Predicting Microdistributions of Steelhead (*Oncorhynchus mykiss*) Parr from Depth and Velocity Preference Criteria: Test of an Assumption of the Instream Flow Incremental Methodology

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We tested an assumption of the Physical Habitat Simulation of the Instream Flow Incremental Methodology (IFIM) that fish select microhabitats based on the quality of one or several hydraulic conditions. We developed preference curves for juvenile steelhead (*Oncorhynchus mykiss*) in Morse Creek, Washington, USA, that accounted for availability of depths and velocities and their utilization by steelhead parr. To allow comparison of intervals among preference curves from different studies, we developed preference indices. We then evaluated the relationship between steelhead parr density and preference or preference indices for depth, velocity, and depth and velocity combined using an independent data set from a different year and an adjacent location in Morse Creek; these indices reflected observed densities of steelhead parr. There was a significant rank correlation between steelhead parr density and preferences or preference indices of steelhead parr for velocity alone and for depth and velocity combined, but not for depth alone. Steelhead parr strongly avoided habitat in which depth preference was 0.0, but velocity preference appeared to influence use of habitat where depth preference was not 0.0. Steelhead parr avoided cells with low preference indices and preferred cells with high preference indices. These relationships support an assumption of the IFIM.

Nous avons vérifié une hypothèse de la simulation de l'habitat physique tirée du *Instream Flow Incremental Methodology* (IFIM) selon laquelle le poisson choisi des micro-habitats en fonction de la qualité d'un ou de plusieurs paramètres hydrauliques. Nous avons établi des courbes de préférence pour des juvéniles de truite arc-en-ciel anadrome (*Oncorhynchus mykiss*) du ruisseau Morse, à Washington (É.-U) qui tenaient compte des profondeurs et des vitesses de l'eau et de leur utilisation par des tacons de cette espèce. Afin de pouvoir comparer les intervalles entre les courbes de préférence des différents études, nous avons établi des indices de préférence. Nous avons ensuite évalué le rapport entre la densité des tacons et la préférence ou les indices de préférence pour la profondeur, la vitesse, la profondeur et la vitesse combinées au moyen d'un ensemble de données indépendantes d'une autre année et d'un emplacement voisin dans le ruisseau Morse : ces indices correspondaient aux densités observées de tacons. Il existait une corrélation des rangs importante entre la densité des tacons et les préférences ou indices de préférence des tacons pour la vitesse seule et pour la profondeur et la vitesse combinées, mais aucune pour la profondeur seulement. Les tacons évitaient fortement l'habitat dans lequel la préférence de profondeur était de 0,0, mais la préférence de vitesse semblait influer sur l'utilisation de l'habitat lorsque la préférence de profondeur était différente de 0,0. Les tacons évitaient les cases présentant des indices de préférences faibles, et recherchaient des cases à indices élevés. Ces rapports renforcent une hypothèse de l'IFIM.

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The Instream Flow Incremental Methodology (IFIM) (Stalnaker 1980; Bovee 1982) is considered the state-of-the-art instream flow method (Loar et al. 1985; Reiser et al. 1989), although several recent reports (Mathur et al. 1985; Scott and Shirvell 1987) have been critical of it. A prominent part of IFIM is the Physical Habitat Simulation (PHABSIM), a set of computer models that can be used to model how some aspects of habitat vary with flow. To use PHABSIM, assumptions about the dynamic equilibrium of channel form and features, about hydraulics, about fish ecology and behavior, and about fish population dynamics are all required.

Among the assumptions in PHABSIM are that fish selectively occupy preferred habitats and that their habitat preferences are based predominantly on their preferences for depth, velocity, substrate, and cover (Bovee and Cochnauer 1977; Stalnaker 1980; Bovee 1986). A testable extension of this assumption is that if (1) the distributions of depths, velocities, substrates, and cover are known and (2) the relative preferences of fish for different values of these habitat components are known, then fish distribution within a stream should be predictable. This study addresses only depth and velocity distribution relative to fish distribution, so it is not a complete test of the assumption. We reasoned that if fish habitat preference were to be useful in predicting fish distribution, prediction should at least be successful under similar conditions (flow and season) to those when preference curves were developed; if not, then predictions at other flows would be questionable.

In this study, we determined depth and velocity preferences of juvenile (parr) steelhead (*Oncorhynchus mykiss*) in a stream segment. For adjacent stream segments, we then predicted fish distribution based on those depth and velocity preferences and compared the predicted and observed fish distributions.

The standard application of PHABSIM calculates fish habitat preference as the product of preferences for depth, velocity, and substrate or cover. Alternative calculations of combined preference are available (Bovee 1982, 1986; Milhous et al. 1984, option 19 in table V.1; Bovee and Zuboy 1988; C. Stalnaker, U.S. Fish and Wildlife Service, personal communication). Some users of PHABSIM in Washington State have suggested that alternative calculations might have more biological significance than the standard calculation. Accordingly, we also evaluated several alternative calculations of fish habitat preference.

