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ARTICLE

Landscape Models of Adult Coho Salmon Density Examined at Four Spatial Extents

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Abstract
Salmon occupy large areas over which comprehensive surveys are not feasible owing to the prohibitive expense of surveying thousands of kilometers of streams. Studies of these populations generally rely on sampling a small portion of the distribution of the species. However, managers often need information about areas that have not been visited. The availability of geographical information systems data on landscape features over broad extents makes it possible to develop models to comprehensively predict the distribution of spawning salmon over large areas. In this study, the density of spawning coho salmon *Oncorhynchus kisutch* was modeled from landscape features at multiple spatial extents to identify regions or conditions needed to conserve populations of threatened fish, identify spatial relationships that might be important in modeling, and evaluate whether seventh-field hydrologic units might serve as a surrogate for delineated catchments. We used geospatial data to quantify landscape characteristics at four spatial

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extents (a 100-m streamside buffer, a 500-m streamside buffer, all adjacent seventh-field hydrologic units [mean area = 18 km^2], and the catchment upstream from the reach [mean area = 17 km^2]). Predictions from models incorporating land use, land ownership, geology, and climate variables were significantly correlated (r = 0.66–0.75, P < 0.0001) with observed adult coho salmon in the study area. In general, coho salmon densities (peak count of adults per kilometer) were greatest in river reaches within landscapes of undeveloped forest land with little area in weak rock types, areas with low densities of cattle and roads, and areas with a relatively large range in winter temperatures. The ability to predict the spatial distribution of coho salmon spawners from landscape data has great utility in guiding conservation, monitoring, and restoration efforts.

For widely distributed, highly variable populations, it is increasingly recognized that a broad-scale perspective is important when relating population characteristics to habitat attributes (e.g., Fausch et al. 2002; Durance et al. 2006; Steel et al. 2010). High-resolution, spatially extensive data on populations and habitats are necessary to understand and manage widely distributed species. However, collecting field data with the necessary spatial extent is expensive and time consuming, and such data are generally lacking. To fill this gap, statistical relationships have been developed that can predict site-specific conditions from landscape characteristics. Characteristics of salmonid populations or their habitats have been successfully modeled from landscape characteristics (e.g., Burnett et al. 2006). Such models can predict site-specific population performance or habitat conditions (Steel et al. 2004), describe broad-scale patterns of population distribution (Feist et al. 2003), suggest mechanisms by which landscape patterns may affect abundance and distribution of fishes (Pess et al. 2002), and benefit efforts to conserve many at-risk populations of migratory fish (NRC 1996).

Many landscape modeling approaches have focused on identifying the best or most appropriate spatial scale for modeling efforts (e.g., Fausch et al. 2002; Burnett et al. 2006; Feist et al. 2010). Catchment size and the mechanism by which a landscape feature may affect in-channel conditions drive the a priori selection of analytical scale. Previous studies have also indicated that a multi-scale approach can reveal the extent over which, and mechanisms by which, landscape conditions affect instream conditions (e.g., Feist et al. 2003; Torgersen and Close 2004; Burnett et al. 2006). Consequently, spatial approaches have been developed that summarize landscape characteristics at multiple spatial extents.

Previous efforts to identify the habitat needs of stream-dwelling fish populations have usually focused on local instream and riparian conditions (Fausch et al. 1988). These studies have improved our understanding of the relationships between instream habitat conditions and coho salmon *Oncorhynchus kisutch* populations. For example, habitat quality, specifically the abundance of large wood and pools, has been used to predict the survival rate and carrying capacity for juvenile coho salmon in Oregon coastal streams (Nickelson and Lawson 1998). During high winter flows, juvenile coho salmon are associated with beaver ponds, dammed pools, and alcoves, and the availability and quality of these types of habitats limit coho salmon production in most Oregon streams (Nickelson et al. 1992a, 1992b; State of Oregon 2005). Addition of large wood and construction of alcoves and dammed pools can result in increased abundance and overwinter survival of juvenile coho salmon (Solazzi et al. 2000; Johnson et al. 2005). Instream relationships depend on population dynamics; when marine survival is low and adult returns are few, only the best freshwater habitats will support viable coho salmon populations (Nickelson 1998; Flitcroft 2007). However, a focus on instream conditions has its limitations.

One limitation of a focus on local, instream conditions is that fine-scale habitat characteristics are dynamic. Wood and sediment, for example, can be washed away or deposited over the course of a single season. That fine-scale habitat features can be altered facilitates instream restoration, but the corollary is that current conditions in the stream are not necessarily a good predictor of the potential condition of a given stream reach. Many landscape characteristics are less mutable than instream characteristics when considered over short periods, and broad-scale variables can be good predictors of the distribution and abundance of fish and aquatic invertebrates (Richards et al. 1996; Creque et al. 2005; Burnett et al. 2007). Fine-scale habitat features are a good source of information to predict current conditions for fish, provided that the data are available, but may not indicate the potential of the stream reach in its optimal state. To predict future potential, regardless of the current conditions of that habitat, then coarser-scale, relatively static landscape features are needed. Also, data on fine-scale in-channel habitat features generally do not exist over broad enough areas to apply models, whereas the possibility exists to develop and apply predictive models that rely on landscape data for broader-scale features as predictor variables. Broader-scale approaches can highlight which watershed conditions may influence stream conditions and fish production, and can help to prioritize restoration activities, even in areas where in-stream habitat is currently poor. Addressing these two needs is critical for conserving freshwater species. 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).

In this paper, we expand the current understanding of how animal populations are linked with landscape conditions by developing and comparing models that predict densities of adult coho salmon from landscape features characterized over four spatial extents across a large region of western Oregon. The

TABLE 1. Geospatial data layers used in model building, predictors, map scale or grid cell size, how predictors were calculated and/or generalized, and sources of data.

Data layer	Predictor	Predictor description	Map scale/grid cell size	Predictor derivation	Data source
Catchment area	AOI	Size of area of influence	1:24,000	Polygon representation of total area upslope of the downstream end of any given index reach. Generated from a U.S. Geological Survey (USGS) 1:24,000 10-m digital elevation model using ArcGIS	Generated for this study
PRISM climate data	MaxTemp	Maximum annual temperature	4,000 m	Air temperature:	Daley et al. (1994)
	Min Temp	Minimum annual temperature		*MaxTemp − MinTemp	
	AnnualRange	Annual temperature range*		**Max − Min in Jun–Aug	
	SummRange	Summer temperature range**		***Max − Min in Dec–Feb	
	WinRange	Winter temperature range***			
	Precip	Mean annual precipitation (mm)			
Forest cover	Big Trees	% Large conifers (>50 cm)	Multiple	Predictive mapping of forest composition using direct-gradient analysis and nearest-neighbor imputation. Thirty-four original vegetation types were generalized to four.	Ohmann and Gregory (2002)
	SmallTrees	% Small trees (<25 cm)			
	Hardwoods	% Hardwoods			
	Remnant	% Remnants			
Land ownership	BLM	% U.S. Bureau of Land Management	Multiple	Land ownership compiled from spatial data from the Oregon Department of Forestry and aggregated into four classes	Burnett et al. (2007)
	USFS	% U.S. Forest Service			
	PrivateInd	% Private industrial (industrial forests)			
	PrivateNI	% Private nonindustrial			
Disturbance	NoDisturb	% Not cut before or during spawner count	25 m	Landsat imagery for a period of over 30 years (to 2004) used to identify change from timber harvesting and fire in western Oregon. Twelve categories were generalized to three.	Lennartz (2005)
	Cut	% Cut prior to or during spawner counts			
	NonForest	% Nonforest			
Geology	Resistant	% Granitics (HU extent only), resistant–sedimentary, or resistant–other (all extents)	1:500,000	USGS classification of geologic map units according to major lithology. Generalized to four classes from the original seven.	Walker et al. (2003)
	Intermediate	% Intermediate sedimentary			
	Weak	% Weak rocks (pyroclastic, schists)			
	Unconsol	% Unconsolidated deposits (landslides, glacial)			
Land use	Ag	% Agricultural	25 m	Combination of forest cover, human development, and zoning	Burnett et al. (2007)
	Rural	% Rural			
Cattle density	CattleDensity	Cattle density (cattle/100 acres)	30 m	Cattle head counts/area of available grazing land by county based on the 1997 Agricultural Census and the National Land Cover Data	Generated for this study

(Continued on next page)

TABLE 1. Continued.

Data layer	Predictor	Predictor description	Map scale/grid cell size	Predictor derivation	Data source
Roads	RoadDen	Road density (km/km^2)	1:24,000	BLM coverage of roads in Oregon (road length divided by the AOI)	Generated for this study
Stream	Flow	Stream flow (m^3/sec)	10 m	Estimated mean annual stream flow at the bottom of the index reach in ft^3 / s.	Clarke et al. (2008)
	Gradient	Stream gradient	10 m	Calculated using USGS 10-m digital elevation model. Defined as upstream elevation minus downstream elevation divided by length of index reach, in percent.	Generated for this study

density of adult coho salmon in this area was selected as the focus of this study for several reasons: (1) there are pervasive public concerns about the persistence of these populations (State of Oregon 2005); (2) detailed knowledge about fine-scale associations between coho salmon and their stream habitats exists for many life history stages (e.g., Nickelson et al. 1992b; Johnson et al. 2005; Burnett et al. 2007); (3) this focus provides an opportunity to adapt and expand on landscape modeling approaches that were developed for other salmonid species or in other regions (e.g., Pess et al. 2002; Feist et al. 2003; Steel et al. 2004); and (4) there are high-quality data layers for both the predictor and the response variables; a large number of survey reaches evenly distributed over a large geographic area have been sampled consistently for decades, and high-resolution geospatial habitat data are available for the region. Our specific objectives are to identify landscape characteristics that predict densities of adult coho salmon, compare model results when landscape characteristics are summarized at different spatial extents, evaluate whether seventh-field hydrologic units can serve as a surrogate for delineated catchments, predict densities of coho salmon across the west slope of the Oregon Coastal Province; and consider the implications of our results for conservation and management.

