AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. **19**: 147–156 (2009)
Published online 4 November 2008 in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/aqc.946

Mixed stream channel morphologies: implications for fish community diversity

CHRISTINA M. CIANFRANI[a,*], S. MAŽEIKA P. SULLIVAN[b], W. CULLY HESSION[c] and MARY C. WATZIN[d]
[a] *School of Natural Science, Hampshire College, 893 West Street, Amherst, MA 01002, USA*
[b] *School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, OH 43210, USA*
[c] *Biological Systems Engineering, Virginia Tech, 304 Seitz Hall, Blacksburg, VA 24061, USA*
[d] *Rubenstein School of Environment and Natural Resources, Aiken Center, University of Vermont, Burlington, VT 05405, USA*

ABSTRACT

1. Stream classification systems are widely used in stream management and restoration. Whereas the principal morphological types of these classification systems are increasingly recognized for their ecological connections, the roles of intermediate and mixed morphologies are still poorly understood, yet may be biologically significant.
2. Twenty-five stream reaches in north-western Vermont were classified by channel morphology to determine whether fish community diversity differed among pool-riffle, mixed (i.e. pool-riffle/cascade, pool-riffle/other) and forced pool-riffle stream morphological groups. Stream reach surveys included cross-sectional surveys, longitudinal profiles, bed substrate characterization, and fish surveys.
3. Three fish community diversity measures were calculated: (1) species richness (S); (2) Shannon–Weaver Index (H'); and (3) Simpson's Index ($1/D$). Multivariate analysis of covariance (MANCOVA) followed by analysis of variance (ANOVA) were used to explore potential differences in fish diversity among stream morphological groups. Fish diversity was significantly different for all three community diversity measures ($P \leqslant 0.05$), with pool-riffle/cascade morphology consistently exhibiting the greatest fish diversity and forced pool-riffle the lowest.
4. These results suggest that fish community diversity is significantly associated with distinct channel morphologies. Generally, pool-riffle/cascade and pool-riffle/other stream morphological groups supported habitats that fostered greater species diversity than more homogeneous and uniform pool-riffle reaches. The observed patterns of diversity are likely to be the result of habitat patches created by variations in flow and other physical characteristics in reaches of mixed morphologies.
5. These results support fish sampling schemes that incorporate morphological heterogeneity, such as proportional-distance designation. Sampling strategies that focus on homogeneous reaches may underestimate diversity, and misrepresent stream condition when fish community data are used in indices of biological integrity (IBIs). Reaches of mixed stream morphologies should be recognized as areas of biological importance in stream and catchment management and in conservation efforts.

Received 17 May 2007; Revised 3 December 2007; Accepted 8 December 2007

KEY WORDS: fish community diversity; mixed morphologies; pool-riffle; rivers/streams; stream classification

INTRODUCTION

Numerous stream classification schemes are used throughout the world to conceptualize stream structure and process, develop restoration strategies, and aid in the general management of streams and catchments (Kondolf, 1995; see reviews in Mosley, 1987 and Thorne, 1997). Many of these classification systems focus on aspects of fluvial geomorphology. Frissell *et al.* (1986) described a hierarchical

*Correspondence to: Christina M. Cianfrani, School of Natural Science, Hampshire College, 893 West Street, Amherst, MA 01002. E-mail: ccianfrani@hampshire.edu

system identifying key variables that determine the major characteristics of stream networks and catchments. Rosgen (1996) used key physical measurements (i.e. entrenchment ratio, width to depth ratio, dominant channel materials, slope, bed features, sinuosity, and meander width ratio) to classify stream reaches. Pegg and Pierce (2002) classified reaches of the Missouri River and the Lower Yellowstone River according to flow characteristics. Montgomery and Buffington (1997) developed a widely-used classification system for mountain drainage basins based on the differences in channel morphology correlated with stream slope and roughness resulting from variations in transport capacity and sediment supply.

While Montgomery and Buffington's (1997) classification system was designed for mountain drainage basins in the Pacific Northwest, it has been successfully applied in other areas in the USA (VTDEC, 2002; Whiting and King, 2003; Sullivan *et al*., 2006). Their system was designed to be process-based and applicable across regions of similar geography. Using diagnostic stream features identified in the field, Montgomery and Buffington (1997) identified seven major channel morphological types: colluvial; bedrock; cascade; step-pool; plane-bed; pool-riffle; and dune-ripple. Major diagnostic features included: bed material; bedform pattern; dominant roughness elements; dominant sediment sources; sediment storage elements; confinement; and pool spacing (Montgomery and Buffington, 1997). They recognized that these channel morphological types exist along a longitudinal gradient with intermediate morphologies acting as transitional zones between major channel types. The importance of the intermediate morphologies depends upon the application of the classification (Montgomery and Buffington, 1997). In addition, they identified 'forced' morphologies that are created by obstructions to flow (e.g. large woody debris), and identified forced pool-riffle and forced step-pool in mountain regions (Montgomery and Buffington, 1997).

The variety of geomorphic, hydraulic, and hydrological influences on stream channels creates a mosaic of habitat patches and transitional zones distributed across the riverscape (Copp, 1989; Amoros and Bornette, 2002; Ward *et al*., 2002). Ward and Wiens (2001) described three major patterns of connectivity in river systems: (1) longitudinal (e.g. headwaters–estuary); (2) lateral (e.g. channel–upland, upland–floodplain); and (3) vertical (e.g. aquifer–channel, soil). Along the longitudinal gradient of alluvial channels, Montgomery and Buffington (1997) identified a series of intermediate alluvial channel morphological types (i.e. riffle-bar, riffle-step, and cascade-pool) that share characteristics with the principal morphological types (i.e. cascade, step-pool, plane-bed, pool-riffle, dune-ripple), but that differ sufficiently to be atypical of the channel type as a whole.