Study Site

Our study site was located about 3 km upstream from the mouth of Morse Creek, near Port Angeles, on the north slope of the Olympic Mountains, Washington. Morse Creek is a small (mean annual flow 3.58 m^3/s, drainage area ~146 km^2, mainstem length 26.1 km) steep stream (average gradient >6%) that flows into the Juan de Fuca Strait within sight of its source in alpine snowfields. In preliminary sampling, we had learned that this study area had a high density of juvenile steelhead relative to other streams we have sampled in Washington state. Morse Creek is typical of many streams where PHABSIM has been used to determine instream flow requirements for hydroelectric projects.

Morse Creek is fed by extensive snowfields on the north side of Hurricane Ridge (near 1950 m above mean sea level) in Olympic National Park. Snowmelt peaks in June (median June flow = 5.5 m^3/s) and continues through July. Low flows occur from late August through October, depending on onset of autumn rains, with the lowest monthly median flow of 1.0 m^3/s in September. Highest flows occur with heavy rains during November–January (Williams et al. 1985).

The study site consisted of three adjacent segments, each about 150 m long. In the middle segment, we measured depths and velocities available to and used by juvenile steelhead during September 1987 and developed preference curves. The middle segment consisted of two pools, up to 2 m deep with gravel and cobble substrate, separated by a bedrock chute. The right bank was a cutbank. The left bank was a gravel bar. We observed gradual transitions of pool, run, and riffle habitats.

We sampled two adjacent test segments immediately upstream and downstream, respectively, of the habitat preference curve development segment during September 1989 to compare the distribution and habitat preference of steelhead parr with the preference curves developed 2 yr previously. In the test segments the left banks were cutbanks and the right banks were gravel bars. Each test segment had a longer pool and a shorter pool with gravel and cobble substrate. One of the lower pools was about 2 m deep, but the upper pools did not exceed about 1.5 m during our sampling. In at least one pool in the upper and lower segments, there was a gradual transition into runs and riffles. The upper segment contained a small bedrock chute. All three segments contained some bedrock outcrops.

Flow at the study site on the date of preference curve development in 1987 was 0.86 m^3/s, and stream width averaged 12.6 m with a range from 7.4 to 25.2 m. On the date of our distribution test in 1989, flow was 0.69 m^3/s, and stream width averaged 11.4 m with a range from 5.8 to 17.5 m.

The stream is inhabited by steelhead, anadromous cutthroat trout (*Oncorhynchus clarki*), chinook (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), and pink salmon (*O. gorbuscha*), and Dolly Varden (*Salvelinus malma*), as well as unidentified sculpins (*Cottus* sp.). Juvenile steelhead fry (~30–60 mm total length (TL)), and parr (~75–200 mm TL) and coho salmon (~50–100 mm TL) are numerically dominant, with both species occupying pools and steelhead predominating in riffles and runs.

Methods

Habitat Preference Curve Development

We developed habitat preference curves by measuring depths and velocities used by fish (utilization) and available to the fish (availability) and then calculated preference as a normalized ratio of utilization to availability for different intervals of depth and velocity.

On 3–4 September 1987, from midmorning until visibility declined with low sun angle in late afternoon, two observers snorkeled upstream through two pools, two bedrock chutes, and a riffle, marking positions of steelhead parr with weighted flags. They swam in parallel, covering the full width of the stream. Water clarity was sufficient that we could see clearly underwater across the stream. We marked fish positions only after we were certain the fish were not being disturbed, that is, they displayed behavior such as feeding, territorial defense, and returning to position after the position was marked.

After flags were placed, we measured depth and mean column velocity (velocity at 0.6 depth) and estimated substrate composition at each of 104 flags. We used a top-setting wading rod with a Swoffer propeller current meter calibrated to read depth and velocity in imperial units (feet and feet per second).

After marking fish positions and measuring habitat use through the entire stream segment, we determined depth and velocity availability by measuring depth and mean column velocity at 182 points at 1.5-m intervals along transects spaced 6.2 m apart along the stream. (In the downstream-most 7.7 m of the site, we measured availability along transects that were 1.5 m apart and adjusted availability calculations to account for the greater density of measurements in this area.)

We developed depth and velocity preferences, as well as an alternative preference index, from the 1987 data. We established initial intervals of depth and mean column velocity (hereafter, velocity) at 0.03-m and 3-cm/s intervals and then tabulated observed numbers of parr into these initial intervals. We tabulated depth or velocity availability measurements into the same initial intervals and then calculated what percentage of total depth or velocity availability occurred in each interval.

We calculated expected numbers of parr in each initial interval by multiplying total number of observed parr by the percentage of depth or velocity availability in an interval. As used throughout this paper, the term "expected number of parr" or "expected number" means the number of parr that should have occurred in an interval of depth or velocity if the parr had distributed themselves in proportion to the availability of the interval. We combined intervals until expected numbers of parr in each interval exceeded five, except that the final interval was not combined with the preceding interval if the expected value in the final interval exceeded two parr. We combined intervals to avoid dividing either by zero or by very small numbers in the next step.

