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Seasonal Microhabitat Use by Juvenile Spring Chinook Salmon in the Yakima River Basin, Washington

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ABSTRACT: Microhabitat data were collected at focal positions of juvenile spring chinook salmon (*Oncorhynchus tshawytscha*) in the Yakima River basin, Washington, during spring, summer, fall, and winter. Significant seasonal differences were noted in most microhabitat characteristics including depth, mean column and focal velocity, focal height, substrate, instream cover, and distance to bank. Juvenile chinook selected positions farther offshore over larger substrates in deeper water as the seasons progressed. Focal and mean column velocities increased in the summer, but decreased again in the fall and winter. Spring and winter focal positions were closely associated with instream cover, but summer positions were not. Seasonal differences in microhabitat use dictate the need for multiple, season-specific Habitat Suitability Criteria (HSC) for instream flow studies involving large, regulated river systems. For example, the use of summer HSC to model fish habitat in spring or winter could produce inappropriate instream flow recommendations.

KEY WORDS: Chinook salmon, criteria curves, habitat suitability criteria, instream flow, *Oncorhynchus tshawytscha*, seasonal microhabitat, Yakima River.

INTRODUCTION

The Yakima River is one of the principal tributaries entering the middle Columbia River, and it has historically supported large returns of anadromous salmonids each year. Currently the Yakima River basin is a highly developed agricultural center, where six major storage reservoirs and eight major diversion dams manage streamflows to provide flood control and irrigation deliveries. In recent years the annual escapement of spring-run chinook salmon (*Oncorhynchus tshawytscha*) has averaged <5,000 fish per year (U. S. Bureau of Reclamation 1998). Flow alterations related to agricultural uses, watershed degradations, downriver and ocean harvest, and other factors have been associated with this decline. Significant effort has subsequently been allocated to restore the depleted runs of chinook salmon to their headwater

spawning areas in the Yakima River basin (Clune and Dauble 1991).

In the early 1980s, an instream flow study was conducted to determine if streamflow releases from the basin's storage and diversion dams could improve the existing habitat quality in the Yakima River basin (Parametrix and Hardin-Davis 1984). A Physical Habitat Simulation (PHABSIM) analysis was conducted that utilized Habitat Suitability Criteria (HSC) developed during the summer in the upper Yakima River and in a major tributary to the Naches River (Stempel 1984). The relation between streamflow and an index to fish habitat is referred to as Weighted Usable Area (WUA) and is a primary result of the PHABSIM analysis. The WUA function is affected by characteristics of the stream channel and by methods used to develop and calibrate the



model (Shirvell 1986; Williams 1996; Bovee et al. 1998; Railsback 1999). Weighted Usable Area is particularly sensitive to the HSC, which are combined with depths and velocities in a hydraulic model to produce the WUA index (Bovee 1986; Modde and Hardy 1992).

Habitat Suitability Criteria describe the microhabitat requirements of fish, which typically include the variables water depth, water velocity, substrate composition, and cover. Most HSC are constructed independently for each variable through a frequency analysis of the microhabitats where fish are observed. The frequency distribution is converted into a curve where the range of optimal habitat is given a value of 1.0 and the range of unsuitable habitat is valued at zero. The range of habitat intermediate to the optimal and unsuitable ranges is valued accordingly on a scale from 1 to 0.

Juvenile salmonids, including chinook, are known to exhibit changes in habitat selection as they grow and as environmental character-

istics, such as water temperature and streamflow, change through the seasons (Hartman 1965; Chapman and Bjornn 1969; Everest and Chapman 1972; Campbell and Neuner 1985; Baltz et al. 1991). In larger rivers, these seasonal changes in habitat use may also result in an offshore movement away from the stream margins (Lister and Genoe 1970). Additional information on the habitat requirements of juvenile chinook was deemed necessary in order to fully evaluate the effects of streamflow regulation on the habitat suitability of the Yakima River throughout its basin and over several seasons. The objective of this study was to develop site-specific HSC from a wide range of habitats and over four seasons in order to more fully describe habitat use in the Yakima River basin through the juvenile rearing phase of chinook salmon. In addition, the use of mid-channel habitats by juvenile chinook was evaluated because the original PHABSIM analysis treated mid-channel areas as unsuitable.

STUDY AREA

The Yakima River basin was separated into four segments based on spawning and rearing distributions of chinook, stream size, and watershed characteristics (Figure 1). Currently, most chinook in the Yakima Basin spawn in the upper mainstem Yakima, the Cle Elum River, or the Naches River and several of its principal tributaries (Major and Mighell 1969; Patten et al. 1970). Juveniles rear throughout the upper and middle segments of the Yakima River and the Naches River, but high water temperatures in the lower segment typically restricts the use of this area to winter rearing or spring outmigration (Patten et al. 1970; Fast et al. 1991).

The Yakima River basin is a 6,155-mi² watershed on the east side of the Cascade Mountains with high precipitation at its headwaters (annual mean >128 in), but low precipitation (annual mean <8 in) in the agricultural floodplains of the lower basin. The mainstem Yakima River averages 100 ft to over 200 ft in width as it flows southeast approximately 215 mi from its headwaters at 5,000 ft msl to its confluence with the Columbia River at 340 ft msl (Figure 1). The upper segment is mountainous with a well-developed coniferous riparian zone. The Cle Elum River is a large, regulated tributary entering

the upper segment with approximately 8 mi of habitat available to anadromous fish below Cle Elum Dam. The middle segment of the Yakima River alternates between deep chaparral canyons and a wide agricultural floodplain near Ellensburg. The lower segment flows through a highly developed agricultural floodplain. Lowland deciduous trees are common throughout the floodplain reaches of the middle and lower segments, and riprap armoring is common along stream banks in the canyon reaches of the middle segment. The Naches River is the largest tributary to the Yakima River and flows southeast for 45 mi to its confluence with the Yakima River. The upper 27 mi of the Naches River are mountainous, but the lower portion flows through an agricultural floodplain. The mean annual streamflow (unregulated) of the Yakima River is estimated at 900 cfs above the Cle Elum River and 5,300 cfs at the Columbia River (Bureau of Reclamation 1998). Mean monthly flows for both rivers were historically highest during spring snowmelt and lowest during late summer, but high flows in the Yakima River now occur in the summer months due to upstream storage and releases to meet irrigation demands.

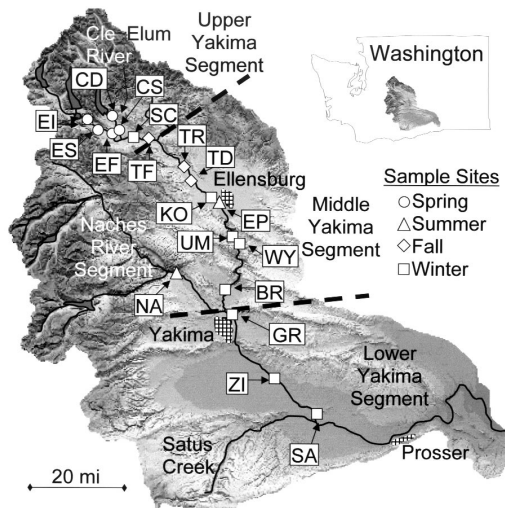


FIGURE 1. The Yakima River basin showing the study segments and the seasonal habitat suitability criteria (HSC) study sites represented by letter code (see Table 2). Watershed image courtesy of U.S. Bureau of Reclamation and U.S. Geological Survey.

In addition to chinook salmon, resident rainbow trout and anadromous steelhead (*O. mykiss*), cutthroat trout (*O. clarkii*), mountain whitefish (*Prosopium williamsoni*), redbreast shiners (*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and sculpins (*Cottus spp.*) dominate the fish fauna of the upper and middle segments of the Yakima River (Patten et al. 1970). Chiselmouth (*Acrocheilus alutaceus*), bridgelip and largescale suckers (*Catostomus columbianus* and *C. macrocheilus*) and northern pikeminnow (*Ptychocheilus oregonensis*) are also abundant in the middle and lower segments, and smallmouth bass (*Micropterus dolomieu*) and carp (*Cyprinus carpio*) are common below Prosser (Figure 1).

METHODS

Habitat Suitability Criteria were developed for juvenile chinook during four seasons using direct observation methodologies in randomly selected habitat units in the Yakima River basin.

