

Hierarchical Modeling of Late-Summer Weight and Summer Abundance of Juvenile Coho Salmon across a Stream Network

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Abstract.—Spatial variation in stream habitat quality can lead to network-level patterns in the survival and growth of juvenile coho salmon *Oncorhynchus kisutch* that provide important insights into the factors influencing the freshwater population dynamics of this species. Our objectives were to quantify the relationships among summer habitat conditions, coho salmon density, and coho salmon parr abundance and weight across an extensive stream network over 3 years. We used hierarchical linear models to assess the factors influencing coho salmon weight and abundance at the levels of individual fish (fork length and parasite burden), habitat unit (surface area, cover, and density), reach (temperature and density) and stream (total nitrogen, soluble reactive phosphorus, and discharge). Habitat-unit-level surface area and stream-level minimum discharge were important predictors of both the abundance and weight of coho salmon parr. An area \times discharge interaction term was also important in models of weight and reflected network-level patterns of the highest abundances and highest parr condition in the middle portions of the basin. In these locations, streamflow, habitat area, and temperature were moderate compared with the warmer, higher-discharge downstream reaches and cooler, lower-discharge (or even intermittent) upstream reaches. We conclude that in the study basin coho salmon parr weight was limited by habitat unit density and minimum summer discharge in the headwaters and abundance was limited primarily by space (pool area) in the headwaters and warm summer temperatures in the lower portions of the basin.

Alteration and loss of stream-rearing habitats for anadromous salmonids has been identified as a primary factor limiting present day abundances and distributions of Pacific salmon *Oncorhynchus* spp. in the Pacific Northwest (National Research Council 1996). For salmon species such as coho salmon *O. kisutch* that spend a year or more in freshwater before ocean residency, the availability and quality of overwintering habitat strongly limit juvenile survival and smolt production (Nickelson and Lawson 1998). However, the effects of winter habitat conditions on juvenile survival are partly mediated by summer habitat conditions via effects on late-summer weight and condition of individuals before overwintering. For example, coho salmon overwinter survival rates increase with fish size (Quinn and Peterson 1996; Ebersole et al. 2006). Overwinter survival can also be

dependent upon fish condition. Lipid stores in juvenile rainbow trout *O. mykiss* were found to be a good predictor of overwinter survival by providing the energetic reserves necessary to avoid starvation (Biro et al. 2004). Although winter habitat conditions may be the primary influence on smolt population dynamics, overwinter survival might also be affected by late-summer size, condition, and abundance of juvenile salmon, all of which reflect cumulative stresses and opportunities during the summer rearing period.

Throughout much of the Pacific Northwest, summer precipitation is minimal and streamflows typically decline substantially from spring through late summer, which results in the contraction of stream surface area and volume. Smaller streams may become intermittent, with surface water limited to isolated pools. Coincident with this stream shrinkage is a decline in macroinvertebrate drift and food availability for juvenile salmonids, and subsequent declines in growth rates (Harvey et al. 2006). Increased competition for available food and space resources leads to increased rates of emigration or mortality (Chapman 1966; Mason 1976). Growth rates may be further reduced where juvenile salmonid densities remain high (Mason 1976), and mortality can directly result from pool dewatering in intermittent streams (May and Lee 2004). As a result, during the low-flow summer period in the

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Pacific Northwest, coho salmon populations can be strongly regulated by density-dependent survival and growth (Fransen et al. 1993).

Many of the factors influencing summer survival and growth of salmonids have been relatively well studied, at least in isolation. For example, high water temperature currently limits the distribution and abundance of coho salmon, especially near the southern margin of their range in northern California (Welsh et al. 2001; Madej et al. 2006) and southern Oregon (Weitkamp et al. 1995). But water temperature and other habitat modifications are often spatially correlated across Pacific Northwest landscapes, and the role of temperature relative to other habitat factors is not always clear. Additionally, the influence of temperature on salmonid weight or abundance across stream networks has seldom been examined in combination with other aspects of stream habitat, including physical structure, water chemistry, and streamflow. The role of juvenile fish density further obscures habitat effects (Lobon-Cervia 2005), and discerning effects of habitat conditions on density-regulated populations is challenging owing to self-thinning, redistribution, or other biotic responses (Dunham and Vinyard 1997b; Grant et al. 1998). These studies illustrate that measures of abundance and size offer differing insights into processes regulating juvenile salmonid production. Both types of metrics are important to consider when assessing the influences of habitat quality and quantity on juvenile coho salmon populations (Fransen et al. 1993). But exclusive reliance on one or the other can lead to misleading results (e.g., vanHorne 1983).

The response of stream salmonids to habitat conditions is complex and multi-scalar (Schlosser and Angermeier 1995; Poff and Huryn 1998), as fish probably respond to micro-habitat conditions that are, in turn, influenced by reach- and stream-level processes (sensu Frissell et al. 1986). This requires a hierarchical view with respect to both study design and analysis of fish-habitat relationships (Frissell et al. 1986; Fausch et al. 2002; Lowe et al. 2006). Variation in habitat quality or quantity across a stream network may result in varying patterns of juvenile salmon size, abundance, or both, depending upon the nature of resource tracking used by the fish and the spatial scale of ecological responses (Folt et al. 1998). Despite many studies on the ecology and life history of juvenile coho salmon, little is known regarding factors influencing late-summer abundance and condition of juvenile coho salmon at multiple spatial scales. To our knowledge, never have both abundance and size of juvenile salmon been considered concurrently within a hierarchical framework.

We examined both late-summer weight (hereafter, weight) and summer abundance (hereafter, abundance) of coho salmon parr across a stream network that included perennial and intermittent tributaries of a perennial main stem over 3 years. The objectives of this study were to: (1) identify spatial (individual level to basin level) variation in coho salmon weight and summer parr abundance across different portions of the stream network, (2) explore the degree of variation in weight and abundance at the individual and habitat unit levels that could be explained using density and habitat characteristics summarized at multiple levels, and (3) evaluate the relative importance of these characteristics in estimating weight and abundance of coho salmon parr.

Study Area

The West Fork Smith River (WFSR) basin is one of seven coastal Oregon basins in which adult and juvenile salmon populations are intensively monitored by the Oregon Department of Fish and Wildlife (ODFW) (Jepsen et al. 2006). We selected the basin for this study because ODFW's monitoring presence provided an important context for our multi-year study that would be helpful in understanding the relevance of our findings elsewhere. Additionally, the WFSR provided the diverse array of stream habitat conditions we sought, including variability in streamflow (perennial and intermittent streams). The WFSR drains a 67-km² basin in the Umpqua River basin of the Oregon Coast Range (Figure 1). Basin vegetation is composed of relatively young multi-aged forest, dominated by Douglas fir *Pseudotsuga menziesii* in the uplands, with mixed conifer and broadleaf species, predominantly red alder *Alnus rubra* and bigleaf maple *Acer macrophyllum*, in the riparian areas. The WFSR has an elevation range from 60 to 850 m, and is underlain by Tyee sandstone bedrock. Mean annual basin precipitation of 2,057 mm occurs predominately as rain during the late fall through spring. Surface streamflow sometimes ceases in parts of the stream network during the summer dry season (Wigington et al. 2006).

Intensive forest harvest and road building activities have occurred in the WFSR basin, similar to that in other Oregon coastal basins (Reeves et al. 2002). These activities have resulted in reduced in-stream large woody debris, altered stream channels, and associated losses of spawning and rearing habitat for salmon (USDI 1997). Additionally, splash-damming occurred in the WFSR during the late 1800s through the early 1900s. Splash-damming was a practice of driving logs down river channels on artificial spates created by releasing water from temporary dams. The debris-filled spates and channel clearing associated with this

