

Juvenile Coho Salmon Growth and Survival across Stream Network Seasonal Habitats

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Abstract.—Understanding watershed-scale variation in juvenile salmonid survival and growth can provide insights into factors influencing demographics and can help target restoration and mitigation efforts for imperiled fish populations. We assessed growth, movement, and apparent overwinter survival of individually tagged juvenile coho salmon *Oncorhynchus kisutch* in a coastal Oregon watershed from June 2002 to June 2003 and related growth and survival parameters to stream characteristics. Fall body size of juvenile coho salmon was a good predictor of smolt size and survival, but smolt size was also influenced by overwintering location. This was due to strong spatial patterns in winter growth rates associated with residency and movement into a small intermittent tributary. Though nearly dry in midsummer, this stream supported high densities of spawning coho salmon in the fall, and juveniles rearing there exhibited relatively high growth rates and emigrated as larger smolts. Improved winter growth and survival of juvenile coho salmon utilizing tributary habitats underscore the importance of maintaining connectivity between seasonal habitats and providing a diversity of sheltering and foraging opportunities, particularly where main-stem habitats have been simplified by human land uses.

Individual variability and behavioral flexibility in foraging tactics, movement, and habitat use are common traits among stream salmonids (Grant and Noakes 1987; Nielsen 1992; Bradford and Taylor 1997; Nislow et al. 1998; Bujold et al. 2004). This flexibility can be advantageous for fish in heterogeneous habitats and can allow multiple strategies for successful growth during critical periods (Dill 1983). Growth is influenced by a wide array of factors and serves as a sensitive indicator of environmental quality (Busacker et al. 1990). In heterogeneous stream

environments, spatial variability in temperature, food availability, and fish density can produce high variability in growth rates among individuals within a cohort (Gibson 2002).

Accelerated growth can foster increased survival for juvenile fish. Larger size may confer an advantage for surviving the physical action of disturbances such as flooding (Pearsons et al. 1992; Bell et al. 2001) and for competing for limited resources such as food or refuge space (Allee 1981; Fausch and White 1986; Hughes 1998). For juvenile coho salmon *Oncorhynchus kisutch* in Pacific Northwest coastal streams, high streamflows associated with winter storms are believed to be a primary factor limiting overwinter survival, having strong effects on smolt production (Nickelson and

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Received June 1, 2005; accepted July 11, 2006
Published online November 20, 2006

Lawson 1998). Quinn and Peterson (1996) found that overwinter survival of juvenile coho salmon was size dependent; larger individuals at the end of summer were more likely to survive to smolt the following spring. The survival advantage of larger fish may be attributable to their greater ability to resist displacement from refuge habitats during floods (Pearsons et al. 1992) or to behavioral exclusion of smaller individuals from refuge habitats via formation of residency hierarchies (Armstrong and Griffiths 2001).

The influence of body size on fitness may be linked across life stages. For example, Hi and Steward (2002) found that early growth rate can strongly influence subsequent life history. Hoar (1976) observed that juvenile anadromous salmonids failing to meet a threshold size may fail to successfully smolt the following spring. Early ocean survival of coho salmon may be size dependent, especially during years of poor ocean feeding conditions (Holtby et al. 1990). Thus, body size may be important throughout the early life history of coho salmon and may reflect processes regulating production throughout the summer, winter, and smolt emigration periods.

Understanding variation in size and growth rate and subsequent effects on survival at the watershed scale is particularly valuable for at-risk species that require accurate and efficient allocation of restoration actions (Lawler and Schumaker 2004). Because the success and fitness of individuals is the ultimate index of habitat quality (Winker et al. 1995), understanding spatial variation in body size may provide glimpses into habitat quality for fish. Furthermore, quantifying individual growth rates and movement patterns may illuminate the various strategies used by fish to optimize fitness in a variable environment (Kocik and Ferreri 1998).

Understanding the ecology of free-ranging fish has benefited tremendously from recent advances in fish tagging and detection technology, particularly passive integrated transponder (PIT) tags that enable refined estimates of survival, movement, and growth of large numbers of stream fishes over relatively large study areas (Zydlewski et al. 2001; Gibbons and Andrews 2004). Here, we report seasonal growth, movement, and survival of individually tagged juvenile coho salmon in a coastal Oregon stream. The objectives of this study were to (1) determine relative abundance and overwinter residency of individually tagged juvenile coho salmon within study locations, including extent of movement between main-stem and tributary habitats, (2) characterize spatial variation in juvenile coho salmon seasonal growth and overwinter survival, (3) relate variation in survival to environmental attributes of the stream network, (4) compare growth rates and

coho salmon smolt sizes to winter movement or residency patterns, and (5) identify the relative contribution of fall size of juvenile coho salmon to smolt size and overwinter survival.

Methods

Study area.—The West Fork Smith River is a perennial stream draining a 69-km² watershed in the Umpqua River basin of the Oregon Coast Range (Figure 1). Watershed vegetation consists of relatively young, multiaged forest dominated by Douglas fir *Pseudotsuga menziesii*, with mixed broadleaf-conifer species in the riparian areas, including red alder *Alnus rubra* and bigleaf maple *Acer macrophyllum*. The West Fork Smith River has an elevation range from 60 to 850 m and is underlain by Tyee sandstone bedrock. Precipitation occurs predominately as rain during the late fall through spring. Surface streamflow may cease in parts of the stream network during the summer dry season.

The West Fork Smith River has been subject to intensive forest harvest and road building activities similar to those of other Oregon coastal basins (Reeves et al. 2002). These activities have resulted in reductions in instream large wood, alterations to stream channels, and associated losses of spawning and rearing habitat for salmon (U.S. Bureau of Land Management, Coos Bay District Office, North Bend, Oregon, unpublished). Additionally, splash damming occurred in the West Fork Smith River during the late 1800s through the early 1900s. This 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 resulted in channel simplification in the lower main stem through loss of wood and streambed scouring to bedrock. Consequently, this portion of the river has relatively little wood and gravel in the stream channel. The Bureau of Land Management has invested heavily in boulder weir and large wood restoration structures to remedy some of these habitat losses.

Additional habitat variability occurs among the West Fork Smith River tributaries because of differences in streamflow. Moore, Crane, and Coon creeks have very low flows during summer months. Surface flow at the tributary mouth ceased at Moore and Crane creeks during the summer of 2002. Beaver Creek, Gold Creek, Church Creek, Tributary 1, and the upper West Fork all maintained flows during summer months. Each of the primary tributaries flows through a culvert near its confluence with the main-stem West Fork Smith River. Historically, some of these culverts were believed to be at least partial barriers to fish movement. Each culvert