Study Site Selection

Collection of HSC data is a labor-intensive procedure that is inefficient where fish densities are very low. Spring, summer, and fall sampling occurred within stream segments where a concurrent distribution and abundance study revealed adequate densities of juvenile chinook (Thomas R. Payne & Associates 1995a), and where streamflow and turbidity characteristics allowed the use of direct observation methodologies. For the spring survey in 1990, individual habitat units were selected by stratified random sampling from within habitat type strata in the upper segment of the mainstem Yakima River and the Cle Elum River where much of the spawning takes place (Figure 1). When the summer survey was conducted in 1990, juveniles had widely dispersed downstream from spawning areas and consequently habitat "clusters" (contiguous habitat units of each habitat type) were randomly selected from all available clusters in the middle segment of the Yakima

River and from the Naches River. Sampling areas were selected from habitat clusters to reduce travel time between individual habitat units and to ensure that all habitat types were represented in the HSC data. Habitat clusters were likewise randomly selected from upper and middle segments of the Yakima River during fall surveys conducted in 1989 and 1990. Distribution and abundance information for juvenile chinook was lacking during winter months; therefore study sites were selected in 1994 after further dividing the mainstem Yakima River into nine evenly partitioned reaches. One cluster was randomly selected from each of the nine reaches (three in the lower segment, four in the middle segment, and two in the upper segment) from among the available clusters that were known to contain some form of winter hiding cover, such as large woody debris or boulder/riprap banks.

The lower segment and the Naches River were not sampled during all seasons because low fish densities, high streamflows, and/or poor water quality limited the feasibility of collecting HSC data in those areas. Additional area was sometimes surveyed in habitat units upstream or downstream of the selected cluster to equalize sampling effort among habitat types.

Sampling Effort

Sampling effort was stratified by season, study site, habitat type, and time of day. Habitat types were deep pool (>6 ft), shallow pool, deep run (>6 ft), shallow run, and riffle. Sampling was conducted with approximately equal effort (measured in ft² of observation area) among habitat types to ensure that all available combinations of depth and velocity (deep versus shallow, fast versus slow) were equally represented in the HSC data. Equal area sampling within habitat types helped to minimize biases by allowing the relative quality of the different habitat types to dictate the form of the HSC data. Thus, if a species or life stage prefers shallow and fast habitat, and all habitat types are sampled with equal effort, most fish observations would probably occur in riffles and fewest would occur in deep pools. In theory, when data are then pooled among habitat types, the numerous shallow/fast observations from the riffles will dominate the HSC form and the fish's preference will be evident.

Although physical habitat characteristics varied widely among locations and seasonal periods, the large size of the Yakima River and the sampling of five habitat types at each study site ensured that areas of shallow, deep, fast, and slow water were represented in the HSC data. Also, at most study sites the thalwegs of deep pools and riffles were deeper and faster, respectively, than where the majority of fish were observed.

Habitat Suitability Criteria data were collected during daylight hours (typically 1000 to 1700 hrs) for spring, summer, and fall surveys when juveniles were most likely to be occupying feeding positions. During the winter in interior rivers, juvenile chinook are typi-

cally concealed deep within cover during daylight hours and are therefore unavailable for direct observation methodologies (Contor and Griffith 1995). Under cover of darkness, many juveniles emerge into the water column where they can be observed using underwater lights. Presumably these nocturnal positions are related to feeding behavior (Riehle and Griffith 1993); therefore, winter HSC data were collected only after dark (beginning 30 min after sunset) when the fishes' exact focal positions could be identified and evaluated.

Data Collection

Divers wearing mask and snorkel or SCUBA gear collected all HSC data from undisturbed juvenile chinook while traversing transects. A combination of bank transects and cross-sectional transects was surveyed at each study site. When an undisturbed chinook was observed within the transect area, the diver estimated the fish's fork length to the nearest cm (with reference to a ruler), estimated its nose height above the bottom (ft), and categorized its behavior as feeding, holding (stationary swimming), or resting (on the bottom). A numbered lead marker was then placed on the substrate underneath the fish's nose position, and the diver continued the survey. After completion of the transect, each marker was relocated and the following data were recorded: total water depth; mean column velocity; fish nose velocity; substrate characteristics in a 1-ft² area surrounding the marker (using the code described by Bovee and Cochnauer 1977); and the dominant type of six categories of instream object cover within 5 ft of the marker (Table 1). Distance (ft) from the marker to the nearest stream bank

TABLE 1
Substrate and instream object cover codes.

Substrate (in)	Code	Cover type (in)
	0	None Present
ORG - Organic detritus	1	Cobble (3.0–12.0)
MUD - Mud or clay (<0.002)	2	Boulder (>12.0)
SLT - Silt (0.002–0.02)	3	Riparian Vegetation
SND - Sand (0.02–0.25)	4	Woody Debris
GRV - Gravel (0.25–3.0)	5	Other
COB - Cobble (3.0–12.0)	6	
BLD - Boulder (>12.0)	7	
BED - Bedrock	8	

was measured during summer, fall, and winter surveys when fish were found to occupy offshore positions. Velocities were measured using a rotating-cup meter on a top-setting wading rod, except during SCUBA surveys when nose velocities were measured with a cup meter attached to a 30-in hand-held probe.

Data Analysis

Habitat Suitability Criteria data were treated separately by season but were pooled among study sites and habitat types within seasons. The data were organized into frequency histograms using bin intervals of 0.2 ft for depths and nose heights, 0.2 fps for mean column and nose velocities, 0.5 (no units) for the substrate code, and 5.0 ft for distance to bank. Histograms for cover were based on the six discrete cover codes.

Habitat Suitability Criteria curves were developed for depth, mean column velocity, and substrate by fitting 4th-order polynomial regression models to the histograms. Polynomials were used to construct HSC because they are readily available, provide statistics describing goodness-of-fit, and because 4th-order models generally provide a visually realistic fit to the typically skewed HSC data. However, polynomials often do not perform well toward the extreme ends of the distributions where sample sizes are small (e.g., in deep or fast water). To alleviate the unrealistic undulations that sometimes resulted at the distribution tails, the polynomial curve was terminated when predicted suitabilities descended to 0.2 in deeper water, faster water, and finer substrates. A straight line was then drawn to the last recorded observation. Modifications to regression curves were also nec-

essary in two other situations: (1) where polynomials failed to describe the steep ascending suitability of shallow water for recently emerged chinook fry, a new model was generated after excluding the data from the first bin (14 observations at >0 to 0.19 ft) and the suitability was then drawn from the predicted value at the second bin (95 observations from 0.2 to 0.39 ft) down to zero suitability at zero depth; and (2) where a high, isolated spike occurred in the winter substrate data that required eliminating that bin in order to fit the remaining data and then drawing a line from the fitted curve to capture the isolated spike. All modified lines are shown in relation to the regression curves.

Habitat Suitability Criteria curves were not generated for focal velocity, focal height, or distance to bank because these variables are poorly modeled or unsuitable for use with a PHABSIM analysis. The study design did not account for differences in the availability of instream object cover among habitat types or study sites. Because cover was highly variable between sample areas, no attempt was made to assign relative suitabilities (HSC curves) to the cover data.

Comparisons of seasonal use of habitat variables were made with Kruskal-Wallis (KW) tests (Biostat, Sigma Soft™) on the histogram data. The Kruskal-Wallis test is a nonparametric analysis of variance that evaluates the relative "locations" of the ranked habitat data rather than the parametric means (Sokal and Rolf 1969). When significant seasonal effects were found (at $P < 0.05$), a-posteriori multiple comparisons tests were performed using a non-parametric Tukey's Honestly Significant Difference (HSD) test. The significance level for all multiple comparisons tests was $P = 0.05$.

RESULTS

Study Site Characteristics

Habitat characteristics varied among seasons and among study sites within seasons (Table 2). In general, seasonal data from the upper basin (spring and fall) were collected from smaller channels at lower streamflows than were data collected from middle and lower segments (summer and winter). Water temperatures also differed according to seasons, where temperatures were in the low to mid-30s° F during the winter, the low to mid-

40s° F during the spring, the 50s° F during the fall, and from the 50s to 60s° F during the summer.

Within seasons, channel characteristics (width, flow, and slope) varied among some study sites. During the spring, the two Easton mainstem sites were sampled at relatively high flows (483 cfs), whereas the neighboring Cle Elum River was regulated at low flows (132 cfs). Consequently, most Easton data were collected in close proximity to woody



TABLE 2
Sampling and habitat characteristics at study sites.

