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[Article]

Modeling Stream Network-Scale Variation in Coho Salmon Overwinter Survival and Smolt Size

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Abstract.—We used multiple regression and hierarchical mixed-effects models to examine spatial patterns of overwinter survival and size at smolting in juvenile coho salmon *Oncorhynchus kisutch* in relation to habitat attributes across an extensive stream network in southwestern Oregon over 3 years. Contributing basin area explained the majority of spatial variation ($R^2 = 0.57$–0.63) in coho salmon overwinter survival (range = 0.02–0.63), with highest survival rates observed in smaller headwater and intermittent streams. Other habitat attributes, including proportional pool area, percent exposed bedrock substrate, percent broadleaf canopy cover, and adult salmon carcass density, were relatively poor predictors of survival. Indices of individual fish condition, including fall parr fork length, condition factor, and parasite infestation rates, were also relatively uninformative in coho salmon overwinter survival models. Coho salmon smolt length was primarily a function of length at the time of fall tagging, but stream type, contributing basin area (positive effect), thermal history (positive effect), and black spot infestation (i.e., trematode metacercariae; negative effect) were also important. The consistent, broad spatial gradients in overwinter survival observed in this study can help guide efforts designed to enhance coho salmon production in coastal streams and suggest that habitat protection, restoration, and enhancement strategies will be best guided by a whole-basin context.

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Populations of Pacific salmon *Oncorhynchus* spp. in the Pacific Northwest spend from several months to several years in freshwater before emigrating to the Pacific Ocean. Habitat conditions within freshwater can strongly influence population dynamics, particularly for species such as coho salmon *O. kisutch* that overwinter in small streams and rivers as juveniles before moving to the ocean as smolts in late winter through spring (Nickelson and Lawson 1998). Declines in population productivity and subsequent listings of multiple stocks of Pacific salmon under the U.S. Endangered Species Act are, in large part, attributed to loss of suitable freshwater habitat and decreased quality of existing habitat associated with human land use activities (NRC 1996).

Recovery plans and restoration actions are underway throughout the Pacific Northwest in response to population declines (e.g., ODFW 2007). The scientific basis for recovery actions in these plans and the ultimate success of the actions rely upon understanding the factors influencing population productivity. Effective targeting and prioritizing of specific restoration actions require knowing how population dynamics of juvenile salmonids are spatially distributed across the landscape.

Comparisons of coho salmon smolt production among drainage basins in the Pacific Northwest have revealed broad patterns of smolt abundance related to stream size, reflecting a general pattern of space limitation in streams (Bradford et al. 1997). Sharma and Hilborn (2001) followed the approach of Bradford et al. (1997) but incorporated additional habitat measures and found that indices of gradient, pool area, and road density were correlated with smolt abundance. However, additional research has shown that within basins, population densities of juvenile salmonids can be spatially heterogeneous at scales of 100–1,000 m. For example, densities of juvenile Atlantic salmon *Salmo salar* may be strongly correlated with spatial patterns of adult spawning (Armstrong 2005), reflecting both biotic (behavior of spawners) and abiotic (distribution of suitable spawning substrate) factors. Network-scale patterns of juvenile Atlantic salmon production illustrate the complementary role of spatially heterogeneous habitats for mobile fish that may exploit different habitats seasonally (Kocik and Ferreri 1998). Similar associations of juvenile Pacific salmon abundance and distribution with habitat conditions are well represented in the literature (Rosenfeld et al. 2000; Pess et al. 2002) and have contributed significantly toward understanding factors potentially influencing freshwater productivity (Reeves et al. 1995; Nickelson and Lawson 1998). Much less is known regarding the spatial structure of juvenile survival because this is more difficult to quantify across entire stream networks than are spatial patterns of abundance or presence–absence (Rosenfeld and Hatfield 2006). Quantifying survival across different habitat conditions within freshwater stream systems may provide additional insight into factors influencing freshwater productivity beyond that provided by surveys of abundance alone.

The size of salmon smolts leaving freshwater habitats also can be an important index of stock productivity. Variation in smolt size within a basin can result from differences in thermal regime and food availability, with larger smolts produced from relatively warm, low-gradient floodplain habitats (e.g., Peterson 1982). Trophic subsidies in the form of terrestrial invertebrate inputs from riparian vegetation (Baxter et al. 2005) or marine-derived nutrients (MDN) associated with the carcasses, eggs, and fry from spawning adult salmon (Wipfli et al. 2003) can also contribute to increased winter growth and smolt size. Parasite loads can negatively affect juvenile salmonid growth and survival (Jacobson et al. 2008) and may be more prevalent in warmer portions of coastal Oregon basins (Cairns et al. 2005). While survival of coho salmon smolts at the time of ocean entry can vary widely among years due to changing biophysical conditions within the marine environment (Briscoe et al. 2005), within-year survival can be positively influenced by smolt size (Holtby et al. 1990). Thus, the degree to which smolt size varies spatially within freshwater systems in response to heterogeneous rearing conditions is an important complement to understanding network-scale variation in survival.

We describe spatial patterns in juvenile coho salmon survival across a 67-km^2 basin over 3 years. We also examine patterns in coho salmon smolt length, as survival may be size dependent both during the overwinter freshwater period (Holtby 1988; Quinn and Peterson 1996) and during migration to and within the ocean environment (Holtby et al. 1990). Our specific objectives were to (1) characterize spatial patterns in overwinter survival and smolt length of coho salmon across years and (2) relate survival and smolt length to abiotic and biotic characteristics of study sites.

Methods

Study area.—The West Fork Smith River is a perennial stream draining a 67-km^2 basin in the Umpqua River drainage 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 broadleaf–conifer species, predominantly red

