THESIS

THE EFFECT OF DEPTH-VELOCITY CORRELATIONS ON AQUATIC PHYSICAL HABITAT USABILITY ESTIMATES

Submitted by
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY CHARLES G. PREWITT, ENTITLED THE EFFECT OF DEPTH-VELOCITY CORRELATIONS ON AQUATIC PHYSICAL HABITAT USABILITY ESTIMATES, BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF THESIS

THE EFFECT OF DEPTH-VELOCITY CORRELATIONS ON AQUATIC PHYSICAL HABITAT USABILITY ESTIMATES

Recent developments in instream flow evaluations have resulted in a variety of assessment methodologies. Of these, the Instream Flow Incremental Methodology permitted consideration of both physical habitat parameters (e.g., depth, velocity, substrate and temperature) and preferences for certain values of these parameters by selected organisms. This methodology was based on the PHABSIM (Physical HABitat SIMulation) computer system, which allowed 1) prediction of depths, velocities and associated substrates at a stream reach; 2) determination of weighting factors for the predicted values from preference curves constructed for each organism or group of organisms; and 3) application of a joint weighting factor (obtained by multiplying the individual weighting factors) to the surface area of the stream reach to obtain weighted usable area (WUA) for that reach. WUA is an indicator of the extent of available preferred physical habitat and a valuable tool in streamflow assessments.

Calculation of joint preference factors by multiplication was statistically permissible only if the variables were uncorrelated. Using the original calculation approach, variable correlations were assumed to be zero, but might actually be quite high. To test the hypothesis that two-variable (depth-velocity) correlations greater than zero did not significantly affect WUA results, a study was designed to account for effects of increased levels of correlation upon WUA calculated using various preference curves in a variety of stream types and channel characteristics.

In the entire data set, the hypothesis was supported only to a correlation level of .2, a level unlikely to occur. However, results were more consistent in medium and large streams than in small streams. Further, in medium and large streams with complex channel configuration, users could expect independent depth-velocity curves to give results similar to correlated curves even if the actual correlation level was 0.4 or in many cases 0.6. Indicators of simple and complex channel conditions and discharge ranges of small, medium and large streams were given.

Ecological (niche and guild theory) inferences related to habitat requirements and impact analysis were briefly discussed, and hypotheses regarding habitat diversity and stability presented. Definition of a fundamental niche using a multivariate statistical approach was suggested as a tool in predicting effects of environmental changes upon usable habitat.

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INTRODUCTION

Substantial effort has recently been expended to determine the effects of various streamflow quantities upon aquatic life. The need to quantify streamflow requirements has supported much State and Federal agency activity in the development of "methodologies" for evaluation of various stream discharges in terms of fish habitat or population effects.

Most such methodologies have allowed evaluation of changes in physical parameters of a stream with changes in flow; some have provided methods for evaluating these changes in terms of fish preferences for various physical habitat parameters. All have, to some extent, been criticized for their inability to deal with all parameters thought to play important roles in determining the quality of instream habitat.

Early in the study of streamflow requirements, Collings (1974) and Thompson (1974) determined that, for spawning of Pacific salmon in the American Northwest, depth, velocity and substrate were the major physical habitat components. Bietz (1981) and Gorman and Karr (1978) found that significant amounts of variation in spawning location and community diversity could be explained by distributions in depth, velocity and substrate.

Hynes (1970) listed these variables among others as major elements in stream fish habitat. Gore (1978), Williams and Winget (1979) and Radford and Hartland-Rowe (1971) emphasized substrate and velocity suitability for invertebrate production in streams. Stalnaker (1979) stressed the importance of depth, velocity and substrate distributions for fishery maintenance. Because findings supported use of a limited set of variables, and because depth, velocity and substrate were the three influential physical variables most likely to change with changes in stream discharge, many early methodologies were based upon them.

In early studies, measurements of depth, velocity and substrate were taken at various flows to determine the value of the measured flow as fish habitat (Waters 1976; Bovee 1974). Time and money restrictions demanded that these parameters be simulated at various flows using computer modeling techniques developed for simulation of velocities and depths in floodplain and channel design studies. A U. S. Bureau of Reclamation flood routing program (Water Surface Profile) allowed simulation of depths, velocities and substrates at multiple, spatially-related cross-sections across a relatively-wide range of unmeasured flows (Spence 1975; Dooly 1976; White 1975; Elser 1976; Cochnauer 1976) and received wide usage. This program allowed rapid simulation of depths and velocities at various flows but did not allow evaluation of predicted values as available habitat.

Biological Criteria.

Collings (1974) presented binary representations of fish habitat preferences by assigning a weighting of one to parameter values within the preferred range and a weighting of zero to values outside the preferred range. Bovee (1974, 1978) and Bovee and Cochnauer (1977) demonstrated preferences as curves which allowed evaluation of less than optimum parameter states. Still, no method for quickly coupling computer-predicted depths, velocities and substrates with preference curves was available.

The Cooperative Instream Flow Service Group (CIFSG) of the U. S. Fish and Wildlife Service was formed in part to develop a methodology which could be used to evaluate various streamflows in terms of available fish habitat. The result of this effort was the Incremental Methodology (Bovee 1982) which was based upon the PHABSIM (Physical HABitat SIMulation) computer system (Milhous 1979; Milhous, Wegner and Waddel 1981). This system reduced previous data processing problems by use of the computer program HABTAT (Main 1978a),which coupled hydraulic simulation output, as predicted depth (d), velocity (v) and associated substrate (s), with d, v and s preference curves for numerous target species (Bovee 1978).

The PHABSIM system required field measurement of d, v and s at certain points (verticals) on a stream cross-section (Figure 1). Locations of verticals and cross-sections were determined by the spatial distribution of

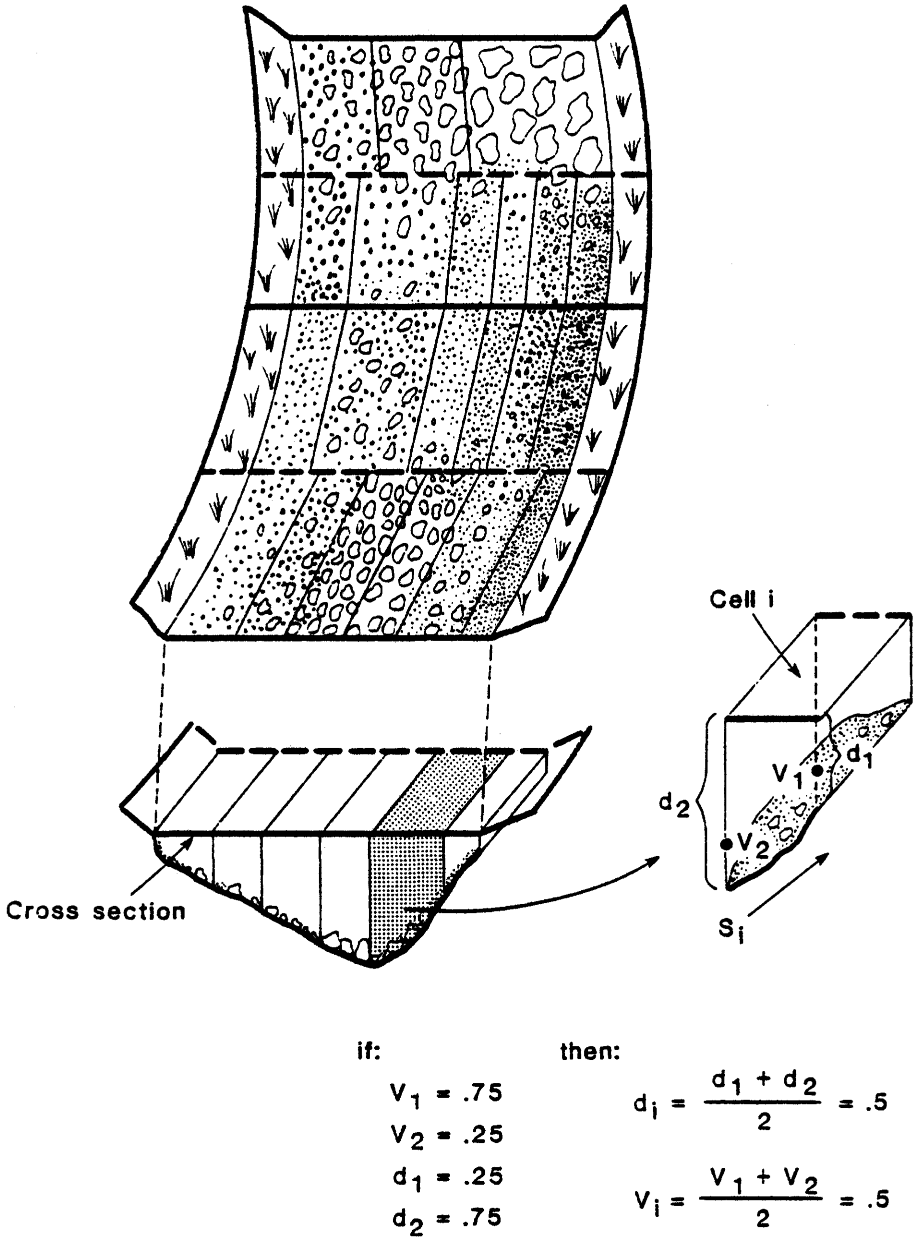


Figure 1. PHABSIM representation of stream physical habitat by placement of cross sections and verticals.

d-v-s combinations in the measured habitat. Measurements were taken such that d, v and s could be predicted (using a computer model) at flows other than those actually measured.

Predicted d, v and s for each cell were located on preference curves for the target species using either a univariate or multivariate approach (Figure 2). In the univariate approach, independent 2-dimensional curves for each variable were used, and from these, preference factors for various d, v and s values obtained. The individual preference factors were multiplied to obtain a joint preference factor. In the multivariate approach, the preference curves were defined by a preference function which expressed the preferences jointly. Solution of the function for various d, v and s values also resulted in a joint preference factor, but one which reflected interactions between the variables (Voos 1981).

Either joint preference factor could be applied to the surface area of the cell to obtain Weighted Usable Area (WUA) for that cell. The WUAs for the individual cells were then summed to obtain a total WUA for the reach at the modeled discharge.

WUA indicated the relative usability of the stream reach in terms of preferred physical habitat for the target species (Stalnaker 1979). Use of the univariate curves had become the standard analytic approach because 1) data for their construction could be derived from literature,

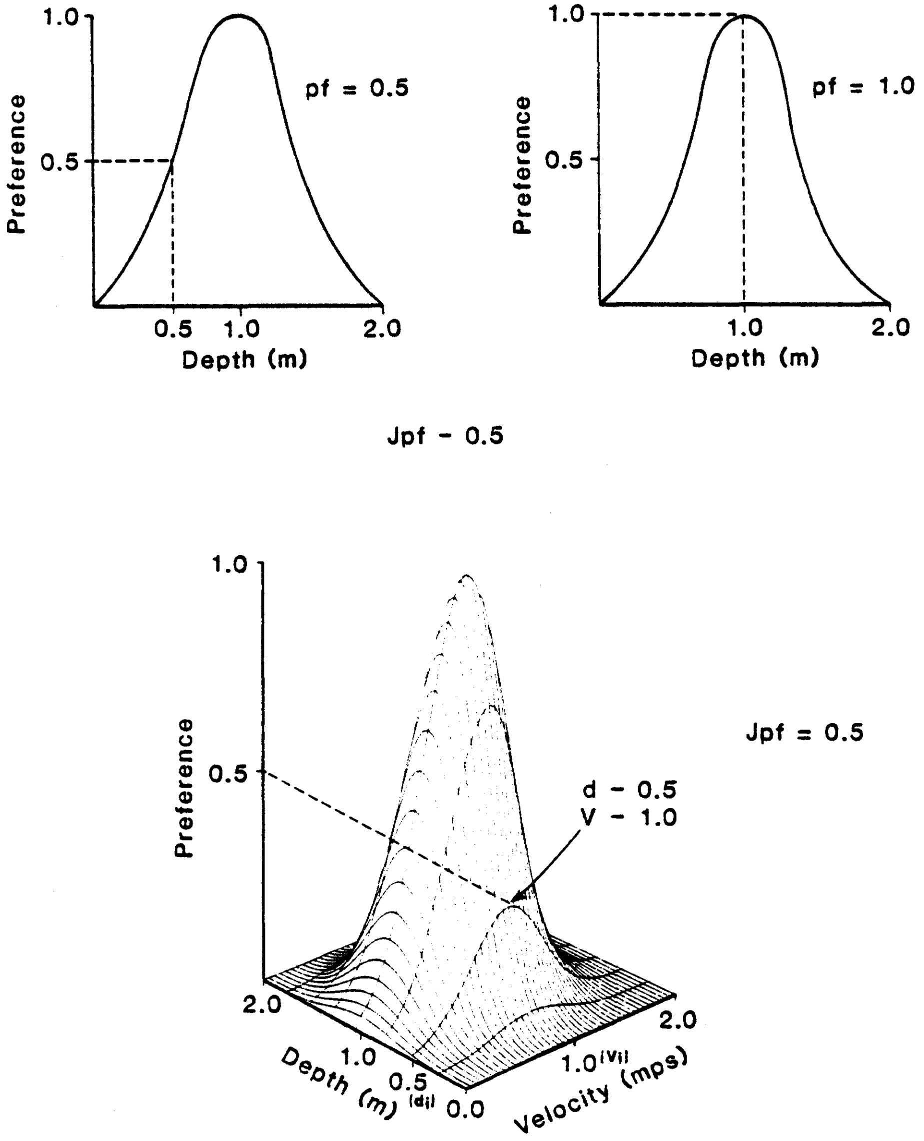


Figure 2. Method for determining joint preference factor (jpf) for depth and velocity using univariate (above) and bivariate (below) approaches.

through general opinion or from estimation (Bovee and Cochnauer 1977), and 2) the PHABSIM system had been widely accepted. Hundreds of applications had resulted in general satisfaction with results based upon the use of the univariate approach.

Statistical problems with the univariate calculation technique were voiced during a formal critique of elements of the methodology (Patten 1979). Specifically, multiplication of preference factors to obtain joint preference was considered conceptually equivalent to determining a joint probability for two independent events, permissible only if the variables were entirely uncorrelated (Mood, Graybill and Boes 1964). If, for example, a fish species preferred high water velocities only in shallow water, a strong negative correlation between d and v would result. WUA calculated using the univariate approach might differ significantly from WUA calculated using the multivariate approach which reflected this correlation. Some examination of the effects of d, v and s correlations was presented by Orth (1980) and Voos (1981), but effect of correlations on WUA under a rigid set of conditions had not been studied.

