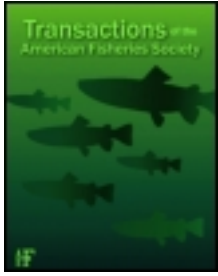


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ARTICLE

Using a Stream Network Census of Fish and Habitat to Assess Models of Juvenile Salmonid Distribution

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Abstract

We censused juvenile salmonids and stream habitat over two consecutive summers to test the ability of habitat models to explain the distribution of juvenile Coho Salmon *Oncorhynchus kisutch*, young-of-the-year (age-0) steelhead *O. mykiss*, and steelhead parr (age ≥ 1) within a network consisting of several different-sized streams. Our network-scale habitat models explained 27, 11, and 19% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively, but strong levels of spatial autocorrelation were typically present in the residuals. Explanatory power of base habitat models increased and spatial autocorrelation decreased with the sequential inclusion of variables accounting for the effects of stream size, year, stream, reach location, and a tertiary interaction term. Stream-scale models were highly variable. Fish–habitat associations were rarely linear and ranged from negative to positive; the variable accounting for location of the habitat within a stream was often more important than the habitat variables. The limited success of our network-scale models was apparently related to variation in the strength and shape of fish–habitat associations across and within streams and years. These results indicate that there are several potential limitations to extrapolating models to broader areas based only on spatially limited surveys.

Stream habitat models can be a useful tool for predicting the density and distribution of salmonids (Fausch et al. 1988; Railsback et al. 2003; Rosenfeld 2003). The models assume that fish selectively occupy habitats (e.g., pools) with particular characteristics (e.g., depth), and if the fish–habitat associations are known, the density and distribution of fish can be predicted based on the quantity and distribution of those habitats (Beecher et al. 1993; Knapp 1999; Van Horne 2002). The utility of a

model therefore depends on the strength and consistency of the surrogate for fish distribution: the fish–habitat associations. For single reaches or streams, habitat models may effectively predict fish density and distribution by using a few habitat variables, but models generally perform poorly when applied broadly to several streams because of variation in fish–habitat associations within streams and between streams and years (Fausch et al. 1988; Dunham and Vinyard 1997; Gibson et al.

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2008). Nonetheless, models that are derived from a subsample of reaches or streams are commonly expanded to unsampled areas to predict fish distributions at larger scales that are more relevant to recovery and restoration, such as the stream network (Fausch et al. 2002). A potential concern with this approach is that agreement between models and the actual distribution of fishes is rarely tested at the stream network scale, so the extent and effects of variability in fish–habitat associations on larger-scale predictions remain poorly understood.

One challenge to evaluating how well stream habitat models predict fish distribution at the network scale is a lack of spatially extensive and continuous data. Salmonid and stream habitat data have traditionally been collected for a single species or life stage in short reaches (e.g., 100–1,000 m) located at widely spaced intervals in one stream or similarly sized streams, often during only a single year (Fausch et al. 2002). Although this approach is typically based on logical sampling designs, it presents three problems for model predictions at more extensive scales. First, the distribution of salmonids is often patchy, and sampling of short and sparsely located reaches could miss aggregations, voids, and the upper and lower limits of fish presence, thereby misrepresenting large-scale distribution patterns (Torgersen et al. 2012) and potentially confounding model predictions (Dunham and Vinyard 1997; Angermeier et al. 2002). Second, focusing on a single species or life stage may miss important variability in assemblage patterns because different salmonid species and age-classes may use different parts of a network (Gibson et al. 2008; Reeves et al. 2011; Brenkman et al. 2012; Kanno et al. 2012). Lastly, fish–habitat associations can vary extensively between different stream sizes, different streams, reach locations within streams, and years (Fausch et al. 1988; Dunham and Vinyard 1997; Rosenfeld et al. 2000). Sparse sampling of reaches or streams in only a single year may therefore oversimplify fish–habitat associations and underestimate the potential influences of space and time on model effectiveness (Clinchy 2002; Isaak and Thurow 2006; Torgersen et al. 2012).

One way to address some of these limitations is to collect continuous data (i.e., census) over long sections (e.g., 40–70 km) of a stream for multiple species of salmonids (Torgersen et al. 2006; Brenkman et al. 2012; Reeves et al. 2011; Kanno et al. 2012) to more closely match the scale at which (1) salmonids carry out their freshwater life cycle (Rieman and Dunham 2000) and (2) managers make decisions (Beechie and Bolton 1999). A census of several streams of varying sizes seems particularly applicable to evaluating how network-scale patterns in fish and habitat distribution match stream habitat model predictions. To date, however, most studies that have censused fish and stream habitat have focused on associations between salmonids and habitat along the longitudinal profiles of individual medium to large streams (Torgersen et al. 1999, 2006; Brenkman et al. 2012) or small streams (Gresswell et al. 2006; Reeves et al. 2011; Kanno et al. 2012). Few studies have used census data to test how well habitat characteristics predict the density and distribution of salmonids across a network of both smaller and larger

streams over multiple years, but results for adult salmonids have provided novel insights into the extent to which space, time, and the space \times time interaction can potentially influence fish distribution models at larger scales (Isaak and Thurow 2006).

Census data could also be used to evaluate the extent and effects of spatial autocorrelation (Torgersen et al. 2008, 2012), which occurs when measurements in adjacent areas are more similar to each other than measurements in distant areas (Legendre 1993). The phenomenon can inflate apparent explanatory power and increase the chance of type I errors (false positives; Legendre et al. 2002). The patchy distributions of salmonids and their associations with habitat are prone to spatial autocorrelation that may violate assumptions about the independence of survey reaches (Dunham and Vinyard 1997; Dunham et al. 2002), but this problem is rarely accounted for when modeling aquatic organisms (e.g., Segurado et al. 2006).

Stream habitat models are commonly applied to draw inferences about juvenile salmonids that spend long periods in freshwater, such as Coho Salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* (anadromous Rainbow Trout). These two species co-exist in many networks, and their associations with habitat are well studied (Everest et al. 1985; Bisson et al. 1988; Bjornn and Reiser 1991) and have been extensively modeled (Porter et al. 2000; Rosenfeld et al. 2000; Sharma and Hilborn 2001; Burnett 2001), although more so for juvenile Coho Salmon than for steelhead. However, censuses of both species and stream habitat in the same network are limited to long but disjoint sections of river in a single year (Scarnecchia and Roper 2000) and a single-thread small stream over multiple years (Reeves et al. 2011), with each study reporting somewhat contrasting findings. Furthermore, we are not aware of previous research using census data to test how stream size, stream, location, and year influence the ability of stream habitat models to explain the distribution and density of juvenile Coho Salmon and steelhead at the network scale. Such tests are needed, however, to understand the level of uncertainty that might be expected by managers and scientists when using a model to predict the density and distribution of salmonids across several streams.

In this study, we tested the ability of habitat models to explain the network-scale distribution of juvenile Coho Salmon and two size-classes of juvenile steelhead. To accomplish this, we censused stream habitat characteristics and juvenile salmonids in over 60% of the linear stream kilometers available to anadromous salmonids in the Calawah River, Washington, during two summers. The objectives were to (1) determine how well models consisting of several instream habitat characteristics predicted juvenile salmonid distribution at the network scale; (2) test for spatial autocorrelation and the effects of stream size, stream, reach location within a stream, and year on network-scale models; and (3) test the extent to which juvenile salmonid distribution at the stream scale is a function of individual habitat characteristics or of the location of the habitat within the stream. The high-resolution data set provided a unique opportunity to assess the strength and consistency of fish–habitat associations across

multiple streams. We discuss the results and their implications for stream habitat modeling and stream conservation actions.

