RIVER RESEARCH AND APPLICATIONS

River. Res. Applic. **24**: 885–899 (2008)

Published online 16 April 2008 in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/rra.1085

SPATIAL DISTRIBUTION AND GEOMORPHIC CONDITION OF FISH HABITAT IN STREAMS: AN ANALYSIS USING HYDRAULIC MODELLING AND GEOSTATISTICS

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ABSTRACT

Reach-scale physical habitat assessment scores are increasingly used to make decisions about management. We characterized the spatial distribution of hydraulic habitat characteristics at the reach and sub-reach scales for four fish species using detailed two-dimensional hydraulic models and spatial analysis techniques (semi-variogram analyses). We next explored whether these hydraulic characteristics were correlated with commonly used reach-scale geomorphic assessment (RGA) scores, rapid habitat assessment (RHA) scores, or indices of fish biodiversity and abundance. River2D was used to calculate weighted usable areas (WUAs) at median flows, Q_{50}, for six Vermont streams using modelled velocity, depth estimates, channel bed data and habitat suitability curves for blacknose dace (*Rhinichthys atratulus*), brown trout (*Salmo trutta*), common shiner (*Notropis cornutus*) and white sucker (*Catostomus commersoni*) at both the adult and spawn stages. All stream reaches exhibited different spatial distributions of WUA ranging from uniform distribution of patches of high WUA to irregular distribution of more isolated patches. Streams with discontinuous, distinct patches of high score WUA had lower fish biotic integrity measured with the State of Vermont's Mixed Water Index of Biotic Integrity (MWIBI) than streams with a more uniform distribution of high WUA. In fact, the distribution of usable habitats may be a determining factor for fish communities. A relationship between predicted WUAs averaged at the reach scale and RGA or RHA scores was not found. Future research is needed to identify the appropriate spatial scales to capture the connections between usable patches of stream channel habitat. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: geomorphology; instream habitat; geostatistics; hydraulic modelling; spatial variability

Received 29 December 2006; Revised 28 September 2007; Accepted 8 October 2007

INTRODUCTION

Human activities have significantly impacted river corridors, degrading water quality, decreasing water storage and conveyance capacity, and altering habitat quantity and quality (National Research Council, 1992, 1999). As stream and river managers work to reverse these changes, they are increasingly using reach-scale assessment protocols to prioritize interventions. Geomorphic assessment protocols based on Schumm (1977), Rosgen (1996) and Montgomery and Buffington (1997) have become particularly common and are being used to score river and stream reaches from reference (excellent) to poor condition. While some evidence suggests that stream geomorphic conditions, or specific characteristics contributing to those conditions, can have important implications for ecosystem integrity (Lammert and Allan, 1999; Roy *et al*., 2003a,b; Sullivan *et al*., 2004, 2006a,b; Chessman *et al*., 2006; Doyle, 2006); the linkages between geomorphic condition, biological health and aquatic habitat are still poorly understood (Sweeney *et al*., 2004; Lepori *et al*., 2005; Chessman *et al*., 2006), and the assumption that good geomorphic conditions translate directly into better aquatic habitat and biodiversity is oversimplified or misleading at best.

'Habitat' includes many physical, chemical and biological components. Many studies have used physical characteristics of the stream, or the physical living space, as a surrogate for habitat (see review: Maddock, 1999).

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Channel depth, width and water velocity are related variables that together define the hydraulics and the morphology of streams (Statzner *et al*., 1988; Stewardson and McMahon, 2002). Instream hydraulics have been linked to both macroinvertebrate (Statzner *et al*., 1988; Thomson *et al*., 2001) and fish distribution, and indeed serve as the main predictors of habitat in the Instream Flow Incremental Methodology (IFIM) for assessing and classifying habitat quality for fish (Bovee, 1982; Bovee *et al*., 1998). In this method, weighted usable areas (WUA) are calculated to quantify fish habitat by species based on Habitat Suitability Index (HSI) curves, generally at the reach scale. Environmental managers worldwide now use the approach routinely as part of environmental assessments and decision making (Tharme, 2003).

The spatial distribution of instream habitat, however, may be as important as it's overall quantity and quality. Analyses of this distribution are a reflection of the scale that is selected. A number of reach-scale studies have shown that instream habitat heterogeneity is important for maintaining healthy aquatic ecosystems (Statzner *et al*., 1988; National Research Council, 1992; Palmer and Poff, 1997; Kemp *et al*., 1999; Rhoads *et al*., 2003; Stewart *et al*., 2005). Others have explored instream habitat heterogeneity at different spatial scales, from the watershed to the local patch (Statzner and Higler, 1986; Pringle *et al*., 1988; Statzner *et al*., 1988; Poff and Ward, 1990; Harper *et al*., 1992; Palmer and Poff, 1997; Newson *et al*., 1998; Padmore, 1998; Kemp *et al*., 2000; Crowder and Diplas, 2000a,b), but few of these studies explicitly acknowledge the scale dependence of their measurements.

More recently, statistical techniques such as cluster analysis (Emery *et al*., 2003), occurrence matrices (Kemp *et al*. 1999), and other approaches have been used to define habitat patches of differing velocity and depth. Spatially dependent hydraulic metrics have also been developed to quantify stream habitat distribution based on the average rate of change of kinetic energy, vorticity and circulation (Crowder and Diplas, 2000a, 2002a,b, 2006). Geostatistical methods have been used to quantify the spatial distribution of different parameters in streams (Oliver and Webster, 1986; Robert and Richards, 1988; Madej, 1999; Bartley and Rutherford, 2002). Clearly, hydraulics affect geomorphic features and both are related to aquatic habitat quality, but the ability of various stream assessment methods, at various scales, to capture habitat characteristics important to fish needs additional analysis. If the key physical characteristics of habitat that drive assessment indicators can be identified, aquatic resource managers might use these tools more effectively in stream restoration and conservation strategies.

The overall goal of this research was to explore the linkages between hydraulics, instream geomorphic condition and fish habitat and biodiversity at the reach and sub-reach scales. At the reach scale, we used rapid geomorphic and habitat assessments and WUA to characterize the physical habitat. We also examined WUA at the sub-reach scale to determine the distribution of patches of usable habitat. Reach-scale WUA does not account for the spatial structure (auto-correlation) and distribution of habitat features that define suitable patch-scale for selected fish at all life stages. To establish patch sizes, we generated semi-variograms in one dimension along the stream thalweg. Our specific objectives were twofold: (i) to characterize the spatial distribution of hydraulic habitat characteristics (WUA) at the reach and sub-reach scales for four fish species using detailed two-dimensional hydraulic models and geostatistics, and (ii) to determine if these hydraulic characteristics were correlated with commonly used reach-scale, geomorphic assessment (RGA) scores, rapid habitat assessment (RHA) scores or indices of fish biodiversity and abundance.