METHODS

Study area.—We conducted our analyses for the region where the Oregon coastal coho evolutionarily significant unit (ESU; Weitkamp et al. 1995) overlaps the Oregon Coastal Province (Figure 1; 20,305 km^2). The Oregon Coastal Province is underlain primarily by marine sandstones and shales or basaltic volcanic rocks. Mountains dominate the area except for interior river valleys and a few locations where there is a prominent coastal plain. Elevations range from 0 to 1,250 m, though most coho salmon habitat occurs in low gradient reaches at lower elevations. The climate is temperate maritime with mild, wet winters and warm, dry summers. The study area supports a highly productive forest dominated by conifers, especially Douglas-fir *Psuedotsuga menziesii*. Forests span early successional to old-growth seral stages, but most of the current forestland is in relatively young seral stands, and the larger river valleys have been cleared for agriculture (Ohmann and Gregory 2002). Burnett et al. (2007) identified that roughly half of the riparian areas adjacent to streams that they modeled and that provide high intrinsic potential habitat for coho salmon are nonforested or have been recently logged.

About one-third of the land is publicly managed, and the remainder is owned privately (Spies et al. 2007). Close to 90% of the stream reaches that have the highest potential to produce coho salmon occur on private lands (State of Oregon 2005; Burnett et al. 2007). Logging, channelization, road building, and conversion of forested lands to agriculture has left reaches that historically supported coho salmon with a scarcity of large wood (Wing and Skaugset 2002), a lack of conifers, lessened connectivity with off-channel alcoves and flood plains, and excess accumulations of fine sediment and gravels (State of Oregon 2005). A more detailed description of the Oregon Coastal Province can be found in Burnett et al. (2007).

Index surveys of coho salmon spawner abundance.—The Oregon coastal coho ESU encompasses all coastal basins in Oregon south of the Columbia River to Cape Blanco (Necanicum River through Sixes River; Weitkamp et al. 1995). This includes 18 independent coho salmon populations and another 41 dependent populations (Lawson et al. 2004). An independent population is defined as a population that can sustain itself without inputs from other populations and is relatively unaffected by immigration from and emigration to other populations. Dependent populations are those that are dependent on immigration from surrounding populations to persist or are highly affected by immigration from and emigration to other populations (Lawson et al. 2004). Three independent populations (Siltcoos Lake, Tahkenitch Lake, and Tenmile Lake) were excluded from the study area because the high productivity observed in those populations is believed to be a product of rearing habitat in coastal lakes rather than of conditions in streams.

The Oregon Department of Fish and Wildlife (ODFW) has monitored spawning salmon in index reaches of Oregon coastal streams since 1950 (Jacobs and Cooney 1997). Easily accessible stream reaches that consistently supported many coho salmon adults were selected to index abundances of spawners. The surveyed length of stream varied between 0.8 and 4.5 km with an average ± SE of 1.8 ± 0.2 km surveyed. Because index reaches were not selected with a probability sample design, the range of reaches that support spawning fish is not fully represented. Index reaches are annually surveyed every 7–10 d from mid-October until late January. Live and dead coho salmon adults are recorded on each visit. Our analysis used annual counts of the maximum number of adult coho salmon observed on a single visit to a stream reach (peak counts) recorded at each of 44 index reaches in river basins. The index reaches were georeferenced to the Coastal Landscape Analysis and Modeling Study (CLAMS) modeled stream network, which was modeled using 10-m drainage-enforced (DE) digital elevation models (DEMs) (Clarke et al. 2008). Georeferencing and stream network modeling were carried out with geographical information systems (GIS, Environmental Systems Research Institute ArcMap version 9.1). Peak spawner counts were standardized by dividing the number of fish present by the length of the index reach surveyed (no. fish/km).

Geospatial data layers.—We used geospatial data layers that represented inherent (e.g., climate, topography, and rock type) and management-related (e.g., land cover, use, and ownership) characteristics of landscapes (Table 1). These characteristics are thought to influence the distribution and abundance of coho salmon in the Oregon Coastal Province. For example, coho salmon prefer small, low-gradient tributaries for building redds (Burner 1951), and thus stream gradient and mean annual flow were considered as potential predictor variables in our modeling. The geospatial data layers we used are similar to those examined in other studies of landscape modeling for streams (e.g., Steel et al. 2004; Van Sickle et al. 2004; Burnett et al. 2006).

The suite of landscape variables was summarized at each of four spatial extents: a 100-m streamside buffer, a 500-m streamside buffer, all adjacent seventh-field hydrologic units (HUs; mean area = 18 km^2), and the entire catchment flowing into a given study reach (mean area = 17 km^2) (Figure 1). In Figure 1 the collection of seventh-field HUs is larger than the catchment, but in some cases the catchment encompassed a greater area than the HUs.

All catchments were independent (as were all units at other spatial scales). We expected that processes acting immediately adjacent to the channel (e.g., tree mortality in riparian stands) would be most important in models using predictors at the two streamside buffer extents, while models at the two larger extents would reflect hill slope processes (e.g., surface erosion and landslides). The streamside buffers extended 100 or 500 m on either side of each index reach as delineated in GIS with a DEM-derived stream network (Clarke et al. 2008). The 100-m buffer was used because it approximates the height of mature trees in the study region and is the width of riparian management areas for fish-bearing streams under the Northwest Forest Plan (USDA and USDI 1994). The 500-m buffer was used primarily for consistency with previous work (Feist et al. 2003). The catchment extent was used because conditions in a stream are a function of landscape characteristics in the surrounding catchment (Hynes 1975; Frissell et al. 1986; Naiman et al. 2000). The HU extent was used because HUs are similar in size to catchments and have already been defined for all streams. Existing HUs may be used in future modeling efforts, eliminating the need to delineate reach-specific catchments.

Model development.—The response data were time series of density estimates at each site; thus, we used a repeated-measures design, with the landscape variables measured between sites only and the density estimates measured within sites. The data from 1981 to 1997 were selected because they coincided with the period represented by several of the geospatial data layers used in this study and because the Pacific Decadal Oscillation (PDO) index, which serves as an indicator of ocean productivity, was relatively consistent throughout this period (Mantua et al. 1997). The correlation among density estimates at a particular site was modeled with an ARMA(1,1) correlation structure and sites were assumed to be independent; thus, the unscaled covariance matrix is block diagonal with ARMA(1,1) blocks corresponding to each site (Littell et al. 1996). Akaike's information criterion (AIC) was used to select this 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 were fit with maximum likelihood procedures using Proc Mixed in Statistical Analysis Software (SAS).

To select the set of best models from multiple potential predictors, we followed a four-step approach that was repeated for each of the four spatial extents. The dependent variable in all cases was the peak count of coho salmon adults per kilometer in each site in each year, which was log transformed to meet normality assumptions (hereafter called peak spawner densities). As a first step, we fit the null model (intercept only), then all one-variable models and all combinations of two-variable models. Quadratic terms were included as a potential second variable and at this stage models were fit both with and without intercepts. All two-variable models with an AIC score less than that of the null model were retained. The AIC is a tool for model selection that provides a measure of the goodness of fit of statistical models by weighing the complexity of a model against its maximum likelihood (Burnham and Anderson 2002). We also assessed whether the intercept term improved model fit. We then created and fit three-variable models from the retained two-variable models by adding singly all other variables. Second, we identified a set of candidate models using the difference in AIC values, termed ΔAIC, between each model and the low-

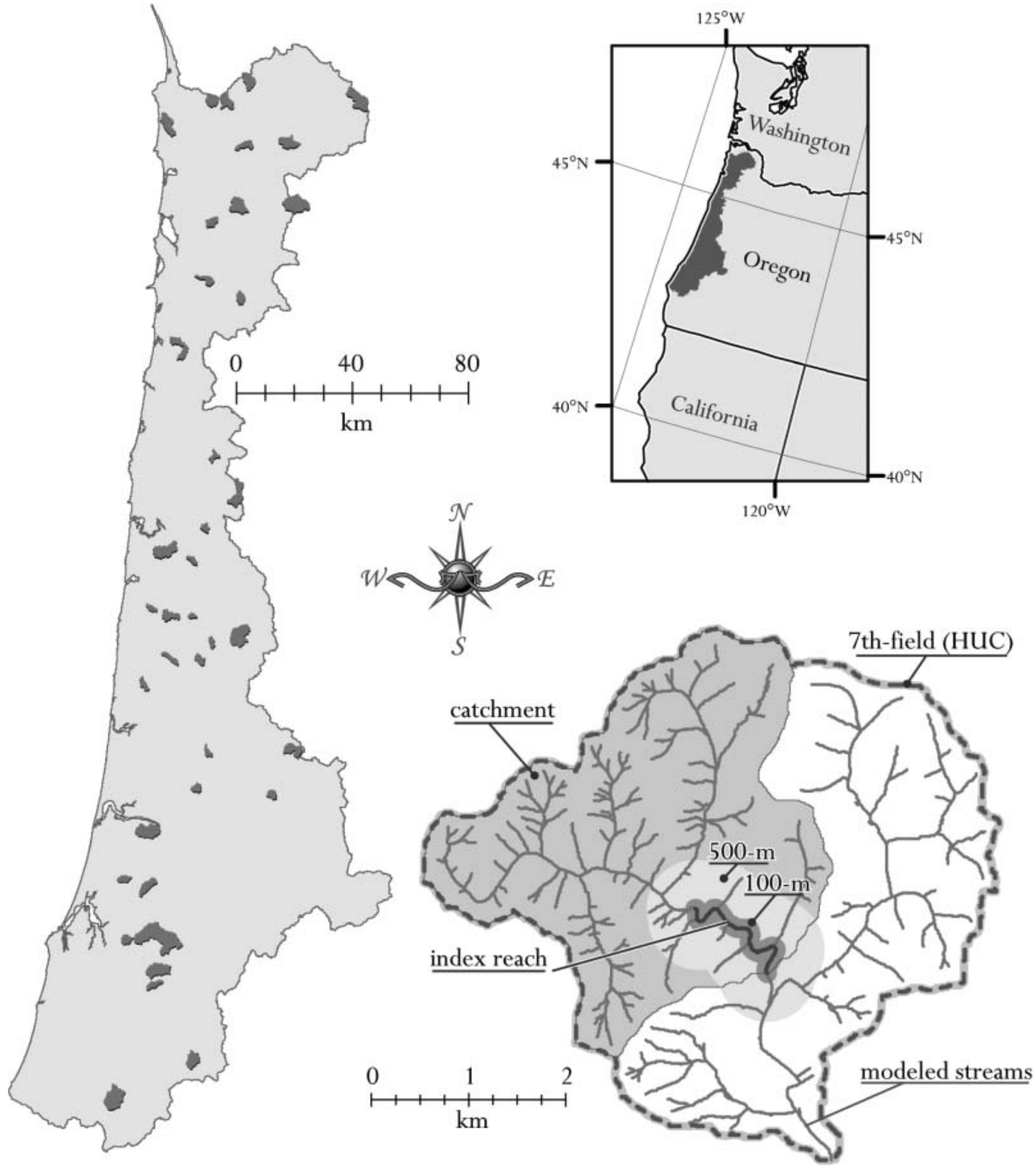

FIGURE 1. Extent of the area of inference included in the models and illustration of the four spatial extents used for modeling. Delineated catchments for coho salmon spawner index sites are indicated by dark gray shading.

