression model explaining observations across reaches given the residual variation.

Table 3. Classification results from single-year logistic models to explain reach-level presence vs. absence of coho salmon spawners.

Year	Predicted	Observed 0	Observed +	Proportion correctly classified (0 vs. +)	Proportion correctly classified overall	Landscape predictors
1998	0	14	2	**0.48**	0.79	AnnualRange, CowDensity, Precip
	+	15	49	0.96		
1999	0	5	3	**0.28**	0.81	Mafic, Public, Resistant
	+	13	63	0.95		
2000	0	6	2	**0.38**	0.86	CowDensity, Flow, BLM
	+	10	67	0.97		
2001	0	4	1	**0.68**	0.96	Landslide, Precip, AnnualRange
	+	2	71	0.99		
2002	0	3	1	**0.75**	0.98	CowDensity, Flow, Unconsolidated
	+	1	85	0.99		
2004	0	1	2	**0.10**	0.87	Renmant, SmallTrees, Cut
	+	9	74	0.97		
2005	0	1	1	**0.17**	0.92	AnnualRange, Elevation, CowDensity
	+	5	70	0.99		
2006	0	2	0	**0.25**	0.93	NonForest, Roads
	+	6	76	1.0		

Note: Counts are of stream reaches with zero spawners (0) and at least one spawner (+) in each year. The proportion of reaches correctly classified and the predictive power are provided for reaches with zero spawners (bold; specificity) and with at least one spawner (nonbold text; sensitivity). The overall proportion of correctly classified reaches includes reaches with zero spawners and reaches with spawners. Landscape predictors are defined in Table 1. There is no model for 2003 because spawners were observed in all reaches surveyed that year.

Table 4. Results of mixed modeling for coho salmon density (spawners per kilometre) using reaches from the Oregon Plan data set where spawners were present.

Model	R^2	AIC	AIC weight
$-0.0776 \times Ag + 0.796 \times IntPotential + 0.0216 \times WinTRange$	0.303	1603.0	0.438
$1.681 - 0.215 \times Ag + 0.00918 \times Ag^2 + 0.842 \times IntPotential$	0.306	1604.6	0.192
$-0.0310 \times NonForest + 0.0216 \times WinTRange + 0.823 \times IntPotential$	0.289	1604.6	0.191
$-0.0173 \times PrivateNI + 0.0231 \times WinTRange + 0.772 \times IntPotential$	0.287	1604.8	0.178

Note: AIC weights indicate the relative strength of the models and enable model users to apply a weighted average of the predictions from the best models. Landscape predictors are defined in Table 1.

teristics, and in particular anthropogenic impacts, can influence the abundance of coho salmon spawners.

Our landscape models built using the Oregon Plan data set, though informative, were not as strong as previously published analyses based on index data. When the data were analyzed using the same techniques as Pess et al. (2002), no significant relationships were detected. At first, we found this surprising because we expected that a large, probabilistically sampled data set would yield models that were both more accurate and more precise than a smaller index data set. There are several potential explanations for the lack of model fit. First, the Oregon Plan data were collected over a large area lacking strong gradients in geological characteris-

tics, climate, or land use. If the study region had encompassed highly urbanized areas and a range of geologies, we might have been better able to detect the influence of landscape features on coho salmon abundance. Note that Firman et al. (2011) found stronger models over this same geographic area using only opportunistically sampled index reaches. Second, the probabilistic nature of the sample meant that we surveyed a wide range of coho salmon habitat suitability. All reaches in the Oregon Plan data set can be considered coho salmon spawning streams because spawners were observed in at least 1 year; however, many reaches were only occupied in some years. The index reaches used in previous modeling of coho salmon (Pess et al. 2002; Fir-

Table 5. Comparison of landscape models across three adult coho salmon data sets.