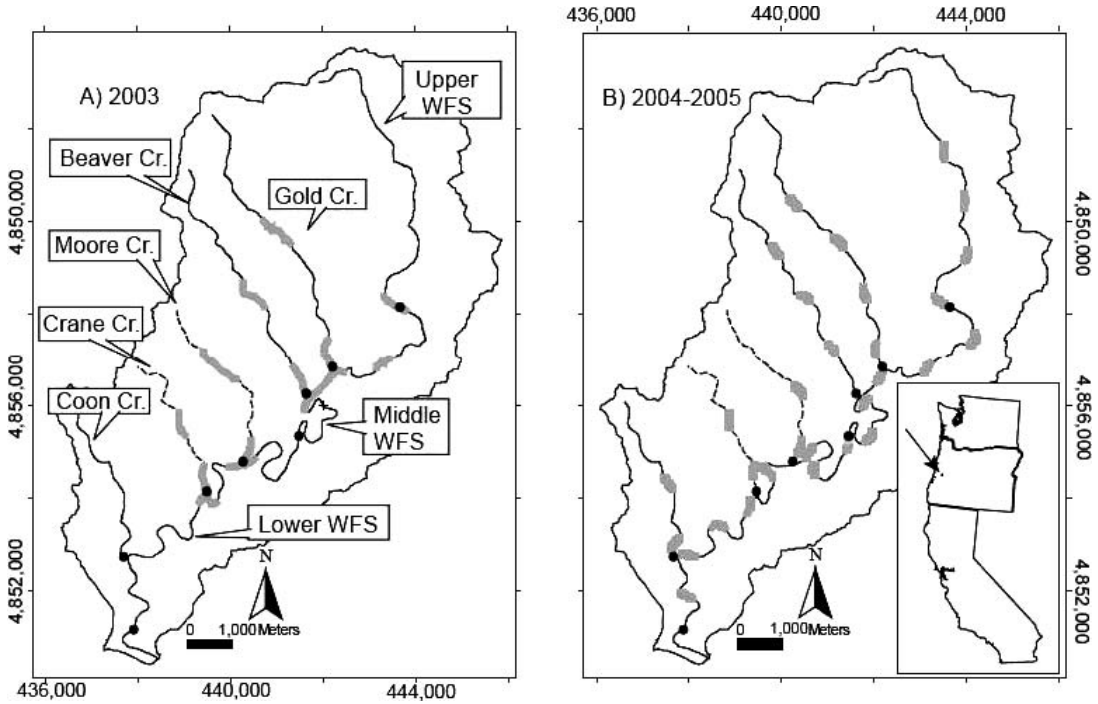


FIGURE 1.—Locations of the study reaches (thick gray segments) within the West Fork Smith River (WFS) in (A) 2003 and (B) 2004 and 2005. Stream-level sampling points (e.g., for chemistry and discharge) are denoted by circles; intermittent streams are denoted by dashed lines.

practice simplified channels in the lower main stem by removing wood and scouring the streambed to bedrock. Consequently, this portion of the river has relatively little wood or gravel in the stream channel. The U.S. Bureau of Land Management has invested heavily in boulder-weir and large-wood restoration structures to remedy some of these habitat losses (Roni et al. 2008).

Differences in streamflow within the WFSR stream network create additional habitat variability (Wigington et al. 2006). Douglas County has operated a stream gauge on the WFSR main stem near the mouth since 1981. Additionally, in 2003–2005, we measured streamflow quarterly in the tributaries using Swoffer flowmeters (Swoffer Instruments, Seattle, Washington) mounted on wading rods (Gordon et al. 1992). Highest streamflows occur during the wet season of November through March. Summer streamflows are low because of the lack of precipitation during this period. We defined three classes of streams within the basin based upon summer streamflow characteristics owing to the hypothesized importance of summer streamflow to juvenile salmonid ecology. Moore and Crane creeks were classified as intermittent tributaries (Figure 1), characterized by low flows during summer months when surface flow ceases as early as July and only isolated pools remain in some sections until rains

commence in the fall. Beaver Creek, Gold Creek, Coon Creek, and the upper WFSR (above Gold Creek) were classified as perennial tributaries (Figure 1), and maintained flows during all summer months. The WFSR below the confluence of Gold Creek was classified as main stem, and was distinguished from the perennial tributaries on the basis of low summer streamflow, which was more than doubled (2005 minimum flow = 0.07 m³/s) below the confluence of Gold Creek (2005 minimum flow = 0.02 m³/s) and the upper West Fork (2005 minimum flow = 0.02 m³/s). Annual differences in streamflow also occur; summer streamflow in 2003 was particularly low. In the main stem, minimum summer streamflows at the gauging station near the mouth of the WFSR were 0.04, 0.09, and 0.09 m³/s during 2003, 2004, and 2005, respectively. The highest summer water temperatures observed during this study also occurred during the low-flow period of 2003 and exceeded 25°C in the lower main stem (J. L. Ebersole, unpublished data).

Methods

Sampling Design

We used a hierarchical, nested sampling design (Figure 2) that consisted of four levels: individual fish, habitat units (individual pool morphologic units, after

Bisson et al. 1982; mean length = 20 m), reaches (mean length = 530 m), and streams (mean length = 6.4 km). Locations of study reaches varied by year. Study reaches were subjectively chosen in 2003 ($n = 17$), but were systematically selected with a random start from throughout the stream network in 2004 and 2005 ($n = 30$) (Figure 1).

Individual level.—Coho salmon parr ($n = 29,277$) were collected between August 19 and September 30 each year to determine weight, length, and condition. A beach seine was used to collect fish from each individual pool within each study reach. Captured fish were anesthetized using tricaine methanesulfonate at a concentration of 80 mg/L, buffered with NaHCO_3 at a concentration of 125 mg/L. Fish were measured for fork length (FL) to the nearest millimeter, weighed to the nearest 0.01 g on an electronic balance, and visually assessed for presence or absence of black spot infestation (a *Neascus*-type trematode parasite; Cairns et al. 2005). Fish were released to their habitat unit of capture following recovery.

Habitat-unit level.—The distribution and relative abundance of coho salmon parr were estimated within the WFSR basin by conducting a snorkel survey during July–August of 2003, 2004, and 2005 in every pool and glide habitat unit within each study reach ($n = 682$, 768, and 788 habitat units in 2003, 2004, and 2005, respectively). Snorkelers used the protocol of Thurow (1994), moving upstream and visually estimating abundances of coho salmon. Visual bias was corrected by comparing snorkeler counts in a subset of pools and glides with more accurate estimates using multiple-pass removal methods (Zippin 1958) by means of electro-fishing within those same units. Correction factors ranged from 1.5 to 1.9 (mean = 1.7).

Physical habitat was characterized at the habitat unit level by measuring (1) unit maximum depth, mean width, and length to calculate surface area, (2) visually estimating cover provided by overhanging vegetation, expressed as percent of total habitat unit area, and (3) visually estimating percent of unit area with cover provided by in-stream objects such as wood or interstitial spaces.

Reach level.—Stream temperatures were recorded using an array of Onset StowAway TidbiT temperature data loggers (Onset Computing, Pocasset, Massachusetts) deployed at each of the study reaches. This provided a continuous, 30-min interval record of the ambient water temperature regime. Duplicate loggers were placed at approximately 20% of the sites for quality assurance purposes. Before deployment, we tested each temperature logger in a laboratory water bath against a National Institute of Standards and Technology (NIST)-traceable digital thermistor at three

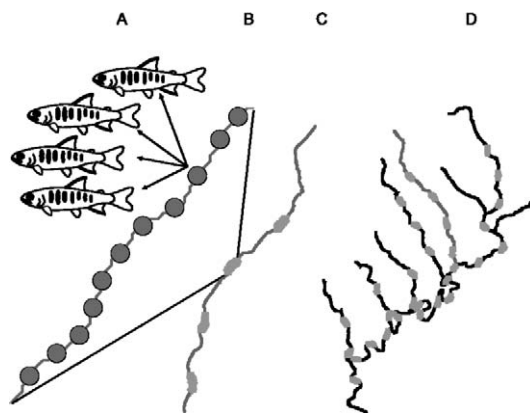


FIGURE 2.—Hierarchy of (A) individual coho salmon within (B) habitat units, (C) focal reaches, and (D) streams in the West Fork Smith River basin.

temperatures, representing the typical range of field conditions encountered. The accuracy and resolution were approximately $\pm 0.2^\circ\text{C}$. We summarized stream temperatures at each location as the maximum weekly (7-d running average) maximum temperature (MWMT).

Stream level.—We measured stream discharge and collected water chemistry samples monthly at stations distributed among the main stem and tributaries (Figure 1). Chemistry values were averaged for the summer period (June–August), except for 2005 when samples were only taken in May and September. Samples were filtered in the laboratory within 24 h of sampling (0.25 μm polycarbonate membrane filters; Whatman, Inc., Newton, Massachusetts). To determine total nitrogen (N), we performed persulfate digestion (Cabrera and Beare 1993) followed by automated colorimetric analysis for nitrate (USEPA 1987, method 353.2). Soluble reactive phosphorus (SRP) was determined by automated colorimetric analysis (USEPA 1987, method 365.1).

Statistical Analysis

To understand the factors that influence weight and abundance of coho salmon parr, we used hierarchical linear models (HLMs). As in standard regression approaches, an HLM model relates the response variable (e.g., coho salmon abundance in this study) to independent variables derived at the same hierarchical level (e.g., pool area). This relationship is termed the base model. We were interested in examining higher-level effects (e.g., reach-level or stream-level effects) in our models. The HLM models differ from traditional regression techniques by incorporating higher-level effects that may help explain variability

TABLE 1.—Variables and associated hypotheses used to construct coho salmon weight models.