est AIC score among all models. Candidate models included all models with a ΔAIC value of less than 4. For the third step, we applied three criteria to remove models from the candidate list that had various forms of model instability. Models with high collinearity were identified by calculating a condition index for the set of variables in the model (Belsley et al. 1980), and those with a condition index greater than 10 were rejected. Models that were unstable owing to data points with high leverage were identified with Cook's D (Cook 1977), and those with data points for which Cook's D was greater than 1.00 were eliminated. Cross-validation analysis was used to eliminate models with low predictive power. We generated 1,000 bootstrap validation sets by randomly selecting 90% of the observations. We then fit the model for each data set, predicting the response for the remaining 10% of the observations and calculating the correlation between these observed and predicted values. Models for which the mean correlation for the 1,000 bootstrap samples, $\overline{V}$, was lower than the lower bound of the 95% confidence interval (CI) of the mean of $\overline{V}$ across all candidate models were eliminated. Fourth, we selected the set of best models from those that met all three of the above criteria by ranking them according to ascending AIC and calculating AIC weights (Burnham and Anderson 2002). The best models comprising the set were those where 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. We also estimated generalized R^2 values for each of the mixed models in the set of best models using the approach of Nagelkerke (1991). This statistic is analogous to the coefficient of determination calculated from sums of squares, but instead compares the likelihood of the model with that of the null (intercept only) model. We used the natural log of the mean of the peak spawner density to examine correlations between predictor variables individually at each spatial extent.

Predictions.—The index sites were not a statistical sample of the population, which hindered our ability to make inferences. However, we believed that it would be instructive to view spatial patterns of predictions. Final predictions of peak spawner densities at each extent used a weighted average of the predictions from each of the models in the best set. Weights in the weighted average were AIC weights, recalculated for the set of best models. Thus, we generated four predictions, one from the set of models at each spatial extent, of peak spawner density for each of 100 randomly selected stream segments within the distribution of coho salmon spawning habitat in the province. We reported the mean and coefficient of variation (CV = 100 × SD/mean) for the four predictions at each location. We also generated predictions from the catchment extent models applied to seventh-field HUs within the province. This approach was used to provide consistency with previous work. In both cases, the reported prediction was back-transformed to number of fish per kilometer.

RESULTS

Correlations

Correlation matrices for predictor and response variables are presented in Tables 2 and 3. At each of the four spatial extents, predictor variables describing land management (e.g., percent area in agriculture and percent area in nonforest) or land management and ownership (e.g., percent area in big trees and percent area in U.S. Forest Service [USFS] jurisdiction) tended to be highly correlated. Predictor variables describing inherent characteristics (e.g., summer temperature range and maximum annual temperature) also tended to be correlated at each extent. Although patterns of correlation were similar among extents, some differences were apparent. For example, the percent area in large diameter trees was highly correlated ($r = -0.61$) with road density at only the 500-m buffer extent. High correlations ($r \geq |0.60|$) were more prevalent in the catchment and HU extents than in the two buffer extents, and more high correlations were observed for the 500-m than for the 100-m buffers.

The response variable, peak spawner density, was generally correlated with the parameter-elevation regressions on independent slopes model (PRISM) climate predictor variables at each extent examined, and most specifically with winter temperature range, maximum annual temperature, and mean annual precipitation. For each of the correlated groups of predictors, only the variable with the highest correlation (or partial correlation) with peak spawner density appears in a given final model because of the elimination of models with moderate to high condition indices.

Models

Fifteen models met the criteria set out in Methods (Table 4) and these were used to predict relative peak spawner densities. Of these, six models described the 100-m buffer extent, two described the 500-m buffer extent, five described the HU extent, and two described the catchment extent. The difference in fit between each model and a "null" model, the generalized R^2, ranged from about 40% to 46%, with models generally explaining the most variation at the HU extent and the least variation at the 500-m buffer extent (Table 4). The correlations between observed and predicted values from bootstrap validation, $\overline{V}$, ranged from 0.66 to 0.75 (Figure 2).

No single variable appeared in all 15 models to predict peak spawner density; however, winter temperature range occurred in 13 of the models (Table 4). The percent area in weak rock also appeared in multiple models at each extent. Cattle density appeared in models at each buffer extent, while road density appeared only at the catchment extent. Land ownership variables (i.e., percent area in U.S. Bureau of Land Management [BLM], private nonindustrial, or private industrial) appeared in models at all extents except the 500-m buffer extent. The management-related variable, percent area in nonforest, also appeared in models at the HU extent, as did the percent area in hardwoods. Another management-related variable, percent area in small diameter trees, appeared in one model at the 100-m buffer extent.

Predictions

Predicted versus observed responses were correlated at all extents (Figure 2). The correlation between observed densities and predictions was greatest at the HU extent, but the differences among spatial extents were small. The models were also applied to 100 randomly selected sites within the study area. Geographic representation of the back-transformed mean prediction of the four modeled extents indicated that predicted peak spawner densities were higher in the southern portion of the study area (Figure 3a), while the CV among the four weighted averages was highest in the northernmost region of the study area (Figure 3b). The weighted-average model for the catchment extent was used to map predicted densities for all seventh-field HUs in the study area (Figure 3c). The model predictions for HUs were placed into categories based on the range of variation observed in the index reaches. Categories of poor, below average, above average, and best represent the first, second, third, and fourth quartiles, respectively, of the observed mean densities in the index watersheds. Predicted spawner densities of fewer than 2.5 fish/km are indicated as "not occupied", and the model was not applied (n/a) when the values of one or more predictor variables fell outside of the range observed at the sites used to construct the models (Figure 3c). Relatively

TABLE 2. Correlations (r) between predictor variables at the 100-m (above diagonal) and 500-m (below diagonal) buffer extents. Response is defined as the natural logarithm of the mean peak coho salmon spawner count in standard index reaches between 1981 and 1997; all other variables are defined in Table 1 ($N = 44$). Dark grey cells with white text indicate $r \geq 0.6$, light grey cells $r \leq -0.6$.