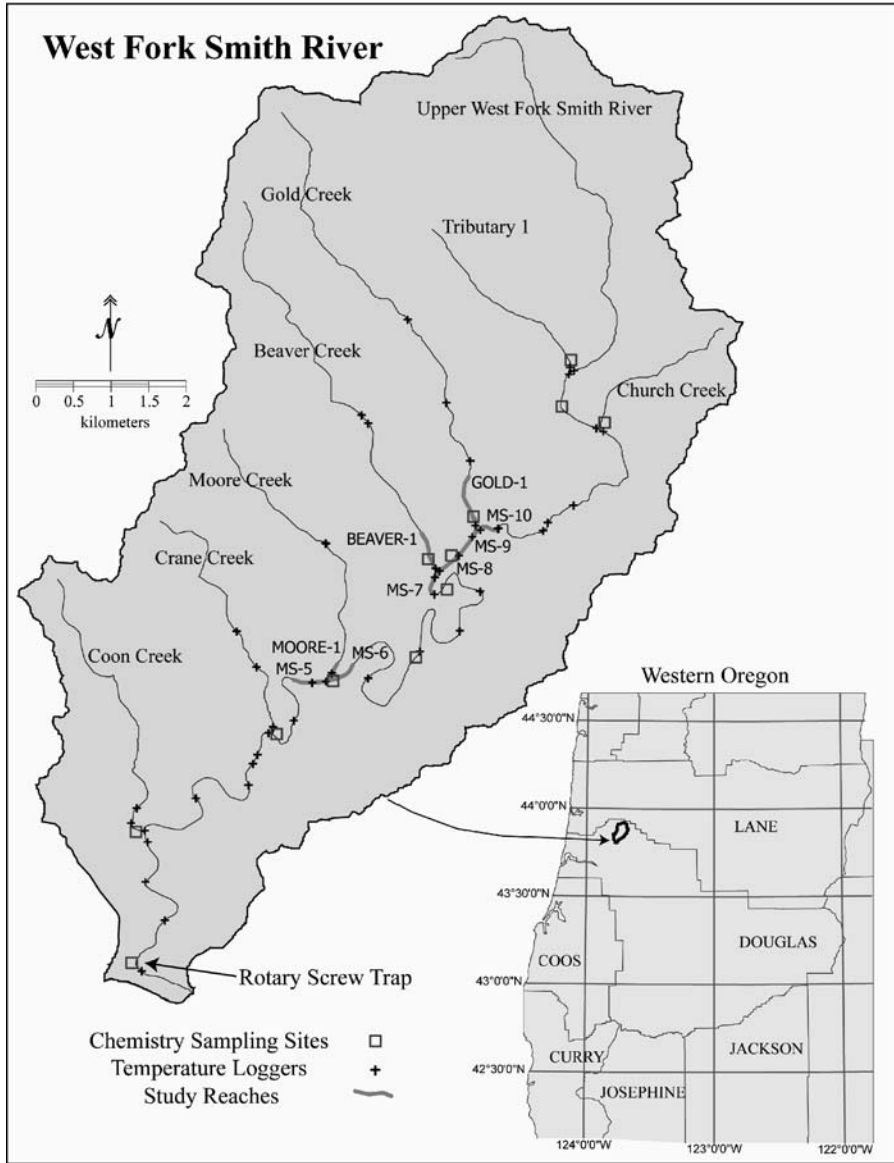


FIGURE 1.—Map of the West Fork Smith River basin, Oregon, showing locations of study reaches, temperature loggers, and water chemistry sampling locations.

has been resized and replaced within the past 20 years such that movement of juvenile and adult fish between the main stem and each tributary is believed to be uninhibited by current culverts (Pat Olmstead, Bureau of Land Management, Coos Bay District, personal communication).

In the main stem, summer and early autumn mean monthly streamflow ranged from 0.31 m³/s in June to 0.04 m³/s in October 2002. Winter (December 2002–March 2003) mean monthly streamflow ranged from

7.90 to 4.08 m³/s, and there were three major events of peak daily streamflow greater than 35 m³/s.

Fish species present in this basin include coho salmon; a small introduced run of fall Chinook salmon *O. tshawytscha*; winter steelhead *O. mykiss*; both sea-run and resident cutthroat trout *O. clarkii*; sculpins *Cottus* spp.; speckled dace *Rhinichthys osculus*; Umpqua dace *R. evermanni*; reidside shiner *Richardsonius balteatus*; largescale sucker *Catostomus macrocheilus*; Umpqua pikeminnow *Ptychocheilus umpqua*;

western brook lamprey *Lampetra richardsoni*; and Pacific lamprey *L. tridentata*. The West Fork Smith River is one of seven monitoring basins maintained by the Oregon Department of Fish and Wildlife (ODFW) for which the agency has annually estimated numbers of adult coho salmon and steelhead spawners and eggs deposited, and numbers of out-migrating coho salmon, steelhead, and cutthroat trout smolts since 1998 (Solazzi et al. 2003). Hatchery-produced coho salmon and steelhead occasionally stray into the basin but represent less than 1% of the spawning population.

Stream habitat characterization.—We surveyed habitat in the West Fork Smith River including Coon, Crane, Moore, Beaver, and Gold creeks (47-km total stream length) in June–July 2002. Individual habitat units ($N = 3,756$) were classified by type (Bisson et al. 1982), numbered, and measured for surface area and maximum depth. Individually labeled aluminum tags were placed at approximately 50-m intervals along the length of the stream network to provide reference locations for subsequent fish marking and relocation data.

We selected tributary–main-stem confluence areas at Gold, Beaver, and Moore creeks (Figure 1) for intensive fish marking and habitat characterization. Each confluence was subdivided into a main-stem reach below the tributary junction, a main-stem reach above the tributary junction, and a reach in the tributary immediately above the junction. Reaches ranged from 364 to 813 m in length.

We characterized each reach for channel dimensions, substrate, riparian vegetation, and bank cover using physical assessment procedures developed for the U.S. Environmental Protection Agency's (USEPA) Environmental Monitoring and Assessment Program (see Kaufmann 2002 for details). This procedure was structured to provide rapid but quantifiable information on stream geometry and bank and riparian conditions gathered via longitudinal thalweg profiles and systematically spaced channel transects. Pool spacing, a commonly used metric to evaluate channel morphology (Montgomery et al. 1995), was calculated by dividing the reach length by both the number of pools and the average channel width (after Quinn and Peterson 1996).

Temperature and stream water chemistry.—Stream temperatures were recorded using an array of Onset StowAway Tidbit temperature data loggers (Onset Computing, Pocasset, Massachusetts) deployed at 43 locations in the West Fork Smith River stream network beginning in June 2002 (Figure 1), including each of the intensive study reaches, to obtain a continuous, 30-min interval record of the ambient water temperature regime. Duplicate loggers were placed at approximate-

ly 20% of the sites for quality assurance purposes. Prior to 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 $\pm 0.2^\circ\text{C}$. Temperatures at each location were summarized as the highest 7-d running average maximum stream temperature (maximum weekly maximum temperature [MWMT]); this metric is used by Oregon Department of Environmental Quality to establish state water quality standards (Sturdevant 1998).

Water chemistry is a potentially important but neglected aspect of "habitat" for stream fishes since stream nutrient levels have been shown to influence stream productivity in some areas of the Pacific Northwest (Perrin et al. 1987; Slaney et al. 2003). We collected water chemistry samples monthly at stations distributed among the main stem and tributaries (Figure 1). To determine total dissolved nitrogen 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). We summarized nonflow weighted total N and P as mean concentration values during the wet season (November 2002–May 2003) for total dissolved nitrogen and SRP to capture high rates of nitrogen flushing during winter storm events.