Data set	Oregon Plan data set (abundance only)	Firman data set	Pess data set
Model fitting procedure	Mixed model	Mixed model	Hierarchical linear model
Strongest predictors	Ag	Roads	%agriculture
	IntPotential	NonForest	%till
	WinTRange	PrivateInd	%bedrock
	NonForest	WinTRange	%urban
	PrivateNI	Weak	
		Hardwoods	
Model Fit	0.30	0.43	<0–0.41*

Note: The results from data sets of Firman et al. (2011) and Pess et al. (2002) describe watershed-scale analyses. Results from Firman et al. (2011) combine both of their large-scale analyses (hydrologic unit and watershed). Model fit was estimated as the average model fit across the set of best models. The range of R^2 reported for hierarchical linear models from Pess et al. (2002) is the adjusted R^2 across years; those reported for mixed models are generalized R^2 (Nagelkerke 1991). For definitions of predictors in the Pess data set, see Pess et al. 2002. Landscape predictors for the Oregon Plan data set and the Firman et al. (2011) data set are defined in Table 1.

*Estimated from data in figure 5 of Pess et al. (2002).

man et al. 2011) tended to represent the most suitable areas, originally selected to monitor particular areas where large numbers of fish were known to occur. These index data are known to provide biased estimates of population performance (Courbois et al. 2008).

Several other factors could have reduced performance of our coho salmon abundance models, including metapopulation dynamics and missing variables. Salmon abundances might not be correlated with current habitat or landscape characteristics when metapopulation dynamics support populations in low-quality habitats (Cooper and Mangel 1999). Our analysis covers such a large area that substantial straying of fish into the study reaches from outside the entire study area is unlikely; however, straying among streams and reaches within the study area could cloud relationships between coho salmon abundance and landscape characteristics. In addition, there may be other variables, for example, landscape characteristics that drive the distribution of off-channel habitat that were not included in our analysis and that might have improved model performance.

Understanding coho salmon occupancy

We were not able to detect a strong or consistent relationship between landscape characteristics and coho salmon occupancy, suggesting that occupancy and abundance may be driven by different factors. Our prediction errors may be based on limitations of the data collection methods or the statistical model (algorithmic errors) or on processes deriving from the ecology of the study subject (biotic errors) (Fielding and Bell 1997). Given that we have multiple years of randomly selected observations across a broad spatial extent, we assume that at least some, if not most, of our errors are biotic errors.

Our logistic models failed to properly classify occupied and unoccupied reaches. Over the 8 modeled years, we observed 16 different potential predictors with no one predictor observed in more than 50% of the models. Although we cannot consider each year an independent analysis, the relatively consistent failures suggest a more general phenomenon than if we had only modeled data from 1 or 2 years. Because there was no consistency in landscape predictors across years, we did not go further and develop a mixed model that

incorporated temporal covariance. Instead, we spent our analytical energy attempting to find a modeling structure that might improve performance in some years or explain performance across years. We also explored additional potential predictor variables to find a landscape-scale feature with some ability to predict whether coho salmon would occupy a particular reach in a particular year.

We considered whether there might be a density-dependent relationship between patterns of occupancy and the number of returning spawners. We might expect such an effect if, for example, some reaches were only occupied in years of high spawner returns. Isaak and Thurow (2006) were able to demonstrate changes in occupancy with changes in Chinook salmon population size in Idaho. Jacobs et al. (2002) suggest a similar pattern for Oregon coastal coho salmon. They suggest that relationships between index reaches and random reaches are not linear because in high population years, the index reaches are saturated but there is still room in other less suitable reaches. We do see a range in run sizes in our data such that habitat was likely nearly or fully seeded in several years of our analysis. Meengs and Lackey (2005) estimated historical run sizes for Oregon coastal coho salmon and considered in detail the relationship between current coho salmon populations and available habitat. They concluded that in good ocean years, for example 2001–2003, coho salmon populations are near the maximum that can be supported with available habitat. We therefore would have expected all suitable habitats to be occupied either in 2002 when a large number of fish returned or by 2003 when the progeny of strong year classes began to return. We did see the best model performance (specificity) in 2001 and in 2002. Population size may provide a partial explanation, but the data do not support a simple relationship in which one type of reach is consistently unoccupied in years of lower returns.