Scale	Variable	Description	Hypothesis	Mean (range)
Individual coho salmon	Weight	Wet mass (g)	Response variable	3.28 (0.4–16.2)
	Length	Fork length (mm)	Base model; weight increases with length	63.8 (34–110)
	Black spot	Infestation by <i>Neascus</i>	Presence of parasite load decreases weight	Categorical (0,1)
Habitat unit	Area	Habitat unit surface area (m ²)	Increased habitat area increases foraging opportunities	198.5 (4.4–1328.7)
	Coho salmon density	Number of coho salmon parr/m ² calculated for habitat unit	Density-dependent competition; increased habitat unit density lowers weight	0.9 (0–14)
	Overhead cover	Visual estimate of percent of habitat unit area influenced by overhanging structure (%)	Increased depth and cover reduce competition, increase weight	17.7 (0–100)
	Substrate cover	Visual estimate of percent of habitat unit area influenced by underwater structure (%)	Increased depth and cover reduce competition, increase weight	11.9 (0–65)
Reach	Temperature	Maximum weekly (7-d running average) maximum temperature (°C)	Temperature regulates metabolism and growth; dome-shaped relationship with weight	18.62 (11.4–24.0)
	Coho salmon density	Number of coho salmon parr/m ² calculated for entire reach	Density-dependent competition; increased reach density lowers weight	1.0 (0.1–4.5)
Stream	Total N	Total dissolved nitrogen (mg/L)	Increased availability enhances productivity, increases weight	0.07 (0.04–0.12)
	SRP	Soluble reactive phosphorus (µg/L)	Increased availability enhances productivity, increases weight	6.3 (2–11)
	Minimum summer discharge	Minimum summer discharge as estimated by stage–discharge relationships (m ³ /s)	Increased minimum flow reduces crowding and increases food availability, increasing weight	0.04 (0–0.09)

in the base-model regression slopes and intercepts (Wagner et al. 2006), such as may occur between different streams (Dunham and Vinyard 1997a). Thus, the base model variables directly influence the response variable as in standard regression, while higher-level variables influence the response variable indirectly, through their effect on the intercept and coefficients of the base models. Conceptually, the analytical framework is consistent with the ecological theory of hierarchy in stream systems (Lowe et al. 2006), and shows promise for enhancing understanding of the spatial scaling of fish–habitat relationships (Deschênes and Rodríguez 2007).

Given the lack of basis for generating a priori structured models across multiple levels, we pursued an exploratory rather than confirmatory (*sensu* Burnham and Anderson 2002) approach. For this reason, we used a priori selected variables to consider all possible model subsets. This approach is in contrast to a confirmatory analysis where a small set of a priori models are constructed and tested with data. The analysis included several steps: (1) a priori selection of variables hypothesized to be associated with coho salmon weight and abundance at multiple levels, (2) development of all possible models incorporating the a priori selected variables, (3) selection of a confidence model set using an information-theoretic model

approach for model selection, and (4) prediction and model testing of the confidence models with an independent data set including an evaluation of the relative influence of independent variables. Each step is described in detail in the following sections.

Variable selection and model development.—Independent variables that could directly or indirectly predict weight and summer parr abundance were identified at the individual (weight only), habitat unit, reach, and stream levels, based on hypothesized relationships and previous research (Tables 1, 2). Combinations of these predictor variables across multiple levels and their interactions have not been quantitatively studied, so we developed candidate models that included all possible ecologically reasonable combinations of a priori specified predictor variables. We also explicitly included the interaction of discharge and area in the weight analysis to test the hypothesis that habitat area for foraging becomes increasingly important as discharge, and associated macroinvertebrate prey drift, declines and inter- and intraspecific competition become enhanced (e.g., Harvey and Nakamoto 1996). We also included a (temperature)² term for both the abundance and weight analyses, to allow for a dome-shaped relationship of temperature that may peak at ecologically “optimal” temperatures (Isaak and Hubert 2004).

TABLE 2.—Variables and associated hypotheses used to construct coho salmon abundance models.

Scale	Variable	Description	Hypothesis	Mean (range)
Habitat unit	Coho salmon abundance	Estimated number of coho salmon parr in habitat unit	Response variable	34.3 (0–643)
	Area	Habitat unit surface area (m ²)	Base model; coho salmon abundance is space limited	59.39 (0.4–1,334.0)
	Overhead cover	Visual estimate of percent of habitat unit area influenced by overhanging structure (%)	Availability of cover provides visual isolation and reduces competition, allowing increased abundance	17.7 (0–100)
	Substrate cover	Visual estimate of percent of habitat unit area influenced by underwater structure (%)	Availability of cover provides visual isolation and reduces competition, allowing increased abundance	11.9 (0–65)
Reach	Temperature	Maximum weekly (7-d running average) maximum temperature (°C)	Temperature regulates metabolism and growth; dome-shaped relationship	18.62 (11.4–24.0)
Stream	Total N	Total dissolved nitrogen (mg/L)	Increased nutrient availability enhances productivity, increasing abundance	0.07 (0.04–0.12)
	SRP	Soluble reactive phosphorus (µg/L)	Increased nutrient availability enhances productivity, increasing abundance	6.3 (2–11)
	Minimum summer discharge	Minimum summer discharge as estimated by stage–discharge relationships (m ³ /s)	Lower minimum flow increases food availability, increasing abundance	0.04 (0–0.09)

We used the standard length-to-weight equation (Anderson and Neumann 1996), log transformed to create a linear relationship between length to weight, to develop the following base model for weight of individual coho salmon:

$$\log(\text{weight}) = \log(\beta_0) + \beta_1 \cdot \log(\text{length}). \quad (1)$$

We fit this base model to habitat units that contained at least 10 individual coho salmon parr. The model intercept parameter (β_0) was allowed to vary among habitat units, reaches, and streams, and corresponding habitat unit-, reach-, and stream-level predictors were used to explain the variation in β_0 . This analysis allowed for a random stream, reach, and habitat-unit effect on β_0 . The model parameter β_1 was fixed (using a basin-wide mean observed value of 3.094) because we were unable to achieve model convergence with a varying β_1 , and among-habitat unit variation was negligible across the basin.

We fit the abundance data using a three-level hierarchical linear model. Individual-level dependent variables were excluded, since abundance was defined at the habitat unit level. Area was hypothesized to be a strong factor, based upon previous research that has shown that summer populations of juvenile salmonids may be space-limited (Chapman 1966; Nickelson and Hafele 1978; Bowlby and Roff 1986). Thus, to understand the influence of higher-level habitat factors we first needed to account for the area effect at the habitat unit level in our base model:

$$\text{abundance} = \beta_0 + \beta_1(\text{habitat unit area}). \quad (2)$$

The three-level model allowed for heterogeneous intercepts among reaches and streams, as well as heterogeneous coefficients (β_0 and β_1) for habitat-unit-

level area. This analysis allowed for random stream and reach effects on β_0 and β_1 . Models for coho salmon weight and abundance were fit and parameters estimated using the NLME4 package via maximum likelihood and an unstructured covariance in the R program (R Development Core Team 2007).

We did not incorporate our a priori stream type classification (intermittent, perennial, main stem) into the modeling framework given very small sample sizes ($n = 2, 4, \text{ and } 2$, respectively), and did not statistically compare stream types for this reason. Rather, we summarized patterns of physical habitat, coho salmon abundance, and weight among these streams types to emphasize larger-scale patterns and hypothesized processes that may be occurring within these stream types (e.g., Tables 1, 2).

Model selection.—We used an information theoretic approach (Burnham and Anderson 2002) to perform model selection for weight and parr abundance. We calculated the Akaike information criterion (AIC) for each model that incorporated a penalty for the number of fixed and random effects that were contained in each model (Burnham and Anderson 2002). The AIC values were not adjusted for small sample size, given the large (>40) ratio of sample size to the number of model parameters (Burnham and Anderson 2002), and that this measure of model fit has been shown to give unstable results (Richards 2005). We calculated the weight of evidence for each candidate model as described in Burnham and Anderson (2002) for candidate models of weight and abundance.