Given the popularity and utility of stream classification systems in the management and conservation of streams and catchments (Kondolf, 1995; Rosgen, 1996; Brierley *et al*., 2002; Snelder and Biggs, 2002; McDonnell and Woods, 2004; Thomson *et al*., 2004), it is crucial that these systems are accurately used in representing biological as well as physical patterns (Chessman *et al*., 2006). To improve understanding of the relative contribution of distinct channel morphologies to stream fish diversity, this study explored the difference between fish community diversity of pool-riffle morphologies and reaches characterized by a heterogeneous mixture of morphologies using Montgomery and Buffington's (1997) classification system as the basis for assigning channel morphological types. Although Montgomery and Buffington's (1997) primary channel morphological types adequately capture principal morphologies along the drainage network, insufficient evidence exists to determine if these morphologies are as appropriate for fish communities. Because of the unique hybrid nature of the habitat of mixed morphologies, it is hypothesized that reaches with mixed morphologies would exhibit higher fish community diversity than pool-riffle channel types.

METHODS

Study area

Data were collected from 25 stream reaches located in 25 independent catchments within the Lake Champlain Basin in north-western Vermont (Figure 1). These catchments are typical of those found in temperate mixed-use glaciated regions, and ranged in size from approximately 4 km^2 to 510 km^2 with an average of about 100 km^2 (Table 1). The majority of the stream reaches were 3rd to 5th order (based on USGS 1:24,000-scale maps) with predominantly pool-riffle structure. Pool-riffle systems were chosen because they represent the dominant channel morphological type in catchments of the Lake Champlain Basin and have been identified as important habitat types for riverine fish diversity (Brussock *et al*., 1985). Adjacent riparian land use in the study reaches included forests, grassy meadows, pasture, and agricultural land with no active grazing. The Lake Champlain Basin is dominated by forest (64%) and agriculture (16%), with areas of open water (10%), wetlands (4%), and increasing urban areas (6%) (LCBP, 2004).

The Lake Champlain Basin in north-western Vermont comprises three major geological regions: the Champlain Lowland; the Vermont Piedmont; and the Green Mountains. During the last ice age, the Lake Champlain Basin underwent glaciation with ice covering the entire basin. Average annual precipitation in the basin is 850 mm, although higher elevations can receive as much as 1500 mm, and snowfall averages 1000 mm annually (Allen, 1974; Shanley and Denner, 1999). Precipitation is distributed fairly evenly throughout the year; however, during the winter months precipitation is stored in the snow pack and released during the spring snowmelt, generally generating the most significant hydrologic event of the year (Shanley and Denner, 1999).

Geomorphic assessment

Quantitative geomorphic assessments were completed for each of the 25 stream reaches in the summers of 2003 and 2004 following procedures outlined in Cianfrani *et al*. (2004) and Hession *et al*. (2003). The assessments included longitudinal and cross-sectional surveys, with reach lengths averaging 10 to 20 bankfull widths (Harrelson *et al*., 1994; Kondolf and Micheli, 1995; Montgomery, 1997). A Trimble (Sunnyvale, CA) Geoexplorer XT GPS unit was used to record the locations of the top and bottom of each reach, as well as rebar

DOI: 10.1002/aqc

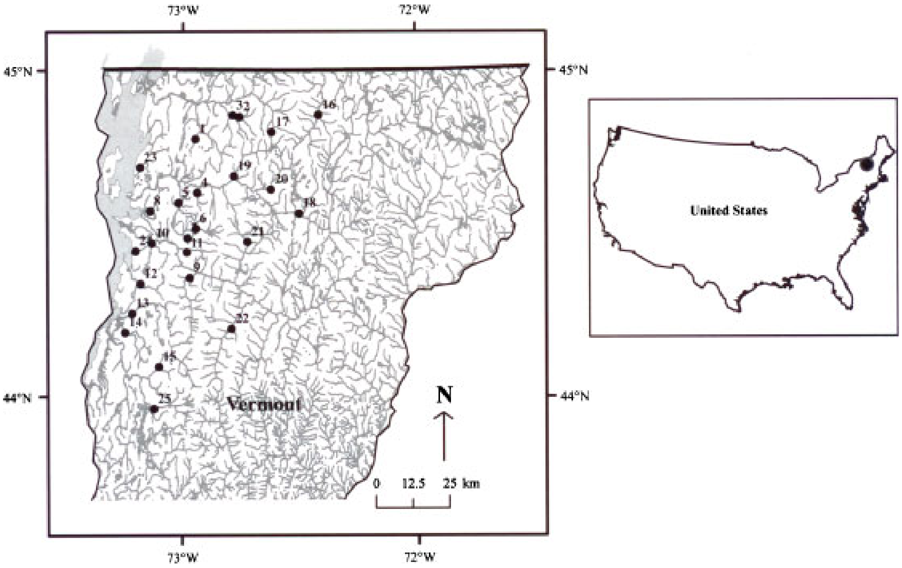

Figure 1. Location of stream reaches in the Lake Champlain Basin, Vermont.

markers at two permanent cross-sections. Wolman's (1954) pebble-count method was used to estimate median bed grain size for each reach. The number of large woody debris (LWD) pieces within the bankfull channel greater than 0.10 m diameter and 1.0 m length were counted (Montgomery *et al*., 1995).

Visual surveys of the stream reaches and surrounding riparian areas were completed to ensure collection of all parameters necessary to classify stream reaches according to Montgomery and Buffington's (1997) classification system. This included assessing dominant roughness elements, dominant sediment sources, sediment storage elements, and typical confinement characteristics.

Classification of stream reaches

Montgomery and Buffington's (1997) classification system predominantly categorizes channel morphologies into cascade, step-pool, plane-bed, pool-riffle, and dune-ripple, which generally progress in a downstream fashion. This general pattern of the progression of channel morphological types was also observed in Vermont, from the headwaters to the confluence with Lake Champlain (cascade to dune-ripple). However, local conditions often created channel morphological types that deviated from the expected longitudinal sequence (e.g. cascade downstream of pool-riffle). Types were always assigned based on the local diagnostic features within each stream reach. If more than one morphological type was present within a stream reach, all major channel types were listed. Modifications were made to Montgomery and Buffington's (1997) classification criteria to account for regional differences. Channel morphological types adapted from the original classification for use in Vermont streams are described below.