Variable	Response	AOI	Flow	Gradient	CattleDensity	RoadDen	Cut	NoDisturb	NonForest	BigTrees	SmallTress	Hardwoods	Remnant	MaxTemp	MinTemp	AnnualRange	SummRange	WinRange	Precip	Ag	Rural	BLM	PrivateInd	PrivateNI	USFS	Weak	Intermediate	Resistant	Unconsol
Response		−0.10	−0.21	−0.30	−0.30	0.05	−0.18	0.06	0.01	0.28	−0.46	0.13	−0.05	0.55	0.45	0.34	0.40	0.56	−0.53	0.10	−0.35	0.37	0.01	0.08	−0.13	−0.38	0.22	0.20	−0.41
AOI	−0.13		0.25	−0.08	−0.03	−0.19	0.26	−0.17	0.05	−0.12	0.19	0.16	0.10	−0.11	−0.15	0.02	−0.03	0.03	0.09	0.04	−0.15	0.02	−0.14	−0.03	0.02	0.35	−0.08	−0.14	−0.14
Flow	−0.21	0.23		−0.04	0.32	0.15	−0.02	0.04	−0.07	−0.36	0.21	0.06	−0.03	−0.51	−0.50	−0.13	−0.34	−0.21	0.45	−0.15	0.04	−0.10	−0.10	−0.10	−0.24	0.42	0.06	−0.35	0.04
Gradient	−0.30	−0.05	−0.04		0.34	−0.07	0.15	−0.17	0.09	−0.01	0.30	−0.33	−0.14	−0.38	−0.33	−0.06	−0.21	−0.34	0.19	0.06	0.21	0.04	0.08	−0.28	0.05	0.35	0.10	−0.35	0.10
CattleDensity	−0.30	−0.02	0.32	0.34		0.16	−0.16	−0.11	0.09	−0.22	0.30	−0.05	0.10	−0.39	−0.39	−0.18	−0.23	−0.04	0.23	−0.12	0.42	−0.07	−0.03	−0.01	−0.25	0.12	0.03	−0.18	0.29
RoadDen	0.15	−0.02	0.26	0.22	0.23		0.09	0.07	−0.10	−0.38	0.20	−0.11	0.02	−0.02	−0.12	0.13	0.06	0.28	−0.18	−0.15	0.13	0.14	0.06	0.00	−0.47	0.01	0.26	−0.23	0.09
Cut	−0.21	0.09	−0.15	0.07	−0.13	0.17		−0.20	−0.07	−0.23	0.22	−0.04	0.08	−0.19	−0.19	−0.17	−0.15	−0.01	0.21	−0.10	0.01	0.01	0.15	−0.09	−0.06	0.42	−0.12	−0.21	0.05
No Disturb	0.03	−0.03	0.05	−0.19	−0.13	−0.40	−0.41		−0.87	0.09	−0.12	0.19	−0.66	−0.03	0.02	0.05	−0.05	−0.20	0.05	−0.49	−0.44	0.16	−0.01	−0.41	0.12	−0.17	−0.07	0.27	−0.37
NonForest	0.02	0.01	−0.14	0.16	0.07	−0.02	0.02	−0.60		0.05	0.00	−0.21	0.51	0.15	0.16	−0.09	0.04	0.13	−0.09	0.60	0.44	−0.20	−0.20	0.53	−0.03	−0.04	0.15	−0.16	0.31
BigTrees	0.18	−0.03	−0.43	−0.14	−0.25	−0.61	−0.32	0.33	0.03		−0.50	0.00	−0.23	0.38	0.46	0.00	0.08	0.08	−0.10	0.01	−0.01	0.29	−0.46	0.06	0.62	−0.39	−0.08	0.36	−0.12
SmallTrees	−0.17	0.01	0.00	0.41	0.08	0.55	0.58	−0.43	0.08	−0.61		−0.41	−0.05	−0.34	−0.41	0.16	0.08	−0.38	0.10	−0.20	0.33	−0.05	0.34	−0.22	−0.25	0.50	−0.06	−0.37	0.29
Hardwoods	0.14	0.13	−0.01	−0.21	−0.05	−0.21	0.09	0.05	−0.06	0.05	−0.20		0.03	0.23	0.26	−0.16	−0.09	0.31	0.09	0.01	−0.21	−0.06	−0.16	0.30	0.06	−0.30	−0.28	0.46	−0.14
Remnant	−0.06	−0.06	0.08	−0.03	0.18	0.32	0.22	−0.83	0.33	−0.29	0.22	−0.03		0.09	0.05	−0.17	−0.04	0.36	−0.04	0.18	0.21	−0.16	−0.08	0.47	−0.15	0.08	−0.12	−0.02	0.25
MaxTemp	0.56	−0.12	−0.51	−0.38	−0.38	−0.06	−0.07	0.07	0.14	0.37	−0.16	0.24	−0.10		0.93	0.37	0.65	0.54	−0.58	0.34	−0.17	0.29	−0.10	0.39	0.12	−0.61	0.03	0.43	−0.13
MinTemp	0.45	−0.15	−0.50	−0.33	−0.39	−0.24	−0.07	0.16	0.17	0.49	−0.21	0.27	−0.23	0.93		0.06	0.37	0.40	−0.46	0.32	−0.08	0.24	−0.18	0.39	0.27	−0.66	0.02	0.47	−0.08
AnnualRange	0.35	0.02	−0.12	−0.07	−0.18	0.31	−0.21	0.05	−0.15	−0.12	−0.01	−0.14	0.02	0.36	0.06		0.90	0.08	−0.43	0.12	−0.35	0.32	0.10	−0.04	−0.30	−0.03	0.07	0.03	−0.25
SummRange	0.41	−0.02	−0.33	−0.22	−0.23	0.21	−0.14	−0.03	0.00	0.01	−0.04	−0.05	0.07	0.65	0.37	0.90		0.23	−0.53	0.23	−0.25	0.28	0.13	0.15	−0.20	−0.21	0.01	0.18	−0.17
WinRange	0.56	0.00	−0.21	−0.34	−0.04	0.26	0.12	−0.24	0.10	0.03	0.00	0.32	0.24	0.54	0.40	0.08	0.22		−0.45	0.18	−0.08	0.11	−0.08	0.36	−0.07	−0.30	0.16	0.10	−0.07
Precip	−0.53	0.08	0.45	0.20	0.25	−0.07	0.07	−0.05	−0.10	−0.09	−0.01	0.01	0.19	−0.57	−0.46	−0.42	−0.52	−0.44		−0.15	0.01	−0.26	0.00	−0.19	0.10	0.52	−0.30	−0.14	0.02
Ag	0.11	0.00	−0.19	0.23	−0.01	0.01	−0.08	−0.42	0.76	0.11	0.03	−0.03	0.09	0.22	0.27	−0.05	0.07	0.04	−0.13		−0.05	−0.13	−0.09	0.39	−0.05	−0.11	0.22	−0.07	−0.07
Rural	−0.41	−0.13	0.00	0.18	0.36	0.04	0.29	−0.37	0.39	−0.14	0.22	−0.13	0.24	−0.14	−0.08	−0.28	−0.19	−0.05	0.03	0.06		−0.09	−0.06	0.24	0.01	−0.05	0.11	−0.26	0.84
BLM	0.36	0.00	−0.15	−0.01	−0.03	0.18	0.03	0.20	−0.25	0.08	−0.05	0.09	−0.26	0.33	0.26	0.36	0.36	0.07	−0.29	−0.17	−0.11		−0.18	−0.26	−0.18	−0.16	0.10	0.05	−0.07
PrivateInd	0.08	−0.17	0.04	0.14	−0.03	0.52	0.25	−0.37	−0.16	−0.49	0.53	−0.28	0.35	−0.13	−0.26	0.17	0.14	0.06	0.00	−0.13	0.01	−0.07		−0.47	−0.24	0.19	0.00	−0.13	0.00
PrivateNI	0.00	−0.04	−0.09	−0.25	0.03	−0.07	0.05	−0.32	0.60	0.00	−0.15	0.41	0.27	0.31	0.31	−0.11	0.07	0.40	−0.17	0.35	0.36	−0.28	−0.39		−0.04	−0.24	−0.02	0.13	0.18
USFS	−0.15	−0.01	−0.32	−0.02	−0.31	−0.51	−0.11	0.19	0.00	0.68	−0.30	−0.02	−0.15	0.21	0.40	−0.29	−0.15	−0.19	0.11	0.14	−0.09	−0.30	−0.32	0.01		−0.17	−0.18	0.27	−0.08
Weak	−0.39	0.34	0.42	0.38	0.21	0.39	0.20	−0.31	−0.01	−0.41	0.38	−0.35	0.31	−0.63	−0.68	−0.05	−0.24	−0.32	0.51	−0.02	−0.04	−0.18	0.25	−0.22	−0.21		−0.16	−0.56	−0.07
Intermediate	0.23	−0.08	0.04	0.13	0.03	0.29	−0.25	0.11	0.08	−0.14	−0.06	−0.29	−0.20	0.05	0.02	0.12	0.05	0.17	−0.30	0.09	0.08	0.08	0.07	0.00	−0.17	−0.17		−0.69	0.16
Resistant	0.22	−0.14	−0.35	−0.39	−0.25	−0.49	−0.02	0.21	−0.12	0.44	−0.25	0.51	−0.12	0.46	0.49	0.04	0.20	0.12	−0.14	−0.03	−0.30	0.10	−0.25	0.08	0.35	−0.56	−0.67		−0.32
Unconsol	−0.39	−0.15	0.07	0.08	0.27	−0.03	0.24	−0.26	0.27	−0.17	0.10	−0.15	0.19	−0.15	−0.08	−0.30	−0.21	−0.07	0.01	−0.09	0.94	−0.10	0.05	0.28	−0.11	−0.09	0.16	−0.34	

TABLE 3. Correlations between predictor variables at the seventh−field hydrologic unit (above diagonal) and catchment (below diagonal) extents. See Table 2 for other details.