STUDY AREA

Our study area was the Lake Champlain Basin, a glaciated watershed in northwestern Vermont where annual average precipitation ranges from 76 cm in the valleys to 127 cm in the higher elevations of the Green Mountains (LCBP, 2004). Much of this precipitation is stored in the form of snow throughout the winter months and released at snowmelt during the spring. Land use is mixed, and includes 64% forest, 16% agriculture, 10% open water, 6% urban and 4% wetlands (Lake Champlain Basin Program, 2004). Within the Lake Champlain Basin, we selected six independent study reaches that were expected to vary in geomorphic condition from good to poor according to the Vermont RGA protocols (VTANR, 2004). Drainage areas ranged from 22.7 km^2 to 36.8 km^2, and reach lengths varied from 90 m to 120 m as measured along the thalweg. Stream widths at bankfull stage ranged from 6.6 m to 14 m (Table I).

DOI: 10.1002/rra

Table I. Drainage area, bankfull widths, stream length, measured flows used for calibration and simulated Q_{50}, bed particle grain size used for calibration, and model calibration error for each stream

Stream name	Vermont center	Drainage area (km^2)	Bankfull width (m)	Stream length modelled (m)	Measured flow (m^3/s)	Modelled Q_{50} (m^3/s)	Bed grain size, D_{84} (mm)	Model calibration error (%)
Allen Brook	Williston	27.9	6.6	120	0.102	0.376	6.32	0.3
Beaver Brook	Cambridge	30.5	14.5	100	0.051	0.412	6.96	4.4
Fairfield River	Fairfield	36.8	8.4	110	0.029	0.497	8.51	0.5
Lee River	Jericho	34.8	10.8	90	0.928	0.471	8.02	0.2
Mill Brook	Jericho	33.4	12.2	100	0.946	0.451	7.66	0.8
Stone Bridge	Georgia	22.7	7.8	97	0.072	0.307	5.07	0.8

METHODS

Hydraulic modelling

The River2D model (Blackburn and Steffler, 2002; Blackburn *et al*., 2002) was selected for the hydraulic analyses. This is a depth averaged, two-dimensional hydrodynamic and fish habitat model designed using the St. Venant shallow water equations for use in natural streams. A key criterion in the model selection process was the ability of the model to calculate in-stream habitat parameters based on the PHABSIM WUA methodology introduced by Bovee (1982). To support the modelling, detailed stream bed topography was collected approximately every 0.5–1 m^2 using a total station surveying system and used to create a computational mesh for each of the six streams. Mesh sizes ranged between 34 957 and 55 497 nodes (~0.15 m node spacing).

Bed particle-size distributions for each stream reach were determined using a modified Wolman method (Wolman, 1954; Potyondy and Hardy, 1994; Kondolf, 1997) and a Wentworth gravelometer. Separate pebble counts were completed for at least two riffle, two pool and two run features for each stream reach, for a total of 600 particles sampled per reach. Supplemental field observations and particle-size classes were mapped to guide the assignment of bed roughness zones during the calibration process. Distributed velocity measurements were collected approximately every 5–10 m throughout each stream reach for calibration purposes. Discharge was estimated using multiple velocity measurements (~0.2 m increments) at two selected stream cross sections.

Calibration required matching the modelled flows to the measured flows and field-measured velocities. The bed elevation difference limit was set at 0.5 m per finite element cell. All model simulations generated flow values within 4% of the measured values (Table I). Although, this difference is well within the model error; some of the error may be attributed to groundwater flux along the lateral edge boundaries in the model. Bed roughness values were initialized to the field measured D_{84} bed grain size value (Chappell *et al*., 2003; Table I), and these did not need to be adjusted during the calibration process for four of the six stream reaches. The values were adjusted to slightly larger values for two streams, Allen Brook and Mill Brook, in keeping with user manual recommendations (Blackburn and Steffler, 2002).

Once calibrated, the model was run at a median discharge of Q_{50}. Average rather than stressful flows were examined because fish spend a greater amount of time at flows closer to the median. Also, preliminary analyses with extreme flows (Q_{min} and Q_{bf}) indicated little suitable habitat. At Q_{min}, many areas of our six stream reaches did not have the necessary depth or velocity needed by the four selected fish species.

Because instream gages were not available for these streams, discharge values were extrapolated from East Orange Branch River (EOB), a USGS gaged watershed in East Orange, Vermont with a similar drainage area (23.1 km^2). Discharge values measured and used for the model simulations are shown in Table I.

Habitat modelling

WUA is a predicted indicator of the relative amount of habitat available for the particular fish species based on HSI curves (Bovee, 1982). HSI curves developed by the U.S. Fish and Wildlife Service (Trial *et al*., 1983a,b;

DOI: 10.1002/rra

Twomey *et al*., 1984; Raleigh *et al*., 1986) and in some cases, locally adapted for Massachusetts (Parasiewicz and Walker, 2008, Submitted for Publication) were used as input to the River2D model to simulate habitat for blacknose dace (*Rhinichthys atratulus*), brown trout (*Salmo trutta*), common shiner (*Notropis cornutus*) and white sucker (*Catostomus commersoni*) in both the spawn and adult life stages. Blacknose dace, common shiner and white sucker are all native species commonly found in the streams of Vermont, and brown trout is a sport fish of considerable management interest in Vermont.

To calculate the WUA, individual indices for velocity (VSI), depth (DSI) and channel index or substrate size (CiSI) ranging between 0 and 1 were obtained from each of the species HSI curves for each location. These individual indices were then multiplied to calculate a composite suitability index (CSI) for each species for each desired spatial location along the stream reach (Steffler and Blackburn, 2002):

$$\mathrm{CSI} = \mathrm{VSI} \times \mathrm{DSI} \times \mathrm{CiSI} \tag{1}$$

This composite suitability index was then multiplied by the contributing area, the local area surrounding each model node, to produce a WUA at the model mesh scale:

$$\mathrm{WUA} = \mathrm{CSI} \times \mathrm{Area} \tag{2}$$

Since the model predicts WUA for all nodes in each of the computational meshes, WUA may be scaled up (averaged) for any larger, user-defined area.