For convenience in this paper, correlations between variables in either univariate or multivariate preference expressions will be denoted by the symbol ρ_p. In the univariate approach, ρ_p must always equal 0. In the multivariate approach, ρ_p may equal 0 or may range from -1 to +1.

Hypothesis Testing.

The null hypothesis was that WUA calculated using the univariate approach did not differ significantly from WUA calculated using a multivariate approach, where ρ_p might equal .2, .4 or even .8, with all other factors equal. The results of the testing, however, were to be of value in helping PHABSIM users determine the reliability of results using the univariate approach. Therefore, beyond the testing of the primary hypothesis, the following questions were addressed.

1. If variable correlations did affect WUA values, at which level of ρ_p were results likely to become unreliable?

2. Were there situations in which changes in WUA might be acceptable?

3. Could PHABSIM users who desired to use the univariate approach because of cost and time constraints use certain indicators to evaluate the reliability of their results?

Study Design.

The study was designed not only to provide a very generalized test of the primary hypothesis but also to answer the user-related questions in as broad an applicational setting as possible. The following steps were taken to ensure a sufficiently-broad experimental base.

1. Study sites sufficient to represent small, medium and large streams were selected. Within each size classification, a "simple" and a "complex" site were selected. "Simple" stream reaches were those with apparently homogeneous channel structures (adjacent depths and velocities were quite similar across the channel), while "complex" reaches were those with heterogeneous channel structures (adjacent depths and velocities were not always similar). Depth and velocity measurements for use in the PHABSIM system were taken at these sites, and hydraulic models were calibrated to predict d and v at unmeasured flows.

2. Based on literature review and actual data, three velocity and five depth preference curves were drawn. These curves were to represent actual preferences as if an investigator had accounted for the habitat availability where the fish were observed, as recommended by Voos (1981). Substrate was not included because 1) the strongest actual correlations had been observed between depth and velocity (Bietz 1981, Hardy 1982); 2) using simple correlation coefficients, only variable pairs could be considered; and 3) if multiple correlations had been considered, results would have been greatly complicated.

3. Exponential polynomial functions were fit to the individual univariate depth and velocity curves.

4. The individual depth and velocity curves were combined into five preference sets, which were assumed to represent physical habitat guild preferences, ranging from preferences for slow, shallow water through preferences for moderate depth and velocities to those for very deep and fast water. The univariate depth and velocity function coefficients were combined to produce bivariate guild preference functions with depth-velocity correlations (ρ_p) equal to 0.

5. Through a parameterization process, ρ_p values ranging from 0 to .8 were assigned to the bivariate guild functions, resulting in five functions (one each for ρ_p levels of 0, .2, .4, .6 and .8) for each guild. Only d-v correlations changed with these functions; the original preference ranges and optima remained.

6. The function fitting from 3 above and the parameterization from 5 above were checked by visual examination of 2- and 3-dimensional function plots.

7. For each of the six stream types, WUA was calculated for each correlation level (0.0 - 0.8) of each guild at five or six discharge levels expected to occur at the site. WUA calculated from functions with

correlation greater than 0 was expressed as a percentage of WUA calculated using the 0 correlation function.

8. At each correlation level (including 0) the mean of the WUA percentages for the five or six flows was calculated. This mean and the coefficient of variation (standard deviation-mean quotient) were used as the bases for hypothesis testing.

A maximum acceptable level of 20 percent deviation from WUA calculated using the univariate approach ($\rho_p = 0$) was specified. The percent deviation values were denoted by the symbol delta (δ). If δ was greater than 20 percent, the ρ_p level associated with that δ was considered too high to support the primary hypothesis. The coefficient of variation value (cv) gave insights into the amount of expected WUA variation across the range of flows. Because PHABSIM users routinely calculate WUA for all flows within the expected range, high cv values might indicate unreliable results even if δ were less than 20.

MATERIALS AND METHODS

Physical Habitat Measurement Sites.

To determine the extent to which WUA changed under various conditions in the environment, six physical habitat measurement sites were selected. To determine the effect of stream size and complexity, the sites were characterized as small, medium or large, and within each category, a simple and a complex reach were selected. Of interest at each site were physical dimensions, hydraulic characteristics and complexity. Also, the d-v correlation (denoted ρ_h for correlation between measured d-v values in the habitat) was of interest as a further indicator of complexity. In most cases, ρ_h value was expected to be higher in a simple channel because in such channels, as depth of flow increased, velocity usually increased. This relationship was not consistent in complex channels, usually resulting in low ρ_h values.

Physical habitat was measured at stations on the Elk, Yampa and Colorado Rivers in Northwestern Colorado and on the Red River in Northern New Mexico. The Elk and Red River sites were representative of small streams located high in their respective watersheds.

The Elk River reach was selected because of its apparently simple channel and assumed high ρ_h value. The Red

River reach was selected as a contrast to the Elk River reach because of its extreme apparent channel complexity.

Yampa River sampling locations were chosen to demonstrate both simple and complex characteristics in medium-sized streams at intermediate watershed locations. The Yampa site near Maybell, Colorado, represented a simple, cobble-substrate reach. The ρ_h value here was expected to be high.

The Yampa station near Lily, Colorado, was a unique, highly complex habitat of the same relative size as the Maybell station. Located approximately 3 km downstream from the mouth of Cross-Mountain Gorge, this site had an entirely alluvial channel with high apparent complexity and assumed low ρ_h.

The selected large river reaches were on the Colorado River downstream from Grand Junction, Colorado. The Colorado River reach known as Black Rocks was the most complex of all the reaches measured (ρ_h was assumed to be quite low). Known to have depths in excess of 20 m, this reach was characterized by a predominantly bedrock bed incised in granitic gneiss. While the main channel was quite deep, extensive lateral channel areas were shallow with numerous potholes and irregularities.

The sampling site near Moab, Utah, was chosen to represent simple (high ρ_h) channel conditions in a large river.

It was similar to the Maybell reach on the Yampa River but had an alluvial bed composed primarily of silt and mud.

Physical Habitat Measurement Techniques.

The measured variables (d and v) and the widths and lengths at each site were determined at multiple cross-sections at low, medium and high flow, using standard cross-sectional water measurement techniques (U. S. Bureau of Reclamation 1967; Grover and Harrington 1966). At each site, four to six cross-section locations were selected to fit the PHABSIM assumption that the depth, velocity and width of each cross-section extended one-half the distance to each adjacent (up- or downstream) cross-section. Clearly, complex reaches required more cross-sections than simple reaches for proper definition of features (Bovee and Milhous 1978; Trihey and Wegner 1981).

In the shallow, wadeable stream reaches and at low flows at certain large river cross-sections, depth and velocity were measured at from six to 40 points using a calibrated wading rod and either a Price AA anemometer-type or a March-McBirney electromagnetic direct-readout current meter. Mean column water velocities were obtained by measuring at 0.6 of the water column depth (from the surface) in water less than 0.91 m deep and by averaging measurements taken at 0.2 and 0.8 of the water column depth in water greater than 0.91 m deep.

In waters too deep to wade, depths and velocities were measured using the standard U. S. Geological Survey

(USGS) boat measurement system. A rigid cross-piece and extendable boom were mounted on an aluminum boat which was affixed to a 3.2-mm steel cable which spanned the river at the cross-section location. A calibrated reel (USGS Model A-55) was used to lower a sounding weight to a desired depth or to the bottom to determine depth at a given point on the cross-section. The current meter was attached to the sounding weight, and velocities were measured at depths to which the weight was lowered. Depths and velocities were obtained at the same distance from a bankside reference point regardless of the discharge at the time of measurement.

To ensure dimensional integrity, all water surface and ground-point elevations were determined relative to an elevation benchmark using standard differential leveling techniques (Bouchard and Moffitt 1965). Where water depth prevented measurement of ground elevations using the surveying rod, sounded depths were subtracted from water surface elevations to obtain stream-bed elevations.

Prediction of Depths and Velocities at Unmeasured Discharges.

At each cross-section, stage (water surface elevation) and mean column velocities were predicted using a regression computer program, IFG-4 (Main 1978b). This program calculated regression coefficients for the log-log stage-discharge relationship at each cross-section and for the velocity-discharge relationship at each vertical on the cross-section. The stage power function was of the form:

$$S = aQ^b$$

where:

S = predicted stage,

a = intercept of the stage-discharge curve,

b = slope of the stage-discharge curve, and

Q = discharge.

Similarly, velocities at the verticals were predicted using:

$$V = cQ^d$$

where:

V = predicted velocity,

c = intercept of the velocity-discharge curve,

d = slope of the velocity discharge curve, and

Q = discharge.

Given predicted stage in terms of water surface elevations, depths were determined by subtraction of known bed elevations from the stage.

Fish Preference Curves.

Since reliable individual species preference curves were not available for fishes inhabiting two of the rivers used as physical habitat sites (the Yampa and Colorado), simulated curve sets, sufficient in scope and number to represent most possible fish preferences, were used.

Certain selected preference curve functions were based upon the expected preferences of the various life history stages of Colorado squawfish (*Ptychocheilus lucius*), humpback chub (*Gila cypha*), and razorback sucker (*Xyrauchen texanus*), because these native fish species evolved within many of the measured physical habitats.

The preference curves used throughout this study, however, should be thought of as representative of the physical habitat preferences of assemblages of fish, definable as guilds (Balon 1975), rather than the preferences of individual species.

The approach to development of the curve sets was to first represent basic preference ranges for the individual variables. Three velocity categories were initially assumed (Figure 3).

The V_1 curve was intended to simulate an extremely restrictive velocity preference, probably characteristic of fish larvae or adult fishes with strong standing-water preferences. V_2 was a less restrictive velocity curve to demonstrate preferences of advanced larvae or juveniles of lotic fishes or adults preferring quiet water. V_3 was probably applicable to adults of a variety of riverine species with rather broad velocity tolerances but slightly diminished preferences for standing water.

The depth curves were developed similarly. The D_1 curve represented preferences of extremely small fish, perhaps to escape predation or to avoid higher velocities often associated with deeper water (Figure 4). D_2 was a less-restrictive depth curve, applicable to juvenile fishes

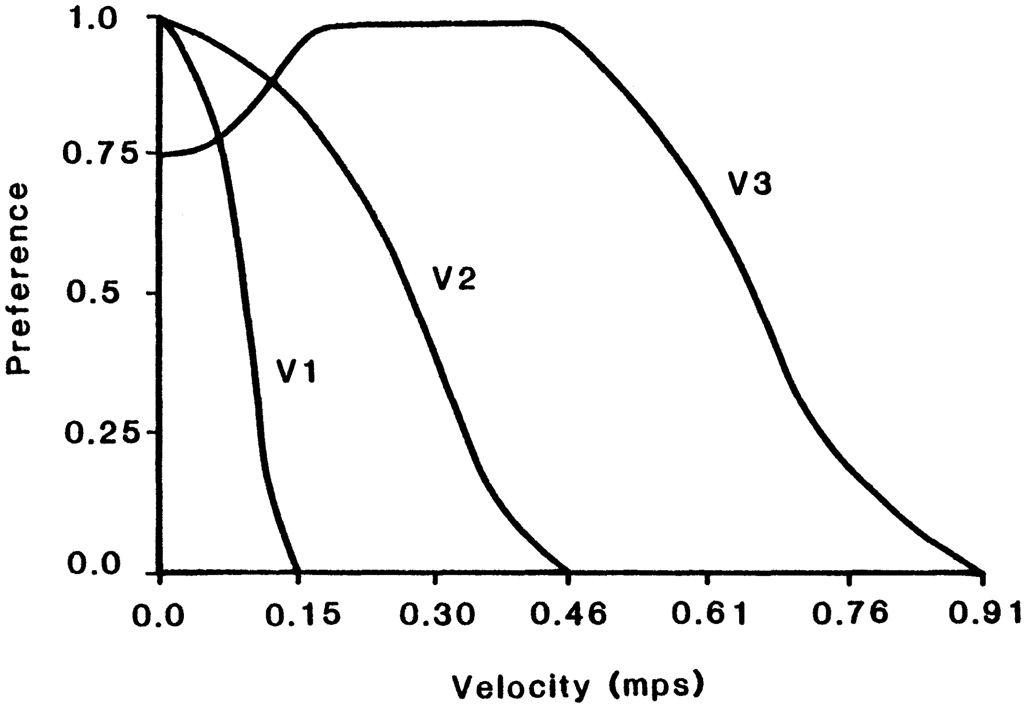


Figure 3. Assumed appearances of the V_1, V_2 and V_3 preference curves.

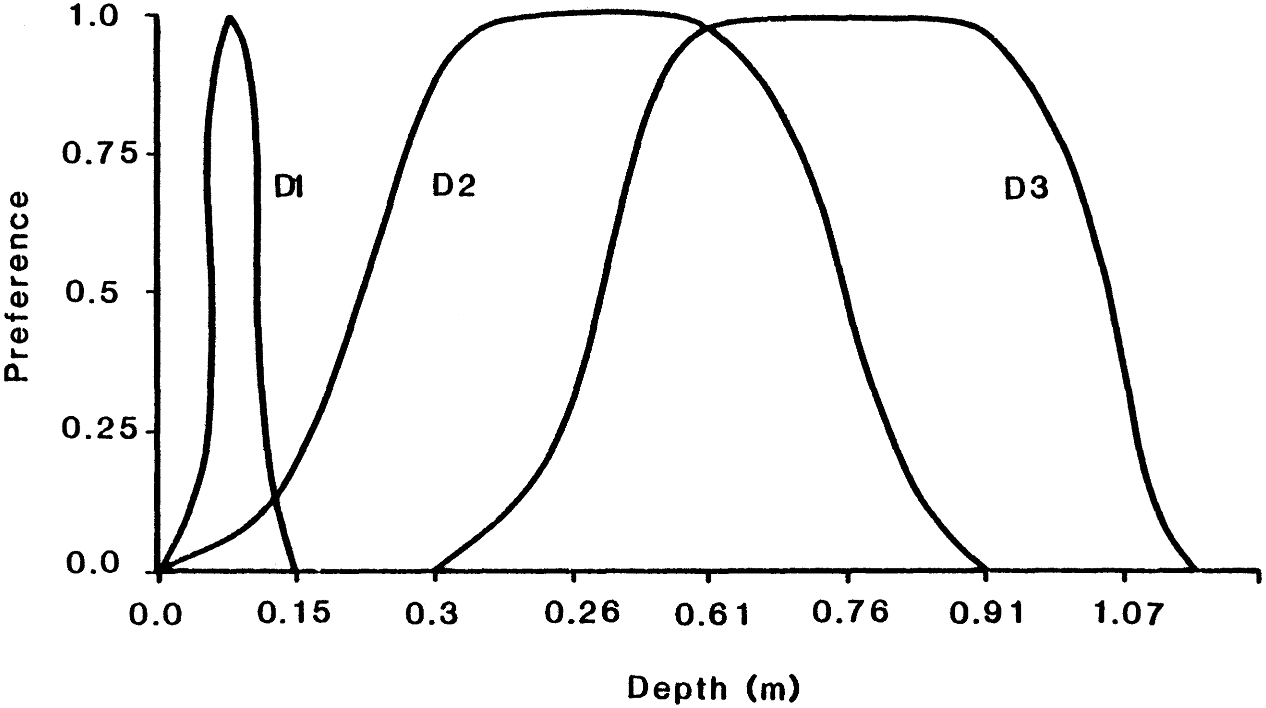


Figure 4. Assumed appearances of the D_1, D_2 and D_3 preference curves.

or groups whose feeding behavior required depths less than 0.9 m or whose spawning activities were normally conducted in shallow water.