Season	Study site	River mile	Sampling dates	Stream-flow	Water temp	#Habitats sampled	Avg area/habitat type	# HSC points
Spring				(cfs)	(°F)		(ft ²)	
EI	Easton I-90 Bridge	201.0	4/29–30/90	483	43	10	3,741	60
ES	Easton Side Channel	196.4	5/3/90	20	46	–	1,798	52
EF	Easton Fishing Access	195.2	5/1/90	483	44	6	2,360	58
CD	Cle Elum Diversion	6.4	4/25–27/90	132	41–45	10	6,203	105
CS	Cle Elum Slide	3.3	4/27–28/90	132	44	5	2,909	70
Summer								
EP	Ellensburg City Park	153.1	7/2–6/90	2,360	58–63	8	8,178	310
NA	Naches	13.0	7/8–10/90	810	53	7	4,041	93
Fall								
TF	Teaway Fishing Access	176.1	10/6–11/89&90	375	49–58	12	20,563	106
TR	Thorp Railroad Trestle	165.2	10/10/90	390	51–54	5	7,941	71
TD	Thorp Diversion Dam	161.4	10/2–5/90	450	54–59	12	21,077	72
Winter								
EI	Easton I-90 Bridge	201.8	2/15/94	126	34	4	2,475	15
SC	South Cle Elum	181.0	2/9/94	363	33	4	2,300	30
KO	Ellensburg KOA	155.9	2/14/94	466	n/a	4	2,200	3
UM	Umtanum Creek	139.0	2/13/94	591	38	4	1,600	20
WY	Wymer	135.8	2/7/94	620	33	4	1,660	4
BR	Burbank Creek	129.8	2/6/94	630	34	4	1,550	12
GR	Yakima Greenway	113.3	2/2/94	1,319	34	4	1,375	3
ZI	Zillah	91.0	2/3/94	1,074	35	4	1,300	3
SA	Satus Creek	72.6	2/11/94	1,774	38	4	1,425	0

debris and riparian vegetation associated with the stream banks, whereas the Cle Elum River data were mostly collected along exposed bars. Large differences in channel characteristics and water temperatures also occurred between the two summer study sites, where the Naches site was smaller, steeper, and colder (from 5 to 10° F) than the Ellensburg site. In the fall, portions of the Teaway site were dominated by jams of large woody debris that were generally lacking at the Thorp sites. The wide range of locations sampled during the winter season produced large differences in habitat characteristics between study sites.

Despite many differences among study sites within seasons, the equal area sampling design helped to ensure that the full range of available depths and velocities were repre-

sented in the data. With the exception of the small side channel site at Easton, all other sites included sampled areas of habitat that were deeper and faster than the range of most observed focal positions.

Seasonal Fish Observations

Differences in fish sizes among seasons are most evident between the spring survey and subsequent surveys (Table 3). Although fall juveniles averaged only 1.6 cm longer than summer juveniles, the fall median was 2 cm larger than the summer median. Individual fish lengths were not estimated during the winter survey. The number of HSC observations collected in spring, summer, and fall seasons all exceeded the 150–200 observations suggested as a minimum for developing site-



TABLE 3

Basic statistics for habitat suitability criteria variables by season. "n/a" is data not collected.

Variable	Season	n	Mean	Median	SD	Range
Fish length (cm)	Spring	345	3.0	3.0	0.19	2–4
	Summer	403	7.5	7.0	1.11	4–12
	Fall	249	9.1	9.0	0.73	7–11
	Winter	90	n/a	n/a	n/a	n/a
Water depth (ft)	Spring	345	0.86	0.60	0.71	0.05–4.40
	Summer	403	2.03	1.90	1.02	0.05–7.00
	Fall	248	2.80	2.45	1.29	0.80–10.10
	Winter	90	2.69	2.13	2.22	0.10–13.00
Focal height (ft off bottom)	Spring	345	0.4	0.2	0.37	0.0–3.5
	Summer	403	0.5	0.4	0.41	0.0–2.2
	Fall	248	0.8	0.5	0.61	0.2–3.4
	Winter	90	0.2	0.0	0.34	0.0–1.8
Mean column velocity (fps)	Spring	345	0.24	0.16	0.25	0.00–1.33
	Summer	402	1.31	1.24	0.71	0.14–4.32
	Fall	249	0.99	0.95	0.56	0.00–3.23
	Winter	90	0.22	0.12	0.24	0.00–1.24
Focal velocity (fps)	Spring	345	0.22	0.15	0.22	0.00–1.19
	Summer	402	1.01	0.93	0.51	0.07–2.74
	Fall	249	0.80	0.79	0.42	0.00–1.84
	Winter	84	0.12	0.05	0.17	0.00–0.76
Substrate	Spring	344	4.6	4.9	1.47	1.0–8.0
	Summer	403	5.1	5.3	1.18	1.0–7.0
	Fall	249	5.5	5.6	0.98	1.0–7.0
	Winter	90	5.0	5.1	1.60	1.0–7.6
Distance from bank (ft)	Spring	345	n/a	n/a	n/a	n/a
	Summer	378	8.7	5.1	10.1	0.0–66.5
	Fall	222	16.0	11.0	14.5	0.0–70.0
	Winter	90	7.3	6.0	5.6	0.0–27.0

specific HSC (Bovee 1986). In winter, the low fish densities that were found at most study sites resulted in only 90 observations (Table 2). Consequently, the winter data are more subject to biases resulting from low sample size. Spring and fall surveys yielded HSC observations from among most study sites in relatively equal numbers (within seasons), but data from summer and winter surveys are more dominated by observations from fewer study areas. Overall, the HSC data collected during this study are most representative of habitat use in the upper and middle segments of the Yakima River during the spring, summer, and fall seasons. The winter data, although limit-

ed in scope, describe a major change in habitat selection and provide a useful comparison with earlier seasons when growth and activity of juvenile chinook are greater.

Seasonal Habitat Selection

Water Depth. The overall "locations" of ranked depths were different among seasons (KW, $P < 0.001$). In the spring, the distribution of depths selected by juvenile chinook was highly skewed towards shallow water, where most fish were observed at depths between 0.2–0.4 ft (Figure 2). By summer, the larger juvenile chinook were rarely observed at depths <0.5 ft



and were most common at depths between 0.7–4.1 ft. The mean depth of juvenile focal positions was greatest in the fall (Table 3), when fish were rarely observed at depths <1.0 ft, but were relatively common at depths >4.0 ft. Juvenile chinook utilized the widest range of depths (0.08–13.00 ft) during the winter survey. Although most juveniles observed during the winter selected depths similar to those used during the summer, the use of depths >4.0 ft remained relatively high as was seen in the fall. Multiple comparison tests indicated that summer and winter locations were not different from each other, but the spring and fall locations were unique (Tukey's HSD, $P < 0.05$).

Each of the polynomial HSC curves were modified to encompass isolated observations in deeper water (e.g., dotted lines in Figure 2). When comparing the modified HSC curves from each of the four seasons (Figure 3, Table 4), the distinctness of the spring curve is evident. The summer and winter curves are very similar in appearance up to the peak, but diverge

afterwards with the winter curve maintaining higher suitability at deeper depths. The fall curve produces the highest suitabilities of deeper water until depths exceed 6 ft, where the winter curve maintains higher suitability into deeper water.

Mean Column Velocity. The ranked locations of mean column velocities selected by juvenile chinook differed among seasons (KW, $P < 0.001$), however velocities measured at spring and winter focal positions were similar (Tukey's HSD, $P > 0.05$). Approximately 99% of all spring and winter focal positions occurred at mean column velocities of <1.0 fps, and 60% of positions had velocities <0.20 fps (Figure 4). In summer and fall, average velocities at juvenile focal positions were approximately 1.0 fps or greater (Table 3), and less than 6% of juveniles selected velocities <0.20 fps. Summer and fall velocities were different from each other and from spring and winter velocities (Tukey's HSD, $P < 0.05$).

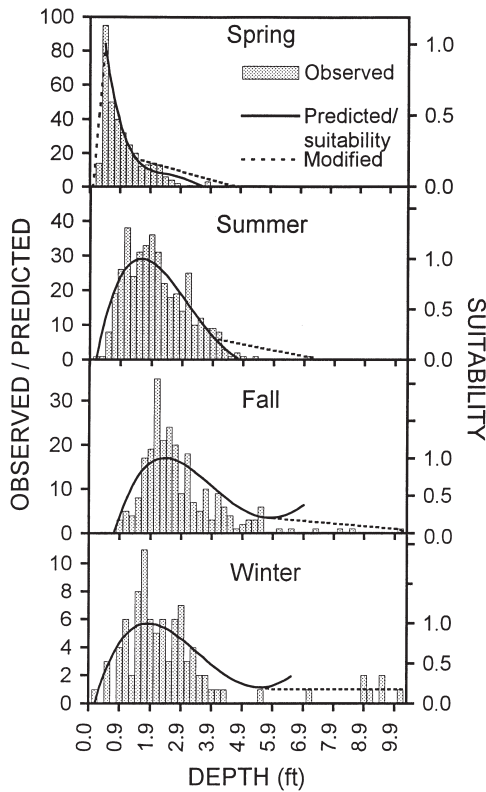


FIGURE 2. Depths at focal positions selected by juvenile chinook (bars) according to season. Solid line is predicted depth (left axis) based on polynomial regression, normalized to suitability (right axis). Dotted line is modified suitability.

