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Fish use of ecohydraulic-based mesohabitat units in a low-gradient Illinois stream: implications for stream restoration

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ABSTRACT

1. A classification scheme for ecohydraulic-based mesohabitat units was developed for a summer low-flow period. Mesohabitat unit designations were based on the integration of three-dimensional channel hydraulics, geomorphic maintenance processes of bed morphology, and biological resource needs of fish. Ecological relevance of the units was evaluated by a study of fish mesohabitat use patterns, and species relationships to feeding guild. By portraying the stream as a mosaic of hydraulic habitat patches that provide specific biotic resource needs, this study's aim was to advance how ecological information may be incorporated into the stream restoration design process.

2. Nine mesohabitat units were designated, including pool-front, -mid, and -rear units, scour pool, simple and complex riffles, glide, submerged point bar, and channel expansion marginal deadwater. Physical habitat structure differed among the nine mesohabitat units by length, water depth, and bed slope and complexity. Fish were collected in specific unit volumes by use of prepositioned areal electrofishing devices, in which distinct patterns of fish mesohabitat use were observed.

3. A key finding was the differences in fish assemblages among the pool units, in which fish densities were greatest in the pool-front and scour pool units. Also, fish density in the pool-front unit was positively correlated with pool entrance slope. Biomass was greatest in the pool-front and -mid units, and it was correlated with maximum mid-pool depth. Density and biomass were generally lowest in the pool-rear unit. Other unique relationships were also observed among the mesohabitat units.

4. Based on feeding guild, patterns of fish mesohabitat use were observed for this summer low-flow period; insectivores dominantly used pool-front and scour pool units, herbivores dominantly used complex riffle units, and piscivores used pool-front and -mid units.

5. Useful ecological information was derived from fish species-habitat relationships observed in this study, linking mesohabitat units with species requirements for food resources. Such findings support advancements to ecological design strategies for stream restoration that promote hydraulic habitat diversity.

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INTRODUCTION

Stream habitat classification schemes are commonly used in aquatic resource inventories to assess habitat condition and ecological health (Barbour *et al*., 1999). Inventory data collected are used to compute a quality index value for a stream reach, which provides environmental regulatory authorities a means to manage water resources, locating streams with good habitat quality to be protected and streams with poor habitat quality to be restored (Raven *et al*., 1998). Although these assessment programmes are essential for aquatic resource conservation regionally, a critical need exists for habitat classification schemes to support restoration design within a local ecosystem framework (Rabeni and Sowa, 1996; Maddock, 1999; Palmer *et al*., 2005). An ecohydraulic-based habitat classification scheme provides such a framework; however, the scheme must be validated so that habitat–biota relationships provide useful information necessary for restoration (Thomson *et al*., 2001; Clarke *et al*., 2003; Clifford *et al*., 2006).

The habitat scale most relevant to stream restoration, and most studied geomorphologically and ecologically, is that of mesohabitats within a reach planform. The mesohabitat scale has been termed the 'pool-riffle' scale by Frissell *et al*. (1986), the channel geomorphic unit scale by Gregory *et al*. (1991), and the bar unit (pool-riffle-bar structure) by Frothingham *et al*. (2002). Fishery biologists typically classify mesohabitats as: backwaters, pools, riffles, glides, runs, chutes, rapids, cascades, and falls (Hawkins *et al*., 1993; Bain and Stevenson, 1999). More recently, mesohabitats were classified similarly to these units, but from an ecohydraulics perspective as physical biotopes incorporating hydraulic biotopes (Padmore, 1998; Wadeson and Rowntree, 1998). Hydraulic biotopes include a secondary set of flow-type classifications, which include: scarcely perceptible flow, smooth boundary turbulent, rippled surface, unbroken standing waves, broken standing waves, upwelling chute, and free falling (Newson *et al*., 1998). Physical biotopes can be differentiated by hydraulic metrics (e.g. shear velocity and Froude number) computed from velocity point measurements. However, a biological validation of patterns of fish use has not been correlated with the physical biotopes (Clifford *et al*., 2006).

Patterns of fish habitat use are generally observed among pool, riffle, glide, and run classifications (Bain *et al*., 1988; Aadland, 1993; Rabeni and Jacobson, 1993). In addition, habitat suitability criteria that relate fish species preferences to point measurements of velocity, depth, and substrate are commonly used in physical habitat simulation (PHABSIM) models to compute estimates of usable habitat area (Bovee *et al*., 1998). These preference criteria have been a useful 'ecohydraulics' tool correlating the likelihood of fish occurrence with local hydraulics. However, PHABSIM has been criticized for its reliance on hydraulic point measurements because studies show that fish use of habitat space is dependent on many abiotic and biotic factors, bounded and integrated more appropriately at a mesohabitat scale (Jackson *et al*., 2001; Parasiewicz, 2001; Rashleigh *et al*., 2005). An ecohydraulics view of the mesohabitat scale would therefore constitute 'patches' of hydraulic habitats with common three-dimensional flow patterns, more than local summaries of point measurements of velocity and depth.

