Habitat effects on depth and velocity frequency distributions: Implications for modeling hydraulic variation and fish habitat suitability in streams

Jordan S. Rosenfeld a,⁎, Kate Campbell b, Elaine S. Leung b, Joanna Bernhardt b, John Post c

a Ministry of Environment, Province of British Columbia, 2202 Main Mall, Vancouver, BC, Canada V6T 1Z4
b BC Conservation Foundation, #206 – 17564 56A Avenue, Surrey, BC, Canada V3S 1G3
c Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

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A B S T R A C T

Describing the velocity and depth attributes of stream channels is a basic goal of theoretical and applied hydrology and is also essential for modeling biological processes in streams. We applied frequency distributions (gamma probability functions fit to point velocity and depth data) to evaluate their ability to describe variation in hydraulic conditions at the channel unit scale among contrasting habitat types (pools, glides, riffles, and runs) at different flows in a small trout stream. Velocity and depth distributions differed systematically between habitat types, with linear regression explaining 65% and 72%, respectively, of variation in gamma distribution parameters related to skewness and kurtosis; however, distribution parameters were not significantly related to discharge. Relative depth explained 68–79% of the variation in slopes of at-a-station hydraulic geometry relationships between different habitat types. Differentiation of habitat types in a velocity–depth phase space was reduced at high flows, and differences in hydraulic geometry exponents were consistent with flow convergence at high discharge. Modeling variance in velocity and depth using locally derived gamma distributions, in conjunction with simple hydraulic geometry, provided accurate estimates of reach average habitat suitability for trout. Frequency distributions derived from a set of New Zealand streams provided much poorer estimates of habitat suitability. Frequency distributions are useful as an heuristic tool for understanding and modeling drivers of spatial variation in hydraulics, and provide a simple method to model hydraulic conditions in streams. However, general transferability of frequency distributions between streams would be improved by validating and refining existing relationships between distribution parameters and easily measured stream characteristics, like habitat type, channel size, gradient, and substrate caliber.

1. Introduction

Describing the velocity and depth attributes of stream channels is a basic goal of theoretical and applied hydrology, and is also critical for modeling the distribution of biological processes ranging from algal production to fish distribution (Statzner et al., 1988; Peterson and Stevenson, 1992; Jowett, 1997; Lamouroux et al.,1999). Hydraulic attributes can be characterized using measures of central tendency (e.g., mean velocity and depth) or measures of dispersion (variance around the mean; e.g., Madej, 1999; Mossop and Bradford, 2006). Simple empirical approaches like hydraulic geometry predict how channel average velocity and depth change with increasing discharge, and are extremely useful shortcut methods for estimating how average hydraulic conditions change with flow (Jowett, 1998; Jowett et al., 2008). However, in many cases variance around the mean may exert stronger control on physical and biological processes than the mean itself. The abundance or persistence of different species of fish, for instance, may depend on the upper or lower distribution of depths or velocities rather than channel averages.

While simple estimates of parameter variance can be used for improving hydraulic models, the implicit assumption of symmetry (normality) is generally unfounded, and probability distributions that reflect realistic skewness and kurtosis capture far more information than a simple standard deviation. To refine predictions of habitat attributes without increasing data needs, researchers have fit a variety of standardized probability (density) functions around mean velocity and depth values to increase the precision of simple habitat models (e.g., Dingman, 1989; Rao et al., 1993; Lamouroux et al., 1995; Lamouroux, 1998; Lamouroux et al., 1998) found that a variable mixture of a normal and exponential distribution performed best, and Lamouroux et al. (1995) provided predictive regression models to estimate distribution shape parameters based on reach Froude number and channel relative roughness. More recently, Schweizer et al. (2007a) also used a mixture of a normal and lognormal distribution to model depth and velocity probability distributions using a similar approach.
The ability of probability distributions to quantify the proportion of habitat above or below particular velocity thresholds makes them especially appealing for modeling biological processes in streams, because habitat suitability may be closely related to velocity and depth thresholds (e.g., Moore and Gregory, 1988). If frequency distributions are transferable between streams or if their properties (e.g., width, skewness, kurtosis) can be modeled based on simple channel attributes such as roughness, channel size, or relative discharge (e.g., Lamouroux et al., 1995; Schweizer et al., 2007a), then they offer the possibility of a simple statistical approach for modeling instream hydraulic habitat, as demonstrated by their successful application to predicting fish community structure (Lamouroux et al., 1998, 1999) and the outcome of different river restoration scenarios (Schweizer et al., 2007b). Consequently, probability approaches for describing distributions of depth and velocity have seen increasing application in modeling habitat availability for fish, assessment of instream flow needs, and stream restoration design (Lamouroux et al., 1999; Schweizer et al., 2007b). Data requirements are simple and may be limited to an estimate of mean channel velocity and depth (e.g., from hydraulic geometry), to which standardized frequency distributions can be applied to estimate variance around the mean (Schweizer et al., 2007a; Saraeva and Hardy, 2009).