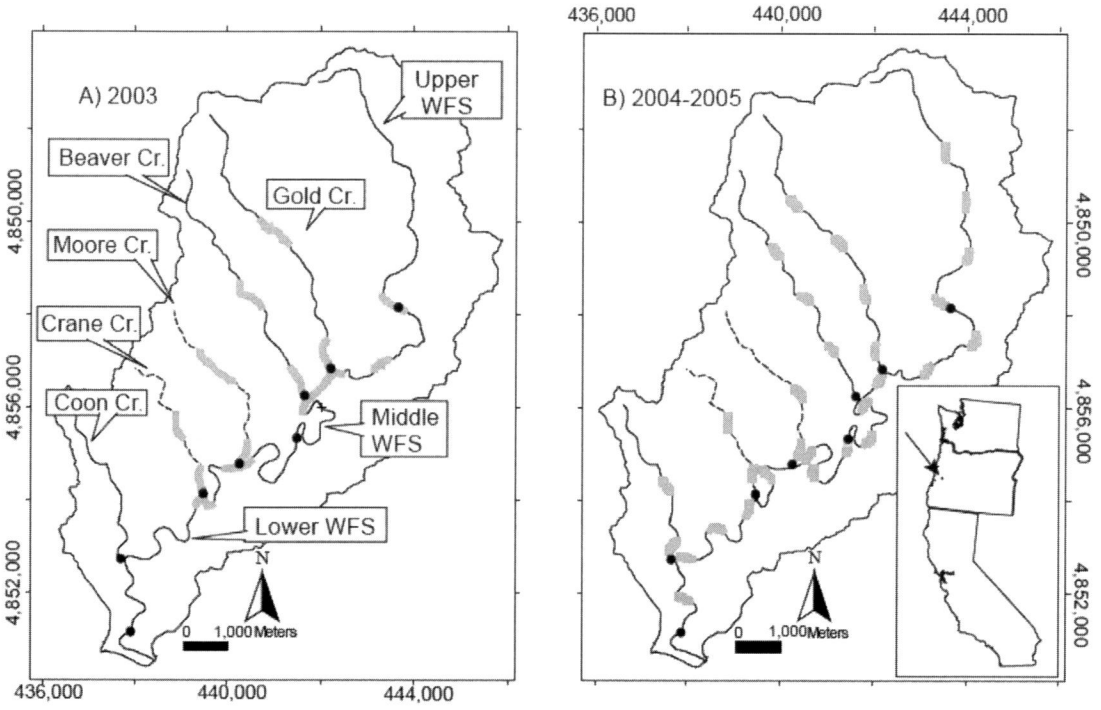

FIGURE 1.—Locations of study reaches (gray-shaded segments) within the West Fork Smith River (WFS), Oregon, in **(A)** 2003 and **(B)** 2004 and 2005. Stream-level sampling points (e.g., chemistry, discharge) are denoted by solid circles. Intermittent streams are denoted by dashed lines. Inset shows general location of study area in western Oregon.

alder *Alnus rubra* and bigleaf maple *Acer macrophyllum*, in the riparian areas. The West Fork Smith River 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 West Fork Smith River basin, similar to other Oregon coastal basins (Reeves et al. 2002). Recent watershed assessments concluded that these activities have reduced instream large wood and altered stream channels, with associated losses of spawning and rearing habitat for salmon (U.S. Department of the Interior, Bureau of Land Management, 1997, unpublished document). Additionally, splash-damming occurred in the West Fork Smith River 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 practice simplified channels in the lower main stem, removing wood and scouring streams down to bedrock. Consequently, splash-dammed portions of the river have relatively little wood and gravel in the stream channel. The U.S. Bureau of Land Management has invested heavily in boulder weir and large wood restoration structures in an attempt to remedy some of these habitat losses (e.g., Roni et al. 2008).

Differences in streamflow within the West Fork Smith River stream network create additional habitat variability (Wigington et al. 2006). Moore Creek, Crane Creek, and smaller streams, including many not shown in Figure 1, become intermittent or dry during late July through September, when streamflows at the gauging station near the mouth of the West Fork Smith River decline to less than 0.03 m^3/s. Highest streamflows occur during November through March, when winter maximum streamflows at the gauging station can exceed 50 m^3/s (Figure 2).

Sampling reaches ($n = 18$) were subjectively chosen in 2003 to encompass major tributary junctions and associated upstream and downstream reaches, in addition to reaches distributed throughout the headwater portions of the main stem and tributaries (Figure 1A). In 2004 and 2005, a systematic sample ($n = 30$) of reaches was taken from throughout the entire stream

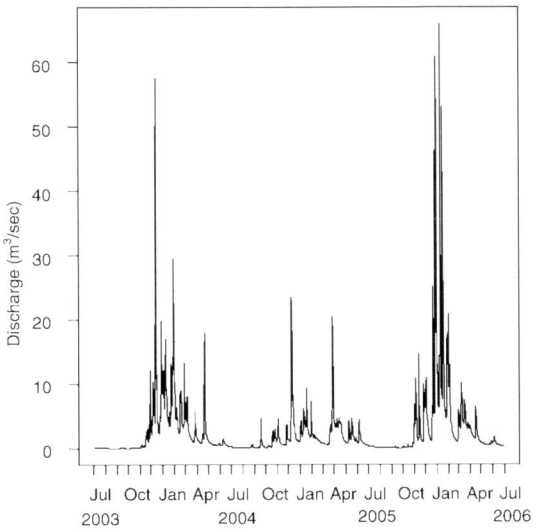

FIGURE 2.—Discharge (m^3/s) for the West Fork Smith River, Oregon, from July 2003 through June 2006.

network accessible to anadromous salmonids to provide a randomized sample of habitat conditions (Figure 1B). Reaches averaged 400 m in length, and contained at least three pool–riffle sequences. Stream widths (bankfull channel dimensions) averaged 10.6 m (range = 4.1–19.3 m) and channel slopes averaged 1.5% (range = 0.2–6.7%). Additional physical characteristics of study sites are provided in Table 1.

Estimating overwinter survival and smolt length.—Juvenile coho salmon were collected for passive integrated transponder (PIT) tagging from each study reach between August 15 and October 31 in 2003, 2004, and 2005. We attempted to tag approximately 400 juvenile coho salmon from each study reach. We collected fish by seining individual habitat units repeatedly until no more fish were captured or until sufficient numbers were captured to meet tagging goals. 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 (BS) infestation (caused by trematode metacercariae not identified to genus; Cairns et al. 2005; Rodnick et al. 2008). Individuals of at least 60 mm FL were implanted with PIT tags, using a 12-gauge hypodermic needle to insert the tag posterior to the tip of the pectoral fin (PTSC 1999). Following tagging, fish were placed in an instream live well and observed for complete recovery before being returned to their habitat unit of origin.

TABLE 1.—Mean (SD) physical characteristics of study sites in intermittent, perennial, and main-stem streams of the West Fork Smith River basin, Oregon.

Characteristic	Intermittent	Perennial	Main stem
Active channel width (m)	6.0 (1.03)	7.8 (2.22)	15.0 (1.90)
Channel slope (%)	1.7 (0.63)	2.3 (1.62)	0.7 (0.30)
Contributing basin area (ha)	373 (81.7)	796 (509.1)	4,466 (1,107.5)
Channel bedrock (%)	15.1 (8.60)	18.1 (16.28)	42.7 (14.78)
Pool area (%)	49.6 (8.43)	41.3 (15.04)	51.5 (21.59)
Basin broadleaf cover (%)	28 (1.5)	16 (5.1)	16 (2.0)

We recaptured PIT-tagged coho salmon at a rotary screw trap near the mouth of the West Fork Smith River from early February through early June in 2004, 2005, and 2006. We attempted to scan every coho salmon smolt captured in the trap for PIT tags, but during periods of high capture rates this was not feasible. During these periods, the proportion of coho salmon smolts that were scanned was recorded but was never less than 95%. Recaptured PIT-tagged coho salmon smolts were measured for length and weight. Trap efficiency was determined by applying a caudal fin clip to a sample of smolts captured in the trap and transporting them 400 m upstream. These fin-clipped individuals were released at dusk using an automated mechanism (Miller et al. 2000). The rate of recapture of fin-clipped smolts was taken as an approximation of trap efficiency and was estimated on a weekly basis. Efficiency of the smolt trap over this period averaged 0.37 (range = 0.34–0.39).

Apparent survival was estimated for each tagged group per reach by dividing the number of PIT-tagged fish recovered at the rotary screw trap by the number tagged in the fall, after correcting for trap efficiency using the weekly efficiency estimate. Because not every coho salmon smolt was scanned for a PIT tag, we estimated the total number of PIT-tagged individuals captured in the smolt trap by dividing the known recaptures by the scan rate. We use the term apparent survival to describe our survival estimates because such estimates are a function of survival and fidelity to the study area (Burnham et al. 1987). Because we were unable to operate the screw trap during the winter high-flow period due to risk of damage from floating debris, we were unable to account for fish that may have emigrated from the basin before early February in each year. We also did not include fish that resided for two winters in freshwater before emigration; these fish represented 0.6% of the total catch of tagged smolts at the smolt trap.