To develop preference curves that account for distribution of available habitat and its utilization by steelhead parr, we divided observed number of parr (Ob) by expected number of parr (E) for each interval. To generate a preference factor between 0.0 and 1.0, the Ob/E ratio in each interval was normalized by dividing each Ob/E ratio by the maximum Ob/E ratio. That is, $P = (\mathrm{Ob}/E) / (\mathrm{Ob}/E_{\max})$. In this way, the most preferred interval had a preference of 1.0, and less preferred intervals had preferences between 0.0 and 1.0. Preferences were calculated for depth ($P[d]$) and velocity ($P[v]$) and then preference for depth and velocity combined was calculated as $P[dv] = P[d] \times P[v]$.

To minimize the subjectivity in fitting data to a curve, we did not smooth the preference curves. In most studies, preference curves are smoothed to follow a continuous distribution assumed to reflect fish behavior.

To allow comparison of intervals among preference curves from different studies, we developed a preference index. A preference index (PI) is developed from Ob/E ratios in intervals before they are normalized into a preference curve. We think of where Ob/E = 1 as a threshold between avoidance and preference. Ob/E = 1 where fish occur in a depth, velocity, or depth–velocity interval in direct proportion to the area of stream channel available in the interval. Ob/E < 1 where fish occur less often than expected based on availability of a habitat interval and suggests habitat avoidance, while Ob/E > 1 where fish occur more often than expected and suggests habitat preference. To develop a preference index, Ob/E ratios in intervals are divided into sections where Ob/E < 1 and Ob/E > 1. We assigned PI = 0.5 as the threshold or midpoint of the depth preference index (PI[d]) and velocity preference index (PI[v]). To generate a PI factor between 0 and 1, preference indices for depth or velocity below the threshold were calculated as $\mathrm{PI} = 0.5 \times \mathrm{Ob}/E$, and preference indices above the threshold were calculated as $\mathrm{PI} = 0.5 + 0.5 [([\mathrm{Ob}/E] - 1) / ([\mathrm{Ob}/E_{\max}] - 1)]$. In this way, PI < 0.5 in depth or velocity intervals avoided by fish and PI > 0.5 in depth or velocity intervals preferred by fish. The preference index for depth and velocity combined is calculated as $\mathrm{PI}[dv] = \mathrm{PI}[d] \times \mathrm{PI}[v]$, and the PI[$dv$] threshold is the product of the PI[d] and PI[v] thresholds, i.e., 0.5 × 0.5 = 0.25.

If no interval had Ob/E = 1 exactly, we found the interval with the Ob/E ratio closest to 1.0 and averaged the midpoints of the adjacent intervals above and below that interval to calculate the threshold. The threshold can occur in an interval with a normalized preference (P) anywhere between 0.0 and 1.0.

Predicting Steelhead Parr Distribution

In two adjacent sections of Morse Creek in a different year (1989), we measured depth and velocity distribution, predicted the distribution of steelhead parr using the preference curves we developed in Morse Creek 2 yr previously, and then measured steelhead parr distribution to test the predictions. We reasoned that steelhead parr density would be higher where fish habitat preferences were higher and that density would be lower where habitat preferences were lower.

On 27 September 1989, an observer counted parr by snorkeling along transects in the test segments that were adjacent upstream and downstream to the preference curve development segment. Parr were counted in the immediate vicinity (within 1.23 m of transect) of all points on a randomly placed grid in the stream; we then measured depths and velocities at those points. We calculated steelhead parr preferences for those points using preference factors determined in 1987 and discussed in the Preference Curve Development portion of this paper.

In the morning, we established transects across the stream at 15.4-m intervals along a line extending downstream from the lower end of the 1987 study reach. In the afternoon, we established transects across the stream at 6.2-m intervals along a line extending upstream from the upper end of the 1987 study reach because we had missed many concentrations of fish using 15.4-m intervals. Our starting transects were set at random distances along the line. We progressed upstream until underwater visibility declined with low sun angle in late afternoon.

At each transect, we visually identified the opposite end; then, one observer entered the water downstream from one end of the transect, snorkeled slowly up to the end of the transect, and then snorkeled across it, marking with weighted flags the positions of any steelhead parr that appeared to be within 1.23 m of the transect. (To be certain that we recorded data on all fish that were within 1.23 m of the transect, we marked some fish positions farther than 1.23 m from the transect, but later discarded those observations when distance from the transect was determined.)

After marking positions of any steelhead parr near a transect, we measured depth and velocity at 0.9-m intervals along the transect, beginning from the upstream/downstream line, regardless of the distance to water's edge from the line. We measured the distance from each marker (parr position) to the transect and used the nearest measurements of depth and velocity on the transect to represent the cell containing the parr.

The sampling procedure used in September 1989 yielded a series of cells along each transect. Each measurement point on a transect was the center of two cells, one rectangular (0.9 × 2.46 m) and one square (0.9 × 0.9 m); the larger rectangular cell encompassed the smaller square cell. Consistent with PHABSIM, depth and velocity at the measurement point were assumed to be representative of depth and velocity throughout the cell. This assumption was probably more true for smaller square cells and less true for the larger rectangular cells, as more points in the larger cells were farther from the measurement point. By using the larger rectangular cells, however, we doubled the number of fish and cells occupied by fish, and thus provided more powerful tests at the greater risk that some fish in a cell occupied depths and velocities that differed substantially from those at the measurement point for the cell.