Stream reach characterization

Since its inception in 1999, the Vermont Agency of Natural Resources' (VTANR) River Management Programme has been developing and testing protocols for conducting fluvial geomorphic and physical habitat assessments.[1] They created an assessment tool that can be used for managing erosion hazards, reducing downstream sediment and nutrient loads, and protecting and restoring aquatic habitat. The protocols include both a field-based RGA and a RHA (VTDEC, 2004). The RGA score is an index for channel stability that includes a channel evolution model (Schumm, 1977), and a stream classification using the Rosgen (1996) and Montgomery and Buffington (1997) systems. Each reach was assessed and assigned a score from 0 (worst condition) to 20 (reference condition) for each of four geomorphic adjustment processes, including: vertical adjustments (channel degradation (incision) and channel aggradation) and lateral adjustments (over-widened channel and change in planform). Each of the individual reach scores were then summed for an overall RGA score, ranging from 0 to 80 for each stream reach.

Vermont's RHA protocols are based, in part, on the Rapid Bioassessment Protocols developed by the U.S. Environmental Protection Agency (Plafkin *et al*., 1989; Barbour *et al*., 1999). The RHA score considers epifaunal substrate and available instream cover, degree of embeddedness, the mixture of velocity and depth regimes, amount of sediment deposition, status of channel flow, degree of channel alteration, frequency of riffles, bank stability, vegetative protection and the width of the riparian vegetative zone. Each habitat parameter included in the RHA was assigned a value from 0 to 20. In conjunction with one another, these values were aggregated to formulate an overall habitat evaluation ranging from 0 to 200. Higher assessment values indicate better aquatic habitat conditions.

Biological data collection

Fish sampling is described in Sullivan *et al*. (2006a). Briefly, three to four representative locations (sites typical of the reach at large) in each reach were sampled, primarily capturing pools and deeper, slow runs. Sampling locations were selected at equal intervals along the reach length, and were randomly distributed among left, centre and right channel positions. For this data collection, a larger 250 m reach was used that contained the approximately 100 m modelled reach. All sampling was performed using a 1.22 m (4 ft) × 12.19 m (40 ft) bag seine with 76.2 mm

[1]Nationally recognized in a USEPA-COE sponsored study of the physical stream assessment methodologies for use in the Clean Water Act Section 404 Programme. The study found that the Vermont approach deserved the highest overall score of the 44 protocols examined nationwide.

DOI: 10.1002/rra

(3/16 in) mesh. At each sampling location, all fish were counted and identified to the species level. A random sample of 150 fish was weighed and measured.

Total fish numbers and two biodiversity indices were used to compare with modelled habitat parameters at each of the stream reaches. The Shannon-Weaver index (H') (Shannon and Weaver, 1963) is a widely used (Magurran, 1988; Rosenzweig, 1995) information index that includes both the number of species and their evenness. Higher H' values are a result of both greater number of species and a more even distribution of these species in the community. The Mixed Water Index of Biotic Integrity (MWIBI) is a locally adapted Index of Biotic Integrity (IBI) for medium-sized wadeable streams based on Karr (1981), and used by the State of Vermont in its biomonitoring programme. It combines species richness and composition, trophic condition and fish abundance (VTDEC, 2004).

Statistical methods

Semi-variogram analysis. The spatial distribution of the WUA was explored using semi-variogram analyses to determine patch size (e.g. examine the spatial structure of hydraulic parameters) along the thalweg. Many stream studies use a one-dimensional approach focused on the thalweg to consider spatial pattern (Oliver and Webster, 1986; Robert and Richards, 1988; Madej, 1999; Bartley and Rutherford, 2002). The spatial structure (range of correlation) of an auto-correlated variable can be described by an experimental semi-variogram (defined in more detail below). The experimental structure is then best fit by a model semi-variogram and can later be used to estimate the parameter value and its associated error variance at unknown locations (de Marsily, 1986; Isaaks and Srivastava, 1989; Goovaerts, 1998). Because we had detailed spatial data from the hydraulic modelling, interpolation of parameter values was not our goal. Instead, we used the experimental and modelled semi-variograms primarily to describe the spatial structure of the data. The analysis was coded and developed in Matlab 7.1 (The Mathworks, Natick, Massachusetts, USA).

The semi-variance, $\gamma(h)$, is defined as the spatial dissimilarity between a parameter separated by a distance h:

$$\gamma(h) = \frac{1}{2N(h)} \sum [u(a) - u(a+h)]^2 \tag{3}$$

where $N(h)$ is the number of data pairs separated by the distance, h, and $u(a)$ and $u(a+h)$ are the parameter values at locations (a) and some distance ($a+h$) away. The difference in distance between each data point and every other data point is calculated, and the pairs of data are binned. The x-axis represents the separation distance between pairs of binned data points; while, the y-axis plots the corresponding average variance of the parameter being investigated. For example, all pairs of points separated by a distance ranging between 0 and 5 m are included in the first bin. The average variance for the parameter values associated with each bin (range of data) is plotted as a single point along the y-axis. The resulting plot is known as the experimental semi-variogram.

Once we calculated values for all bin sizes, a semi-variogram model was fit to the experimental semi-variogram by adjusting three model parameters known as the nugget, range and sill. The nugget is the discontinuity shown at the origin of the plot; and represents measurement error or the general variability within the measured parameter that is not spatially dependent. The range, a, defines the distance at which the variable is no longer correlated (referred to as the limit of spatial dependence). The semi-variance associated with the plateau is defined as the sill, where larger sill values indicate greater variance in the measured parameter.

Quantification of habitat patches. The semi-variograms and plan-view distributions of WUA for each of the six streams were used to rank the streams in order of WUA patchiness. Streams associated with distinctly separate patches of WUA were ranked first, while streams with more uniformly distributed WUA were ranked last. The ranking was performed using the sinusoidal pattern of the semi-variograms. Semi-variograms that exhibited distinct sine waves with high sill values received a patch-ordered rank closer to 1. The rank decreased with decreasing amplitude until no distinct amplitude or sinusoidal pattern could be observed in the semi-variograms. Streams with distinct patches of WUA had higher sill values associated with their semi-variograms and a more distinct periodic function. Velocity and residual depth profiles were also analyzed using this technique, as alternative non-species specific parameters describing the instream hydraulics.