Cascade. Characteristics of these segments included tumbling flow, high relative slope (within the segment), large particle size, steep bedrock areas, slightly or moderately confined channel, and no obvious sediment storage elements. Most of the stream reaches were 3rd to 5th order streams, and lower in the catchment than typical for this channel type. Therefore, complete cascade reaches were not found within the project stream reaches. However, bedrock outcroppings and large boulder areas created cascade-type segments within the stream reaches, usually at the upper or lower ends of the defined reach.

Step-Pool. Characteristics for these segments included steeper relative local slope, steps formed by large clasts with pools below (steps may have spanned all or most of the channel), slightly confined channel, average width to depth ratios (for study stream reaches), and lower pool spacing. As with the cascade channel type, average reach slopes in the study streams were lower than typical (according to Montgomery and Buffington (1997)) for step-pool reaches (generally about 0.01 $m\,m^{-1}$).

Plane-Bed. These segments were typified by featureless, straight reaches with higher relative roughness than present in pool-riffle or dune-ripple. Typical substrate was gravel or cobble. Some stream segments were unconfined whereas others were confined. Slopes for this channel type were lower than those found by Montgomery and Buffington (1997). For the study stream reaches, plane-bed morphology was found at slopes as low as 0.0009 to 0.01 $m\,m^{-1}$.

Pool-Riffle. Pool-riffle channel types in this study were similar to those described by Montgomery and Buffington (1997). Stream reaches had slopes less than 0.01 $m\,m^{-1}$, alternating pool-riffle bedforms, active floodplains, and unconfined channels. Typical bed storage occurred in bars that alternated along the length of the channel. Dominant substrate was primarily coarse gravel. The main difference seen in the study stream reaches was the pool spacing. While Montgomery and Buffington (1997) have identified the standard distance to be 5–7 channel widths, our pool-riffle streams exhibited much closer pool spacing, often in the range of 2–5 channel widths.

Dune-Ripple. Segments characterized as dune-ripple had low slope, were often highly sinuous and had significant bank erosion contributing fine particles to the stream channel.

DOI: 10.1002/aqc

Table 1. Stream reach characteristics

Site #	Site name	Drainage area (km^2)[a]	Reach length (m)	Sinuosity (mm^{-1})	Bankfull width (m)	Bankfull cross-sectional area (m^2)	Bankfull width to depth ratio
1	Fairfield River	36.8	217	1.1	8.4	4.3	16.7
2	Tyler Branch	43.9	177	1.5	15.8	9.6	26.1
3	Bogue Brook	32.0	176	1.2	12.3	2.9	52.3
4	Beaver Brook	30.5	270	2.8	14.5	7.2	29.1
5	Rogers Brook	16.6	259	1.2	6.7	2.6	17.6
6	Browns River	52.8	275	1.1	19.8	7.1	54.8
7	Lee River	34.8	250	1.3	10.8	4.5	26.2
8	Malletts Creek	43.7	393	1.2	10.8	5.5	21.1
9	Huntington River	160.8	326	1.1	22.0	14.3	33.7
10	Allen Brook	27.9	211	2.0	6.6	3.7	11.9
11	Mill Brook	33.4	251	1.1	12.2	4.5	32.7
12	LaPlatte River	80.9	250	1.5	13.8	7.6	25.1
13	Lewis Creek	195.6	255	1.0	24.5	15.9	37.8
14	Little Otter Creek	148.2	313	1.3	17.1	7.4	39.8
15	New Haven River	219.5	324	1.2	20.9	13.7	31.9
16	Missisquoi River	173.6	340	1.5	25.8	10.5	63.4
17	South Branch	3.7	174	1.3	10.1	4.3	24.0
18	Lamoille River	509.2	548	1.1	35.2	24.2	51.1
19	North Branch Lamoille River	150.4	472	1.1	26.3	14.8	46.9
20	Gihon River	139.4	297	1.1	23.7	16.3	34.3
21	West Branch Waterbury River	58.7	349	1.2	14.6	8.8	24.1
22	Mad River	240.0	420	1.3	33.2	39.6	27.8
23	Stone Bridge Brook	22.7	174	1.4	7.8	3.4	18.1
24	Potash Brook	15.8	190	1.3	8.3	3.9	17.7
25	Middlebury River	121.4	377	1.5	23.9	11.9	47.9

[a] Upstream from bottom of study reach.

Dominant substrate type was sand and small gravel. Active bed transport was visible even at low flow.

After assigning a channel morphological type or types, each stream reach was assigned to one of four stream morphological groups: (1) pool-riffle; (2) pool-riffle/cascade; (3) pool-riffle/other; or (4) forced pool-riffle. Pool-riffle stream reaches were characterized along their entire length by typical pool-riffle structure, and stream segments both above and below the stream reach were also characterized as pool-riffle. Stream reaches of mixed morphologies (i.e. pool-riffle/cascade and pool-riffle/other) contained more than one recognizable channel morphological type throughout their length (Figure 2). Pool-riffle/cascade stream reaches often had a cascade segment at the upper end or above the top of the reach and/or at the lower end or below the reach. Pool-riffle/other stream reaches contained pool-riffle structure mixed with features typical of step-pool, plane-bed, or dune-ripple, again often at the upper or lower ends of the stream reaches. Forced pool-riffle stream reaches contained amounts of LWD significant enough to force pool-riffle structure throughout the stream reach in areas that otherwise would have exhibited different channel morphological types given their slope and sediment characteristics (Montgomery and Buffington, 1997).