We transcribed data on location, depth, velocity, preferences, and preference indices for each cell, and number of parr within square cells and within rectangular cells to a database. The steelhead parr preference factors and preference index factors associated with a cell were based on preference factors and preference index factors calculated during the development of the preference curves and preference indices for steelhead parr in Morse Creek during 1987. Each cell was thus associated with three preference factors ($P[d]$, $P[v]$, $P[dv]$) and three preference index factors (PI[d], PI[v], PI[dv]). The preference factors and preference index factors were sorted by value and then combined into intervals to bring the expected number of parr in an interval to at least five and as close to five as possible in the final interval. In this section of the study, combined preference intervals are generally broader than the combined intervals during preference curve development because, while the range of habitat measurements was about the same in the two portions of the study, we observed 50 parr during this portion compared with 104 parr during preference curve development.

The preference for a preference interval was calculated as the sum of the products of each preference or preference index and

TABLE 1. Depth and velocity preferences (*P*) and preference indices (PI) for steelhead parr in Morse Creek, September 1987.

Depth (*d*) interval (m)	Proportion of total area available in interval	Number of parr					Velocity (*v*) interval (cm/s)	Proportion of total area available in interval	Number of parr				
		Observed (Ob)	Expected (*E*)	Ob/*E*	*P*[*d*]	PI[*d*]			Observed (Ob)	Expected (*E*)	Ob/*E*	*P*[*v*]	PI[*v*]
<0.15	0.35	0	36.4	0.00	0.00	0.00	<3.0	0.24	9	25.2	0.36	0.18	0.18
0.15–0.18	0.10	2	10.7	0.19	0.04	0.10	3.0–8.8	0.10	7	9.7	0.72	0.36	0.36
0.18–0.24	0.10	4	10.0	0.40	0.08	0.20	9.1–11.9	0.07	5	7.4	0.68	0.34	0.34
0.24–0.27	0.08	14	8.3	1.68	0.35	0.59	12.2–14.9	0.05	1	5.4	0.19	0.09	0.10
0.27–0.30	0.07	6	7.3	0.82	0.17	0.41	15.2–21.0	0.08	9	8.2	1.09	0.55	0.55
0.30–0.33	0.05	13	5.2	2.50	0.53	0.70	21.3–27.1	0.05	10	5.0	1.98	1.00	1.00
0.34–0.39	0.07	8	7.7	1.04	0.22	0.51	27.4–33.2	0.08	15	7.9	1.90	0.96	0.96
0.40–0.48	0.05	12	5.5	2.18	0.46	0.66	33.5–39.3	0.06	8	6.0	1.32	0.67	0.66
0.49–0.76	0.09	26	9.3	2.78	0.59	0.74	39.6–45.4	0.07	11	6.9	1.60	0.81	0.81
>0.76	0.04	19	4.0	4.74	1.00	1.00	45.7–51.5	0.06	10	5.7	1.75	0.88	0.88
							51.8–60.7	0.06	9	7.0	1.28	0.65	0.64
							61.0–106.4	0.08	9	7.4	1.22	0.62	0.61
							>106.4	0.02	1	2.0	0.50	0.25	0.25

the proportion of the combined preference interval area made up by each component preference interval. For example, a combined preference interval covering 0.2–0.3 might be made up of two component preference intervals, one at 0.2 with three as the expected number of parr and the other at 0.3 with two as the expected number of parr. The preference for the combined 0.2–0.3 preference interval would be $(3/5 \times 0.2) + (2/5 \times 0.3) = 0.24$.

In each combined preference interval, we calculated parr density as number of parr observed divided by the number of cells in that interval.

Our null hypothesis was that there was no significant relationship between rank of parr density and rank of preferences ($P[d]$, $P[v]$, $P[dv]$) or between rank of parr density and rank of preference indices (PI[d], PI[v], PI[dv]) for that combined preference interval. We considered rank correlations significant where $p < 0.05$ and marginally significant where $p < 0.10$. We used Kendall's tau to test for rank correlation because the data did not appear to be normally distributed.

A second null hypothesis was that parr would be distributed above or below the avoidance–preference threshold in proportion to the number of measurements (cells) in a preference interval and independent of preference index (PI[d], PI[v] or PI[dv]). For each preference interval, we calculated the expected number of parr within 0.45 m and within 1.23 m by multiplying total number of parr observed by the proportion of total number of measurements that were within that preference interval. We used chi-square tests of distribution and considered chi-square values significant where $p < 0.05$ and marginally significant where $p < 0.10$.