D_3 was a less restrictive curve with a significantly higher optimum depth but low preference for areas usually considered "pools" (Figure 4). The D_4 curve represented preferences for moderate depths, perhaps typical of benthic species which were found on the substrate of a pool in which "D_3 species" would occupy a shallower level in the water column (Figure 5). The D_5 curve (Figure 5) represented a truly depth-tolerant species group with optimum preference near 12 m and tolerances of depths to 21 m, a value selected because it approximated depths in the deepest reaches of the studied physical habitats.

Curve Sets for Physical Habitat Guild Preferences.

Certain combinations of the depth-velocity curves were based upon expected guild preferences. For example, the early larval stages of most cyprinid and catostomid species, because of their small size and poor swimming competency, could not tolerate even moderate velocities and probably would prefer standing water if it were available. Vanicek and Kramer (1969) stated that Colorado squawfish "young were most often taken in still, shallow pools, near shore." Sigler and Miller (1964) and Miller (1964) reported squawfish young in moderate current and shallow water. Hagen and Banks (1963) captured young squawfish only in "quiet backwaters." Taba, Murphy and Frost (1965) reported that young

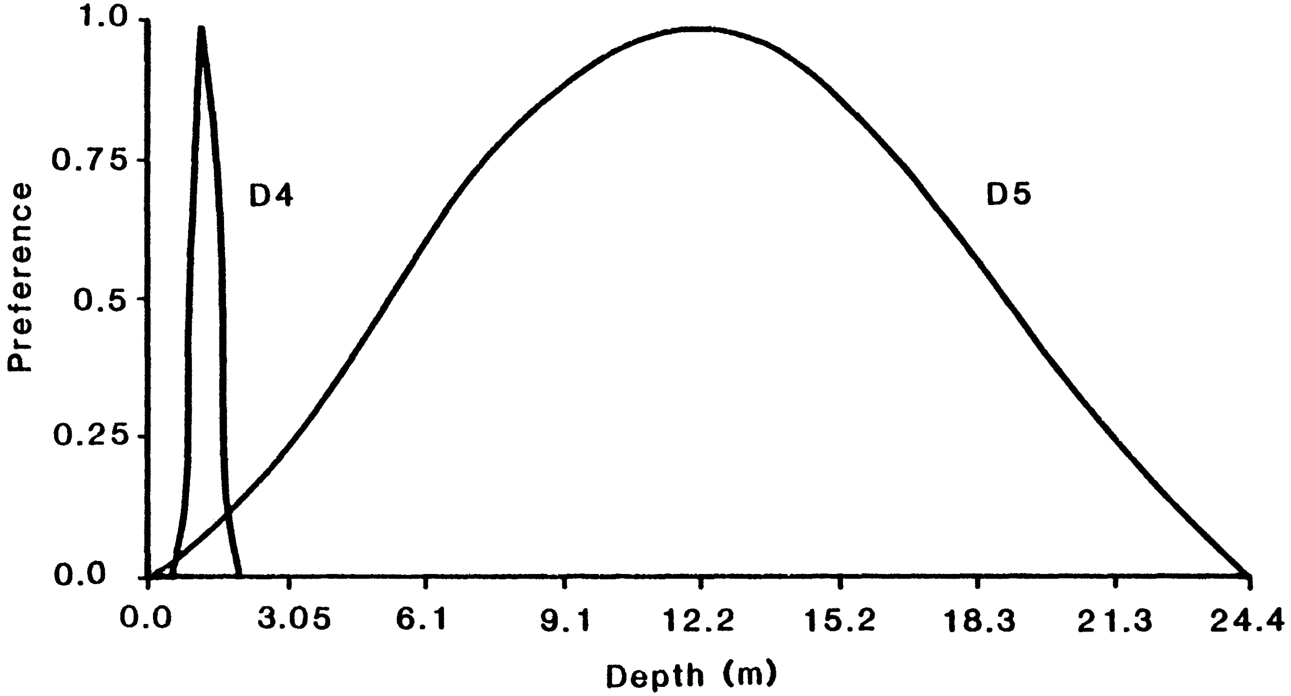


Figure 5. Assumed appearances of the D_4 and D_5 preference curves.

squawfish were "much in evidence in quiet backwaters." Prewitt, Wick and Snyder (1978) captured all cyprinid and catostomid larvae in the Yampa, White, Gunnison and Colorado Rivers in slow, shallow side-channel and backwater areas. Holden and Stalnaker (1975) reported young Colorado squawfish in water 60 to 90 cm deep which was quite slow.

A strong concensus toward characterizing preferences of young cyprinids and catostomids as slow, shallow water was evident. Therefore, a highly-restricted depth and velocity curve set (referred to as the V_1 D_1 guild) was assumed.

Salmonid species known to inhabit the headwater reaches of the studied area were rainbow trout (_Salmo gairdneri_), brown trout (_Salmo trutta_) and mountain whitefish (_Prosopium williamsoni_). Preferences of rainbow trout "fry" were available primarily from unpublished file data (Oregon State Game Commission 1969; Hanson 1977). Similar data for brown trout and mountain whitefish (Cochnauer 1977; Gosse, Wydoski and Helm 1977) indicated that "fry" of all three species preferred velocities between 0 and 45 cm/sec (cms) and depths no greater than 60 cm. Bovee (1978) presented univariate curves for larvae of these species which showed preference for moderately slow, rather shallow water. The V_2 D_2 guild combination was assumed to be applicable to salmonid larvae and to early cyprinid or catostomid juveniles.

The V_3 D_3 and V_2 D_4 guild combinations demonstrated preferences of adult fish for moderate riverine conditions. The V_3 D_3 guild curve was considered appropriate for adult salmonids, especially those adapted to conditions in small, relatively-swift streams. This guild curve was similar to many of the salmonid curves presented by Bovee (1978).

The V_2 D_4 guild curve represented preferences of species favoring slow, moderately-deep water, such as Colorado squawfish or razorback sucker adults. Vanicek and Kramer (1969) found adult squawfish in "pools, eddies and runs" but not in shallow, swift water. Hagen and Banks (1963) captured adult squawfish in "all types of water." Sigler and Miller (1964) found squawfish in water "with strong current...3 to 4 feet deep." Smith (1959) found many squawfish in a pool at depths of at least 4.5 m. Carlson, Prewitt, Wick, Snyder, Ames and Fronk (1979) described conditions at capture locations of several squawfish; velocities ranged from 0 to 1 mps and depths from .15 m to 3 m.

Sealing, Kidd, Burdick, Sutton, McMaster and Jophet (1975) reported capture of several humpback chubs from the Black Rocks reach of the Colorado River. This reach was at least 21 m deep in the main channel; velocities during the high flow regime exceeded 3.4 mps but were less than 0.1 mps during the low flow regime. Adult humpback chubs appeared to be far more numerous in or quite near extremely deep areas and the

V_3 D_5 guild combination was assigned to fish with the apparent preferences of the humpback chub.

It is important to restate that the simulated preferences were not necessarily those of any particular fish species. The purpose of the technique was to allow use of several data sources to develop guild curve sets which demonstrated the total range of preferences likely to be found among riverine fish species. Development of preference curves for the native fish species of the Upper Colorado River Basin is not an objective of this paper.

The Exponential Polynomial Function.

To develop the preference functions it was necessary to construct probability density functions which had certain attributes. First, the integral of the function over the range of the variable(s) was to equal one. Second, the value for any solution of the function was not to be less than 0. And,third, when dealing jointly with two or more variables, it was desirable to calculate a term or coefficient which expressed the interactions (correlations) between pairs of the variables.

The traditional polynomial frequency distribution $f(x) = a_0 + a_1x + a_2 x^2 \ldots\ldots a_n s^4$, $a < x < b$ (where a and b were finite limits on x) did not easily meet the above requirements for several reasons. First, transformation of the function to yield an integral equal to one resulted in a more complex function; second, f(x) might assume values less than 0; and third, it was difficult to calculate a term or coefficient which expressed correlations between variable pairs.

In dealing with normal frequency distributions, the familiar normal curve function was appropriate:

$$f(x) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{1}{2}\left(\frac{\bar{x}-\mu}{\sigma}\right)^2}$$

where:

μ = the sample mean,

$\bar{x}$ = the population mean, and

σ = the sample variance.

This model satisfied all three desired attributes but was not flexible; the original data distribution must have been approximately normal and unimodal.

This model was a member of the "exponential family"; because the functional portion was an exponent, f(x) could not assume values less than zero. Also, the term

$$\frac{1}{\sqrt{2\pi\sigma}}$$

served as a normalization factor which brought the integral of f(x) equal to one in a simple way.

Combining desirable attributes of the above model with the flexibility to express non-normal and multimodal distributions was the exponential polynomial of the form:

$$f(x) = \frac{1}{N} e^{\{-(a_1 + a_2x^2 + \ldots a_nx^n)\}}$$

where:

N = the normalization factor which ensured $\int f(x)dx=1$

When dealing with more than one variable, the exponential polynomial allowed inclusion of as many terms as could be conveniently calculated and provided the multivariate capabilities desired in this study. Each variable could be expressed to a power or powers necessary to allow proper data fit in the case of non-normal or multimodal distributions.

The simplest expression of the bivariate case in which the variables were normally distributed and independent (uncorrelated) could be expressed:

$$f(x,y) = \frac{1}{N} e^{\{-(a_1x + a_2y + a_3x^2 + a_4y^2)\}}$$

where:

a_1, a_2, a_3, a_4 were polynomial coefficients.

Given data collected such that, for each observation of an undisturbed organism, the value of both (or more) variables was known, a similar function which expressed the correlation between the pairs of variables could be developed:

$$f(x,y) = \frac{1}{N} e^{\{-(a_1x + a_2y + a_3x^2 + a_4y^2 + a_5xy)\}}$$

where:

a_5 = the cross-product coefficient which expressed correlations between variable pairs.

Matz (1978) stated that the fourth-order exponential polynomial could be used to fit environmental variables with bell-shaped, decaying, increasing or multimodal distributions. Burnham, Anderson and Laake (1982), Voos (1981), Jensen (1979) and Crain (1976) described environmental applications of such a model.

Exponential Polynomial Curve Fitting.

After the univariate depth and velocity curves were hand-drawn, their digitized coordinates were input to a computer program (CRVDAT) which, by randomization and rejection process, constructed a hypothetical "sample" which duplicated the essential shape of the original curve and provided data somewhat of the form encountered in actual field situations where depth and velocity were measured at the location of observed fish.

The depth and velocity samples were used as input to a computer program (XPOLY, Voos 1981) which calculated exponential polynomial coefficients using the maximum likelihood technique (Matz 1978). The actual least squares calculation process was described in Marquart (1963). Coefficients for each variable distribution were calculated independently, resulting in two functions of the form:

$$f(v) = \frac{1}{N} e^{\{-(a_1 v + a_2 v^2)\}} \text{ for velocity, and}$$

$$f(d) = \frac{1}{N} e^{\{-(a_3 d + a_4 d^2)\}} \text{ for depth,}$$

where:

a_1 and a_2 = velocity coefficients,
a_3 and a_4 = depth coefficients,
v = velocity,
d = depth, and
N = normalization factor.

Initial bivariate exponential polynomial equations for the five selected guild preferences were developed by simply combining the univariate equations to produce:

$$f(v,d) = \frac{1}{N} e^{\{-(a_1 v + a_3 d + a_2 v^2 + a_4 d^2)\}}$$

assuming no interaction between the variables.

Development of Depth-Velocity Correlations for Guild Preference Expressions.

To display a range of possible depth-velocity interactions, it was necessary to modify the coefficients of the exponential polynomials which fit the original curves. The initial coefficients were parameterized about the mean (μ) and standard deviation (σ) of the univariate curves by the following process:

Recall the initial bivariate function

$$f(x,y) = \frac{1}{N} e^{\{-(a_1x + a_2y + a_3x^2 + a_4y^2 + a_5xy)\}}$$

where:

x = velocity,

y = depth,

a_1 through a_4 = polynomial coefficients,

a_5 = the cross-product coefficient (initially zero), and

N = the normalization factor, ensuring

$$\int\int f(x,y)dxy = 1$$

If the correlation coefficient (ρ_p) was equal to zero, μ and σ for the two parameters could be found using the following equations:

$$a_3 = \frac{1}{2\sigma x^2}, \quad \mu x = -a_1\sigma x^2;$$

$$a_4 = \frac{1}{2\sigma y^2}, \quad y = -a_2\sigma y^2;$$

$$a_1 = \frac{-\mu x}{\sigma x^2}, \quad \sigma x = \frac{1}{\sqrt{2a_3}};$$

$$a_2 = \frac{-\mu y}{\sigma x^2}, \quad \sigma y = \frac{1}{\sqrt{2a_4}}$$

These relationships were derived from the parameterized bivariate normal distribution (Morrison 1967; Cooly and Lohnes 1971).

