

Habitat connectivity, complexity, and quality: predicting adult coho salmon occupancy and abundance

Kara J. Anlauf-Dunn, Eric J. Ward, Matt Strickland, and Kim Jones

Abstract: The distribution, quality, and connectivity of instream habitat can influence adult salmon occupancy and abundance patterns and alter population dynamics. In this study, we evaluated the relationships between adult coho salmon (*Oncorhynchus kisutch*) occupancy and abundance with instream habitat conditions, including measures of spawning gravel, habitat complexity, and juvenile rearing habitat. We used corresponding adult salmon spawning and instream habitat data collected within coastal Oregon watersheds as part of a long-term monitoring program. We modeled two processes as a function of habitat characteristics: the number of coho salmon when they were present and the occupancy probabilities of coho salmon. The results from both submodels were then combined into an estimate of total abundance at each site. Adult coho salmon occupancy was best predicted by the capacity of the habitat to support parr during the winter, complex pools, percent bedrock, and site distance to the ocean. Although lacking the predictive capacity of the occupancy model, increases in adult coho counts at sites were also influenced by the site distance to the ocean, and there is evidence that both percent gravel and complex pools may also be valuable predictors. By taking advantage of long-term datasets with broad spatial range, using an integrative approach across coho salmon life stages, and utilizing innovative Bayesian modeling techniques, this study is a unique approach to understanding a complicated ecological narrative. Combined, our results indicate the spatial distribution and proximity of spawning and rearing habitats may maximize productivity for coho salmon in coastal Oregon watersheds.

Résumé : La répartition, la qualité et la connectivité des habitats dans les cours d'eau peuvent influencer l'occupation par les saumons adultes et la distribution de leur abondance et modifier la dynamique de leurs populations. Nous avons évalué les relations entre l'occupation et l'abondance des saumons cohos adultes (*Oncorhynchus kisutch*) et des conditions relatives à l'habitat dans le cours d'eau, y compris des mesures du gravier utilisé pour le frai, de la complexité de l'habitat et de l'habitat d'élevage des juvéniles. Nous avons utilisé des données correspondantes sur le frai de saumons adultes et sur l'habitat dans le cours d'eau recueillies dans des bassins versants côtiers de l'Oregon dans le cadre d'un programme de surveillance à long terme. Nous avons modélisé deux processus en fonction des caractéristiques de l'habitat, soit le nombre de saumons cohos quand ces derniers étaient présents et les probabilités d'occupation par des saumons cohos. Les résultats des deux sous-modèles ont ensuite été combinés pour obtenir une estimation de l'abondance totale dans chaque site. La capacité de l'habitat de supporter les tacons durant l'hiver, la présence de fosses complexes, le pourcentage de substrat rocheux en place et la distance séparant le site de l'océan étaient les meilleurs prédicteurs de l'occupation par des saumons cohos adultes. Si elles n'ont pas la capacité de prédiction du modèle d'occupation, les augmentations du nombre des saumons cohos adultes dans les sites étaient également influencées par la distance par rapport à l'océan, et les résultats indiquent que le pourcentage de gravier et les fosses complexes pourraient aussi constituer des prédicteurs utiles. En combinant l'utilisation d'ensembles de données de longue durée à grande couverture spatiale, une approche intégrée couvrant les différentes étapes du cycle de vie du saumon coho et des méthodes de modélisation bayésiennes novatrices, l'étude constitue une approche singulière pour mieux comprendre une situation écologique complexe. Nos résultats combinés indiquent que la répartition spatiale et la proximité des habitats de frai et d'élevage pourraient maximiser la productivité du saumon coho dans les bassins versants côtiers de l'Oregon. [Traduit par la Rédaction]

Introduction

Salmonids have complex life histories, utilizing distinct habitats at each life stage. Stream reaches that provide sufficient habitat for each coho salmon (*Oncorhynchus kisutch*) life stage (adequate spawning gravels, depths, and flows and complex refuge habitats) may be the most productive (Mull and Wilzbach 2007; Flitcroft et al. 2012). Yet how the distribution and condition of those habitat features can influence salmonid dynamics within river basins is still not well understood. One challenge to this understanding is the lack of temporally and spatially extensive data. While a few studies

exist with spatially continuous data (Anderson et al. 2008; Flitcroft et al. 2012; McMillan et al. 2013), they are often limited in study duration, which can underestimate the importance of time (Isaak and Thurow 2006). A complete understanding of salmonid dynamics is likely best viewed with a broad spatial and temporal lens.

Recent studies have focused on how natural and anthropogenic features at larger spatial scales influence the dynamics of adult salmonid occupancy and abundance in the Pacific Northwest (Reeves et al. 1995; Pess et al. 2002; Firman et al. 2011; Steel et al. 2012). Densities of coho salmon tend to be higher in areas

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dominated by forest cover, with less agricultural land use, and where sedimentary (versus volcanic) geologies prevail (Firman et al. 2011; Steel et al. 2012). The habitat conditions that influence adult salmonid occupancy and abundance are hierarchical; landscape scale features such as climate, geology, geomorphology, or land use account for only a portion of the variability in adult salmonid spawning location, timing, and (or) abundance (Steel et al. 2012). Controls operating at landscape scales bound the distribution of conditions at smaller scales (Beechie et al. 2008). Therefore, landscape features may help explain patterns in maximum fish abundance, but finer-scale habitat features, measured within a stream reach or specific types of habitat, are necessary to further illuminate differences in site occupancy and abundance (Montgomery et al. 1999). Further, temporal variation can affect relationships at all spatial scales clouding our ability to disentangle the value of individual habitat features. Variation in stream habitat is typically higher spatially than temporally, and while much of the variation in adult abundance also occurs between stream reaches, considerable variation occurs between years (Anlauf et al. 2011; Steel et al. 2012). The location of both landscape and fine-scale habitat features along the stream network could provide the context for understanding how habitat conditions can affect the dynamics of occupancy and abundance both spatially and temporally. The inclusion of reach location has been shown to be important in understanding juvenile salmonid distributions and could be used to understand differences in adult abundances at individual sites (McMillan et al. 2013).

Ocean regimes strongly regulate salmonid productivity at large spatial and temporal scales; however, over half of the variability in coho salmon recruitment is thought to be related to the freshwater phase of the life cycle (Lawson 1993). For coho salmon, the location of spawning is controlled by suitable holding and spawning habitats at finer spatial scales, dictated by characteristics inherent to different channel types (Montgomery et al. 1999), stream discharge, and hyporheic flow exchange (Beechie et al. 2008). Juvenile coho rear in mainstem and secondary channel pool habitats that improve in quality with increases in complexity (Bjornn and Reiser 1991; Nickelson et al. 1992). Structurally complex stream habitats provide velocity refuge and cover supporting higher capacities of juvenile salmonids (Nickelson et al. 1992; Nickelson and Lawson 1998) and also have a strong association with spawning site selection (Beechie et al. 2008; Bisson et al. 2009). Complex habitats are typified by a number of stream conditions such as off-channel habitats, a diversity of habitat types, instream roughness (e.g., woody debris), and a range of substrate compositions (Schlosser 1991). Stream habitat complexity exists at multiple spatial (channel unit, reach, stream network) and temporal (daily, seasonal, annual) scales influencing the distribution, persistence, and productivity of fish species (Schlosser 1991; Fausch et al. 2002). While the number of adults that can spawn in a stream is a function of the size of an area suitable for spawning and building redds, the long-term productivity and freshwater survival of coho salmon may depend on the spatial distribution of salmonid spawning habitats relative to these high-quality rearing habitats that persist over time (Flitcroft et al. 2014).