Results

Habitat Preference Curves

We measured depths and velocities at locations of 104 steelhead parr in Morse Creek during September 1987. Most parr were at locations with depths greater than 0.24 m and with velocities between 15 and 106 cm/s (Table 1). When habitat availability was considered, steelhead parr preferred (i.e., Ob/*E* ratio > 1) these same intervals of depth and velocity, except that the depth interval 0.27–0.30 m was not preferred by parr (Table 1). The most-used interval differed from the most-preferred interval for both depth and velocity. The highest numbers of parr in an interval were observed at locations with depths of 0.49–0.76 m, but the depths most preferred by parr (i.e., having the highest Ob/*E* ratio) were in the >0.76 m depth interval. Similarly, more parr were observed at locations with velocities of 27.4–33.2 cm/s, but the velocities most preferred by parr were in the 21.3–27.1 cm/s velocity interval. In addition, steelhead parr avoided (i.e., Ob/*E* ratio < 1) the most available depths (those <0.24 m) and velocities (those <21 cm/s), the shallowest depths and slowest velocities available (Table 1). Depth and velocity preference curves for steelhead parr in Morse Creek are shown in Fig. 1.

For 179 locations on transects in Morse Creek, we measured a maximum depth of 1.2 m and a maximum velocity of 160 cm/s. We observed steelhead parr at a maximum depth of 1.7 m and at a maximum velocity of 139 cm/s. Maximum depth at locations of steelhead parr in Morse Creek was probably limited by stream size and maximum depth available at the flow during the study ($0.86\ m^3/s$). Maximum velocity at locations of steelhead parr was less likely a function of maximum velocity available, as indicated by the declining Ob/*E* ratio at higher velocities (Table 1).

Predicting Steelhead Parr Distribution

On 27 September 1989, we observed and marked locations of 50 parr in 40 rectangular (2.4×0.9 m) cells. This included 25 parr in 21 square (0.9×0.9 m) cells.

Depth and velocity are significant factors influencing the spatial distribution of steelhead parr in Morse Creek during late summer low flow. Steelhead parr avoided cells with low preference indices and occurred in greater numbers than expected in cells with high preference indices. When we compared preference indices less than the threshold of 0.5 (PI values < 0.5) with preference indices greater than the threshold of 0.5 (PI values > 0.5), steelhead parr occurred significantly less frequently than expected in square and rectangular cells with PI[v] < 0.5 and significantly less frequently than expected in rectangular cells with PI[d] < 0.5. Similarly, steelhead parr preferred square and rectangular cells with PI[v] > 0.5 and preferred rectangular cells with PI[d] > 0.5 (chi-square tests, $p < 0.05$). Although parr occurred less frequently than expected in square cells with PI[d] < 0.5, the relationship was not significant (Table 2). When depth

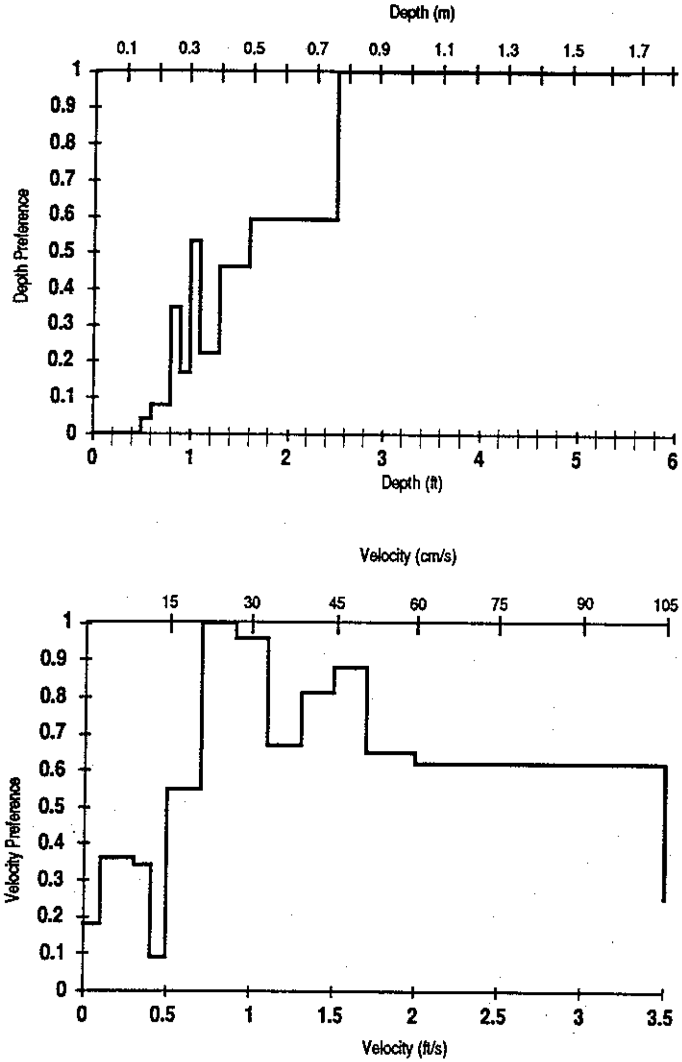

FIG. 1. Depth (upper panel) and velocity (lower panel) preference curves for steelhead parr in Morse Creek, September 1987. Preference curves were not smoothed.

and velocity are combined, the appropriate threshold between avoidance and preference is $0.5 \times 0.5 = 0.25$; steelhead parr occurred significantly less frequently than expected in square and rectangular cells having $\mathrm{PI}[dv] < 0.25$, and parr preferred cells having $\mathrm{PI}[dv] > 0.25$ ($p < 0.01$, Table 2).