Abundance of adult salmon spawners and salmon carcasses was estimated for each reach by ODFW crews using standardized spawner survey protocols (ODFW 2005). To furnish an index of potential benefits associated with marine-derived nutrient deposition provided by spawning salmon (Wipfli et al. 2003), spawner 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 mean weight of adult coho salmon captured at the adult trap on the main-stem West Fork Smith River.

Fish tagging and recovery.—We estimated coho salmon distribution and relative abundance within the West Fork Smith watershed by conducting a systematic snorkel survey in every fifth pool throughout the main stem and major tributaries in July 2002 ($n = 570$ pools). Snorkelers used the protocol of Thurow (1994), moving upstream and visually estimating abundances of coho salmon. We used a backpack electrofishing unit to derive estimates of coho salmon abundance in riffles and glides, and in a subset of pools to determine visual bias. Visual bias was corrected by comparing

snorkeler counts within several habitat units to more accurate estimates using electrofishing multiple-pass removal methods (Zippin 1958) within those same units (Hankin and Reeves 1988). Mean snorkeling efficiency was 0.69. Basinwide estimates of coho salmon density were derived by expanding snorkeling density estimates from pools and electrofishing density estimates from riffles and glides (approximately 24% of the total stream area) to unsampled stream areas within each tributary and main-stem reach using the methods of Hankin and Reeves (1988).

Fish were collected for PIT tagging from each study reach in three discrete time periods: August 19–September 4, October 15–26, and November 13–14, 2002. 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 and weighed to the nearest 0.01 g on an electronic balance. Individuals 60-mm FL or larger were implanted with PIT tags using a 12-gauge hypodermic needle to insert the tag posterior to the tip of the pectoral fin (PIT Tag Steering Committee 1999). After tagging, fish were placed in an instream live well and were observed for complete recovery prior to return to their habitat unit of origin.

We recaptured PIT-tagged coho salmon throughout the subsequent winter and spring using three methods. First, we used night seining (Gries and Letcher 2002) during winter base flow conditions in November 2002 through January 2003. Second, we used wire mesh minnow traps to capture fish within those same locations during higher winter flow conditions in January–March 2003. Minnow traps were baited with fresh steelhead eggs that had been soaked in an iotophore bath for 30 min. Eggs were enclosed in a fine mesh bag and suspended within each trap. Third, a rotary screw trap near the mouth of the West Fork Smith River was operated from February 7 to June 6, 2003. Trap efficiency was determined by releasing a sample of marked fish above the trap and determining rate of recapture. A caudal fin clip was applied to all fish caught. Newly caught fish were marked and released 100 m upstream of the trap using an automatic mechanism that released fish at dusk (Miller et al. 2000), while recaptured fish were released 100 m downstream of the trap. Efficiency of the smolt trap over this period, estimated on a weekly basis, averaged 0.31 (range = 0.15–0.54). Coho salmon juveniles

captured during these recapture efforts were scanned for PIT tags and measured for length and weight.

In addition to the capture techniques described above, stationary PIT tag monitoring stations were positioned in three tributary streams (Gold, Beaver, and Moore creeks) near the junction with the main-stem West Fork Smith River. Each monitoring station consisted of a Destron-Fearing FS1001 transceiver powered by deep-cycle batteries. A rectangular antenna (3.3×1.2 m) was positioned perpendicular to the streamflow and bracketed with weir panels to capture all but the highest streamflows. Tagged fish passing through the antenna field were recorded (PIT tag identification number, date, and time) continuously by a laptop computer attached to the transceiver. Computer malfunction and antenna damage due to high streamflows resulted in missing data for 7 d at Beaver Creek, 21 d at Moore Creek, and 27 d at Gold Creek during the overwintering period. Efficiencies of the antennas during the smolt out-migration period, estimated from known capture or antenna detections of fish in the tributaries and subsequently captured at the smolt trap, were 0.50 in Moore Creek, 0.61 in Beaver Creek, and 0.82 in Gold Creek.

Data analysis.—Valid associations of fish growth or survival to environmental characteristics of the stream network are dependent upon assumptions of fish location over the period of interest (Winker et al. 1995). For our study, movement of juvenile coho salmon to locations outside of the study reaches where they were tagged contributed complexity to the analysis of factors associated with growth and survival. We assumed overwinter location of juvenile coho salmon based on where fish were observed during the overwintering period with the following restrictions. We defined the overwinter period beginning with the onset of increased streamflow ($>10 \text{ m}^3/\text{s}$ in the main stem) after the first fall rain (November 8, 2002) and ending with the onset of the smolt monitoring period (February 7, 2003). Individuals were assumed to remain within locations where they were last observed during the overwintering period unless otherwise observed to leave the site (e.g., detected at the PIT tag monitoring stations) or recaptured in another location. Individuals not observed during the overwintering period were not assigned an overwinter location. Individuals that moved among multiple study sites were not assigned a specific overwinter location but were classified as mobile. We estimated the number of PIT-tagged coho salmon entering each tributary from the main stem by expanding the number of main-stem-tagged coho salmon detected at each tributary antenna location after November 14 (date on which all antennas were installed and functional) to account for antenna efficiency and

duration of monitoring. Counts of unique detections were divided by antenna efficiency, and the resultant product was expanded proportional to the number of days when the antenna was not operational. Location data were thus summarized by origin (e.g., location of first capture and tagging), any subsequent recapture, and presumed overwintering location.

Multiple recaptures—detections of PIT-tagged coho salmon allowed determination of specific growth rates and movement throughout the fall and winter period until emigration from the West Fork Smith River as smolts. Instantaneous growth rates for each fish were calculated by

$$100 \times (\log_e W_2 - \log_e W_1) (T_2 - T_1)^{-1},$$

where W_1 is weight at capture (g), W_2 is weight at recapture (g), and $(T_2 - T_1)$ represents the number of days between tagging and recapture (Busacker et al. 1990).

Only growth rates measured over time periods exceeding 28 d were used in analyses to minimize influence of tagging and handling effects on growth. We defined two growth seasons based upon visual observation of growth curves and timing of recaptures: (1) a winter period with relatively moderate growth rates (November 13–March 19) and (2) a spring period of relatively rapid growth (March 20–June 6). We compared fall parr size, spring smolt size, winter growth rate, and spring growth rate among reaches using one-way analysis of variance (ANOVA) for each size or growth variable, followed by Bonferroni-adjusted Fisher's least-significant-difference test (Ramsey and Schafer 1997:156). Differences were considered significant at P -values equal to 0.05. Logarithmic transformation was performed on fish length and weight data to normalize variances. To assess relative fish length within a study reach, we calculated the deviation of each individual from the mean length of all fish sampled within a given reach. This index, termed delta length (δ_L), is potentially more sensitive to effects of density dependence or social interactions than measures of absolute size (Zabel and Achord 2004). As a measure of fish condition factor, Fulton's K ($[10,000 \cdot \text{length in mm}] / \text{weight in g}$) was considered appropriate given similar length distributions among the groups assessed (Bolger and Connolly 1989). To assess potential bias in growth estimates associated with size-dependent survival, size-dependent sampling probability, or both, we compared length frequency distributions (at time of tagging) of all coho salmon recaptured for growth estimates and all coho salmon tagged, but not recaptured, using a chi-square test (Zar 1984).