Nickelson and Lawson (1998) modeled the population viability of coho salmon in Oregon Coast basins based on assumptions of spatial connectivity between spawning and rearing habitats and metapopulation dynamics. Patterns of adult occupancy and abundance varied between basins and over time, but modeled viability of the populations was directly associated with quality of juvenile rearing habitats during years or decades of poor ocean survival. Distribution and abundance contract and expand within a basin, with some patches consistently occupied with spawning adults, while other patches wax and wane (Lewis et al. 2012; Peacock and Holt 2012). Further, the distribution or dispersal of juveniles into non-natal habitats can fluctuate as a result of competition and habitat quality (Anderson et al. 2008). The modeling by Nickelson

and Lawson (1998) implied that a spatial structure and relationship between juvenile and adult habitat exists, though to date no empirical relationship has been demonstrated. Furthermore, Nickelson and Lawson (1998) suggested that a better understanding of spatial relationships and metapopulation dynamics would improve viability modeling for management. Being able to identify habitat thresholds across life histories and life stages may also provide some clarity on restoration approach and prioritization.

In this paper, we examine an extensive overlapping dataset of adult spawner and instream habitat to evaluate the relationship between adult occupancy and abundance with stream network and habitat features. Our objectives were to (i) develop a predictive model of adult abundance given habitat conditions, (ii) determine whether the inclusion of complexity metrics further our understanding of occupancy and abundance patterns, and (iii) identify whether different habitat metrics might differentially influence occupancy and abundance. We used adult coho salmon spawning and instream habitat data collected over a broad spatial extent and a wide time period in Oregon Coast watersheds. Coho salmon on the Oregon Coast are a model species for study because they are listed as a threatened species under the Endangered Species Act (ESA); therefore, harvest has been suppressed or eliminated for the majority of the monitoring period, and few major impoundments exist that substantially impede freshwater survival. The long-term, spatially and temporally explicit datasets and the use of an integrative approach across coho salmon life stages is a unique attempt to understand this complicated ecological narrative.

Methods

Study area and data

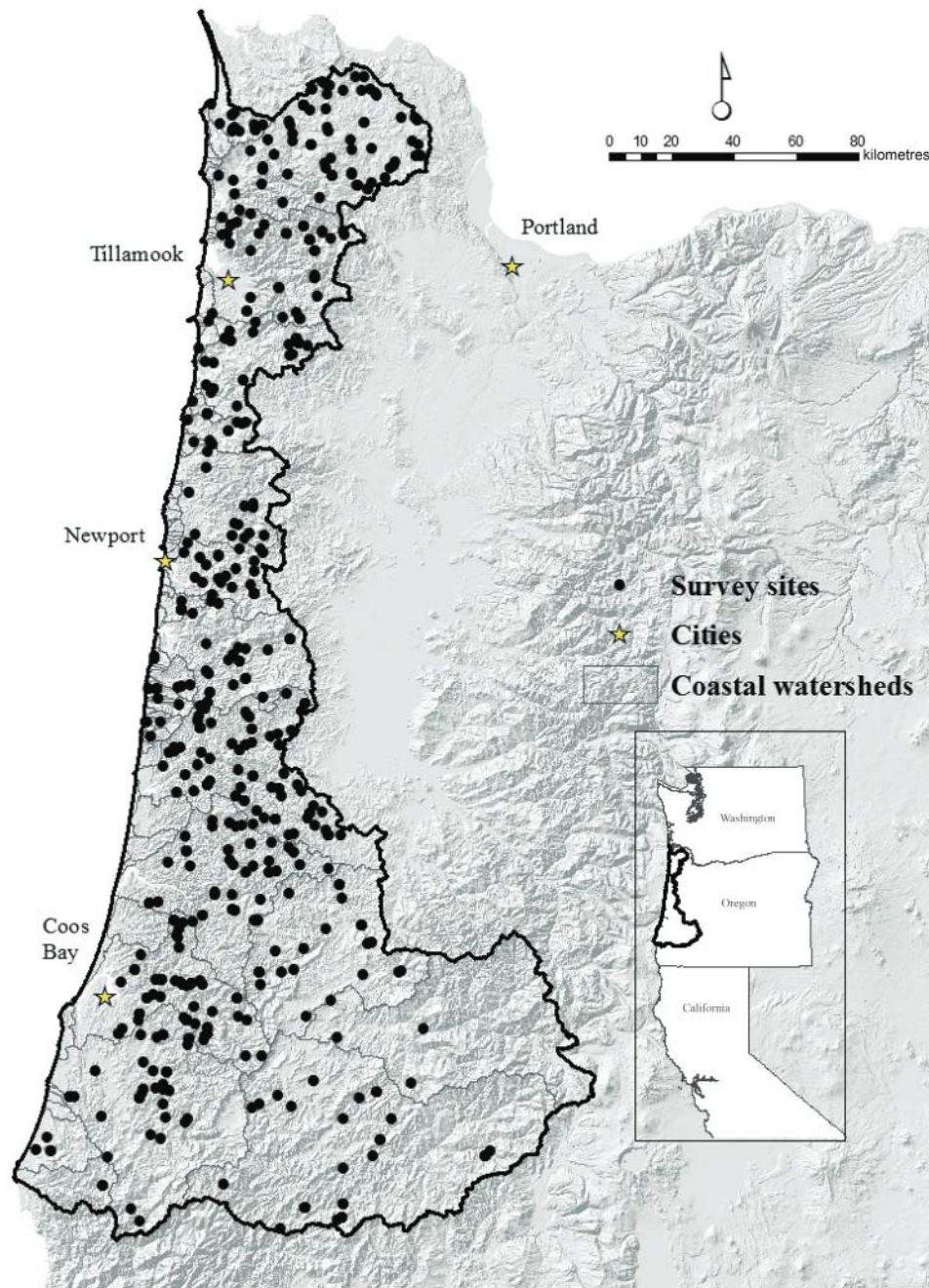
Adult salmon and instream habitat data were collected within wadeable streams in coastal watersheds in the Oregon Coast Coho Salmon Evolutionary Significant Unit (ESU) (Weitkamp et al. 1995) (Fig. 1). This region is primarily underlain by marine sandstones, basaltic volcanic rock, and intrusive igneous rock (Spies et al. 2002). The Oregon Coast is characterized by a maritime climate with narrow fluctuations in temperatures, seasonally and diurnally (Spies et al. 2002). Precipitation falls primarily as rain in the winter months. Conifer forests are the dominant land cover throughout the coastal watersheds, although agricultural lands are common in the lowlands of all basins. As a result, aquatic systems have been modified primarily by forest management and agricultural land use activities.

Sites were selected using a generalized random tessellation stratified (GRTS) design (Stevens 2002; Stevens and Olsen 2004). Sites were randomly assigned to four temporal strata and visited annually, every 3 years, every 9 years, or only once. Based on that design, systematic sampling along a 1:24 000 scale hydrography line work was applied, resulting in points (GRTS points) that are both random and spatially balanced. Salmonid spawning and stream habitat survey reaches were then established, encompassing the GRTS point within the survey bounds. Reach boundaries were associated with natural features (major stream confluences, changes in valley morphology) when feasible. Only survey sites within the currently known distribution of coho salmon were included in this analysis.

Physical habitat data

Instream habitat data were collected by the Oregon Department of Fish and Wildlife (ODFW) between June and September (1999–2011). These data are collected to monitor the status and trends of coastal stream habitats. Survey reaches averaged 1 km in length (range 0.38–1.4 km). Each reach was visited once during the season. At each reach location, surveyors recorded data related to channel morphology, substrate compositions, volume of instream wood, and the adjacent riparian vegetation (Moore et al. 2007). All data were collected within discrete geomorphic habitat

Fig. 1. Survey sites, cities, and coastal watersheds boundaries within the Oregon Coast Coho Salmon Evolutionary Significant Unit (ESU).



units (Hawkins et al. 1993) and were summarized at the reach scale for this analysis. An estimate of habitat capacity with respect to the production potential of juvenile coho salmon was also included in the analysis. The estimate of winter parr capacity (parr·km⁻¹) is an integrated variable derived from the Habitat Limiting Factors Models (Nickelson and Lawson 1998). The model estimates parr density based on stream habitat type and surface area. Winter parr estimates were based on a modeled relationship from summer habitat data (Anlauf et al. 2009). Table 1 summarizes all the metrics selected for this analysis.