Next, the values μ_x, σ_x, μ_y and σ_y were input to the following equations with values of ρ_p ranging from 0 to 0.8 to obtain coefficients which described bivariate curves whose means and standard deviations did not change regardless of the assigned value of ρ_p and the resultant cross-product coefficient.

These equations were:

$$a_1 = -\mu x \sigma y^2 + \rho \mu_y \sigma_x \sigma_y,$$

$$a_2 = -\mu_y \sigma_x^2 + \rho \mu x \sigma_x \sigma_y,$$

$$a_3 = \frac{1}{2(1-\rho^2)} \sigma x^2,$$

$$a_4 = \frac{1}{2(1-\rho^2)} \sigma y^2, \text{ and}$$

$$a_5 = \frac{-\rho}{(1-\rho^2)} \sigma x \sigma y.$$

The numerous calculations were performed with a programmable hand calculator but could be done more conveniently with a FORTRAN IV computer program.

Function Coefficient Evaluation.

The calculated function coefficients were checked for accuracy by comparing marginal and density distribution plots. Marginal plots represented the univariate distributions of the individual variables (d, v) and were useful in confirming that the function-fitting process accurately retained the ranges and optima of the hand-drawn curves. Density plots represented the bivariate distributions with preference implied by density on the Z axis. These plots were useful in demonstrating the effect of increased ρ_p values in the final guild preference functions.

Experimental Design and Display of Results.

Initially, a WUA array of the following form was produced for each guild preference at each physical habitat sampling site:

	$\rho_p = 0$	$\rho_p = .2$	$\rho_p = .4$	$\rho_p = .6$	$\rho_p = .8$
Q_1	$WUA_{1},\ _{0}$				
Q_2	$WUA_{2},\ _{0}$				
Q_3					
Q_4					
Q_5				$WUA_{5},\ _{.6}$	$WUA_{5},\ _{.8}$
Q_6	$WUA_{6},\ _{0}$			$WUA_{6},\ _{.6}$	$WUA_{6},\ _{.8}$
	$\bar{X}\ WUA,\ _{0}$	$\bar{X}\ WUA,\ _{.2}$	$\bar{X}\ WUA,\ _{.4}$	$\bar{X}\ WUA,\ _{.6}$	$\bar{X}\ WUA,\ _{.8}$

where:

$\rho_p = 0 \ldots .8$ = preference function with correlation coefficient = 0... .8,

$Q_1 \ldots Q_6$ = discharge levels selected to cover the expected range of flows,

$WUA_{1 \ldots 6},\ 0 \ldots (.8)$ = WUA calculated using preference function with $\rho p = 0 \ldots (.8)$.

$\bar{X}$ WUA,$_{0\ldots\ .8}$ = mean WUA for all flows at a given level of ρ_p.

Because WUA values at the various sites differed significantly in absolute value, they were expressed as percentages of the WUA at $\rho_p = 0$.

The mean WUA percentages for $Q_1 \ldots Q_n$ for each level were calculated. This mean value was then expressed as a deviation from 100 percent value which was defined by WUA at $\rho_p = 0$. The deviation values (denoted by δ) were used in hypothesis testing. Robson and Regier (1964) had suggested various confidence levels (.10, .20 and .50) for use in screening, management and population research applications of Petersen population estimations. While WUA results expressed as δ values were not population estimates, they were usability estimates of a given habitat, and therefore possible surrogates of population. Also, PHABSIM is normally used in a screening or management mode, and the 20 percent confidence level suggested by the authors for management purposes did not conflict with estimates made by PHABSIM users of its general reliability level. Therefore, the value of δ was to be less than 20 if the effects of changes in ρ_p were to be considered insignificant. No standard was placed upon cv values, except that lower values were considered better.

RESULTS

Physical Habitat Measurement.

The six physical habitat measurement sites displayed a very broad range of conditions. The smallest site, in terms of volume and dimensions was the Red River (Table 1). Maximum depth and velocity were moderate, but their distribution was quite complex. Coefficient of variation values (cv) for the two variables were comparatively high (>0.6). This site displayed a highly complex channel structure limited in depth and velocity and was described as "small-complex".

Similar in size, but not in structure, was the Elk River reach. Mean depths and velocities were not extreme (depths were actually less than those at the Red River), but distribution of the variables was quite normal and predictable. As expected, depth and velocity cv values were quite low (<0.4) at the three measured discharges (Table 1). This was a limited, simple habitat and was described as "small-simple".

The Yampa Maybell reach was much larger than either the Red or Elk River reaches but resembled the Elk River reach in its simple channel characteristics. Both variables were quite normally distributed with the highest frequency

Table 1. Hydraulic and dimensional characteristics at the six physical habitat measurement sites (ρ_h = d-v correlation coefficient, cms=m^3/sec.)

Station	Discharge (cms)	Velocity (cv)	Depth (cv)	Velocity mean (mps)	Depth mean (m)	Depth maximum (m)	Width (m)	ρ_h
Elk (small-simple)	1.70	.32	.44	.208	.204	.805	32.61	.042
	5.66	.28	.3	.518	.430	1.079	36.88	.269
	14.16	.36	.33	.628	.518	1.201	39.32	.603
Yampa-Maybell (medium-simple)	4.53	.27	.25	.271	.247	.183	46.64	.288
	25.49	.25	.33	.625	.521	.908	66.45	.698
	113.28	.23	.36	1.207	.905	1.487	73.46	.637
Moab (large-simple)	113.28	.38	.39	.591	1.48	3.00	89.61	.47
	198.24	.36	.32	.899	2.53	4.39	94.18	.61
	424.8	.27	.26	1.305	3.52	5.43	96.92	.72
Red (small-complex)	1.13	.62	.65	.50	.40	1.17	10.2	.58
	2.27	.60	.60	.57	.45	1.23	10.8	.57
	3.40	.63	.55	.65	.49	1.29	11.1	.47
Yampa-Lily (medium-complex)	4.53	.52	.57	.167	1.338	4.289	43.89	.18
	22.66	.29	.72	.387	1.716	4.697	55.74	.13
	113.28	.53	.80	.832	1.737	5.803	75.89	.47
Black Rocks (large-complex)	101.95	.84	.83	.405	3.188	14.26	73.76	.48
	118.94	.64	.81	.381	3.25	14.36	74.67	.42
	212.40	.72	.75	1.88	3.57	14.87	78.94	.58

of depths in the less-than-1 m range. Again, cv values for depth and velocity were quite low (<0.3) (Table 1). Maximum velocities were high, probably because of the low roughness of the channel. This was a moderately-sized simple habitat with uniform normal distribution of depth and velocity.

The Yampa Lily Park reach, while the same size as that at Maybell, was much more complex. Depth and velocity distributions were broad and in some cases multimodal, with good representations in both the deep and shallow portions. Maximum depths and velocities were quite high, and cv values of both variables greater (>0.5) than at the Maybell station. This reach was called "medium-complex".

The Colorado River reach at Moab had a very simple channel despite its large size. The depth distribution was skewed toward greater depths because of the deeply incised characteristics of the reach. Very little shallow water was encountered. Similarly, velocities, while moderate to high in most portions of the reach, were quite uniform. Velocity and depth cv values were quite low (<0.4) at all flows (Table 1). This reach was described as "large-simple".

The Black Rocks reach of the Colorado River, while approximately the same size as the Moab reach, was the most diverse of the entire study. Extremely complex channel characteristics and a vast range of depths were exhibited while velocity cv values were nearly twice those at Moab (Table 1). This was a "large-complex" habitat.

Calculated ρ_h values varied with discharge more than did cv values (Table 1). At high and medium flows, however, ρ_h for simple channels was usually greater than 0.6 and less than 0.6 in complex channels.

Exponential Polynomial Curve-Fitting.

Marginal plots of the V_1 and V_2 functions showed very good fit to the original hand-drawn curves. The V_1 function produced a curve slightly different from the original, especially in the maximum-preference region, but differences were considered insignificant (Figure 6). The V_2 function provided a near-perfect data fit (Figure 7).

The V_3 function produced a curve of quite different shape than the hand-drawn curve, but the range and region of optimum preference were retained (Figure 8). The much narrower curve peak resulted from use of second order polynomial coefficients. Third- or fourth-order coefficients might have allowed much closer curve fit but would have required very complex mathematics during the parameterization process.

Plots of the depth functions showed the same narrowing in the region of optimum preference (Figures 9-13), again because of the restriction to second-order coefficients. The D_5 curve (Figure 13) retained much of the shape of the original curve. The ranges and optima of the hand-drawn curves were retained.

The initial curve fitting process was considered successful because it was possible to construct simple functions

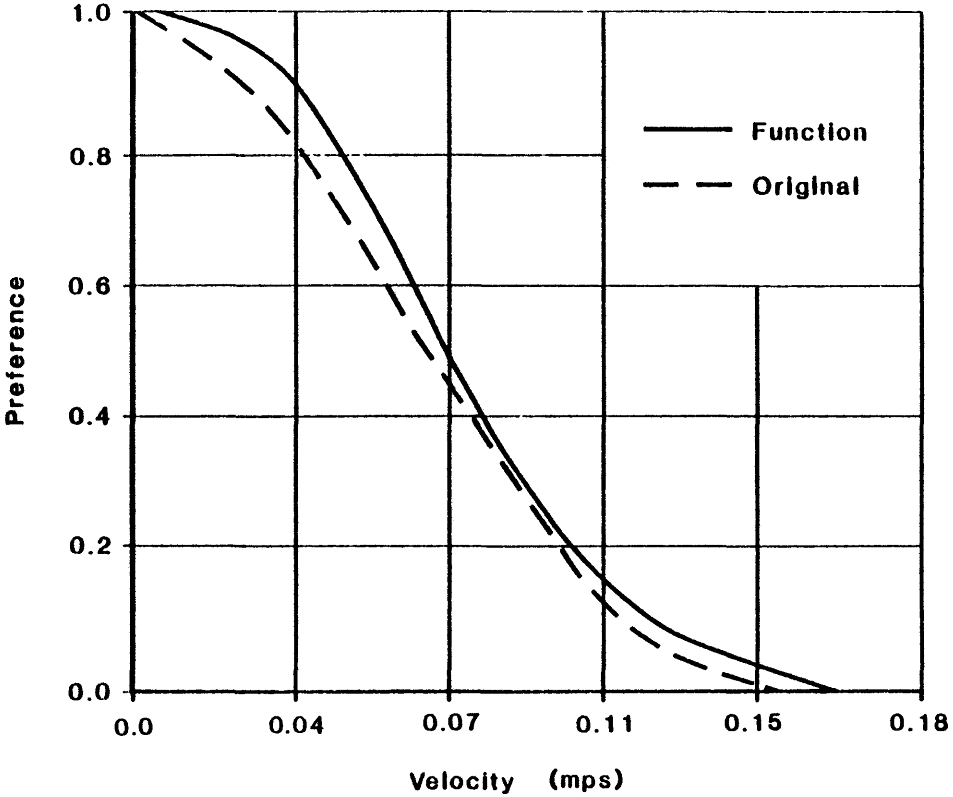


Figure 6. Marginal distribution plot of V_1 preference function with original V_1 curve for comparison.

$$f(V_1) = \frac{1}{.2614} e^{\{-(2.1v + 20.3v^2)\}}.$$

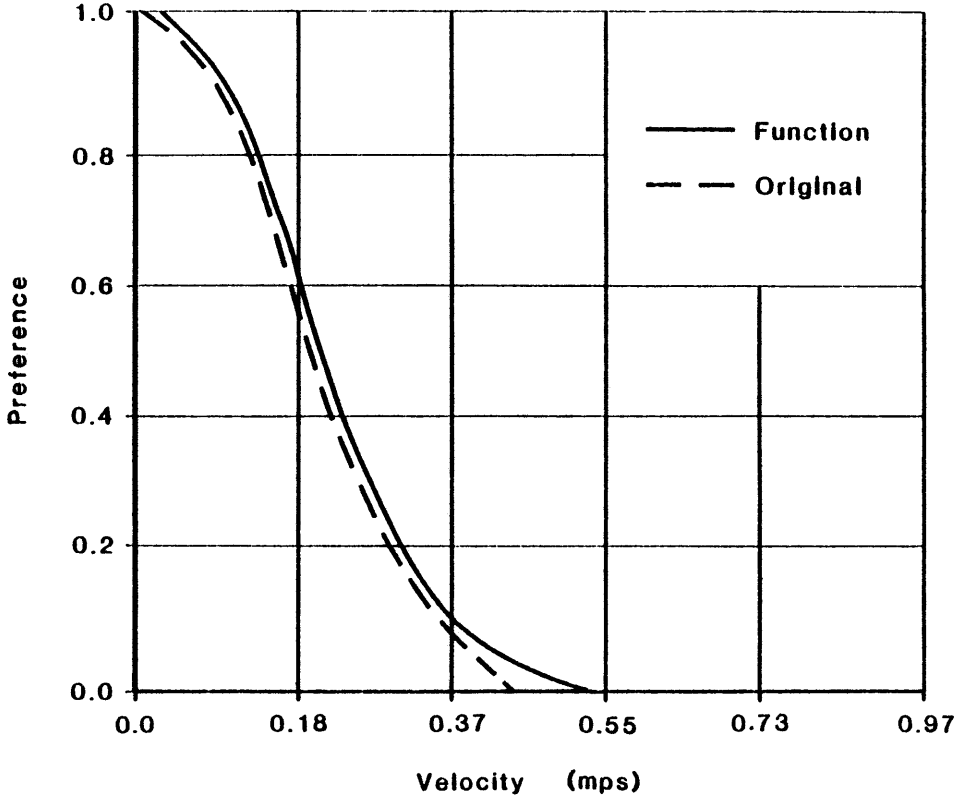


Figure 7. Marginal distribution plot of V_2 preference function with original V_2 curve for comparison.