Stewardson and McMahon (2002) expanded the application of univariate probability distributions to consider how bivariate velocity–depth distributions correlate with channel structure. They hypothesized that longitudinally homogenous channels (i.e. continuous glide or run dominated by transverse variation in depth) would exhibit a positive correlation between depth and velocity (highest depths and velocities at the thalweg), and normally distributed depth and velocity distributions (Fig. 1A); whereas channels dominated by longitudinal variation in depth (alternating pools and riffles) should show a negative relationship between velocity and depth (highest velocities in riffles, lowest velocities in pools; Fig. 1B) and highly skewed depth and velocity distributions (Lamouroux, 1998; Schweizer et al., 2007a). Stewardson and McMahon (2002) and later Schweizer et al. (2007a) showed that bivariate velocity–depth plots can indeed serve as useful diagnostics of channel structure, and that the shape of reach-scale velocity–depth distributions are closely related to the proportion of pool and riffle habitat.

In this paper we consider how velocity–depth distributions differ between the constituent habitat types (channel units) that collectively determine reach-scale hydraulic attributes in small streams (Rabeni and Jacobson, 1993). We also test some of the implicit assumptions of earlier studies, e.g., that the skewed distributions and negative relationship between velocity and depth in highly structured (pool–riffle) channels are the outcome of superimposing generally positive velocity–depth relationships for individual habitat types that occupy different parts of the velocity–depth phase space (Fig. 2B; Kemp et al., 1999). We also test some basic assumptions of stream hydrology, e.g., that frequency distributions become more normally distributed with increasing stream discharge (Fig. 2A; Lamouroux et al., 1995; Schweizer et al., 2007a), and that increasing discharge leads to convergence of hydraulic conditions in different habitat types (Fig. 2B), as characterized by different at-a-station hydraulic geometry relationships (Hogan and Church, 1989; Rosenfeld et al., 2007) and increasing overlap of hydraulic conditions in different habitat types at high flow (Fig. 2B).

Our specific geomorphic goals in applying the frequency distribution approach at the habitat level are (i) to quantify differences in the underlying hydraulic conditions between fundamental habitat types (pools, glides, runs, and riffles) in a small stream using depth and velocity frequency distributions, and (ii) to understand how the hydraulic attributes of constituent habitats affect the larger hydraulic characteristics of the reach. Our more applied objective is to assess the usefulness of depth and velocity frequency distributions for modeling habitat suitability for cutthroat trout (Oncorhynchus clarki clarki) at low and high flows in a small trout stream; and to test the transferability of frequency distributions generated elsewhere.

2. Methods

2.1. Study site

We measured velocity and depth distributions in different channel units (habitat types; Peterson and Rabeni, 2001) in a 1 km reach of Husdon Creek, a small coastal stream on the Sunshine Coast of British Columbia, 50 km north of the city of Vancouver, Canada (UTM 448650E 5478500 N). Husdon Creek has an average bankfull channel width of 3.4 m, a summer low flow of 0.02–0.03 m³·s⁻¹, a bankfull discharge of 0.6 m³·s⁻¹, and drains a 3.4 km² watershed of second growth conifer forest. The reach of stream used for measurements had ~75% of its gradient.

Fig. 1. Hypothesized effects of transverse and longitudinal variation in depth on joint velocity–depth frequency distributions (after Stewardson and McMahon, 2002; and Schweizer et al., 2007a). A positive relationship between velocity and depth is expected when transverse variation in depth dominates (A), and a negative relationship is expected when longitudinal variation dominates (i.e., pronounced pool–riffle structure) (B).

Fig. 2. Expected changes in habitat attributes associated with increasing discharge. Frequency distributions of depth and velocity are predicted to become more normal as average depth and velocity increase (A), different habitat types are expected to show greater overlap in a velocity–depth phase space at higher flows (B), and depths and velocities in different habitat types are expected to converge or even reverse at high discharge (B). Note that the negative relationship between velocity and depth may be an emergent property of superimposing positive velocity–depth relationships for habitat types that occupy different areas of the velocity–depth phase space.
canopy cover; a 1% gradient; substrate dominated by gravel, sand, and cobble; and abundant large wood (0.37 pieces of large wood per linear meter) in a forced pool–riffle channel. Hudson Creek typifies the small stream habitat where juvenile anadromous coastal cutthroat trout and coho salmon (*Oncorhynchus kisutch*) are most abundant (Rosenfeld et al., 2000), with summer densities of trout and coho averaging 0.9 and 0.2 fish m$^{-2}$, respectively (J. Rosenfeld, unpublished data).

### 2.2. Study design and sampling methods

We characterized differences between habitat types by measuring velocity and depth in five replicate riffle, run, glide, and pool channel units (total $n = 20$) during summer low flow (July 2001) and four of the same replicate riffles, runs, glides, and pools (total $n = 16$) during winter high flows (December 2001). Depth and water velocity (at 60% of total depth) were measured at 20 cm intervals on multiple transects spaced 20 cm apart in each channel unit (essentially measuring velocity and depth at the nodes of a 20 cm square grid superimposed on each habitat unit) using a meter stick and a Marsh–McBirney model 2000 flow meter. Channel unit lengths ranged from 1.1 to 9.2 m, with 67 to 435 paired velocity and depth measurements in each channel unit, for a total of 3365 and 5192 paired point velocity and depth measurements at summer low flow and winter high flow, respectively. Discharge range during low and high flow sampling was 0.02–0.03 and 0.17–0.64 m$^{-3}$ s$^{-1}$, respectively, with 0.64 m$^{-3}$ s$^{-1}$ approaching bankfull discharge. Low flow conditions are considered to be particularly important to juvenile salmonid rearing in small coastal streams, as this is often when habitat and food are most limiting (e.g., Rosenfeld and Boss, 2001). Time constraints precluded collection of additional data at intermediate flows.