Coho salmon data

Spawning survey data were collected by ODFW from mid-October through the end of January (1998–2010). These data were collected to monitor adult coho salmon abundances in Oregon

Coast watersheds. Spawning survey reaches averaged 1.4 km in length (range 0.24–2.0 km). Each reach was visited every 7–10 days to capture the peak and variability of run timing between sites. The numbers of live and dead coho salmon were recorded at each survey visit (Lewis et al. 2012).

In this study, peak counts of coho salmon were used as the best metric of spawning abundance because these numbers were available for each reach (Table 2). These data represent the maximum number of fish observed at a reach during the survey period. While these values may not accurately characterize the temporal distribution of fish within a reach, they represent the maximum number of fish that were present at a point in time during that season. We excluded two reaches influenced by Tahkenitch Lake on the mid-south coast and one reach where the spawning survey was greater than 2 km.

Table 1. Description of the habitat variables used as covariates in the analyses.

Habitat variable	Description	Transformation	Model
Complex pools	No. of pools per kilometre with greater than or equal to three pieces of wood ^a	log10(x)	Occupancy and positive
Distance to the ocean	Distance from the random GRTS point (site) to the ocean; measured in a GIS	None	Occupancy and positive
Percent bedrock	Weighted percentage of bedrock substrates (by habitat area) for all habitat unit types	log10(x)	Occupancy
Percent gravel	Weighted percentage of gravel substrates (by habitat area) for all habitat unit types	None	Positive
Riffle depth	Mean depth (m) of all riffle habitat units	None	Occupancy and positive
Winter parr·km ⁻¹	Modeled estimate of winter parr per kilometre of stream based on habitat conditions; Habitat Limiting Factors Model (HLFM) ^b	log10(x)	Occupancy
Wood volume	Wood volume (m ³) per 100 m stream length	log10(x)	Positive

Note: All data, except for distance to ocean, are collected at the habitat unit scale and summarized at the reach scale.

^aCountable wood pieces are greater than or equal to 3 m in length and 0.15 m in diameter at breast height.

^bNickelson and Lawson 1998.

Table 2. Summary of coho salmon peak count data collected at spawning survey sites by spawning year.

Year	Count of sites	Median peak count	Mean peak count	SD peak count	% of sites occupied
1998	54	1.0	3.98	6.26	59.26
1999	45	4.0	6.13	10.93	77.78
2000	44	3.5	9.61	17.43	75.00
2001	43	7.0	12.42	16.08	86.05
2002	42	17.0	24.33	23.61	92.86
2003	21	13.0	26.52	35.42	95.24
2004	43	11.0	19.56	25.50	88.37
2005	42	13.0	19.00	21.30	92.68
2006	47	3.0	7.17	11.22	76.60
2007	61	2.0	3.16	3.91	65.57
2008	72	8.0	12.85	15.20	86.11
2009	80	8.0	16.58	24.94	81.25
2010	58	11.0	20.40	28.20	94.83

One additional, non-field-based metric was considered in the analysis to account for position of a reach within the watershed. The distance to the ocean from the GRTS point was calculated by measuring the distance along the stream network using the same 1:24 000 scale hydrography line work in a geographic information system (GIS). This variable can also have particular importance when there are potential habitat accessibility issues in a given year because of precipitation and timing of high or low flow conditions relative to the spawning period.

Habitat variable selection

Nineteen habitat variables were initially considered as predictors given relationships that have appeared in the literature. Nonmetric multidimensional scaling (NMDS) was used as an exploratory tool to elucidate patterns between these instream habitat variables and the occupancy and positive datasets (Tong 2001; McCune and Grace 2002). Through this analysis we were able to reduce the partially redundant set of habitat variables to identify those with the strongest potential influence. In this study, NMDS was conducted each year and the habitat variables where the distance to the biological metric was minimized (clustering) were selected for subsequent analyses. The analysis was run separately using the occupancy dataset and then the positive dataset. A scree plot was produced to determine the appropriate number of dimensions on which to calculate stress (the measure of goodness of fit). Stress values from NMDS are considered good if they are between 5 and 10 and fair if they are between 10 and 20. Analyses were conducted using the vegan library in R (Oksanen et al. 2012).

Modeling approach

The modeling strategy used in this study predicted site-level abundance using instream habitat covariates. Only sites where both instream habitat data and adult data were available each year were used. Across the entire dataset, the distribution of coho spawners was both skewed and zero-inflated (0 fish were observed at 19% of the sites across the 13-year study period). We assumed the zeros represented the absence of spawners rather than detection error because of the revisit frequency to each site. To account for the zero-inflated data, we separated the modeling of abundance into two submodels, relating covariates to the occupancy dataset and positive dataset (values > 0). We used a delta-generalized linear mixed effects model (GLMM) distribution to model coho occupancy and the positive values. Occupancy and positive datasets are assumed to follow Bernoulli (binomial) and lognormal distributions, respectively. Because occupancy is treated as a binary response, the statistical model is equivalent to logistic regression. The results from both submodels are then combined into an estimate of total abundance. This process of separating the nonzeros from the zeros, which are assumed to have a lognormal distribution, has been widely used in fisheries and related fields (Aitchinson 1955; Pennington 1983; Stefannsson 1996; Thorson and Ward 2013). This provided the opportunity to also evaluate whether occupancy and positive values of peak coho spawners were driven by different instream habitat variables and conditions.

We first modeled the probability of a site being occupied (occupancy model) using a binomial GLMM with a logit link, $\text{logit}(p_{i,t}) = B_0 + s_{i,t} + y_{i,t} + BX$, where B_0 represents a global intercept (or the mean occupancy across sites), the habitat covariates and respective fixed effects coefficients are represented by X and B , the random site deviations are $s_{i,t} \sim \text{Normal}(0, \sigma_{\text{site}})$, and the random year deviations are $y_{i,t} \sim \text{Normal}(0, \sigma_{\text{year}})$. The instream habitat covariates selected by NMDS were complex pools, distance to the ocean, percent bedrock, riffle depth, and estimated winter parr capacity (Table 1). Second, we modeled the positive values of peak coho spawners given the habitat conditions using a lognormal GLMM with log-link (positive model). The form of the model is $\text{log}(u_{i,t}) = B_0 + s_{i,t} + y_{i,t} + BX$, where the parameters have the same representation as in the occupancy model. Because the distribution of coho is assumed to be lognormally distributed, the variance parameter of the lognormal was also estimated. The instream habitat covariates selected by NMDS were complex pools, distance to the ocean, percent gravel, riffle depth, and wood volume (Table 1). Several of the habitat variables were transformed to normalize the residuals (Table 1).

Parameters for both submodels were estimated in a Bayesian framework. Markov chain Monte Carlo (MCMC) methods were

Table 3. Posterior distribution means, standard deviation (SD), and 95% credible intervals for occupancy model.

Metric	Mean	SD	Lower 95% CI	Upper 95% CI	Pr(x > 0)
Winter parr·km ⁻¹	0.854	0.314	0.285	1.522	0.998
Distance to ocean	0.022	0.022	0.005	0.043	0.995
Percent bedrock	0.176	0.077	0.024	0.333	0.988
Complex pools	0.245	0.097	0.064	0.447	0.995
Riffle depth	-1.633	2.526	-6.649	3.266	0.257
Site effects (SD)	2.622	0.584	1.626	3.952	
Year effects (SD)	1.475	0.471	0.823	2.610	
Residual effects (SD)	0.003	0.000	0.003	0.003	

Note: The proportion of the posterior distribution that is greater than zero, Pr(x > 0), is also quantified. Habitat metrics are ordered by magnitude of importance (evaluating one covariate while holding all other standardized covariates at a mean of 0).

used to generate random samples from the distributions of parameter values for both the fixed (habitat covariates) and random effects (variance terms). Weakly informative priors were specified for the coefficients (vague normal) and the variance parameters (inverse gamma). An offset term was included to account for differing spawning survey lengths; however, these lengths were similar across reaches. Random effects in year and site were modeled as normally distributed with uniform priors assigned to the random effect standard deviations (Gelman 2006). For both models, we ran five chains for 10 000 iterations. Once the model runs were complete, we evaluated MCMC convergence and autocorrelation diagnostics by visually inspecting plots of the sampled chains and calculating the Gelman–Rubin R statistic (Gelman 2006). Convergence for the latter is assumed when the value is close to 1.