Fish surveys

Fish were sampled at three to four locations with the number of sampling locations varying in proportion to reach length. Sampling locations were selected to represent the major flow habitats (e.g. pool, riffle, run) in order to reflect the flow composition of the entire reach (VTDEC, 2004). Samples were collected using a 1.22 m (4 ft) $\times$ 12.19 m (40 ft) bag seine with 3.175 mm (1/8 in) mesh, with a consistent collection effort ($\sim$15% of wetted area) at each reach (Sullivan *et al.*, 2006). Fish were sampled working downstream to upstream to prevent disturbing collection areas before sampling (Matthews and Hill, 1979). After seining each location (three or four collections per reach), 150 individual fish from each sampling location were haphazardly subsampled (450–600 total number of fish for each reach) and identified to species. Young-of-the-year were not included in the analysis.

Numerical and statistical analysis

Three common community diversity measures (Magurran, 1988) were used to compare fish diversity among the four stream morphological groups. Community measures included: (1) species richness (S) — the number of species; (2) Shannon-Weaver index (H') — a multifactor information index of community diversity incorporating both number of species and their evenness (Shannon and Weaver, 1963); and (3) Simpson's Index ($1/D$) — a multifactor dominance index differentially assigning weight to common species (Simpson, 1949). In all three indices, higher values represent greater diversity.

Multivariate analysis of covariance (MANCOVA) was used to test for differences among the four groups (pool-riffle, pool-riffle/cascade, pool-riffle/other, and forced pool-riffle) with group as the main effect. The covariate (drainage area) and the interaction effect (morphological group $\times$ drainage area) were used to ensure that there was no significant difference in the mean drainage area between groups, a factor that has been shown to strongly govern fish community diversity (Angermeier and Schlosser, 1989). Univariate analyses of variance (ANOVA) were then performed as *post hoc* tests of differences in fish community diversity among groups. Finally, Tukey–Kramer Honestly Significant Difference (HSD) (Tukey,

DOI: 10.1002/aqc

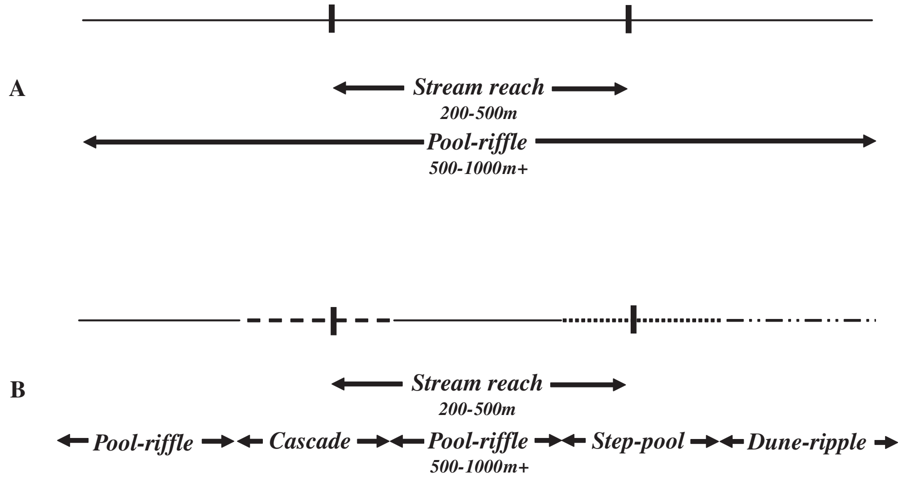

Figure 2. Uniform pool-riffle (A) and mixed stream morphological groups (B) as defined for stream reaches.

1953; Kramer, 1956) comparisons for all stream morphological groups for each fish community diversity measure were completed to test for differences between the individual stream morphological groups. All statistical analyses were performed using JMP 5.0.1.2 Statistical Discovery Software (SAS Institute, Inc., Cary, NC).

All data were tested to ensure that they met assumptions for both MANCOVA and ANOVA (Kuehl, 2000; Afifi *et al*., 2004). When necessary, square (x^2) and logarithmic transformations were used to normalize data (Afifi *et al*., 2004). All data were tested at the $\alpha = 0.05$ level.

RESULTS

Morphological classification

Based on the diagnostic features, a variety of channel morphological types were found across the stream reaches (Table 2). Eight stream reaches were classified as pool-riffle. The remaining 17 stream reaches exhibited characteristics of two or more distinct channel morphological types or forced morphologies, and were classified as: pool-riffle/cascade (six stream reaches); pool-riffle/other (six stream reaches); and forced pool-riffle (five stream reaches). For example, Mallets Creek (pool-riffle/cascade) exhibited typical pool-riffle morphology throughout the middle of the reach; however, a bedrock cascade was located at the upper end of the reach. The upper section of Allen Brook (pool-riffle/other) had pool-riffle morphology, but features more typical of a dune-ripple morphology dominated towards the downstream end of the reach.

Fish diversity

Fish community diversity varied across the sites (Table 3). Species richness (S) ranged from 1 to 16 ($\bar{X} = 8.12$, $SD = 3.42$), Shannon–Weaver (H') from 0 to 2 ($\bar{X} = 1.36$, $SD = 0.46$), and Simpson's ($1/D$) ranged from 1 to 5.60 ($\bar{X} = 3.22$, $SD = 1.14$). Across all three diversity measures, Stone Bridge Brook (pool-riffle/cascade) supported the highest community diversity and South Branch (forced pool-riffle) the lowest.

A significant difference was found in the fish community diversity indices among stream morphological groups (MANCOVA, $P = 0.01$, Table 4). Drainage area and the interaction of drainage area with group were not found to be significant covariates in the analysis. Subsequent ANOVA indicated that S and H' exhibited the greatest differences among morphological groups ($F = 12.50$, $F = 12.80$, respectively; Table 4).