Each channel unit was classified during summer low flow as a pool (0% gradient, low current velocity, deep), glide (0–1% gradient, slow current velocity, minimal surface water disturbance), run (1–2% gradient, high current velocity, turbulent flow), or riffle (1–3% gradient, high current velocity, water surface broken by protruding substrata, shallow) as described in Johnston and Slaney (1996) and Moore et al. (1997). Average Froude number in pools, glides, runs, and riffles were 0.08, 0.13, 0.17, and 0.30, respectively; and average Froude number for all habitats was 0.16 and 0.19 at low and high discharge. Sampled channel units were dispersed throughout the reach (i.e., rarely contiguous) and were chosen to be representative of their class; habitat units that were anomalous, excessively complex (e.g., with islands or side-channels created by wood jams), or did not consist of a single channel-spanning habitat type were not included; we recommend explicitly sampling these complex habitats in future studies to provide a more robust test of frequency distribution models. The same channel units were measured during winter high flow; channel unit length did not change between seasons, but channel width and the number of point measurements were higher in winter because of elevated discharge.

### 2.3. Data analysis

#### 2.3.1. Modeling velocity and depth frequency distributions

A variety of functions have been used to describe velocity and depth distributions in streams, including negative exponential, normal, lognormal, gamma, and combinations thereof (Lamouroux et al., 1995; Lamouroux, 1998; Schweizer et al., 2007a). Although several recent papers have successfully modeled depth and velocity distributions as a mixture of normal and lognormal distributions, we chose to use a simple 2-parameter gamma distribution. The gamma distribution is flexible and can fit a variety of distributions ranging from near-normal to strongly skewed using a single function with different parameter values. Gamma distributions produce a fit that is similar to combined functions (e.g., Lamouroux, 1998), and differences in distribution parameter values between habitats allow for quantitative comparisons and easy transfer and application in modeling. Nothing is intrinsically superior about the gamma distribution, but it is convenient because gamma distributions are simple to fit using readily available statistical packages, whereas mixed distribution models (e.g., Lamouroux, 1998; Schweizer et al., 2007a) require custom modeling to fit the mixing parameter.

The gamma probability density function is a 2-parameter distribution that ranges in shape from nearly symmetrical to nearly logarithmic or negative exponential (right-skewed) depending on the scale and shape parameter values. The shape parameter ($k$) determines the degree of skewness ($2/k$) and kurtosis ($6/k^2$), such that a smaller shape parameter creates a more skewed distribution and a larger shape parameter creates a more symmetric one. The scale parameter ($\theta$) determines the width of the distribution; a larger scale parameter horizontally stretches the distribution. The mean of a gamma distribution equals $k\theta$, and the variance is $k\theta^2$.

We fit gamma distributions to velocity and depth data for individual channel units during high and low discharge, and for larger virtual stream reaches created by concatenating all of the individual channel units sampled during either high or low flow, allowing us to compare frequency distributions at the channel unit and reach scales. We created virtual reaches only because our sampled habitat units were not contiguous. However, these virtual reaches had proportions of habitat type by area (35% pool at summer low flow) similar to the larger sample reach in Hudson Creek (~40% pool at summer low flow), so their properties should be representative of reach-scale attributes. Following Schweizer et al. (2007a), we standardized all depth and velocity values within a habitat unit by dividing by the average depth or velocity in that unit; for reach-scale distributions, we standardized distributions by dividing point data by the reach average velocity or depth. Standardizing distributions allows them to become scale independent (i.e. expressed in terms of deviations from the mean rather than as absolute depth or velocity), thereby facilitating comparisons and transferability of frequency distributions; note, however, that the mean and variance of depth or velocity are used to convert standardized distributions back to scaled ones for modeling purposes.

Because gamma density functions can only be fit to positive values, and because three-dimensional flow structures (e.g., backeddies or turbulence) can create negative velocities, we transformed the standardized data by adding 2 to all standardized velocity and depth values before fitting gamma distributions (effectively right-shifting the center of standardized distributions to three times the standardized mean). Consequently, use of the gamma distribution parameters as presented later in this paper requires a simple back-transformation, i.e. subtracting a value of 2 standardized means to recenter the predicted distribution over the mean (i.e., to restore the negative values). Because shape and scale parameters are sensitive to the mean distribution value (distribution mean $= k\theta$), we also transformed depth in the same way to allow direct comparison of shape and scale parameters between velocity and depth distributions.

We visually illustrated the fit of our gamma functions by plotting them over observed depth and velocity frequency distributions for high and low discharge reaches. We also compared our gamma distributions to the mixed normal–lognormal distributions for velocity and depth calculated according to the predictive equations proposed by Schweizer et al. (2007a):

$$f(v) = (1 - S_{max}) \cdot N_v(\mu_{LN}, \sigma_{LN}) + (S_{max}) \cdot LN_v(\mu_{LN}, \sigma_{LN})$$

where $v$ is standardized velocity (point velocity/mean velocity), $N_v$ is the probability density function for the normal distribution, $LN_v$ is the probability density function for the lognormal distribution, $\mu_{LN} = \mu_{LN} = 1$, $\sigma_{LN} = 0.52$, $\sigma_{LN} = 1.19$, and

$$f(d) = (1 - S_{max}) \cdot N_d(\mu_{LN}, \sigma_{LN}) + (S_{max}) \cdot LN_d(\mu_{LN}, \sigma_{LN})$$

where $d$ is standardized depth (point depth/mean depth), $\mu_{LN} = \mu_{LN} = 1$, $\sigma_{LN} = 0.52$, $\sigma_{LN} = 1.09$, and

$$\ln(S_{max} / 1 - S_{max}) = -4.72 - 2.84 \cdot \ln(Fr)$$
where $Fr$ is the Froude number (mean velocity / (9.8 · depth)0.5). Schweizer et al. (2007a) based these relationships on best fit joint velocity and depth frequency distributions from 92 stream reaches in New Zealand, and our purpose was to evaluate their transferability to a novel stream (Hudson Creek).