Overall model performance was evaluated by calculating the percent deviance and reviewing diagnostic plots. Following recommendations from Pearce and Ferrier (2000), calibration plots (assessing predicted probabilities of occurrence relative to observed proportions of sites occupied) and receiver operating curves (ROC) (relative proportions of correctly and incorrectly classified predictions) were evaluated. The area under the ROC curve (AUC) was also reported (AUC values near 1 indicate good model performance; Freeman 2012). To examine hot spots in coho occurrence, Geostatistical Analyst in ArcMap (ESRI 2013) was used to spatially interpolate the predicted probabilities across the study area. The distribution of the random year effects was evaluated for each submodel, with year deviations plotted along with estimates of annual percent marine survival. Percent marine survival was calculated each year from adult and smolt data collected at ODFW life cycle monitoring trap sites along the Oregon Coast (see Suring et al. 2012 for methods).

In the final step of the modeling process, we obtained the site-level abundance estimates. This was done by multiplying the posterior distributions of the occupancy probabilities for each site with the corresponding positive model estimates. We used the JAGS (Plummer 2003) and the R2jags libraries for the modeling (Su and Yajima 2012) and the Presence/Absence Model Evaluation (PresenceAbsence) library in R to assess model diagnostics (Freeman 2012).

Results

There were 651 sites in the dataset with 21–80 sites visited per year (Table 2). We used all 651 sites to model coho occupancy (presence or absence) and 530 sites to model the positive values of peak coho spawners. The latter dataset ranged from 20 to 65 sites per year. Stream size (active channel width) and gradient across all sites averaged 8.64 m (95% CI: 8.26 m, 9.02 m) and 2.39% (95% CI: 2.21%, 2.57%), respectively.

Habitat covariate selection

The habitat dataset was reduced to five covariates for both the occupancy and the positive datasets by selecting the habitat covariates that appeared most frequently across time in association

with fish metrics in the NMDS. Three of these covariates (distance to the ocean, complex pools, and riffle depth) were the same in each model (Table 1). Adequate stress was achieved with three dimensions, values ranging from 7.5 to 13.3 for the occupancy ordination and 7.5 to 11.4 for the positive ordination (McCune and Grace 2002).

Occupancy model

The percentage of sites occupied ranged from 59% (1998) to 94% (2003) (median = 86% occupied) over the 13-year time period (Table 2). We observed strong effects of the habitat covariates, with all but one of the habitat covariates having credible intervals not overlapping zero. Estimated winter parr capacity, complex pools, percent bedrock, and site distance to the ocean were strongly associated with adult coho occupancy, each with posterior probabilities of a positive effect, Pr(x > 0), being greater than 0.990 (Table 3; Fig. 2). Based on measures of deviance, 48% of the variation was accounted for with these covariates and estimates of the site and year effects. To estimate the marginal effects of each covariate, we held the standardized values at a mean of 0 and varied the parameter of interest across its observed range (Fig. 2). For most of our habitat covariates (estimated winter parr capacity, site distance to the ocean, percent complex pools, and percent bedrock), extremely high values of the habitat covariate predict occupancy rates near 100%; where these metrics differ is how rapidly occupancy declines at lower levels (Fig. 2). Evidence of that analysis suggests that estimated winter parr capacity and percent complex pools had the highest relative importance.

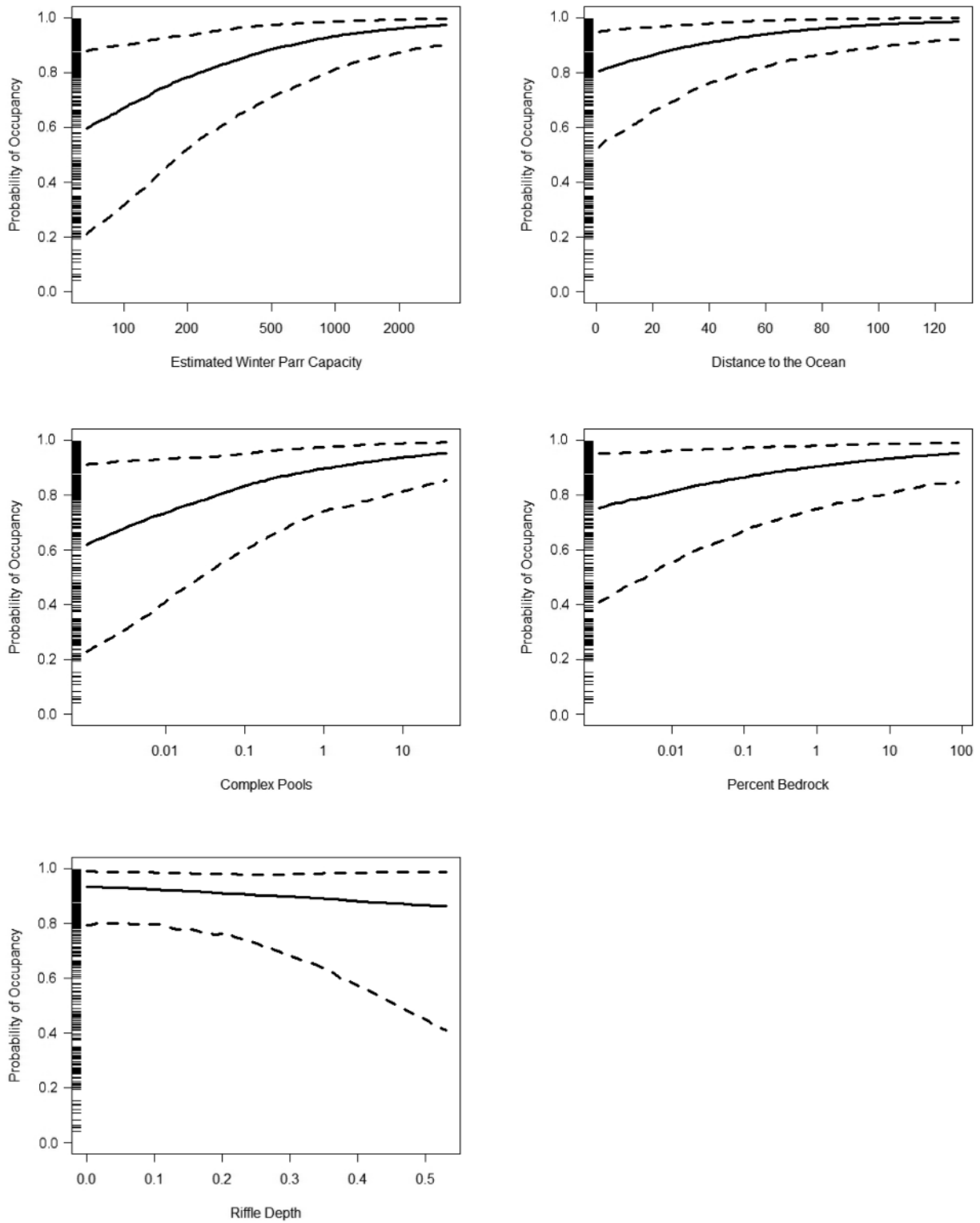
The patterns of occupancy varied over time (Fig. 3a), loosely tracking with estimates of marine survival (Suring et al. 2012). Though the estimated year deviations fluctuated, the variability in the year effects was small (mean with credible intervals: 0.810 ≤ 1.436 ≤ 2.683). Relative to year-to-year variation, the mean standard deviation of the site effects was almost twice as high (Table 3), suggesting that most of the factors affecting variation in coho occupancy are static. Using Geostatistical Analyst in ArcMap (ESRI 2013), predicted probabilities of occupancy were interpolated across the study area (Fig. 4). Locations with a higher probability of occupancy by coho salmon appear patchy on the landscape (Fig. 4).