METHODS

Survey Site and Salmonid Populations

The Calawah River basin (196 km²) is a tributary of the greater Quillayute River basin, which is part of the temperate rainforest that stretches across the western side of the Olympic Peninsula (Figure 1). The main-stem Calawah River is formed by the South Fork (SF) Calawah River and North Fork (NF) Calawah River. Elk Creek flows into the main-stem Calawah River, whereas the Sitkum River, Hyas Creek, and Lost Creek drain into the SF Calawah River. The streams are variable in channel length and width, with “rivers” being longer and larger than “creeks” (Tables 1, 2). The NF Calawah River was unique because an extensive section of stream (~12 river kilometers [RKM]) naturally goes dry during the summer, and we considered sections at either end separately because of the differences in width and slope; hereafter, these sections are referred to as the lower and upper NF Calawah River. The stream network is large enough to contain numerous tributaries with differing characteristics and exceptional bank-to-bank water clarity for snorkeling, yet it is small enough (wetted width < 25 m) to be adequately surveyed by a small crew (diver and bank walker) within a relatively short period of time (~3 weeks).

The Calawah River supports naturally spawning populations of summer and winter steelhead, fall and summer Chinook Salmon *O. tshawytscha*, fall Coho Salmon, resident Rainbow Trout, Coastal Cutthroat Trout *O. clarkii clarkii*, and a small number of Chum Salmon *O. keta* and river-type Sockeye Salmon

O. nerka. We focused on enumerating juvenile Coho Salmon and steelhead because (1) they are the most abundant species, (2) they have extended freshwater rearing periods, and (3) respective associations with stream habitat may vary between species and within size-classes (e.g., age 0 versus age 1; Everest et al. 1985; Bjornn and Reiser 1991). Little information exists on juvenile Coho Salmon or steelhead in this network, but adult steelhead spawn primarily in the larger main-stem Calawah, SF Calawah, Sitkum, and lower NF Calawah rivers, while fall Coho Salmon spawn primarily in the creeks and throughout the entire NF Calawah River (Quileute Tribe and Washington Department of Fish and Wildlife, unpublished annual steelhead redd surveys, 1995–2003).

Data Collection

Extent of surveys.—Our goal each summer was to census fish and stream habitat across all stream habitats that were available to juvenile anadromous salmonids in the SF Calawah River, NF Calawah River, Sitkum River, Elk Creek, Hyas Creek, and Lost Creek (Figure 1). Surveys in small and large streams (except for Elk Creek, Lost Creek, and the SF Calawah River) ended at the uppermost falls constituting a barrier to anadromous salmonids. We continued surveys for a minimum of 1.5 km upstream of assumed barrier falls to confirm a lack of anadromous salmonids. The upper 0.7 km of Elk Creek and the upper 0.4 km of Lost Creek were not surveyed because depths were consistently too shallow for snorkeling (<0.2 m deep). The upper SF Calawah River inside the Olympic National Park was not sampled because the habitat is in pristine condition, whereas the vast majority of areas outside the park drain a mosaic of commercial timberlands in various stages of growth and harvest (Smith 2000), and such variation in land use patterns would potentially

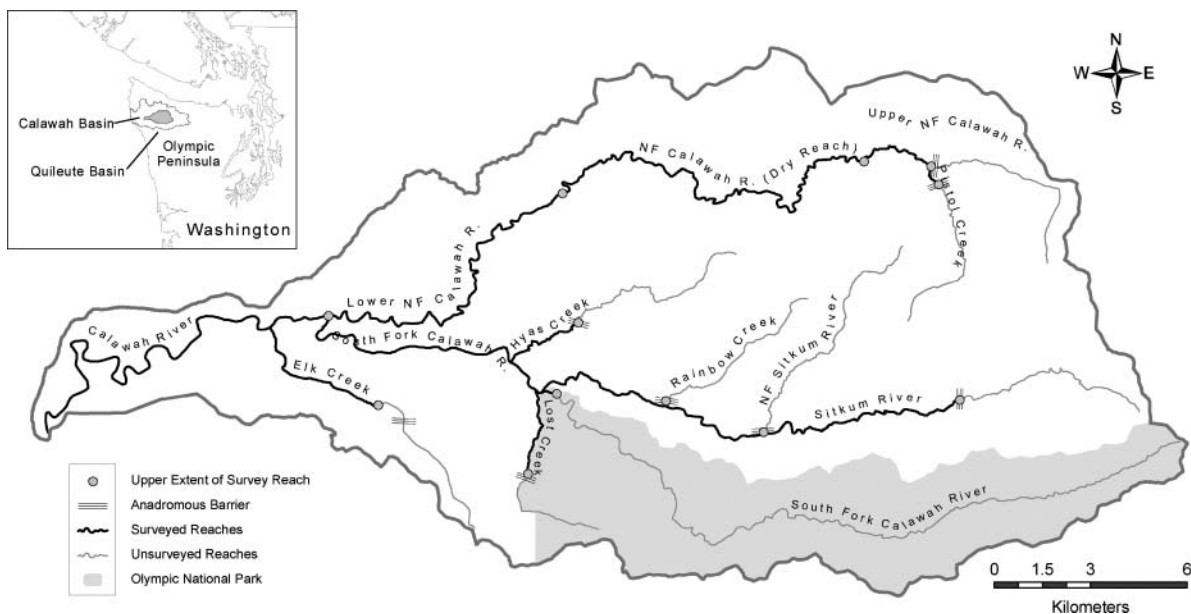


FIGURE 1. Map of the Calawah River basin, Washington, and the stream lengths surveyed during the summers of 2002 and 2003.

TABLE 1. Summary of stream features in the Calawah River system, including stream size-class (small or large), length of stream that was accessible to anadromous salmonids in summer (stream), average total length of stream surveyed in 2002 and 2003 (surveyed), number of habitat units surveyed and number of reaches generated with habitat units (*n* units/reaches), mean (\pm SD) length of reaches for which habitat and fish data were generated, and the percentage of stream length that was not surveyed because it was too shallow for snorkeling (<0.2 m deep).

Stream	Type	Length (km)		<i>n</i> units/reaches		Mean reach length (m)		% of stream <0.2 m deep	
		Stream	Surveyed	2002	2003	2002	2003	2002	2003
South Fork Calawah River	Large	24.8	9.9	84/10	81/10	982 \pm 308	992 \pm 304	0	0
Lower North Fork Calawah River	Large	13.0	13.0	114/12	125/12	1,056 \pm 150	1,025 \pm 190	16	17
Sitkum River	Large	15.9	15.9	242/12	326/16	1,016 \pm 135	997 \pm 164	0	2
Upper North Fork Calawah River	Small	2.9	2.9	173/23	167/23	223 \pm 26	213 \pm 31	7	16
Elk Creek	Small	6.4	4.9	102/14	109/14	211 \pm 26	212 \pm 22	0	2
Hyas Creek	Small	3.0	3.0	114/14	103/14	211 \pm 23	211 \pm 23	3	18
Lost Creek	Small	3.5	2.9	75/15	66/12	202 \pm 31	204 \pm 38	6	4

impose an additional layer of complexity on the fish–habitat associations (Pess et al. 2002; Anlauf et al. 2011). A two-man crew completed the surveys in 22 d during 2002 and in 24 d during 2003.

Juvenile salmonid surveys.—We used snorkel surveys to census the distribution and abundance of salmonids in all habitat units greater than 0.2 m in depth (Dolloff et al. 1993; Thurow 1994). All units were sampled by the same experienced diver and habitat recorder to reduce bias associated with multiple surveyors (Hankin and Reeves 1988; Thompson and Mapstone 1997). Salmonids were classified based on species and size (estimated FL) as juvenile Coho Salmon, young-of-the-year trout (hereafter, age-0 steelhead; <70 mm), and age-1 and older steelhead parr (hereafter, steelhead parr; 70–200 mm; J. McMillan, unpublished data); larger parr (>200 mm) that could have matured as resident Rainbow Trout (e.g., McMillan et al. 2007) were excluded. We classified age-0 trout as steelhead, but we acknowledge that some of the small trout were presumably Coastal Cutthroat Trout; however, at that size it is difficult to distinguish the species (Thurow 1994). Thus, we assumed that most (>85%) of the age-0 fish were steelhead offspring based on comparisons of adult abundance estimates for both species (WDFW 2012; J. R. McMillan, unpublished data).