Variable	Response	AOI	Flow	Gradient	CattleDensity	Road Den	Cut	NoDisturb	NonForest	BigTrees	SmallTress	Hardwoods	Remnant	MaxTemp	MinTemp	AnnualRange	SummRange	WinRange	Precip	Ag	Rural	BLM	PrivateInd	PrivateNI	USFS	Weak	Intermediate	Resistant	Unconsol
Response		0.03	−0.21	−0.30	−0.30	−0.03	−0.01	−0.17	0.19	0.14	0.01	0.20	0.18	0.55	0.45	0.32	0.37	0.57	−0.51	0.14	−0.17	0.34	0.24	0.06	−0.20	−0.39	0.21	0.20	−0.29
AOI	0.13		0.37	−0.34	−0.07	−0.11	−0.12	−0.24	0.34	−0.14	−0.12	0.25	0.31	−0.17	−0.17	−0.16	−0.23	0.21	0.11	0.13	0.21	−0.31	0.00	0.36	−0.12	0.06	−0.04	−0.02	−0.06
Flow	−0.21	0.77		−0.04	0.32	0.22	−0.11	−0.02	−0.07	−0.46	0.00	−0.13	0.00	−0.50	−0.49	−0.09	−0.29	−0.20	0.47	−0.03	−0.05	−0.23	0.23	−0.06	−0.33	0.37	0.06	−0.36	0.21
Gradient	−0.30	−0.18	−0.04		0.34	0.17	0.17	−0.06	−0.12	−0.18	0.45	−0.22	−0.04	−0.39	−0.34	−0.07	−0.24	−0.36	0.23	−0.02	0.01	−0.04	0.03	−0.24	−0.03	0.39	0.26	−0.49	0.06
CattleDensity	−0.30	0.16	0.32	0.34		0.33	−0.09	0.05	−0.07	−0.16	0.08	−0.05	−0.06	−0.38	−0.39	−0.15	−0.22	−0.08	0.34	−0.03	0.25	0.05	−0.12	−0.12	−0.25	0.24	−0.02	−0.19	0.13
RoadDen	−0.16	0.39	0.35	0.21	0.31		0.54	−0.51	−0.14	−0.35	0.31	−0.16	0.30	−0.15	−0.31	0.23	0.20	0.16	−0.01	−0.16	0.18	0.26	0.40	−0.10	−0.37	0.48	−0.02	−0.40	0.26
Cut	−0.01	−0.10	−0.08	0.11	−0.11	0.43		−0.58	0.01	−0.21	0.56	0.03	0.23	−0.04	−0.08	−0.10	0.00	0.09	0.00	−0.07	0.14	0.19	0.32	−0.03	−0.13	0.50	−0.16	−0.29	−0.09
NoDisturb	−0.09	−0.02	0.06	−0.13	0.03	−0.54	−0.70		−0.43	0.38	−0.45	−0.19	−0.86	0.00	0.13	−0.11	−0.18	−0.30	0.14	−0.33	−0.25	0.06	−0.42	−0.38	0.30	−0.41	0.17	0.23	−0.03
NonForest	0.12	−0.07	−0.14	0.00	−0.09	−0.16	−0.11	−0.06		0.07	−0.04	0.47	0.35	0.22	0.29	−0.22	−0.05	0.11	−0.16	0.82	0.47	−0.07	−0.21	0.62	−0.02	−0.10	−0.17	0.18	0.02
BigTrees	0.21	−0.24	−0.48	−0.18	−0.16	−0.45	−0.35	0.42	0.18		−0.45	0.15	−0.24	0.52	0.62	−0.11	0.04	0.16	−0.32	0.14	−0.09	0.23	−0.62	−0.01	0.63	−0.40	−0.17	0.46	−0.32
SmallTrees	−0.03	0.02	0.06	0.43	0.08	0.38	0.64	−0.54	−0.17	−0.51		−0.18	0.20	−0.08	−0.12	−0.02	0.01	0.01	0.02	−0.07	0.18	−0.03	0.56	−0.11	−0.26	0.30	0.35	−0.47	0.01
Hardwoods	0.14	−0.17	−0.26	−0.15	−0.09	−0.23	0.10	0.06	0.13	0.21	−0.16		0.26	0.38	0.42	−0.20	−0.02	0.40	−0.21	0.41	0.18	0.17	−0.41	0.69	−0.01	−0.35	−0.31	0.49	−0.16
Remnant	0.11	0.06	−0.07	0.10	−0.07	0.34	0.36	−0.84	0.13	−0.25	0.25	−0.03		0.11	−0.03	0.16	0.20	0.41	−0.21	0.23	0.18	−0.19	0.25	0.47	−0.18	0.24	−0.23	−0.05	0.01
MaxTemp	0.54	−0.14	−0.53	−0.39	−0.38	−0.32	−0.06	0.10	0.22	0.54	−0.13	0.34	−0.01		0.94	0.29	0.61	0.51	−0.65	0.19	−0.02	0.39	−0.20	0.28	0.23	−0.61	−0.10	0.58	−0.27
MinTemp	0.45	−0.19	−0.50	−0.33	−0.38	−0.43	−0.09	0.26	0.21	0.62	−0.15	0.38	−0.18	0.95		0.01	0.35	0.39	−0.55	0.27	0.03	0.29	−0.33	0.28	0.41	−0.62	−0.09	0.58	−0.23
AnnualRange	0.34	0.17	−0.10	−0.11	−0.17	0.19	−0.15	−0.21	0.02	−0.12	−0.06	−0.21	0.28	0.27	0.02		0.88	0.04	−0.41	−0.18	−0.36	0.39	0.16	−0.11	−0.31	−0.11	0.12	0.04	−0.28
SummRange	0.38	−0.05	−0.37	−0.27	−0.23	0.06	−0.04	−0.25	0.16	0.06	−0.04	−0.05	0.28	0.60	0.36	0.86		0.17	−0.53	−0.03	−0.22	0.45	0.10	0.07	−0.15	−0.28	−0.03	0.27	−0.25
WinRange	0.56	0.10	−0.25	−0.37	−0.09	−0.03	0.11	−0.19	0.06	0.27	−0.03	0.41	0.25	0.52	0.40	0.03	0.18		−0.45	0.01	0.12	0.16	0.16	0.30	−0.22	−0.30	−0.03	0.27	−0.12
Precip	−0.50	−0.06	0.51	0.21	0.38	0.12	0.04	−0.01	−0.12	−0.33	0.08	−0.18	−0.07	−0.65	−0.57	−0.42	−0.53	−0.43		−0.12	0.03	−0.41	0.14	−0.21	0.05	0.44	−0.13	−0.30	0.25
Ag	0.00	−0.07	−0.14	0.05	−0.17	−0.10	−0.12	−0.03	0.71	0.17	−0.22	0.08	0.09	0.30	0.28	0.18	0.31	−0.01	−0.15		0.14	−0.02	−0.27	0.61	0.07	−0.04	−0.16	0.13	0.04
Rural	−0.19	−0.07	0.01	0.25	0.42	0.20	0.02	0.00	0.16	0.05	0.13	0.01	−0.11	−0.11	−0.05	−0.29	−0.18	−0.08	0.18	−0.07		−0.14	0.01	0.23	−0.11	−0.06	−0.08	0.06	0.37
BLM	0.41	0.07	−0.11	−0.10	0.03	0.29	0.13	−0.01	−0.12	0.10	0.00	0.16	−0.07	0.38	0.29	0.40	0.40	0.17	−0.40	0.00	−0.13		−0.14	−0.13	−0.36	−0.18	0.00	0.16	−0.15
PrivateInd	0.11	0.22	0.25	0.13	−0.07	0.44	0.36	−0.53	−0.26	−0.63	0.59	−0.42	0.26	−0.32	−0.41	0.14	0.03	−0.04	0.18	−0.23	−0.03	−0.04		−0.31	−0.44	0.23	0.34	−0.42	0.21
PrivateNI	0.07	0.07	−0.08	−0.27	−0.06	−0.05	−0.06	0.00	0.32	0.06	−0.15	0.44	0.10	0.26	0.16	0.12	0.26	0.37	−0.21	0.31	0.03	−0.10	−0.31		0.00	−0.14	−0.20	0.24	0.03
USFS	−0.19	−0.34	−0.33	0.01	−0.24	−0.38	−0.17	0.27	0.14	0.62	−0.27	0.07	−0.21	0.26	0.43	−0.32	−0.12	−0.20	0.04	0.19	0.15	−0.38	−0.40	−0.05		−0.10	−0.21	0.23	−0.13
Weak	−0.38	0.08	0.38	0.39	0.25	0.52	0.44	−0.44	−0.05	−0.41	0.34	−0.37	0.39	−0.60	−0.60	−0.14	−0.29	−0.31	0.46	−0.09	0.18	−0.20	0.23	−0.17	−0.08		−0.12	−0.75	0.22
Intermediate	0.18	0.12	0.06	0.27	−0.03	−0.02	−0.19	0.12	−0.08	−0.18	0.32	−0.28	−0.19	−0.16	−0.14	0.09	−0.07	−0.08	−0.09	−0.02	−0.03	−0.04	0.32	−0.09	−0.20	−0.14		−0.56	0.08
Resistant	0.20	−0.15	−0.37	−0.51	−0.20	−0.45	−0.25	0.29	0.10	0.48	−0.50	0.49	−0.20	0.62	0.60	0.08	0.31	0.31	−0.34	0.09	−0.14	0.20	−0.42	0.20	0.21	−0.75	−0.55		−0.32
Unconsol	−0.06	0.03	0.13	−0.13	0.02	0.27	−0.08	0.05	−0.06	−0.24	−0.04	−0.01	−0.11	−0.07	−0.04	−0.25	−0.16	0.09	0.10	0.00	0.10	−0.04	0.24	0.04	−0.16	−0.12	0.14	−0.06	

TABLE 4. Results of model development to predict the natural logarithm of peak coho salmon spawner densities. Shown are the Akaike information criterion (AIC) values, generalized R^2 values, average correlations from bootstrap validation, and model weights. Variables are defined in Table 1.

Extent	Model	AIC	R^2	$\overline{\overline{V}}$[a]	Weight[b]
100-m buffer	0.0065BLM − 0.017SmallTrees + 0.024WinRange	1,742.75	42.87	0.696	0.320
	0.0062BLM − 0.016CattleDensity + 0.025WinRange	1,743.88	41.38	0.693	0.182
	0.0058BLM − 0.0056Weak + 0.023WinRange	1,744.48	40.58	0.695	0.135
	–0.015CattleDensity − 0.0055Weak + 0.027WinRange	1,744.60	40.41	0.695	0.127
	0.0085BLM + 0.0050PrivateNI + 0.020WinRange	1,744.64	40.35	0.698	0.124
	–0.030Weak + 0.00026Weak^2 + 0.024WinRange	1,744.83	40.10	0.697	0.113
500-m buffer	–0.026Weak + 0.00023Weak^2 + 0.025WinRange	1,744.56	40.47	0.696	0.524
	–0.013CattleDensity − 0.0056Weak + 0.027WinRange	1,744.76	40.20	0.697	0.476
HU	0.0070PrivateInd − 0.011Weak + 0.022WinRange	1,742.18	43.61	0.697	0.259
	1.41 + 0.046NonForest + 0.011PrivateInd − 0.013Weak	1,742.35	45.90	0.696	0.238
	–0.033Weak + 0.00034Weak^2 + 0.025WinRange	1,742.38	43.35	0.697	0.235
	1.10 + 0.043Hardwoods + 0.012PrivateInd − 0.011Weak	1,743.48	44.50	0.696	0.135
	0.031NonForest − 0.0079Weak + 0.023WinRange	1,743.52	41.86	0.694	0.133
Catchment	0.0067PrivateInd − 0.36RoadDen + 0.031WinRange	1,743.48	41.91	0.695	0.517
	–0.029*Weak + 0.00027Weak^2 + 0.025WinRange	1,743.62	41.73	0.694	0.483

[a]Average correlation from bootstrap validation.
[b]Model-averaging weight derived from AIC.

