Comparison of Preference Curves and Habitat Utilization Curves Based on Simulated Habitat Use

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ABSTRACT: Two techniques for calculating depth and velocity suitability using simulated fish distributions were compared. Fish were distributed across natural, normal, and uniform depth and velocity distributions based on assigned depth and velocity suitabilities. Depth and velocity preferences (category III, accounting for habitat availability) matched assigned suitabilities in all cases as well or better than utilization, but utilization suitabilities matched assigned suitabilities equally well in the uniform distribution. A secondary fish distribution generated from the preferences did not differ significantly from the original simulated fish distributions, although the secondary distribution generated from utilization suitabilities differed significantly from the original distribution. Preferences were superior to utilization in matching assigned suitability and duplicating original fish distributions when available combinations of depth and velocity could not be sampled uniformly.

KEY WORDS: Depth, fish, habitat suitability, IFIM, instream flow, PHABSIM, preference, simulation, utilization, velocity.

INTRODUCTION

The Instream Flow Incremental Methodology (IFIM) is widely used by regulatory agencies to provide a basis for recommending or requiring instream flows (Reiser et al. 1989). The Physical Habitat Simulation system (PHABSIM), a central part of the IFIM, estimates the amount of physical microhabitat available for different species and life stages of aquatic organisms at different streamflows (Bovee 1982). The core of the PHABSIM consists of a hydraulic model (e.g., WSP or IFG4) and a habitat model (e.g., HABTAT, HABTAV, or HABTAE). The hydraulic model predicts depth and velocity distribution in relation to distribution of substrate and/or cover at different flows. The habitat model integrates habitat quality of combinations of depth, velocity, substrate, and/or cover into an index of habitat quantity, weighted usable area (WUA). Habitat quality of different values of depth, velocity, substrate, and/or cover are entered into the habitat models as habitat suitability criteria.

Habitat suitability criteria or curves are a series of weighting factors assigned to different values of each habitat variable that is measured or predicted. Weighting factors range from 0.00, for uninhabitable values, to 1.00, for optimal values for the life-stage and species of interest (Bovee and Cochnauer 1977). Results of PHABSIM studies are sensitive to suitability criteria; the relation between WUA and flow peaks at different flows when suitability curves differ (e.g., Beecher 1987).

Bovee (1986) distinguished three different categories of habitat suitability criteria. Category I suitability criteria are based on professional judgment (e.g., Jirka and Homa 1990). Category II suitability criteria are utilization frequencies, which do not account for habitat availability. Category III suitability criteria (preference curves) are those in which habitat utilization data are corrected for habitat availability (Bovee 1986).

Both utilization criteria (e.g., Loar et al. 1985; Sheppard and Johnson 1985; Modde and Hardy 1992) and preference criteria (e.g., Baldrige and Amos 1981; Orth et al. 1981; DeGraaf and Bain 1986; Baltz et al. 1991; Helfrich et al. 1991; Bozek and Rahel 1991, 1992) have been published. There is controversy over the merits of the use of the two types of habitat suitability criteria in PHABSIM (Moyle and Baltz 1985; Parsons and Hubert 1988; Morhardt and Hanson 1988; Bartholow and Slauson, Parsons and Hubert 1990; Rubin et al. 1991).

If the PHABSIM is a valid simulation of fish habitat, and if fish occupy habitat with higher depth and velocity suitability, then PHABSIM should be able to predict fish distribution in a stream segment (Milhous et al. 1984; Beecher et al. 1993). If so, then accuracy of prediction should depend on accuracy of habitat suitability determinations, other factors considered.

The purpose of this paper is to evaluate the relative merits of habitat preference (Type III) and utilization (Type II) suitability criteria with computer simulation of fish distribution. The objective of suitability determination is to measure and calculate as accurately as possible the true suitability of different values of habitat variables such as depth and velocity. Two standards for evaluation are matching true suitability and duplicating true fish distribution (e.g., Beecher et al. 1993). We cannot know true suitabilities for real fish; only with hypothetical fish and assigned suitabilities can we know "true" suitability.