2.3.2. Relationship between habitat type and gamma distribution parameters

We tested for habitat (pool, glide, run, and riffle) and discharge (low vs. high) effects on shape and scale gamma distribution parameters for velocity and depth separately using two-factor Analysis of Variance (ANOVA), with habitat and discharge as factors and shape and scale parameters as response variables. To further test for habitat and discharge effects on distribution parameters, we converted habitat and discharge classes to dimensionless variables in terms of relative depth (average habitat unit depth divided by bankfull depth) and relative discharge (discharge at time of channel unit measurement divided by bankfull discharge). We then regressed shape and scale parameters for depth and velocity separately against relative depth and relative discharge.

We developed combined predictive models for velocity and depth scale and shape parameters using ANOVA by modeling shape or scale vs. metric (velocity or depth), habitat (pool, glide, run, or riffle), and discharge (low vs. high). We further tested for discharge effects on scale and shape parameters using a paired t-test, by subtracting low flow scale or shape parameter values from high flow parameter values for each individual channel unit, and testing to see if differences between flows were significantly different from zero (i.e. consistently higher or lower at a particular flow). All data analysis and transformations were performed using SAS software (SAS Institute, 1989). All analyses were tested to ensure assumptions of normality and equal variance at $p = 0.05$, which was assessed using the Shapiro–Wilke statistic, a frequency histogram of residuals (SAS Institute, 1989), and the presence of a significant correlation between the absolute value of residuals and observed values. Variables were log10 transformed to meet assumption of normality as necessary.

2.3.3. Effects of increasing discharge on habitat attributes

We tested for differences in the rate of change of velocity and depth on a rising hydrograph by comparing slopes of at-a-station hydraulic geometry relationships in different habitat types (e.g., Rosenfeld et al., 2007). Expectations were that increases in depth with discharge would be fastest in riffles and slowest in pools, whereas increases in velocity would be fastest in pools and slowest in riffles (leading to flow convergence or velocity reversal in pools and riffles at high flows; Keller, 1971; Knighton, 1998; Rosenfeld et al., 2007). To provide more generally transferable functions for modeling changes in average velocity and depth in different habitat types, we modeled habitat effects on the slope of hydraulic geometry relationships using relative habitat depth (average channel unit depth/bankfull depth; $n = 16$) as the independent dimensionless variable.

To test the prediction that correlations between velocity and depth would become more positive with increasing discharge (when longitudinal variation in depth declines at higher flows), we used a t-test to compare velocity and depth correlation coefficients at low vs. high discharge in individual channel units (total $n = 36, 20$ low flow and 16 high flow channel units). We also used a paired t-test to assess whether the average slope of the velocity–depth relationship increased at high vs. low discharge (for each of $n = 4$ habitat types).

We used velocity–depth plots (after Schweizer et al., 2007a) to assess the predictions of (i) a shift from a negative reach-scale correlation between velocity and depth at low flow to a positive correlation at high flow (Fig. 2B), and (ii) convergence of hydraulic conditions in different habitat types at high flow (Fig. 2B).

2.3.4. Applying gamma frequency distributions to model fish habitat suitability

The weighted useable area (WUA; Parasiewicz and Dunbar, 2001) method models habitat availability for fish by obtaining discrete estimates of velocity and depth over defined polygons or segments of stream habitat in the reach to be assessed. Published habitat suitability curves for velocity and depth are then used to estimate habitat suitability (ranging from 0 to 1) in each polygon based on observed velocity and depth values, and the habitat suitability values are multiplied by polygon area to derive an estimate of WUA in each polygon; polygon estimates are then summed to give a reach estimate of WUA (Parasiewicz and Dunbar, 2001). Although the WUA approach has significant shortcomings that are well described elsewhere (Mathur et al., 1985; Railsback et al., 2003; Anderson et al., 2006), it is a convenient model for evaluating the application of frequency distributions to modeling fish habitat.

We evaluated the accuracy of frequency distributions for model fish habitat using a data reduction approach (i.e., by comparing predictions based on a complete vs. reduced data set). First, we derived detailed estimates of habitat suitability for trout in our high and low flow reaches by using published depth and velocity habitat suitability curves for juvenile trout (Raleigh et al., 1984) to calculate habitat suitability at each paired velocity and depth measurement collected on the 20 cm × 20 cm grid in each channel unit. These habitat suitability values were then averaged to create a “true” reference value of habitat suitability (for both depth and velocity) in our virtual low and high discharge reaches (20 sampled channel units concatenated at summer low flow, 16 concatenated at winter high flow for a reach length of ~70 m, a typical scale for calculating reach WUA).