$$f(V_2) = \frac{1}{.7155} e^{\{-(-.376v + 2.08v^2)\}}.$$

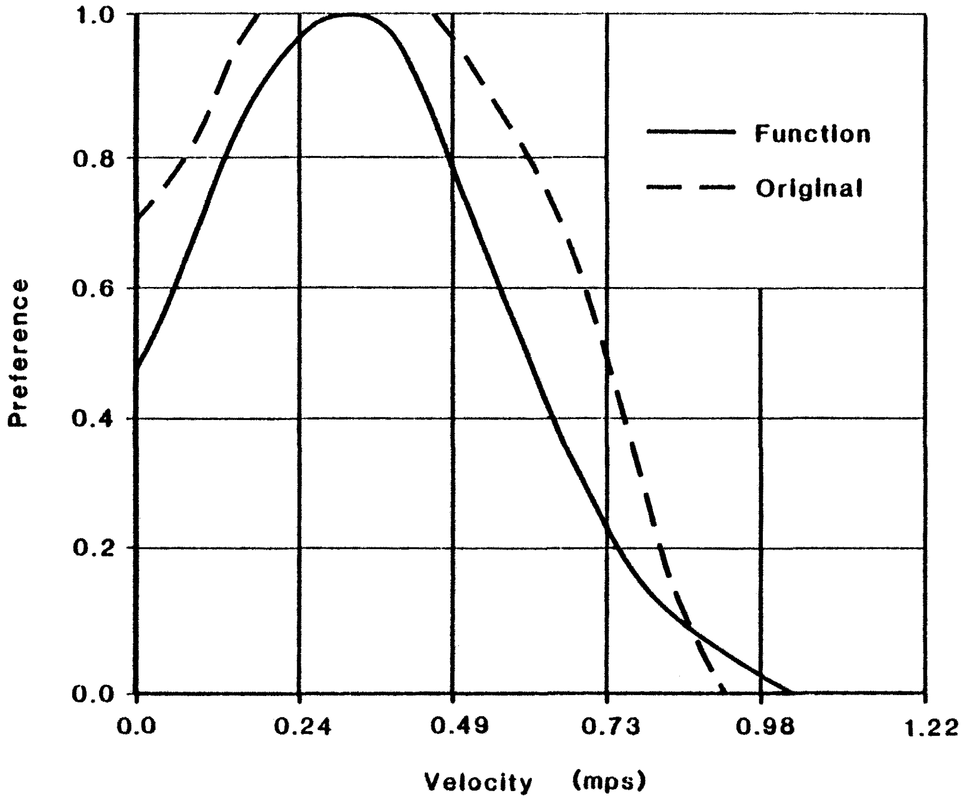


Figure 8. Marginal distribution plot of V_3 preference function with original V_3 curve for comparison.

$$f(V_3) = \frac{1}{3.977} e^{\{-(-1.61v + .804v^2)\}}.$$

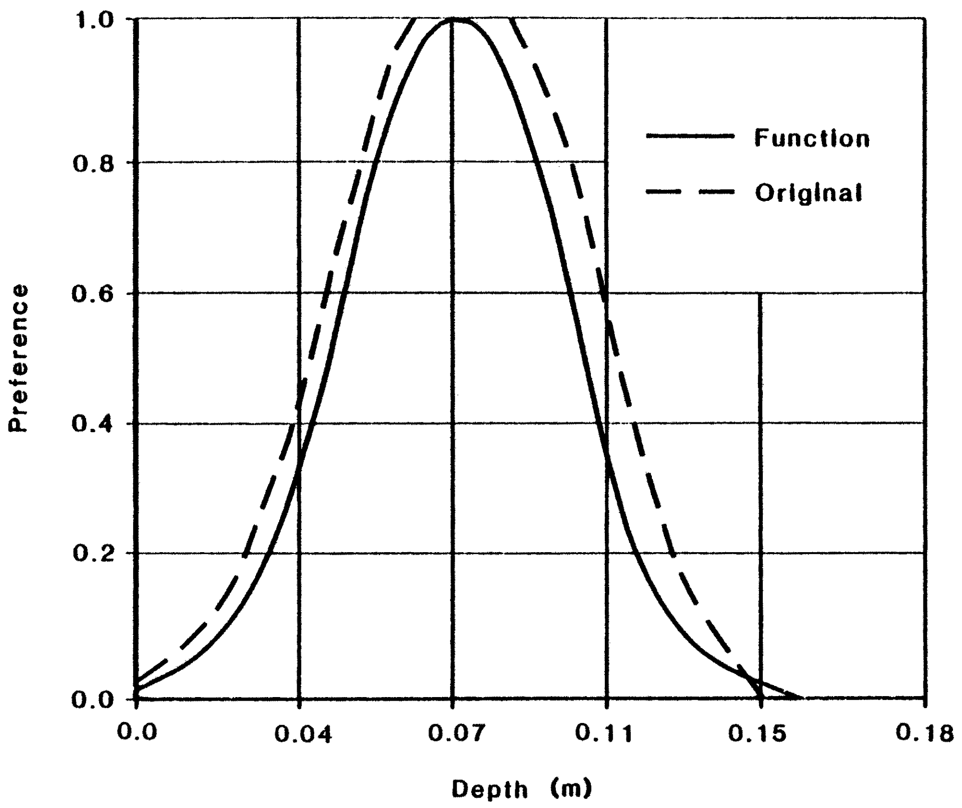


Figure 9. Marginal Distribution plot of D_1 preference function with original D_1 curve for comparison.

$$f(D_1) = \frac{1}{31.94} e^{\{-(-40.6d + 83.0d^2)\}}.$$

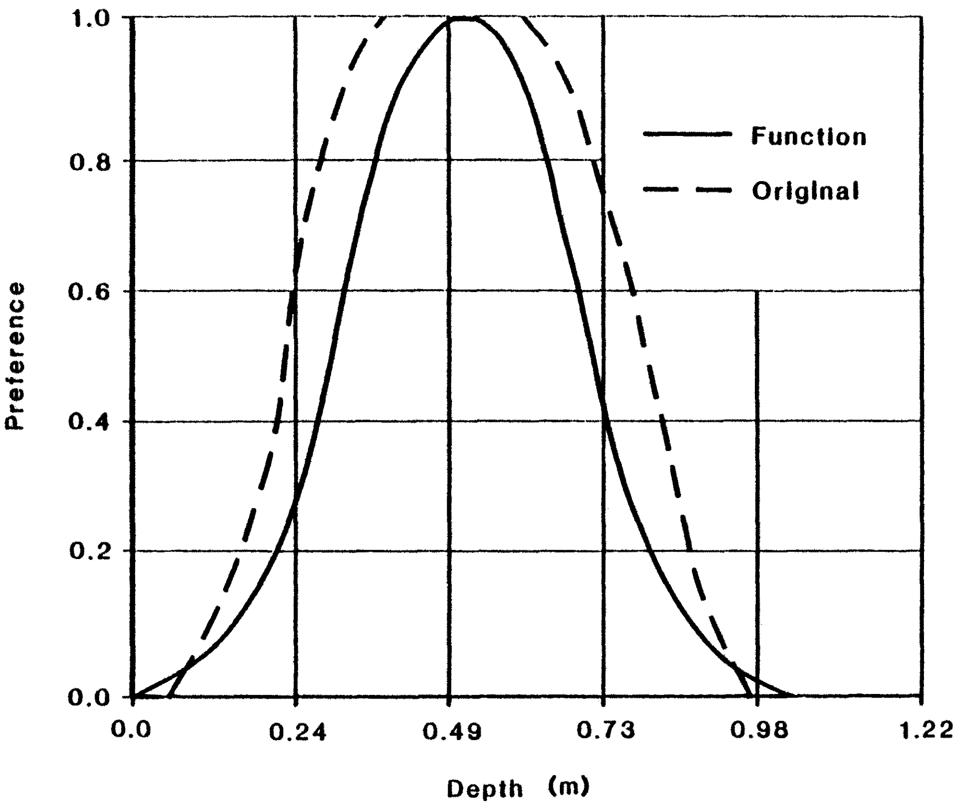


Figure 10. Marginal distribution plot of D_2 preference function with original D_2 curve for comparison.

$$f(D_2) = \frac{1}{76.62} e^{\{-(-5.15d + 1.65d^2)\}}.$$

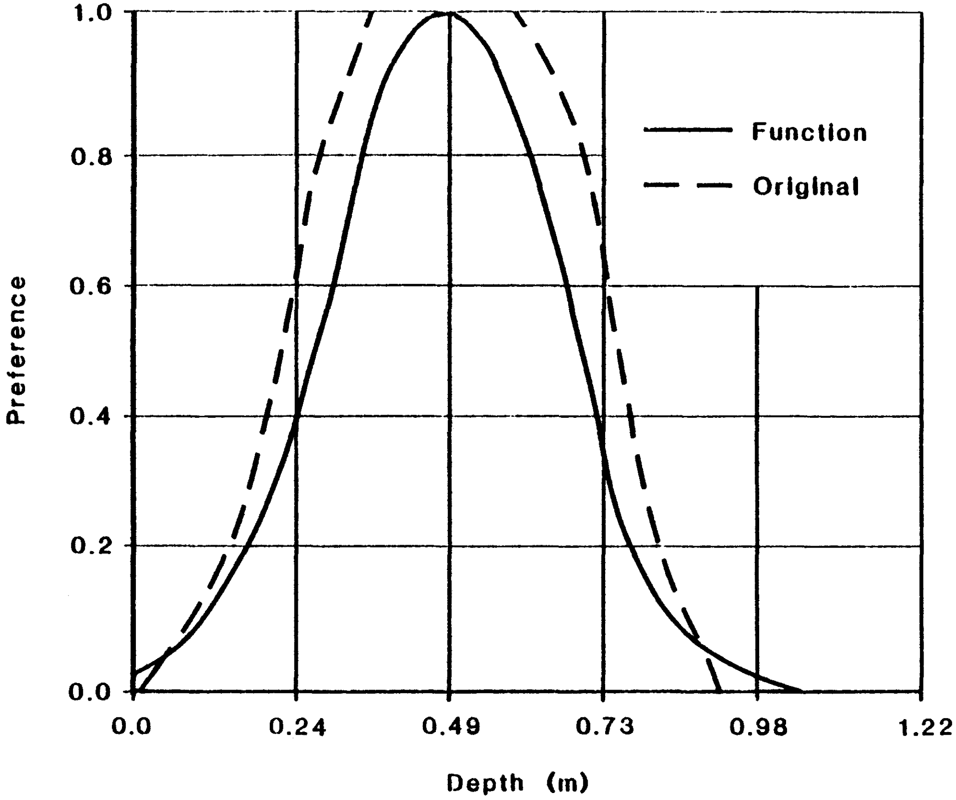


Figure 11. Marginal distribution plot of D_3 preference function with original D_3 curve for comparison.

$$f(D_3) = \frac{1}{.537E05} e^{\{-(-8.58d = 1.74d^2)\}}.$$

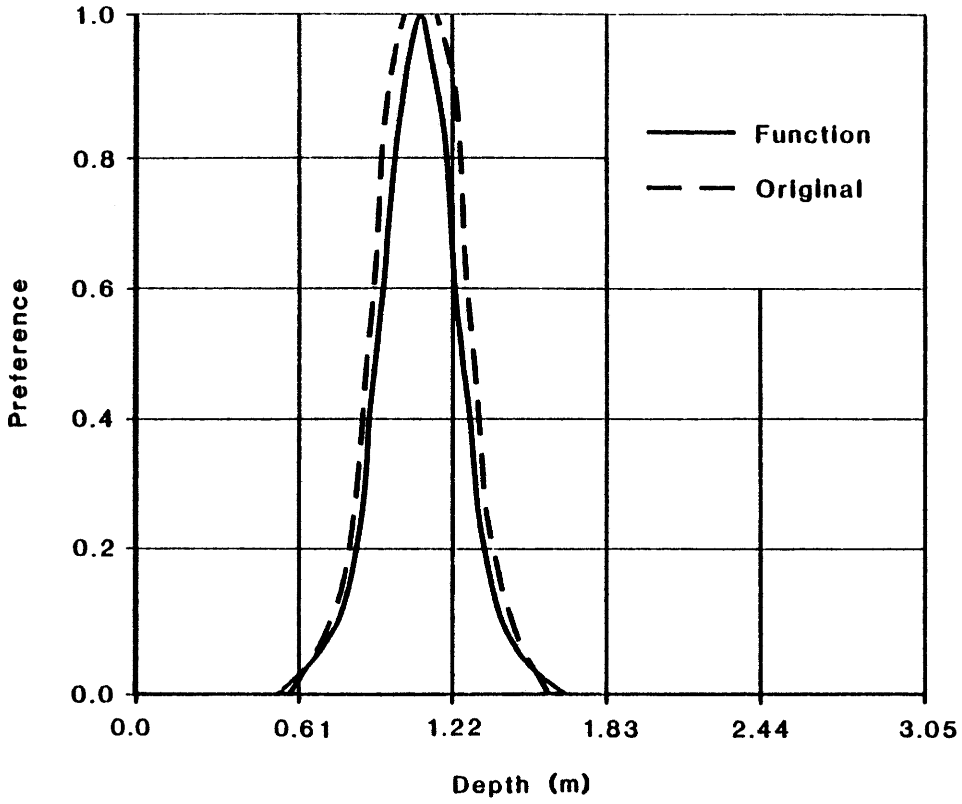


Figure 12. Marginal distribution plot of D_4 preference function with original D_2 curve for comparison.

$$f(D_4) = \frac{1}{.157E12} e^{\{-(-14.3d + 2.01d^2)\}}.$$

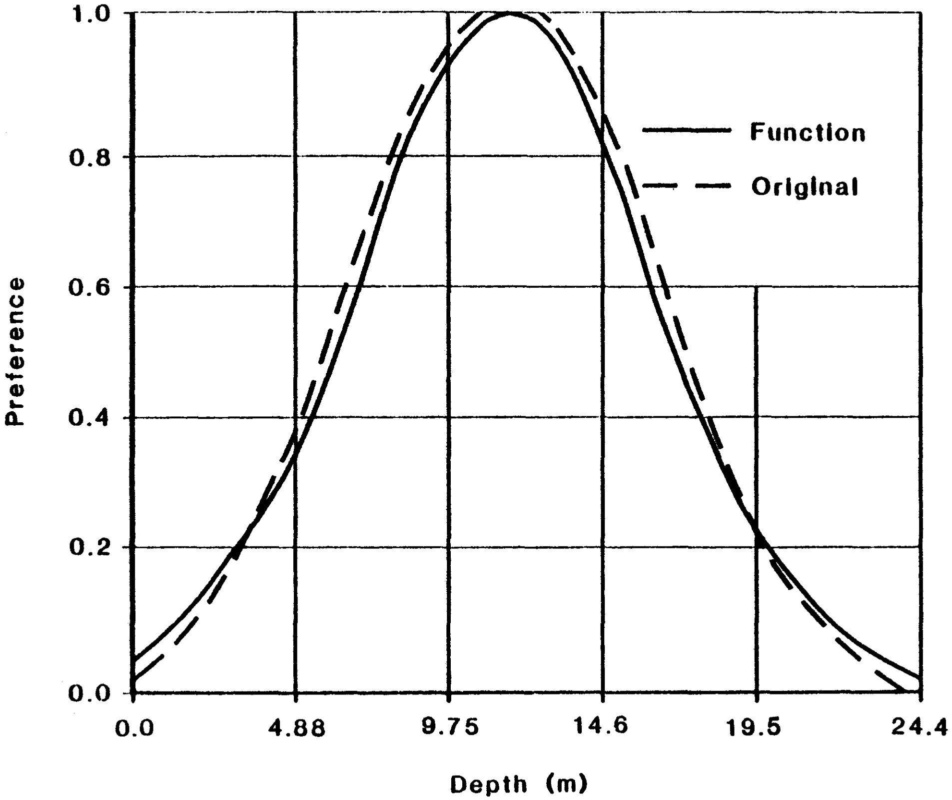


Figure 13. Marginal distribution plot of D_5 preference function with original D_5 curve for comparison.

$$f(D_5) = \frac{1}{798.3} e^{\{-(.162d + .00215d^2)\}}.$$

which essentially retained the characteristics of an extremely broad range of preference curves. Those desiring more precise curve fitting could use the XPOLY program to calculate higher-order coefficients.