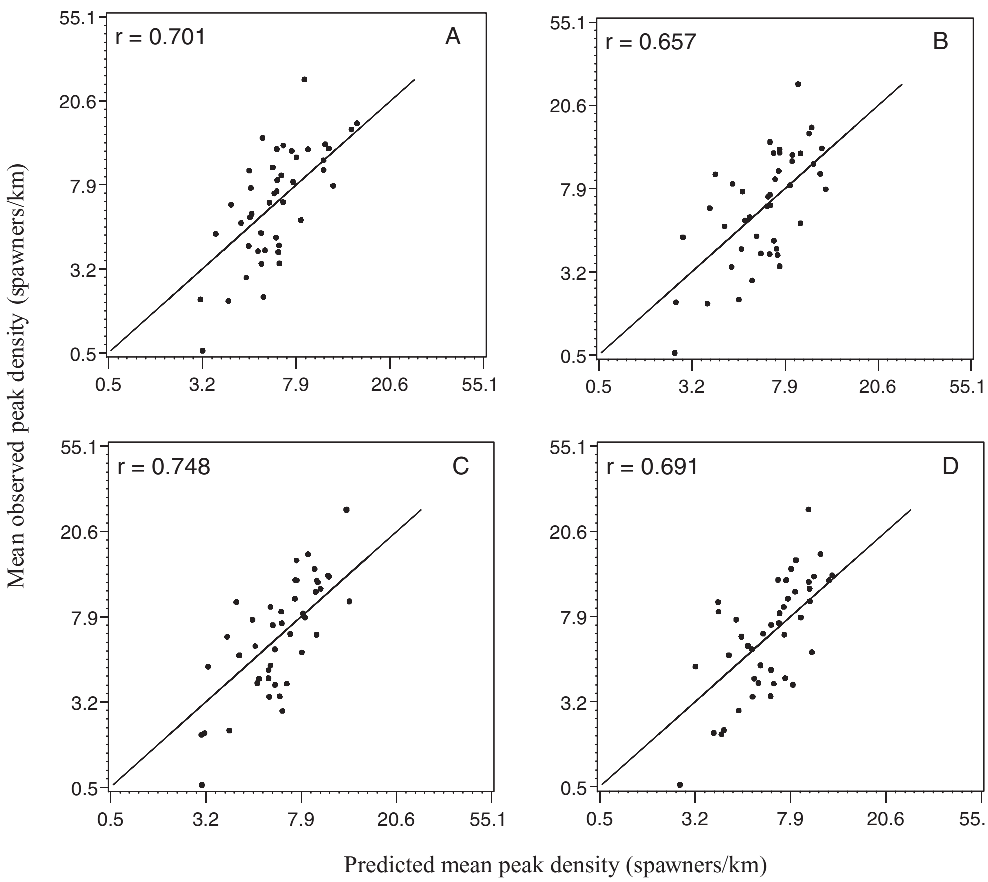

FIGURE 2. Plots of observed versus predicted mean coho salmon peak spawner density at the **(A)** 100-m buffer scale, **(B)** 500-m buffer scale, **(C)** seventh-field hydrologic unit scale, and **(D)** catchment scale. The observed densities were averaged over 17 years for each sample reach. A 1:1 line is included for reference; r = the correlation between the observed and predicted densities.

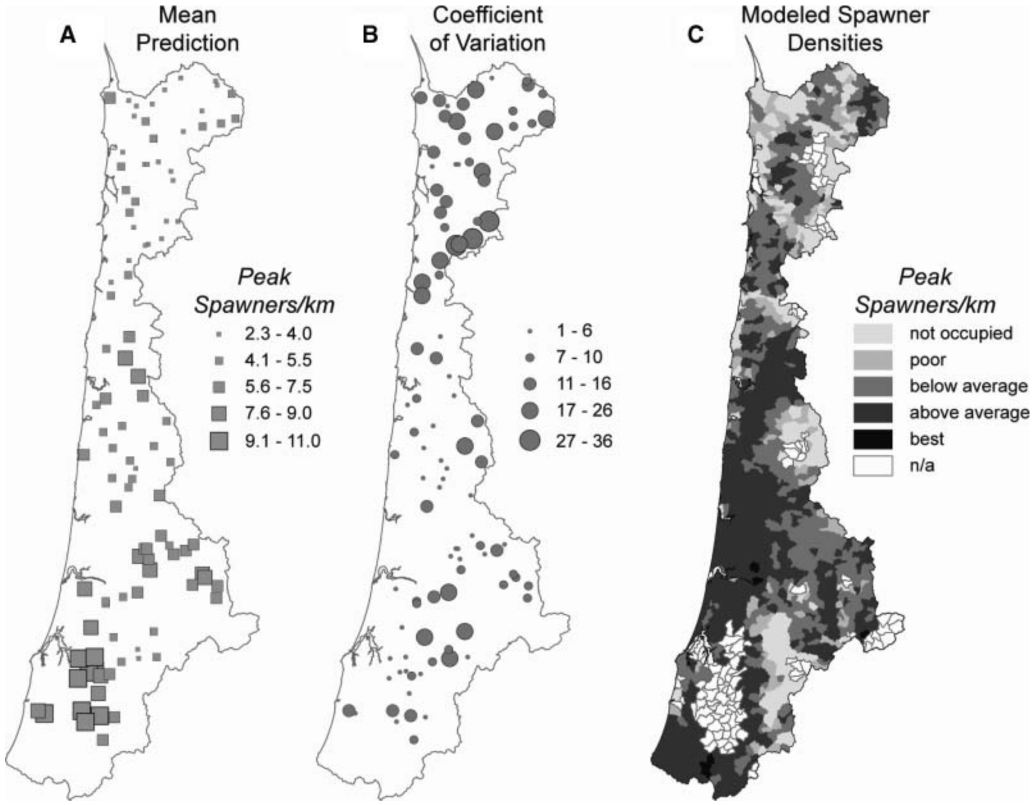

FIGURE 3. Predictions of coho salmon peak spawner density (number of spawners/km). Panel **(A)** shows the mean predictions (from four spatial extents) of spawner density at randomly selected stream segments, panel **(B)** the coefficients of variation among the predictions from the average models at each of the four spatial extents, and panel **(C)** the predicted spawner densities based on the average model from the catchment extent.

low peak spawner densities were predicted in the central portion and near the northern edge of the study area, and the highest densities were predicted in the southern part of the study area.

DISCUSSION

Relative Performance of Landscape Models

Our research contributes to a growing body of literature that examines the relationships between landscape characteristics and salmon populations. Like earlier studies in other regions (e.g., Pess et al. 2002; Feist et al. 2003; Steel et al. 2004), we found that landscape characteristics could explain a substantial percentage of the variation in salmon densities. It is often difficult to make strict comparisons among model performances because modeling approaches and model structures often differ, as do extents over which models apply and the pool of landscape attributes that are available. Furthermore, interpretation of correlations is often not straightforward. However, the performance of our models was comparable, if not stronger, than other landscape models (Table 5). Attributes appearing in models from these studies differ, perhaps reflecting the unavailability of consistent landscape data or that different species are sensitive to different landscape features, or that landscape controls differ in different regions.

Landscape Characteristics Associated with Adult Coho Salmon Distribution

The most important variable in our models is an indicator of climate. The predicted range of winter temperatures was a positive predictor of peak spawner densities at each spatial extent, appearing as a predictor in all but one of our models. Minimum temperature, maximum temperature, annual temperature range, and winter temperature range are all higher in the southern portion of the study area than in the northern portion, and this difference was most pronounced for the winter temperature range. In general, temperatures tend to be milder in the southern portion of the area and warm up earlier. Warmer winter temperatures can accelerate juvenile growth, which produces larger coho salmon smolts (Scrivener and Andersen 1982), and large coho salmon smolts may survive better than small smolts when ocean conditions are relatively poor (Holtby et al. 1990), a situation that existed for the period when we modeled peak spawner densities. More smolts may have returned as adults to areas experiencing wider ranges of winter temperatures that favored greater overwinter growth and larger smolts. It is also possible that winter temperature range may simply be correlated with a key variable that we did not examine. Local ocean production might be partially responsible for spatial patterns in peak spawner densities (Logerwell et al. 2003).

TABLE 5. Comparison of model performance with those of similar landscape models in the literature.

Data set	Species	Study area	Max R^2	Strongest predictors	Model fit (average R^2)	Reference
$N_{sites} = 44$, $N_{years} = 17$; Oregon coast, 1981–1997	Coho salmon	20,305 km^2	0.44	Road density, % nonforest, % private industrial, winter temperature range, mixed geology	0.42	Current study
$N_{sites} = 22$, $N_{years} = 1$; Kalamazoo River, Michigan, 1981–1997	Total fish density	3,232 km^2	0.24	% agriculture in local stream corridor	0.24	Moerke and Lamberti (2006)
$N_{sites} = 54$, $N_{years} = 15$; Snohomish River, Washington, 1984–1998	Coho salmon	4,610 km^2	0.48	% agriculture, % till, % bedrock, % urban	0.18[a]	Pess et al. (2002)
$N_{sites} = 23$, $N_{years} = 18$; Salmon River, Idaho, 1960–1977	Spring –summer Chinook salmon	36,260 km^2	0.30	Presence of wetlands, mean air temperature, % sedimentary geology, Sum of hill slope <1.5%	0.26	Feist et al. (2003)
$N_{sites} = 27$, $N_{years} = 20$; Willamette River, Oregon, 1979–1999	Winter steelhead	7,857 km^2	0.37[b]	% alluvium, % hill slope, % landslide, % young forest, % mafic soil, % agriculture	0.35[b]	Steel et al. (2004)

[a]Estimated from data reported in a figure.
[b]Estimated from reported data (square of correlation).

Ocean recoveries of marked adult hatchery salmon indicate a separation in distribution patterns for coho salmon originating in northern Oregon versus central Oregon (Weitkamp and Neely 2002), which is consistent with latitudinal patterns exhibited in winter temperature ranges and peak spawner densities.

Geology plays a prominent role in these models because the erodability of the substrate influences channel morphology (Hack 1957; Hicks 1990) and sediment loading within a stream (Bond 2004). Over one-half of all models at each of the four spatial extents showed a negative relationship between peak spawner densities and the percent of weak rock types (schists and pyroclastic deposits). These rock types erode easily and contribute to fine sediment loading in streams (Hack 1957). Increased fine sediments have been cited as a major cause of the degradation of salmonid spawning and rearing habitat (Nehlsen et al. 1991; Frissell 1993) because they become embedded in spawning gravels, which results in a decrease in dissolved oxygen and water exchange (Cederholm and Reid 1987). This results in altered behavior and decreased growth and survival of juvenile salmonids (Crouse et al. 1981; Bisson and Bilby 1982) and causes a shift in invertebrates toward burrowing taxa, which are unavailable as prey (Suttle et al. 2004). The density of Chinook salmon *O. tshawytscha* redds was negatively related to sedimentary geology in previous landscape models (Feist et al. 2003).