Characterizing habitat conditions.—Stream temperatures were recorded using an array of Onset StowAway TidbiT temperature data loggers (Onset Computer Corporation, Pocasset, Massachusetts) deployed at each of the study reaches for the duration of the study period. This provided a continuous, 30-min-interval record of the ambient water temperature. 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 traceable digital thermistor at three temperatures representing the typical range of field conditions encountered. The accuracy and resolution were approximately ±0.2°C. We estimated the thermal history (T) of each smolt before the date of emigration by calculating cumulative degree-days (above 0°C; Neuheimer and Taggart 2007) experienced by each smolt from January 1 until the date of capture at the smolt trap, based upon temperatures recorded at the reach where each fish was tagged. This estimate assumes each fish remained in the reach of origin (or thermally similar environment) during this period, which is an unlikely scenario for all individuals (Ebersole et al. 2006) but a necessary assumption given the lack of detailed location data for all fish. However, cumulative degree-day estimates for individual fish were much more sensitive to date of emigration than to specific location, due to relatively modest differences in temperature among sites, particularly during late winter and early spring, and substantial increases in temperature through late spring. As a result, by mid-May, the cumulative degree-days from the coldest site attained values equivalent to the cumulative degree-days from the warmest site within 4 d. Thus, our degree-day estimate primarily indexes date of emigration, with a modest correction (within a few days) for presumed location of winter residency.

Aspects of the physical habitat at the reach level were quantified during summer 2003 and 2004 to estimate habitat conditions influencing survival during the onset of winter storm flows for winter 2003–2004 and 2004–2005, respectively. We used physical assessment procedures developed for the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (Kaufmann 2002) to measure channel slope, active channel width, large wood volume, and the percent of streambed surface area composed of exposed bedrock from point measurements. We calculated the percent of reach area classified as pool (PA; after Bisson et al. 1982). Physical habitat data were not collected in 2005 due to budget constraints. Winter streamflows were mild in 2004 (Figure 2), and visual observation and comparison of site photographs indicated that changes in bed forms (locations of gravel bars, individual pools) were relatively minor (J. L. Ebersole, personal observations). Therefore, we assumed that percent pool and percent channel bedrock estimates obtained in 2004 reasonably represented conditions during the onset of winter 2005–2006 storm events.

We measured stream discharge monthly to quarterly at stations distributed among the main stem and tributaries (Figure 1). Basin area was determined for each reach and stream location using standard geographical information systems (GIS) tools (ESRI 1998). Standardized discharge relationships were established between each discharge station and the main flow gauge over a range of streamflows, and the coefficient of this relationship (specific to each stream) was used to weight the basin area estimate for each reach. This provided an index we termed effective basin area (A_E) that accounted for differences in the discharge–area relationships (regression slope coefficient range = 0.71–1.18) among study sites while capturing variation in contributing basin area among sites.

Abundance of adult salmon spawners and salmon carcasses was estimated for each reach by Oregon Department of Fish and Wildlife (ODFW) crews using standardized spawner survey protocols (ODFW 2005). These were conducted at approximately 5–7-d intervals during the late-fall–winter period when adult coho salmon returned to the West Smith Fork River to spawn (generally early November through January). To provide an index of potential benefits to juvenile coho salmon resident in the streams at the time of spawning, we estimated MDN deposition provided by spawning adults (Wipfli et al. 2003). Carcass estimates were converted to estimates of spawner carcass and egg biomass (kg/m^2) deposited within each reach. This was estimated by multiplying carcass survey abundance estimates by the estimated mean weight of adult coho salmon captured at the adult trap on the main-stem West Fork Smith River. Coho salmon spawner weights in grams were estimated from measured FLs in millimeters with the formula derived by Holtby and Healey (1986): $\log_{10}\text{weight} = 3.3183 \cdot (\log_{10}\text{FL}) - 5.843$.

To account for potential trophic benefits to salmonids associated with presence of deciduous riparian canopy cover in both near riparian areas and upland deciduous forest stands (e.g., Wipfli and Gregovich 2002; Wipfli and Musslewhite 2004), we estimated the proportional broadleaf cover for the contributing basin area upstream of each sampling reach using GIS. Land cover within the West Fork Smith River basin was

TABLE 2.—A set of a priori working hypotheses for factors influencing overwinter survival in juvenile coho salmon of the West Fork Smith River basin, Oregon. Direction of hypothesized effect is denoted by + (positive) or − (negative).

Hypothesis	Rationale	Variables
Habitat limiting	Survival is best explained by winter habitat-based smolt capacity[a]	% pool area (+) % bedrock substrate (−)
Habitat, food, flow limiting >	Significant additional explanatory power is gained by also considering discharge[b] (measures of flow "favorability") and trophic opportunities[c]	Effective basin area (−) Carcass biomass density (+) Basin broadleaf canopy cover (+)
Summer conditions limiting	Summer habitat conditions can influence overwinter survival via effects on fish size or condition[d], and parasite load[e] prior to overwintering	% of parr above critical length or condition thresholds (+) % of parr infested with parasites (−)

[a] Quinn and Peterson (1996); Nickelson (1998); Ebersole et al. (2006).
[b] Bell et al. (2001).
[c] Bilby et al. (1998); Piccolo and Wipfli (2002).
[d] Ebersole et al. (2006).
[e] Cairns et al. (2005).

obtained from the Coastal Landscape Analysis and Modeling Study (www.fsl.orst.edu/clams/index.htm, accessed June 2001). This raster vegetation layer integrates field plots, environmental data, and 1996 Landsat thematic mapper imagery (Ohmann and Gregory 2002) to produce forest classes based on land cover (forest, open, and woodlands), forest type (broadleaf, conifer, and mixed broadleaf–conifer), and diameter of trees in conifer and mixed forests (small, medium, large, and very large). To categorize basin area above the sampling point, we checked perimeters using the 10-m-digital elevation model and 1:24,000 hydrology layer and clipped out the vegetation layer using ArcGIS (ESRI 1998). We quantified the percent of broadleaf forest as a proportion of the basin area upstream from each study site.

Statistical analysis.—We developed a set of candidate multiple linear regression models to explain variation in overwinter survival and smolt length for coho salmon. Survival was summarized at the reach scale and related to reach-level biotic and abiotic factors. Models were based upon ecologically reasonable multiple working hypotheses derived from previous studies on overwinter survival and growth of coho salmon in the region (Tables 2, 3). We summarized coho salmon parr length and condition at the reach scale by calculating the percentage of individuals within each reach that exceeded hypothesized critical thresholds of length or condition factor. We used 80 mm as the threshold for fall parr length (% suitable FL, FL_S), based upon previously reported size-dependent overwinter survival of juvenile coho salmon that increased markedly above 80 mm (Ebersole et al. 2006). Physiological condition (e.g., energy content) can also influence overwinter survival in juvenile salmonids (Gardiner and Geddes 1980). We included Fulton's condition factor K, calculated as $[(\text{weight, g}) \times 10^5]/(\text{length, mm})^3$, (Ricker 1975) in our models as an index of physiological condition. Although an imperfect measure of physiological status (Sutton et al. 2000), we found that K was positively associated with sustained swimming performance and blood lipid content in coho salmon parr from the West Fork Smith River (Rodnick et al. 2008). Lacking published relationships of parr K and overwinter survival rates

TABLE 3.—Set of a priori working hypotheses for factors influencing coho salmon smolt length in the West Fork Smith River basin, Oregon. Direction of hypothesized effect is denoted by + (positive) or − (negative).