Guild Preference Curve Sets with Varying ρ_p Values.

The mathematical transformations described earlier were successful in producing joint preference functions which retained the ranges and optima of the univariate functions while allowing changes in the value of ρ_p. The V_1 D_1 guild density plot duplicated the ranges and optima of the univariate curves (Figure 14). Also, the effects of ρ_p values between 0.2 and 0.8 were clearly demonstrated (Figure 15). Similar density plots were produced for all other guild functions and the same changes in the axes of the plots were noted. Therefore, only the V_1 D_1 plots were presented. Density plots for the remaining guilds showed retention of the individual depth-velocity curve characteristics (Figure 16).

Increasing ρ values changed both the plot axis and the volume under the plot surface (usually known as "response surface") (Mead and Pike 1975). The V_1 D_1 and V_2 D_2 function volumes changed by respective factors of 1.8 and 25 with the greatest change occurring between ρ_p values of 0.4 and 0.9 (Tables 2 and 3). Volumes for the other functions changed by smaller factors, but the changes were always greatest between ρ_p values of 0.4 to 0.9 (Tables 4 and 5).

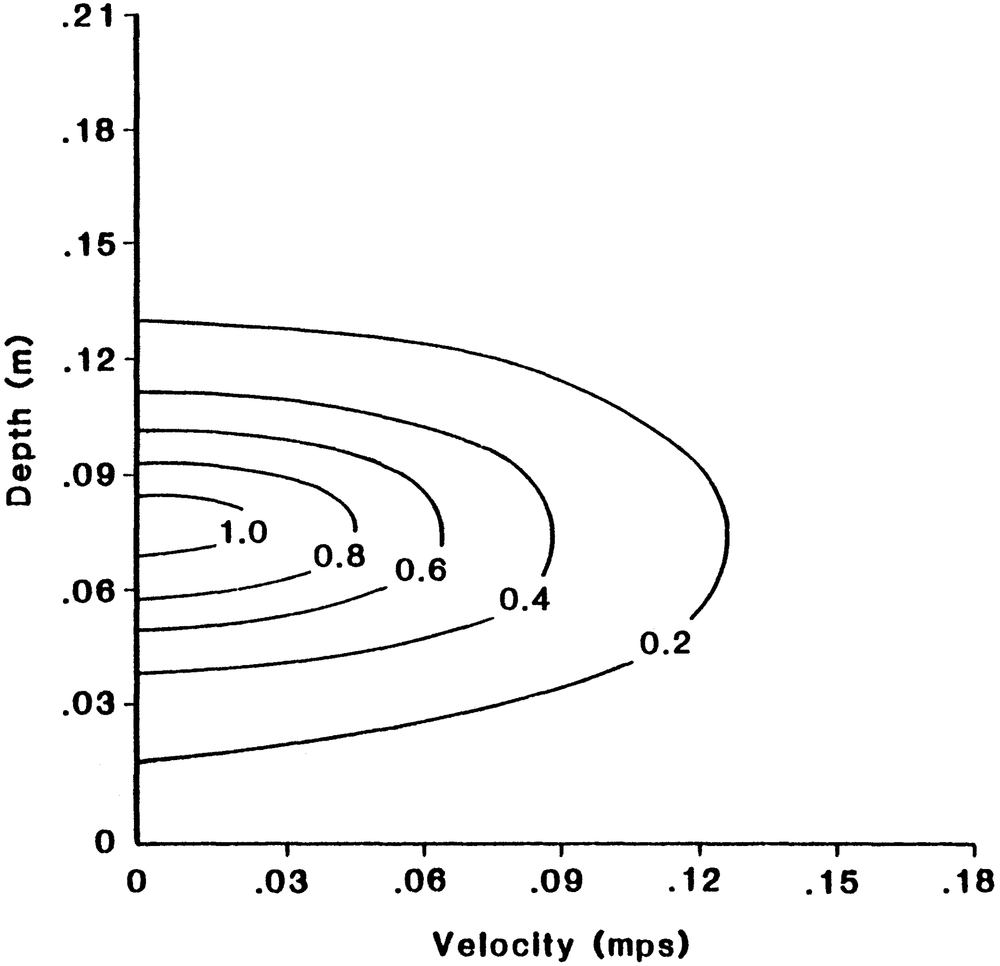
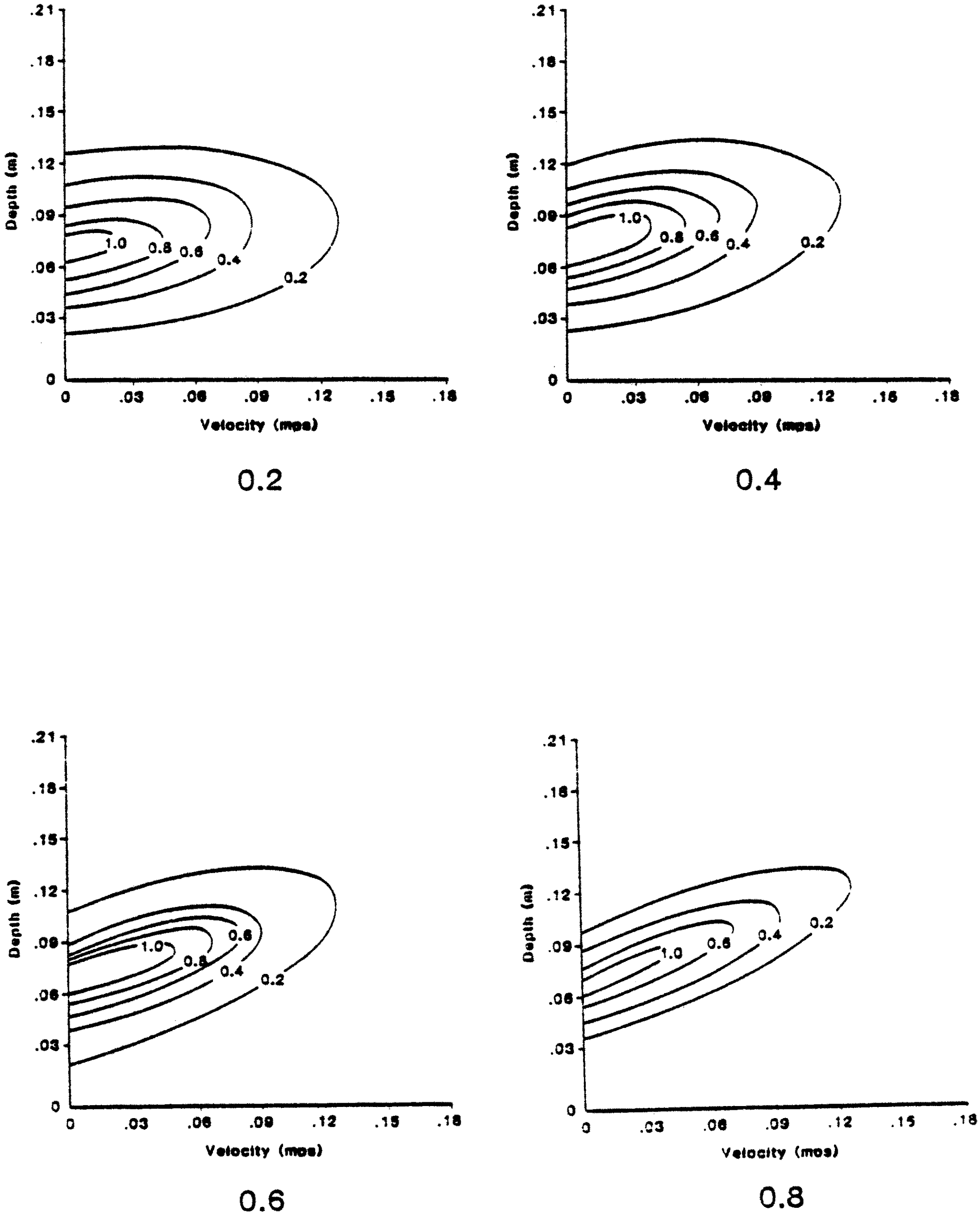


Figure 14. Density plot of V_1 D_1 guild preference function, $\rho_p = 0$.

$$f(V_1D_1,0) = \frac{1}{150} e^{\{-(2.01v + 40.6 + 20.3v^2 + 83.0d^2)\}}$$



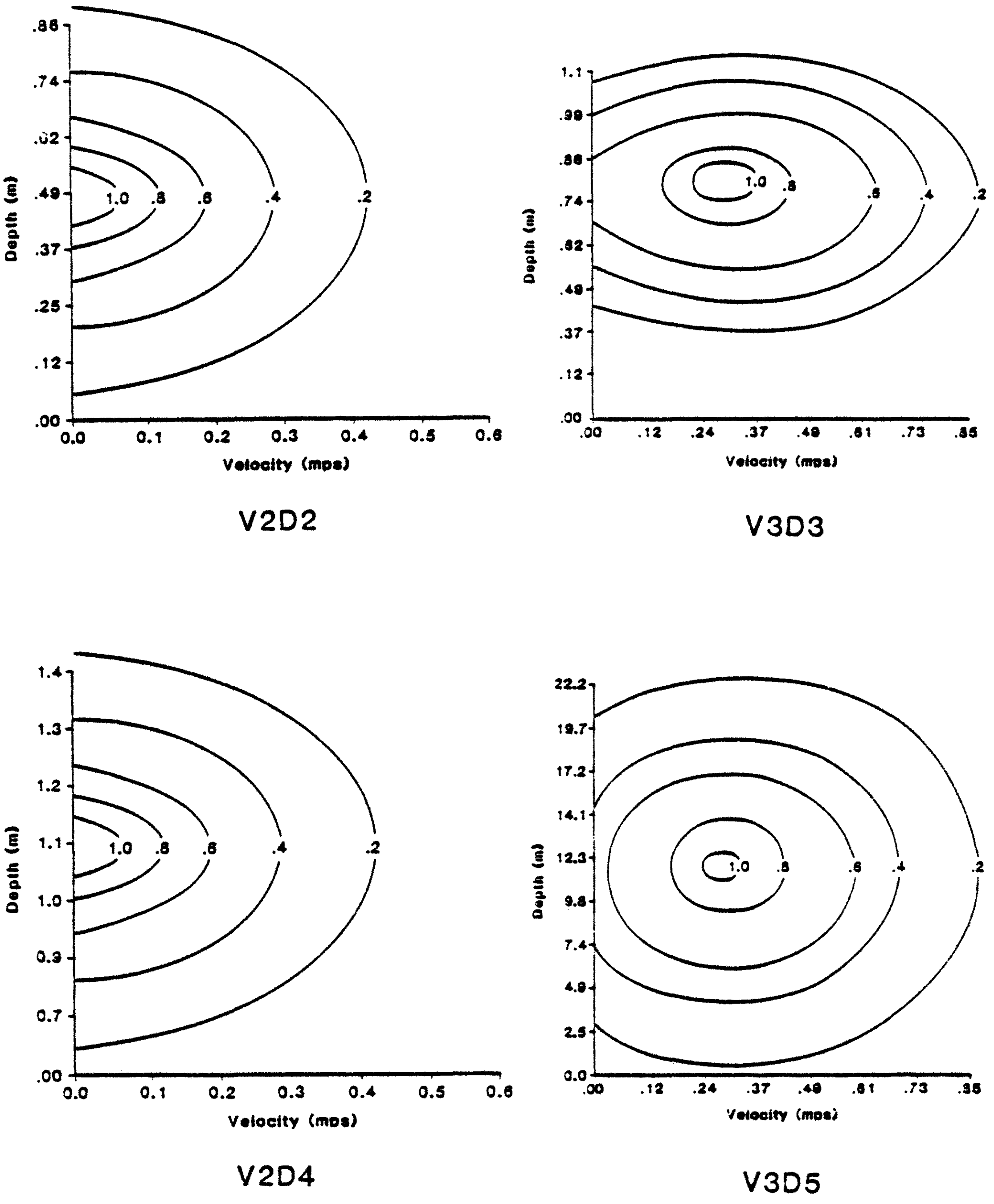
0.2

0.4

0.6

0.8

Figure 15. Density plots of V_1 D_1 guild preference function with ρ_p = .2, .4, .6 and .8.



V2D2

V3D3

V2D4

V3D5

Figure 16. Density plots of V_2 D_2, V_3 D_3, V_2 D_4 and V_3 D_5 guild preference functions.

Table 2. Volumes under response surfaces for $V_1 D_1$ preference function, ρ_p= .9 through -.9.

ρ_p	1/N	Volume	Normalized Volume
.9	2.512E10	.823E08	.0026
.4	.0026	17.4	.0453
.1	.0080	5.91	.0476
-.1	.0059	8.16	.048
-.4	884E-06	50.3	.044
-.9	5.92E15	.308E13	.0018

Table 3. Volumes under response surfaces for V_2 D_2 preference function, $\rho_p = .9$ through $-.9$.

ρ_p	1/N	Volume	Normalized Volume
.9	6.28E-09	.677E08	.0425
.4	.0106	84.6	.9
.1	.0178	54.6	.975
-.1	.0154	70.4	1.083
-.4			
-.9	4.44E-11	.970E11	.0431

Table 4. Volumes under response surfaces for V_3 D_3 preference function, $\rho_p = .9$ through $-.9$.