Stream habitat surveys.—We identified habitat units as pools and nonpools according to Bisson et al. (1982), and we measured characteristics that were important for juvenile Coho Salmon and steelhead habitat use, including habitat unit depth, wetted habitat unit width, habitat unit gradient (Everest et al. 1985; Bjornn and Reiser 1991), and stream valley width (Burnett et al. 2007). Wetted width and length of each habitat unit were measured across a single transect, with width being measured at a spot that was approximately average for the unit (Hankin and Reeves 1988). We measured habitat unit gradient with a laser range finder and a stadia rod, and maximum depth was

measured at the single deepest location. Stream channel (i.e., bankfull) depth and width as well as floodprone width (stream width at a discharge twice that of the maximum bankfull depth) were measured with a laser range finder, and the valley width index (VWI) was then calculated as floodprone width divided by bankfull width (Grant and Swanson 1995).

Statistical Analyses

Stream habitat and salmonid variables.—We used the habitat-unit-scale data to generate response and predictor variables at the reach scale for 2002 and 2003. First, working upstream from the mouth, we delineated each small stream into approximately 200-m reaches and each large stream into approximately 1,000-m reaches (Table 1); these reach lengths are similar to those used in traditional noncensus studies (Fausch et al. 2002). Because we did not use block nets and fish may have moved between units to avoid the diver (Peterson et al. 2005), aggregation of the data into reaches also reduced the potential for fish movement to influence habitat associations at smaller scales. We also aggregated data into reaches because fish use different habitat units within a given area to survive, grow, and develop over the course of a year (e.g., habitat complementation; Angermeier and Schlosser 1989; Schlosser and Angermeier 1995), making longer stream reaches more inclusive of the surrounding habitat potential. Reach lengths varied slightly because we placed the upstream boundary of each reach at natural breaks in habitat units rather than artificially dividing a unit (and its fish) into partial units to achieve uniformity. Second, for each reach and year, we calculated the weighted mean of five habitat metrics, including the percentage of the reach length in pool habitat, mean habitat unit depth, mean wetted width, mean unit gradient, and mean VWI (Table 2). We then calculated the number of juvenile Coho Salmon, age-0 steelhead, and steelhead parr per linear meter of stream (our measure of density) to represent

TABLE 2. Descriptions and expected influence of variables considered in generalized additive models for predicting the density (fish/linear meter) of juvenile Coho Salmon, age-0 steelhead, and steelhead parr (age ≥ 1).

Variable	Description	Expected influence
<i>Stream habitat</i>		
Percent pool (%)	(Length of reaches consisting of pool habitat)/(reach length)	Influences availability of slow-water habitats ^{a,b}
Mean depth (m)	Habitat unit depth \times (unit length/ reach length)	Influences extent of vertical cover and habitat area ^{a,b}
Mean width (m)	Habitat unit width \times (unit length/ reach length)	Influences available habitat area ^{a,b}
Stream channel gradient (%)	Rise over run for entire reach length	Influences stream velocity and substrate size ^c
Mean valley width index (VWI)	(Habitat unit VWI \times unit length)/ (reach length)	Influences availability of secondary streams ^d
<i>Time, size, stream, and space</i>		
Year	Year in which sampling was conducted	Fish-habitat associations may vary annually ^e
Stream size	Small (wetted width < 7 m) or large (wetted width > 7 m) streams	Fish-habitat associations may vary by stream size ^{e,f}
Stream	Geographically distinct tributary or stream section	Fish-habitat associations may vary by stream ^{e,f}
River kilometer	Longitudinal location of reach midpoint within each stream	Accounts for spatial autocorrelation in the model ^g

^aBisson et al. 1988.^bBjornn and Reiser 1991.^cMontgomery et al. 1999.^dGrant and Swanson 1995.^eFausch et al. 1988.^fDunham and Vinyard 1997.^gSegurado et al. 2006.

reach-scale variation in distribution (Table 3). The caveat to the density estimate is that we were unable to enumerate salmonids via snorkeling in units with depths less than 0.2 m, and age-0 steelhead often use shallow habitats (Bjornn and Reiser 1991).

Modeling approach.—We used generalized additive models (GAMs; Wood 2011) to examine correlations between juvenile salmonid density and the five stream habitat variables (Table 4). Generalized additive models offer a flexible approach to modeling that requires minimal assumptions about the shape of the relationships and allows for a range of possible error distributions and links (Efron and Tibshirani 1991). Results of other studies using GAMs (e.g., Knapp and Preisler 1999; Stoner et al. 2001) suggest that the approach has considerable utility in the development of models to predict fish distributions based on habitat characteristics because the shape of the response is rarely known prior to the analysis. We used the GAM function implemented in R (R Development Core Team 2011) with the mgcv package (Wood 2001). The default smoothing function, thin-plate penalized regression splines, and smoothing parameter estimation method (generalized cross validation criterion) were used (Wood 2003). We assumed normally distributed errors with the identity link, and we examined the model residuals to check this assumption.

Network-scale models.—We first fit GAMs at the scale of the entire stream network to examine the ability of a common

set of five stream habitat variables (Table 4) to explain variation in the density (i.e., fish per linear meter) of juvenile Coho Salmon, age-0 steelhead, and steelhead parr. We then gradually added complexity to the model by first allowing the habitat variable relationships to vary by stream size and then adding year, stream, the reach location \times stream interaction, and lastly the location \times stream \times year interaction.

The habitat portion of the model is either expressed as a sum of smoother terms (where s = smooth function),

$$\begin{aligned} \text{Density (fish/m)} = & \beta_0 + s_1(\% \text{ pool}) + s_2(\text{mean depth}) \\ & + s_3(\text{mean width}) + s_4(\text{mean slope}) \\ & + s_5(\text{mean VWI}), \end{aligned} \quad (1)$$

or as a sum of smoother terms that vary by stream size (see Table 4),

$$\text{Density (fish/m)} = \beta_0 + s_1(\% \text{ pool [stream size]}) + \dots \quad (2)$$

Here, the term $s_1(\% \text{ pool [stream size]})$ indicates separate relationships (smooths) for each level of the stream size factor (i.e., small stream or large stream). This is analogous to a fixed interaction term in a standard linear model. In all cases, the habitat variable relationships were limited to smooths of four

TABLE 3. Analysis of deviance results for generalized additive models constructed for the entire Calawah River stream network, with iterative influences of stream size, time, stream, and space and their interaction on the base habitat model; the model deviance, df, delta Akaike's information criterion (Δ AIC), R^2 values, and Moran's I -statistic (a measure of spatial autocorrelation in model residuals; see Methods) for 2002 and 2003 are presented.

Model	Model		Δ AIC	R^2	Moran's I	
	Deviance	df			2002	2003
Coho Salmon						
Null model	160.0	1.0	247	0.00	0.56	0.68
Habitat	112.7	9.3	193	0.27	0.54	0.58
Habitat \times stream size	96.7	13.8	171	0.35	0.58	0.38
(Habitat \times stream size) + year	90.9	14.8	161	0.39	0.54	0.33
(Habitat \times stream size) + year + stream	67.3	20.3	111	0.53	0.22	0.25
(Habitat \times stream size) + year + (location \times stream)	50.8	31.0	76	0.63	0.25	0.14
(Habitat \times stream size) + (location \times stream \times year)	28.3	51.7	0	0.76	0.04	-0.19
Age-0 steelhead						
Null model	44.7	1.0	113	0.00	0.25	0.52
Habitat	38.0	9.4	97	0.11	0.20	0.40
Habitat \times stream size	34.9	16.4	94	0.16	0.16	0.33
(Habitat \times stream size) + year	30.8	17.0	70	0.25	0.18	0.26
(Habitat \times stream size) + year + stream	24.9	20.4	34	0.38	0.11	0.12
(Habitat \times stream size) + year + (location \times stream)	23.5	28.2	38	0.39	0.11	0.10
(Habitat \times stream size) + (location \times stream \times year)	16.4	45.2	0	0.53	-0.25	-0.10
Steelhead parr						
Null model	3.6	1.0	263	0.00	0.24	0.71
Habitat	2.8	9.5	230	0.19	0.27	0.70
Habitat \times stream size	2.0	18.2	180	0.39	0.11	0.68
(Habitat \times stream size) + year	1.8	19.6	167	0.43	0.07	0.65
(Habitat \times stream size) + year + stream	1.4	23.3	112	0.58	0.19	0.43
(Habitat \times stream size) + year + (location \times stream)	1.3	32.7	116	0.58	0.16	0.40
(Habitat \times stream size) + (location \times stream \times year)	0.6	49.2	0	0.78	-0.30	0.01