Ecologically, hydraulic habitat patches also need to be defined by biota use as an expression of species traits and life histories as developed in the patch dynamic concept (Poff, 1997; Newson and Newson, 2000). Kemp *et al*. (1999) distinguished mesohabitat units classified by this idea as 'functional habitats', in which distinct patterns of aquatic biota use were correlated with hydraulic biotopes. The patch dynamics concept constructively supports this functional habitat idea because it recognizes that character and dimensions of hydraulic habitat patches change with flow stage and morphological complexity, and basic biological needs of biota change accordingly (Townsend *et al*., 1997). Application of this concept provides a better means to classify ecologically relevant mesohabitat units for stream restoration assessment and design, in which the use of such habitats by biota is linked to species requirements for survival at various life stages and at multiple flow stages (Newson *et al*., 1998; Schwartz, 2002). A classification of mesohabitat units that holistically integrates geomorphic, hydraulic, and ecological factors is essential for improving the ecological performance of restoration designs (Rabeni and Jacobson, 1993; Chessman *et al*., 2006).

Objectives of this research were: (1) to classify mesohabitat units in a low-gradient Illinois stream based on the integration of three-dimensional (3D) channel hydraulics, geomorphic maintenance processes of bed morphology, and biological resource needs of fish species; (2) to characterize patterns of fish use for the newly defined mesohabitat units during summer low-flow; and (3) to evaluate whether these mesohabitat units provide useful ecological information that can be applied to stream restoration design. In order to accomplish the biological objective, uniquely designed pre-positioned areal electrofishing devices (PAEDs) were used to immobilize and collect fish in specific mesohabitat unit volumes (Schwartz and Herricks, 2004).

METHODS

Study area

The study site was a third-order stream in the upper Embarras River basin, a 476-km^2 basin area located approximately

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15 km south of Urbana, Illinois, USA (Figure 1). Regionally, the Embarras River basin lies in a gently sloping landscape formed by Pleistocene glaciation, and primarily drains agricultural lands. Mechanized row-crop agriculture for corn and soybean production has been practised in the basin for more than 80 years. Within the 1-km study reach, a riparian zone of native and exotic grasses, approximately 150 m in width, lies between each stream bank and agricultural fields. The study reach was unique in this region of Illinois because its meandering channel planform remains unaltered. Upstream and downstream of the study reach, the channel had been straightened and maintained for drainage control.

Because the study reach had not been channelized, floodplain surfaces at multiple elevations have developed over a long fluvial geomorphic history, including concave bank benches and remnant channels. Bankfull width ranged between 6 and 8 m. Over the study reach the average bed slope was 0.00075. Bed substrates were comprised of pebble, sand, and silt. Flows for this stream range from $0.15\,m^3\,s^{-1}$ during summer dry periods to approximately $12\,m^3\,s^{-1}$ at near bankfull stage (Frothingham, 2000). During the study, Embarras River daily flows were continuously near normal stage, approximately equal to the 46-year median as reported by a US Geological Survey gauging station (Station No. 03343400; located 20 km downstream of the study site).

Study design

This study focused on an ecological analysis of fish habitat use during the summer low-flow stage only, although it was part of a larger project applying ecohydraulic habitat patch concepts at multiple flow stages and seasons (Schwartz, 2002; Schwartz and Herricks, 2005). The study was designed to test whether a newly developed mesohabitat classification scheme based on ecohydraulic concepts provided useful morphological and ecological information to support stream restoration design. Analysis of fish habitat use data was conducted by means of a spatial approach, in which fish were sampled in a brief 2-week, low-flow period uninterrupted by stormflows. This period constituted a common ecological season where fish are not migrating and are mostly engaged in feeding activities (Angermeier, 1982; Schlosser, 1985; Aadland, 1993). The basic study approach was as follows:

1. Develop an ecohydraulic-based mesohabitat classification scheme for the low-flow stage, and morphological criteria for use in field habitat surveys.
2. Delineate mesohabitat units in the study reach based on unit morphological criteria, and measure physical characteristics of length, width, depth, and bed slope for each unit delineated.