ρ_p	1/N	Volume	Normalized Volume
.9	2.0E-14	.375E14	.75
.4	1.56E-05	.145E-6	2.269
.1	2.036E-05	.118E06	2.40
-.1	6.33E-06	.379E06	2.399
-.4	1.73E-07	.129E08	2.23
-.9	1.11E-38	.90E38	1.047

Table 5. Volumes under response surface for V_3 D_5 preference function, ρ_p = .9 through -.9.

ρ_p	1/N	Volume	Normalized Volume
.9	4.83E-03	.579E04	27.97
.4	.0045	1290	58.63
.1	.027	2460	66.48
-.1	.0175	3780	66.32
-.4	2.68E-03	23000	61.66
-.9	4.05E-16	.712E17	28.82

Effects of Increasing ρ_p Value upon δ and cv.

Calculated δ values ranged from less than 1 to greater than 99 (Appendix I), indicating that variable correlation had a clear effect upon WUA when the entire data set was considered. At the .2 correlation level, however, most of the results met the deviation standard (Figure 17). Results at the .4 level were less acceptable, while at the .6 level, slightly more than one-fourth of the results met the hypothesis standard. At the .8 level, only 3 percent of the δ values were acceptable. Without considering further stratifications, ρ_p levels could probably not exceed 0.2 without severly reducing the reliability of the results.

Results differed significantly among various stream sizes. In small streams (Figure 17), correlations greater than .2 resulted in uniformly high δ values. Results in medium and large streams were much better (Figure 17), and correlations as high as 0.6 resulted in acceptable outcome in more than half the trials.

Consideration of channel complexity allowed for elimination of even more variability in δ (Figure 18). Clearly, complex channel results were consistently better than those in simple channels.

In medium or large streams with complex channels, very high percentages of the trials were acceptable, even at a level of 0.6 (Figure 19). The small stream simple channel results are shown because they represented one of few cases in which simple channel results were superior.

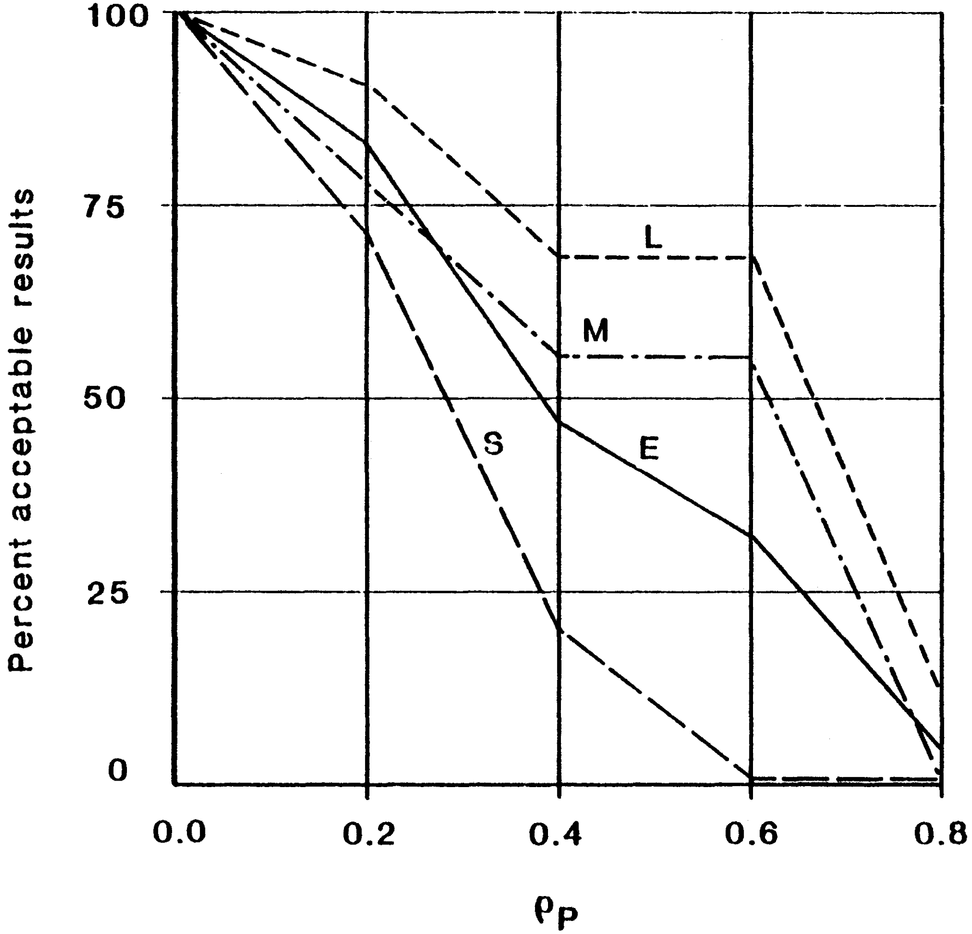


Figure 17. Percent acceptable results ($\delta<20$) in the entire (E) data set ($n=120$), large streams ($n=40$), medium streams ($n=40$), and small streams ($n=60$).

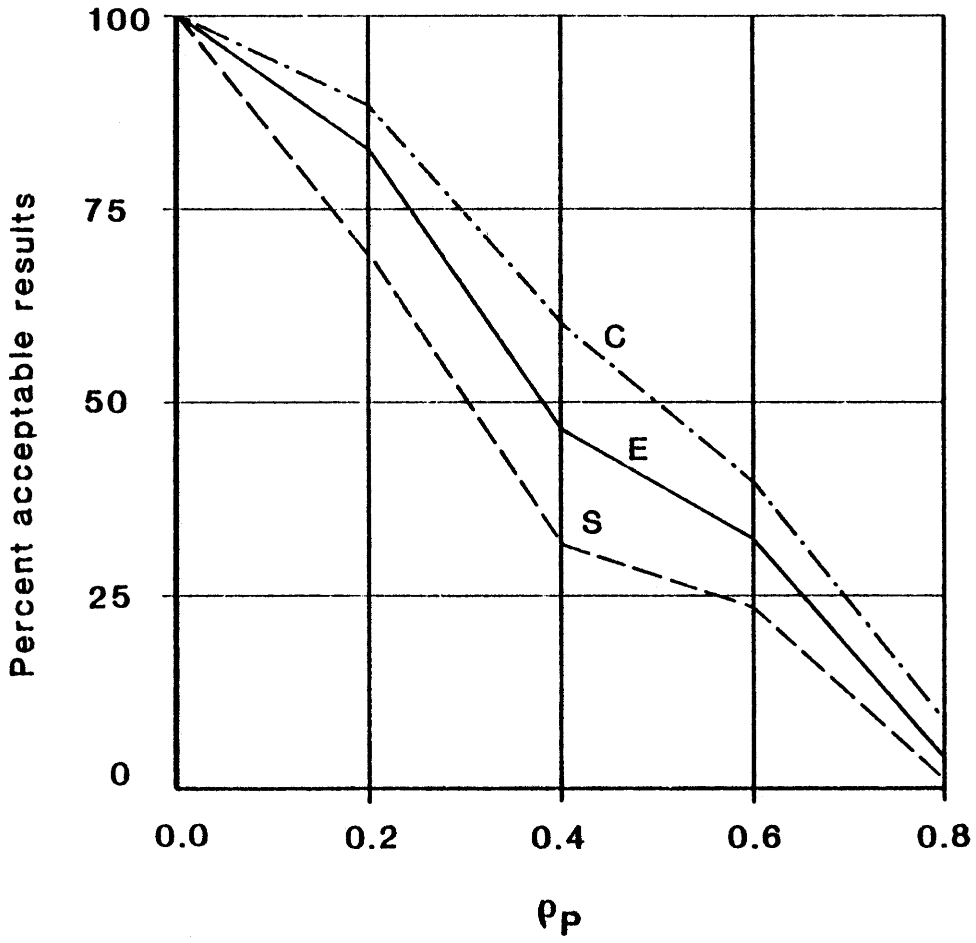


Figure 18. Percent acceptable results (δ<20) in the entire data set (n=120), simple streams (n=60) and complex streams (n=60).

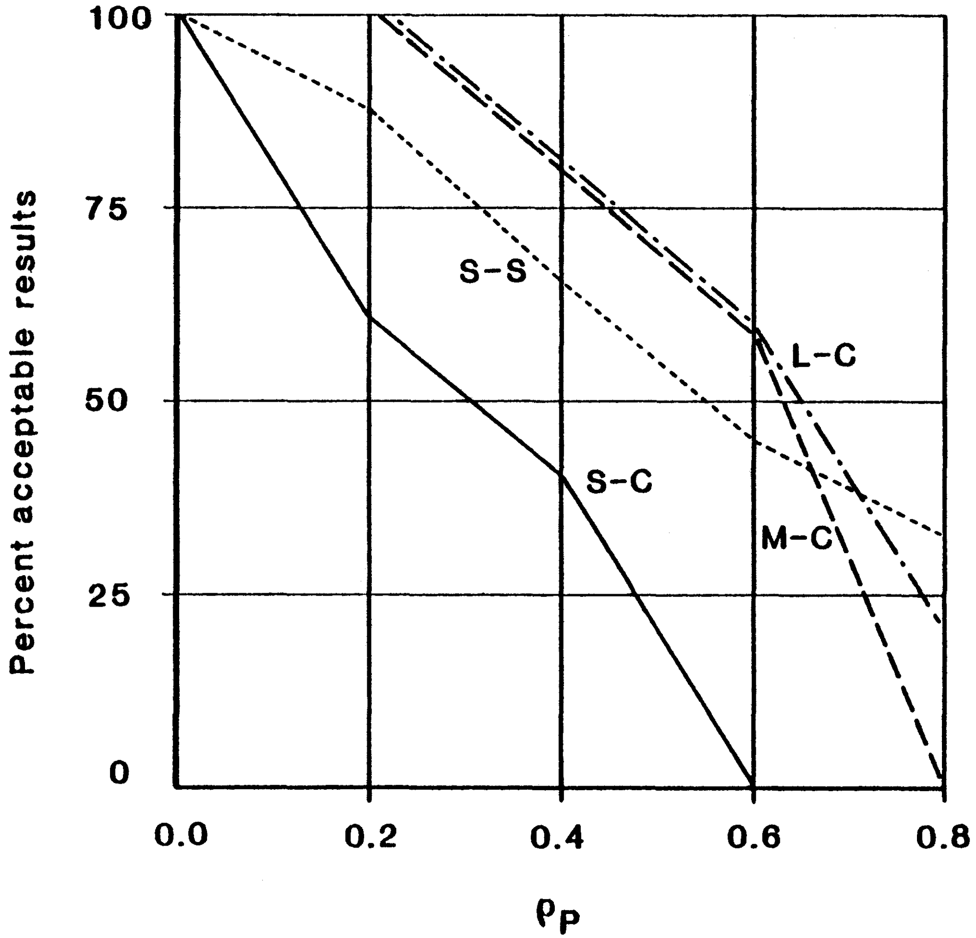


Figure 19. Percent acceptable results (δ<20) in small, medium and large streams with complex channel structures (n=20 in each case, S-S=Small-Simple).

In a 3 x 2 analysis of variance (AOV), the stream sizes and channel complexities had highly significant ($p>.955$) effects upon variation in δ (Table 6). Of the two, channel complexity had a slightly more significant effect.

Among the various preference curves, results for the V_1 D_1 guild were remarkably consistent, especially in the simple channel (Table 7), another situation in which simple channel effects were more favorable than those in the complex channels. The V_2 D_2, V_3 D_3 and V_2 D_4 guild results were quite similar and slightly better in complex channel situations (Table 7). Results for the V_3 D_5 guild curves were considerably poorer, especially in the simple channel situations.

cv Value Comparisons.

Because no arbitrary standard was set for cv results, only comparative evaluation was performed. The mean cv for the data was 26.28 (Table 8), with small and medium size streams showing even more average deviation. The large streams had considerably lower cv values (Table 8).

The simple channel cv values were highest of all data partitions while complex channel cv values were about one-half those in simple channels. Results for all stream sizes in complex channels were dramatically better than those in the data set as a whole. If a maximum cv value of 20 were imposed, it would have been met consistently in the large

Table 6. Two-way analysis of variance of δ values resulting from stream size and channel complexity.

Source	Degrees of Freedom	Sum of Squares	Mean Square
Total	120	228,269.60	
Mean	1	143,104.06	
Total (corrected)	119	85,165.54	
Streams	2	7,720.29	3860.15
Complexity	1	6,434.17	6423.17
Error	116	77,-45.25	667.63

$$F_{size} = \frac{3860.15}{667.63} = 5.78 \ (F,2,116) \quad p>0.95$$

$$F_{complexity} = \frac{6423.17}{667.63} = 9.62 \ (F,1,116) \quad p>0.99$$

Table 7. Mean δ for individual guild preference curves in simple and complex channel structures.

	$\bar{X}$		$\bar{\bar{X}}$
Curve	Simple	Complex	
V_1 D_1	6.86	17.25	12.06
V_2 D_2	40.75	23.00	31.88
V_3 D_3	33.56	27.33	30.45
V_2 D_4	33.25	31.70	32.48
V_3 D_5	68.62	28.24	48.43

Table 8. Comparison of mean cv values from various data partitions.

Data Partition	Mean cv Value
Entire Data Set	26.28
Small Streams	28.17
Medium Streams	28.83
Large Streams	21.85
Simple Channel	40.34
Complex Channel	23.82
Complex Small	10.57
Complex Medium	7.89
Complex Large	5.37

streams or in streams of any size with complex channel structures.

Significance of effects of stream size and channel structure upon variation in cv was tested with a 3 x 2 AOV. Again, results were highly significant with the F statistic indicating that cv values were more influenced by channel complexity than stream size (Table 9).

Table 9. Two-way analysis of variance of cv values resulting from stream size and channel complexity.

Source	Degrees of Freedom	Sum of Squares	Mean Square
Total	120	160,919.11	
Mean	1		
Total (corrected)	119	82,882.00	
Size	2	28,023.00	14,011.00
Complexity	1	56,387.00	56,387.00
Error	116	54,859.00	472.92

$$F_{size} = \frac{14,011}{472.92} = 29.63 \quad p>0.99$$

$$F_{complexity} = \frac{56,387}{472.92} = 119.23 \quad p>0.99$$

DISCUSSION

The primary hypothesis, that ρ_p values greater than 0 did not affect WUA, was not supported. Users of univariate preference curves in a variety of possible settings could not expect reliable results in enough cases to warrant unrestricted use. Answers to the questions posed in the Introduction, however, may be of value in guiding users who either must use univariate curves or decide when conditions warrant the extra expense involved in development of multivariate curves.