Variable correlation. Pearson's correlation coefficients were used to explore relationships between the WUA variables and the RGA, RHA and fish biodiversity indices. Pairs of variables that had correlation coefficients above

DOI: 10.1002/rra

0.75 were examined further to determine significance in a bivariate linear regression. Relationships having a p-values < 0.05 were deemed to be statistically significant.

RESULTS

Spatial structure of hydraulic parameters

The WUA of habitat for blacknose dace, brown trout, common shiner and white sucker in each of the six stream reaches varied considerably (Table II). As an example, the nodal distribution of WUA for the spawn and adult life stages of the four species are shown for Beaver Brook (Figure 1). Differences associated with the life stages (spawn and adult) of a particular species were primarily expressed as changes in magnitude of the WUA. With the exception of brown trout, the magnitude of the total reach-scale WUA was higher for the spawn life stage than the adult life stage.

The simulated WUA was distributed in patches throughout the stream reach. These distributed patches were generally associated with the location of riffles and pools. Areas of high WUA existed in the riffle areas for blacknose dace (Figure 1a,e) and common shiner (Figure 1b,f), and in the pools for brown trout and white sucker (Figure 1c,d,g,h). The spatial distribution of the hydraulics associated with the riffle-pool structure was described using the semi-variogram analysis. The best-fit, semi-variogram model parameters (i.e. ranges, sills and nuggets) for the four fish species for all streams are provided in Table III. For streams characterized by distinct patches of WUA along the thalweg, the range values indicate the approximate distance over which an average patch is spatially correlated.

The plan-view distribution of WUA for blacknose dace and the semi-variograms describing the spatial structure of WUA for Beaver Brook and Mill Brook are shown in Figure 2. These two streams represent the two WUA distribution extremes; Beaver Brook had the most distinct patches, and Mill Brook, the most uniform distribution.

Semi-variograms with sinusoidal structure (Figure 2d) were used to identify periodicity and quantify the length of correlation of patch distribution. Beaver Brook had large patches of good habitat (high WUA) for the spawn life stage of blacknose dace located at riffles, separated by areas of low WUA associated with the pools. The periodic spacing of the first two peaks of the semi-variogram suggests an approximate spacing of 13 m riffles separated by 17 m pools. These measurements are the distance between sine peaks on the semi-variogram, as shown in Figure 2d. Physical characterization data from the larger 250 m reach of Beaver Brook where fish seining was conducted, showed an average riffle spacing of 17.9 m. There were eight riffles in this stretch, and if the one unusually long 51 m riffle was excluded, the average riffle size was 14 m (Watzin, unpublished work). These numbers correspond extraordinarily well to the modelled results. Mill Brook had more evenly distributed areas of WUA and the semi-variogram exhibited a single range value of ~25 m long. Field measurements in Mill Brook showed just two small pools over the entire 250 m reach and 14 riffles and runs of various sizes (Watzin, unpublished work).

Because local WUA values were calculated at all model nodes (~0.15 m density, ranging from 34 957 to 55 497 points per stream reach), these may be summed over any user-defined area to calculate WUA at any sub-reach scale.

Table II. Reach-averaged WUA values calculated per 100 m of stream length for each of the four species modelled at adult and spawn life stages

	Blacknose dace		Brown trout		Common shiner		White sucker	
	Adult	Spawn	Adult	Spawn	Adult	Spawn	Adult	Spawn
Allen Brook	34	154	139	156	39	57	25	119
Beaver Brook	36	161	159	141	33	67	19	116
Fairfield River	57	278	49	17	60	27	42	39
Lee River	59	272	54	8	36	104	21	74
Mill Brook	165	552	104	0	135	1	99	25
Stone Bridge	53	219	37	38	23	86	12	56