We then reduced the detailed velocity and depth measurements to a single reach-average value of velocity and depth for calculating habitat suitability in the low and high flow reaches based on a single reach average velocity and depth estimate. A third habitat suitability estimate was then derived by applying a gamma distribution to include variation around these reach average values for velocity and depth, allowing us to compare habitat suitability estimates based on gamma distributions with those based on either reach average velocity and depth values alone, or the detailed benchmark habitat data (average suitability values from 5192 and 3365 point measurements at high and low flows, respectively). If predictions of habitat suitability based on gamma distributions are accurate, then frequency distributions may be a parsimonious approach for modeling habitat suitability or other habitat attributes when only reach-average metrics of velocity and depth are available. To evaluate the transferability of the frequency distribution relationships from Schweizer et al. (2007a), we also estimated habitat suitability using mixed normal–lognormal distributions based on data from New Zealand streams (Eqs. (1)–(3) above).

Because total stream habitat areas are constant within each of the high and low flow comparisons described above, we present the results in terms of the estimated habitat suitability (HS) values for the three modeling approaches (i.e. WUA = HS × Area; variation is driven entirely by differences in estimated habitat suitability values because area is constant in these scenarios).

3. Results

3.1. Relationship between habitat type and gamma distribution parameters

Gamma distribution shape and scale parameters (Table 1) were both significantly different between depth and velocity frequency distributions ($F_{1,67} = 112, P = 0.0001$ for shape, $F_{1,67} = 146, P = 0.0001$ for scale). Shape and scale parameters also differed across habitats ($F_{2,66} = 5.1, P = 0.003$ for shape, $F_{3,66} = 146, P = 0.0001$ for scale). While the skew and width of distributions differed systematically between habitats (as represented by shape and scale parameters of gamma distributions), distribution
asymmetry and width was always higher at the reach scale than for individual habitat types (Table 1). However, discharge had no significant effect on either shape or scale parameters, either as a class (low vs. high discharge) or continuous (relative discharge) variable. The predictive regression equations for predicting shape ($F_{\text{sh}} = 31.8, P < 0.0001, R^2 = 0.65$) and scale ($F_{\text{scale}} = 42.6, P < 0.0001, R^2 = 0.72$) gamma distribution parameters as a function of habitat and metric variables were

\[
\text{shape} = 23.3 + \text{habitat} + \text{metric} 
\]

where coefficients for habitat are run = 0, riffle = −3.8, glide = −5.6, and pool = −15.9, and coefficients for metric are velocity = 0 and depth = 32.5.

\[
\log_{10}(\text{scale}) = -0.77 + \text{habitat} + \text{metric} 
\]

where coefficients for habitat are run = 0, riffle = −0.004, glide = −0.48, and pool = −0.237, and coefficients for metric are velocity = 0 and depth = −0.485.

Habitat coefficients for parameters in Eqs. (4) and (5) are generally negatively correlated with habitat depth (pools have the lowest shape and highest scale coefficients, i.e. distributions in deep habitats are more right-skewed and wider), but regressions with relative depth substituted for habitat class variables were not significant ($F_{\text{sh}} = 0.33, P = 0.57$ for shape, $F_{\text{scale}} = 1.36, P = 0.26$ for scale). However, Froude number was a significant continuous habitat variable in regression for both shape ($F_{\text{sh}} = 51.4, P < 0.0001, R^2 = 0.60$) and scale ($F_{\text{scale}} = 65.0, P < 0.0001, R^2 = 0.65$):

\[
\text{shape} = 11.7 + 31.9 \cdot \text{Froude number} + \text{metric} 
\]

where coefficients for metric are velocity = 0 and depth = 32.5.

\[
\log_{10}(\text{scale}) = -0.61 - 0.60 \cdot \text{Froude number} + \text{metric} 
\]

where coefficients for metric are velocity = 0 and depth = −0.485.

Gamma distributions at the reach scale provided a reasonable fit to depth and velocity distributions (Fig. 3; $R^2$ values for the gamma distribution models illustrated in Fig. 3 range from 0.62 to 0.86 with a mean of 0.75). Frequency distributions estimated using the mixed normal–lognormal density functions provided by Schweizer et al. (2007a) tended to overestimate depth and velocity, particularly at low flows, and provided a generally poorer fit than the gamma distributions ($R^2$ values for the mixed normal–lognormal models illustrated in Fig. 3 range from 0.42 to 0.75 with a mean of 0.51). However, the predictive equations from Schweizer et al. (2007a) provided a reasonable first approximation of the general shape and spread of the distribution considering they come from generally larger streams in a different hydrogeomorphic context.

Shape and scale parameters at the reach scale were generally outside the range of parameter values for individual habitat types at both low and high flows (Table 1), and were generally more skewed (smaller shape parameter) than distributions within individual habitat types. These results indicate that the greater width and skew of reach-scale distributions is a consequence of superimposing several more normally distributed distributions that differ in their means (e.g., as illustrated in Fig. 2B).

High and low flow shape parameters were not significantly or consistently different in a paired comparison ($t$-test) across all habitats, and the non-significant tendency was for depths to become slightly less skewed ($k_{\text{winter}} - k_{\text{summer}} = 4.1, t_{116} = 0.95, P = 0.35$) and velocities to become slightly more skewed ($k_{\text{winter}} - k_{\text{summer}} = -4.6, t_{116} = -2.0, P = 0.06$) at higher flows.