dimensions. This effectively limits the df, allowing control over the upper bound of model complexity. Since we were primarily interested in the explanatory power of habitat variables as a whole rather than that of individual variables, we did not enter the habitat variables into the model individually. We tested for year and stream effects by including the terms "year" and "stream" as simple categorical variables (2002 or 2003; Elk Creek, Hyas Creek, etc.). Location was defined as the distance upstream from the lowermost point in the stream to the midpoint of the reach and is expressed in units of reach lengths. The effect of location on density varies by stream, $s_6(\text{location}[\text{stream}])$, or by stream and year, $s_6(\text{location}[\text{stream-year}])$, where "stream-year" is a separate category for each stream \times year combination (7 streams \times 2 years = 14 combinations). The full model is

$$\begin{aligned}
 \text{Density (fish/m)} &= \beta_0 + s_1(\% \text{ pool}[\text{stream size}]) + s_2(\text{mean depth}[\text{stream size}]) \\
 &+ s_3(\text{mean width}[\text{stream size}]) + s_4(\text{mean slope}[\text{stream size}]) \\
 &+ s_5(\text{mean VWI}[\text{stream size}]) + s_6(\text{location}[\text{stream-year}]).
 \end{aligned}
 \tag{3}$$

Here, the dimension of the location smooth is constrained to five. For each model, we calculated the deviance, the df, the delta Akaike's information criterion (Δ AIC; Burnham and Anderson 2002), and the R^2 (proportion of total variability in fish density that was explained by the model). Evaluation of model performance was based primarily on Δ AIC.

Spatial autocorrelation is a common statistical property in ecological data that poses problems because correlated data violate the assumption of independence, which is a key assumption for parametric statistical tests (Legendre 1993; Legendre et al. 2002). To account for this, we quantified the degree to which the individual models explained the spatial structure in fish density among reaches by calculating Moran's I -statistic for the model residuals. Moran's I -values of 0–0.20, 0.21–0.50, 0.51–0.70, and 0.71–1.0 indicate that spatial autocorrelation is absent, weakly positive, moderately positive, or strongly positive, respectively, and vice versa if values are negative for negative spatial autocorrelation (Legendre et al. 2002).

Stream-scale models.—Next, we fit GAMs at the stream scale to test the extent to which juvenile salmonid distribution was a function of individual habitat characteristics in comparison with

TABLE 4. Coefficient of determination (R^2) and statistical significance (values in bold indicate $P < 0.05$) of individual habitat variables and reach location (river kilometer [RKM]) in generalized additive models for each stream (2002 and 2003 combined) when modeled individually (Indiv.) and with RKM (w/RKM). Year is included as a main effect (NA = not applicable because fish abundance was too low for modeling).

Variable	Elk Creek		Hyas Creek		Lost Creek		Upper North Fork Calawah River		Lower North Fork Calawah River		South Fork Calawah River		Sitkum River	
	Indiv.	w/RKM	Indiv.	w/RKM	Indiv.	w/RKM	Indiv.	w/RKM	Indiv.	w/RKM	Indiv.	w/RKM	Indiv.	w/RKM
Coho Salmon														
Percent pool	0.48	0.82	0.09	0.51	0.58	0.68	0.21	0.75	0.14	0.63	0.03	0.09	0.09	0.58
Mean depth	0.35	0.84	0.00	0.53	0.36	0.70	0.06	0.76	0.39	0.66	0.02	0.03	0.04	0.77
Mean width	0.33	0.82	0.41	0.54	0.09	0.67	0.09	0.66	0.10	0.65	0.16	0.78	0.22	0.58
Gradient	0.52	0.84	0.45	0.52	0.04	0.78	0.36	0.68	0.21	0.52	0.13	0.17	0.05	0.75
Mean VWI	0.38	0.78	0.27	0.51	0.05	0.76	0.84	0.88	0.06	0.58	0.05	0.82	0.02	0.67
RKM	0.74		0.53		0.60		0.67		0.54		0.60		0.67	
Age-0 steelhead														
Percent pool	0.07	0.69	0.22	0.27	0.20	0.38	0.32	0.56	0.08	0.41	0.26	0.47	0.13	0.26
Mean depth	0.26	0.67	0.11	0.23	-0.04	0.35	0.00	0.11	0.20	0.30	0.10	0.47	0.05	0.29
Mean width	0.12	0.70	0.36	0.46	0.01	0.38	0.15	0.15	0.14	0.33	0.09	0.43	0.05	0.25
Gradient	0.07	0.66	0.37	0.28	0.16	0.32	0.01	0.12	0.08	0.33	0.00	0.55	0.50	0.69
Mean VWI	0.30	0.63	0.00	0.30	0.07	0.33	0.03	0.13	0.04	0.20	0.55	0.72	0.04	0.26
RKM	0.63		0.22		0.34		0.15		0.23		0.43		0.28	
Steelhead parr														
Percent pool	0.19	0.37	0.65	0.62	0.25	0.41	0.00	0.76	NA	NA	0.25	0.32	0.04	0.17
Mean depth	0.12	0.36	0.67	0.66	0.02	0.31	0.04	0.74	NA	NA	0.08	0.33	0.00	0.30
Mean width	0.28	0.51	0.11	0.69	0.03	0.29	0.12	0.63	NA	NA	0.03	0.33	0.11	0.16
Gradient	0.23	0.38	0.70	0.68	0.02	0.11	0.03	0.60	NA	NA	0.04	0.35	0.59	0.84
Mean VWI	0.07	0.36	0.03	0.65	0.10	0.23	0.04	0.66	NA	NA	0.38	0.54	0.04	0.15
RKM	0.36		0.63		0.15		0.63		NA		0.35		0.18	

the location of the habitat (i.e., stream reach) within the stream. First, we fit GAMs for each stream and each habitat variable individually to investigate the potential for variation in fish-habitat associations among streams. Second, we evaluated the effect of space within a stream by adding a reach location term to each model (e.g., Legendre et al. 2002). We used P -values and R^2 for each variable (e.g., Fausch et al. 1988) to compare and contrast the relative effects of each habitat variable versus reach location. Year was included in all models as a main effect.

Due to the continuous spatial sampling design, we recognize the danger of overfitting and type I error; therefore, the R^2 values should be viewed as upper bounds of any potential fish-habitat associations at the network and stream scales. By entering location in the GAMs as a smoother term (e.g., Knapp and Preisler 1999), we allowed for fish-habitat associations and the effects of reach location to be compared in a common framework.

RESULTS

Extent of Census, Stream Habitat, and Juvenile Salmonids

We censused stream habitat and juvenile Coho Salmon and steelhead across 52.5 km of stream habitat in 2002 and 54.6 km in 2003, which accounted for slightly more than 60% of the linear stream network that was accessible (total of ~84 linear kilometers of stream) to juvenile salmonids during summer

(Figure 1; Table 1). Cumulatively, we sampled 95% and 93% of the linear length of stream in 2002 and 2003, respectively, and only in a few streams did shallow depths (depth < 0.2 m) preclude sampling of more than 10% of the habitat (Table 1). Close bank observation suggested that few fish used shallow habitats in the small streams, whereas age-0 steelhead were rare to abundant in such habitats within the large streams.