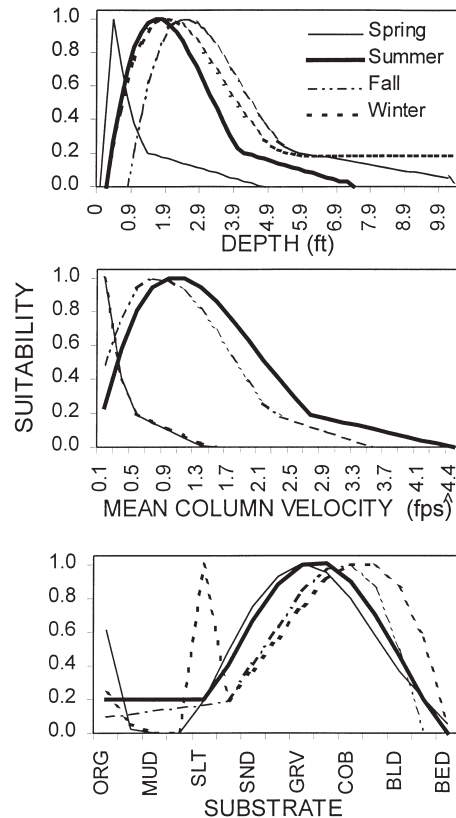


FIGURE 3. Comparison of seasonal depth, mean column velocity, and substrate habitat suitability criteria for juvenile chinook in the Yakima River.



TABLE 4

Seasonal depth (ft), mean column velocity (fps), and substrate habitat suitability criteria values for juvenile chinook.

Depth	Spring	Summer	Fall	Winter	Velocity	Spring	Summer	Fall	Winter
0.0	0.00				0.0	1.00	0.01	0.29	1.00
0.1	0.50	0.00		0.00	0.1	1.00	0.24	0.48	1.00
0.3	1.00	0.27		0.25	0.3	0.41	0.58	0.77	0.39
0.5	0.73	0.51		0.45	0.5	0.19	0.81	0.93	0.20
0.7	0.53	0.69	0.00	0.62	0.7	0.15	0.94	1.00	0.16
0.9	0.38	0.83	0.22	0.76	0.9	0.10	1.00	0.99	0.11
1.1	0.28	0.92	0.44	0.86	1.1	0.06	1.00	0.92	0.07
1.3	0.20	0.98	0.62	0.93	1.3	0.01	0.94	0.81	0.02
1.5	0.19	1.00	0.76	0.97	1.5	0.00	0.86	0.68	0.00
1.7	0.18	1.00	0.87	1.00	1.7		0.75	0.54	
1.9	0.16	0.97	0.94	1.00	1.9		0.63	0.39	
2.1	0.15	0.92	0.98	0.99	2.1		0.51	0.26	
2.3	0.14	0.86	1.00	0.96	2.3		0.39	0.18	
2.5	0.13	0.79	1.00	0.92	2.5		0.29	0.15	
2.7	0.12	0.71	0.97	0.87	2.7		0.19	0.12	
2.9	0.10	0.63	0.94	0.81	3.5		0.11	0.00	
3.1	0.09	0.55	0.89	0.75	>4.4		0.00		
3.3	0.08	0.46	0.83	0.68	Substrate				
3.5	0.07	0.38	0.77	0.62	1.0	0.61	0.20	0.10	0.23
3.7	0.06	0.30	0.70	0.55	1.5	0.02	0.20	0.12	0.06
3.9	0.04	0.23	0.63	0.49	2.0	0.00	0.20	0.14	0.00
4.1	0.03	0.20	0.56	0.43	2.5	0.00	0.20	0.15	0.00
4.3	0.02	0.19	0.49	0.37	3.0	0.19	0.20	0.17	1.00
4.5	0.01	0.18	0.43	0.32	3.5	0.48	0.40	0.19	0.20
4.7	0.00	0.16	0.37	0.28	4.0	0.75	0.67	0.40	0.38
4.9		0.15	0.32	0.25	4.5	0.93	0.88	0.63	0.57
5.1		0.14	0.28	0.22	5.0	1.00	0.99	0.84	0.76
5.3		0.13	0.24	0.21	5.5	0.95	1.00	0.97	0.91
5.5		0.12	0.22	0.20	6.0	0.80	0.90	1.00	1.00
5.7		0.10	0.21	0.19	6.5	0.59	0.71	0.86	1.00
5.9		0.09	0.20	0.18	7.0	0.37	0.46	0.49	0.86
7.3		0.00	0.15	0.18	7.5	0.21	0.20	0.00	0.56
>10.2			0.00	0.18	8.0	0.05	0.00	0.00	0.05

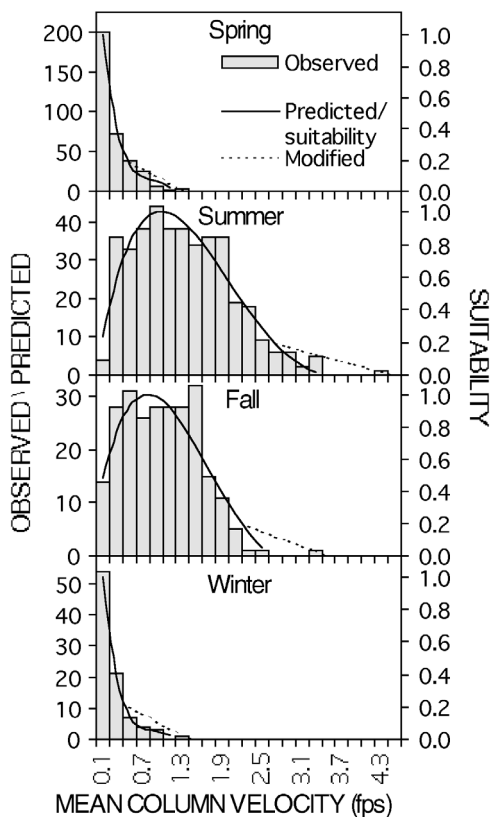


FIGURE 4. Mean column velocities at focal positions selected by juvenile chinook (bars) according to season. Solid line is predicted velocity (left axis) based on polynomial regression, normalized to suitability (right axis). Dotted line is modified suitability.

The curvilinear nature of the polynomial curves did not reflect the broad range of velocities that were most commonly selected during summer and fall seasons (e.g., from 0.3 fps to 1.9 fps in summer), but rather produced a single peak in the middle of the range (Figure 4). The few isolated observations in higher velocities were encompassed with minor modifications to the polynomial curves. When plotted together, the spring and winter HSC curves are almost indistinguishable (Figure 3). The summer curve appears similar in shape to the fall curve, but is somewhat broader and shifted approximately 0.3 fps toward faster water (Table 4). Although the juvenile chinook averaged 1.6 cm longer in the fall than in the summer, the warmer water temperatures encountered at Ellensburg (Table 2) may have resulted in greater use of higher velocities than seen at the fall study sites.

Substrate. The ranked locations of dominant substrates were different among seasons (KW,

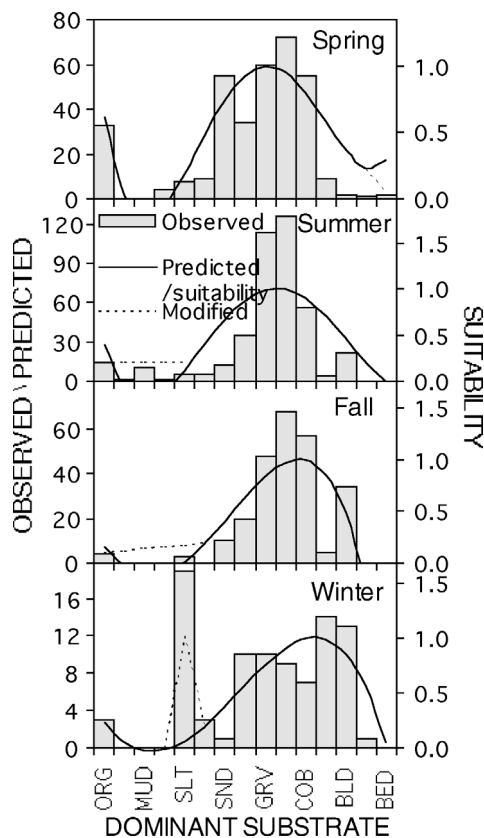


FIGURE 5. Dominant substrate at focal positions selected by juvenile chinook (bars) according to season. Solid line is predicted substrate (left axis) based on polynomial regression, normalized to suitability (right axis). Dotted line is modified suitability.