![Fig. 3. Reach-scale frequency distributions (scaled to a maximum of one) of depth (upper panels) and velocity (lower panels) at low (A, C) and high (B, D) flows in Husdon Creek. Solid lines represent frequency distributions fit using gamma functions. Broken lines represent frequency distributions fit using predictive models from Schweizer et al. (2007a). See text for details.](image)

![Fig. 4. Standardized frequency distributions for depth and velocity at low (solid line) and high (broken line) discharge.](image)

Table 1
Shape and scale parameters for velocity and depth distributions for different habitat types at low (summer) and high (winter) flows. A larger shape parameter value indicates a more symmetric distribution; a larger scale parameter indicates a wider distribution.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Shape</th>
<th>Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pool</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low flow</td>
<td>32.2</td>
<td>0.09</td>
</tr>
<tr>
<td>High flow</td>
<td>44.8</td>
<td>0.07</td>
</tr>
<tr>
<td>Glide</td>
<td>56.6</td>
<td>0.06</td>
</tr>
<tr>
<td>Low flow</td>
<td>56.2</td>
<td>0.06</td>
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<tr>
<td>High flow</td>
<td>59.9</td>
<td>0.05</td>
</tr>
<tr>
<td>Run</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low flow</td>
<td>42.1</td>
<td>0.08</td>
</tr>
<tr>
<td>High flow</td>
<td>59.9</td>
<td>0.05</td>
</tr>
<tr>
<td>Reach average</td>
<td>17.6</td>
<td>0.17</td>
</tr>
<tr>
<td>High flow</td>
<td>28.6</td>
<td>0.11</td>
</tr>
</tbody>
</table>
3.2. Effects of increasing discharge on habitat attributes

The prediction of increasing symmetry (normality) of velocity and depth distributions at high discharge (e.g., Fig. 2A) was poorly supported over the range of flows observed in this study. Although depth distributions became slightly less skewed at higher discharge (Fig. 4), both depth and velocity distributions remained strongly asymmetrical at high flow. However, overlap between habitats in the velocity–depth phase space (Fig. 5) greatly increased with discharge as predicted, and the reach-scale correlation between velocity and depth changed from negative at low flow to weakly positive at high flow (Table 2; Fig. 5) as hydraulic conditions in all habitats converged with increasing discharge. Similarly, the coefficient of variation in Froude number among all channel units declined from 0.67 at low flow to 0.51 at high flow, despite an increase in mean average Froude number from 0.16 to 0.19 at higher flows.

Correlations between velocity and depth at low flow were positive as expected in both run and riffle habitats, but weakly negative in pools and glides (Fig. 6; Table 2). As expected, the correlation between velocity and depth generally increased within all habitats at high flow, resulting in a significant increase in slope of the velocity–depth relationship at high discharge (Table 2; paired t-test by habitat type, \( t_{13} = 3.5, P < 0.04 \)).

The slope of hydraulic geometry relationships predicting mean velocity and depth in different habitats showed strong evidence of hydraulic convergence at high flows (particularly for pools and riffles; Fig. 7), with exponents for mean velocity relationships generally increasing with habitat depth, and exponents for mean depth following the opposite pattern (Table 3). Flow convergence was incomplete, however; with many pools and glides retaining relatively deeper, slower characteristics and riffles retaining shallower, faster attributes even near bankfull discharge. Measurements over a range of higher flows may have contributed to a lack of convergence; however, one run actually decreased in velocity at higher discharge (Fig. 7) because of a channel-spanning log downstream that backed up flow, indicating the importance of downstream hydraulic controls in small streams with abundant wood.

Pools were the most distinct habitat type in terms of their hydraulic geometry exponents, but expressing habitat classes as relative depth (a continuous dimensionless variable) generated significant predictive regressions between relative depth and slope of the discharge-velocity \( (F_{1,13} = 27.4, P < 0.001, R^2 = 0.68) \) and depth-velocity \( (F_{1,13} = 53.1, P < 0.001, R^2 = 0.79) \) relationships:

\[
\log_{10} (v) = -0.78 + (1.28 \cdot \text{relative depth})
\]

\[
\log_{10} (d) = -0.10 - (1.49 \cdot \text{relative depth})
\]

### Table 2

<table>
<thead>
<tr>
<th></th>
<th>Low flow</th>
<th>High flow</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( R^2 )</td>
<td>P</td>
</tr>
<tr>
<td>Pool</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Glide</td>
<td>0.03</td>
<td>0.42</td>
</tr>
<tr>
<td>Run</td>
<td>0.20</td>
<td>0.14</td>
</tr>
<tr>
<td>Riffle</td>
<td>0.25</td>
<td>0.07</td>
</tr>
<tr>
<td>Reach average</td>
<td>0.11</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Each value represents the average of five replicates within each habitat type during the summer, and four replicate habitats in the winter. Reach averages are based on a single correlation with all habitats pooled.

3.3. Applying gamma frequency distributions to model fish habitat availability

Reach-scale estimates of habitat suitability for velocity and depth based on a single reach-average value of depth and velocity were within 8% of the benchmark fine-scale habitat suitability at low discharge, but up to 64% in error at high flow (Table 4). Applying reach-average gamma distributions to mean velocity and depth values generated estimates of habitat suitability that were much closer to the reference values (within 7% at both low and high flows; Table 4), indicating that gamma distributions applied to mean velocities and depths may provide a reasonable representation of habitat conditions with minimal effort. In contrast, the mixed normal–lognormal distributions from Schweizer et al. (2007a) generated large errors in estimated habitat suitability (Table 4), particularly for velocity where the frequency of less suitable higher velocities were considerably overestimated (Fig. 3).