Habitat characteristics were highly variable (Figure 2). Large streams were generally deeper and had narrower VWIs than small streams; variation in mean depth and mean width was greater in large streams than in small streams, while variability in mean VWI was generally greater in small streams (Figure 2). In addition, variation in habitat metrics between streams was generally greater than variation between years within a given stream (Figure 2). Owing to this complexity, no two streams displayed the same habitat characteristics.

All salmonids co-existed and were present up to anadromous barriers throughout most of the stream network (Figure 3a-c). Coho Salmon and age-0 steelhead generally were found at the highest densities, and steelhead parr typically exhibited the lowest densities (Figure 2). Densities within streams were similar among years for all three salmonid groups, with the upper and lower NF Calawah River being the clear exception (Figure 2). Coho Salmon and age-0 steelhead displayed similar distributions that were mostly continuous, although

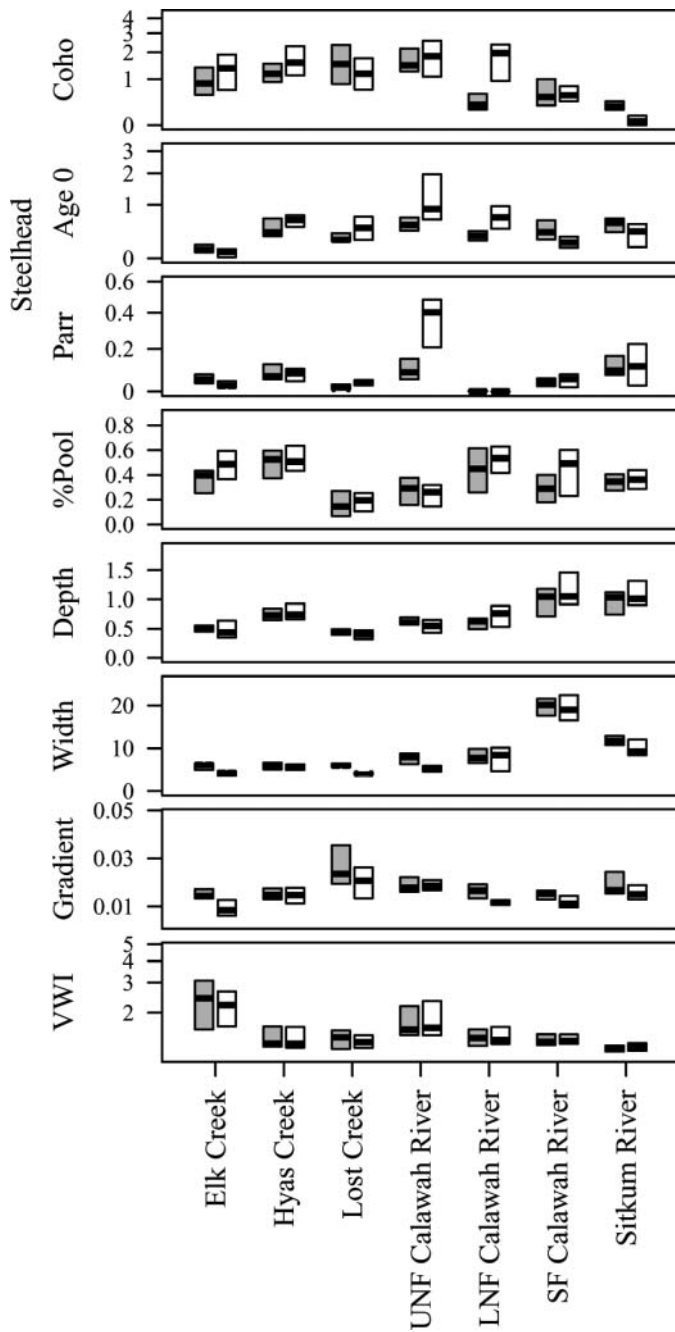


FIGURE 2. Stream-specific metrics (2002 = white boxes; 2003 = gray boxes), including the mean density (fish/linear meter) of Coho Salmon, age-0 steelhead, and larger steelhead parr (age ≥ 1) and the percent pool (% pool), mean depth (m), mean width (m), stream channel gradient (%), and valley width index (VWI). On each box, the top line denotes the 75th percentile, the bottom line represents the 25th percentile, and the middle line denotes the mean (UNF = upper North Fork; LNF = lower North Fork; SF = South Fork).

age-0 steelhead were skewed further towards the headwaters (Figure 3a, b) and Coho Salmon densities were higher in small streams (Figure 2). Steelhead parr had the patchiest distribution and were skewed farthest upstream, with a density spike in

the headwaters that changed locations from 2002 to 2003 (Figure 3c). In addition, the distribution patterns within streams did not necessarily match what was found at the network scale, as Coho Salmon were sometimes patchier and distributed further upstream than both age-classes of juvenile steelhead and vice versa (Figure 3a–c).

Network-Scale Models

Associations between stream habitat and juvenile salmonids.—Generalized additive models using the five stream habitat variables explained 27, 11, and 19% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively (Table 3). We also found weak levels of spatial autocorrelation in model residuals for both size-classes of steelhead in 2002, moderate levels for age-0 steelhead in 2003 and for Coho Salmon in both years, and strong levels for steelhead parr in 2003 (Table 3). The shape of the salmonid response to individual habitat characteristics was typically curvilinear and differed between species and between the steelhead age-classes in some cases (Figure 4). For example, Coho Salmon were positively associated with percent pool habitat, while age-0 steelhead and steelhead parr were not (Figure 4). Furthermore, Coho Salmon had a negative association with channel gradient while steelhead did not, and the curve for steelhead parr peaked at a greater depth than that for Coho Salmon and smaller age-0 steelhead (Figure 4). All salmonids responded similarly to mean VWI (positive) and mean width (negative).

Effect of stream size, time, stream, and reach location.—We found strong effects of stream size, year, stream, and reach location on the network-scale distribution models (Table 3). Sequential inclusion of each variable consistently reduced deviance and improved explanatory power (Table 3). Consequently, the best model for all salmonids was the full model, which included a reach location effect that was allowed to vary by stream and year; this model explained 76, 53, and 78% of the variation in density of juvenile Coho Salmon, age-0 steelhead, and steelhead parr, respectively (Table 3). The reach location \times stream \times year interaction term produced the greatest single improvement in deviance and explanatory power among models and salmonids except for one instance with steelhead parr (Table 3). Inclusion of the reach location variable and its interactions in the full model also accounted for the spatial autocorrelation in model residuals for Coho Salmon in both years and for age-0 steelhead and steelhead parr in 2003. Spatial autocorrelation was weak to nonexistent for age-0 steelhead and steelhead parr in 2002, so the location variable had less of an effect.

Stream-Scale Models

Stream habitat variable consistency and explanatory power.—Single habitat variables explained as much as 70% of the variability in salmonid density in individual streams when reach location within a stream was not considered (Table 4). On average, however, explanatory power tended to be quite low,