$P < 0.001$). In the spring, juvenile chinook selected focal positions overlying a wide range of substrate categories (Table 3, Figure 5). During the summer and fall, relatively few juveniles were associated with substrates smaller than gravel but were most often found over mixtures of gravel and cobble. Juveniles were again associated with a wide range of substrates during the winter season, but with a noticeable increase in the occurrence of silt and boulder substrates. The seemingly contradictory increase in the use of both fine and coarse substrates may be due to the winter juvenile's close association with large cover elements, which are used for daytime concealment (see instream cover below), and slow velocities, which allow the deposition of fines during low flow conditions. Despite the apparent uniqueness of the winter substrate data, the summer and winter mean ranks were not different (Tukey's HSD, $P > 0.05$). Mean ranks of the spring and fall substrates were, however, different from all others (Tukey's HSD, $P < 0.05$).



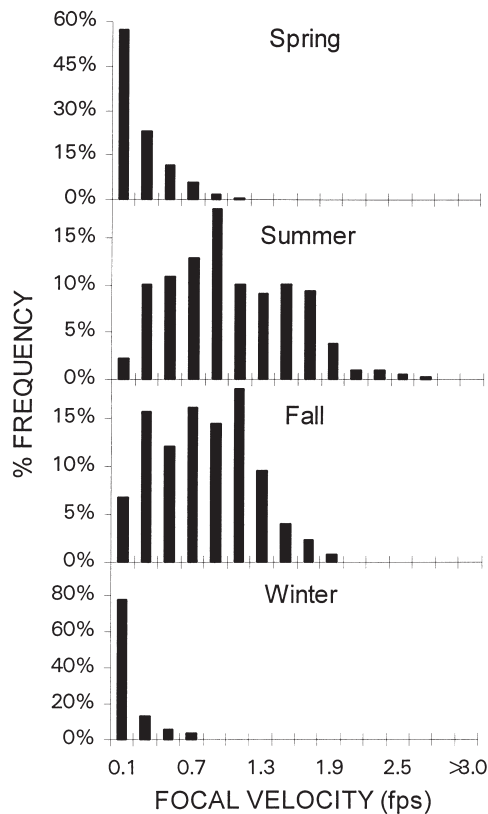


FIGURE 6. Focal velocities at positions selected by juvenile chinook according to season.

Modifications to the polynomial curves were necessary at the ends of the distributions for most data sets and to account for silt substrate in the winter data (Figure 5). When compared, the seasonal HSC curves reflect the increasing suitability of larger substrates during the fall and winter months and the increased suitability of finer substrates (organic matter and silt) during spring and winter (Figure 3, Table 4).

Focal Velocities. The Kruskal-Wallis test indicated that ranked locations of focal velocities differed among seasons ($P < 0.001$). Multiple comparisons tests showed that all seasonal mean ranks were different from each other (Tukey's HSD, $P < 0.05$). In the spring, most juvenile chinook (57%) selected positions with focal velocities < 0.2 fps, and only one fish was observed with a focal velocity of > 1.0 fps (Figure 6). Focal velocities selected by juvenile chinook in the summer ranged from 0.07 to 2.74 fps and were higher than during any other season (Table 3). Only 2% of observations were < 0.2 fps, but 45% exceeded 1.0 fps. In the fall, juveniles used slower velocities (< 0.2 fps) to a

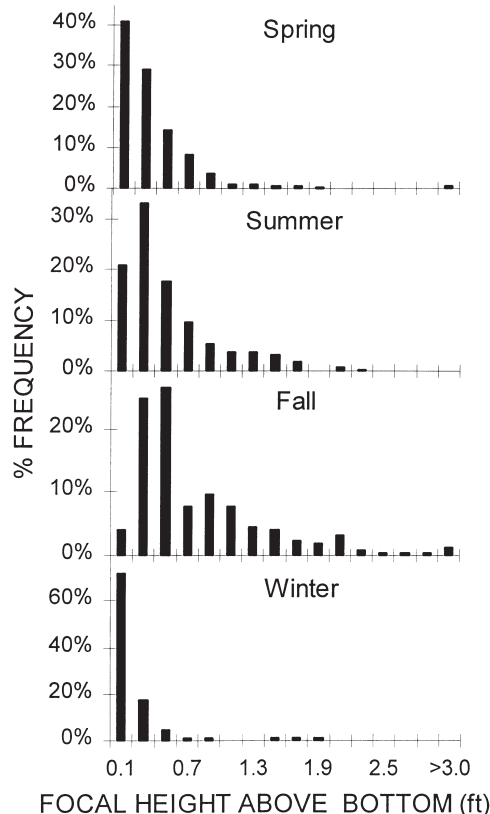


FIGURE 7. Focal heights at positions selected by juvenile chinook according to season.

greater degree (7%) and higher velocities (> 1.0 fps) to a lesser degree (33%) than in the summer. Juvenile chinook selected the slowest and most restricted range of focal velocities during the winter than at any other season. Although the range of mean column velocities selected during winter and spring was similar, the average focal velocity in the winter was only one-half of the average focal velocity in the spring (Table 3).

Focal Height. The ranked locations of focal heights were different among seasons (KW, $P < 0.001$), and all seasonal mean ranks were distinct from each other (Tukey's HSD, $P < 0.05$). In the spring, approximately 40% of juvenile chinook held focal positions < 0.2 ft from the bottom and only 4% held positions > 1.0 ft (Figure 7). By summer, the mean focal height of juvenile chinook was only slightly higher than the positions selected in the spring (Table 3). However, only 21% of fish held positions < 0.2 ft from the stream bottom, and 13% held positions > 1.0 ft. The focal heights selected by juveniles were higher during the fall than dur-

ing all other seasons. The relatively low use of near-bottom positions (4% <0.2 ft) and the high use of off-bottom positions (26% >1.0 ft) is in marked contrast to the spring and winter data (Figure 7). Juvenile chinook held focal positions closer to the stream bottom during the winter than at any other season (Table 3), when over 70% of juveniles were stationed <0.2 ft from the bottom.

The observed trends in focal heights cannot be explained solely by the changes in total water depth at fish locations among seasons (Figure 4). For example, the increase in focal height seen from the spring to the summer (Figure 7) occurred even though the relative focal height (the proportional distance from the surface to the bottom) was lower in the summer (mean=80% of total depth) than in the spring (mean=60%). In the fall, the relative focal height (mean=70%) was intermediate to that of summer (deeper relative positions) and spring (shallower relative positions). Relative focal heights were lowest during the winter when 66% were observed actually in contact with the substrate materials (relative height=100%).

Instream Object Cover. A Kruskal-Wallis test performed on ranked values of instream object cover suggested that ranked locations were different among seasons ($P<0.001$). However, because the presence or type of cover was not a part of the habitat stratification design, the availability of some forms of instream object cover was highly variable between study areas. Consequently, seasonal comparisons are difficult to interpret. For example, in the spring, 39% of juvenile focal positions occurred in proximity to woody debris cover (Figure 8), and a multiple comparisons test indicated that the spring mean rank was higher than all other seasons (Tukey's HSD, $P<0.05$). The relatively high use of woody debris cover in spring when compared to other seasons is due in part to the small juvenile's close association with the stream margin (see Distance to Bank), and because woody debris was more common in the upper segment where spring data were collected than in most downstream segments. No cover was present within 5 ft of focal positions for 23% of spring observations.