Depth and velocity, alone and in combination, are important in determining steelhead parr distribution in Morse Creek. Depth appears to influence steelhead parr distribution mostly in areas with a depth preference of 0.0. A large number of cells had $P[d] = 0.0$ (Table 1) and parr avoided these cells ($p < 0.01$, Table 2). In areas where $P[d] > 0.0$, velocity appears to influence steelhead parr distribution more than depth. Comparisons of the significance levels of preferences and preference indices for depth and velocity ($P[d]$ versus $P[v]$ and $\mathrm{PI}[d]$ versus $\mathrm{PI}[v]$) suggest that velocity provides a better measure of steelhead parr distribution in rectangular cells (Table 3).

Habitat preference and preference indices reflected observed densities of steelhead parr in Morse Creek. There was a significant relationship between steelhead parr density and preferences or preference indices for velocity alone and for depth and velocity combined, but not for depth alone. Rank correlation between steelhead parr habitat preferences and observed parr density in cells was significant for $P[dv]$ and $\mathrm{PI}[dv]$ in rectangular cells ($p < 0.05$) and marginally significant for $P[v]$ and $\mathrm{PI}[v]$ in rectangular cells and for $P[dv]$ and $\mathrm{PI}[dv]$ in square cells ($p < 0.10$), but relationships between $P[d]$ or $\mathrm{PI}[d]$ and parr density were not significant (Table 3). For example, parr density in an interval increased consistently with $P[dv]$ and $\mathrm{PI}[dv]$ in rectangular cells (Table 4; Fig. 2).

Discussion

Habitat Preference Curves

We accounted for availability of different intervals of depth and velocity and their use by steelhead parr when developing preference curves. Although depth and velocity preferences are probably not perceived independently by fish (Mathur et al. 1985; Scott and Shirvell 1987), we chose to treat them independently because it is the standard practice in PHABSIM studies in Washington State, and this study was designed as an initial test of the validity of studies using this approach.

We evaluated mean column velocity as a determinant of steelhead parr distribution because it is the standard method in PHABSIM studies in Washington. Scott and Shirvell (1987) criticized that the use of mean column velocity measured at 0.6 depth was not applicable to fish habitat selection. Shirvell (1989) improved the PHABSIM prediction of chinook salmon spawning locations by using focal point velocity rather than mean column velocity. Baltz et al. (1987, 1991) found that mean column velocity and focal point velocity were highly correlated in California streams. A high correlation ($r = 0.877$, $n = 435$) was found between mean column velocity and focal point velocity for spawning sockeye salmon (*Oncorhynchus nerka*) in Washington (M. Barclay and P. Rittmueller, Cascades Environmental Services, 1111 N. Forest St., Bellingham, Wash., personal communication).

Standard application of PHABSIM includes measurements of substrate or cover in addition to depth and velocity. We did not include substrate and cover but do not believe this seriously compromised the study because substrate and cover did not vary greatly throughout the study reaches. Substrate was relatively uniform with poorly sorted cobble and gravel throughout the study reach, but some boulders and bedrock were present. Only a few larger trout (not steelhead parr) and char were associated with bedrock outcrops, and we estimated that large boulders accounted for less than 1% of the study reach. Cobble, which was widely distributed, provided the main cover. Instream woody debris was absent in this segment of Morse Creek.

Sample size affects resolution of habitat preference curves. Small numbers of fish observations necessitate wider intervals within which to accumulate both observations and expected numbers of observations. As intervals widen, the chance increases that true preferences at the extremes and the midpoint of the range will differ. For example, the depth interval of 0.49–0.76 m was calculated to have a preference of 0.59 (see Table 1), but true depth preference might be greater at 0.76 m and less at 0.49 m or vice versa.

Preference curves developed in this study showed some anomalies that are probably artifacts of small sample size. Depth and velocity preference curves each have more than one peak, while one would expect unimodal curves. If deviations of our preference curves from the true preferences of steelhead parr and our small sample size made our test less likely to detect a

TABLE 2. Chi-square analyses of steelhead parr distribution among cells categorized as avoided (PI < 0.5) or preferred (PI > 0.5) and among cells having depth preferences ($P[d]$) of 0.0 or greater than 0.0.