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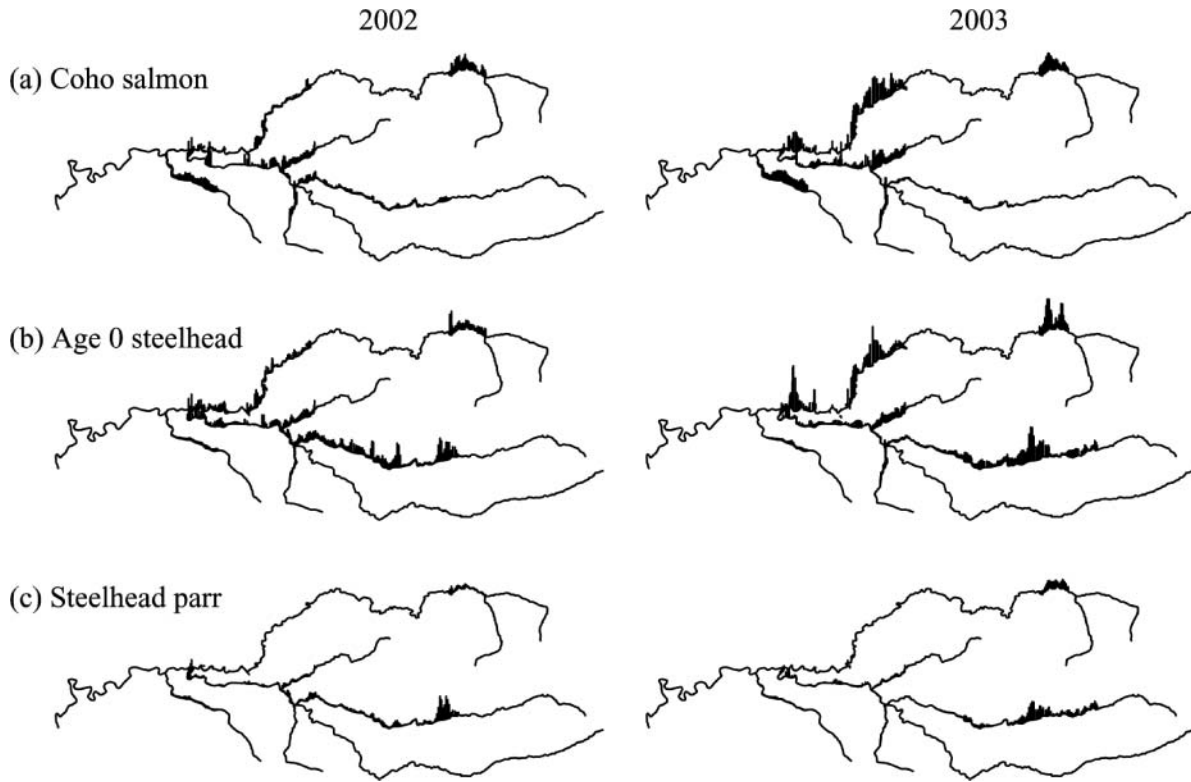


FIGURE 3. Density depicted in 200-m bins (fish/200 linear meters) for (a) juvenile Coho Salmon, (b) age-0 steelhead, and (c) steelhead parr (age ≥ 1) across the Calawah River stream network in 2002 and 2003.

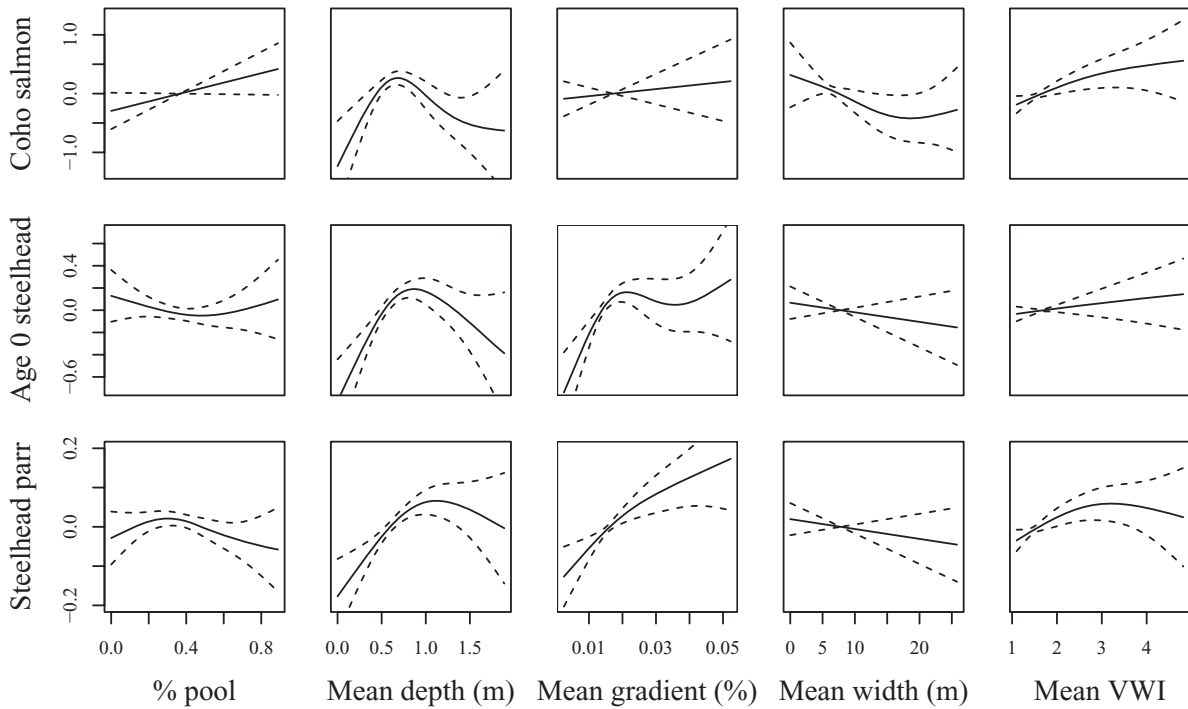


FIGURE 4. Nonparametric response of juvenile Coho Salmon, age-0 steelhead, and steelhead parr (age ≥ 1) densities as a function of percent pool habitat (% pool), mean depth (m), mean stream channel gradient (%), mean wetted width (m), and mean valley width index (VWI) for all streams combined. Dashed lines indicate ± 2 SEs for the smoothed parameter.

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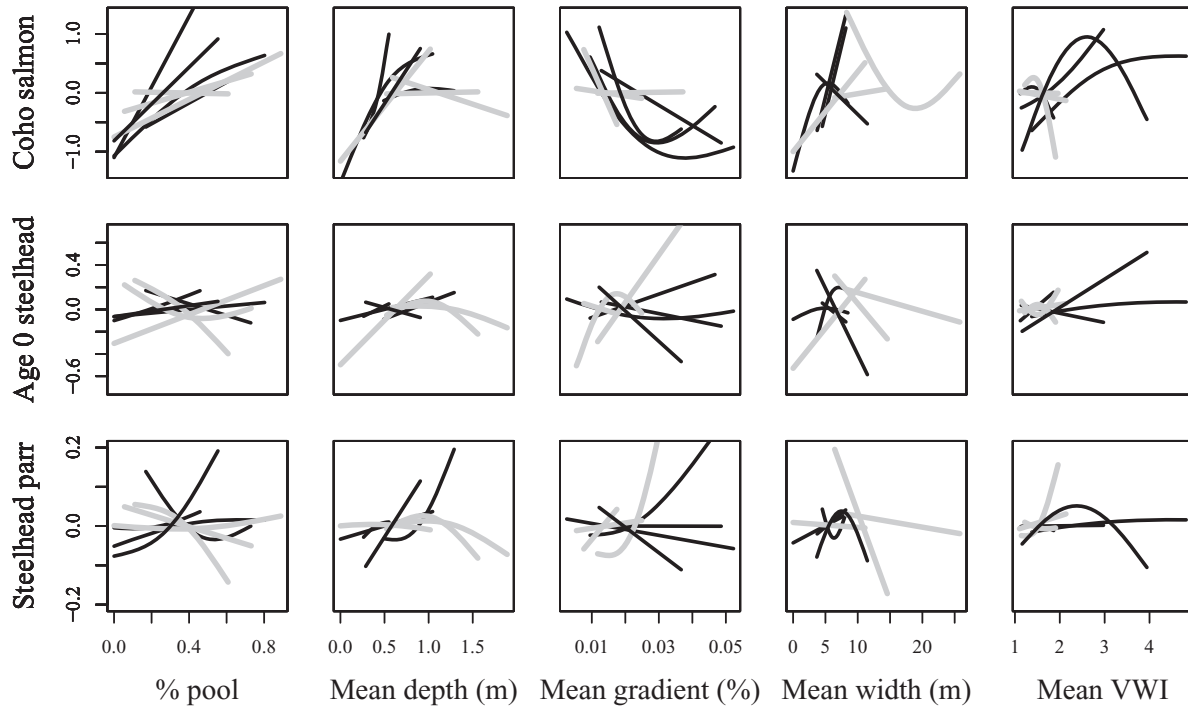


FIGURE 5. Nonparametric response of juvenile Coho Salmon, age-0 steelhead, and steelhead parr (age ≥ 1) densities as a function of percent pool habitat (% pool), mean depth (m), mean stream channel gradient (%), mean wetted width (m), and mean valley width index (VWI) in each individual stream. Gray lines denote small streams; black lines denote large streams.

and no single variable was significant across all of the streams for a given species (Table 4). Although it was low in general, the consistency of fish–habitat associations was highest for Coho Salmon, with all variables (except for mean width) having a significant effect and R^2 values being greater than 20% for three of the seven streams (Table 4). For steelhead parr, only percent pool habitat was significant and this variable had an R^2 of at least 20% for two streams; for age-0 steelhead, the mean depth, stream channel gradient, and mean VWI achieved R^2 values greater than 20% for two streams (Table 4).