For all measures of fish diversity, pool-riffle/cascade supported the highest level of fish diversity, followed by pool-riffle/other, pool-riffle, and forced pool-riffle. Tukey–Kramer HSD comparisons showed that S and H' exhibited the same pattern for comparisons for all pairs of stream morphological groups, while $1/D$ exhibited more overlap among groups (Table 5).

DISCUSSION

Stream classification schemes have proved useful for a variety of purposes across a wide range of geographical areas (Frissell *et al*., 1986; Rosgen, 1996; Montgomery and Buffington, 1997; Pegg and Pierce, 2002). However, because of the variability in local stream characteristics, these systems must be regionalized to fit local conditions and carefully chosen depending on the purpose and use of the classification system. Montgomery and Buffington's (1997) classification system, with some minor modifications, was found to be useful in classifying Vermont streams. The Vermont study stream reaches exhibited the same general morphological characteristics described for each channel type. However, this study showed that multiple channel morphological types were commonly found within a single stream reach, and that these channel types often combined characteristics of pool-riffle and those of other major channel types. These areas of morphological mixing are increasingly being recognized as important in classification systems with an ecological component or that are being used for ecological applications such as habitat restoration (Brussock *et al*., 1985; Ward and Tockner, 2001; Ward *et al*., 2002).

Heterogeneity in lateral, vertical, and longitudinal habitats has been shown to contribute significantly to the biodiversity of stream ecosystems (Gorman and Karr, 1978; Brussock

DOI: 10.1002/aqc

Table 2. Diagnostic features for classification of stream reaches

Site #	Slope (%)	Relative roughness[a]	d_{50} (mm)[b]	Dominant substrate type	Dominant sediment storage element	Floodplain development	Pool spacing (m)	Confinement	Bedform types	Group[c]
1	0.69	0.0059	36	Very Coarse Gravel	bars	yes	2.2	unconfined	pool-riffle	1
2	0.55	0.0047	53	Very Coarse Gravel	bars	yes	1.8	unconfined	pool-riffle	1
3	1.00	0.0004	50	Very Coarse Gravel	pools	limited	1.3	moderate	pool-riffle/cascade	2
4	0.93	0.0019	96	Medium Cobble	pockets, bars	yes	1.4	slight	bedrock/plane bed/pool-riffle	3
5	0.93	0.0029	36	Very Coarse Gravel	bars, bedrock, pockets	yes	5.7	unconfined	cascade/pool-riffle/cascade	2
6	0.59	0.0049	37	Very Coarse Gravel	bars	yes	2.6	unconfined	forced pool-riffle	4
7	1.10	0.0048	31	Coarse Gravel	bars, boulders	no	1.4	slight	forced pool-riffle	4
8	0.44	0.0037	26	Coarse Gravel	bars, bed	yes	4.9	unconfined	cascade/pool-riffle	2
9	0.44	0.0096	32	Coarse Gravel	boulder	no	1.9	moderate	plane bed/cascade	2
10	0.24	0.0200	11	Medium Gravel	bars, bed	yes	3.4	unconfined	pool-riffle/dune-ripple	3
11	0.97	0.0023	33	Very Coarse Gravel	bars	yes	1.4	unconfined	pool-riffle	1
12	0.25	0.0093	32	Coarse Gravel	bars, bed	yes	2.7	unconfined	pool-riffle/dune-ripple	3
13	0.49	0.0034	56	Very Coarse Gravel	boulder	limited	2.4	moderate	cascade/plane bed	2
14	0.10	0.0045	54	Very Coarse Gravel	bars, boulders	limited	4.2	moderate	pool-riffle/plane bed	3
15	0.26	0.0099	33	Very Coarse Gravel	bars	yes	3.3	unconfined	pool-riffle	1
16	0.22	0.0041	66	Small Cobble	bars	yes	2.5	unconfined	pool-riffle	1
17	1.40	0.0054	44	Very Coarse Gravel	pools, bars	yes	2.0	slight	forced pool-riffle	4
18	0.09	0.0076	53	Very Coarse Gravel	bars, bed	yes	7.7	unconfined	pool-riffle/dune-ripple	3
19	0.18	0.0115	31	Coarse Gravel	bars	yes	5.5	unconfined	pool-riffle	1
20	0.30	0.0091	39	Very Coarse Gravel	bars/bedrock	yes	3.4	slight	pool-riffle	1
21	1.40	0.0040	73	Cobble	bars	yes	3.9	unconfined	forced pool-riffle	4
22	0.21	0.0121	60	Very Coarse Gravel	bars, bed	yes	4.0	unconfined	pool-riffle	1
23	2.00	0.0031	66	Small Cobble	bedrock, boulders, bars	yes	1.5	slight	cascade/pool-riffle	2
24	1.10	0.0054	38	Very Coarse Gravel	LWD, pools, bars	yes	1.9	slight	forced pool-riffle	4
25	0.26	0.0050	53	Very Coarse Gravel	bars	yes	3.7	unconfined	pool-riffle/dune-ripple	3

[a]Mean depth/d.
[b]Median bed sediment diameter for stream reach (mm).
[c]Pool-riffle (1), Pool-riffle/cascade (2), Pool-riffle/other (3), Forced pool-riffle (4).

Table 3. Fish community diversity indices at each stream reach

Site #	Site name	Species richness (S)	Shannon-Weaver Index (H′)[a]	Simpson's Index (1/D)
1	Fairfield River	10	1.63	4.09
2	Tyler Branch	6	1.18	2.50
3	Bogue Brook	9	1.58	3.39
4	Beaver Brook	9	1.52	3.01
5	Rogers Brook	14	1.94	5.17
6	Browns River	4	0.77	1.73
7	Lee River	6	1.24	2.53
8	Malletts Creek	11	1.80	4.82
9	Huntington River	9	1.35	2.94
10	Allen Brook	8	1.60	3.91
11	Mill Brook	8	1.23	2.94
12	LaPlatte River	14	1.84	4.09
13	Lewis Creek	8	1.65	4.24
14	Little Otter Creek	8	1.66	4.34
15	New Haven River	7	1.46	3.61
16	Missisquoi River	7	1.44	3.17
17	South Branch	1	0.00	1.00
18	Lamoille River	10	1.59	3.20
19	North Branch Lamoille River	8	1.37	2.72
20	Gihon River	7	1.47	3.49
21	West Branch Waterbury River	4	0.97	2.31
22	Mad River	6	0.68	1.43
23	Stone Bridge Brook	16	2.04	5.60
24	Potash Brook	3	0.68	1.61
25	Middlebury River	10	1.37	2.72

[a] Square transformed in analysis.