	Square cells (0.9 × 0.9 m)			Rectangular cells (0.9 × 2.4 m)		
	Number of parr			Number of parr		
Preference index	Observed (Obs)	Expected (E)	Cell chi-square	Observed (Ob)	Expected (E)	Cell chi-square
PI[d] < 0.5	14	16.53	0.39	23	33.06	3.06
PI[d] > 0.5	11	8.47	0.76	27	16.94	5.98
		Chi-square = 1.15 df = 1, NS			Chi-square = 9.04 df = 1, $p < 0.01$	
PI[v] < 0.5	3	10.89	5.71	7	21.77	10.02
PI[v] > 0.5	22	14.11	4.41	43	28.23	7.73
		Chi-square = 10.12 df = 1, $p < 0.01$			Chi-square = 17.76 df = 1, $p < 0.01$	
PI[dv] < 0.25	10	17.74	3.38	20	35.48	18.30
PI[dv] > 0.25	15	7.26	8.26	30	14.52	4.97
		Chi-square = 11.64 df = 1, $p < 0.01$			Chi-square = 23.27 df = 1, $p < 0.01$	
$P[d]$ = 0.0	3	9.48	4.43	7	18.95	7.54
$P[d]$ > 0.0	22	15.52	2.70	43	31.05	4.60
		Chi-square = 7.13 df = 1, $p < 0.01$			Chi-square = 12.14 df = 1, $p < 0.01$	

TABLE 3. Relationship between steelhead parr density and preference (P) and preference indices (PI) for depth (d), velocity (v), and depth–velocity (dv) combined.

	$P[d]$	$P[v]$	$P[dv]$	PI[d]	PI[v]	PI[dv]
			Parr in square cells (0.9 × 0.9 m)			
Kendall's tau	0.33	0.67	1.00	0.33	0.67	1.00
n	4	4	4	4	4	4
p	NS	NS	0.10	NS	NS	0.10
			Parr in rectangular cells (0.9 × 2.4 m)			
Kendall's tau	0.60	0.73	0.97	0.33	0.73	0.81
n	5	6	6	5	6	7
p	NS	0.10	0.05	NS	0.10	0.05

TABLE 4. Rank of steelhead parr density, rank of depth–velocity preference ($P[dv]$), and rank of depth–velocity preference index (PI[dv]) in rectangular cells (0.9 × 2.4 m) as examples of the data used to test the relationships shown in Table 3.

$P[dv]$			Parr density		$P[dv]$			Parr density	
Interval	Weighted mean of interval	Rank	Parr per cell	Rank	Interval	Weighted mean of interval	Rank	Parr per cell	Rank
0.00	0.00	6	0.07	6	0.00	0.00	7	0.07	7
0.01–0.03	0.02	5	0.10	5	0.02–0.06	0.04	6	0.15	5
0.04–0.07	0.05	4	0.24	3.5	0.07–0.12	0.10	5	0.12	6
0.08–0.14	0.10	3	0.24	3.5	0.13–0.19	0.16	4	0.23	4
0.15–0.29	0.21	2	0.26	2	0.20–0.36	0.30	3	0.27	3
0.30–0.59	0.42	1	0.50	1	0.38–0.51	0.45	2	0.46	1
					>0.51	0.63	1	0.43	2
Kendall's tau = 0.97, $n = 6$, $p < 0.05$					Kendall's tau = 0.81, $n = 7$, $p < 0.05$				

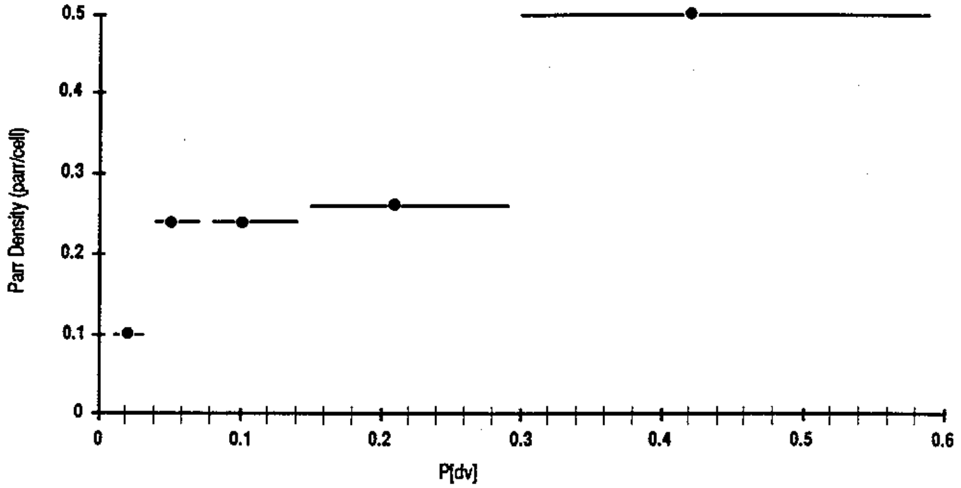

FIG. 2. Relationship between steelhead parr density and depth–velocity preference (*P*[*dv*]) intervals (horizontal lines) in Morse Creek from the data in Table 4. Circles indicate weighted means of *P*[*dv*]) intervals.

relationship between preference factors and fish distribution, the fact that we still found one suggests that the relationship is relatively robust.