Beginning with assigned or true depth and velocity suitabilities for a population of hypothetical fish, and a distribution of depths and velocities, hypothetical fish were distributed (original fish distribution) in a depth and velocity distribution grid according to suitabilities. When depth and velocity utilization and preference suitability criteria were calculated they were compared to a standard of assigned or true depth and velocity suitabilities; the calculated suitability that better matched assigned suitabilities was superior.

A second level of evaluation was to attempt to match the original fish distribution. Calculated utilization and preference suitability criteria were used to distribute fish in the depth and velocity distribution grid. The two resulting fish distributions were compared to the original fish distribution. The closer fit was superior.

Computer simulation is a suitable technique for this comparison because it accounts for assumptions about what governs fish distribution. In many instream flow studies we assume that real fish select habitat based on depth, velocity, and substrate or cover suitabilities. We assume that other behavioral, physiological, and trophic interactions do not influence fish distribution as much as depth, velocity, substrate, or cover, yet we recognize that the other interactions exist. In this simulation, original fish distribution is determined exclusively by the product of depth suitability, velocity suitability, and availability of different combinations of depth and velocity. By definition, the hypothetical fish in this simulation are distributed only according to the product of depth and velocity availabilities and suitabilities. Use of assigned suitability criteria for hypothetical fish rather than suitability criteria for real fish eliminates the extraneous issue of the validity of the suitability criteria.

In this report, I (1) assign depth and velocity suitabilities to hypothetical fish and project their distribution based on assigned suitabilities, (2) calculate utilization suitabilities and preferences, (3) make secondary projections of fish distributions based on preferences and utilization suitabilities, (4) compare utilization suitabilities and preferences to assigned suitabilities, and (5) compare secondary projections to the original projection. The null hypothesis is that utilization and preference suitability would not differ from the assigned (true) suitabilities, and that projected distributions based on preference and utilization suitability did not differ from the original distribution based on assigned suitabilities.

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METHODS

Assigned Habitat Suitabilities

I arrayed a matrix of depth and velocity values in a spreadsheet, with depth held constant in columns and velocity held constant in rows (Table 1). For each depth and each velocity I assigned a suitability value ("assigned suitabilities") from 0.0 to 1.0 (Figure 1). These assigned suitabilities can be considered true suitabilities of the hypothetical fish.

For each combination of depth and velocity I calculated a weighting factor (S[dv]), the product of the assigned suitability for the depth (S[d]) and the velocity (S[v]):

$$S[dv] = S[d] \times S[v] \qquad (1)$$

in Table 1. Assigned suitabilities for depth and velocity were independent. To simplify the simulation, I did not include a substrate suitability in the calculations; this is equivalent to assigning a suitability of 1.0 to all available substrates.

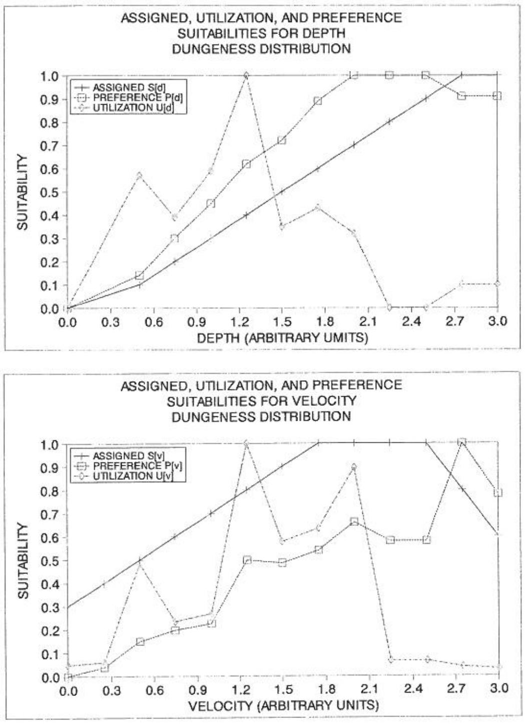

FIGURE 1. *Assigned, derived preference, and utilization suitabilities for depth (A) and velocity (B) in a simulated fish distribution on a depth and velocity distribution from the Dungeness River, Washington.*