Evaluation of the calibration plot (goodness-of-fit plot) for the occupancy model indicates that over 80% of the sites with predicted probability of 0.80 have observed presence (Fig. A1a). Approximately 94% (SD = 0.009%) of the sites were correctly classified, and the model’s ability to predict an occurrence where one actually occurred (sensitivity) was over 99% (Fig. A1b). The AUC value for the mean probability of occupancy was 0.98, indicating good overall model performance.

Positive model

The positive model describes the relationship of habitat covariates to the number of coho salmon present at a site (>1 fish). Fewer habitat features had a strong association with the number of adult

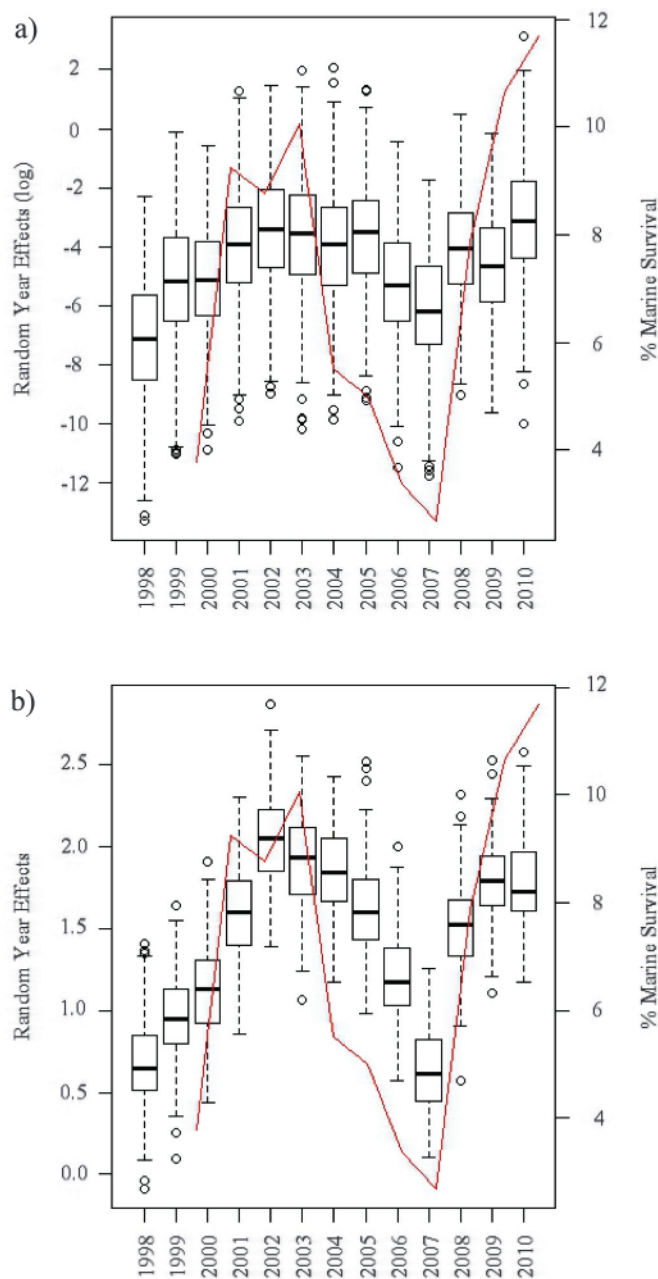
Fig. 2. Effect of individual habitat covariates in the occupancy model. The dashed lines represent the 95% credible intervals. For those covariates that were log-transformed, the x axis has been converted to the original units. The ticks on the y axis represent the estimated occupancy probabilities for a given site.



salmon at a site. The only covariate with estimated 95% credible intervals not overlapping zero was site distance to the ocean; however, there is evidence that percent gravel and complex pools also contributed to an increase in peak counts at a site ($\Pr(\chi > 0)$; Table 4; Fig. 5). Based on measures of deviance, only 11% of the variation was accounted for with these covariates and

estimates of the site and year effects. Like the occupancy model, we again evaluated the marginal impacts of each habitat parameter on the expected number of coho present (Fig. 5). Evidence of this analysis suggests that site distance to the ocean had the highest relative importance, and all other predictor variables had little effect (Fig. 5).

Fig. 3. Boxplot displaying the distribution of year effects from the (a) occupancy model and (b) positive model. The solid line curve is the mean marine survival estimate each year from the ODFW life cycle monitoring trap sites across the coast (1998 and 1999 data not available) (Suring et al. 2012).



The year deviations were estimated to have a large effect, similar to the occupancy model, and the pattern across years was also similar with peaks in 2002 and 2003 and low periods in 1998 and 2007. Because adult abundance is driven in part by ocean conditions, the estimates of the year deviations are likely reflecting this large-scale annual variability (Fig. 3b).

Probability of abundance

Given the posterior distributions coefficients and predicted values from both submodels, we used the results to estimate site-level abundance across all 651 sites. The residuals from this final model were symmetric and centered at zero (Fig. A2) with no discernable spatial patterns across time. However, the variability

around the residuals was much higher in years where the mean peak coho salmon count was higher (e.g., 2002–2003 and 2008–2010). This could indicate a threshold in the model’s predictive capacity given the inherent variability or perhaps that logging the positive counts did not sufficiently stabilize the variance, making our variance mean relationship less flexible.

Discussion

Owing to the persistent and complex pressures threatening the resilience of Pacific salmon, an understanding of the instream habitat conditions that have a major effect on freshwater survival and reproduction is critically important. We found strong relationships between instream habitat characteristics and adult coho salmon occupancy across the 13 years of study, specifically metrics reflecting habitat complexity and juvenile rearing capacity. We could not predict abundance of adults at a site with a high level of certainty, likely in part due to the close relationship with patterns in marine survival. However, both occupancy and abundance were influenced by the location of a spawning site within the stream network relative to its distance to the ocean. Our results indicate that the spatial patterns of habitat complexity and the distribution and proximity of spawning and rearing habitats may maximize productivity for coho salmon in coastal Oregon watersheds by playing a role in the survival of salmon from adult to smolt life stages (Einum et al 2008; Flitcroft et al. 2012).

The metric site distance to the ocean explained variation in both occupancy and the positive count of spawners likely reflecting the connectivity and arrangement of certain types of stream habitats that coincide with the many physical gradients along a stream network (Isaak and Thurow 2006; Flitcroft et al. 2012). In this study, when more adult coho salmon were present, more sites farther from the ocean were occupied and at higher abundances. This implies broader distributions of adult salmon throughout most watersheds and a greater number of occupied sites coinciding with increased adult returns. Flitcroft et al. (2014) explored similar interannual patterns in juvenile coho salmon, noting the summer distribution of juvenile salmonids expanded and contracted relative to size of the adult spawning population, likely driven by habitat characteristics along the network. Alternative theories could suggest that in years with increased adult returns, adult salmon are filling the first suitable habitats encountered or that there are higher-quality habitats distributed lower in the system.

An understanding about the proximity and connectivity of habitat on the landscape has broad implications for salmon productivity. Landscape or network-scaled predictors have been used in previous studies to understand abundance patterns of salmon (Pess et al. 2002; Flitcroft et al. 2012; Steel et al. 2012). Specifically, network variables have been shown to explain juvenile coho salmon densities better than instream habitat variables (Flitcroft et al. 2012), with reach location specifically strengthening network-scale juvenile distribution models (McMillan et al. 2013). We found that site distance to the ocean was the strongest covariate influencing the number of adults present over time. Beechie et al. (2008) noted that stream flows influence the longitudinal position of redds in streams, and in years with higher flows salmon spawn farther upstream where there is more habitat available. Prolonged low flow and drought during peak spawning periods could limit occupancy expansion. These variables cannot explain all of the patterns in coho salmon productivity. Steel et al. (2012) found landscape predictors alone could not consistently explain site occupancy, providing further evidence that patterns of occupancy and abundance are driven by different processes and factors operating at different scales.