Hypothesis	Rationale	Variables
Temperature limiting	Growth is primarily a function of overwinter accumulated temperature units[a]	Cumulative temperature units (+)
Food limiting	Significant additional explanatory power is gained by also considering trophic opportunities[b]	Carcass biomass density (+) Basin broadleaf canopy cover (+)
Summer conditions limiting	Summer habitat conditions can influence smolt size via effects on fall (parr) size and parasite infestation[c] prior to overwintering	Fall parr fork length (+) Black spot infestation (−) (presence or absence)

[a] Larsen et al. (2001).
[b] Bilby et al. (1998); Piccolo and Wipfli (2002).
[c] Cairns et al. (2005).

TABLE 4.—Summary of continuous predictor variables retained for inclusion in models of coho salmon overwinter survival and smolt size in the West Fork Smith River basin, Oregon.

Analysis	Variable	Variable code	Mean	Minimum	Maximum
Both survival and smolt size models	Bedrock substrate (%)	BR	27	0	73
	Effective basin area (ha)	A_E	1,856	183	5,726
	Basin broadleaf cover (%)	BC	18	8	31
	Marine-derived nutrients (carcass biomass density, kg/m^2)	MDN	0.37	0.00	1.81
	Pool area (%)	PA	47	12	96
Survival models only	Suitable condition factor K (% > yearly avg. K)	K_S	49	7	98
	Suitable fork length (FL; % > 80 mm)	FL_S	10	1	32
	Black spot infestation rate (%)	BS	34	0	100
Smolt size models only	Fall (parr) FL (mm)	FL	71	59	106
	Cumulative temperature units (°C × d)	T	883	268	1,412

for coho salmon, we used the basin mean K for each year as the threshold value (% suitable condition, K_S).

We eliminated variables that were redundant (Pearson's product-moment correlation coefficient $r > 0.6$) or that exhibited low variation among sites. These included channel slope, sinuosity, active channel width, and large wood volume. We retained the remaining subset of parameters for inclusion in candidate model sets (Table 4). We developed 108 ecologically plausible models for survival, including only those interactions defined a priori. We allowed for year-specific effects by including interactions with year terms. We also included interactions between the fish size and condition metrics (FL_S and K_S) and the primary physical environmental metrics (A_E, percent bedrock [%BR], and PA) to allow for mediating or exacerbating effects of habitat on survival. The survival response variable was arcsine–square-root transformed for regression assumptions. We controlled for multicollinearity by eliminating combinations of continuous predictor variables with variance inflation values greater than 10 (Neter et al. 1989). The set of candidate models included a global model that contained all of the predictors, reflecting the inclusion of all the possible effects.

Models for coho salmon smolt length required a different analytical approach, as our objective was to relate individual fish size to reach-level predictors. Based upon a priori hypotheses gleaned from previous experience and the literature (Table 3), we fit 43 potential models of coho salmon smolt length using two-level mixed-effects models (Wagner et al. 2006) to include covariates for individual coho salmon and reach-level predictors (Table 4). At the individual coho salmon level, we fit a model relating coho salmon smolt length to individual-level predictors (FL at fall tagging, T, and BS infestation). We also allowed for an interaction between FL and T, with the hypothesis that T will be less important for larger coho salmon smolts that may emigrate earlier (February–March) and experience more uniform winter–early spring temperatures before the onset of rapid spring growth in April and May (e.g., Ebersole et al. 2006). Reach-level predictors then were used to explain variation in the intercepts of the individual-level models. There were missing values for size at fall tagging for 64 fish from two reaches in 2004. These values were replaced with the reach mean, as this was determined by simulation studies to be the least sensitive to model selection results and parameter estimates (M. E. Colvin, unpublished data).

Candidate models were completed using an information theoretic approach (Burnham and Anderson 2002). Akaike's information criterion (AIC) was calculated for each model conditional on the data used to construct the model (Burnham and Anderson 2002). We ranked candidate models according to their AIC, and the AIC difference (ΔAIC) was calculated by subtracting each model's AIC value from the maximum AIC value. We calculated Akaike weights (w_i) to estimate the weight of evidence in favor of each model (Burnham and Anderson 2002).

We reduced the candidate model set to a confidence model set by retaining models if the ratio of the candidate model weight to the weight of the top model was 0.1 or greater (Thompson and Lee 2000; Burnham and Anderson 2002). The confidence model set accounts for uncertainty due to model selection and in parameter estimates and is analogous to a confidence interval (CI). A composite model was constructed for survival, but not smolt length (see next paragraph), with parameters contained in the confidence model set. The parameter estimates for predictor variables were weighted by their corresponding w_i and averaged to make a single parameter, and unconditional standard errors were calculated using the methods of Burnham and Anderson (2002). Confidence intervals were calculated for the weighted parameter estimates.

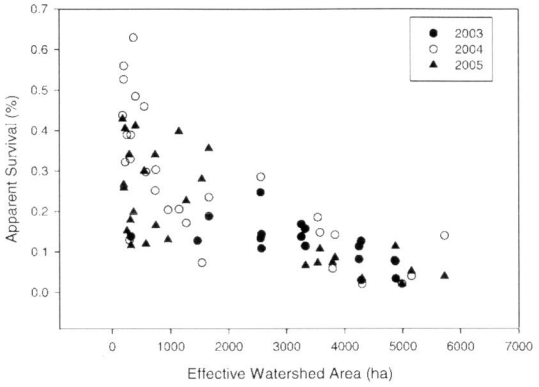

FIGURE 3.—Relationship between apparent survival of passive integrated transponder tagged coho salmon and effective basin area in the West Fork Smith River basin, Oregon, 2003, 2004, and 2005.

Predictor variables were deemed to be interpretable if the CI did not include zero. The relative importance of individual variables was calculated as the sum of the w_i values for the models in which the variables appeared (Burnham and Anderson 2002).

Because it is not appropriate to average estimates of covariates from mixed-effects models, we used a slightly different approach to evaluate predictor variables in the smolt length analysis. We used weighted model predictions to interpret models predicting coho salmon smolt length (Burnham and Anderson 2002). To evaluate the effect of parameter estimates for the mixed-effects model used to evaluate smolt length, we calculated relative importance, as above, but we could not calculate average parameter estimates and CIs. Instead, we calculated the proportion of the candidate model set in which the variable was interpretable (i.e., its CI did not contain zero). In this case, as this number approaches 1, we could be reasonably certain that there was evidence supporting this effect. This measure in concert with relative importance can be used to evaluate the overall importance of the predictors in the mixed-effects models for smolt length and determine whether there was reasonable support for the effects.