DOI: 10.1002/rra

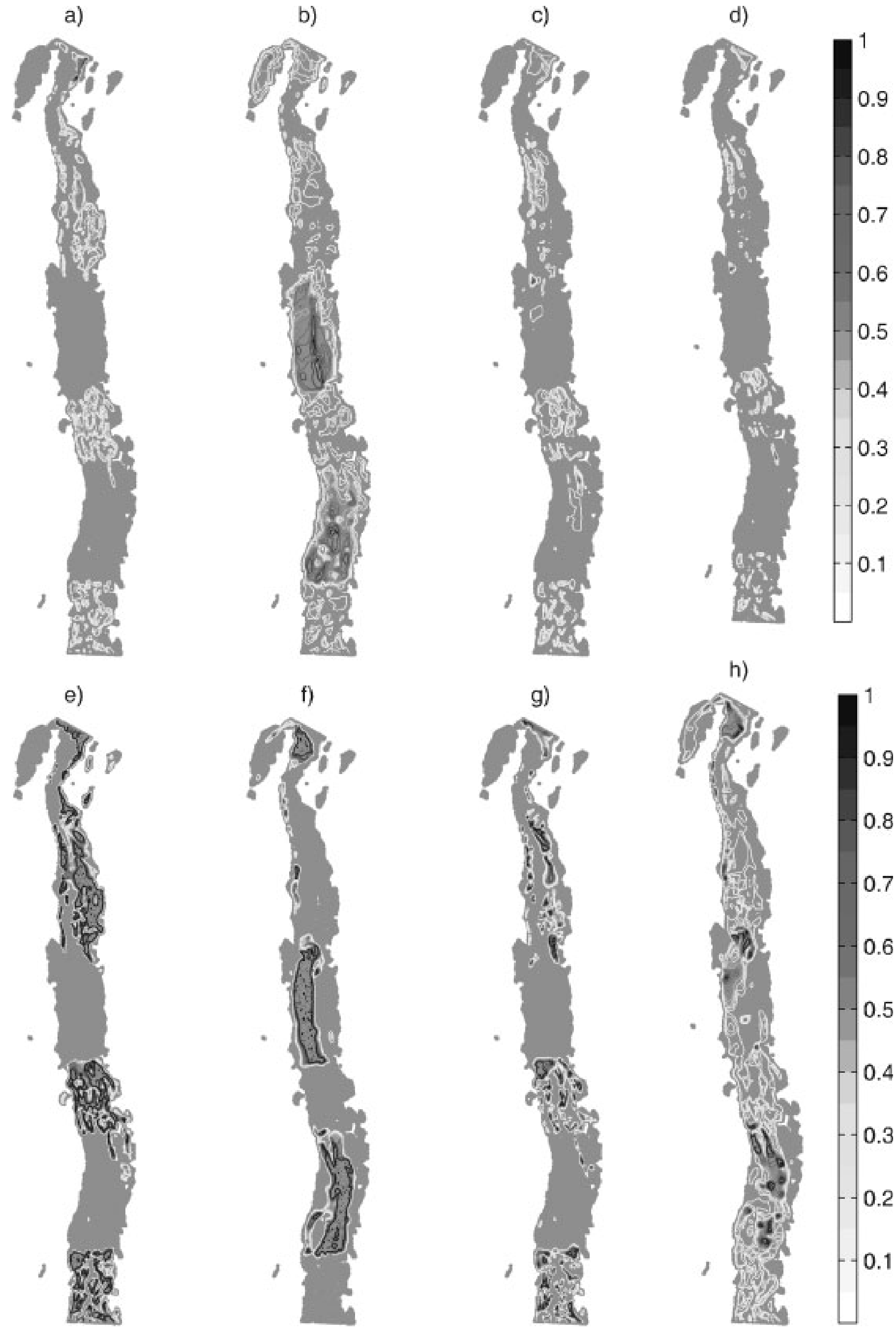

Figure 1. Contrasting WUA distribution for the spawn (top panels) and adult life stages (bottom panels) for (a) and (e) blacknose dace, (b) and (f) brown trout, (c) and (g) common shiner and (d) and (h) white sucker. Numbers represent the reach-averaged WUAs for each species and life stage.

The patch-scale WUA was calculated at increments equivalent to the correlation length (ranges) by summing nodal values of WUA within that range (25 m for Mill Brook, and 13 and 17 m alternately for Beaver Brook). These numbers and the spatial distribution of WUA are illustrated in Figure 2a and c.

We tried to rank each stream according to its longitudinal spatial distribution of WUA (patchiness), quantified using semi-variogram analyses. To rank or classify streams according to their WUA patchiness, a single species and

DOI: 10.1002/rra

Table III. Semi-variogram models and parameters of best-fit range, sill and nugget for all species WUA in one dimension down the thalweg

	Blacknose dace adult				Blacknose dace spawn			
	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model
Allen Brook	4	0.10	0.00	Exponential	10	1.00	0.00	Exponential
Beaver Brook	10	0.05	0.01	Exponential	12	0.90	0.20	Spherical
Fairfield River	10	0.04	0.03	Exponential	10	1.05	0.50	Exponential
Lee River	13	0.17	0.00	Exponential	13	2.25	0.50	Spherical
Mill Brook	25	1.20	0.60	Spherical	25	5.50	3.00	Spherical
Stone Bridge	25	0.13	0.05	Exponential	22	1.05	0.40	Exponential
	Brown trout adult				Brown trout spawn			
	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model
Allen Brook	20	0.70	0.70	Exponential	27	2.20	0.00	Spherical
Beaver Brook	18	1.20	1.20	Spherical	18	2.80	0.00	Spherical
Fairfield River	18	0.22	0.22	Exponential	15	0.90	0.00	Exponential
Lee River	8	0.08	0.08	Spherical	0	0.50	0.00	None
Mill Brook	10	0.17	0.17	Exponential	0	0.00	0.00	Linear
Stone Bridge	5	0.01	0.01	Exponential	>80	Not seen	0.00	Linear
	Common shiner adult				Common shiner spawn			
	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model
Allen Brook	10	0.24	0.00	Exponential	5	0.21	0.00	Exponential
Beaver Brook	12	0.17	0.00	Exponential	9	0.28	0.00	Exponential
Fairfield River	20	1.35	0.00	Spherical	0	0.00	0.00	Linear
Lee River	9	0.16	0.00	Exponential	5	0.80	0.00	Linear
Mill Brook	12	2.00	0.00	Exponential	0	0.00	0.00	Exponential
Stone Bridge	5	0.5	0.00	Exponential	22	0.07	0.00	Exponential
	White sucker adult				White sucker spawn			
	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model	Range (m)	Sill (1×10^4)	Nugget (1×10^4)	Model
Allen Brook	12	0.11	0.00	Exponential	5	0.30	0.00	Exponential
Beaver Brook	12	0.06	0.00	Exponential	10	0.52	0.00	Spherical
Fairfield River	20	0.90	0.00	Exponential	5	0.40	0.00	Exponential
Lee River	11	0.10	0.00	Exponential	11	0.10	0.00	Exponential
Mill Brook	10	1.40	0.00	Exponential	10	0.01	0.00	Exponential
Stone Bridge	8	0.01	0.00	Exponential	6	0.07	0.00	Exponential

life-stage must be selected because differences in WUA distribution vary widely across species and life stages. For example, areas of high WUA exist in the riffle areas for blacknose dace and common shiner, and in the pools for brown trout and white sucker (Figure 1). The semi-variograms for each of the species modelled (Figure 3) illustrate the variability of WUA distributions within a stream reach. An aggregate across species of sinusoidal semi-variograms creates unworkable variability in the magnitudes of semi-variogram ranges and sills.

Therefore, to determine a species-independent patchiness rank, the semi-variograms of bed elevation (detrended by slope), or residual depth, were used to rank order streams (Table IV). Semi-variograms of bed elevation were very similar to WUA semi-variograms and offer the advantage of ease of implementation; the WUA patches