While our results could suggest a density-dependent effect based on the co-occurrence of both adequate spawning and juvenile rearing habitats, we were not able to include other relevant

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Fig. 4. Spatial interpolation of occupancy probabilities across years.

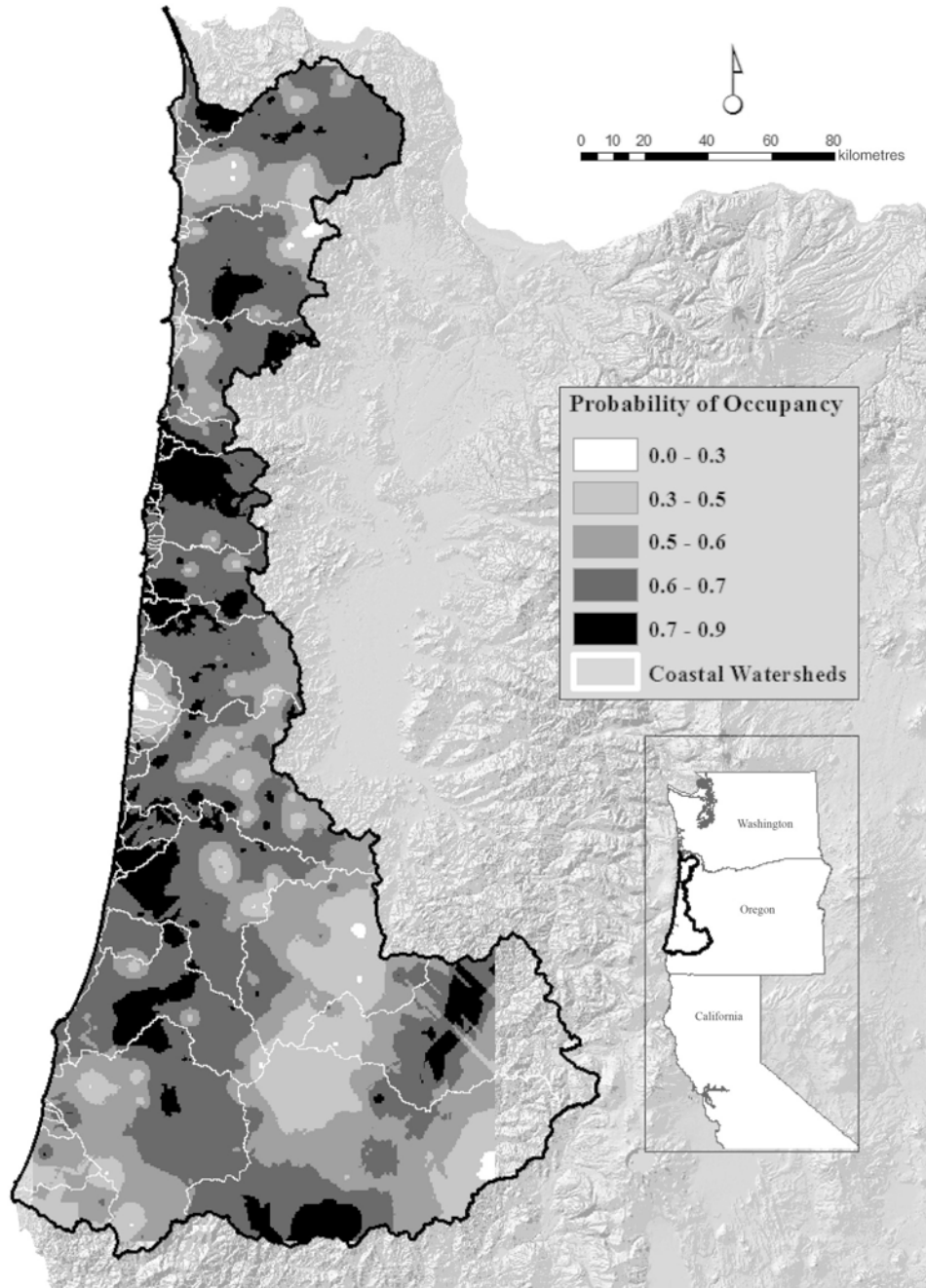
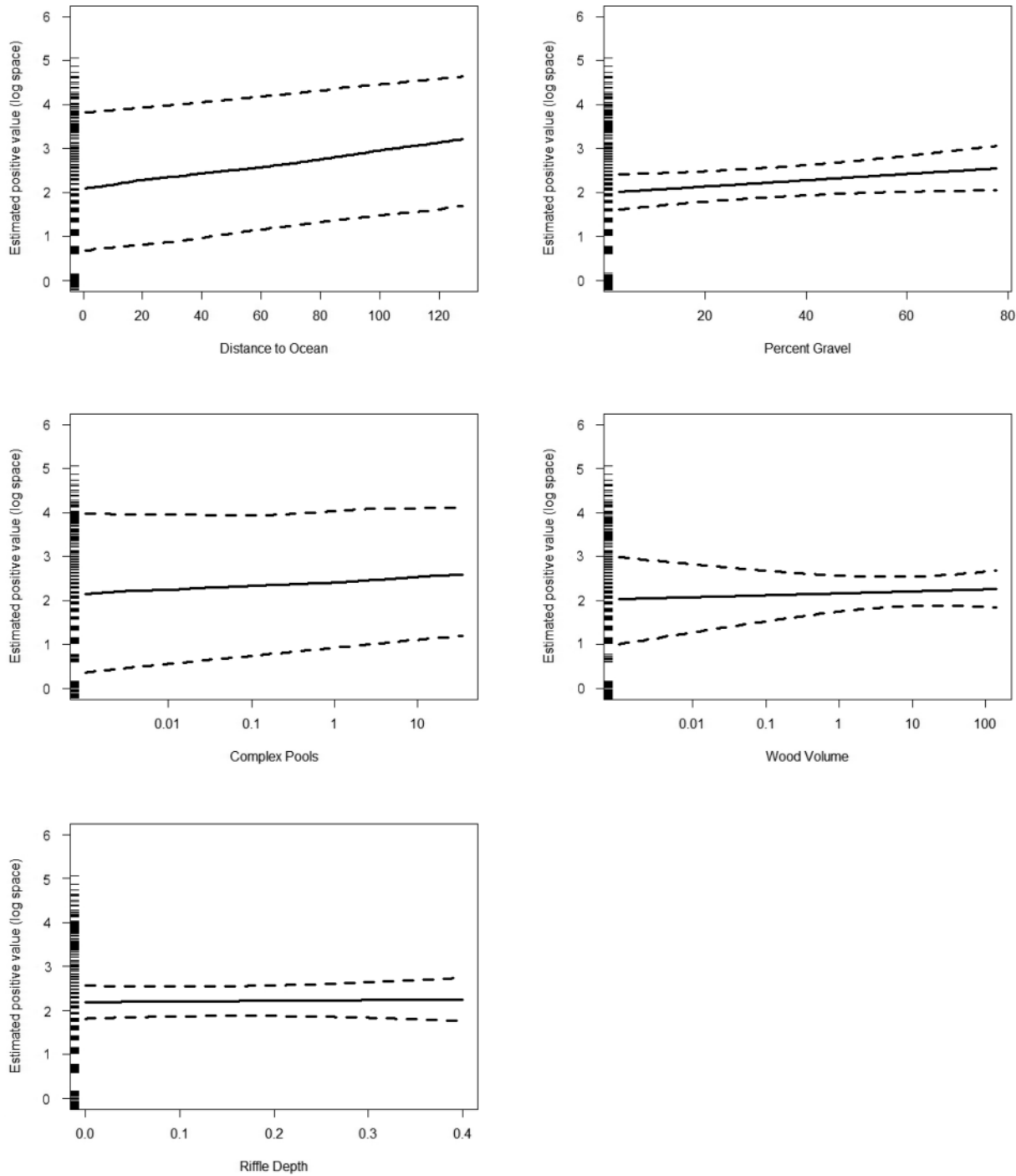


Table 4. Posterior distribution means, standard deviation (SD), and 95% credible intervals for positive model.