Distributions of Depth with Velocity

In a second matrix, a "natural" distribution of available depths and velocities was tabulated as the frequency of each combination of depth and velocity according to a data set from the Dungeness River, Washington (Table 2). Depths and velocities in Tables 2 and 3 are points taken to represent ranges.

Projected Original Fish Distribution

If fish are distributed according to depth and velocity suitabilities, as in default PHABSIM calculations of WUA, then they should be distributed in proportion to the product of the weighting factor (S[dv], Table 1) and the frequency (Table 2 or normal or uniform distribution) of each combination of depth and velocity. Using corresponding cells from each matrix (Table 1 with Table 2 or normal or uniform distribution), I distributed 1,000 fish (subsequently rounded to yield only integers, thus deviating slightly from 1,000) according to assigned depth and velocity suitabilities (Table 3) as follows:

$$n[dv] = k \times F[dv] \times S[d] \times S[v]; \quad (2)$$

where n[dv] is the number of fish at depth d and velocity v; k is a constant to bring total number of fish to 1,000; F[dv] is the frequency of cooccurrence of depth d with velocity v (the sum of all F[dv] is 1.00); S[d] is the assigned suitability for depth d; and S[v] is the assigned suitability for velocity v. The sum of n[dv] is initially 1,000. Values of n[dv] were rounded to the nearest integer as would occur with real fish. Rounding resulted in slightly different numbers of fish (sum of n[dv]).

A similar procedure was used on normal and uniform distributions of depth and velocity. Table 2 was replaced by normal and uniform distributions of depths and velocities in these procedures. In normal and uniform distributions depth and velocity were independent. In the normal distribution, depth and velocity were each distributed normally with mean values in the middle of the ranges, which extended to ±2 s. In the normal distribution the great-

TABLE 1

Weighting factors (S[dv]) for different combinations of depth and velocity are the products of assigned depth and velocity suitabilities (S[dv] = S[d] × S[v]).

	Depth	0.00	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00
	Assigned suitability	0.00	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00	1.00
Velocity	Assigned suitability													
0.00	0.30	0.00	0.00	0.03	0.06	0.09	0.12	0.15	0.18	0.21	0.24	0.27	0.30	0.30
0.25	0.40	0.00	0.00	0.04	0.08	0.12	0.16	0.20	0.24	0.28	0.32	0.36	0.40	0.40
0.50	0.50	0.00	0.00	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50	0.50
0.75	0.60	0.00	0.00	0.06	0.12	0.18	0.24	0.30	0.36	0.42	0.48	0.54	0.60	0.60
1.00	0.70	0.00	0.00	0.07	0.14	0.21	0.28	0.35	0.42	0.49	0.56	0.63	0.70	0.70
1.25	0.80	0.00	0.00	0.08	0.16	0.24	0.32	0.40	0.48	0.56	0.64	0.72	0.80	0.80
1.50	0.90	0.00	0.00	0.09	0.18	0.27	0.36	0.45	0.54	0.63	0.72	0.81	0.90	0.90
1.75	1.00	0.00	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00	1.00
2.00	1.00	0.00	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00	1.00
2.25	1.00	0.00	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00	1.00
2.50	1.00	0.00	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00	1.00
2.75	0.80	0.00	0.00	0.08	0.16	0.24	0.32	0.40	0.48	0.56	0.64	0.72	0.80	0.80
3.00	0.60	0.00	0.00	0.06	0.12	0.18	0.24	0.30	0.36	0.42	0.48	0.54	0.60	0.60

TABLE 2

Frequency of available cells having each combination of depth and velocity, based on English unit data for a site on the Dungeness River, Washington, at 1.4 m^3/sec (mean annual flow = 10.6 m^3/sec).