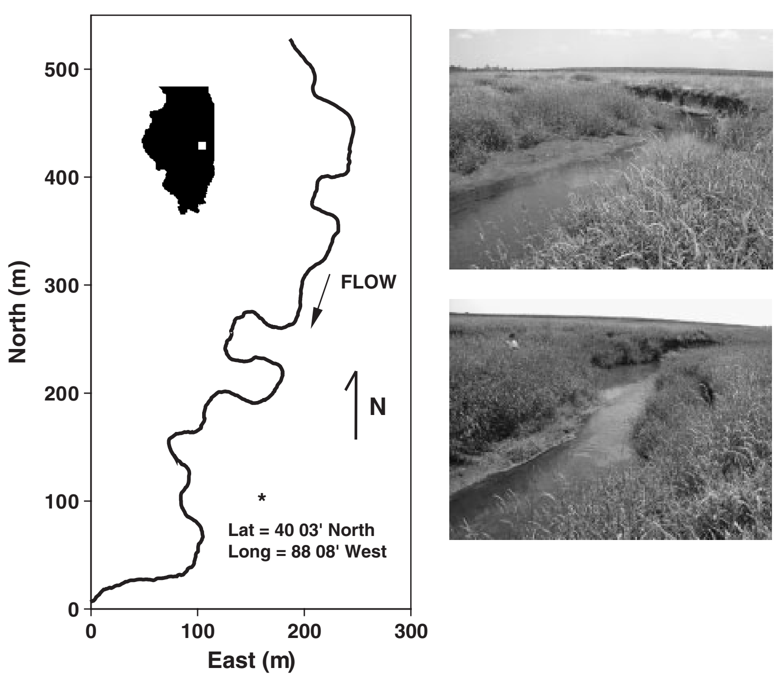

Figure 1. Study site on the upper Embarras River, Illinois, USA, with site photos.

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3. Collect fish in a selected subset of field-delineated mesohabitat units using PAEDs; enumerating species abundance and biomass per unit.
4. Analyse data for patterns of fish habitat use by statistical techniques, including classification and ordination.

Each of these study elements is described in detail below. Additional analyses included exploring data for relationships between physical habitat characteristics of mesohabitat units and fish use, and observing relationships between species occurrence in mesohabitat units and feeding guild. These additional analyses supported the study objectives, identifying potentially important information that could be used in the ecological design for stream restoration.

Ecohydraulic classification of mesohabitat units

An ecohydraulic-based classification scheme for mesohabitat units was developed based on current conceptual understandings of 3D channel hydraulics, biological resource needs of fish species found in low-gradient Illinois streams, and geomorphic maintenance processes of bed morphology. Previously developed mesohabitat classification schemes and descriptions of flow types for physical-hydraulic biotopes were used as a foundation when applicable (Padmore, 1998; Bain and Stevenson, 1999). Existing mesohabitat classifications use point measurements of downstream-oriented velocities, water depth, and bed substrate to distinguish mesohabitat units. This study differs from others in that unit types are conceived as 'patch volumes' with common geomorphic characteristics and 3D velocity patterns, and relative flow depths (Table 1).

Ecologically, development of the classification scheme incorporated the functional habitat idea, identifying the need to link flow types, physical habitat characteristics, and species requirements (Newson *et al.*, 1998). During summer low flow, fish habitat use dominantly relates to feeding position (Angermeier, 1982; Schlosser, 1987, 1988; Bain *et al.*, 1988). Therefore, this study hypothesized feeding strategy to be the

Table 1. Geomorphological and hydraulic characteristics of mesohabitat units in low-gradient streams