Metric	Mean	SD	Lower 95% CI	Upper 95% CI	Pr($x > 0$)
Distance to ocean	0.008	0.002	0.004	0.012	1.000
Percent gravel	0.007	0.004	-0.001	0.015	0.962
Complex pools	0.046	0.031	-0.014	0.109	0.929
Wood volume	0.020	0.051	-0.077	0.122	0.643
Riffle depth	0.148	0.675	-1.192	1.477	0.588
Site effects (SD)	0.726	0.074	0.592	0.773	
Year effects (SD)	0.569	0.163	0.347	0.956	
Residual effects (SD)	0.632	0.067	0.527	0.773	

Note: The proportion of the posterior distribution that is greater than zero, Pr($x > 0$), is also quantified. Habitat metrics are ordered by magnitude of importance (evaluating one covariate while holding all other standardized covariates at a mean of 0).

Fig. 5. Effect of individual habitat covariates in the positive model (on the log scale). The dashed lines represent the 95% credible intervals. For those covariates that were log-transformed, the x axis has been converted to original units. The ticks on the y axis represent the positive values of peak count for a given site.

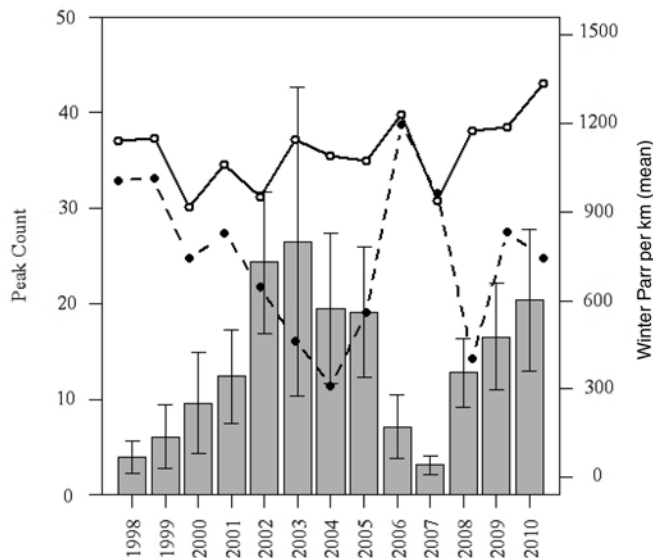


data controlling the biological response such as competition. Intraspecific competition can constrain populations at high densities (Greene and Guilbault 2008), reducing fitness influencing subsequent cohorts (Einum et al. 2008). Further, at higher spawning densities, there may be a shift in the spatial distribution of adults into less optimal habitats (Fig. 6). Density dependence is often not considered to strongly regulate populations of threatened species because it is assumed that population densities are so small relative to historical levels (Achor et al. 2003). However, given the degradation of freshwater habitat conditions, the carry-

ing capacity of most habitats has decreased, enabling for potential density-dependent mortality (Beechie et al. 2008). Further data would be needed to detect an effect of habitat quality on the strength of density dependence.

While the logistic regression was very effective at predicting occupancy, the lognormal model explained very little of the observed variability in abundance among sites where fish were present. The percentage of the sites occupied ranged from 59% (1998) to 95% (2003), and the distribution of fish over time varied across Oregon Coast basins. For example, 80% of the fish occupied only

Fig. 6. Plot of mean peak counts (gray bars) with confidence intervals and mean winter parr capacities at occupied sites (solid line) and unoccupied sites (dashed line) by year. When fish estimates are higher (e.g., 2002–2005, 2010), fish are utilizing all habitats regardless of quality, and the difference between the occupied capacities and the unoccupied capacities is larger. Alternatively, when fish estimates are lower (e.g., 1998, 1999, 2007), fish are utilizing just those higher-quality habitats and the difference is smaller.



11%–50% of the sites in 1998, while in 2010 that value ranged from 28% to 60% (Lewis et al. 2012; Peacock and Holt 2012) (Table A1). Many factors influence this variability, from the spatial and temporal variation in the attraction of a site to stray rates (Peacock and Holt 2012). While these factors could be obscuring some of the relationships between instream habitat and coho salmon abundances, declines in freshwater habitat capacities can result in changes in both coho salmon abundance and distribution, which can negatively impact the overall vigor and resilience of populations.

It has been suggested that limitations on coho salmon production is based on the carrying capacity of physical habitat at the juvenile or presmolt stages (Nickelson and Lawson 1998; Bradford et al. 2000), and basins with moderate and high-quality habitat support long-term viability of coho salmon populations (Nickelson and Lawson 1998). Results of this study support this contention where a capacity threshold in freshwater habitat conditions may limit salmonid productivity at the juvenile life stage. We found that as the habitat capacity for parr during the winter increases, so does the probability of site occupancy by adult coho. Further, fish occupy freshwater habitats with higher predicted parr capacities when adult densities are low, spreading out into habitat with lower predicted parr capacities when returns are high (Fig. 6). While occupied sites had higher estimated winter parr capacities than unoccupied sites, most of the habitat on the Oregon Coast is in the low to moderate range (Anlauf et al. 2009), and the distribution of high-quality habitats does not appear to be random on the landscape. The majority of the highest quality habitats are often concentrated in upper watersheds in part because of reduced land use pressure on public land ownership (Burnett et al. 2007). Stream conditions located lower in the stream network often have highly altered floodplains, substantial land use, and have been affected by the legacy of splash damming and log drives (Miller 2010).

Instream habitat complexity can reflect a variety of habitats that meet the needs of multiple life stages, specifically increasing smolt production by improving overall habitat conditions and

increasing carrying capacity and overwinter survival. We did not find instream wood alone to have a strong relationship with patterns of abundance; however, estimated winter parr capacity and pool complexity, both of which are influenced by instream wood volumes, were strong covariates influencing adult occupancy. Clark et al. (2014) found that adult coho spawning site selection did not have a direct relationship with individual wood restoration structures, but at the reach scale, habitat complexity has been shown to increase because of enhancement projects (Roni and Quinn 2001; Whiteway et al. 2010). Increasing stream complexity is often accomplished by increasing wood volumes; however, this is not the sole means by which more heterogeneous habitats can be restored. In fact, to adapt to a changing climate, Beechie et al. (2012) recommended that restoring floodplain connectivity, stream flow regimes, and re-aggrading incised channels is most likely to increase habitat diversity and resilience in salmonid populations.

This study is an initial attempt at linking the adult freshwater life stage to optimal habitat conditions. Ideally, habitat capacity estimates and thresholds could be used as a road map for locating simplified and degraded habitat and for identifying restoration potential within watersheds. Restoration of instream habitat conditions should not only focus on improving or increasing complexity, but consider the location of the site in the watershed and condition of surrounding stream habitat. While complex habitats may offer maximum production potential, adjacent simplified habitats may prove to be a bottleneck in both restoration and recovery efforts.

Conclusions

The productivity of adults is driven in part by the quality and availability of habitat for juvenile coho salmon. Marine conditions will likely affect all Oregon coho salmon similarly; however, decreased productivity can be attributed to the loss of freshwater habitat suited to meet the needs of multiple life stages and life histories. Adult salmon escapement remains the most common measure of condition and success of the species (Lawson 1993), and while the degradation of instream habitat has had deleterious effects on spawning habitats, change and improvements in instream conditions will likely be most effective at the juvenile salmonid life stage. Restoring stream heterogeneity, habitat complexity, and connectivity will benefit multiple life stages by increasing survival at earlier life stages. Furthering our understanding of life stage specific survival can enable us to think about salmon productivity more completely and provide valuable information on where we should be investing our efforts to conserve salmonid species.