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Fig. 5. Joint velocity–depth plots (after Schweizer et al., 2007a) at low (upper panel) and high (lower panel) discharge. Ellipses represent 95% confidence intervals on point velocity and depth data from pools and riffles.
4. Discussion

Habitat heterogeneity is a defining feature of stream ecosystems, and is usually driven by spatial variation in depth and velocity. Stewardson and McMahon (2002) identified two sources of variation associated with contrasting extremes in channel structure; longitudinal variation in depth (e.g., sequential pools and riffles) associated with structurally complex stream channels, and transverse depth variation (deeper water at the thalweg) associated with simple channels where pools are absent or reduced (Fig. 1). Stewardson and McMahon (2002) and later Schweizer et al. (2007a) showed that channels dominated by lateral vs. longitudinal depth variation had different reach-scale hydraulic signatures, with simple channels showing a positive relationship between velocity and depth, and complex channels showing a negative relationship (Fig. 1).

Our data from Hudson Creek is broadly consistent with these expectations, i.e. there is a strong negative relationship between velocity and depth in a heterogeneous channel with abundant pool habitat. Our analysis also demonstrates that the shape of joint velocity–depth distributions at the reach scale can be understood as a composite of narrower distributions associated with individual habitat types that

![Graph](image)

**Fig. 6.** Standardized velocity–depth distributions for pools, glides, runs, and riffles at low (left panels) and high flows (right panels). Solid black lines represent the relationship between mean velocity and depth with 95% confidence intervals on the predicted mean as solid grey lines. Broken grey lines represent 95% confidence intervals on all data points.

![Graph](image)

**Fig. 7.** Habitat-specific differences in flow-related increases in velocity (upper panel) and depth (lower panel), i.e., hydraulic geometry relationships. Note contrasting slopes between different habitat types (most pronounced between pools and riffles), indicating convergence in depth and velocity among different habitats at higher flows.

| Slope and intercept for hydraulic geometry relationships for velocity, width, and depth by habitat type. Example equation: log(velocity) = intercept + [slope · log(discharge)], or \(v = 10^{(intercept + \text{slope} \times \text{log}(\text{discharge}))} \) (discharge)^slope. Units for depth and width are m, m·s\(^{-1}\) for velocity, and m\(^3\)·s\(^{-1}\) for discharge.

<table>
<thead>
<tr>
<th>Slope</th>
<th>Intercept</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Velocity</td>
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<tr>
<td>Pool</td>
<td>0.58</td>
</tr>
<tr>
<td>Glide</td>
<td>0.29</td>
</tr>
<tr>
<td>Run</td>
<td>0.24</td>
</tr>
<tr>
<td>Rifle</td>
<td>0.25</td>
</tr>
<tr>
<td>Average</td>
<td>0.34</td>
</tr>
</tbody>
</table>

Stewardson and McMahon (2002) identified two sources of variation associated with contrasting extremes in channel structure; longitudinal variation in depth (e.g., sequential pools and riffles) associated with structurally complex stream channels, and transverse depth variation (deeper water at the thalweg) associated with simple channels where pools are absent or reduced (Fig. 1). Stewardson and McMahon (2002) and later Schweizer et al. (2007a) showed that channels dominated by lateral vs. longitudinal depth variation had different reach-scale hydraulic signatures, with simple channels showing a positive relationship between velocity and depth, and complex channels showing a negative relationship (Fig. 1).

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Table 4

<table>
<thead>
<tr>
<th>Reach average velocitya or depthb</th>
<th>True HS</th>
<th>Mean HS</th>
<th>Gamma HS</th>
<th>Schweizer HS</th>
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</thead>
<tbody>
<tr>
<td>Low discharge</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Velocity</td>
<td>0.14</td>
<td>0.74</td>
<td>0.81</td>
<td>0.72</td>
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<tr>
<td></td>
<td>(9%)</td>
<td>(3%)</td>
<td>(4%)</td>
<td>(45%)</td>
</tr>
<tr>
<td>Depth</td>
<td>0.13</td>
<td>0.48</td>
<td>0.52</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>(8%)</td>
<td>(4%)</td>
<td>(4%)</td>
<td>(17%)</td>
</tr>
<tr>
<td>High discharge</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Velocity</td>
<td>0.33</td>
<td>0.44</td>
<td>0.16</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>(64%)</td>
<td>(7%)</td>
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<tr>
<td>Depth</td>
<td>0.32</td>
<td>0.79</td>
<td>1.00</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>(27%)</td>
<td>(4%)</td>
<td>(4%)</td>
<td>(25%)</td>
</tr>
</tbody>
</table>

True HS is calculated using fine-scale velocity and depth data over a 20 cm × 20 cm grid; Mean HS is calculated using only a single reach-average velocity and depth; gamma HS is calculated using a gamma distribution equations from Schweizer et al. (2007a). Error (in parentheses) represents the deviation from the true reference value of habitat suitability calculated using fine-scale velocity and depth data.

a m s⁻¹
b m.

differ in mean depth and velocity (Figs. 2B, 5), i.e. the strong negative relationship between depth and velocity at the reach scale reflects the superimposition of neutral or strongly positive relationships that occupy different parts of the velocity–depth phase space.