1. If variable correlations do affect WUA values, at what levels of correlation are results likely to become unreliable? Considering the range of possible PHABSIM applications, one could expect reliable results only if ρ_p values were 0.2 or less. The majority of multivariate curves presented by Voos (1981), and Hardy (1982) had d-v correlations in the .3 to .6 range. Curves with ρ_p values less than .3 might only result from samples of fish captured or observed in a very broad range of environments or those which lived throughout very complex environments. It is unlikely, then, that users could expect ρ_p to be less than 0.2 in most situations. However, knowledge

of the characteristics of the physical habitat would allow use of univariate curves in certain instances, as described in the following paragraphs.

2. Are there situations in which changes in WUA might be acceptable? Clearly, δ was significantly smaller in medium and large streams and in those with complex channel structures. If actual ρ_p values were to vary between .3 and .6, users applying univariate curves in medium to large streams with complex channels could expect δ and cv to be acceptable in 60 to 80 percent of their applications. Small stream applications were slightly more reliable in the simple channel case but overall results in the two small streams were not acceptable beyond the 0.2 ρ_p level.

Use of a highly-restricted d-v curve set (such as V_1 D_1) appeared to promote reliable results across a very broad range of stream sizes and channel structure combinations. Results for the moderate guild preferences (V_2 D_2, V_3 D_3 and V_2 D_4) were not so consistent and the V_3 D_5 guild curve results were low and rather inconsistent in both simple and complex channels.

3. Are there any indicators by which users of univariate curves might evaluate their results? Data required for the PHABSIM system always include measurement of depth and velocity (and usually substrate as well). Correlation (ρ_h) of the paired d-v measurements are easily

computed. ρ_h values less than .6 were generally calculated at complex reaches, while values greater than .6 were calculated for the simple reaches. ρ_h was not stable over a broad range of discharges, however, and should therefore be used as a structure indicator only at medium to high flows (from 1/2 to bankfull).

The best indicators of habitat complexity were either depth or velocity cv values. Both were extremely stable across a broad range of flows and they separated quite well; simple channel values were always less than 0.5 and complex channel values were always greater than 0.5. Because measurement of numerous velocities at multiple stream transects is costly and time-consuming, and because depth and velocity cv were almost identical, depth measurements alone could be used in an initial estimation of channel complexity.

The stream size categories used in this report should be meaningful in the Rocky Mountain region, but may not be in other regions of the country. The small streams in this study had mean annual discharges of less than 14.15 cms; the medium stream (Yampa River) had mean annual discharge of 42.45 cms. The Colorado River, largest in the region, had a mean annual discharge greater than 198.1 cms. "Medium" could apply to streams with discharges ranging from above 12 to 60 cms. "Large" would be those streams with discharge greater than 60 cms. Channel dimensions, especially width, were not good indicators of stream size, because they may have been established at some time in the past during extreme flood events or before impoundments.

Cause and Effect Relationships - A Proposal.

No clear reasons were available for the improvement of results in medium and large streams. Perhaps larger streams offered a greater degree of complexity or diversity by virtue of size alone than did the more limited environments. Similarly, it was quite difficult to determine why the highly restrictive V_1 D_1 guild curve produced such consistent results. Perhaps it was not the very low depth and velocity preference but simply the highly restrictive range of the preference. It would be valuable to determine whether a very restrictive preference expression in the middle ranges of depths and velocities might produce similarly consistent results.

Some explanation of the effect of habitat complexity is possible, however, and is facilitated by envisioning both the preference and the habitat as response surfaces. The WUA of a study reach at a given flow for a given preference expression is dependent upon the degree of correspondence between the preference response surface and the availability response surface. If the two surfaces coincide completely, the usability (WUA) is equal to the surface area of the reach. For all unions less than complete, the usability is less than the surface area by a factor proportional to the disjunct volume. Theoretically, a particular preference function could be assigned correlation coefficients between 0 and one, and, when placed within a broad and diverse enough depth-velocity environment, provide the same WUA regardless of correlation coefficient.

The opposite situation would occur when an extremely correlated preference function was applied in an extremely correlated (simple or non-diverse) environment. Here minor changes in ρ_p could almost completely eliminate coincidence between the response surfaces and cause major discrepancies between WUA ($\rho_p>0$) and WUA ($\rho_p=0$). Recalling that the volume of the $\rho_p=0$ response surfaces was consistently greater than the volume of all response surfaces with higher correlations, it is possible to envision more stable and predictable usability estimates when applying variable preference functions in highly uncorrelated (complex) environments.

This theory supports the general (but disputed) ecological axiom that environmental diversity implies biological diversity and that diversity implies stability (MacArthur 1955). It was seen that WUA was more predictable within diverse physical habitats than within simple ones. Also, the diverse habitats in all cases offered some usability regardless of the preference curve, ρ_p value or stream discharge level. In two non-diverse habitats, no significant usability was calculated for two suitability curves (Appendix I), suggesting that simplicity promotes an "all or nothing" situation and usability for fewer species.

Physical habitat complexity might also offer opportunity for niche shifts resulting from competition. For example, under competitive stress a species which was originally depth indifferent might shift to a preference for swift water only if it were quite shallow, and slow water only if it were quite deep. The resulting increase in d-v correlation would severely limit the usability of a highly correlated (simple) environment in all cases except that in which the habitat and preference correlations were quite similar. In a complex environment, the shift could probably be made with smaller losses of habitat usability, resulting in suitable conditions for more species or physical habitat guilds.

Niche Theory Inferences.

While this study did not address specific ecological topics, some inferences toward applications of Niche and Guild theories resulted. Hutchinson (1957) proposed a niche definition in which the preferred ranges of important environmental variables received values of one, and all values outside this range received a value of zero. Considered jointly, the numerous important environmental variables and their preferred ranges defined a hyper-volume dimensionally equivalent to the organism's fundamental niche. Hutchinson proposed that, if the important environmental variables were known and measured for numerous observations of the organism, a multivariate model of the niche could be developed.

Hutchinson (1978) proposed that such a model would provide a linear ordering of the environmental variables, but did not offer a mathematical method to demonstrate this. Wangersky (1972) similarly proposed that the hypervolume could be defined by a group of probability density functions, each an estimate of the probability of finding an organism at a given value of the variable in question. Both proposals suggested the advantages of considering several environmental variables jointly, but did not propose specific methods for accomplishing this.

The exponential polynomial model described in this paper and its literature sources provided a sound mathematical approach to modeling a multi-dimensional niche with the variables defined jointly, that is, with interractions explained. To construct a niche model for a given species, a set of potential components would be assumed. Hutchinson (1978) estimated that most species niches could be defined by use of fewer than five variables. Next, numerous measurements or estimates of the variables would be taken at the locations of undisturbed organisms. Then, through a computerized curve-fitting process, exponential polynomial coefficients could be calculated and the resulting model used to determine 1) relative importance of the measured parameters as niche components, 2) degree to which the components interacted, and 3) probable response of the organism to changes in any or all of the niche components. Such a model might serve as a powerful tool in impact analysis or environmental planning.

Guild Theory Inferences.

The process described in this paper might also be valuable in assigning habitat preferences to certain guilds based upon physiological requirements, trophic relationships or perhaps reproductive strategies. For example, the V_1 D_1 curve set (with additional values for substrate) would probably define the physical habitat requirements of a larval cyprinid or catostomid guild. The actual preference function could be derived by analysis of actual observation data, or from literature sources using the mathematical process described in this paper to assign some moderate (but likely) degree of correlation between variable pairs.

Balon (1975) described a reproductive guild (psammophils) which were known to build nests in water less than 40 cm deep with a sand substrate. Based on such information, a guild preference function could be described and derived. Because members of this guild did not spawn over substrates other than sand, a univariate velocity curve similar to V_1 or V_2 might be selected because velocity would necessarily be low in such substrate conditions. Next, a suitable depth curve (perhaps D_3) could be combined with the velocity curve and some likely ρ_p (perhaps .4) could be assigned through the parameterization process. For all situations in which sand was the available substrate, WUA could be calculated using this preference function. In all situations other than those with sand substrate, WUA would be 0.

Guild preferences may in fact be superior to species preferences in many instances. Significant preference distinctions are probably quite broad and only a limited number of depth-velocity-substrate combinations are likely. Use of a few distinctive guild curves precludes problems often encountered in determining the preferences of numerous species because such specific curves often reflect sampling bias, regional anomalies and differences in basic habitat availability. While the guild preference function might differ from functions derived for each guild member separately, it probably more accurately distinguishes the general preferences than would any of the individual curves.

CONCLUSIONS AND RECOMMENDATIONS

This study demonstrated that correlations between variables in a preference expression may have major effects upon WUA values; and other usability estimates derived from calculation of joint preference factors. However, certain conditions were identified which might allow evaluation of results using measurable characteristics of the stream channel and discharge range. Specifically, the following conclusions were drawn.

1. WUA remained within acceptable management limits ($>20\%$ differences if depth-velocity preference correlations were less than .6 in medium to large streams with complex channel structures).
2. WUA remained within acceptable limits for screening and reconnaissance studies ($\delta<50$) in all cases if ρ_p was less than .6.
3. Coefficient of variation (cv) of either depth or velocity in the habitat was a good indicator of channel complexity. The "simple" channel streams in this study had d and v cv values less than .5, and the complex streams had cv values greater than 0.5.
4. Stream size classification based on mean annual discharge was effective for the western geomorphic

provinces included in this study, but other classifications might be more appropriate elsewhere.

A summary of recommended use of univariate or multivariate approach showed that consideration of variable interactions was necessary in less than half the applications used in this thesis (Table 10). For all other situations and for those which are not demonstrated in this paper, it is strongly recommended that users make every effort to account for the effects of variable correlations, preferably by requiring use of multivariate curve functions derived from an unbiased fish obsrevation study.

PHABSIM users should consider the guild preference concept especially as it might apply in high order stream situations with numerous closely-related species. Extensive literature on fish guilds is available, and could be valuable in initially defining habitat preferences.

Finally, theoretical ecologists are urged to review and evaluate the exponential polynomial model for use in defining niche components and predicting niche utilization. The current state of mathematical facility should encourage study design and data collection in this exciting field.

Table 10. Recommended use of univariate (U) or multivariate (M) approach in various applications of PHABSIM. (MAF = mean annual flow)

	Stream Size					
	Small (MAF< 12 cms)		Medium (MAF>12-60 cms)		Large (MAF>60 cms)	
Guild:	V_1D_1	all others	V_1D_1	all others	V_1D_1	all others
Simple (cv<.5)	U+M	M	U+M	M	U+M	M
Complex (cv>.5)	U+M	M	U+M	U+M	U+M	U+M

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Appendix I. Difference (δ) and coefficient of variation(cv) value for simple (S) and complex (C) streams of small size. (ρ_p = .2 ... .8)

		.2		.4		.6		.8	
		S	C	S	C	S	C	S	C
V_1 D_1	δ	2.6	5.6	8.2	12.6	23.5	26.4	42.8	42.6
	cv	10.9	1.5	19.5	3.9	31.6	13.5	46.3	19.1
V_2 D_2	δ	15	14	34.6	32	54	54	74.8	77.6
	cv	3.4	2.8	14.2	7.1	27.6	16.3	64.8	45
V_3 D_3	δ	5.8	6	38.8	39.4	40.0	45.3	49.2	58
	cv	10.4	.7	22.0	3.0	32.9	8.21	44.0	12.7
V_2 D_4	δ	13.4	29.0	51	74	85	94.8	74	99.6
	cv	19.9	17.4	35.5	51.5	50.5	90.9	60.0	≈100.0
V_3 D_5	δ	28.8	26.2	38.8	34.2	70.4	67.6	93	92.8
	cv	22.1	2.9	43.3	6.8	63.8	8.9	81.4	11.5

Appendix I cont. Difference (δ) and coefficient of variation (cv) values for simple (S) and complex (C) streams of medium size.

		.2		.4		.6		.8	
		S	C	S	C	S	C	S	C
V_1 D_1	δ	+12.6	+2	+18.4	2	17.2	21.6	65.4	37.6
	cv	44.2	7.8	80.4	9.5	45.4	10.1	95.5	27.3
V_2 D_2	δ	27	2.2	55	.94	62.2	21	95.5	43.4
	cv	15.9	2.5	36.9	5.8	96.6	11.9	97.3	23.4
V_3 D_3	δ	13.2	1	51.5	30.6	63.74	27.51	82.5	32.6
	cv	10.6	2.5	20.3	5.2	32.1	11.7	43.4	17.3
V_2 D_4	δ	22.7	+7	44.9	1	56.4	12.4	85.1	33
	cv	23.2	4.8	45.5	8.0	61.42	15.7	81.4	31.5
V_3 D_5	δ	38.0	3.4	54.7	+18.2	82.8	2.2	97.1	25
	cv	22.1	11.6	44.2	23.0	71.6	34.3	89.2	51.5

Appendix I cont. Difference (δ) and coefficient of variation (cv) values for simple (S) and complex (C) streams of large size.

		.2		.4		.6		.8	
		S	C	S	C	S	C	S	C
V_1 D_1	δ	13.9	.4	25.6	4.4	35.6	15.4	49.2	31.2
	cv	10.3	5.2	20.8	8.3	43.3	12.9	57.41	33.0
V_2 D_2	δ	3.3	+4.8	11	1.2	21.2	8	36.2	18.8
	cv	19.74	6.2	38.8	4.3	57.4	10.4	77.5	20.7
V_3 D_3	δ	+1.5	3.2	29.3	33.8	28.12	34.1	34.2	42
	cv	6.3	2.8	10.9	5.9	27.0	17.2	40.3	26.5
V_2 D_4	δ	+17.8	+5.4	+15.6	+8.8	19.6	13.8	33.8	39.4
	cv	11.4	5.3	26.9	8.7	77.1	13.9	78.4	22.7
V_3 D_5	δ	33.0	10.2	46.6	8.6	73.6	29.0	92.5	55.4
	cv	3.7	0.4	6.8	1.5	11.9	1.44	33.3	7.3