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Appendix A

Appendix figures (Figs. A1 and A2) and table (Table A1) appear on the following pages.

Fig. A1. (a) Goodness-of-fit plot (calibration plot) for occupancy model where the probability of occurrence is plotted against the observed occurrence. The number of sites is labeled above each point along with the confidence interval around the point. (b) Receiver operating curve (ROC) plotting the true positive rate (sensitivity) against the false positive rate. The area under the ROC curve (AUC) is a measure of model performance with an ROC plot for a good model rising steeply at the origin and leveling off at a value near the maximum of 1.

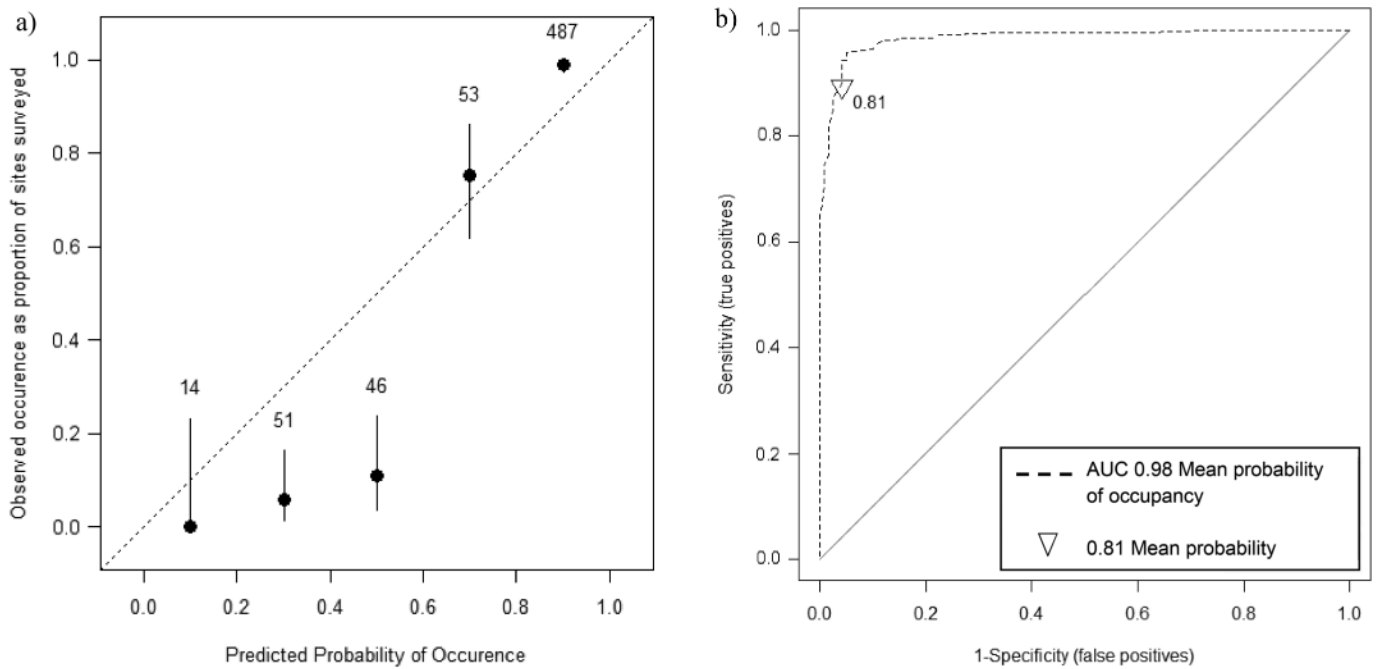
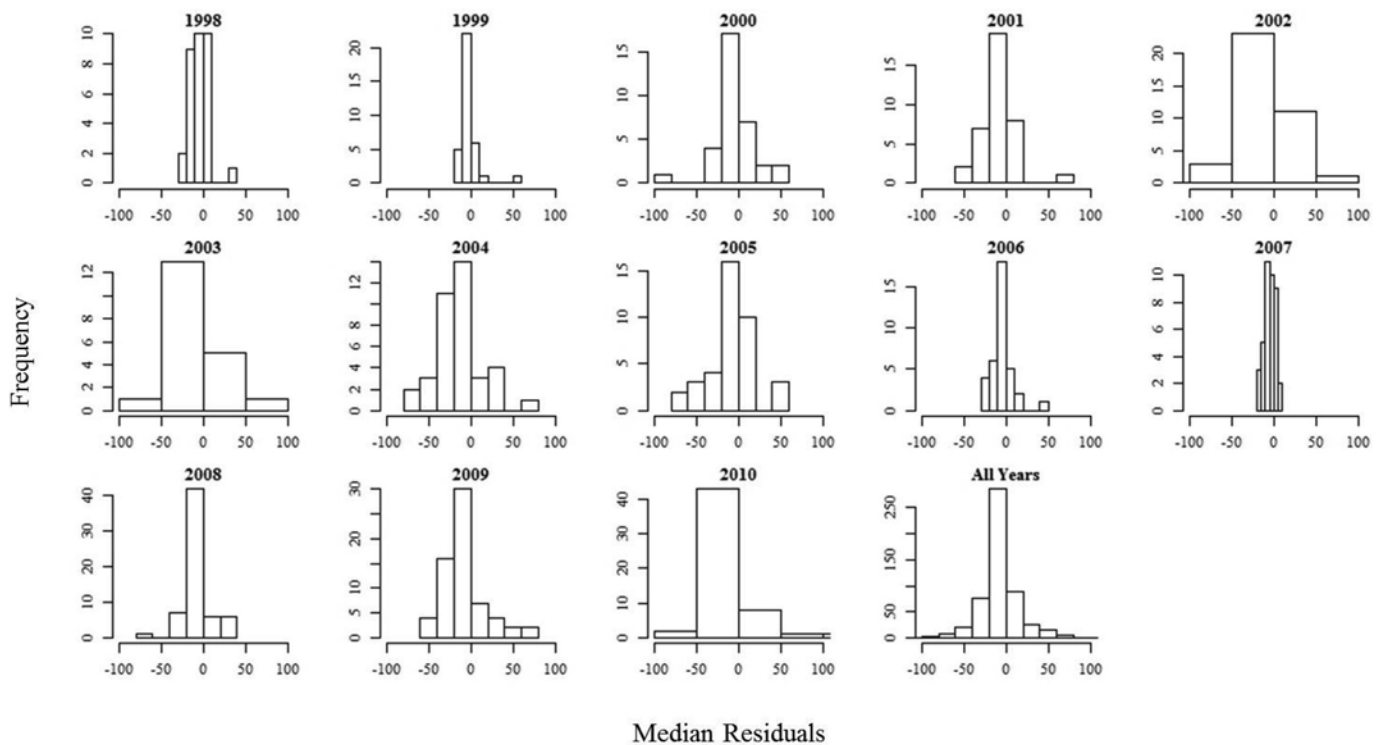


Fig. A2. Histogram of residuals by year from abundance model.



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Table A1. $P_{80\%}$ spatial distribution metric evaluated and detailed by Peacock and Holt (2012).

Year	Minimum $P_{80\%}$	Maximum $P_{80\%}$	Mean $P_{80\%}$
1998	11.10	50.00	28.60
1999	13.30	54.50	32.70
2000	11.60	44.40	28.90
2001	28.90	62.50	40.00
2002	27.90	60.00	39.30
2003	28.00	55.50	42.90
2004	31.50	71.40	43.30
2005	26.60	75.00	49.10
2006	23.80	54.50	38.70
2007	16.60	66.60	36.70
2008	15.70	66.60	44.50
2009	21.40	57.10	38.80
2010	28.50	60.00	43.70

Note: $P_{80\%}$ describes the minimum number of sites comprising 80% of the total spawner abundance.