Table 4. MANCOVA (Wilks' Lambda) test statistics for comparisons of fish community diversity indices for four stream morphological groups followed by univariate ANOVAs as post hoc tests of differences between morphological groups. Group refers to classification as pool-riffle (1), pool-riffle/cascade (2), pool-riffle/other (3), or forced pool-riffle (4).

Source of variation	*Wilks*' Lambda	*F*	NumDF[a]	DenDF[b]	*P*
Whole model	0.13	2.19	21.00	43.62	0.01
Group	0.31	2.52	9.00	36.66	0.02
Drainage area		21.05	3.00	15.00	0.78
Group × Drainage area	0.53	1.23	9.00	36.66	0.31

	df	Sum of Squares	Mean square	*F ratio*	*P*
Species richness					
Group	3	179.90	59.97	12.50	<0.0001
Group	21	100.74	4.80		
C. Total	24	280.64			
Shannon–Weaver Index[c]					
Group	3	17.03	5.68	12.80	<0.0001
Error	21	9.31	0.44		
C.Total	24	26.34			
Simpson's Index					
Group	3	18.44	6.15	9.49	0.0004
Error	21	13.60	0.66		
C. Total	24	32.04			

[a] Numerator Degrees of Freedom.
[b] Denominator Degrees of Freedom.
[c] Square transformed in analysis.

et al., 1985; Schiemer *et al*., 1995; Ward and Tockner, 2001; Ward and Wiens, 2001; Ward *et al*., 2002; Clark *et al*., 2007). The results from this study indicate that longitudinal heterogeneity in the form of reaches of mixed morphologies supports high levels of fish community diversity. Pool-riffle/cascade and pool-riffle/other stream morphological groups supported habitats that fostered greater species diversity than uniform pool-riffle reaches. Forced pool-riffle stream reaches exhibited the lowest species diversity.

All three diversity measures generated similar results. A significant difference was recorded in the number of species (*S*), a fundamental measure of community diversity. This pattern suggests that morphologies containing multiple channel morphological types support habitat suitable for a

DOI: 10.1002/aqc

Table 5. Tukey–Kramer HSD comparisons for all pairs of stream morphological groups for each fish community diversity index

Index/Group		Mean
Species richness		
Pool-riffle/cascade	A	11.2
Pool-riffle/other	AB	9.8
Pool-riffle	B	7.4
Forced pool-riffle	C	3.6
Shannon–Weaver Index		
Pool-riffle/cascade	A	3.0
Pool-riffle/other	AB	2.6
Pool-riffle	B	1.8
Forced pool-riffle	C	0.7
Simpson's Index		
Pool-riffle/cascade	A	4.4
Pool-riffle/other	AB	3.6
Pool-riffle	BC	3.0
Forced pool-riffle	C	1.8

Groups with same letter are not significantly different ($\alpha = 0.05$)

wider variety of species than uniform pool-riffle zones. Both Shannon–Weaver's and Simpson's values were higher in the pool-riffle/cascade and pool-riffle/other stream reaches, indicating that not only did these mixed morphologies support a greater number of species, but also that the number of each species was more evenly distributed than in the pool-riffle reaches. Species evenness is an important component in representing a healthy and resilient trophic structure and in reflecting ecological functioning and productivity (Wilsey and Potvin, 2000; Lyons and Schwartz, 2001; Magurran and Phillip, 2001).

The observed patterns of diversity are probably the result of habitat patches created by variations in flow and other physical characteristics in reaches of mixed morphologies. Pool-riffle reaches and reaches of mixed morphologies exhibited important differences in their morphological and hydraulic characteristics, and a number of these variables have been identified as important in determining the quality of fish habitat, including: water depth; current velocity; flow variability; substrate type and size; cover; roughness elements; confinement; and large woody debris (Poff and Allan, 1995; Dunham and Vinyard, 1997; Leftwich *et al.*, 1997; Montgomery and Buffington, 1997; Pitlick and Van Steeter, 1998; Flebbe, 1999; Inoue and Nunokawa, 2002). Pool-riffle channel types are associated with shallow, faster moving water alternating with deeper, slower moving pools. Generally, coarser particles exist in the riffles relative to the pools. The pool-riffle types contained repeating sets of these characteristics throughout the entire reach. Pool-riffle/cascade and pool-riffle/other morphologies contained a larger variety of characteristics because they were associated with more than one channel morphological type (e.g. slope changed more rapidly in these streams).

Inoue and Nunokawa (2002) found higher abundance of fish in stream reaches with a higher variety of sub-units. While the number or type of sub-units (e.g. patches) was not specifically identified in this study, by definition the pool-riffle/cascade and pool-riffle/other morphologies contained more sub-units than the pool-riffle or forced pool-riffle groups. The results indicate that the number of transitions (or sub-units) may influence the diversity of fish communities as well as their abundance.

Multiple reach selection strategies are used in sampling stream fish communities. Whereas fixed-distance (e.g. Ohio EPA, 1987; Massachusetts DEP, 1995) and representative reach approaches (Plafkin *et al.*, 1989; Meador *et al.*, 1993; USEPA, 1999; VTDEC, 2004) are commonly used, these methods may not capture the habitat and geomorphic variability inherent in the stream network (Williams *et al.*, 2004). Study designs that reduce variability by avoiding 'grey' (e.g. intermediate, transitional, ecotonal, etc.) zones may, in fact, exclude areas of high biological importance. These results support the use of proportional-distance designation (Harrelson *et al.*, 1994; Klemm and Lazorchak, 1995; Kondolf and Micheli, 1995), in which a standard number of stream channel widths is used to measure the stream study reach, and the likelihood of incorporating mixed morphologies is heightened.