In contrast to the spring data, 51% of all juvenile chinook observed during the summer selected focal positions more than 5 ft away from instream cover (Figure 8). Focal positions

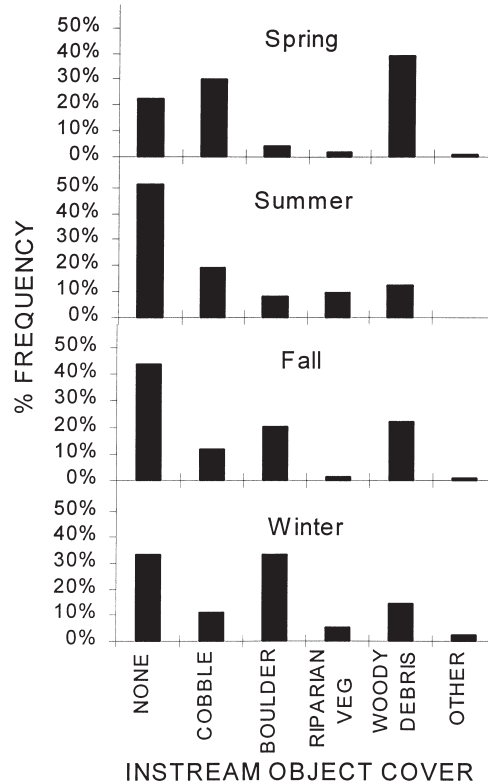


FIGURE 8. Dominant instream object cover at focal positions selected by juvenile chinook according to season.

selected in the fall were also typically over 5 ft from instream object cover (44%). In the winter, an equal proportion of focal positions (33%) contained either boulder cover or no cover. The summer and winter mean ranks were different (Tukey's HSD, $P<0.05$), but the fall mean rank was not different from either the summer mean rank or the winter mean rank.

Despite the large number of winter observations lacking cover (33%), juvenile chinook were only abundant where some form of dense overwintering cover (e.g., boulder/riparian, or woody debris) existed within the habitat unit. The 5-ft area of coverage for evaluating instream cover frequently did not account for the nearby presence of overwintering habitat. Only 7% of all juveniles observed during the winter occurred more than 20 ft away from some form of dense hiding cover.

Distance to Bank. Distance to bank was not measured during the spring survey, but <1% of observations were made from cross-sectional transects. The remaining observations



were all made along bankside transects, which extended an average of 6 ft from the bank in the Yakima and 10 ft in the Cle Elum. The ranked locations of distance to bank were different among the remaining seasons (KW, $P < 0.001$). During the summer, most juveniles continued to occupy nearshore positions, but 24% of observations occurred >10 ft from the bank (Figure 9). Focal positions selected during the fall averaged 16.0 ft from the bank (Table 3), and over 50% of observations occurred >10 ft from shore. The distance to bank was greater during fall than during other seasons (Tukey's HSD, $P < 0.05$). In the winter, most juvenile chinook were again observed near the bank, but 19% of focal positions occurred >10 ft offshore. Many of those fish were in a single deep pool habitat containing a woody debris jam that extended well into the scour hole. Mean ranks for summer and winter bank distances were not different (Tukey's HSD, $P > 0.05$).

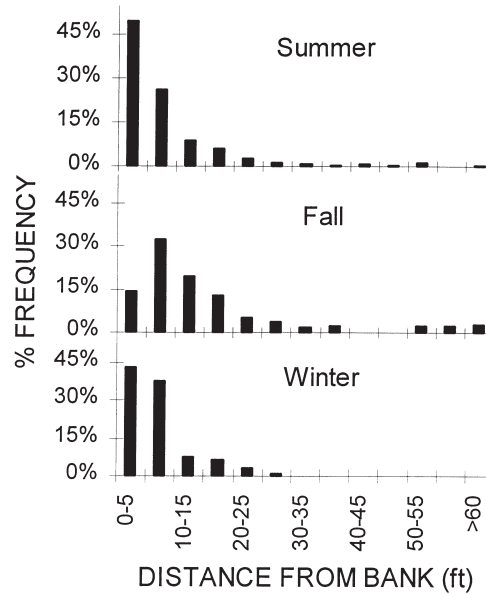


FIGURE 9. Distance to bank from focal positions selected by juvenile chinook according to season.

DISCUSSION

Seasonal Changes in Habitat Use

In the Yakima River, direct observation of juvenile chinook from a habitat-stratified sampling approach in a wide variety of stream reaches provided evidence of size and seasonal-related changes in habitat use. Although this study was not designed to assess the individual effects of fish size, habitat availability, or seasonal variables (e.g., streamflow, water temperature, photoperiod) on habitat use by juvenile chinook, juvenile salmonids have long been known to exhibit size and seasonal-related shifts in habitat use (McCrimmon 1954; Hartman 1965; Chapman and Bjornn 1969). Juvenile chinook in British Columbia and Idaho were observed to move away from stream margins and use deeper and faster water as they grew in size (Lister and Genoe 1970; Everest and Chapman 1972). Because size and seasonal-related habitat shifts occur concurrently, it is frequently difficult to assess the relative role of each factor independently. In an attempt to clarify the specific effects of increasing size on habitat selection by juvenile rainbow trout, Baltz et al. (1991) evaluated focal characteristics in a flow-controlled environment where the physical habitat remained

relatively constant throughout the summer and fall. They found that size effects alone accounted for changes in the use of depth, mean column and focal velocities, focal height, and substrate. When habitat use was adjusted for fish size, seasonal changes in mean column and focal velocities were significant. Many of these changes were thought to result from the fish's changing metabolic needs and foraging efficiency at different temperatures (Smith and Li 1983).

Depth. In the Yakima River, mean depth of focal positions increased by three-fold as juvenile chinook grew from 3 cm in the spring to 9–10 cm in the fall and winter (Table 3). Larger juveniles rarely used the shallow water depths heavily used by smaller juveniles. Other studies have recognized the susceptibility of small fish to predation or displacement by high velocities (McCrimmon 1954; Ottaway and Clarke 1981), and those factors may affect the choice of shallow, nearshore focal positions by chinook fry. Focal positions selected by recently emerged juveniles in the Cle Elum River, however, were also restricted to margin habitats even though larger preda-

tory fishes were rarely observed and the ambient low-flow conditions produced large quantities of low velocity habitat in deeper water.

These data and other studies (Everest and Chapman 1972; Baltz et al. 1991; Riehle and Griffith 1993) indicate an increase in suitability of deeper water for larger juveniles. Some HSC depth curves for juvenile chinook are modified to maintain suitability at 1.0 with increasing depth (Bovee 1978; Hampton 1988; Rubin et al. 1991), which assumes that once a critical depth is reached, all greater depths are equally suitable. In small streams in central Idaho, Rubin et al. (1991) found maximum densities of juvenile chinook in the deepest habitats sampled, which led to an HSC curve that leveled off at 1.0 in deeper water. In the Yakima River, which is considerably deeper than the central Idaho streams, juveniles did appear to use deeper water to a greater degree in fall and winter than in summer. However, despite considerable sampling effort in deep water habitats (all deep pools and deep runs exceeded 6 ft), relatively few fish were found at depths >4 ft. Increased use of deeper water in fall and winter may be related to increased association with large cover objects, such as boulder/rip-rap and large woody debris (Bustard and Narver 1975; Swales et al. 1986). Such cover elements often result in local scour with increased depths (Lisle 1986). Deeper habitat is also directly associated with lower velocities, which are selected for during colder seasons in response to decreased metabolic demands (Smith and Li 1981; Baltz et al. 1991).

Mean Column and Focal Velocity. The seasonal choice of mean column and focal velocities by juvenile chinook in the Yakima River followed the patterns described in other studies (Lister and Genoe 1970; Everest and Chapman 1972; Rimmer et al. 1984; Heggenes and Saltveit 1990; Baltz et al. 1991). In this study, velocities at summer focal positions averaged 5 times greater than velocities during spring (Table 3). The increases in fish size and water temperatures from spring to summer necessitated greater energy intake by juvenile chinook, which is often accomplished by selecting focal positions with higher velocities and drift rates (Chapman and Bjornn 1969; Smith and Li 1983; Hughes and Dill 1990). The increased use of higher velocities with increased size was strongly mediated, however, by declining water temperatures in fall and (especially) winter, as described by Baltz et al.

(1991). Fall mean column and focal velocities averaged 20%–30% than summer velocities, and by winter the velocities selected were even lower than those used by recently emerged fry.

The low velocity requirements of small fry and overwintering juveniles may lead to problems when applying PHABSIM, because suitable habitat (expressed as WUA) is often maximized at near zero flow releases, which may be unrealistic and ecologically damaging. One result of a very low flow regime would be a partial separation of the wetted edge from the riparian zone and the cover provided by vegetation, undercut banks, and high flow-deposited woody debris. Although this condition existed in the Cle Elum River during spring sampling, chinook fry remained abundant along margins of the exposed bars. Loss of bankside cover could be more critical to overwintering juveniles, however, because these fish require cover that is sufficiently dense to escape from direct sunlight during daylight hours (Contor and Griffith 1995).