Habitat unit	Geomorphic characteristics	Water depth	Hydraulic characteristics
Formative geomorphic process: Erosion			
Pool-front	Entrance slope to a pool; downward-directed bed slope oriented with flow.	Moderately deep	Convective acceleration along entrance slope, and strong outward flow in meanders; relatively high turbulence.[1,7,8]
Pool-mid	Topographic low along stream bed; level bed.	Deep	Transition from convective acceleration to deceleration and strong secondary circulation; submergence of high-velocity core; relatively moderate turbulence.[1,7,8]
Pool-rear	Exit slope to a pool; upward-directed bed slope oriented with flow.	Moderately deep	Convective deceleration, and diminishing secondary circulation; relatively low turbulence.[1,7,8]
Local scour pool	Small area of topographic low in bed; length smaller than channel width.	Moderately deep	Local convective acceleration due to deflection and constriction of flow field.[2,5,6]
Formative geomorphic process: Deposition			
Glide	Intermediate bed topographic elevation; level and uniform bed.	Moderately shallow	Uniform downstream velocity vectors; minimal secondary circulation.[3,4,5]
Simple riffle	Topographic intermediate to high along stream bed; lateral bed diversity.	Moderately shallow	Downstream velocities accelerate from increasing bed slope, weak surface-divergent secondary circulation; relatively moderate turbulence.[1,5]
Complex riffle	Topographic high along stream bed; sinuous flow path through alluvium during low flow; diverse bed morphology with small depressions.	Very shallow interspersed with deeper 'pockets'	Downstream velocities accelerate from increasing bed slope, weak surface-divergent secondary circulation relatively moderate turbulence.[1,7,8]
Submerged point bar	Lateral topographic high adjacent to pool, and extending into riffle; can be alternate bar in straight channels.	Shallow	Low velocities due to shoaling and lateral deflection of flow by the point bar; possible flow separation adjacent to or in lee of the point bar.[1,7]
Channel expansion marginal deadwater	Intermediate topographic elevation laterally positioned behind instream or bank structural element; area in lee of obstruction.	Shallow	Separated, stagnant water or slightly recirculating flow in lee of obstacle.[2,3,4,6]

References: [1]Dietrich, 1987; [2]Schmidt *et al.*, 1993; [3]Padmore, 1998; [4]Wadeson and Rowntree, 1998; [5]Bain and Stevenson, 1999; [6]Thompson *et al.*, 1999; [7]Frothingham and Rhoads, 2003; and [8]Rodriguez, 2003.

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primary expression of fish biological needs. In support conceptually, fish species occupation of specific mesohabitats has been correlated with body morphology (body shape, and fin and mouth orientation) and habitat hydraulics (Bisson *et al*., 1988; Allan, 1995).

Within the study site, acoustic Doppler velocity (ADV) measurements and computational fluid dynamics modelling supported development of the mesohabitat classification scheme (Frothingham, 2000; Rodriguez, 2003). These hydraulic data supported mesohabitat characterization and were completed on approximately one-third of the study reach. The 3D flow patterns from Frothingham (2000) were consistent with those observed by others (Thompson, 1986; Dietrich, 1987; Rhoads *et al*., 2003). Conceptually, the key hydraulic principles used were: (1) distinct 3D flow patterns occur through pool-riffle sequences and bar units, generally described as helical flow (Dietrich, 1987; Frothingham and Rhoads, 2003); and (2) local flow acceleration–deceleration patterns are influenced by flow deflection from instream structural elements (Schmidt *et al*., 1993; Thompson *et al*., 1999).

Based on geomorphic maintenance processes of bed morphology, mesohabitat units were categorized into either erosional or depositional categories, referring to whether degradation or aggradation of bed sediments occurs during effective discharges (Table 1). Erosional units included a main channel pool subdivided into front, middle, and rear sections, and a local scour pool. During low flow distinct hydraulic patterns occur through the three sections of a main channel pool including flow acceleration and deceleration and formation of secondary circulation cells (Dietrich, 1987; Rodriguez *et al*., 2004). The scour pool is differentiated from the main channel pool in that the unit length is less than the channel width, and it is observed as local depressions in bed topography. Scour pool units are formed downstream or adjacent to a physical obstruction to the main channel flow, locally causing flow acceleration that erodes the bed sediment during flood flows. Physical obstruction includes bank failures consisting of large blocks of soil and bound grass roots, large woody debris and exposed tree root wads, and human-introduced debris.

Depositional units included glide, simple and complex riffles, submerged point bar, and channel expansion marginal deadwater (Table 1). The glide, simple riffle, and complex riffle are full channel units that represent a topographic high on the stream bed, whereas the submerged point bar and 'channel expansion marginal deadwater' constitute lateral channel units. Glides have uniform, moderately shallow water depths lacking a definite thalweg and any flow obstructions (Bain and Stevenson, 1999). Simple riffles have uneven cross-sections owing to lateral deposition of sediment with a channel thalweg occurring on the opposite side of the channel. They are short units equal to 1 to 2 channel unit widths with moderately shallow water depths. In contrast, complex riffles are distinct channel units with lengths in the order of 5 to 10 times the channel width and topographically higher than glides or simple riffles. During low flow a sinuous thalweg occurs through complex riffles, where non-wetted, exposed lateral gravel bars are sometimes vegetated with grass. Water depths are very shallow except for an occasional small, deep pocket of water within the thalweg, and small surface waves appear. Submerged point bars consist of lateral sediment deposits along the inner bank of meanders or alternative bars in straight channels (Knighton, 1998). The 'channel expansion marginal deadwater' unit occurs in channel locations behind bank failures, and areas where the channel abruptly expands orientated in the direction of flow. Rapid channel expansions commonly occur at floodplain sloughs and concave-bank bench locations (Howard, 1992; Schwartz and Herricks, 2005). As implied by its name, a deadwater area occurs in the lee of the structure, and the unit generally lies laterally adjacent to a scour pool formed by the obstruction.