Depth Velocity	<0.25	0.50	0.75	1.00	1.25	1.50	1.75	1.00	2.25–2.5	2.75+
0.00	.085	.011	.002	.002	.001	.002	.002			
0.25	.085	.011	.002	.002	.001	.002	.002			
0.50	.138	.037	.012	.012	.005			.006		.007
0.75	.027	.033	.003	.003	.008	.001	.001	.003		
1.00	.027	.033	.003	.003	.008	.001	.001	.003		
1.25	.011	.021	.026	.026	.033	.008	.008			
1.50		.039	.008	.008	.015	.004	.004			
1.75		.039	.008	.008	.015	.004	.004			
2.00		.029	.017	.017	.014	.003	.003	.009		
2.25		.004			.002	.001	.001			
2.50		.004			.002	.001	.001			
2.75						.001	.001			
3.00						.001	.001			

est number of cells had mean depth or mean velocity. In the uniform distribution all combinations of depth and velocity had the same frequency; for the uniform distribution, $n[dv] = k \times S[d] \times S[v]$.

Derived Utilization Suitabilities and Derived Habitat Preference

The projected fish distributions (Table 3) were used to derive utilization suitabilities and preferences (Figures 1–3, Table 4) following the procedure used by Beecher et al. (1993). Utilization suitabilities for depth (U[d]) and velocity (U[v]) were calculated as ratios of numbers of fish in an interval (n[d] or n[v]) to the maximum value of n[d] or n[v]:

$$U[d] = n[d]/n[d]_{max},$$

and

$$U[v] = n[v]/n[v]_{max}.$$

Utilization suitabilities range from 0.00 to 1.00.

Derived preferences for depth and velocity were calculated as ratios (scaled to a maximum of 1.00) of projected number of fish in an interval (n[d] or n[v]) to expected number of fish in an interval (E[d] or E[v]) if those fish were distributed only according to frequency (F[d] or F[v]) of that interval (n[d]/E[d] or n[v]/E[v]; Table 4):

$$P[d] = (n[d]/E[d])/(n[d]/E[d])_{max};$$
$$P[v] = (n[v]/E[v])/(n[v]/E[v])_{max}.$$

Expected number of fish in an interval was calculated as:

$$E[d] = F[d] \times \text{sum } n[d, v]),$$

and

$$E[v] = F[v] \times \text{sum } (n[d, v]).$$

Secondary Projections Based on Derived Habitat Preference and Utilization Suitability

Secondary projections of fish into the depth and velocity matrix of Table 2 were made using the preferences and utilization suitabilities from Table 4. The purpose of the secondary projections was comparison of secondary and original projected distributions; the original projection was the expected distribution if the preferences and utilization suitabilities accurately reflected assigned (true) fish suitability or behavior. Projections were made in a similar manner to the generation of Table 3, except that preferences and utilization suitabilities were substituted for assigned suitabilities. I developed two additional matrixes analogous to Table 1 from preferences and utilization suitabilities in Table 4. Using corresponding cells from each matrix (Table 1 analog and Table 2), I distributed fish

TABLE 3.

Projected utilization of depth-velocity combinations based on 1,013 fish distributed proportionately to products of assigned depth and velocity suitabilities (S[d] × S[v]) from Table 1 and frequencies of depth-velocity combinations from Table 2.