Substrate. In the Yakima River, juvenile chinook used greater proportions of larger substrates as the season progressed (Figure 5). In particular, the relative proportion of boulder substrate increased from 1% in spring, to 5% in summer, to 14% in fall and winter. The increasing use of larger substrates as fish grow is widely recognized, but the close correlation between substrate size and water velocity makes it difficult to assess the specific importance of substrate when determining habitat suitability. When controlled for velocity, Lister et al. (1995) found that densities of juvenile chinook in the Thompson River, British Columbia, were influenced by substrate size, particularly in fall as water temperatures declined. Some studies have thus concluded that substrate is an important determining factor in focal point selection (Rimmer et al. 1984; Hayes and Jowett 1994), whereas others have not (Wickham 1967; Gosse and Helm 1982).

Because most juvenile salmonids feed on drifting prey and will defend optimum locations against competitors, larger substrates may affect habitat suitability by increasing habitat complexity through the creation of sheltered feeding stations, visually isolated territories, or refuges from predators (Chapman 1966; Chapman and Bjornn 1969; Bozek and Rahel 1991; Hayes and Jowett 1994).

Refuge from predation or extreme environmental conditions leads to the increasing importance of large, unembedded substrates (or other cover elements) as water temperatures decrease in fall and winter and fish begin exhibiting winter concealment behavior (Bjornn 1971; Contor and Griffith 1995). Although the observation of 30% of winter focal positions over fine substrates would appear to contradict the importance of large bed elements during winter, I found that some juveniles would disperse considerable distances away from their daytime hiding cover in boulder/rip-rap or woody debris if near-zero water velocities extended into the midchannel (e.g., in larger pools). Thus, in winter, fish would sometimes utilize nighttime focal positions that had fine substrates and lacked cover, but would nevertheless require the larger cover elements for daytime hiding. Failing to incorporate such larger-scale substrate and cover elements during a winter PHABSIM study could lead to inflated or biased WUA estimates.

Focal Height. Juvenile chinook in the Yakima River and other locations occupied focal positions close to the substrate after emergence and progressively moved higher off the bottom as they grew (Heggenes and Saltveit 1990; Baltz et al. 1991), yet most fish remained within 1 ft of the bottom at all seasons (Figure 7). The observed changes in focal height were only partially due to the concurrent changes in the total depth selected by juvenile chinook, because the relative height above bottom decreased with fish size and season. Actual and relative focal heights were lowest in winter in the Yakima River when most fish were observed with their pectoral fins resting on the substrate. The combination of deep water and near-bottom focal positions selected by juveniles during the winter is problematic with PHABSIM, which relies on mid-column velocities to estimate habitat suitability (Shirvell 1986; Baltz et al. 1987; Heggenes and Saltveit 1990). Although a modeling option can be used to substitute estimate bottom velocities in place of mean column velocities in PHABSIM, the accuracy of such velocity predictions should be field verified before use because the large cover elements (i.e., boulder/rip-rap, large woody debris) that are characteristic of many winter focal positions could make such predictions unreliable (Bovee et al. 1998).

Instream Object Cover. Evaluating the cover requirements of stream-dwelling salmonids is a difficult procedure, particularly when the cover relationship must be expressed in the simplistic form of HSC (Shirvell 1986). The categorical nature of cover coding systems, the use of cover as protection from predators or other environmental factors (e.g., excessive velocities, sunlight), the potential number of cover code combinations, and the ambiguity of recognizing effective cover elements all lead to nonstandardized coding methodologies (Pacific Gas and Electric Company 1994). Furthermore, the fish-cover relationship may be different or less evident in the relatively deep and cover-rich habitats of steep, cobble/boulder dominated rivers such as the upper and middle Yakima Basin than in shallow, low-gradient, alluvial rivers where cover is lacking or restricted to stream banks.

In this paper, I only evaluated the presence or absence of a dominant type of instream object cover within 5 ft of a focal position. Because instream cover characteristics differed widely between study reaches, I did not assign relative suitabilities to the various cover types used by fish. However, I found—as have many other researchers—that cobbles, boulders, and large woody debris were important cover types used by juvenile chinook (Lister and Genoe 1970; Bjornn 1971; Hillman et al. 1987; Swales et al. 1986). I also found that 45%–50% of summer and fall-rearing juveniles selected focal positions that were not in the immediate proximity of instream cover. Other studies have also shown that instream cover is not always apparent at selected focal positions, particularly as fish grow larger (Bachman 1984; Campbell and Neuner 1985; Hughes and Dill 1990). The importance of evaluating cover at a larger scale than the focal position was readily apparent during the winter study, where the nighttime location of juveniles was related to the presence of daytime hiding cover as much as 30 ft away. Some of the juveniles observed actively feeding during the fall at the Teanaway study site were fish that appeared to have dispersed up to 200 ft upstream from nighttime resting positions in a large woody debris jam (Thomas R. Payne and Associates 1995b). Thus, larger-scale cover elements may have significant effects on the habitat suitability of focal positions during the fall and winter periods.

Distance to Bank. The relative use of offshore positions in the Yakima River increased as fish grew in size, as demonstrated elsewhere (Lyster and Genoe 1970; Everest and Chapman 1972; Hillman et al. 1987). As juvenile chinook grow in size, their increased swimming ability and reduced threat from predation may lead to greater use of midchannel habitats. In the Yakima River, the proportion of fish observed >10 ft from the bank increased from <1% in the spring to 50% in the fall. Over 20% of fall focal positions occurred >20 ft from the bank. Many winter studies have reported that nighttime focal positions are largely restricted to nearshore areas (Griffith and Smith 1993; Riehle and Griffith 1993). Although most fish observed during the winter in the Yakima River occurred <10 ft from the bank, I found that fish dispersed well into the midchannel if water velocities near the bottom remained close to zero. Almost 20% of winter focal positions occurred >10 ft from the bank. In contrast, recently emerged juveniles in the spring were rarely observed more than 10 ft from the bank even when predators were absent and

low-velocity habitat was readily available offshore.

A method sometimes used in PHABSIM studies is to "block-out" the midchannel areas by classifying them as unsuitable, and only assess habitat along the stream margins (Parametrix and Hardin-Davis 1984). I found after surveying 24 cross-sectional transects in low-flow and high-flow reaches in spring that small juveniles rarely occurred in midchannel habitats but were instead restricted to habitats <10–15 ft offshore. During winter, most juveniles appeared to be dependent upon bank-side cover for daytime hiding even though many nighttime focal positions were in midchannel areas. For recently emerged fry and overwintering juveniles, blocking-out midchannel areas and modeling only margin habitat may be an effective approach. For summer and fall rearing, however, I found that many juveniles dispersed into offshore habitats and actively fed during the afternoon and evening. Blocking-out midchannel areas would therefore ignore an important component of juvenile rearing habitat.

CONCLUSIONS

I agree with many researchers that PHABSIM studies should utilize HSC curves that account for changing habitat use over seasons (Campbell and Neuner 1985; Heggenes and Saltveit 1990; Baltz et al. 1991). In the Yakima River, recently emerged chinook fry were restricted to shallow, slow, nearshore habitats even where midchannel habitats appeared suitable. The quantity and quality of margin habitat containing slow velocities and instream cover is important for maintaining high densities of young juveniles (Moore and Gregory 1988; Bozek and Rahel 1991) and may affect survival to later life-stages (LeCren 1973; Nehring and Anderson 1993). Because most rivers exhibit high discharges during fry emergence, a healthy riparian zone with associated instream cover is important to provide habitat complexity and shelter from excessive velocities or predation (McCrimmon 1954; Moore and Gregory 1988; Bozek and Rahel 1991). A lack of such habitat may result in downstream displacement of fry into potentially less suitable water (Chapman 1966; LeCren 1973) and could reduce the overall productivity of a river basin to rear anadro-

mous salmonids. Like Moore and Gregory (1988) and Nehring and Anderson (1993), I have found that many HSC curves that represent "fry" do not adequately describe the slow and narrow range of velocities required by small fry soon after emergence.

Focal positions selected by larger juveniles 3–4 months following emergence in the Yakima River were significantly different than positions used by smaller juveniles in a number of characteristics important to instream flow modeling. Greater depths, faster velocities, and higher use of midchannel habitats were evident at summer focal positions. As water temperatures declined in fall, juvenile chinook used deeper water and slower velocities and were more closely associated with instream cover than in summer. The association with slow velocities and instream cover grew yet stronger during winter. The accessibility of dense, bank-associated cover is important for high quality overwintering habitat (Bustard and Narver 1975; Hillman et al. 1987), but this factor is not always evident at the focal point scale of measurement. Physical Habitat Simulation analyses during

spring and winter seasons must expressly account for these riparian influences.