Apparent survival was estimated for each tagged

group per reach by dividing the number of fish recovered at the rotary screw trap by the number released, after correcting for trap efficiency and the proportion of captured smolts scanned for PIT tags. We use the term "apparent survival" to describe these 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 watershed prior to February 7, 2003. We calculated Pearson's correlation coefficients to examine association among metrics of coho salmon apparent survival and stream reach characteristics, including measures of channel complexity, water temperature, water chemistry, and spawner carcass and egg biomass (Table 1). Experiment-wise error rate was controlled at α equal to 0.05 using the Bonferroni adjustment.

Additionally, we assessed the potential role of fall coho salmon parr size on apparent overwinter survival and detection the following spring by characterizing initial size and condition of known survivors from each reach of origin. Known survivors were classified as any fish detected or captured during the smolt monitoring period of February 7–June 6 (i.e., fish detected on or after February 7 were presumed to have survived the overwintering period). Likelihood ratio tests derived from logistic regression models (Allison 1999) were used to relate fish size and condition in the fall (length, δ_L , weight, and K at the time of PIT tagging) within each tributary to detections of all fall-tagged coho salmon at the Moore, Beaver, or Gold Creek PIT tag antennas during the smolting period. This analysis was restricted to coho salmon tagged within each tributary above each antenna and excluded coho salmon tagged in the main stem due to much lower detection probabilities of main-stem-tagged fish at the tributary antennas and low recapture rates at the smolt trap. To compare smolt weights across locations, we related coho salmon smolt weight to fall parr weight and date of smolt capture using multifactor ANOVA with tagging reach or known overwinter reach as a factor. Fall parr weight was included as a covariate. Date of smolt capture was also included as a covariate due to observed rapid spring growth.

Results

We estimated a total population size of 104,088 (95% confidence interval [CI] = 94,082–114,094) juvenile coho salmon in the West Fork Smith River in midsummer 2002. Juvenile coho salmon were distributed throughout the extent of accessible habitat in the basin in midsummer; highest coho salmon densities

TABLE 1.—Reach-level metrics used to relate coho salmon condition and performance to physical habitat structure, chemistry, water temperature, and spawner and egg biomass in West Fork Smith River, Oregon. Shown are mean, minimum (Min), and maximum (Max) mean values among study reaches ($n = 9$).

Metric	Mean	Min	Max
Juvenile fish condition and performance			
Apparent overwinter survival (%)	10.0	4.2	13.3
Instantaneous overwinter growth rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.58	0.15	0.68
Instantaneous spring growth rate ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	0.84	0.39	1.49
Smolt fork length (mm)	100	95	113
Smolt weight (g)	11.4	9.8	15.5
Physical habitat structure			
Within-channel large wood volume ($\text{m}^3/100 \text{ m}$)	1.4	0.1	6.9
Within-channel large wood frequency (number/100 m)	14.9	2.6	43.9
Exposed bedrock substrate (%)	29	12	62
Riparian canopy density (%)	40	21	56
SD of mean active channel depth (cm)	16	10	25
Total instream fish cover (%)	33	23	46
Baseflow pool area (%)	58	20	96
Pool spacing (channel widths/pool)	5.5	7.6	3.1
Channel gradient (%)	1.1	0.7	1.7
Mean substrate diameter (mm)	61	11	402
Sinuosity	1.14	1.01	1.37
Water chemistry			
Wet season total dissolved nitrogen ($\mu\text{mol/L}$)	33.3	10.2	62.6
Wet season soluble reactive phosphorus ($\mu\text{mol/L}$)	0.23	0.14	0.32
Water temperature			
Maximum weekly average maximum ($^{\circ}\text{C}$)	18.8	16.8	22.1
Adult coho salmon abundance			
Spawner and egg biomass (kg wet weight/m^2)	0.05		0.15

occurred in the tributaries (mean density = 0.66 fish/m², SD = 0.3), intermediate densities in the main stem upstream of Moore Creek (mean = 0.34 fish/m², SD = 0.1), and lowest densities in the main stem downstream of Moore Creek (mean = 0.15 fish/m², SD = 0.02).

Overwinter Location of Tagged Juvenile Coho Salmon

We tagged 3,755 juvenile coho salmon in late summer and early fall 2002, equivalent to approximately 3.6% of the estimated basin population (Table 2). Of these, 1,217 (or 32% of the tagged population) were recaptured or detected by the PIT tag antennas during the overwinter period, allowing classification of overwinter location for these individuals (Table 2). Seventy-nine percent of the juvenile coho salmon detected or captured during the overwinter period were detected within the reach where they were tagged. Seventeen percent overwintered within a reach other than their reach of origin, and the remaining 4% were classified as mobile (i.e., observed in numerous reaches; Table 2).

We detected 147 coho salmon that had been PIT tagged in the main stem at one or more of the tributary antennas (Figure 2). From antenna detection rates, we estimated that 75, 110, and 66 coho salmon that were PIT tagged in the main-stem West Fork Smith River

moved into Moore, Beaver, and Gold creeks, respectively, during the overwinter period. Coho salmon parr tended to use tributaries nearest their main-stem tagging location. Coho salmon from all reaches utilized Moore Creek, fish from all but the lowest reach used Beaver Creek, and only fish from the upper three reaches used Gold Creek (Figure 2). These numbers represent from 3% to 16% of the population originally tagged in the main-stem reaches.

Winter and Spring Growth

Growth rates were estimated for 104 individuals that were recaptured at least once prior to emigration. The mean length at time of tagging of PIT-tagged coho salmon recaptured and remeasured for growth estimation (71.7 mm) was slightly greater than the mean length of coho salmon never recaptured (71.4 mm). The data were not normally distributed, and a chi-square test indicated that the length frequency distributions were not significantly different when fish were grouped in 10-mm intervals ($\chi^2 = 10.4$; $\text{df} = 8$; $P = 0.24$). Instantaneous growth rate during winter and spring was not correlated with fish weight at the time of tagging in the fall (Pearson's $r = 0.03$; $P = 0.33$; $n = 104$).

Mean coho salmon weight increased moderately

TABLE 2.—Proportion of coho salmon observed in an overwintering reach that were tagged in a given reach of origin within the West Fork Smith River basis, Oregon (e.g., 12.8% of fish observed to overwinter in Beaver Creek originated in reach MS-7). Coho salmon observed using multiple reaches over the overwinter period were classified as mobile (*N* given in parentheses).