	Depth	<0.5	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25–2.5	>2.50	Totals
	Assigned depth suitability	0.00	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.8–0.9	1.00	
Velocity	Assigned velocity suitability											
0.00	0.3		3	1	1	1	2	3				11
0.25	0.4		3	1	2	1	3	4				14
0.50	0.5		14	10	14	8			15		50	111
0.75	0.6		15	3	5	15	3	4	9			54
1.00	0.7		18	4	5	17	4	4	10			62
1.25	0.8		13	32	49	81	25	30				230
1.50	0.9		27	12	18	41	16	19				133
1.75	1.0		30	13	20	45	17	21				146
2.00	1.0		22	27	40	44	10	12	51			206
2.25	1.0		3			5	3	4				15
2.50	1.0		3			5	3	4				15
2.75	0.8						4	5				9
3.00	0.6						3	4				7
Totals		0	151	103	154	263	93	114	85	0	50	1,013

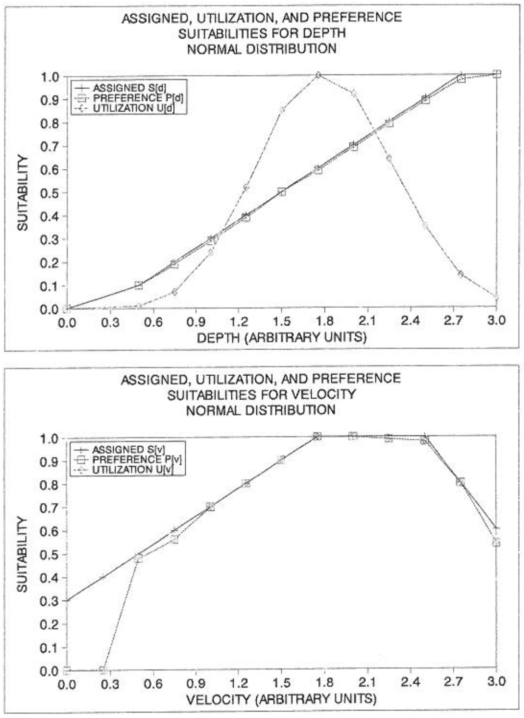

FIGURE 2. *Assigned, derived preference, and utilization suitabilities for depth (A) and velocity (B) in a simulated fish distribution on a normal depth and velocity distribution.*

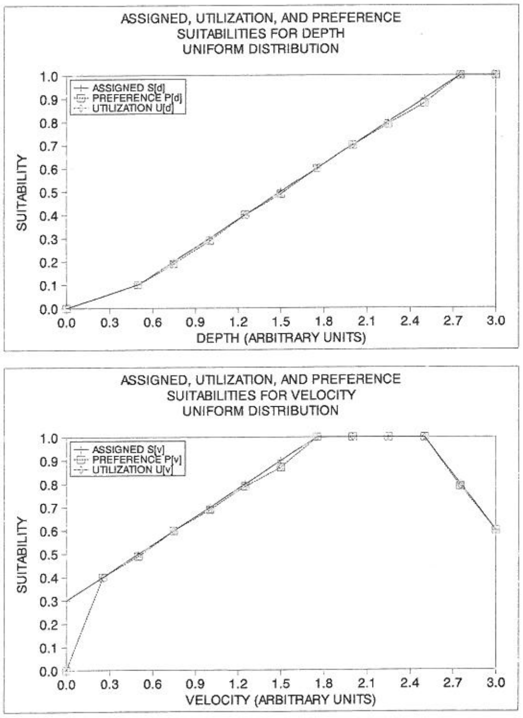

FIGURE 3. *Assigned, derived preference, and utilization suitabilities for depth (A) and velocity (B) in a simulated fish distribution on a uniform depth and velocity distribution.*

TABLE 4

Derivation of depth (P[d]) and velocity preference (P[v]) and utilization suitability (U[d] and U[v]) from projected number of fish (n[d]) or n[v]) in interval d or v in simulated fish distribution (Table 3) and habitat availability (Table 2) based on data for Dungeness River, Washington. Expected number of fish (E[d] or E[v]) is product of frequency of occurrence of interval d or v (F[d] or F[v]) by total number of fish (1,013).