Clearly, the application of a single HSC curve to represent chinook rearing habitat during their entire first year is inappropriate and should be avoided wherever possible. Although the observed differences in seasonal habitat use described in this study are important, in the PHABSIM context it is how these different HSC curves affect estimates of WUA and, ultimately, instream flow decisions that is of greater importance (Williams et al. 1999). I do not show how seasonal-specific HSC would affect WUA projections in this study, but it is evident that the observed changes in habitat use between the fry emergence, sum-

mer and fall rearing, and overwintering periods could have dramatic effects on the outcome of habitat modeling.

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REFERENCES

- Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society* 113: 1–32.
- Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. *Transactions of the American Fisheries Society* 116: 12–20.
- Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. *Transactions of the American Fisheries Society* 120: 166–176.
- Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. *Transactions of the American Fisheries Society* 100: 423–438.
- Bovee, K. D. 1978. Probability-of-use criteria for the family Salmonidae. Instream Flow Information Paper No. 4. Washington, DC: U. S. Fish and Wildlife Service (FWS/OBS-78/07).
- Bovee, K. D. 1986. Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology. Instream Flow Information Paper No. 21. Washington, DC: U. S. Fish and Wildlife Service (Biological Report 86[7]).
- Bovee, K. D., and T. Cochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. Instream Flow Information Paper No. 3. Washington, DC: U.S. Fish and Wildlife Service.
- Bovee, K. D., B. L. Lamb, J. M. Bartholow, C. B. Stalnaker, J. Taylor, and J. Henriksen. 1998. Stream habitat analysis using the instream flow incremental methodology. Washington, DC: U.S. Geological Survey (Biological Resources Division Information and Technology Report [USGS/BRD-1998-0004]).
- Bozek, M. A., and F. J. Rahel. 1991. Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analysis. *Transactions of the American Fisheries Society* 120: 571–581.
- Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 32: 667–680.
- Campbell, R. F., and J. H. Neuner. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain streams. Pages 39–48 in F. W. Olson, R. G. White, and R. H. Hamre, editors. *Symposium on small hydropower and fisheries*. Bethesda, MD: American Fisheries Society.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *American Naturalist* 100: 345–357.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153–176 in T. G. Northcote, editor. *Symposium on Salmon and Trout in Streams*. Vancouver, British Columbia: University of British Columbia (H. R. MacMillan Lectures in Fisheries).
- Clune, T., and D. Dauble. 1991. The Yakima/Klickitat Fisheries Project: A strategy for supplementation of anadromous salmonids. *Fisheries* 16: 28–34.



- Contor, C. R., and J. S. Griffith. 1995. Nocturnal emergence of juvenile rainbow trout from winter concealment relative to light intensity. *Hydrobiologia* 299: 179–183.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29: 91–100.
- Fast, D., J. Hubble, M. Kohn, and B. Watson. 1991. Yakima River chinook enhancement study. Portland, OR: Bonneville Power Administration (Project No. 82–16).
- Gosse, J. C., and W. T. Helm. 1982. A method for measuring microhabitat components for lotic fishes and its application with regard to brown trout. Pages 138–149 in N. B. Armantrout, editor. *Acquisition and utilization of aquatic habitat inventory information*. Portland, OR: American Fisheries Society, Western Division.
- Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. *North American Journal of Fisheries Management* 13: 823–830.
- Hampton, M. 1988. Development of habitat preference criteria for anadromous salmonids of the Trinity River. Sacramento, CA: U. S. Fish and Wildlife Service, Division of Ecological Services.
- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* 22: 1035–1081.
- Hayes, J. W., and I. G. Jowett. 1994. Microhabitat models of large drift feeding brown trout in three New Zealand rivers. *North American Journal of Fisheries Management* 14: 710–725.
- Heggenes, J., and S. J. Saltveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *Journal of Fish Biology* 36: 707–720.
- Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. *Transactions of the American Fisheries Society* 116: 185–195.
- Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: Model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 2039–2048.
- LeCren, E. D. 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behavior. *International Council for the Exploration of the Sea* 164: 241–246.
- Lisle, T. E. 1986. Stabilization of a gravel channel by large streamside obstructions and bedrock bends, Jacoby Creek, Northwestern California. *Geological Society of America Bulletin* 97: 999–1011.
- Lister, D. B., and H. S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. *Journal of the Fisheries Research Board of Canada* 27:1215–1224.
- Lister, D. B., R. J. Beniston, R. Kellerhals, and M. Miles. 1995. Rock size affects juvenile salmonid use of streambank riprap. Pages 621–632 in C. R. Thorne, S. R. Abt, F. J. B. Barends, S. T. Maynard, and K. W. Pilarczyk. *River, Coastal and Shoreline Protection: Erosion Control Using Riprap and Armourstone*. NY: John Wiley and Sons.
- Major, R. L., and J. L. Mighell. 1969. Egg-to-migrant survival of chinook salmon (*Oncorhynchus tshawytscha*) in the Yakima River, Washington. *Fisheries Bulletin*: 67(2): 347–359.
- McCrimmon, H. R. 1954. Stream studies on planted Atlantic salmon. *Journal of the Fisheries Research Board of Canada* 11: 362–403.
- Modde, T., and T. B. Hardy. 1992. Influence of different microhabitat criteria on salmonid habitat simulation. *Rivers* 3: 37–44.
- Moore, K. M. S., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1921–1930.
- Nehring, R. B., and R. M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation System. *Rivers* 4: 1–19.
- Ottaway, E. M., and A. Clarke. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) to downstream displacement by high water velocities. *Journal of Fish Biology* 19: 135–145.
- Pacific Gas and Electric Company. 1994. Evaluation of factors causing variability in habitat suitability criteria for Sierra Nevada trout. San Ramon, CA: Pacific Gas and Electric Company (Environment, Health and Safety Report 009.4–94.5).
- Parametrix, Inc., and Hardin-Davis. 1984. Initial flow recommendations Yakima River Basin. Boise, ID: U. S. Bureau of Reclamation (Document No. 84–1031–0019F).



- Patten, B. G., R. B. Thompson, and W. D. Gronlund. 1970. Distribution and abundance of fish in the Yakima River, Washington, April 1957 to May 1958. Washington DC: U. S. Fish and Wildlife Service (Special Scientific Report Fisheries No. 603).
- Railsback, S. 1999. Reducing uncertainties in instream flow studies. *Fisheries* 24: 24–26.
- Riehle, M. D., and J. S. Griffith. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2119–2128.
- Rimmer, D. M., U. Paim, and R. L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 469–475.
- Rubin, S. P., T. C. Bjornn, and B. Dennis. 1991. Habitat suitability curves for juvenile chinook salmon and steelhead development using a habitat-oriented sampling approach. *Rivers* 2: 12–29.
- Shirvell, C. S. 1986. Pitfalls of physical habitat simulation in the Instream Flow Incremental Methodology. *Canadian Technical Report of Fisheries and Aquatic Sciences*: 1460.
- Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Pages 173–180 in D. L. G. Noakes, editor. *Predators and prey in fishes*. The Hague, Netherlands: Dr. W. Junk Publishers.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. San Francisco, CA: W. H. Freeman and Company.
- Stempel, J. M. 1984. Development of fish preference curves for chinook and rainbow trout in the Yakima River basin. Moses Lake, Washington: U. S. Fish and Wildlife Service (Special Progress Report, January 1984).
- Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Canadian Journal of Zoology* 64: 1506–1514.
- Thomas R. Payne and Associates. 1995a. Distribution and abundance of juvenile chinook salmon in the Yakima River Basin. Final Report to Yakima River Basin Defense Coalition, Yakima, Washington.
- Thomas R. Payne and Associates. 1995b. Diurnal shifts in habitat use by juvenile chinook salmon in the Yakima River Basin, Washington. Final Report to Yakima River Basin Defense Coalition, Yakima, Washington.
- U. S. Bureau of Reclamation. 1998. Draft programmatic environmental impact statement, Yakima River basin water enhancement project. Yakima, WA: U. S. Bureau of Reclamation.
- Wickham, M. G. 1967. Physical microhabitat of stream trout. Master's Thesis. Fort Collins: Colorado State University, Department of Fishery and Wildlife Biology.
- Williams, J. G. 1996. Lost in space: Minimum confidence intervals for idealized PHABSIM studies. *Transactions of the American Fisheries Society* 125: 458–465.
- Williams, J. G., T. P. Speed, and W. F. Forrest. 1999. Comment: Transferability of habitat suitability criteria. *North American Journal of Fisheries Management* 19: 623–625.