Nonforested land is frequently a key model component, perhaps because a substantial percentage (32%) of the area adjacent to reaches with high intrinsic habitat potential for coho salmon has been converted to uses other than forestry (Burnett et al. 2007). Likewise, the positive relationship with ownership by the BLM, private nonindustrial owners, or private industrial forest owners may be explained by the fact that the intrinsic habitat potential for coho salmon tends to be higher for streams on lands under these ownerships than on lands managed by the USFS (Burnett et al. 2007). Our current analysis could not separate the importance of the distribution of lands owned by the BLM from the condition of the land owned by the BLM. In a western Washington landscape that is more urbanized than the Oregon Coastal Province, abundances of coho salmon spawners were positively related to percent forested area (Pess et al. 2002). Many negative effects on stream ecosystems have been associated with conversion of forested lands to agricultural and developed uses (e.g., IMST 2002; Roy et al. 2003; Van Sickle et al. 2004), and these include lower densities of coho salmon (Beechie et al. 1994; Bradford and Irvine 2000; Pess et al. 2002).

Predictor variables indicative of land management, cattle density, and road density were negatively associated with peak spawner densities in many of our models. These results are consistent with a rich literature documenting the types of effects and pathways by which livestock grazing (e.g., Platts 1991; Belsky et al. 1999) and roads (e.g., Everest et al. 1987; Beechie et al. 1994; Paulsen and Fisher 2001) may degrade salmonid freshwater habitats. Low road densities were useful in identifying areas across the interior Columbia River basin with relatively healthy populations of salmon in general (Lee et al. 1997) or high densities of Chinook salmon in particular (Thompson and

Lee 2000). The spatial extent for summarizing landscape characteristics determined which of the two variables appeared in a model; cattle density was a predictor only in models using buffer extents and road density was a predictor only at the catchment extent. Roads are concentrated in areas managed for timber and are often located some distance from the stream. Thus, roads would be more likely to influence models when road densities are summarized to incorporate upslope timberlands. Though cattle grazing is generally confined to low-gradient areas near streams, the grain size for this layer is too large to be able to discern differences between the different spatial extents. The reason that this variable does not appear in models at broader spatial extents may be that variables, such as road density, become stronger drivers and overshadow the influence of cattle density.

Impact of Spatial Extent

In contrast to previous results indicating that broad-scale models had better predictive power for Chinook salmon and steelhead *O. mykiss* (Feist et al. 2003, 2010), we saw little evidence that the spatial extent at which landscape characteristics were summarized affected model results for peak spawner densities of coho salmon. Models at each spatial extent contained similar predictor variables, explained similar amounts of variation, and yielded similar predictions. There were only slight differences between buffers of 100 and 500 m. This may be because (1) values of most predictor variables were fairly highly correlated among spatial extents, given that the study area is managed predominantly for forestry with only small and isolated patches in other land uses; (2) peak spawner densities may respond to broad-scale influences (e.g., climate, ocean conditions) as well as local influences and thus may be less sensitive than other in-channel indicators to the spatial extent at which landscape characteristics are summarized for modeling; and (3) the 100- and 500-m buffer sizes were probably smaller than the resolution of some of these geospatial data layers, increasing the likelihood that predictor variables would be correlated between the two buffer extents. Although spatial extent may influence the ability to model some indicators, such as large wood (Feist et al. 2003; Burnett et al. 2006), it may have little influence on other indicators, such as the density of cutthroat trout *O. clarkii* (Van Sickle et al. 2004).

There was still value in comparing the different spatial extents, however. In particular, doing so enabled us to distinguish indicators of potential management influence that are likely to be informative at local extents from those that are likely to be informative over broader extents (e.g., road density). There was little difference between the HU and catchment extents, and models at the HU extent performed better than models at any other extent. This indicates that existing HUs could be used in future modeling efforts for coho salmon in this region, eliminating the need to delineate reach-specific catchments. Feist et al. (2010) also found that models for Chinook salmon in the Yakima River basin in eastern Washington had similar AIC values at sixth-field HU and catchment extents. However, care should be taken in extending this finding to other regions and species. Catchment and HU extent models of steelhead in the John Day Basin in eastern Oregon varied significantly (the 500-m buffer extent models were more similar to the HU extent models) and the HU extent yielded the highest AIC values (Feist et al. 2010). Which landscape variables correlate with salmon abundance, the extent at which these variables are most important, and the way that variables interact vary with species and region (Feist et al. 2010), the degree to which landscapes have been altered by humans (Wang et al. 2003; Feist et al. 2010), and the spatial correlation between human alterations and natural features (Lucero et al., in press). The resolution of landscape data might also influence which spatial extent would be best for modeling. All of these considerations must be taken into account when deciding on the best spatial extent for modeling.

Predictions

Our aim was not to explicitly predict coho salmon densities or to define mechanistic relationships between landscape variables and fish production, but rather to predict the relative density of adult coho salmon. The response variable for modeling is based on the mean of fish densities over 17 years during which the PDO index was relatively consistent (Mantua et al. 1997). Shifts in the PDO coincide with marked swings in ocean productivity for Pacific salmon. The period of study coincided with a low production regime for salmon along the Oregon coast. Consequently we have a fairly precise estimate of mean density over this period at locations distributed throughout the region. We interpret the results as indicating the relative productivity of stream reaches within the distribution of coho salmon in western Oregon. Those sites with high average scores are expected to support higher relative densities of coho salmon spawners in both good and poor years, compared with those sites with low average scores. These results could be used to identify hypotheses regarding relationships between salmon abundance and landscape characteristics or to identify reaches for further on-the-ground research.

This and all previous landscape modeling attempts for salmonids are hampered by the use of a nonrandom sample. Without a representative sample it is not possible to accurately infer conditions in the rest of the study area. In this sample, sites were selected because they were easily accessible and historically sustained high densities of spawning coho salmon. Consequently, remote and rugged areas and those with poorer habitat would be excluded from the sample. However, although selection of the index reaches was not statistical, they cover a broad range of the conditions represented in the dependent and independent variables. For a predictive model it is most important that the sample encompass the range of conditions present in the region that is modeled. We did not make predictions in areas where conditions were outside of the range in the sample. Our objective was not to characterize all types of habitat,

TABLE 6. Key variables for predicting coho salmon density at multiple spatial scales. Plus signs indicate positive relationships with spawner density, minus signs negative relationships. Variables are defined in Table 1.

Variable	100-m buffer	500-m buffer	Hydrologic units	Watershed
Climate	WinRange (+)	WinRange (+)	WinRange (+)	WinRange (+)
Geology	Weak (–)	Weak (–)	Weak (–)	Weak (–)
Land use	CattleDensity (–)	CattleDensity (–)		RoadDen (–)
Ownership	BLM or PrivateNI (+)		PrivateInd (+)	PrivateInd (+)
Management			NonForest (+)	
Vegetation	SmallTrees (–)		Hardwoods (+)	

but rather to identify areas where conditions are conducive to supporting higher-than-average coho salmon abundances.

Management Implications

The models we developed can assist in decision making for coho salmon management. Mapped predictions of areas likely to support unusually high numbers of coho salmon spawners (Figure 3) are informative for a wide range of purposes. For example, conservation and restoration activities may be targeted to areas predicted to be capable of sustaining high relative densities of coho salmon spawners. Several characteristics that appear as predictors in the models (such as cattle density) can be altered and doing so may facilitate restoration and enhancement of coho salmon production. Additionally, if a site is deemed suitable for a restoration project, our results could be used to better predict how well that restoration site would function, given the landscape conditions in the surrounding area. For example, Steel et al. (2004) were able to use similar models for steelhead to prioritize barrier removal projects by predicting relative redd density in the upstream habitat.

Our results suggest key variables to consider when developing monitoring plans and data collection efforts for coho salmon and their habitats (Table 6). To monitor all components of the population, it will be important to include samples from a wide range of geologic and climatic strata. To tease out the relative impact of land management, it would be informative to collect data on adult spawner abundances or juvenile densities in areas with similar geologic and climatic controls, but that differ only in cattle density in riparian areas or road density in the upland catchments.

Future Directions

This study represents a significant improvement in modeling fish densities based on landscape characteristics. Data sets are rarely available that reflect such a favorable combination of qualities for model building, i.e. comprehensive, generally high-resolution landscape data coupled with a large number of field sites ($N = 44$), evenly distributed throughout a large area (20,305 km^2), with a long and consistent history of data collection (17 of 50 years of data were used for this study). These data sets allowed us to develop models with high correlations between landscape characteristics and peak spawner densities for coho salmon ($r = 0.66$–0.75, $P < 0.001$). However, improvements are still possible. These models were based on index reaches that were not randomly selected. Models based on a statistical sample would be expected to contain a greater range of fish densities and, thus, better predict the relative response of spawner densities across the entire range of potential habitat. Another possible enhancement of the research is to model relationships between landscape characteristics and the abundance of juvenile salmonids. Abundances of adult coho salmon are strongly influenced by ocean conditions during the year of ocean entry (Nickelson 1986; Logerwell et al. 2003). Ocean conditions have less direct influence on juvenile densities. Consequently, relationships between juvenile densities and habitat may be stronger than those between habitat and adults. Finally, it would be instructive to model relationships between instream habitat characteristics observed on the ground and landscape characteristics defined in geospatial data layers. This would allow us to hypothesize the mechanisms by which landscape characteristics influence instream habitat, and thus fish densities, and to predict habitat quality associated with landscape characteristics that may arise under different land management policies.

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REFERENCES

Beechie, T., E. Beamer, and L. Wasserman. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. North American Journal of Fisheries Management 14:797–811.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431.

Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics: identifying influential data and sources of collinearity. Wiley, New York.

Bisson, P. A., and R. E. Bilby. 1982. Avoidance of suspended sediment by juvenile coho salmon. North American Journal of Fisheries Management 4:371–374.

Bond, N. R. 2004. Spatial variation in fine sediment transport in small upland streams: the effects of flow regulation and catchment geology. River Research and Applications 20:705–717.

Bradford, M. J., and J. R. Irvine. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. Canadian Journal of Fisheries and Aquatic Sciences 57:13–16.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish and Wildlife Service Fishery Bulletin 61:97–110.