Reach of origin	Number tagged	Overwintering reach									
		Beaver Creek	Gold Creek	Moore Creek	MS-5	MS-6	MS-7	MS-8	MS-9	MS-10	Mobile
Beaver Creek	478	76.2 (285)	0	0	0	2.1 (1)		0	0	0	2.3 (1)
Gold Creek	531	0.8 (3)	75.6 (152)	0.3 (1)	0	0	0	0	0	0	37.2 (16)
Moore Creek	334	0	0	87.8 (310)	0	0	0	0	0	0	0
MS-5	408	0	0	6.5 (23)	100.0 (3)	2.1 (1)	0	0	0	0	7.0 (3)
MS-6	419	0.3 (1)	0	2.5 (9)	0	87.5 (42)	0	0	0	0	2.3 (1)
MS-7	427	12.8 (48)	0	0.8 (3)	0	2.1 (1)	89.5 (51)	30.0 (3)	0	1.0 (1)	20.9 (9)
MS-8	393	5.3 (20)	3.0 (6)	0.8 (3)	0	0	8.8 (5)	70.0 (7)	0	0	4.7 (2)
MS-9	340	2.9 (11)	7.0 (14)	0.6 (2)	0	2.1 (1)	0	0	90.0 (27)	9.2 (9)	7.0 (3)
MS-10	425	1.6 (6)	14.4 (29)	0.6 (2)	0	4.2 (2)	1.8 (1)	0	10.0 (3)	89.8 (88)	18.6 (8)

from December to March (hereafter “overwinter growth”; mean instantaneous growth rate = 0.58 g·g⁻¹·d⁻¹; SE = 0.03), and rapidly from mid-March through June (hereafter “spring growth”; mean instantaneous growth rate = 0.84 g·g⁻¹·d⁻¹, SE = 0.08; Figure 3). Overwinter growth was estimated from 78 coho salmon recaptured prior to March 19, 2003. Fifteen fish were observed in multiple stream reaches during the overwinter period and were not assigned a

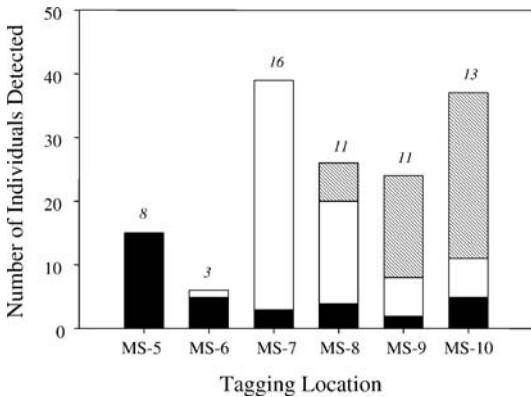


FIGURE 2.—Number of coho salmon parr that were PIT tagged in each of six main-stem West Fork Smith River (Oregon) locations (see Figure 1) and detected at Moore Creek (solid bar), Beaver Creek (unfilled), and Gold Creek (cross-hatched) antennas during the overwinter period. Italicized number above each bar shows the percentage of PIT-tagged fish from each location estimated to have used one or more of the tributaries after accounting for antenna efficiencies.

single overwintering reach but were classified as mobile. Too few (less than four) fish were captured from reaches MS-5, MS-6, MS-8, and MS-9 to allow reach-level assessment of overwinter growth, so fish observed to overwinter within main-stem sites were combined for statistical analysis. Overwinter growth rate was highest for juvenile coho salmon in Moore Creek, lowest in Beaver Creek (ANOVA: $F_{4,72} = 8.77$; $P < 0.01$), and intermediate in Gold Creek, the main stem, and for fish that moved between tributary and main-stem habitats (Table 3).

Spring growth rates were estimated from 26 coho salmon captured at least twice between March 19 and June 6, 2003. Too few coho salmon were captured

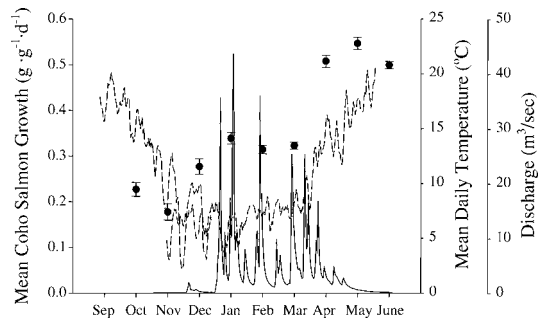


FIGURE 3.—Mean ($\pm 2SE$) instantaneous growth rate of juvenile PIT-tagged coho salmon recaptured during mark-recapture sampling (solid circles) in the West Fork Smith River, Oregon. Also shown is daily discharge (solid line) and daily mean temperature (dashed line) recorded at the location of the rotary smolt trap (see Figure 1).

TABLE 3.—Instantaneous overwinter growth rate ($g \cdot g^{-1} \cdot d^{-1}$) of juvenile coho salmon among overwinter locations within the West Fork Smith River basin, Oregon.

Overwinter location	Count	Mean	SE	95% confidence interval
Beaver Creek	20	0.34	0.057	0.22–0.45
Gold Creek	4	0.42	0.127	0.16–0.68
Moore Creek	36	0.74	0.042	0.65–0.83
Main stem	10	0.56	0.081	0.40–0.73
Mobile ^a	8	0.56	0.090	0.38–0.75

^a Individuals observed moving among tributaries or between the main stem and tributaries during overwinter period.

from individual tributary or individual main-stem reaches to allow comparison among tributaries or among main-stem reaches, so they were grouped into three classes: (1) fish overwintering in main-stem reaches, (2) fish overwintering in tributary reaches, (3) mobile fish observed in multiple reaches, and (4) fish that were not observed during the overwintering period and whose overwintering location could not be confidently assigned. Overall spring growth rates were significantly higher than overwinter growth rates ($t = -4.99$; $P < 0.001$) but did not differ among fish overwintering in tributary reaches, main-stem reaches, or for fish whose overwintering location was unknown (ANOVA: $F_{3,25} = 0.29$, $P = 0.83$; Table 4). Spring growth rate was not correlated with overwinter growth rate for individual fish recaptured during both seasons (Pearson's $r = -0.46$; $P = 0.36$).

Coho Salmon Overwinter Survival

We captured 4386 coho salmon smolts at the rotary screw trap during the spring out-migration between February 7 and June 6, 2003. Of these, 110 coho salmon smolts had been PIT tagged the previous fall, representing 2.5% of the total catch scanned for PIT tags. Based upon measured efficiency of the screw trap, we estimated approximately 16,000 coho salmon smolts emigrated from the watershed and that 375 of these were PIT-tagged fish. Peak emigration occurred

TABLE 4.—Instantaneous spring growth rate ($g \cdot g^{-1} \cdot d^{-1}$) of juvenile coho salmon among overwinter locations within the West Fork Smith River basin, Oregon.

Overwinter location	Count	Mean	SE	95% confidence interval
Main stem	6	0.92	0.111	0.69–1.15
Tributary	8	0.80	0.098	0.60–1.00
Unknown ^a	11	0.82	0.083	0.65–1.00
Mobile ^b	1	0.72	0.276	0.16–1.29

^a Overwinter location not determined.

^b Individuals observed moving among tributaries or between the main stem and tributaries during the overwinter period.