We tested confidence model sets by excluding a random subset (15%) of reaches (for survival model building) and smolts (for smolt length model building) from model development data sets. Survival was predicted for the held-out reaches using the model-averaged estimates. Smolt size was estimated using weighted model predictions for all models in the confidence model set. Plots of predicted versus observed data values for the held-out data were used to visually assess the performance of each model set.

Results

Survival

The best approximating model for coho salmon overwinter survival included a negative relationship with A_E that was apparent in all 3 years (Figure 3). Highest survival rates were consistently observed in reaches with a relatively small basin area, but not all small basins exhibited high survival. Variability in survival rates was high among basins with A_E values less than 2,000 ha (Figure 3). Survival rates in the middle and lower main stem ($A_E > 3{,}000$ ha) never exceeded 0.20. Although we had hypothesized that the basin area effect might differ depending upon FL_S or K_S, this was not apparent from the data (e.g., no interpretable length or condition interaction terms). Interactions between effective basin size and other factors (including year effects) were not important in the confidence model set (Table 5).

The parameter estimate for %BR was negative. This is consistent with earlier findings that %BR was inversely associated with juvenile coho salmon overwinter survival in the West Fork Smith River basin (Ebersole et al. 2006), but high uncertainty in this parameter resulted in a 95% CI that contained zero (Table 5). Similarly, FL_S was positively associated with survival, as predicted, but it was included in only 51% of the top models, it had low relative importance (0.64; Table 5), and its parameter estimate had a wide CI that included zero (Table 5). The remaining predictors had very low relative importance (0.27 or less) and had 95% CIs that were centered at approximately zero.

The model performed very well when applied on the hold-out test data set (Figure 4), indicating that the confidence model set is reasonable and explains a high portion of the variance. The confidence model set also appeared to be robust to year-to-year variation, indicating that the year effect is sufficient to explain variation among years, such as variation that could be caused by differences in winter streamflow over the study period (Figure 2).

Smolt Length

Coho salmon smolt length was proportional to fall FL. Model selection results indicate that an increase in 1 mm in the fall FL was proportional to an approximately 1-mm increase in smolt length (Table 6). This indicates no change in the size structure on average for tagged coho salmon that survived the overwinter period. However, there was considerable uncertainty in this estimate, especially for small coho salmon parr, and many coho salmon that were relatively small in the fall emigrated as relatively large smolts (Figure 5). A significant portion of this

TABLE 5.—Weighted parameter estimates and standard errors for multiple models contained in the confidence model set ($n = 29$) for coho salmon overwinter survival in the West Fork Smith River basin, Oregon. Variable codes are defined in Table 4.

Variable	Models	Relative importance	Model-averaged estimate	SE	Lower 95% confidence limit	Upper 95% confidence limit
Intercept	29	1.00	0.59114	0.06814	0.45758	0.72469
A_E	29	1.00	−0.00551	0.00150	−0.00844	−0.00257
Year = 2004	29	1.00	0.06295	0.05265	−0.04024	0.16614
Year = 2005	29	1.00	−0.01515	0.05031	−0.11375	0.08345
BR	24	0.86	−0.00213	0.00126	−0.00460	0.00034
FL_S	15	0.64	0.23916	0.34925	−0.44537	0.92369
PA	13	0.27	0.00009	0.00031	−0.00051	0.00070
K_S	6	0.11	−0.00687	0.01210	−0.03059	0.01685
BS	3	0.10	0.00620	0.00810	−0.00967	0.02207
BC	2	0.04	0.00114	0.01057	−0.01957	0.02185
MDN	2	0.04	0.00017	0.00312	−0.00595	0.00628
$A_E \times FL_S$	4	0.22	−0.00444	0.00448	−0.01323	0.00435
Year = 2004 × FL_S	4	0.12	0.17309	0.20311	−0.22501	0.57119
Year = 2005 × FL_S	4	0.12	0.06137	0.13634	−0.20587	0.32860
BR × FL_S	2	0.10	−0.00119	0.00150	−0.00414	0.00176
BR × K_S	2	0.04	0.00015	0.00019	−0.00022	0.00053
Year = 2004 × BR	1	0.02	0.00005	0.00009	−0.00012	0.00022
Year = 2004 × A_E	1	0.02	−0.00010	0.00012	−0.00034	0.00014
Year = 2005 × BR	1	0.02	0.00010	0.00012	−0.00014	0.00033
Year = 2005 × A_E	1	0.02	−0.00011	0.00013	−0.00036	0.00014
FL_S × PA	1	0.02	−0.00019	0.00032	−0.00081	0.00044
$K_S \times A_E$	1	0.01	0.00001	0.00004	−0.00007	0.00009

variability was explained by adding T to models of smolt length. The size of a smolt was positively related to cumulative temperature units accrued from January 1 to the day of capture at the smolt trap (Table 6). The median parameter estimate for this effect was 0.06 (Table 6), indicating that an increase of 100 cumulative temperature units before capture at the smolt trap conferred a 6-mm increase in smolt length.

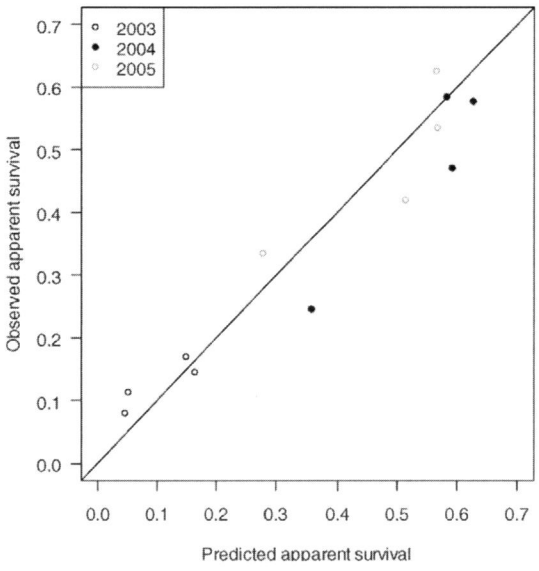

FIGURE 4.—Relationship between predicted and observed coho salmon survival for a set of randomly selected reaches held out for testing of survival models for the West Fork Smith River basin, Oregon.

The relationship between fall FL and smolt length also varied by stream type. Coho salmon smolts from intermittent tributaries were, on average, 4.5 and 7.7 mm longer than smolts originating from perennial streams and the main stem, respectively, given similar fall parr lengths (parameter estimates from Table 6). However, fall coho salmon parr from intermittent sites were significantly smaller than coho salmon parr from perennial sites in 2004 and 2005 and were significantly smaller than parr from main-stem stream sites in 2003 and 2005 (analysis of variance followed by Fisher's least-significant-difference test for pairwise comparisons within years, $P < 0.05$; Table 7). Further, coho salmon smolt length was positively associated with A_E, and smolts in spring were, on average, 7.6 mm longer from main-stem sites and 3.7 mm longer from perennial sites compared with intermittent sites for coho salmon parr tagged in 2004 and 2005 (Table 7). For coho salmon parr tagged in 2003, smolt lengths were not significantly different between intermittent and main-stem sites but were, on average, 3.6 mm shorter from perennial stream sites (Table 7).

We observed a small effect of BS infestation (presence or absence) on smolt length. The median parameter estimate was −1.13 (Table 6), indicating that infested coho salmon smolts were approximately 1 mm smaller than uninfested smolts. This relationship was consistently interpretable (the 95% CI did not include zero) for all 11 models in the confidence model set.