Velocity–depth relationships of individual habitat types vary similarly to reaches: those habitats with minimal longitudinal variation in depth (riffles and runs) show positive relationships between velocity and depth, while deeper habitats (in particular pools) show weakly negative relationships between velocity and depth at low flow (Fig. 6). This is because pools have concave bed profiles that are dominated by longitudinal depth variation, i.e. they include shallow inflow and tailout sections as well as deep habitat. Consequently, pools include a wider diversity of microhabitats than other channel unit types and have the widest velocity and depth distributions as indicated by relatively high scale parameters (Table 1).

Theory predicts that divergence in hydraulic conditions (velocity, depth, Froude number) between habitat types should be greatest at low stream flow and converge as discharge approaches bankfull (Keller, 1971; Knighton, 1998). This is quantitatively expressed as differences in hydraulic geometry exponents between different habitats (Table 3; Fig. 7). Other researchers have observed different hydraulic geometry exponents between pools and riffles (Richards, 1977; Knighton, 1998; Halket and Snelgrove, 2005) that support an inference of hydraulic convergence at high discharge, but they have not modeled hydraulic geometry exponents as a function of a continuous variable like relative flow. Hopefully such a dimensionless relationship will provide some transferability of the habitat-specific gamma function to model distributions rather than a mixture of normal and lognormal distributions as in other studies (e.g., Schweizer et al., 2007a), this was because a gamma distribution is easier to fit with readily available software rather than because of any intrinsic superiority of the gamma function. The advantage of both the gamma or mixed distribution approach is that distribution parameters can, in principle, be regressed against independent variables (like habitat type or Froude number) to develop predictive relationships for selecting appropriate distributions for habitat modeling (e.g., Lamouroux et al., 1998; Schweizer et al., 2007a).

Not surprisingly, velocity and depth distributions based on predictive models from Schweizer et al. (2007a) did not fit Hudson Creek data as well as our locally parameterized gamma functions, considerably overestimating depth and velocity at low flows but generating a reasonable visual fit at higher discharge. Because the Schweizer et al. (2007a) equations are based on a set of New Zealand streams that were generally larger than Hudson Creek, this poorer fit is not surprising. Although their equations would provide a good first-order approximation to variance around mean velocity and depth in Hudson Creek in the absence of local data on frequency distributions, they generated poor estimates of habitat suitability for trout. The general transferability of the Schweizer et al. (2007a) functions would require evaluation over a broader range of additional streams, as does the transferability of the habitat-specific gamma distributions and hydraulic geometry relationships we present here.

In a recent application of frequency distribution equations derived from French streams (Lamouroux et al., 1995; Lamouroux, 1998; Saraeva and Hardy, 2009) predicted habitat suitability for fish in streams of the Nooksack River basin in Washington State. They found that predicted trends in habitat suitability based on hydraulic geometry and frequency distribution equations were generally within 30% of those based on conventional PHABSIM modeling, and concluded that probability distributions were a useful shortcut method for evaluating habitat suitability. However, in several of their streams with unconventional structure (unusually shallow channels, or channels exhibiting abrupt increases in cover or substrate quality at higher flows) habitat suitability trends were grossly misrepresented using probability types at high flow, as differences in depth between habitats are swamped out by increasing stage.

However, the expectation that depth and velocity distributions would show large shifts toward normality at higher flow was not supported in Husdon Creek (Fig. 4). Although a shift of velocity and depth toward a more symmetric distribution at higher flows makes intuitive sense and is consistent with empirical observation elsewhere (e.g., Lamouroux et al., 1995; Schweizer et al., 2007a), the conceptual basis for convergence towards normality at high flows is unclear. A more thorough assessment of how flow interacts with channel structure to affect distribution attributes is needed, because at present the mechanistic basis for predicting how distribution shape changes with channel structure is poorly defined. For example, hydraulic resistance associated with abundant large wood in Husdon Creek may prevent a stronger shift to normality at high flows than would otherwise be expected (e.g., Curran and Wohl, 2003). In general, channel features that increase hydraulic resistance (higher pool frequency, lower flows, larger substrate) appear to produce more right-skewed velocity and depth frequency distributions (Schweizer et al., 2007a).
distribution modeling, highlighting the sensitivity of habitat estimates to errors in assumed distribution shapes for atypical channels.

5. Conclusions

In general, a better understanding of the empirical relationships between distribution attributes (e.g., shape and scale parameter values) and channel size, substrate caliber, gradient, abundance of large wood, and discharge would generate better predictive relationships between habitat and hydraulic characteristics, and would improve our understanding of the abiotic drivers of depth and velocity distribution shapes. It would also greatly improve the predictive ability of the frequency distribution modeling approach. The advantage of this statistical modeling approach is its simplicity and potential application to real channels (Lamouroux et al., 1998, 1999; Saraeva and Hardy, 2009); the disadvantage is a limited ability to adapt predictions to the idiosyncrasies of particular streams, but this is likely also a problem with theoretical models (e.g., Pizzuto, 1991). If frequency distributions are not transferrable between streams without generating large errors, then intensive than other methods. Nevertheless, as demonstrated in this and earlier studies, frequency distributions are useful as an heuristic tool for understanding drivers of temporal and spatial variation in hydraulic conditions, as diagnostics of channel hydraulic attributes, and for simple predictive modeling of fish habitat.

Acknowledgments

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References