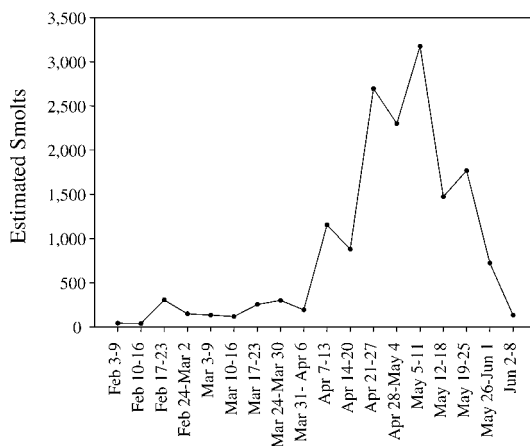


FIGURE 4.—Estimated weekly number of coho salmon smolt out-migrants (excluding fry) based upon captures at the rotary screw trap on the West Fork Smith River, Oregon. The trap was operated from February 7 to June 6, 2003.

during mid-April through late May 2003 (Figure 4). Estimated apparent overwinter survival of PIT-tagged juvenile coho salmon was highest for the three tributaries and upper main-stem reach MS-8 (12–13%); intermediate in upper main-stem reaches MS-7, MS-9, and MS-10 (9–10%); and lowest for the lower main-stem reaches MS-5 and MS-6 (4–6%; Figure 1; Table 5).

Relation of Survival to Stream Characteristics

Apparent overwinter survival was positively correlated with riparian canopy density and adult coho salmon spawner carcass and egg biomass, but negatively associated with percentage of exposed bedrock in the stream channel and MWMT (Table 6). Apparent overwinter survival was not significantly associated with any other physical habitat or water chemistry

TABLE 5.—Apparent overwinter survival of coho salmon tagged with passive integrated transponders (PIT-tags) by reach of origin in the West Fork Smith River basin, Oregon. Also shown are summer parr densities and densities of fall adult coho salmon spawners.

Reach	Summer coho salmon density (number/100 m ²)	Apparent overwinter survival (%)	Spawner carcass and egg biomass density (kg wet weight/m ²)
Beaver Creek	37.5	12	0.08
Gold Creek	61.6	12	0.06
Moore Creek	132.9	13	0.15
MS-5	39.8	4	0.03
MS-6	44.4	6	0.00
MS-7	40.7	10	0.01
MS-8	41.3	13	0.05
MS-9	49.8	9	0.06
MS-10	45.6	10	0.07

TABLE 6.—Pearson’s correlation coefficients between apparent overwinter survival of juvenile coho salmon tagged with passive integrated transponders (PIT-tags) and selected habitat characteristics of study reaches in the West Fork Smith River basin, Oregon. Coefficients in bold type are statistically significant ($P < 0.05$) (MWMT = maximum weekly average maximum daily temperature; LWD = large woody debris).

Variable	MWMT (°C)	LWD volume (m ³ /100 m)	LWD frequency (pieces/100 m)	Total instream fish cover (%)	Riparian canopy density (%)	Sinuosity	Bedrock substrate (%)	Spawner carcass and egg biomass density (kg/m ²)
Survival (%)	-0.85	0.30	0.11	0.23	0.89	0.22	-0.81	0.68
MWMT (°C)		-0.39	-0.14	-0.07	-0.94	-0.10	0.88	-0.66
LWD volume (m ³ /100 m)			0.90	0.49	0.24	-0.11	-0.42	0.21
LWD frequency (pieces/100 m)				0.65	0.01	-0.19	-0.31	0.05
Total instream fish cover (%)					0.34	-0.26	-0.43	0.21
Riparian canopy density (%)						-0.06	-0.91	0.62
Sinuosity							-0.11	0.66
Bedrock substrate (%)								-0.77

characteristic listed in Table 1 ($r < 0.4$, $P > 0.3$ for characteristics not listed in Table 6).

Contribution of Size at Tagging to Overwinter Survival and Smolt Size

Among individual coho salmon tagged within the tributaries, probability of survival was positively associated with FL, condition factor, and reach location at the time of tagging in the fall as indicated by likelihood ratio tests (Table 7). Survival was highest for coho salmon that were larger than 90 mm at the time of tagging (Figure 5). Weight and δ_L , which were correlated with FL, were not significantly associated with survival after accounting for FL and condition factor.

Among coho salmon smolts captured at the rotary screw trap February 7 through June 6 2003, weight was positively associated with parr weight the previous fall and date of smolt sampling. Smolt wet weight differed among reaches of origin, after accounting for fall weight and date of smolt sampling (two-way ANOVA: $F_{8,223} = 3.15$, $P = 0.002$; Table 8). Estimates of smolt FL as a function of fall FL or δ_L after accounting for data of smolt sampling and reach of origin produced similar results (not shown). Smolts originating from Moore Creek were significantly larger than those

originating from all other locations (Figure 6) despite being intermediate with regard to weight at time of tagging in the fall (Figure 7). Smolts overwintering in Moore Creek were significantly larger (weight and length) than smolts overwintering in Beaver Creek, Gold Creek, or main-stem reaches 5–9, but were not significantly larger than smolts observed to overwinter within multiple reaches (mobile fish) or in main-stem reach 10 (Figure 6).

Discussion

The ability to individually tag and track coho salmon from late summer through the spring provided a unique perspective on basin-scale patterns of movement, growth, and survival. We were able to observe upstream movement of juvenile coho salmon tagged in the main stem into tributaries and to document enhanced survival there. Our observations of seasonal immigration by juvenile coho salmon into tributaries and associated improvements in survival are consistent with earlier observations (Bustard and Narver 1975; Kralik and Sowerwine 1977; Tschaplinski and Hartman 1983). Additionally, we were able to document enhanced growth of juvenile coho salmon using Moore Creek, an intermittent tributary, during the winter months.

The ability to track movement of individual coho salmon provided additional insights helpful in interpreting growth and survival data. For example, although Moore Creek was nearly dry in late summer (surface water was restricted to a few isolated pools), fish quickly recolonized newly flooded habitat within 3 d of the first substantial fall rains, including fish that had been previously PIT tagged in the adjacent main stem. Passive integrated transponder-tagged coho salmon originating from reaches as far away as the

TABLE 7.—Likelihood ratio tests for individual fish length and condition factors from a logistic regression model of coho salmon parr overwinter survival in Gold, Beaver, and Moore creeks, Oregon (percentage of deviance explained by model = 8.7; adjusted percentage = 7.6).

Factor	Chi-square	df	P-value
Fork length (mm)	5.64	1	0.018
Condition factor (K)	5.28	1	0.022
Reach of origin	25.13	2	<0.001

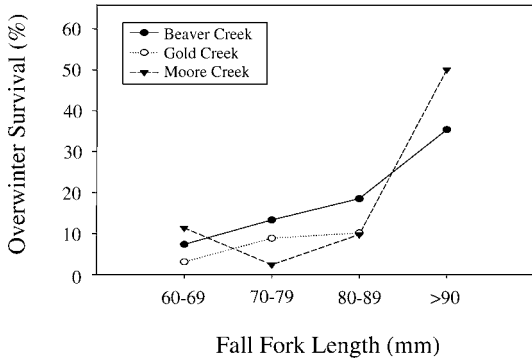


FIGURE 5.—Apparent overwinter survival of coho salmon parr by length-class from Beaver, Gold, and Moore creeks in the West Fork Smith River, Oregon, 2003.

uppermost main-stem reach (over 8,100 m distant) also moved into Moore Creek during the overwintering period (Figure 2). The few fish moving long distances into Moore Creek and the other tributaries, as detected by the stream width antennas, tended not to stay within the tributaries and were observed using multiple reaches over the overwintering period. These observations suggest that juvenile coho salmon use of tributaries may be temporally dynamic, some individuals using a wide array of habitats during the overwinter period. We caution that our estimates of tributary use are likely underestimates because (1) some fish entered tributaries prior to the overwintering period (however, not all antennas were operational prior to November 14 and we did not attempt to estimate immigrants prior to that date), and (2) although antennas at Beaver Creek and Gold Creek are located within 50 m of the stream mouth, the Moore Creek antenna is located 220 m upstream of the confluence with the main stem. Additional fish may

TABLE 8.—Analysis of variance table for coho salmon smolt weight (g) by reach of origin within the West Fork Smith River basin, Oregon, after accounting for sampling date and fall weight.