DOI: 10.1002/rra

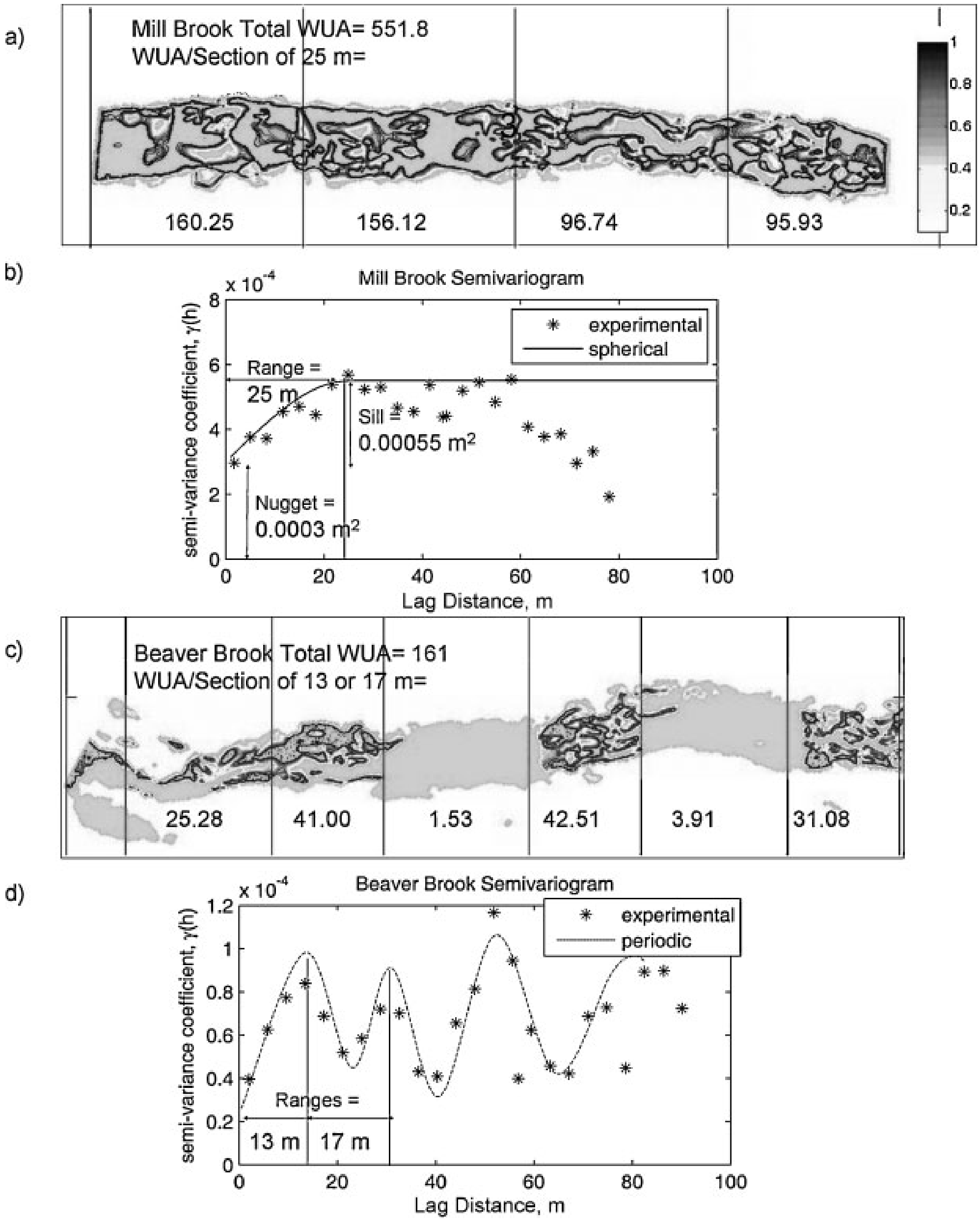

Figure 2. WUA for blacknose dace spawn is visually represented in plan view and calculated at increments corresponding to the semi-variogram ranges for (a) Mill Brook and (c) Beaver Brook. The associated semi-variograms describing the spatial structure of WUA are shown for (b) Mill Brook and (d) Beaver Brook. This figure is available in colour online at www.interscience.wiley.com/journal/rra

corresponded to elevation fluctuations in the individual bedforms. This patchiness rank is based on the magnitude of the semi-variance (sill value) in thalweg residual depth. The periodic semi-variograms of residual depth were best fit with periodic models (Figure 4).

Relationships between hydraulics and reach-level assessment results

There were no significant relationships between the reach-scale RGA score (Table IV) and the modelled reach-scale WUA values, or with the patchiness ranking. Likewise, there was no relationship between the RHA

DOI: 10.1002/rra

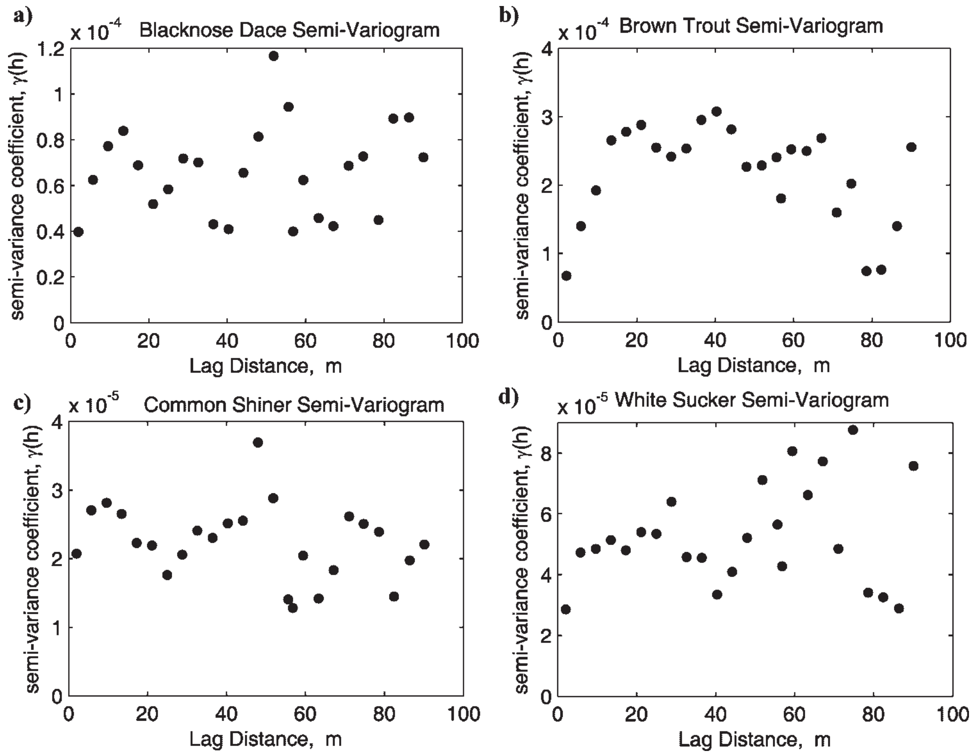

Figure 3. Experimental semi-variograms representing spawn stages of (a) blacknose dace, (b) brown trout, (c) common shiner and (d) white sucker WUA profile in Beaver Brook

scores and the reach-scale WUA or the patchiness ranking. RGA and RHA were strongly and positively associated ($R^2 = 0.85$, $p = 0.009$).