Depth	F[d]	n[d]	E[d]	n[d]/ E[d]	P[d]	U[d]
0.00	0.19	0	189.73	0.00	0.00	0.00
0.25	0.19	0	189.73	0.00	0.00	0.00
0.50	0.26	151	265.41	0.57	0.14	0.57
0.75	0.08	103	83.93	1.23	0.30	0.39
1.00	0.08	154	83.93	1.83	0.45	0.59
1.25	0.10	263	103.93	2.53	0.62	1.00
1.50	0.03	93	31.20	2.98	0.72	0.35
1.75	0.03	114	31.20	3.65	0.89	0.43
2.00	0.02	85	20.67	4.11	1.00	0.32
2.25	0.00	0	0.00	NA	NA	0.00
2.50	0.00	0	0.00	NA	NA	0.00
2.75	0.01	25	6.69	3.74	0.91	0.10
3.00	0.01	25	6.69	3.74	0.91	0.10

Velocity	F[v]	N[v]	E[v]	N[v]/ E[v]	P[v]	U[v]
0.00	0.10	11	106.26	0.10	0.03	0.05
0.25	0.10	14	106.26	0.13	0.04	0.06
0.50	0.22	111	227.01	0.49	0.15	0.48
0.75	0.08	54	80.79	0.67	0.20	0.23
1.00	0.08	62	80.79	0.77	0.23	0.27
1.25	0.13	230	136.05	1.69	0.50	1.00
1.50	0.08	133	80.79	1.65	0.49	0.58
1.75	0.08	146	80.79	1.81	0.54	0.63
2.00	0.09	206	93.60	2.20	0.66	0.90
2.25	0.01	15	7.70	1.95	0.58	0.07
2.50	0.01	15	7.70	1.95	0.58	0.07
2.75	0.00	9	2.68	3.35	1.00	0.04
3.00	0.00	7	2.68	2.61	0.78	0.03

according to depth and velocity preferences (1,003 hypothetical fish) and utilization suitabilities (1,001 hypothetical fish) (Tables 4 and 5) as in equation 2. Because of differences in the areas under suitability curves, the sum of *n*[d,v] after rounding in the preference projection was 1,003, and for the projection based on utilization it was 1,001.

The null hypothesis was that projections based on preference and utilization suitability were not different from the original distribution based on assigned suitability.

TABLE 5

Correlations between assigned suitabilities (S) and derived preferences (P) and utilization suitabilities (U).

		Depth-velocity distributions					
		Dungeness		Normal		Uniform	
Depth	Assigned S[d]	P[d]	U[d]	P[d]	U[d]	P[d]	U[d]
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.50	0.10	0.14	0.57	0.10	0.01	0.10	0.10
0.75	0.20	0.30	0.39	0.19	0.07	0.19	0.19
1.00	0.30	0.45	0.59	0.29	0.24	0.29	0.29
1.25	0.40	0.62	1.00	0.39	0.52	0.40	0.40
1.50	0.50	0.72	0.35	0.50	0.85	0.49	0.49
1.75	0.60	0.89	0.43	0.59	1.00	0.60	0.60
2.00	0.70	1.00	0.32	0.69	0.92	0.70	0.70
2.25	0.80	NA	0.00	0.79	0.64	0.79	0.79
2.50	0.90	NA	0.00	0.89	0.35	0.88	0.88
2.75	1.00	0.91	0.10	0.98	0.14	1.00	1.00
3.00	1.00	0.91	0.10	1.00	0.04	1.00	1.00
$r =$		0.93	−0.27	1.00	0.83	1.00	1.00
$n =$		11	13	13	13	13	13
P		0.05	NS	0.01	0.01	0.01	0.01