Part of the inconsistency in fish–habitat relationships was related to the shape of the response. For example, the response of steelhead parr to percent pool habitat ranged from strongly positive to strongly negative, even among streams of similar sizes, whereas the effect of mean depth was generally positive for steelhead parr in small streams and negative for those in large streams (Figure 5). In fact, outside of mean depth and mean VWI, response curves for age-0 steelhead and steelhead parr generally ranged from strongly negative to strongly positive without a clear pattern between streams of similar sizes (Figure 5). Fish–habitat associations appeared to be more consistent for Coho Salmon, especially with percent pool habitat, but that variable was still not significant for three of the seven streams, and R^2 values were below 10% for three streams and below 25% for five streams (Table 4). The association of Coho Salmon with stream channel gradient was also typically negative, while other responses were inconsistent.

Effects of longitudinal location of habitat.—Location of the survey reach (RKM) was significant for 50% of all streams (for all salmonids combined) and had the highest R^2 , often by a large margin, for 45% of those streams (Table 4). The effects were most pronounced for Coho Salmon, with RKM being significant for five of the seven streams and having the highest R^2 value for four streams, compared with two streams for age-0 steelhead and three streams for steelhead parr (Table 4). River kilometer also influenced the significance of habitat variables. In Hyas Creek, mean wetted width, stream channel gradient, and mean VWI were individually significant for juvenile Coho Salmon but not when RKM was included (Table 4). The patterns were similar for age-0 steelhead and steelhead parr; consequently, RKM was the only significant variable in the Hyas Creek models and in the upper NF Calawah River models for Coho Salmon and steelhead parr.

DISCUSSION

Network-Scale Models

Expansive spatial coverage and a census of a wide variety of streams over multiple years allowed us to test stream habitat models in a way that would not have been possible with traditional sampling schemes. Nonetheless, the fish–habitat associations we reported were generally consistent with prior knowledge, albeit often nonlinear. Percent pool habitat had a positive influence on density of juvenile Coho Salmon, and

channel gradient had a negative influence on density of Coho Salmon and a positive influence on density of age-0 steelhead and steelhead parr (Bjornn and Reiser 1991; Roni and Quinn 2001; Sharma and Hilborn 2001; Burnett et al. 2007), although some studies have found contrasting associations with pools for Coho Salmon and steelhead parr (Bryant and Woodsmith 2009; Reeves et al. 2011). Due to their body shape and fin size, Coho Salmon are less suited for faster-water habitats than the more fusiform steelhead (Bisson et al. 1988; Bjornn and Reiser 1991), and slow-water pools are more common in low-gradient channels (Montgomery et al. 1995). All salmonids had a negative response to wetted width, suggesting that larger streams are less favorable for smaller-sized juveniles (Rosenfeld et al. 2011). All salmonids exhibited a positive response to VWI, presumably because wider valleys offer more secondary and tertiary habitats (Nickelson et al. 1992; Pess et al. 2002). Lastly, larger steelhead parr were associated with deeper water than the smaller age-0 steelhead (e.g., Bjornn and Reiser 1991), perhaps because larger-bodied fish require greater habitat volume to balance the tradeoffs among feeding, competition, and predation (Harvey 1991; Harvey and Nakamoto 1997).

Although fish responses to habitat aligned with much of what is already known, our base stream habitat models explained little of the variation in network-scale distribution of Coho Salmon (27%), age-0 steelhead (11%), and steelhead parr (19%). This was not surprising, however, given that the models were constructed based on data from seven streams with different sizes and habitat characteristics over two summers. Fish-habitat associations can vary extensively in relation to stream size, stream, reach location, and year (Fausch et al. 1988; Dunham and Vinyard 1997; Gibson et al. 2008; Rosenfeld et al. 2011). We observed this also, as the full models that included those factors achieved a substantially greater level of explanatory power than the base habitat models. Among factors, stream size and year had lesser effects individually, and the greatest effect occurred when the reach location \times stream \times year interaction was included in the full models. Using continuous data on the distribution of Chinook Salmon redds, Isaak and Thurow (2006) partitioned the relative importance of variance components that explained variation in redd distribution and they also found a strong effect of river segment. Strong local effects on fish-habitat associations imply that neither habitat type (pools in our case) nor commonly used habitat variables (e.g., depth and width) can necessarily be assumed to effectively explain the distribution of salmonids across streams of differing sizes and characteristics.

A possible limitation of our study is that surveys were conducted during only 2 years. Although stream and reach location can have strong effects on models (Fausch et al. 1988; Dunham and Vinyard 1997) and on the distribution of fish populations (Kocik and Ferreri 1998), we may have underestimated the role of time. A 2-year period is not long enough to capture the full range of variability that could occur over longer periods (Clinchy et al. 2002). For example, Isaak and Thurow (2006) censused stream habitat and fish data to predict the distribution

of spawning Chinook Salmon over a 9-year period and found that inferences drawn from fewer than 3–5 years of study would have underestimated the influence of time relative to space. Thus, the effect of year in our models might have been greater had we sampled over more years.

Ultimately, the full models that accounted for the reach location \times stream \times year interaction achieved a high level of explanatory power. However, the full models did not necessarily tell us why large-scale patterns in salmonid distribution differed between and within streams and years. Rather, we only determined that those patterns in distribution were less related to stream habitat than to the location of the habitat within the network and each stream between years; this result is not entirely surprising because previous studies have found that habitat location can strongly influence growth and survival of juvenile salmonids (Ebersole et al. 2009; Pess et al. 2011). This may have also been the case in our study based on the distributions of the two steelhead size-classes. For example, age-0 steelhead were abundant in many stream reaches where steelhead parr were rare or absent. The young-of-the-year steelhead either survived poorly in or moved away from those areas as they got older, implying that some reaches—and even entire sections of streams, such as the lower NF Calawah River—are sources and sinks (Schlosser and Angermeier 1995). If true, then juvenile distributions might have been more strongly influenced by other factors (e.g., food, competition, predation, and water temperature) that were not measured in our study but that affect growth, survival, and movement (Angermeier and Schlosser 1989; Dunham and Rieman 1999; Railsback and Rose 1999; Keeley 2001).

The unexplained patterns in distribution could also have been influenced by other factors. For instance, we probably consistently undersampled age-0 steelhead; these fish may rely heavily on shallow-water habitats (Bjornn and Reiser 1991), but we were unable to snorkel habitats less than 0.2 m deep, which could have reduced explanatory power. To some degree, distributions of young-of-the-year juveniles also likely reflected differences in the abundance and location of spawning adults (Finstad et al. 2009). We could not determine this because spatially explicit data on redd locations are not available for all sections of individual streams in the Calawah River basin. However, there are escapement data for adults; estimates for adult Coho Salmon in the entire network increased marginally from 2001 to 2002 (escapement = 3,994 and 4,267 adults, respectively), and estimates for adult steelhead decreased by about the same amount (escapement = 4,413 and 3,990 adults, respectively). Thus, we documented large, stream-scale increases in the density and distribution of juvenile Coho Salmon and age-0 steelhead between years when adult abundance was similar, which suggests that egg-to-fry survival may have had a greater effect on juvenile salmonid distribution than the yearly differences in adult abundance.