All models having AIC weights within 10% of the largest model weight were retained for prediction; this group of models is referred to as the confidence model set (Thompson and Lee 2000; Burnham and Anderson 2002). Variables were evaluated using three metrics

that incorporate measures of variable importance within the confidence model set. Proportional occurrence (O_p) is the proportion of models within the confidence model set that contain a given variable. Because inclusion in a high proportion of candidate models does not necessarily indicate statistical significance, we also assessed variable relative weight (W_r), which is a function of the model AIC weight and the proportion of the candidate model set in which the variable was interpretable (I_p). A model variable was deemed interpretable if the 95% confidence interval (CI) did not include zero. We considered variables to be relatively "important" in the confidence model set if they occurred in a majority of the models and the variable W_r was greater than 0.50 or I_p was greater than 0.50, or both.

Model set testing and prediction.—Because using many possible combinations of multi-level predictor variables may lead to spurious relationships, we tested the confidence model set constructed using 2004 and 2005 data on an independent data set collected in 2003. Weighted predictions for the independent data set were made using the confidence model sets for coho salmon weight and summer parr abundance. Weighted model predictions were then plotted and visually compared with observed values for departures from unity.

The parameter estimates for individual predictors contained in the confidence model set were not averaged, as this is inappropriate for mixed models where parameter estimates are a function of upper level predictors (Burnham and Anderson 2002). Instead, we determined the effect of multi-level predictors on coho salmon parr weight and abundance by taking the AIC-weighted average of the model predictions. This approach was advantageous, as it can be difficult to understand how higher-level factors potentially interact on both intercepts and coefficients in hierarchical models, especially when there are multiple models within the confidence model set. In some cases an upper-level predictor may have a positive effect on the coefficient but a negative effect on the intercept. We used weighted model predictions to further investigate the relative effect of influential variables on the dependent variables. To do this we calculated the predicted response in the dependent variables associated with an increase from the 25% to 75% quartiles (hereafter interquartile increase) for selected independent variables. This was repeated for each model in the confidence model set, and summarized as a mean response with observed variation. Owing to interactions with individual fish length or habitat area, the estimated effects of individual predictor variables were not always uniform across the range of fish lengths or habitat unit areas examined. To further clarify

estimated effects, we plotted the estimated effects of each independent variable across increments of individual length from 51 to 80 mm, and across a range of small (50 m²), medium (110 m²), and large (170 m²) habitat unit areas.

Results

Late-Summer Weight

We developed 1,609 models relating coho salmon parr weight to individual, habitat unit-, reach-, and stream-level variables and their interactions, of which 98 were included in the confidence model set. When applied to the 2003 data set, the confidence model set explained nearly 94% of the variation in individual coho salmon parr weight, and fit well across main-stem, perennial, and intermittent streams (Figure 3, left panel).

As expected, individual-level variation in coho salmon parr weight was consistently explained by length (Table 3). At the individual level, coho salmon parr with black spot parasite did not differ in weight from uninfested individuals at similar lengths, and the parameter estimates for black spot were not consistently interpretable (e.g., the CI included zero; Table 3).

Habitat-unit-level variables that were relatively important in explaining variation in β_0 for equation (1) (coho salmon parr weight) included habitat unit area, and habitat unit coho salmon density (Table 4). The estimated effects of these two variables on coho salmon weight were positive for area, and negative for habitat-unit-level density across the range of fish length classes examined, although these effects were small (<0.05 g per interquartile increase; Figure 4). Variables included to capture the hypothesized effects of depth, overhead cover, and substrate cover were not supported in the confidence model set (all $W_r \leq 0.20$ and all $I_p = 0$; Table 4).

At the reach level, temperature was the most important variable examined to explain variation in β_0 from equation (1), but was relatively uninformative ($W_r = 0.43$ and $I_p = 0.38$; Table 4). The squared-temperature and reach-level coho salmon density variables did not contribute meaningfully to the confidence model set and their coefficients were not interpretable (Table 4).

Stream-averaged late-summer weights of coho salmon parr in the WFSR were consistently highest in the perennial tributaries and main-stem WFSR from 2003 to 2005 (mean = 3.4 g; Table 5). Coho salmon weights in the intermittent streams Moore and Crane creeks averaged 0.9 g lower (mean = 2.5 g). Important stream-level effects on coho salmon parr weight included minimum discharge and SRP (Table 4). Minimum

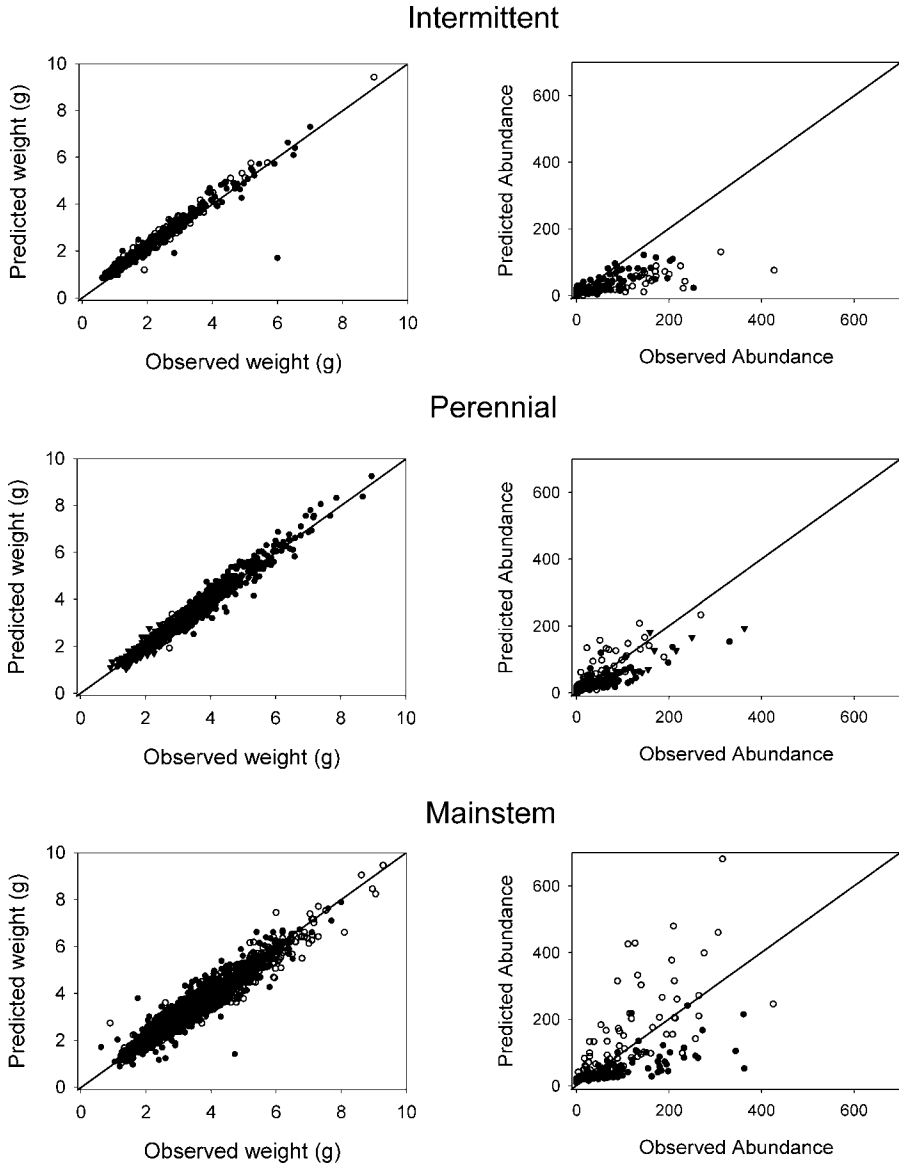


FIGURE 3.—Habitat unit coho salmon weight and abundance at the end of summer in intermittent, perennial, and main-stem reaches as estimated by models constructed from data collected in 2004 and 2005 (predicted) and applied to data collected in 2003 (observed). The 45° lines represent perfect prediction. Data from individual streams are plotted with unique symbols.

discharge had a positive effect on weight across the range of fish length classes examined (Figure 4). The SRP also had a positive effect on weight (Figure 4), and was marginally important in the confidence model set ($W_r=0.47, I_p=0.51$; Table 4). Stream-level total N was included in less than one-third of the confidence models, and its effect was not interpretable (Table 4).

A multi-level interaction term of habitat-unit area and stream-level minimum discharge was important in the confidence model set ($W_r=0.59, I_p=1.00$; Table 4), and

indicated that streams with lower minimum discharge were more sensitive to the positive effect of habitat-unit area on the β_0 term from equation (1) (Figure 5).