The confidence model set effectively predicted FL for randomly selected smolts (Figure 6), although the fit varied by year ($R^2 = 0.56$, 0.74, and 0.73 for 2003,

TABLE 6.—Parameter summary for coho salmon smolt length analysis for the confidence model set. Variable codes are defined in Table 4.

Variable	Number of models	Relative importance	Median parameter estimate	Proportion interpretable
Intercept	11	1.00	13.0360	1
A_E	11	1.00	0.3083	1
T	11	1.00	0.0604	1
Stream type = main stem	11	1.00	−7.6749	1
Stream type = perennial	11	1.00	−4.5437	1
Black spot = present	11	1.00	−1.1359	1
FL	11	1.00	0.9743	1
FL × T	11	1.00	−0.0005	1
Tag year = 2004	11	1.00	0.1383	0
Tag year = 2005	11	1.00	−0.7072	0
BR	4	0.25	0.0161	0
MDN	4	0.24	0.7426	0
BC	4	0.23	0.7026	0
PA	4	0.23	−0.0011	0

2004, and 2005, respectively). Small coho salmon smolts (<100 mm FL) were overpredicted in 2004 and 2005 and larger smolts (>105 mm FL) were underpredicted in 2004.

Discussion

Overwinter Survival

High winter streamflows and associated displacement, injury, or exhaustion of juvenile coho salmon and other salmonids are thought to be a major cause of mortality in Oregon coastal streams (Bilby and Bisson 1987; Lawson et al. 2004), but this effect can be moderated by complex habitats that provide structural refuges or off-channel alcoves and beaver ponds (Nickelson et al. 1992a; Bell et al. 2001). We had anticipated that patterns of overwinter survival within a coastal Oregon basin would be, at least in part, explained by variation in physical habitat conditions. We found little evidence of relationships of survival with measures of channel substrate composition or PA. Indices of site nutrient or trophic status (carcass biomass density, percent broadleaf cover) also provided little insight into patterns of survival. Instead, much of the variation in overwinter survival was associated with A_E, and patterns of survival within the West Fork Smith River primarily reflected an upstream gradient of increasing survival probability that was consistent across years.

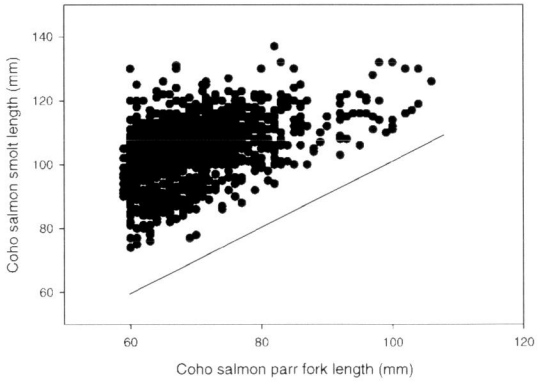

FIGURE 5.—Relationship between coho salmon smolt fork length and parr fork length at the time of fall tagging in the West Fork Smith River basin, Oregon. Line denotes domain of zero net growth.

Our a priori rationale for including the A_E metric was to incorporate a measure of winter discharge and to capture the hypothesized effect of high winter streamflows. Surprisingly, while overall survival rates were slightly higher in 2004, a strong relationship with A_E was still apparent (Figure 3) despite relatively modest winter streamflows during that year (Figure 2). This strong consistent relationship may reflect the overwhelming influence of winter discharge in the West Fork Smith River, which may be particularly sensitive to streamflow effects given the legacy of splash-damming and other basin modifications that have simplified the habitats in the basin, particularly in the lower main stem (Ebersole et al. 2006). Evidence from generalized trends of juvenile salmonid habitat suitability along longitudinal gradients of stream discharge suggests that suitability declines downstream with predictable increases in velocity and depth, barring local heterogeneity in channel form and structure (e.g., off-channel habitat and flow refugia; Rosenfeld et al. 2007). Similarly, spatial peaks in optimal habitat for stream salmonids are likely to shift upstream with increases in discharge (Rosenfeld et al. 2007). Lacking off-channel low-velocity habitats or other flow refugia (K. Jones, ODFW, unpublished data), our downstream study sites that contain low to modest densities of coho salmon parr in the summer months may contain very little suitable habitat for juvenile coho salmon during

TABLE 7.—Mean (SD) juvenile coho salmon survival, length, condition factor K, and marine-derived nutrient availability (spawner and egg biomass) from intermittent (Int), perennial (Per), and main-stem (MS) sites in the West Fork Smith River basin, Oregon, for fish tagged in 2003, 2004, and 2005. Within-year fall fork length (FL) and smolt FL comparisons sharing a common letter are not significantly different ($P > 0.05$).

	2003			2004		
Variable	Int	Per	MS	Int	Per	MS
Apparent survival	0.21 (0.07)	0.25 (0.09)	0.14 (0.04)	0.41 (0.09)	0.38 (0.15)	0.14 (0.08)
Fall parr FL (mm)	69.4 z (5.8)	71.3 zy (8.5)	71.1 y (7.3)	67.6 z (7.2)	70.2 y (8.4)	68.3 z (5.9)
Smolt FL (mm)	107.7 y (9.8)	104.9 z (8.4)	109.4 y (8.4)	100.3 z (10.9)	103.8 y (10.3)	109.3 x (8.8)
Black spot infestation rate	0.01 (0.01)	0.14 (0.27)	0.59 (0.38)	0.00 (0.00)	0.21 (0.31)	0.72 (0.29)
Fall parr FL > 80 mm	0.05 (0.02)	0.09 (0.04)	0.07 (0.04)	0.07 (0.04)	0.07 (0.06)	0.04 (0.02)
Fall parr K > median K	0.13 (0.05)	0.36 (0.08)	0.60 (0.08)	0.55 (0.29)	0.41 (0.26)	0.56 (0.28)
Spawner and egg biomass (kg/m^2)	0.60 (0.48)	0.58 (0.23)	0.29 (0.16)	0.13 (0.06)	0.21 (0.17)	0.10 (0.08)

winter peak streamflows, contributing to low survival rates observed there.

In bedrock-dominated channels, interstitial cover provided by coarse substrates or complex bedforms may be lacking, and high winter streamflows in these larger channels may restrict suitable winter rearing areas for salmonids to channel margins and tributaries (Hartman 1965). In previous research in this basin, the proportion of bedrock in the stream channel was negatively associated with overwinter survival during a single year (Ebersole et al. 2006). In this study, which encompassed multiple years and a more spatially extensive sample of the basin, bedrock was important but not consistently interpretable in survival models, indicating that an effect may have been present but could not be reliably detected from these data.

Pool availability, indexed by percent PA in our study, may similarly reflect channel geomorphic complexity and availability of potential refuges from varying winter streamflows (Nickelson et al. 1992b; Bell et al. 2001) and has been positively associated with coho salmon smolt production elsewhere (Sharma and Hilborn 2001). In this study, PA was not associated with survival of coho salmon parr, indicating that in this basin PA alone was a poor predictor of survival. The failure of this metric to explain variation in survival may also be in part due to the relatively simple channel morphology of the lower main-stem West Fork Smith River.