Predicting Steelhead Parr Distribution

Steelhead parr distribution during late summer low flow in Morse Creek was consistent with an assumption used in PHABSIM that depth and velocity preferences govern the usability and the use of habitat. Out of 12 analyses, the highest rank correlations were between density and the combined preference factor (*P*[*dv*]) and combined preference index (PI[*dv*]) (Table 3). We believe that the higher significance for *P*[*dv*] and PI[*dv*] indicates that preference for depth and velocity combined is a better predictor of steelhead parr habitat preference than the other predictors we evaluated.

In this study, depth and velocity preferences were determined in the same stream as the test of predictions of fish distribution. The test of depth and velocity as predictors of habitat use was statistically independent of preference curve development, both spatially and temporally, but conditions were very similar (adjacent parts of same stream with similar habitat at similar streamflow).

Hardy et al. (1982) found positive correlations between predicted and observed distributions of native and introduced fishes in a spring-fed Nevada stream. Their predictions were based on depth and velocity only. Hardy et al. (1982) noted that cover distribution appeared to account for discrepancies between observed and predicted fish distributions. In a Michigan stream, Gowan (1984) found more brown trout (*Salmo trutta*) near transects with higher average weighted usable area (WUA, based on preferences for depth, velocity, and substrate) than in transects with lower average WUA. Scott and Shirvell (1987) questioned Gowan's conclusions because some trout occupied areas with preference values near zero, and some habitats with high preference values were not occupied, and further, Shirvell (1987) determined that the Michigan results were based on inappropriate data manipulation.

Shirvell (1989) tested the ability of PHABSIM to predict chinook salmon spawning distribution in a segment of the Nechaco River, British Columbia. In one of six simulations, he found a correlation coefficient of 0.80 between transect WUA and number of spawning salmon on the transect, but the same simulation incorrectly predicted that areas were unusable where over 50% of spawning had historically occurred.

In this study, as in those by Gowan (1984) and Shirvell (1989), we observed some fish in cells with preference factors of zero and some unoccupied cells that had high preference factors. Sampling artifacts during preference curve development and single-point representation of a cell may have contributed to this imprecision. In PHABSIM studies, measurement points on transects are assumed to be representative of a cell; however, streams are not homogeneous and few cells are uniform in depth, velocity, and substrate. A measurement at the center of a cell may indicate a preference of zero, but part of the cell might have a higher "true" preference and could possibly account for the presence of fish in a cell for which the preference is counted as zero. Similarly, most of a cell might have a true preference of zero, while the measurement at the center indicates a nonzero preference. In addition, the seeding rate of a stream can affect utilization of habitat by fish. Wild steelhead spawner escapement in Morse Creek that produced the parr observed in 1987 and 1989 met the escapement goal.

Alternative Habitat Preference Index (PI)

We tested an alternative habitat preference index (PI) to accommodate some PHABSIM users' suggestion that a "neutral" preference value of 0.5 should be comparable between studies and should be a dividing point between preferred habitat ($Ob/E > 1$) and avoided habitat ($Ob/E < 1$) (Bozek and Rahel 1991). If PIs at a given depth or velocity or substrate class in separate studies are all above 0.5, then they are all preferred habitat; if they are all below 0.5, then they are all avoided habitat.

In our study, PI was about as useful as the standard preference factor (*P*) in predicting steelhead parr distribution. When PIs for depth, velocity, and substrate or cover are multiplied together in the standard application of PHABSIM, it should be noted that the combined "neutral" PI is 0.125.

Assumptions of PHABSIM

Basic assumptions in IFIM are that (1) distribution of depth and velocity in relation to somewhat fixed channel features (substrate, cover) contributes to determining the quality of different areas or microhabitats to fish (Stalnaker 1980; Bovee 1982;

Milhous et al. 1984), (2) fish select microhabitats based on quality as determined by depth, velocity, substrate, and cover (possibly in conjunction with other features) (Stalnaker 1980; Bovee 1982; Milhous et al. 1984), (3) changes in flow directly change the quality of different microhabitats by changing depth and velocity distribution, while fish preferences for these attributes remain unchanged (Stalnaker 1980; Bovee 1982), and (4) fish populations are influenced by the history of the quality of the habitats they experience through one or more generations (Bovee 1982, 1988).

This study, together with studies by Hardy et al. (1982) and perhaps Gowan (1984), supports basic assumption (2) above. Shirvell's (1989) correlation between transect suitability and salmon redds near transects also provides limited support for this assumption, but PHABSIM's calculation of habitat suitability for chinook salmon spawning does not adequately predict spawning sites, thus casting doubt on this assumption for spawning habitat. Although none of these studies found perfect matches between fish use and indices of habitat quality, the number of positive associations suggests that this assumption is reasonable.

One of the secondary assumptions of a standard application of PHABSIM is that cell preference is a product of separate preferences for depth, velocity, and substrate. Shirvell (1989) speculated that his simulations of salmon spawning habitat may have been inaccurate because other hydraulic or topographic features were not incorporated into the calculation of WUA. This study supports reliance on calculation of combined preference as a product of separate preferences for depth and velocity. We also found depth and velocity preferences to be useful alone. Substrate measurements were not made in this study.

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