Summer Abundance

We developed 2,180 models relating abundance to habitat unit, reach, and stream-level variables and their interactions, of which 19 were included in the confidence model set. When applied to the 2003 data set, the set of confidence models explained about 31%

TABLE 3.—Summary of predictor variables contained in the base confidence model sets for coho salmon parr end-of-summer weight and summer abundance. Proportional occurrence is the proportion of models in the set that include the variable of interest. Relative weight is a function of the model AIC weight and the proportion of models in which the variable parameter estimate is interpretable. A parameter is interpretable if the 95% confidence interval for the estimate does not include zero. Variables for which relative weight or the proportion of models that are interpretable exceed 0.50 are indicated by bold italics.

Variable	Proportional occurrence	Relative weight	Proportion of models interpretable
End-of-summer weight			
<i>Length</i>	1.00	1.00	1.00
Black spot	0.20	0.16	0
Abundance			
<i>Area</i>	1.00	1.00	0.11
<i>Overhead cover</i>	0.94	0.97	1.00
Substrate cover	0.39	0.24	0.00

of the variation in coho salmon abundance across all habitat units, with model fit varying by stream type (Figure 3, right panel). In particular, abundances in Moore Creek and Crane Creek, the two intermittent tributaries, were substantially underestimated by the model in 2003.

The base model for coho salmon parr summer abundance included area (equation 2), which was consistently important but not consistently interpretable in the candidate model set (Table 3). This is probably due to the fact that the relationship between habitat unit area and abundance varied by stream type despite a consistently positive association between these variables (Figure 6). At the habitat-unit level, overhead cover was consistently included in the confidence model set, and its very small positive effect on

abundance was always interpretable ($W_r = 0.97$, $I_p = 1.00$; Table 3). Substrate cover did not contribute meaningfully to models of coho salmon abundance (Table 3).

Several higher-level factors had indirect effects on the area–abundance relationship (β_1 from equation 2, i.e., density) through their influence on the base model intercept (β_0) or coefficients (β_1 from equation 2), or both. To illustrate the effects of interquartile increases in influential variables, separate abundance estimates were made for small (50 m²), medium (110 m²), and large (170 m²) habitat unit-area classes (Figure 7). At the reach level, both temperature and (temperature)² had important effects on the area–abundance intercept (Table 6). The modeled estimated effect of reach-level temperature on abundance was positive for small habitat areas (Figure 7A), but negligible for larger habitat areas (Figure 7B, C). The (temperature)² term was important in the confidence model set and reflected highest densities from intermittent streams with intermediate temperatures (Figure 8A).

At the stream level, both minimum discharge and total N had high relative weights and were consistently interpretable (Table 6). Owing to high variation in parameter estimates across the confidence model set, stream-level 95% CIs for the effect of SRP on abundance was not consistently interpretable (Table 6). The estimated effect of stream-level total N on abundance was positive for small, medium, and large habitat unit-area classes (Figure 7), and in part reflected higher total N values for some intermittent and perennial streams (Figure 8B). Stream-level minimum discharge was negatively associated with abundance for all area classes (Figure 7) and reflected strong differences in discharge among stream types (Figure 8C).

Habitat-unit level abundances of coho salmon parr

TABLE 4.—Summary of higher-level predictor variables included in the confidence model sets for coho salmon parr end-of-summer weight. Higher-level predictor variables can affect weight indirectly through their effect on the intercepts of the base models (Table 3). The coefficients were fixed for this analysis. See Table 3 for additional details.

Level	Variable	Proportional occurrence	Relative variable weight	Indirect effects on intercept: proportion interpretable
Habitat unit	<i>Area</i>	0.60	0.64	0.85
	<i>Density</i>	0.90	0.93	1.00
	<i>Depth</i>	0.22	0.20	0.00
	Overhead cover	0.15	0.12	0.00
	Substrate cover	0.18	0.14	0.00
Reach	Temperature	0.51	0.43	0.38
	(Temperature) ²	0.07	0.05	0.00
	Density	0.01	0.01	0.00
Stream	Total N	0.32	0.32	0.00
	<i>SRP</i>	0.46	0.47	0.51
	<i>Minimum discharge</i>	0.78	0.81	0.63
Multilevel interaction	<i>Area × minimum discharge</i>	0.52	0.59	1.00

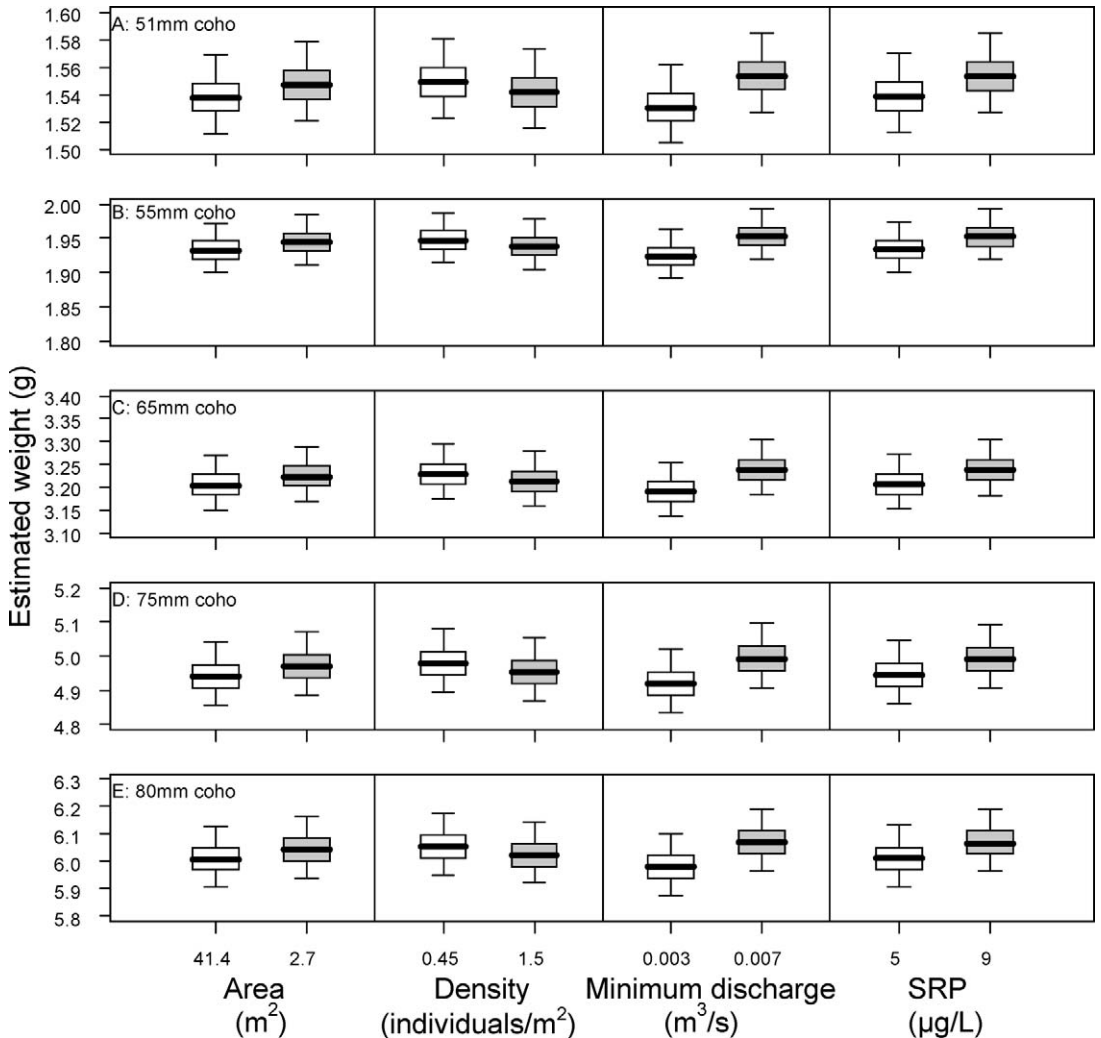


FIGURE 4.—Modeled effects of habitat-unit-level area, habitat-unit-level density, stream-level minimum summer discharge, and stream-level soluble reactive phosphorous (SRP) on the weights of individual juvenile coho salmon ranging from (A–E) 51 to 80 mm FL. Each independent variable was set at the 25% (low; unshaded) and 75% (high; shaded) quartile values observed in the data to illustrate the estimated effect of an interquartile increase in each factor on parr weight. Box plots enclose upper and lower quartiles, and whiskers extend to maximum and minimum values. The thick black lines show the median. Note the differences in the scales of the y-axes.

were highest in 2003 and lowest in 2005 in all streams (Table 5). Differences in abundances paralleled differences in density among streams. Although mean densities of coho salmon parr varied among years, streams were similarly ranked based on these densities regardless of year. In each year, densities were lowest in the main stem or the perennial tributary of Gold Creek, and were highest in the intermittent tributaries or the perennial tributaries of Coon Creek and upper WFSR (Table 5).