As noted previously (Ebersole et al. 2006), large wood is relatively uncommon in the West Fork Smith River, and where wood is present it is relatively ineffective at trapping sediment or altering channel bedforms. This is particularly true in the main stem due to high winter streamflow energy and a predominantly bedrock-dominated channel. We did not include measures of wood availability as a candidate factor for this reason, although we note that numerous researchers have found wood availability to be a good predictor of overwinter distribution (Harvey 1998), abundance (Roni and Quinn 2001), and survival (Quinn and Peterson 1996; Solazzi et al. 2000) of juvenile salmonids elsewhere. The absence of large wood is probably an artifact of past land use history, especially splash-damming, exacerbated by the high-energy winter streamflows that typify streams in the region. Thus, our results may not represent other stream settings where large wood is more common.

We found little support for our hypothesis that summer conditions significantly influenced overwinter survival of coho salmon parr. The proportion of coho salmon above a critical length (FL_S) or K (K_S) before overwintering had low relative "importance" in the confidence model set and CIs that included zero, contrary to our expectations. Hurst (2007) in a recent review proposed that refined predictions of fall size effects on winter mortality in fish will require a better understanding of mechanisms that can be highly variable in space and time. Researchers have found mixed results when analyzing the influence of size in fall on overwinter survival of juvenile salmonids, and results appear to be dependent upon winter severity. In two independent studies, overwinter survival of juvenile coho salmon (Quinn and Peterson 1996) and cutthroat trout *Oncorhynchus clarkii* (Boss and Richardson 2002) was not clearly size dependent during relatively mild winters, but size-dependent mortality was detected during years of more severe winter conditions (Quinn and Peterson 1996).

We had assumed an absolute size dependence in overwinter survival, based upon previous analyses (Ebersole et al. 2006), but if relative size (sensu Zabel and Achord 2004) was more important, due to competition or other density-dependent winter mortality mechanisms, our absolute size metrics (FL_S and K_S) might fail to capture important aspects of juvenile size that could be driving mortality. Additionally, fall size may be a poor predictor of overwinter survival where significant opportunities for winter growth occur (Hurst 2007), particularly when growth potential is spatially

TABLE 7.—Extended.

Variable	2005		
	Int	Per	MS
Apparent survival	0.20 (0.06)	0.28 (0.11)	0.07 (0.04)
Fall parr FL (mm)	69.2 z (6.9)	71.8 y (9.6)	72.7 y (7.2)
Smolt FL (mm)	102.3 z (11.4)	106.2 y (9.4)	108.5 x (8.3)
Black spot infestation rate	0.00 (0.00)	0.15 (0.33)	0.69 (0.35)
Fall parr FL > 80 mm	0.05 (0.03)	0.12 (0.10)	0.13 (0.08)
Fall parr K > median K	0.54 (0.26)	0.49 (0.22)	0.60 (0.26)
Spawner and egg biomass (kg/m^2)	0.31 (0.08)	0.37 (0.22)	0.12 (0.16)

variable (e.g., Ebersole et al. 2006). While basinwide correlations of fall size to smolt length were evident, this relationship was quite variable (e.g., Figure 5), indicating significant individual variability in winter growth rates. As observed previously (Ebersole et al. 2006; Wigington et al. 2006), high growth rates of coho salmon parr overwintering in intermittent streams allowed relatively small parr to "catch up" in growth and emigrate at a larger size than would be predicted solely based upon fall size. Additionally, our measure of fish physiological status, K, can often be an imperfect index of energy status (Sutton et al. 2000). While K has been positively associated with swimming performance and blood lipid content in coho salmon parr during the summer in the West Fork Smith River (Rodnick et al. 2008), this relationship has not been examined for overwintering coho salmon juveniles.

We observed no detectable effect of BS infestation on overwinter survival, contrary to our expectations. Reaches with high infestation rates were generally located lower in the basin in the main-stem West Fork Smith River, where summer water temperatures were higher; this is consistent with observations by Cairns et al. (2005). These reaches also tended to have lower overwinter survival rates, but our model selection results indicate that this pattern of survival was most adequately described by the reach-scale predictor A_E.

As an observational study across wide gradients in habitat conditions, this study was challenged by correlated gradients in streamflow (as indexed by A_E), channel width, channel depth, velocity, and channel slope. These are aspects of basin and channel geometry that together can be viewed as providing a template for stream salmonid habitat (Rosenfeld et al. 2007). These features were probably correlated with other habitat attributes that we did not measure. For this reason, we emphasize that these results are associative and probably reflect the response of coho salmon parr survival to a suite of environmental and biotic factors that covary from headwaters to downstream reaches. This covariation was best captured by the single metric A_E, indicating that among our study sites A_E was an effective predictor of coho salmon parr overwinter survival.

Smolt Length

We had hypothesized that coho salmon smolt length would be a function of a combination of accumulated thermal units, trophic opportunities, and effects of

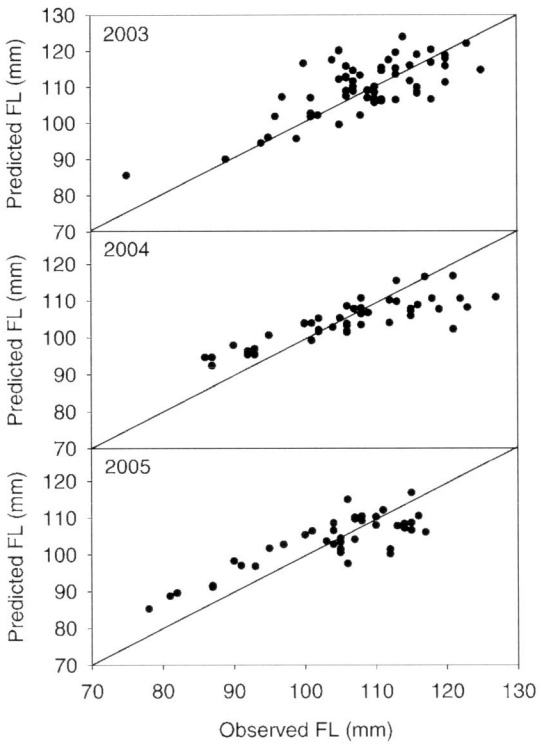

FIGURE 6.—Model test of randomly selected data points held out from development of the coho salmon smolt fork length (FL) confidence model set. The line represents a 1:1 relationship between observed and predicted FL.

previous summer conditions. Our modeling results provide evidence supporting thermal and summer condition effects, but we found no evidence to support a trophic benefit associated with spawner biomass density or basin broadleaf canopy cover.

Numerous researchers have documented enhanced overwinter growth of juvenile salmonids in streams associated with inputs of salmon-derived nutrients and food resources (Bilby et al. 1998; Lang et al. 2006), while others have found little or no evidence of growth effects (Wilzbach et al. 2005; Shaff 2006). Presumably, effects of salmon-derived input on juvenile salmonid growth can vary depending on local density effects and on degree, type, and timing of inputs in relation to local food web dynamics (Compton et al. 2006). Our failure to detect a significant reach-level effect of MDN availability on smolt size may indicate that MDN biomass availability is insufficient under current salmon returns. However, we observed MDN biomass loadings averaging 0.37 kg/m^2 and ranging up to 1.18 kg/m^2. We expected that these loading values would be sufficient to detect an effect of MDN, given that Bilby et al. (2001) found that carcass biomass loading levels of 0.15 kg/m^2 were sufficient to detect MDN uptake in western Washington streams. Ongoing stable isotope analysis of coho salmon parr and smolt tissue from our study sites reveals significant individual variation in MDN signatures, with some fish showing significant enrichment (M. Robbins Church, unpublished data). Uptake of MDN is not associated with increased size or K among these fish, however, suggesting that other factors more strongly influence fish size within and among our sites.