The total reach-scale WUA estimates were generally not good predictors of fish community structure (H', MWIBI) using any of our four selected fish species. Only one significant association was found, and this was a negative association between adult brown trout WUA and MWIBI ($R^2 = -0.66$, $p = 0.049$). However, the comparison of MWIBI with the rank-ordered patchiness showed a *positive* trend (Figure 5), suggesting that streams with more uniformly distributed habitat (e.g. Mill Brook) had the highest biotic integrity.

A significant relationship was found between the actual number of fish counted and reach-scale WUA for blacknose dace ($R^2 = 0.96$, $p < 0.001$ for adult-stage WUA and $R^2 = 0.97$, $p < 0.001$ for spawn-stage WUA). Although many common shiner were counted during the field surveys, no significant relationship was found between the abundance of this fish and the simulated reach-scale WUA. We were unable to evaluate the relationship

Table IV. Stream reach RGA and RHA scores, Patchiness Rank and the associated biodiversity and fish count data

	RGA	RHA	Patchiness rank	Shannon-Weaver's H'	MWIBI	Blacknose dace #	Brown trout #	Common shiner #	White sucker #
Allen Brook	32.0	101	2	1.597	21	3	0	18	0
Beaver Brook	57.0	155	1	1.519	21	17	0	51	5
Fairfield River	61.0	153	3	1.627	23	33	0	43	93
Lee River	47.5	133	5	1.239	27	25	0	3	0
Mill Brook	48.0	149	6	1.229	23	85	3	35	1
Stone Bridge	60.0	149	4	2.038	25	21	0	14	1

DOI: 10.1002/rra

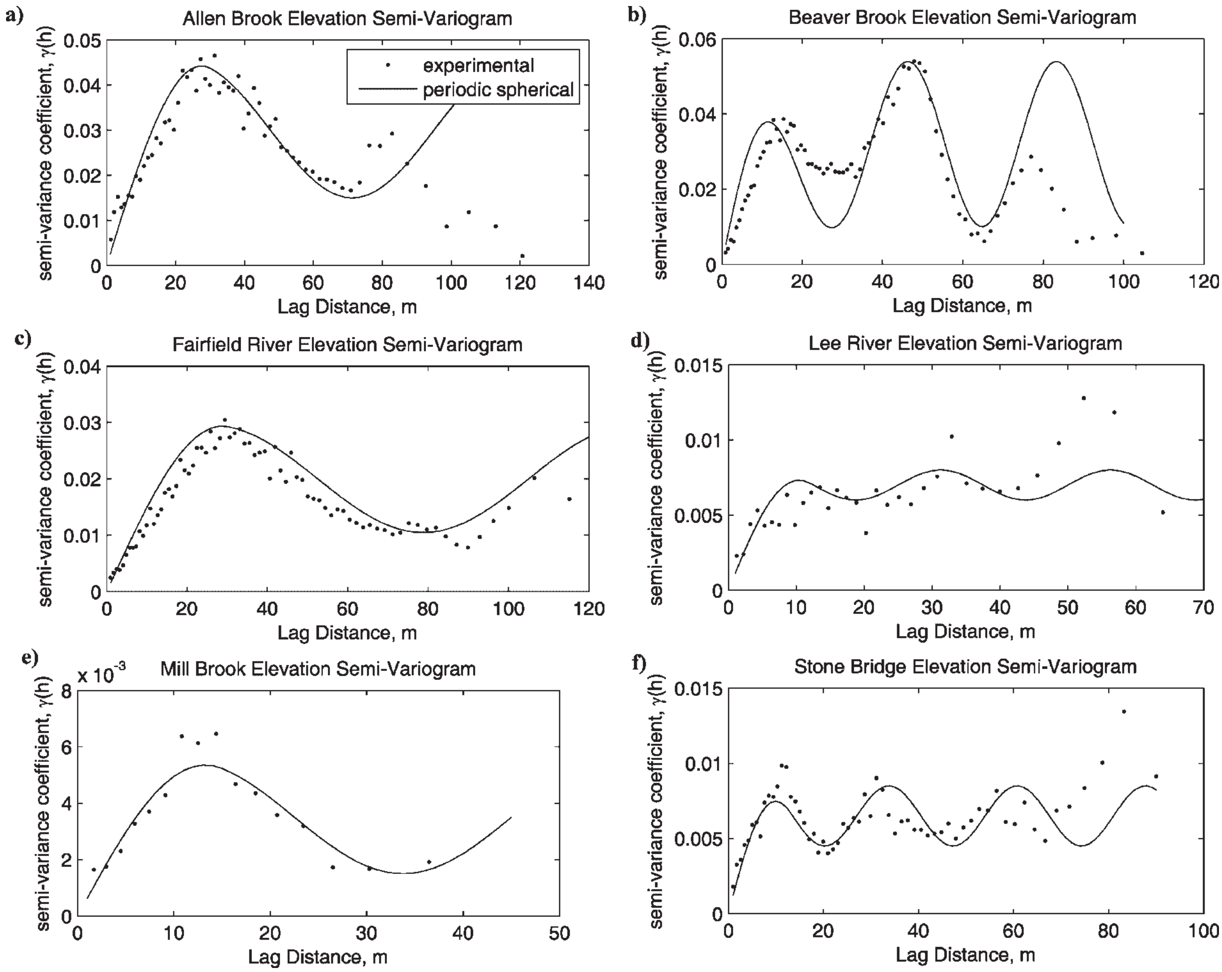

Figure 4. Semi-variograms fitted with periodic functions describing the bed elevation profile down the thalweg after being detrended by slope

between brown trout and white sucker numbers and WUA because very few of these fish were collected at our six sites (Table IV). However, the lack of relationship between WUA and brown trout may be significantly affected by fishing and stocking practices in Vermont.

SUMMARY AND DISCUSSION

Variations in the distribution of WUA were expected both between reaches and among the four species modelled. Differences in the magnitude of WUA between the spawn and adult life stages reflect preferences for different combinations of depth, velocity and substrate size. For streams with distinct patches of usable habitat, areas of high WUA tended to occur in riffles and/or pools. Riffles had high WUA for blacknose dace and common shiner, and pools had high WUA for brown trout and white sucker at the median flow examined. The observed distributions of patches associated with estimates of WUA are similar to the spatial information gathered in meso-scale assessments as described by Harper *et al*. (1992), Newson *et al*. (1998), Padmore (1998) and Parasiewicz (2001).