We also found moderate to strong levels of spatial autocorrelation in the residuals of most network-scale models, suggesting that the survey reaches were not spatially independent.

Nonindependence can produce correlation coefficients that are biased and overly precise (Legendre et al. 2002). However, Moran's I -values were generally reduced to negligible levels ($I < \pm 0.25$) by including stream, reach location, and the associated interaction terms. Although this approach accounted for spatial autocorrelation, inclusion of the site-specific variables eliminated transferability to other streams (Segurado et al. 2006); consequently, our inferences are limited to the sites we sampled and the interactions with the habitat characteristics we measured. Future modeling efforts may thus consider including spatial autocorrelation into regressive models to improve predictive success (Betts et al. 2006).

Stream-Scale Models

Models for individual streams can achieve a high level of explanatory power and precision by incorporating a few habitat variables (Fausch et al. 1988). In our study, individual habitat variables for each stream explained up to 70% of the variation in salmonid density, but on average, explanatory power was low and no single variable was significant across all streams for any of the three salmonid groups. Further, the shape and direction of the responses were inconsistent. For instance, the effect of VWI on Coho Salmon and the effect of channel gradient on age-0 steelhead and steelhead parr ranged from strong to weak and from strongly positive to strongly negative depending on the stream—something that is not often observed in fish–habitat associations (Bjornn and Reiser 1991; Burnett et al. 2007). The stream-specific responses of fish to habitat indicate that models based on multiple streams can oversimplify variability in fish–habitat associations. In our case, oversimplification of fish responses was one reason why the network-scale models struggled to effectively predict the distribution of juvenile Coho Salmon and steelhead.

The only fairly consistent response—that between Coho Salmon density and percent pool habitat—did not necessarily produce a strong correlation. Percent pool habitat explained less than 10% of the variation in Coho Salmon density for three of the seven streams and less than 22% for five of the streams. Previous habitat use studies (Bisson et al. 1988; Bjornn and Reiser 1991) and models based on traditional sampling schemes (Rosenfeld et al. 2000; Sharma and Hilborn 2001) and census data (Reeves et al. 2011) have reported stronger correlations between pools and Coho Salmon. Notably, however, the associations between Coho Salmon and pool habitat were stronger in smaller streams than in larger ones. Similarly, steelhead parr were positively associated with depth in small streams, while the association was nonexistent to negative in large streams. This finding suggests that age-class differences in habitat use can influence distribution (Kanno et al. 2012) and that relatively small fish (e.g., juveniles) may prefer deeper water in shallower streams than in deeper streams and vice versa (Rosenfeld et al. 2011). The results underscore the idea that strong effects of stream and stream size can potentially limit how well a single model can be

applied across different areas (Fausch et al. 1988; Porter et al. 2000; Rosenfeld et al. 2000, 2007).

Part of the variability we found in fish–habitat associations between streams could also be related to differences in fish density rather than to actual differences in habitat selection. For example, many suitable habitats may be unoccupied at very low densities, while many potential sinks may be occupied at high densities (Van Horne 1983; Angermeier and Schlosser 1989). Additionally, Rosenfeld et al. (2005) found that density altered the habitat selection and suitability curves for juvenile Coho Salmon. In our study, the escapement goals in 2001 and 2002 for spawning Coho Salmon and winter steelhead were both easily achieved, and escapement levels were among the highest observed for the Calawah River during the period of record (1980–2012; WDFW 2012). Perhaps consequently, fish were more thoroughly distributed and habitat that would not be used in years with lesser adult abundances was selected during the years of our study, when adult abundance was higher. Overall, though, the effects of density appear to be negligible considering that we sampled several streams with a wide range of densities, but models generally performed poorly for all streams and for all species and life stages. Nonetheless, we also acknowledge that inferences based on habitat selection in nature may provide different results from stream to stream and from year to year based on organism abundance (Hobbs and Hanley 1990).

Perhaps most importantly, we found that fish–habitat associations were dramatically weakened when habitat was allowed to compete with reach location. Previous models based on traditionally collected data (Dunham and Vinyard 1997) and models using continuous data for salmonids (Isaak and Thurow 2006; Ebersole et al. 2009) and nonsalmonids (Grenouillet et al. 2004) have also noted that location within a network can influence fish distribution. Although the location variable did not allow us to identify the underlying reason for the correlation, it did allow us to determine that individual fish–habitat associations were generally weak or nonsignificant after location was included in the full model. This is important because without accounting for location, we would have had an artificially high level of certainty in many of the fish–habitat associations (Legendre et al. 2002). This type of reach effect could limit how effectively correlations drawn from a subsample of reaches can be expanded to larger scales, such as entire streams or networks, and it highlights how the interpretation of models can be biased if the surrounding context of fish and habitat is not considered (Dunham and Vinyard 1997).

Implications

Stream habitat models are commonly generated from a subsample of reaches and streams and then are widely applied to other streams and networks to predict the distribution and density of salmonids (Fausch et al. 1988; Dunham and Vinyard 1997; Porter et al. 2000; Rosenfeld 2003). This approach would have had little success in our study. Stream habitat models performed poorly until we accounted for an interaction between

fish–habitat associations and the location of habitat within streams, the latter of which often violated assumptions about sample independence of the survey reaches and inflated effects of habitat characteristics. These results raise two cautionary points. First, fish–habitat associations that are drawn from multiple streams or from streams other than those in which the data were collected cannot be presumed to be representative of stream-scale variability across a network, so the testing of assumptions is important for establishing a level of certainty (Fausch et al. 1988; Porter et al. 2000; Van Horne 2002). Second, even if fish–habitat associations are known, accounting for the spatial and temporal context of those associations within individual streams may be necessary to effectively predict potentially dramatic troughs and aggregations in the network-scale distribution of salmonids (Dunham and Vinyard 1997; Angermeier et al. 2002; Isaak and Thurow 2006; Torgersen et al. 2012).

Uncertainty due to a lack of testing has implications for the use of stream habitat models to guide management and restoration in unsampled areas and across streams of differing sizes (Fausch et al. 1988). Steelhead parr in our study offer one example. Effects of percent pool habitat ranged from strongly negative to strongly positive between streams and were not entirely consistent within a stream, suggesting that the benefits of manipulating stream channels to create more pool habitat may vary depending on the stream, at least when only summer is considered. In addition, even when the density of steelhead parr was positively correlated with pools, the location of the habitat generally mattered more than the amount. Interactions between fish–habitat associations and space are relatively common and can influence growth and survival across a variety of scales (Ebersole et al. 2009; Pess et al. 2011). If this variability is common in networks, then restoring watershed-scale processes that regulate natural habitat formation may be more effective than manipulating short reaches and expecting the fish to exhibit uniform responses (Beechie and Bolton 1999; Feist et al. 2003).

An increasing focus on larger scales in restoration efforts, combined with strong stream and spatial effects on fish–habitat associations and nonindependence among survey reaches, poses challenges for future modeling and sampling. Our rather complete data set reveals that we know less about the influences on fish distribution than what we have been led to believe—that is, from models based on less spatially exhaustive data. Still, we were only able to detect patterns rather than identify mechanisms, and without understanding the processes it is hard to know why space was so important in our models (Clinchy et al. 2002). Nonetheless, future research that couples intensive, traditional-scale sampling of fish condition and survival with extensive censuses of fish and habitat distribution over multiple years could prove valuable for untangling patterns and processes (Dunham et al. 2002; Isaak and Thurow 2006; Ebersole et al. 2009; Torgersen et al. 2012). One possible way to accomplish this is through integrated population models that rely on repeated

count data to estimate various parameters (e.g., abundance or survival) associated with population dynamics over time (Dail and Madsen 2011; Schaub and Abadi 2011). Such models are increasingly being applied to understand changes in populations of birds and mammals (Schaub and Abadi 2011), and the models may be further improved by explicitly including spatial autocorrelation (Betts et al. 2006). Such an approach could help to clarify the level of uncertainty that can be expected by scientists and managers when applying habitat models broadly across streams, locations, and times.

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