Source	Sum of squares	df	Mean square	F-ratio	P-value
Covariates					
Date of capture	2,229.62	1	2,229.62	548.34	<0.01
Fall weight (g)	368.97	1	368.97	90.74	<0.01
Main effects					
Reach of origin	101.42	8	12.68	3.12	0.002
Residual	906.75	223	4.07		
Total (corrected)	3,629.82	233			

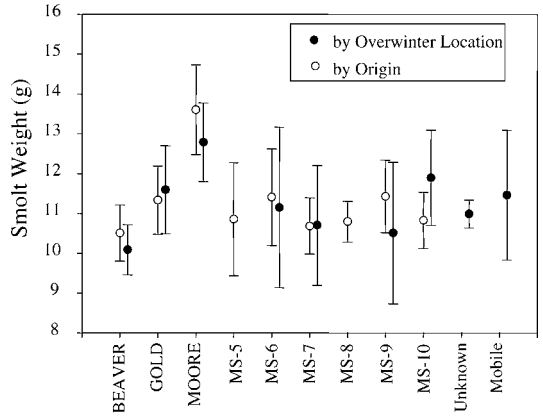


FIGURE 6.—Mean coho salmon smolt weight ($\pm 95\%$ Bonferroni CI) by reach of origin (open symbols; see Figure 1 for locations) and known overwintering reach (filled symbols) in the West Fork Smith River system, Oregon, 2003.

have used Moore Creek below the antenna and were not detected.

Mobile fish, which could not be assigned a single overwintering habitat location, exhibited high variation in smolt weight and did not differ from individuals from specific overwintering locations (Figure 6). High individual variation in movement patterns and duration of residency in different habitats likely contributed to this pattern.

Spatial variability in overwinter survival at the stream network scale has been previously documented for juvenile coho salmon, primarily associated with higher survival in habitats containing off-channel wetlands or lakes (Peterson 1982; Brown and Hartman 1988; Quinn and Peterson 1996). Our study differs

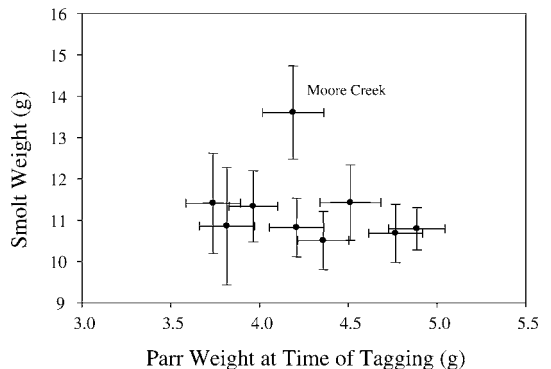


FIGURE 7.—Mean coho salmon weight (g) at the time of PIT tagging (2002) and mean smolt weight (g; 2003) by reach of origin within the West Fork Smith River system, Oregon. Shown are Bonferroni-adjusted CIs.

from previous research in that we found higher survival within tributaries in a basin where flood plain wetlands and off-channel ponds or lakes are unavailable. The overwinter survival rates we observed are lower than published values for Washington, British Columbia, and Alaska streams (25–42%; e.g., Bustard and Narver 1975; Crone and Bond 1976; Quinn and Peterson 1996) but are within the range observed for Oregon coastal streams that were not enhanced by habitat rehabilitation (11–13%; Solazzi et al. 2000).

Variation in apparent overwinter survival among reaches was related to a group of intercorrelated physical habitat factors, including riparian canopy density, percent bedrock substrate, and maximum temperatures during the preceding summer. These factors covary spatially such that stream sections that had less dense riparian canopy cover also tended to have a higher proportion of bedrock substrate and higher summer stream temperatures. Each of these factors has been associated with habitat quality for stream salmonids in previous studies through both direct and indirect effects on food availability, cover, and fish physiological performance (e.g., Wipfli 1997; Sullivan et al. 2000; Armstrong and Griffiths 2001). For example, percent bedrock may provide an index of availability of hydraulic refuges for juvenile salmon. Juvenile salmonids are known to seek shelter during low stream temperatures and during high discharge events. Interstitial spaces in boulder and cobble substrates can allow individuals to avoid displacement due to reduced swimming ability at low temperatures and high stream velocities (McMahon and Hartman 1989; Valdimarsson et al. 1997). These shelters can be lacking from smooth bedrock channels.

Because coho salmon require gravel for spawning and egg deposition, the negative association of spawner density with percent bedrock is hardly surprising. Low spawner densities may have contributed to reduced overwinter survival by decreasing availability of carcass material and eggs to the diet of juvenile coho salmon, decreasing overwinter growth rates and opportunities for accumulation of lipids (Heintz et al. 2004).

Proportion of exposed bedrock was positively correlated with maximum temperature among the study reaches. Bedrock may influence stream temperatures by restricting opportunities for hyporheic flow and storage and by reducing the accompanying thermal buffering effect that hyporheic storage can provide (Poole and Berman 2001). High stream temperatures may have indirectly reduced overwinter survival by reducing fitness of juvenile coho salmon prior to the overwinter period through temperature-mediated stressors (e.g., Thomas et al. 1986).

We did not observe significant correlations between apparent overwinter survival and other indices of channel complexity (e.g., sinuosity, large woody debris abundance, pool spacing) or cover despite an abundance of previous research that has demonstrated such relationships (e.g., McMahon and Hartman 1989; Nickelson et al. 1992; Quinn and Peterson 1996; Cederholm et al. 1997; Solazzi et al. 2000). Much of the West Fork Smith River has been subject to harvest of riparian conifers and removal of large wood from stream channels over the past half century (U.S. Bureau of Land Management, Coos Bay District Office, unpublished). Much of the riparian forest is composed of red alder, which is typically much smaller and provides a much shorter-lived presence as a structural agent within stream channels compared with conifer species (Bilby and Bisson 1998). Observed large woody debris loadings across our sites were low (0.02 to 0.50 pieces/m), similar to the relatively low values observed for stream channels in clear-cut forests of the Pacific Northwest surveyed by Montgomery et al. (1995). Under current channel and riparian conditions, the smaller pieces of wood that are present, particularly in high-energy, bedrock-dominated channels, may be relatively ineffective at accumulating sediment and providing hydraulic complexity favorable for formation of suitable winter rearing habitats for juvenile salmonids (Bilby and Bisson 1998).