Key indicators of community composition and ecosystem condition may be missed by only sampling homogeneous reaches. For example, Karr's (1981) index of biological integrity (IBI) — based on fish community characteristics (i.e. abundance, condition, and community composition), has been regionally modified and is used by many state and government agencies in stream monitoring and assessment protocols (e.g. VTDEC, 2004). The possibility of additional fish species and changes in density and age-class structure in reaches of mixed morphologies would alter IBI scores, with potentially significant ecological implications.

Therefore, if stream classification systems are to be used for ecological applications: (1) reaches of mixed morphologies must be recognized as important in maintaining stream fish diversity; and (2) a classification system must be used that is of sufficient resolution to identify sub-units within a stream reach in order to quantify the heterogeneity of the habitat. Finally, given their potential to support higher fish community diversity, these zones of morphological mixing should be recognized in stream or catchment management programmes as important areas for protection or restoration.

ACKNOWLEDGEMENTS

The research was supported in part by grants from the US Environmental Protection Agency STAR Grants program R 83059501-0, and the Vermont Experimental Program to Stimulate Competitive Research (VT EPSCoR) grant number EPS 0236976 Graduate Research Assistantship. We thank Andrea Pearce, Laura Allen, Jenn Gagnon, Tracy Owen, Jessica Clark, Chelsea Ransom, Elizabeth Royer, Brian Ellrott, and Eric Howe for their field assistance. The authors would also like to thank David Montgomery and Philip Boon for their helpful reviews of the manuscript.

REFERENCES

Afifi A, Clark VA, May S. 2004. *Computer-Aided Multivariate Analysis*, 4th edn. Chapman and Hall/CRC: New York.

Allen G. 1974. Soil Survey of Chittenden County, VT. United States Department of Agriculture, Soil Conservation Service, Washington, DC.

Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**: 761–776.

Angermeier PL, Schlosser IJ. 1989. Species-area relationships for stream fishes. *Ecology* **70**: 1450–1462.

Brierley G, Fryirs K, Outhet D, Massey C. 2002. Application of the river styles framework as a basis for river management in New South Wales, Australia. *Applied Geography* **22**: 91–122.

Brussock PP, Brown AV, Dixon JC. 1985. Channel form and stream ecosystem models. *Water Resources Bulletin* **21**: 859–866.

Chessman BC, Fryirs KA, Brierley GJ. 2006. Linking geomorphic character, behaviour and condition to fluvial biodiversity: implications for river management. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **16**: 267–288.

Cianfrani CM, Hession WC, Watzin MC. 2004. Evaluating aquatic habitat quality using channel morphology and watershed-scale modeling techniques. In *Critical Transitions in Water and Environmental Resources Management*, *Proceedings of the World Water and Environmental Resources Congress*, Sehlke G, Hayes DF, Stevens DK (eds). American Society of Civil Engineers: Reston, VA.

Clark JS, Rizzo DM, Watzin MC, Hession WC. 2008. Spatial distribution and geomorphic condition of fish habitat in streams: an analysis using hydraulic modeling and geostatistics. *River Research and Applications* **24**: 885–889.

Copp GH. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. *Environmental Biology of Fishes* **26**: 1–27.

Dunham JB, Vinyard GL. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. *Transactions of the American Fisheries Society* **126**: 323–329.

Flebbe PA. 1999. Trout use of woody debris and habitat in wine spring creek, North Carolina. *Forest Ecology and Management* **114**: 367–376.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* **10**: 199–214.

Gorman OT, Karr JR. 1978. Habitat structure and stream fish communities. *Ecology* **59**: 507–515.

Harrelson CC, Rawlins CL, Potyondy JP. 1994. Stream Channel Reference Sites; An Illustrated Guide to Field Technique. General Technical Report RM-245. US Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Hession WC, Pizzuto JE, Johnson TE, Horwitz RJ. 2003. Influence of bank vegetation on channel morphology in rural and urban watersheds. *Geology* **31**: 147–150.

Inoue M, Nunokawa M. 2002. Effects on longitudinal variations in stream habitat structure on fish abundance: an analysis based on subunit-scale habitat classification. *Freshwater Biology* **47**: 1594–1607.

Karr JR. 1981. Assessment of biotic integrity using fish communities. *Fisheries* **66**: 21–27.

Klemm DJ, Lazorchak JM. 1995. Environmental Monitoring and Assessment Program — Surface Waters: Field Operations and Methods for Measuring the Ecological Conditions of Wadeable Streams. EPA/620/R-94/004. Environmental Monitoring Systems Laboratory, Office of Research and Development, US Environmental Protection Agency, Cincinnati, OH.

Kondolf GM. 1995. Geomorphological stream channel classification in aquatic habitat restoration: uses and limitations. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **5**: 127–141.

Kondolf GM, Micheli ER. 1995. Evaluating stream restoration projects. *Environmental Management* **19**: 1–15.

Kramer CY. 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* **12**: 309–310.

Kuehl RO. 2000. Design of Experiments: Statistical Principles of Research Design and Analysis, 2nd edn. Brooks/Cole: Belmont, CA.

LCBP. 2004. Lake Champlain Basin Atlas: Land Use. Lake Champlain Basin Program, Grand Isle, VT. Retrieved 2005, from http://www.lcbp.org/Atlas/HTML/so_landuse.htm

Leftwich KN, Angermeier PL, Dolloff CA. 1997. Factors influencing behavior and transferability of habitat models for a benthic stream fish. *Transactions of the American Fisheries Society* **126**: 725–734.