Allen Brook and Beaver Brook had the lowest numbers of blacknose dace. These two streams also had the lowest WUA at the reach scale and the most distinctly isolated patches of WUA at the sub-reach scale (thus 1st and 2nd patchiness rankings; Table IV). Blacknose dace are small fish that prefer moving water and swim readily, but don't

DOI: 10.1002/rra

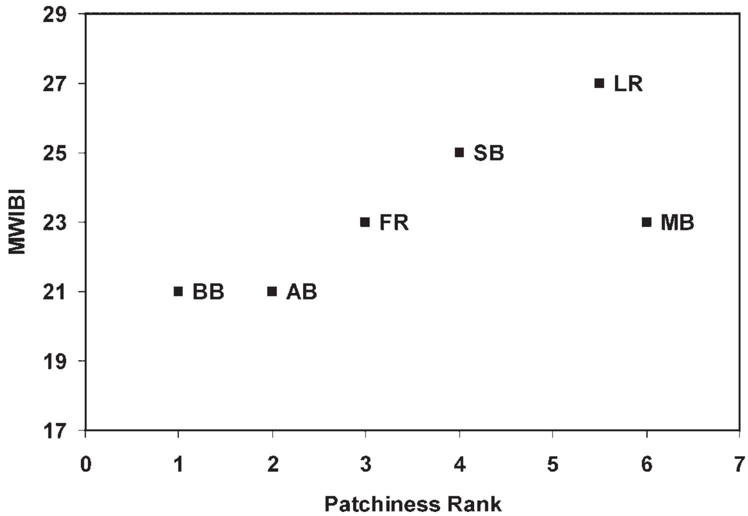

Figure 5. General positive relationship between MWIBI (Mixed Water Index of Biotic Integrity) and patch-ordered rank

like the quieter pool or shallow run sections that separated riffles in these two streams (Trial *et al*., 1983a; Larson *et al*., 2002; Nelson *et al*., 2003). The highest number of blacknose dace (Table IV) was found in Mill Brook, which had more uniform and continuous patches of riffle and run with moving water, in addition to one of the highest reach-scale WUA scores.

The reach-scale WUA scores for blacknose dace were significantly correlated with the number of fish counted in the field, but no statistically significant relationship was found between the reach-scale WUA scores for common shiner and the number of this fish counted in the field. Whereas blacknose dace have relatively simple requirements for moving water, common shiner need both riffles and pools, as well as adequate spacing between them; and this may not be captured in a simple reach-scale WUA.

None of the univariate HSI curves used in this study include the interaction between physical characteristics in the calculation of WUA. Recent research by Parasiewicz (2001) suggests that models that incorporate this interaction might provide significantly better predictions of usable habitat. We also argue that connectedness and the spatial variability of instream habitats are key characteristics that must be considered, at both the individual species and community level. The lack of correlation between our biodiversity and biotic integrity measures and reach-scale WUA may in part be because these spatial aspects were not included in these WUA scores. When we used the semi-variograms and analysis of spatial heterogeneity down the thalweg to calculate a hydraulic patchiness rank, we found that MWIBI was positively associated with this rank (Figure 5).

When streams are managed to provide healthy instream habitat, often one target species is chosen to represent the whole ecosystem. We found little support for the notion that habitat for one species can represent others, especially at the reach scale. Neither H' nor MWIBI was strongly associated with any of the reach-scale WUA scores for the four individual fish species. Only when we looked at the sub-reach scale and considered the spatial distribution of habitat, we were able to find general associations with biotic integrity. The techniques of geospatial analysis may offer great promise for linking habitat values and fish distribution in streams with varying hydraulic characteristics. Again, the general association between the MWIBI and patchiness ranking may reflect the fact that in these small, wadeable streams, habitat connectivity is extremely important for a variety of species.

CONCLUSIONS AND FUTURE WORK

An additional goal of this research was to investigate the relationships among reach-scale stream geomorphic condition (RGA score), reach-scale stream habitat condition (RHA score) and reach-scale in-stream hydraulic habitat availability and condition. We found that reach-scale WUA was generally not significantly correlated with

DOI: 10.1002/rra

RGA or RHA score. We did find a significant relationship between RGA and RHA, as did Sullivan *et al*. (2004). However, the lack of strong relationships between either RGA or RHA and reach-scale WUA suggest that these two groups of measures (RGA/RHA and WUA) are not quantifying the same habitat characteristics.

There are a number of inherent complications in quantifying variability within streams because of the hierarchy of scales and the non-linear nature of these systems. Directional anisotropy of variability within streams may reflect habitat characteristics important to different species. Several studies have shown that a one-dimensional approach does not consider the variation across the stream versus downstream (Stewardson and McMahon, 2002; Chappell *et al*., 2003; Rhoads *et al*., 2003). A closer look at the directional anisotropy of habitat parameters (i.e. across vs. longitudinally down the stream) could help capture differences in heterogeneity associated with the stream axis. An interesting approach would be to select a series of thresholds for WUA and re-explore the relationships between the threshold-averaged WUA scores and the various biotic measures. This threshold analysis could use indicator kriging coupled with multivariate statistics.

Neither simple physical habitat measures (i.e. velocity, depth, bed substrate) or analysis of the spatial distribution of physical habitat address the time scale over which geomorphic processes affect fish distribution. There is a tremendous need for studies that focus on both spatial and temporal heterogeneity within streams, and the processes that create this heterogeneity. To explain biotic integrity, a dataset that included the distribution of biota over space as well as time is necessary; but to our knowledge such datasets are almost completely lacking.

This study shows that physical and geomorphological characteristics affecting biotic communities are complex. It suggests that simple indices of physical habitat at the reach scale, such as semi-quantitative geomorphic and habitat assessment scores and modelled WUA, do not capture the scales of response of fish and that spatial distribution of habitats, size and their connectedness are also important. In fact, the distribution of usable habitats may be a determining factor for fish distribution. Additional research focused on multiple spatial scales, and exploring the sizes and connections between usable patches of stream channel habitat is urgently needed.

ACKNOWLEDGEMENTS

Funding for this project was provided by the National Center for Environmental (NCER) STAR Program, EPA, grant number R83059501-0, the U.S. Forest Service through the Northeastern States Research Cooperative and in part by a Graduate Research Assistantship from the Vermont NSF Experimental Program to Stimulate Competitive Research (EPSCoR).

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