Discussion

Hierarchical models for weight and abundance across a stream network over multiple years provided differing insights into factors influencing coho salmon populations. Although the two model sets shared several common factors, including stream-level minimum summer discharge, reach-level temperature, and habitat-unit area, the direction and relative magnitude of the predicted effects on the response variables differed. The models also contained important vari-

TABLE 5.—Mean (SD) stream-level, end-of-summer weight (g), summer abundance (number per habitat unit), and density (number/m²) of coho salmon parr in the West Fork Smith River (WFSR) watershed in 2003, 2004, and 2005.

Site	2003			2004		
	Weight	Abundance	Density	Weight	Abundance	Density
Main-stem						
Lower WFSR	3.06 (1.07)	94.67 (100.8)	0.64 (0.7)	3.2 (1.22)	79.12 (101.16)	0.46 (0.32)
Middle WFSR	3.71 (1.25)	102.73 (92.27)	0.52 (0.35)	3.12 (1.2)	97.96 (94.24)	0.73 (0.52)
Perennial tributaries						
Coon Creek				2.87 (1.88)	27.13 (34.33)	1.79 (1.64)
Beaver Creek	2.97 (1.52)	35.09 (46.58)	0.99 (0.87)	2.83 (2.03)	30.05 (34.47)	1.2 (0.94)
Gold Creek	3.49 (1.17)	21.36 (39.12)	0.72 (0.73)	3.28 (1.12)	15.55 (25.82)	0.6 (0.63)
Upper WFSR	2.9 (1.12)	101.16 (90.22)	1.14 (0.56)	2.95 (1.3)	31.85 (55.57)	1.29 (1.12)
Intermittent tributaries						
Moore Creek	1.83 (1.05)	80.8 (86.65)	3.98 (3.99)	2.33 (1.49)	53.33 (61.79)	2.88 (2.86)
Crane Creek	2.29 (1.49)	41.79 (52.47)	2.98 (3.33)	2.6 (1.47)	28.46 (38.21)	1.58 (1.48)

ables unique to each set. Although the availability of food and space has long been recognized as a fundamental driver of stream salmonid population dynamics (Chapman 1966), the processes of competition, self-thinning, and redistribution can greatly challenge attempts to link environmental conditions to biotic responses. By analyzing spatial variation in both weight and abundance in relation to habitat and fish-density variables across multiple hierarchical levels, we were able highlight the ways in which weight and abundance responded to important environmental factors differently, or in concert, across a stream network. In the following discussion, we address factors associated with weight and abundance at each hierarchical level.

Individual-Level Effects on Weight

Our base models for coho salmon parr weight included FL and presence of black spot infestation. Not surprisingly, length explained a high proportion of the variation in individual coho salmon weight, and was an essential component of the base models. Contrary to our hypothesis, occurrence of black spot was not associated with reduced individual weight after accounting for length. In a companion study, Rodnick et al. (2008) found that black spot was not associated with variation in swimming ability. Using histology and microscopic examination, Rodnick et al. (2008) identified high levels of infestation by three additional parasites among coho salmon from the WFSR, including *Myxobolus kisutchi*, the kidney parasite *Nanophyetus*, and *M. insidiosus*. Thus, it is apparent that our gross external examination for *Neascus* as evidenced by black spot did not fully account for total

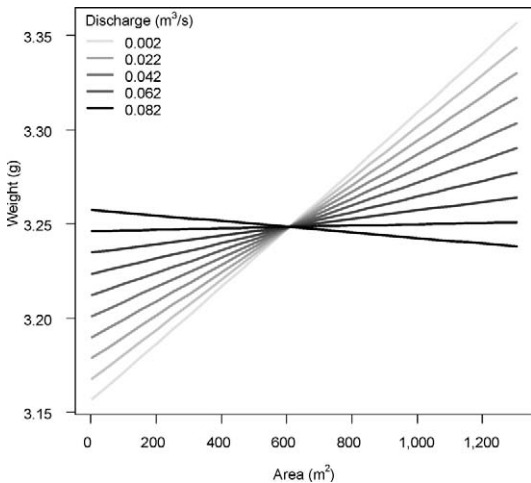


FIGURE 5.—Effects of the multilevel interaction between habitat unit area and minimum summer discharge on coho salmon parr weight. The predicted values are the weights for an average-sized (65-mm) parr across the range of observed habitat unit areas and minimum discharge values.

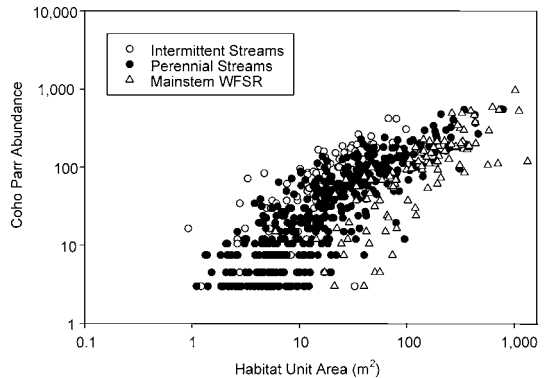


FIGURE 6.—Relationships between log-transformed habitat-unit-level coho salmon parr abundance and log-transformed habitat unit surface area for intermittent, perennial, and mainstem locations in the West Fork Smith River (WFSR) basin.

TABLE 5.—Extended.

Site	2005		
	Weight	Abundance	Density
Main-stem			
Lower WFSR	4.01 (1.38)	64.89 (85.24)	0.25 (0.19)
Middle WFSR	4.24 (1.4)	59.44 (54.09)	0.42 (0.49)
Perennial tributaries			
Coon Creek	3.04 (1.94)	18.75 (26.24)	1 (1.11)
Beaver Creek	4.11 (2.43)	17.52 (36.23)	0.54 (0.47)
Gold Creek	4.37 (1.52)	9.96 (13.28)	0.49 (0.57)
Upper WFSR	3.31 (1.61)	17.78 (24.4)	0.72 (0.61)
Intermittent tributaries			
Moore Creek	3.25 (1.42)	21.46 (31.05)	0.67 (0.59)
Crane Creek	2.89 (1.22)	12.5 (17.51)	0.66 (0.74)

parasite loads experienced by juvenile coho salmon in this study. Previous research in the WFSR has found that portions of the watershed with high levels of *Neascus* infestation (as reported by Cairns et al. 2005)

are also areas of poor overwinter survival (Ebersole et al. 2006). Combined, results of these studies provide equivocal evidence for a substantive effect of *Neascus* on juvenile coho salmon performance. However, the presence of high loadings of other parasites more difficult to quantify supports calls for more comprehensive physiological investigations into the effects of parasite loadings on juvenile salmonids in the study region (Rodnick et al. 2008).

Habitat-Unit-Level Effects

We considered effects of coho salmon parr density on weight indirectly by using density to explain variation in the intercepts from equation (1) (β_0) at both habitat unit and reach levels, and found important effects of density at the habitat unit level. We had hypothesized that higher densities of juvenile coho salmon would be associated with lower mean weights