		Depth-velocity distributions					
		Dungeness		Normal		Uniform	
Velocity	Assigned S[v]	P[v]	U[v]	P[v]	U[v]	P[v]	U[v]
0.00	0.30	0.00	0.05	0.00	0.00	0.00	0.00
0.25	0.40	0.04	0.06	0.00	0.00	0.40	0.40
0.50	0.50	0.15	0.48	0.48	0.40	0.49	0.49
0.75	0.60	0.20	0.23	0.56	0.13	0.60	0.60
1.00	0.70	0.23	0.27	0.70	0.34	0.69	0.69
1.25	0.80	0.50	1.00	0.80	0.62	0.79	0.79
1.50	0.90	0.49	0.58	0.90	0.90	0.87	0.87
1.75	1.00	0.54	0.63	1.00	1.00	1.00	1.00
2.00	1.00	0.66	0.90	1.00	0.78	1.00	1.00
2.25	1.00	0.58	0.07	0.99	0.47	1.00	1.00
2.50	1.00	0.58	0.07	0.98	0.23	1.00	1.00
2.75	0.80	1.00	0.04	0.80	0.07	0.79	0.79
3.00	0.60	0.78	0.03	0.54	0.01	0.60	0.60
$r =$		0.67	0.39	0.93	0.75	0.97	0.97
$n =$		13	13	13	13	13	13
P		0.05	NS	0.01	0.01	0.01	0.01

I compared distributions of secondary projections of fish with the original projection based on assigned suitability using chi-square analysis. Values in the original projection (Table 3) were the expected values for secondary projections.

RESULTS

Assigned suitabilities were closer to derived preferences than to utilization suitabilities for the natural depth-velocity distribution (Figure 1, Table 5). In the normal distribution, both preference and utilization suitabilities were close to assigned suitabilities for velocity, but depth preference was much closer to assigned suitability than was utilization (Figure 2, Table 5). Preference and utilization suitabilities matched assigned suitabilities equally well in the uniform distribution (Figure 3, Table 5). Depth and velocity preferences were significantly correlated ($r \geq 0.65$, $P \leq 0.05$; Table 5) with assigned depth and velocity suitabilities in the natural depth-velocity distribution as well as in the normal and uniform distributions. Likewise, utilization suitabilities were significantly correlated with assigned depth and velocity suitabilities in the normal and uniform distributions ($r \geq 0.75$, $P < 0.01$; Table 5). By contrast, utilization suitabilities were poorly correlated with assigned suitabilities in the natural Dungeness River depth-velocity distribution (depth: $r = -0.27$, velocity: $r = 0.39$, $P > 0.05$; Table 5). Correlations between preferences and assigned suitabilities were lowest in the natural example (Table 5). In the natural distribution, patterns of preferences and assigned suitabilities were similar, with peak preferences near peak assigned suitabilities, but they were not identical (Figure 1). In this simulation, the relative difference between preference and assigned suitability at a given interval is greater for velocity than for depth.

The original projected fish distribution based on assigned suitabilities did not differ significantly (chi-square = 7.94, df = 54, $P > 0.995$) from the secondary projection based on preference curves in the natural depth-velocity distribution. However, the secondary projection based on utilization suitabilities differed from the original projection (chi-square = 700.5, df = 54, $P \ll 0.001$). The secondary projection based on utilization suitabilities resulted in more fish in shallow depths (<1.5) and fewer fish in deep water (≥1.5) than in the original projection.

DISCUSSION

This simulation supports the use of preference curves over utilization curves in PHABSIM studies, except where availability is uniformly distributed as a result of study design (e.g., Rubin et al. 1991). The higher correlation of assigned suitabilities with preference than with utilization suitabilities and the better match of original fish projection with the secondary projection based on preference indicate that calculated preferences are superior to utilization suitabilities.

In the uniform distribution of depth and velocity, utilization suitabilities closely matched assigned suitabilities and preferences (Table 5). Consequently, a sampling strategy such as that used and recommended by Rubin et al. (1991), which samples all combinations of depth and velocity equally, will yield good representations of true preference from utilization. Their sampling strategy requires a relatively high density of the target fish, and they recommend accounting for availability in preference calculation for less abundant fish (Rubin et al. 1991). With the exception of some salmonid fry (Rubin et al. 1991) and spawning pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye or kokanee salmon (*O. nerka*), salmonid densities in Washington are too low to allow equal effort sampling without an extraordinarily large effort.