Many unmeasured factors might improve our understanding of occupancy in the future. We were unable to model reach selection dynamics of individual fish, such as attraction of arriving fish to established territories or the order by which spawning habitats are filled. If such dynamics are unrelated to landscape characteristics, they might improve model fit. Individual variability in habitat selection can certainly lead to poor models linking habitat to presence vs. ab-

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sence dynamics (Fielding and Bell 1997). Spatial correlation between sites may also obscure observed correlations.

An enhanced conceptual model of coho salmon spawning and implications for future research and monitoring

Landscape characteristics are correlated with spawner abundance in good reaches (e.g., index reaches) and within occupied reaches. Landscape models have successfully identified correlations between landscape characteristics and spawner abundances for multiple species (e.g., Feist et al. 2003; Steel et al. 2004; Bilby and Mollot 2008) across a range of good habitat. Our results suggest that there is an additional process driving occupancy that cannot be explained by the landscape predictors used in this study. We suggest that a complete conceptual model of coho salmon spawning distribution should include both (*i*) a mechanism explaining why any salmon are present in a particular reach and in a particular year, and (*ii*) the suite of factors, including landscape-scale conditions, that explain how many salmon are present in occupied sites. A better understanding of occupancy will be useful for developing a full understanding of the drivers of spatial structure and the relationship between spatial structure and population performance.

In our study area, we propose that there is an as yet unexplained process by which perfectly good reaches remain unoccupied in some years. Alternatively, poor reaches may be occupied because spawners happen to stray into them. This random process may be driven by population size, local flow events during a key migration window, competition, or even by small-scale habitat fluctuations, such as gravel movements that impede or open particular reaches in particular years. As far as we know, this is the first multiyear, probabilistically sampled data set covering such a large spatial extent. Without similar data sets in other regions, we cannot determine whether there might be landscape-scale drivers of occupancy in other regions or for other species. A take-home message of our study is that these kinds of data need to be collected over many areas and for all species of concern. Unbiased data from the full range of potential habitats is necessary to ensure that species management plans and actions are based on a complete understanding of species–habitat relationships.

A better understanding of occupancy will eventually require studies in multiple locations. Ideal locations in which to study occupancy might include newly opened habitat in close proximity to healthy populations, areas with increasing coho salmon populations, and locations with particularly dynamic habitat conditions. Further, research on moderately suitable and rarely occupied reaches will also be essential to untangle these relationships. We encourage the development of data-gathering programs to test whether these same patterns occur in other species of salmonids, in regions that have a completely different topography, and in areas where landscape predictors have an even stronger relationship with abundance.

Probabilistically sampled spawner surveys are ideal for exploring relationships between fish and landscapes that can be extrapolated to the full population of potential reaches. We have long been aware that index reaches cannot be used to provide unbiased estimates of population performance trends (Thurow 2000; Jacobs et al. 2002). Our results further demonstrate that index reaches provide a biased perspective of

landscape-scale human impacts on fish populations. They may provide information about coho salmon abundance in occupied reaches, but they provide little insight on occupancy or spatial structure.

A great deal of research has gone into designing the spatially balanced, probabilistic sampling scheme that generated the Oregon Plan data set (e.g., Stevens 2002; Stevens and Olsen 2004). Using a simulation study, Courbois et al. (2008) demonstrated that the generalized random-tessellation stratified design used to collect this data set is increasingly accurate at larger population sizes when only 5%–10% of the population can be surveyed. Our results suggest that modifications of random designs to collect further data about occupied reaches might provide useful information. Adaptive cluster sampling, for example, is one possible approach (Thompson 1990). Other slight modifications might be particularly useful for depressed or declining populations. For these populations, increased sampling effort to distinguish occupied from unoccupied reaches could yield ecological insights that have the potential to improve management. Future research to identify those human impacts that limit occupancy of threatened and endangered species could enable small on-the-ground changes that increase connectivity between populations, improve spatial structure, and increase population growth rates and (or) resilience.

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