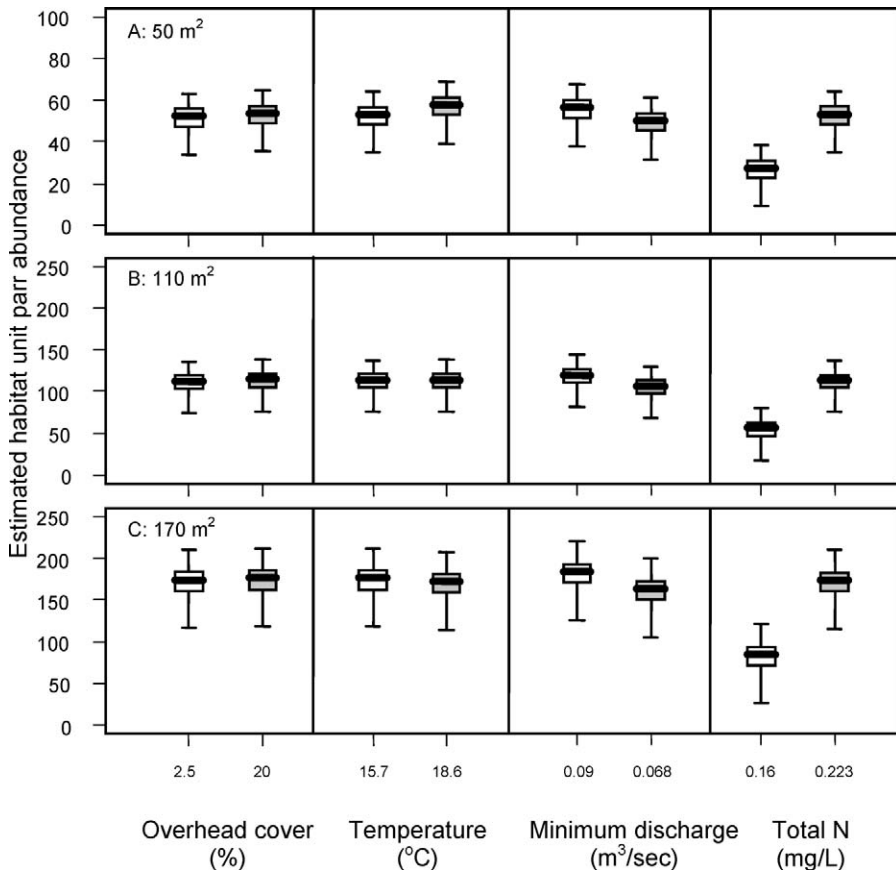


FIGURE 7.—Modeled effects of habitat-unit-level overhead cover, reach-level stream temperature, stream-level minimum summer discharge, and stream-level total nitrogen on the habitat unit abundances of juvenile coho salmon in (A) small (50-m²), (B) medium-size (110-m²), and (C) large (170-m²) habitat unit areas. Estimates were derived only from models in which the 95% confidence intervals of the parameters did not include zero. See Figure 4 for additional details.

TABLE 6.—Summary of higher-level predictor variables included in the confidence model sets for coho salmon parr abundance. Higher-level predictor variables can affect abundance indirectly through their effect on the intercepts or coefficients of the base models (Table 3). See Table 3 for additional details.

Level	Variable	Proportional occurrence	Relative variable weight	Indirect effects: proportion interpretable	
				Intercept	Coefficient
Reach	<i>Temperature</i>	0.89	0.96	0.69	0.00
	<i>(Temperature)²</i>	0.39	0.43	0.71	0.00
Stream	<i>Total N</i>	1.00	1.00	0.00	1.00
	SRP	0.44	0.31	0.13	0.00
	<i>Minimum discharge</i>	0.50	0.40	0.22	0.56

at both levels. Density dependence at the habitat unit level has been observed by numerous authors in stream settings where movement between habitat units was either inhibited by experimental barriers (Harvey et al. 2005), or naturally limited by shallow intervening riffles or dry sections of streambed (May and Lee 2004). Perennial flow and connection between habitat units was maintained in all streams except Moore and Crane creeks. In these streams, where flow becomes intermittent during summers of the driest years, habitat-unit-level coho salmon densities approached or exceeded 3 fish/m². Despite relatively high densities in some locations, we observed that many habitat units contained at least a few relatively large, robust individuals (J.L.E., personal observation). Additionally, the modeled effect of density on the intercept β_0 for the weight equation was small (Figure 4). We speculate that these observations could be due to condition-dependent mortality. Maintenance of body reserves and condition under high densities could be observed among survivors if starvation-induced mortality was occurring at a higher rate for low-condition fish. The finding by Rosenfeld et al. (2005) that dominant fish could maintain condition under reduced food supply at the expense of sub-dominant fish suggests that sub-dominant (e.g., lower condition) individuals might be the first to be affected under starvation or other stressful conditions (Fagerlund et al. 1981). This could occur if sub-dominant fish are forced into lower quality microhabitats where food resources are lower or predation risks are higher (Grant et al. 1998; Jenkins et al. 1999). Within our data, the maximum coefficient of condition within individual habitat units always exceeded 1.2 across the full range of densities observed (J.L.E., unpublished data). This value is a relatively “good” condition factor for coho salmon parr, equivalent to that observed for coho salmon provided with supplemental salmon carcass additions in the studies of Bilby et al. (1998). This relatively high maximum within-habitat unit condition factor is consistent with the hypothesis that at least a few dominant individuals were always able to maintain

good condition despite locally high densities of conspecifics. More detailed observational or experimental studies of behavior and foraging divergence among individuals within habitat units (e.g., Nielsen 1992) could further elucidate causal mechanisms.

For the abundance analysis, base models were constructed to account for the hypothesized direct effects of habitat-unit-level area (equation 2). As expected, abundance was primarily influenced by area with larger habitat units having proportionately greater numbers of parr. We additionally hypothesized that for habitat units of a given area, the availability of cover may allow increased abundances of juvenile coho salmon by providing visual isolation and protection from predators (e.g., Bugert et al. 1991). Other investigators have used various definitions of “cover” when evaluating effects on stream salmonids and we distinguished between cover provided by overhanging vegetation and that provided by substrate complexity. We found that overhead cover, but not substrate cover, was important in our models of abundance. Giannico and Healey (1999) observed that juvenile coho salmon in experimental streams preferred pool units with cover, but experienced reduced foraging efficiency in microhabitats with overhead cover, perhaps owing to reduced visibility of prey items. We did not detect an effect of overhead or substrate cover on coho salmon weight. The observations of Giannico and Healey (1999) would be consistent with the positive effects of overhead cover on habitat unit abundance, but not individual condition, of coho salmon parr observed in our study.

Reach-Level Effects

As previously discussed, we observed habitat unit-level effects of coho salmon parr density on parr weight. We did not observe reach-scale effects of density. Jenkins et al. (1999) observed reach level, instead of habitat unit-level effects of density on brown trout *Salmo trutta* growth in a California stream, and attributed the scale of the effect to the observed ability of fish to move among habitat units. Our observation of

habitat-unit rather than reach-level density dependence suggests that movement among habitat units was limited in our streams. Kahler et al. (2001) documented between-pool movement of coho salmon during low-flow periods in streams where summer streamflows were higher ($0.1\text{--}0.27\text{ m}^3/\text{s}$) than observed in this study ($0\text{--}0.09\text{ m}^3/\text{s}$), perhaps indicating that the lack of an observed reach-level effect of density may reflect the particularly low streamflows that occur in our study streams during the summer months.

We had hypothesized that the reach-level (temperature)² term would be an important predictor in both model sets. This was because we expected dome-shaped temperature effects (e.g., Isaak and Hubert 2004) on both weight and abundance across the range of temperatures observed, which spanned physiological optimal temperatures for growth ($13\text{--}18^\circ\text{C}$; McCullough 1999). The (temperature)² term was not important in the model set for weight, but it was important in the abundance analysis, and we observed highest densities of coho salmon parr at intermediate temperatures ($18\text{--}20^\circ\text{C}$; Figure 8C). Reach-level temperature had a slightly positive effect on the intercepts for the weight–length relationship and habitat-unit abundance. However, the temperature effect on abundance was only evident for habitat units with smaller habitat surface areas and was negligible for intermediate habitats and negative for habitat units with surface area exceeding 110 m^2 (Figure 7). These results indicate that the positive effects of temperature on weight and abundance were primarily restricted to the smaller streams, all of which were cooler than 20°C .

Stream-Level Effects

For both the coho salmon parr weight and abundance analyses, stream-level minimum discharge was an important component of our hierarchical models. Summer stream shrinkage from June through September is coincident with declines in macroinvertebrate drift and food availability for juvenile salmonids, and subsequent declines in growth rates (Harvey et al. 2006). Our observation of reduced weight at lower discharge levels is consistent with in-stream experiments conducted by Harvey et al. (2006) on juvenile steelhead (anadromous rainbow trout), in which flow and subsequent invertebrate prey drift rates were manipulated.