Habitat utilization could match preference, but usually does not. The species' entire range of depth and velocity suitability is seldom encompassed by equally available combinations of depths and velocities at the flow at which they are being observed and measured. For example, no fish could use the cells with the highest suitability (lower right of Tables 1, 2, and 3) because no part of the reach of the Dungeness River had the combination of depths and velocities corresponding to suitabilities of 1.00 for both depth and velocity at the flow sampled. In the normal distribution fewer fish were in deeper depths because fewer deeper depths were available, resulting in a poor match between depth utilization and assigned suitability.

Two factors appear to cause deviation of preference from assigned suitability. The first is deviation of codistribution of depth and velocity from random normal or uniform distribution. The second is the occurrence of true suitabilities of 0.0 for one of the habitat attributes (i.e., depth), which drives down the preferences for the other habitat attribute (i.e., velocity).

The first factor is shown by the much

closer match between preference and assigned suitability in the normal and uniform simulations, compared to the "natural" example (Figures 1–3; Table 5). If velocity and depth are correlated so that fast water is associated with deep water, then a fish that prefers fast water will appear to prefer deep water even if its depth preference is catholic. Such a false preference could lead the PHABSIM to overestimate flow needed to maximize habitat. However, Beecher et al. (1993, 1995) successfully predicted steelhead (*Oncorhynchus mykiss*) parr density in cells of different depths and velocities at different times and flows. Steelhead parr density predictions were based on depth and velocity preference curves developed from an independent sample of about 100 steelhead parr in the same stream (Beecher et al. 1993, 1995). The errors that may have entered the preference curves did not prevent a reasonable match between fish distribution and distribution of WUA. Thus, although habitat preference curves are subject to error, the "natural" simulation in this study and a related field test suggest that the PHABSIM can be useful for approximating habitat as used by fish in those cases where the habitat variables used in the PHABSIM are the attributes to which fish are responding.

A solution to the second factor was proposed by Baldrige and Amos (1981), who recommended deleting unusable values (e.g., those velocities associated with depths having preferences of 0.0, from summation of availability). Their procedure should improve the match. In the normal and uniform distributions, the correlations between assigned and preference suitabilities were higher for depth than for velocity (Table 5).

Sample sizes in these simulations were larger than most applications of the PHABSIM in Washington, where numbers of fish of any one species and life stage observed in suitability curve verification studies usually range from 20 to 200. Smaller sample size reduces resolution of preference curves; bin width will be wider with smaller sample size because a larger part of the available habitat must be sampled to accumulate the requisite expected number of fish in a bin.

Simulations in this study were based on the assumption that depth and velocity suitabilities were the only factors influencing fish distribution. With hypothetical fish, whose behavior is dictated by the model, this assumption is accurate. However, Shirvell (1989) found that the PHABSIM was inaccurate in predicting chinook salmon (*O. tshawytscha*) spawning distribution, possibly because salmon were orienting to topography or flow through gravel, which are not modeled in the PHABSIM. Habitat suitability curves for PHABSIM studies are only valid if behavior of the fish is understood and relevant habitat variables are addressed. We must understand the importance of depth, velocity, substrate, or cover relative to other habitat variables; if different habitat variables are determining fish habitat selection, then use of the standard PHABSIM habitat variables will yield misleading results.

In conclusion, use of Category III preference criteria is superior to utilization (Category II) suitability criteria unless very high fish density is found and sampling is equally distributed over all combinations of depth and velocity. However, the habitat variables for which suitability is being determined must be important for habitat selection by the target species if the resulting PHABSIM model is to produce useful simulations.

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