Lyons KG, Schwartz MW. 2001. Rare species loss alters ecosystem function — invasion resistance. *Ecology Letters* **4**: 358–365.

Magurran AE. 1988. *Ecological Diversity and its Measurement*. Princeton University Press: Princeton, NJ.

Magurran AE, Phillip DA. 2001. Implications of species loss in freshwater fish assemblages. *Ecography* **24**: 645–650.

Massachusetts DEP. 1995. Massachusetts DEP Preliminary Biological Monitoring and Assessment Protocols for Wadable Rivers and Streams. Massachusetts Department of Environmental Protection, North Grafton, MA.

Matthews WJ, Hill LG. 1979. Influence of physico-chemical factors on habitat selection by red shiners, *Notropis lutrensis* (Pisces: Cyprinidae). *Copeia* **1979**: 70–81.

McDonnell JJ, Woods R. 2004. On the need for catchment classification. *Journal of Hydrology* **299**: 2–3.

Meador MR, Cuffney TE, Gurtz ME. 1993. Methods for Sampling Fish Communities as Part of the National Water-Quality Assessment Program. US Geological Survey OFR 93-104, Denver, CO.

Montgomery DR. 1997. River management: what's best on the banks? *Nature* **388**: 328–329.

Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* **109**: 596–611.

Montgomery DR, Buffington JM, Smith RD, Schmidt KM, Pess G. 1995. Pool spacing in forest channels. *Water Resources Research* **31**: 1097–1105.

Mosley MP. 1987. The classification and characterization of rivers. In *River Channels*, *Environment and Process*, Richards K (ed.). Basil Blackwell: Oxford; 295–320.

Ohio EPA. 1987. Biological Criteria for the Protection of Aquatic Life: Volumes I-III. Ohio Environmental Protection Agency: Columbus, OH.

Pegg MA, Pierce CL. 2002. Classification of reaches in the Missouri and Lower Yellowstone Rivers based on flow characteristics. *River Research and Applications* **18**: 31–42.

Pitlick J, Van Steeter MM. 1998. Geomorphology and endangered fish habitats of the Upper Colorado River 2. Linking sediment transport to habitat maintenance. *Water Resources Research* **34**: 303–316.

Plafkin JL, Barbour MT, Porter FD, Gross SK, Hughes RM. 1989. Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish. EPA 440-4-89-001. US Environmental Protection Agency, Washington, DC.

Poff NL, Allan JD. 1995. Functional-organization of stream fish assemblages in relation to hydrological variability. *Ecology* **76**: 606–627.

Rosgen DL. 1996. *Applied River Morphology*. Wildland Hydrology: Pagosa Springs, CO.

Schiemer F, Zalewski M, Thorpe JE. 1995. Land inland water ecotones — intermediate habitats critical for conservation and management. *Hydrobiologia* **303**: 259–264.

Shanley JB, Denner JC. 1999. The hydrology of the Lake Champlain Basin. In *Lake Champlain in Transition*: *from Research Toward Restoration*, Manley TO, Manley PL (eds). American Geophysical Union: Washington, DC; 41–66.

Shannon CE, Weaver W. 1963. *The Mathematical Theory of Communication*. University of Illinois Press: Urbana, IL.

Simpson EH. 1949. Measurement of diversity. *Nature* **163**: 688.

Snelder TH, Biggs BJF. 2002. Multiscale river environment classification for water resources management. *Journal of the American Water Resources Association* **38**: 1225–1239.

Sullivan SMP, Watzin MC, Hession WC. 2006. Influence of stream geomorphic condition on fish communities in Vermont, USA. *Freshwater Biology* **51**: 1811–1826.

Thomson JR, Taylor MP, Brierley GJ. 2004. Are river styles ecologically meaningful? A test of the ecological significance of a geomorphic river characterization scheme. *Aquatic Conservation*: *Marine and Freshwater Ecosystems* **14**: 25–48.

Thorne CR. 1997. Channel types and morphological classification. In *Applied Fluvial Geomorphology for River Engineering and Management*, Thorne, CR, Hey, RD, Newson, MD (eds). John Wiley: Chichester; 175–222.

Tukey JW. 1953. The problem of multiple comparisons. Unpublished report. Princeton University.

USEPA. 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish. EPA 841-B-99-002.US Environmental Protection Agency, Washington, DC.

VTDEC. 2002. *Stream Geomorphic Assessment Phase 2 Handbook*. *Rapid Stream Assessment — Field Protocols* (*draft*). Vermont Agency of Natural Resources, Department of Environmental Conservation: Waterbury, VT.

VTDEC. 2004. Biocriteria for Fish and Macroinvertebrate Assemblages in Vermont Wadeable Streams and Rivers — Development Phase. Vermont Agency of Natural Resources, Department of Environmental Conservation: Waterbury, VT.

Ward JV, Tockner K. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* **46**: 807–819.

Ward JV, Tockner K, Arscott DB, Claret C. 2002. Riverine landscape diversity. *Freshwater Biology* **47**: 517–539.

Ward JV, Wiens JA. 2001. Ecotones of riverine ecosystems: role and typology, spatio-temporal dynamics, and river regulation. *Ecohydrology and Hydrobiology* **1**: 25–36.

Whiting PJ, King JG. 2003. Surface particle sizes on armoured gravel streambeds: effects of supply and hydraulics. *Earth Surface Processes and Landforms* **28**: 1459–1471.

Williams LR, Warren ML, Adams SB, Arvai JL, Taylor CM. 2004. Basin visual estimation technique (BVET) and representative reach approaches to wadeable stream surveys: methodological limitations and future directions. *Fisheries* **29**: 12–22.

Wilsey BJ, Potvin C. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology* **81**: 887–892.

Wolman MG. 1954. A method of sampling coarse river-bed material. *Transactions — American Geophysical Union* **35**: 951–956.

DOI: 10.1002/aqc