Habitat-unit area became a stronger factor influencing body condition in streams with lower stream-level discharge, as indicated by the multi-level interaction of habitat-unit area and discharge (Table 4). This indicated that streams with lower discharge were more sensitive to the positive effects of increased habitat-unit area (Figure 5). A possible explanation for this finding

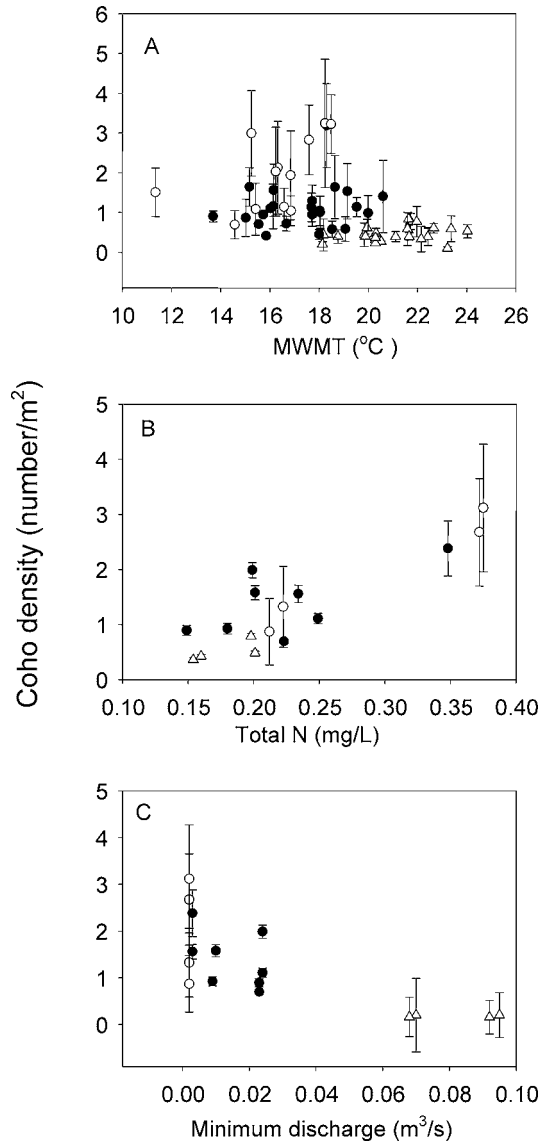


FIGURE 8.—Relationships between coho salmon parr density and (A) the maximum weekly maximum temperature (MWMT), (B) total N, and (C) the minimum discharge for intermittent (open circles), perennial (solid circles), and mainstem locations (triangles). The data in panels (A) and (B) are stream-level means, those in panel (C) reach-level means.

is that as discharge declines and pools become isolated or nearly so, the cumulative stresses experienced by fish crowded into a shrinking habitat may increase in a nonlinear fashion. For example, territorial-based hierarchies that allow resource partitioning under stable conditions may break down with increasing densities, forcing individuals into continuous contests for desirable foraging locations or microhabitats (e.g., three-

spine sticklebacks *Gasterosteus aculeatus*, Sneddon et al. 2006). Given the inability to emigrate from such conditions, a reduction in growth (and ultimately survival) would be expected.

While we observed increased weight with increased discharge (Figure 4), which is consistent with this hypothesis, we did not observe increased abundance with increased discharge. On the contrary, abundance was negatively associated with discharge (Figure 7). In the WFSR, minimum summer discharge was associated with increases in stream size, increasing from small intermittent tributaries, to perennial tributaries and the main stem (Figure 8B). As noted previously, stream-level patterns of temperature also tended to increase along this gradient, but the relationship of coho salmon parr density to temperature was dome-shaped (Figure 8C). So while abundance generally increased with pool area (and associated increases in overall stream size, minimum discharge, and temperature), density declined, particularly as habitat units exceeded 110 m² and temperatures exceeded 20°C.

We had hypothesized that total N and SRP would be positively associated with both weight and abundance of juvenile coho salmon. We observed positive associations of total N and abundance, and positive associations of SRP with weight. The mechanism for the effect of stream water total N on coho salmon abundance is not clear. Algal production is not expected to be limited by stream total N levels in the WFSR, since molar total N:SRP ratios ranged from 34 to more than 100 in our stream water, much higher than the empirically based threshold of less than 10 for N limitation (Shanz and Juon 1983). This suggests that if nutrients limit algal production, then SRP is expected to be limiting. Indeed, SRP was an important factor positively associated with weight. One possible explanation for the relationship of abundance to total N is that total N is correlated with some other stream characteristic, and is not a direct cause of the increase in abundance. For example, dissolved nitrogen in some Oregon Coast Range streams is positively correlated with the proportion of red alder cover in the basin (Compton et al. 2003). Preliminary analyses indicate that this is also the case in the WFSR (J. E. Compton and M. R. Church, unpublished data). Red alder is a nitrogen-fixing tree that grows quickly in moist disturbed areas, and is common along stream corridors in the Coast Range. Presence of alder in riparian areas increases litterfall quantity and nutrient content relative to coniferous canopy cover (Volk et al. 2003), as well as production of terrestrial invertebrates (Wipfli and Gregovich 2002) and salmonids (Piccolo and Wipfli 2002). Thus, the association of total N and coho salmon abundance may reflect the food web benefits

provided by alder-dominated basins and riparian areas. While the estimated effect of SRP on weight was positive, as expected, we caution that linking salmonid abundances or weights to stream nutrient levels is fraught with potential confounding factors (Compton et al. 2006). A much more satisfactory approach, which we were unable to accomplish owing to logistical constraints, would also incorporate direct measures of prey availability for juvenile coho salmon (e.g., Piccolo and Wipfli 2002; Wipfli and Gregovich 2002).

Caveats

An important caveat to consider when interpreting these density data is that our measures of density were obtained in July–August, whereas fish weight and length data were collected mid-August–September. It is quite likely that the densities observed during July did not consistently index the cumulative density-dependent stresses experienced by coho salmon parr across all study sites through August and September. This would be particularly true for sites where rates of emigration, mortality, or stream shrinkage were atypical. Owing to the 1-month interval between abundance estimates and collection of weight data, we were unable to obtain robust estimates of biomass, which could have provided further insights into habitat quality effects on juvenile salmonids (Rosenfeld 2003; Harvey et al. 2005).

Although our HLM approach possesses several advantages for analyzing inherently hierarchical stream fish-habitat relationships, as with any observational field study, several caveats are in order. First, the population characteristics (weight, abundance, and distribution) of juvenile fish are inherently dynamic. Our samples represent a single point in time during late summer, when we assumed that the weights and abundances of coho salmon parr reflected without bias the cumulative stresses of the preceding summer period. Although this may be a relatively reasonable assumption, we also know that the effects of the cumulative stresses associated with high temperatures, crowding, or habitat shrinkage were probably more advanced in the small, intermittent streams. Second, our models fit well for length:weight ratios when tested against an independent data set from a different year. This is to be expected, given the relatively robust relationship of length to weight and the high percentage of variation explained in the base model. In contrast, models for abundance:area ratios exhibited much poorer predictive ability. A more robust test would apply this modeling approach to a set of basins differing in land use, geology, or climate to determine generality of these findings. Third, we assumed that individual fish measured and weighed in early

September experienced the net cumulative stresses and densities assigned to a given location. Variation in cumulative stressor exposure could be introduced if fish moved substantially between reaches, or if mortality rates differed among reaches, or if some individuals used thermal refugia. The latter has been observed in the lower WFSR when temperatures exceeded 20°C, although available refuge space was very restricted and probably supported relatively few individuals (Raskauskas 2005). Fourth, although we used 3 years of data representing three cohorts of coho salmon, this study occurred during a period when coho salmon spawner returns, and hence basin seeding, were at high levels relative to the late 1990s when coho salmon populations were severely depressed coast-wide (ODFW 2007). Thus, the habitat associations observed during our study period may not reflect habitat associations that might be expected under much lower population sizes.

Conclusions

These results illustrate how environmental factors and their relative influence vary within a basin (e.g., between intermittent streams, perennial streams, and the main stem), and how these effects can be captured using HLM approaches. Not all of the factors influencing weight and abundance were consistent between the two model-building efforts, illustrating that spatial patterns of parr weight and abundance reveal slightly different aspects of the ecology of juvenile coho salmon. But several factors were shared between models, notably minimum discharge and habitat unit area.

The consistent and strong effects of discharge and area on both weight and abundance observed in this study could inform efforts to protect and enhance habitat for coho salmon. Coho salmon recovery efforts are guided by an understanding of the factors limiting production (ODFW 2007). These findings illustrate how a broad-scale factor, streamflow, can regulate juvenile salmon population abundance and body size via multiple direct (physical space) and indirect (physiology, food availability) pathways, leading to basin-level gradients in abundance and weight. In the WFSR basin, low summer streamflows were associated with space and food limitation in the headwaters, and temperature limitation in the lower basin. These findings have direct management implications for the WFSR and other basins that may share these patterns, and can help direct restoration efforts more effectively, by focusing on appropriate locations within stream networks for specific restoration actions. In the lower portions of the WFSR, increases in summer habitat rearing area may have minimal effects on abundance

and weight if water temperatures remain high. Conversely, increases in abundance in the headwaters due to habitat improvement or increased adult escape-ment could be offset by decreases in weight depending upon the strength of density dependence. This would be expected particularly if simultaneous improvements in food quality or availability do not occur. A fully contextual view of the processes maintaining stream habitats for salmon (e.g., Lake et al. 2007), including factors influencing food and space, will best guide habitat management and restoration under continued land-use and climate change pressures.

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