Smolt length was strongly influenced by length at the time of fall tagging, although there was significant scatter in this relationship, particularly for small fish, suggesting substantial variation in individual growth rate. Additional variation in smolt length was explained by stream type. We found that smolt length was higher than would be predicted based on fall length alone for intermittent streams relative to perennial and main-stem sites. In previous research, we observed elevated growth rates for coho salmon overwintering in intermittent streams (Ebersole et al. 2006). In the West Fork Smith River, intermittent streams are also heavily used by adult coho salmon for spawning, which is hypothesized as an additional trophic resource for juvenile salmonids (Wigington et al. 2006). However, as previously noted, we did not observe a significant MDN effect at the reach scale on smolt length in this study. Rather, stream type (a stream-scale factor) better explained variation in smolt length, suggesting that some other unmeasured attribute responsible for differences in growth rate may differ between stream types.

Smolt length was also a function of accumulated thermal units. The period from March through June is a period of rapid growth among coho salmon juveniles in the West Fork Smith River (Ebersole et al. 2006), coincident with rapid increases in water temperature that encompass the optimal temperatures for coho salmon growth (12–17°C; Everson 1973). This is also a period of high annual macroinvertebrate production, emergence, and drift in Oregon Coast Range streams, allowing substantial growth for stream fishes (Robillard 2006).

Locations lower in the basin (higher A_E) tended to produce larger smolts. Bradford et al. (1997) found a similar pattern in a regional review of coho salmon smolt production. They hypothesized that larger smolt size might be attributed to higher water temperatures, longer growing seasons, and more productive off-channel habitats in lower-gradient downstream river reaches. Off-channel habitats are very rare in the lower reaches of the West Fork Smith River, so use of floodplain ponds and wetlands adjacent to the main stem is an unlikely contributor in our system. Small tributaries are available, however, and immigration of main-stem fish into intermittent tributaries during the winter months could be an alternative tactic for some fish in the lower main stem and probably contributes to growth of coho salmon parr originally tagged in the main stem (Ebersole et al. 2006). Low survival rates observed in the lower main stem also mean that winter densities in the lower main stem are probably quite low, thereby reducing the likelihood of density-dependent effects on winter growth (Roni and Quinn 2001) and enhancing growth potential for the remaining survivors.

Infestation by BS was associated with a slight (1-mm) decrease in smolt length. This effect probably reflects the influence of conditions during the preceding summer, when BS infestation occurs during warming temperatures and peaks at temperatures exceeding 18°C (Cairns et al. 2005). The biological significance of this effect on postsmolt survival is unknown. Given that we detected no deleterious effect of BS infestation on overwinter survival, it is possible that this parasite's effects are relatively benign. However, given the slight effect we observed on smolt size and given the difficulty of detecting deleterious effects of parasites on fish using observational studies such as ours (Bakke and Harris 1998), it is premature to conclude absence of an effect. Ongoing research by fish pathologists (Rodnick et al. 2008) has shown that BS is just one of several parasites prevalent among juvenile coho salmon in our study sites. Accurately

assessing parasite effects on fish health and performance probably will require controlled experimental tests.

Caveats

It is important to emphasize that we modeled survival, not production, in this analysis. As a result, the effect of density on observed patterns of survival was not explicitly modeled. As noted previously in this discussion, the availability of such suitable winter rearing habitat is believed to be limiting in many coastal Oregon basins, such that limited habitat capacity effectively constrains survival, which may often be density dependent (Nickelson 1998). We were unable to obtain robust estimates of winter coho salmon densities in the West Fork Smith River, but in related research we have estimated summer densities across the study area over this same time period and found that density was inversely associated with basin area (J.L.E., unpublished data). If summer densities are reflective of winter densities, then this pattern would reinforce the importance of smaller basins in supporting overall production of coho salmon smolts in the West Fork Smith River. Incorporation of winter density estimates and reach-specific estimates of smolt production would be a valuable contribution to future research and could help refine estimates of habitat effects that were not interpretable in this analysis.

Our reliance on PIT tags to assess overwinter survival introduces a potential bias. We were unable to tag coho salmon parr less than 60 mm FL, and thus our estimates of survival can only be applied to fish above this size. The proportion of coho salmon parr less than 60 mm FL within each sampling reach at the time of PIT tagging ranged from 5% (lower main stem) to 34% (upper Crane Creek). Given the size-dependent survival observed in previous studies in this basin (Ebersole et al. 2006), it is likely that survival estimates are biased upwards, particularly for reaches with a high proportion of small coho salmon parr. We are unable to account for this potential bias and stress that our survival estimates are for coho salmon parr greater than 60 mm FL only.

We have no data on emigration of coho salmon out of the basin before the installation of the rotary smolt trap in early February of each year. The majority of coho salmon smolts in the Oregon coastal region appear to emigrate during the months of April and May (Jepsen et al. 2006) as is typical throughout the range of the species (Sandercock 1991). However, fall downstream movement of juvenile coho salmon has been observed in nearby basins and has been hypothesized to be a result of fish displacement from shrinking habitats upstream (Rodgers et al. 1987) or juveniles that are actively redistributing to lower-gradient overwintering habitats (Miller and Sadro 2003). Based on limited winter trapping, smolt emigration before early February is believed to be a very small component of the total emigration (B. A. Miller, personal observation). In our analysis, coho salmon that may have emigrated before the installation of the rotary smolt trap in late winter are treated as mortalities.

Implications

Management objectives for Oregon coastal coho salmon populations include restoration of self-sustaining populations capable of resilience in the face of environmental change (ODFW 2007). This will require freshwater conditions that allow survival during high-streamflow winter storm events, as well as the production of large, energetically robust smolts capable of surviving early ocean-rearing conditions during unfavorable years. In the West Fork Smith River, intermittent and perennial headwater portions of the stream network, where both summer densities and overwinter survival rates are high, make up approximately 69% of the total stream length and 45% of the total stream summer base flow area (J.L.E., unpublished data). These streams may be particularly important in supporting coho salmon smolt production from the basin. Intermittent streams in particular may be especially important for providing productive growth and rearing habitats for coho salmon parr that would otherwise suffer size disadvantages (see also Wigington et al. 2006).

Current habitat conditions in the main-stem West Fork Smith River, which is characterized by exposed bedrock channels with low habitat complexity, appear to limit coho salmon production to a few (but large) smolts. Improved overwinter survival in the main-stem West Fork Smith River could provide substantial benefits to coho salmon populations, although the challenges are substantial and costs are high due to the legacy of past management. Freshwater habitat protection and restoration efforts among main-stem, tributary, and headwater locations in the West Fork Smith River and in similar basins of the Oregon Coast Range will be best allocated based upon understanding of spatial patterns of survival and smolt production, such as provided by this study.

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