Burnett, K. M., G. H. Reeves, S. Clarke, and K. Christiansen. 2006. Pages 175–197 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Comparing riparian and catchment influences on stream habitat in a forested, montane landscape. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Burnett, K. M., G. H. Reeves, D. J. Miller, S. Clarke, K. Vance-Borland, and K. Christiansen. 2007. Distribution of salmon-habitat potential relative to landscape characteristics and implications for conservation. Ecological Applications 17:66–80.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cederholm, C. J., and L. M. Reid. 1987. Impact of forest management on coho salmon *(Oncorhynchus kisutch)* population of the Clearwater River, Washington. University of Washington, Project Summary, Seattle.

Clarke, S. E., K. M. Burnett, and D. J. Miller. 2008. Modeling streams and hydrogeomorphic attributes in Oregon from digital and field data. Journal of the American Water Resources Association 44:1–20.

Cook, R. D. 1977. Detection of influential observations in linear regression. Technometrics 19:15–18.

Creque, S. M., E. S. Rutherford, and T. G. Zorn. 2005. Use of GIS-derived landscape-scale habitat features to explain spatial patterns of fish density in Michigan rivers. North American Journal of Fisheries Management 25:1411–1425.

Crouse, M. R., C. A. Callahan, K. W. Malueg, and S. E. Dominquez. 1981. Effects of fine sediments on growth of juvenile coho salmon in laboratory streams. Transactions of the American Fisheries Society 110:281–286.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Durance, I., C. Lepichon, and S. J. Ormerod. 2006. Recognizing the importance of scale in the ecology and management of riverine fish. River Research and Applications 22:1143–1152.

Everest, F. H., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98–142 *in* E. O. Salo and T. W. Cundy, editors. Forestry and fishery interactions. University of Washington Press, Seattle,

Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. U.S. Forest Service General Technical Report PNW-GTR-213.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Feist, B. E., E. A. Steel, D. W. Jensen, and D. N. D. Sather. 2010. Does the scale of our observational window affect our conclusions about correlations between endangered salmon populations and their habitat? Landscape Ecology 25:727–743.

Feist, B. E., E. A. Steel, G. R. Pess, and R. E. Bilby. 2003. The influence of scale on salmon habitat restoration priorities. Animal Conservation 6:271–282.

Flitcroft, R. L. 2007. Regions to streams: spatial and temporal variation in stream occupancy patterns of coho salmon *(Oncorhynchus kisutch)* on the Oregon coast. Doctoral dissertation. Oregon State University, Corvallis.

Frissell, C. A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (USA). Conservation Biology 7:342–354.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Hack, J. T. 1957. Studies of longitudinal stream profiles in Virginia and Maryland. U.S. Geological Survey, Professional Paper 294-B.

Hicks, B. J. 1990. The influence of geology and timber harvest on channel morphology and salmonid populations in Oregon Coast range streams. Doctoral dissertation. Oregon State University, Corvallis.

Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47:2181–2194.

Hynes, H. B. N. 1975. The stream and its valley. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 19:1–15.

IMST (Independent Multidisciplinary Science Team). 2002. Recovery of wild salmonids in western Oregon lowlands. Oregon Governor's Natural Resources Office, Technical Report 2002-1 to the Oregon Plan for Salmon and Watersheds, Salem.

Jacobs, S. E. and C. X. Cooney. 1997. Oregon coastal spawning surveys, 1994 and 1995. Oregon Department of Fish and Wildlife, Information Report 97-5, Portland.

Johnson, S. L., J. D. Rodgers, M. F. Solazzi, and T. E. Nickelson. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus* spp.) in an Oregon coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62:412–424.

Lawson, P. W., E. P. Bjorkstedt, M. W. Chilcote, C. W. Huntington, J. S. Mills, K. M. S. Moore, T. E. Nickelson, G. H. Reeves, H. A. Stout, T. C. Wainwright, and L. A. Weitkamp. 2004. Identification of historical populations of coho salmon (*Oncorhynchus kisutch*) in the Oregon coast evolutionary significant unit. NOAA Technical Memorandum NMFS-NWFSC-79.

Lee, D. C., J. R. Sedell, B. E. Rieman, R. F. Thurow, and J. E. Williams. 1997. Broad scale assessment of aquatic species and habitats. U.S. Forest Service, General Technical Report PNW-GTR-405:1057–1496.

Lennartz, S. 2005. Oregon forest land change mapping. Sanborn Mapping Solutions, Portland, Oregon.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS® system for mixed models. SAS Institute, Cary, NorthCarolina.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12;554–568.

Lucero, Y. E., A. Steel, K. M. Burnett, and K. Christiansen. In press. Untangling human development and natural gradients: implications of underlying correlation structure for linking landscapes and riverine ecosystems. River Systems.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Moerke, A. H., and G. A. Lambarti. 2006. Scale-dependent influences on water quality, habitat and fish communities in streams of the Kalamazoo River basin, Michigan (USA). Aquatic Science 68:193–205.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Naiman, R. J., S. R. Elliott, J. M. Helfield, and T. C. O'Keefe. 2000. Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. Hydrobiologia 410:79–86.

Nehlsen, W., J. E. Williams, J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the

Oregon production area. Canadian Journal of Fisheries and Aquatic Sciences 43:527–535.

Nickelson, T. E. 1998. A habitat-based assessment of coho salmon production potential and spawner escapement needs for Oregon coastal streams. Oregon Department of Fish and Wildlife, Information Report 1–15, Salem.

Nickelson, T. E., and P. W. Lawson. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. Canadian Journal of Fisheries and Aquatic Sciences 55:2383–2392.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992a. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

Nickelson, T. E., M. R. Solazzi, S. L. Johnson, and J. D. Rodgers. 1992b. An approach to determining stream carrying capacity and limiting habitat for coho salmon (*Oncorhynchus kisutch*). Pages 251–260 *in* L. Berg and P. W. Delaney, editors. Proceedings of the coho workshop. Department of Fisheries and Oceans, Vancouver.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Canadian Journal of Forest Research 32:725–741.

Paulsen, C. M., and T. R. Fisher. 2001. Statistical relationship between Snake River spring/summer Chinook salmon parr-to-smolt survival and indices of land use. Transactions of the American Fisheries Society 130: 347–358.

Pess, G. R., D. R. Montgomery, E. A. Steel, R. E. Bilby, B. E. Feist, and H. M. Greenberg. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Washington, USA. Canadian Journal of Fisheries and Aquatic Sciences 59: 613–623.

Platts, W. S. 1991. Livestock grazing. Pages 389–423 *in* W. S. Platts, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Bethesda, Maryland.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53:295–311.

Roy, A. H., M. C. Freeman, J. L. Meyer, and D. S. Leigh. 2003. Patterns of land use change in upland and riparian areas in the Etowah River basin. Pages 331–334 *in* K. J. Hatcher, editor. Proceedings of the conference on 2003 Georgia water resources. University of Georgia, Athens.

Scrivener, J. C., and B. C. Andersen. 1982. Logging impacts and some mechanisms which determine the size of spring and summer populations of coho salmon fry in Carnation Creek. Pages 257–272 *in* G. F. Hartman, editor. Proceedings of the Carnation Creek workshop: a ten year review. Department of Fisheries and Oceans, Nanaimo, British Columbia.

Solazzi, M. F., T. E. Nickelson, S. L. Johnson, and J. D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57:906–914.

Spies, T. A., K. N. Johnson, K. M. Burnett, J. L. Ohmann, B. C. McComb, G. H. Reeves, P. Bettinger, J. D. Kline, and B. Garber-Yonts. 2007. Cumulative ecological and socioeconomic effects of forest policies in coastal Oregon. Ecological Applications 17:5–7.

State of Oregon. 2005. Oregon coastal coho assessment: parts 1, 2, 3A and 3B. Oregon Department of Fish and Wildlife, Salem.

Steel, E. A., B. E. Feist, D. W. Jensen, G. R. Pess, M. B. Sheer, J. B. Brauner, and R. E. Bilby. 2004. Landscape models to understand steelhead (*Oncorhynchus mykiss*) distribution and help prioritize barrier removals in the Willamette basin, Oregon, USA. Canadian Journal of Fisheries and Aquatic Sciences 61:999–1011.

Steel, E. A., R. M. Hughes, A. H. Fullerton, S. Schmutz, J. A. Young, M. Fukushima, S. Muhar, M. Poppe, B. E. Feist, and C. Trautwein. 2010. Are we meeting the challenges of landscape-scale riverine research? A review—living reviews in landscape research 4:1. Available: landscaperesearch.livingreviews.org/Articles/lrlr-2010-1/. (July 2010).

Suttle, K. B., M. E. Power, J. M. Levine, and C. McNeely. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecological Applications 14:969–974.

Thompson, W. L., and D. C. Lee. 2000. Modeling relationships between landscape-level attributes and snorkel counts of Chinook salmon and steelhead parr in Idaho. Canadian Journal of Fisheries and Aquatic Sciences 57:1834–1842.

Torgersen, C. E., and D. A. Close. 2004. Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology 49:614–630.

Van Sickle, J., J. Baker, A. Hierlihy, P. Bayley, S. Gregory, P. Haggerty, L. Ashkenas, and J. Li. 2004. Projecting the biological conditions of streams under alternative scenarios of human land use. Ecological Applications 14:368–380.

Walker, G. W., N. S. MacLeod, R. J. Miller, G. L. Raines, and K. A. Connors. 2003. Spatial digital database for the geologic map of Oregon. U.S. Geological Survey, Open-File Report 03-67, Menlo Park, California.

Weitkamp, L., and K. Neely. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Sciences 59:1100–1115.

Weitkamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon and California. NOAA Technical Memorandum NMFS-NWFSC-24.

Wang, L. Z., J. Lyons, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela, and P. M. Stewart. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the northern lakes and forest ecoregion, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 60:491–505.

Wing, M. C., and A. Skaugset. 2002. Relationships of channel characteristics, land ownership, and land use patterns to large woody debris in western Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 59:196–807.