For the cohort we examined, apparent survival and growth were linked not only to overwintering conditions but also to conditions during the preceding summer (i.e., summer maximum temperatures). Annual variation in climate, streamflow regimes, and population abundances most likely influences the relative contribution of summer versus winter effects on coho salmon production (Lawson et al. 2004). The 2002–2003 cohort year experienced moderate winter streamflows but low summer flows during the freshwater portion of its life cycle. During water years (October–September) 2001–2002 and 2002–2003, maximum daily discharges and maximum 7-d high discharges were in the 57–65th percentiles of 23 years of streamflow records. Summer–fall 2002 minimum discharge was the 78th percentile. We hypothesize that the relative influence of summer stream temperatures might be expected to be more severe under even warmer and drier climatic conditions with warmer and lower summer streamflows (Eaton and Scheller 1996).

In the West Fork Smith River, variation in spring smolt size was associated with fall parr size but was also influenced by overwintering location due to spatial patterns of overwinter growth rates, especially in Moore Creek. Growth of all fish increased rapidly in the spring, coinciding with increasing stream temper-

atures and decreasing streamflow (Figure 3). The largest smolt sizes were associated with fish remaining in and moving into Moore Creek during the winter months. Streamflows in Moore Creek were intermittent during summer, but this tributary had some of the highest densities of spawning coho salmon during November–December. Coho salmon spawner carcass and egg biomass densities in Moore Creek in 2002 approached 0.15 kg wet mass/m² (Table 5), the level hypothesized by Bilby et al. (2001) at which trophic incorporation of marine-derived nutrients in juvenile salmon becomes asymptotic. Direct consumption of eggs, carcass material, or newly emerged coho salmon fry may have contributed to the elevated growth rates and smolt sizes observed for fish using Moore Creek, and we have observed eggs and fry in the diet of juvenile coho salmon from the West Fork Smith River (M.R.C., unpublished data).

We observed increased apparent survival with juvenile coho salmon body size. These results are consistent with previous findings relating overwinter survival of juvenile salmonids to fall size (Quinn and Peterson 1996; Miyakoshi et al. 2003). An exception to this trend was noted for Moore Creek, an intermittent stream that had intermediate size coho salmon parr in the fall but produced the largest smolts and had the highest overwinter survival rates, in part due to higher winter growth rates. Where density-dependent processes and competitive interactions are likely (e.g., within socially organized species like coho salmon [Chapman 1962]), relative length may be a better predictor of success than absolute length. Zabel and Achord (2004) were able to separate potential effects of relative versus absolute body size on juvenile Chinook salmon survival and found that relative size had better explanatory power. Absolute body size (FL) was a better predictor of overwinter survival than relative size (δ_L) in the present study. This may indicate that size-dependent factors (e.g., increased energy reserves or physical capability to withstand physical stress) are relatively more important than density-dependent mechanisms of survival (e.g., size-mediated competition for limited refuge space) for overwintering coho salmon in the West Fork Smith River. This conclusion is supported by our finding that body condition factor (K) was also positively associated with apparent survival, after accounting for FL.

We caution that our observed pattern of size-dependent apparent survival may be biased by sampling. The fate of displaced fish is often problematic for survival models of free-ranging fish (Burnham et al. 1987), and this study is no exception. Due to high flood flows and heavy debris loads, we were unable to operate a rotary screw trap during the winter months,

and the tributary PIT antennas were periodically disabled during high streamflows. Although the majority of coho salmon smolts appeared to emigrate during the months of April and May in 2003 (Figure 4) as is typical throughout the range of the species (Sandercock 1991), we have no data on emigration of coho salmon out of the basin prior to the installation of the trap on February 7, 2003. However, in a basin near our study area, Rodgers et al. (1987) observed fall downstream migration of lower-condition coho salmon. The fate of these fish, thought to be displaced by competitively superior conspecifics, is unknown. In our analysis, coho salmon that may have emigrated prior to February 7 are treated as mortalities. Sampling effects could also potentially bias growth rate estimates due to size-dependent survival, size-dependent capture probability, or both. Among recaptured coho salmon, instantaneous growth rate was not correlated with fish weight at the time of tagging, and length frequencies of the sample recaptured for individual growth estimates did not differ from the initial tagging population, indicating that bias associated with size-dependent survival or capture probabilities was not likely.

Seasonal movement into tributaries may be particularly important in watersheds where main-stem habitats have been simplified by logging, splash damming, and other activities (Tschaplinski and Hartman 1983). Like many river systems in coastal Oregon, a history of splash damming in the main-stem West Fork Smith River below Beaver Creek is believed to have contributed to loss of in-channel sediment and large wood structure and an increase in the reaches with predominately bedrock channels (U.S. Bureau of Land Management, Coos Bay District Office, unpublished). These changes to Oregon coastal streams have contributed to declines in the productive capacity of freshwater rearing habitats for coho salmon and other salmon species (Reeves et al. 2002). In the West Fork Smith River, contrasts in habitat conditions and apparent overwinter survival between main-stem and tributary habitat are highest in the lower portion of the network (e.g., downstream of Beaver Creek) where main-stem channels are predominantly bedrock and lack substantial cover and low-velocity refuge areas during winter floods. These conditions contrast sharply with habitat conditions within Moore Creek, a heavily alluviated channel with more moderate winter flows. Concordant main-stem apparent overwinter survival rates are approximately one-third the rate observed in Moore Creek.

These results provide additional evidence that small tributaries may be important to overwintering coho salmon, particularly when they are close to main-stem habitats of low habitat quality. If higher growth rates

are typical of small tributaries, as supported by these observations and as suggested by Brown and McMahon (1988), such habitats may contribute disproportionately to smolt recruitment, particularly during periods of poor ocean conditions when smolt survival is particularly size dependent (Holtby et al. 1990). The importance of small tributaries at the watershed scale likely varies annually with climatic conditions. During wetter years, small tributaries may retain surface flow year-round, allowing improved summer survival and subsequently higher densities of juvenile salmonids prior to the overwinter period. Under these conditions, the relative advantages of fall immigration into such tributaries may be reduced.

These results also indicate the potential importance of connectivity between main-stem and tributary habitats, particularly where main-stem habitats have been simplified through loss of channel structure and coarse sediments, and experience high summer water temperatures. Impassible road culverts make many small tributaries throughout the Pacific Northwest presently disconnected from downstream waters in basins like the study watershed. This is recognized as a major opportunity for habitat restoration and salmon recovery in the region, though guidance is needed for prioritizing culvert removal and passage improvements given the sheer number of currently disconnected tributaries (Roni et al. 2002). High heterogeneity in habitat conditions between proximal tributary and main-stem habitat conditions may allow for a diverse range of seasonal rearing habitats for juvenile salmonids. These results support continuing efforts to protect, maintain, and restore seasonally productive habitats, and connectivity between them.

Acknowledgments

John Bartosz, Steve Hendricks, Clayton Oyler, Nancy Raskauskas, Chad Meengs, Jason Meyers, and Ross St. Clair assisted with fish and habitat sampling. Patti Haggerty provided geographical information system coverages and distance matrices. Gordon Reeves, Robert Ozretich, and two anonymous reviewers provided helpful reviews of earlier drafts of this manuscript. We thank Roseburg Resources for access to private lands. Pat Olmstead of the Coos Bay District Bureau of Land Management provided logistical support. The information in this document has been funded by the USEPA. It has been subjected to review by the National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the USEPA, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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