Physical habitat surveys

As guided by the classification criteria in Table 1, a visual survey was conducted within the study reach, in which mesohabitat units were delineated and unit boundaries flagged (Bisson and Montgomery, 1996; Kaufmann *et al*., 1999). Within the 1.0-km study reach, 107 channel units were mapped in linearly sequenced order, and 138 units were mapped in total, including the laterally positioned units (submerged point bar and channel expansion marginal deadwater). With a total station, plan (x, y) coordinates and elevations (z) were obtained along the thalweg at 1-m intervals, bed slope breaks, and flagged unit boundaries, which provided the data to compute habitat unit lengths and bed slopes. With a survey tape or rod, wetted channel widths, and average and maximum water depths were measured at each unit, and unit lengths for scour pool, submerged point bar, and marginal deadwater units.

Habitat-specific fish collection

With PAEDs, fish were sampled at 70 units among the nine types of mesohabitat unit. A PAED includes an electrode pair placed in the stream with wires extending to the bank area that are connected to a 2.0-kW power source. PAEDs were placed in units so that the fish immobilization range covered the delineated unit volume. Schwartz and Herricks (2004) described in detail protocols for placing electrode pairs with different rod lengths in order to sample unit volumes varying in shape. Data on PAED placement were recorded for each sample and used to compute the sample area and volume. Data included electrode lengths, orientation (parallel or series) and distance between electrodes, and voltage output. Specific conductance was measured daily with a Chemtrix Type 700 meter (Chemtrix, Hillsboro, Oregon, USA) because it also affects the immobilization range.

Sampling continued daily for a 2-week sample period (23 July to 2 August 2001). Each day, six to eight electrode pairs were placed in the study reach far enough apart so that collection activity would not disturb an adjacent mesohabitat unit not yet sampled, typically a distance equivalent to 6–10 mesohabitat units. After placement of PAEDs, mesohabitat units were sampled starting downstream and working upstream ensuring that electrodes were left undisturbed several hours prior to activation. Once electrodes were activated, two to three netters entered the stream to capture immobilized fish from the mesohabitat unit. Collected fish were measured for standard length to the nearest mm, and weighed with an Ohaus CS2000 scale (Ohaus, Pine Brook, New Jersey, USA). Fish were released to their captured location, except for a few individuals retained for verifying species identification.

Data analysis

Physical habitat characteristics of mesohabitat units were summarized using basic descriptive statistics. Unit characteristics included length, width, average depth, maximum depth, and slope. A coefficient of variance (CV) was computed for depth measurements to characterize bed heterogeneity. Comparisons between habitat units for selected characteristics were completed by a two-sample independent *t*-test (SPSS v.14).

Fish data collected at each habitat unit were summarized by species into fish density (No./100 m^2), biomass ($g\,m^{-2}$), species richness by adult and young-of-the-year (YOY), and diversity (Shannon diversity index, H; Legendre and Legendre, 1998). Statistical comparisons between habitat units for selected biometrics used a two-sample independent *t*-test (SPSS v.14). In this study, YOY fish were designated as less than 1 g and 35 mm in total length for all families except Centrarchidae. Centrarchidae YOY were designated as less than 3 g and less than 45 mm in total length. In addition, for each species and adult/YOY age group, frequency of occurrence per habitat unit type was compiled, and arranged by feeding guild. Feeding guild designations were based on Smith (1979) and Barbour *et al*. (1999), and included herbivore, omnivore, insectivore, and piscivore. Pearson *r* linear correlations were calculated between maximum depth and bed slope characteristics of pool-type mesohabitat units (front, mid, rear, and scour), and total fish density and biomass (SPSS v.14).

Four statistical analyses were performed to evaluate whether distinct patterns of fish habitat use emerged among the nine different types of mesohabitat units as sampled by PAEDs. The four analyses were: (1) a two-way frequency table using the Pearson chi-square statistic, completed in a computer spreadsheet (Legendre and Legendre, 1998); (2) hierarchical agglomerative cluster analysis, Ward's method with Euclidean distance; (3) principal components analysis (PCA), distance-based bi-plots with Euclidean distances and correlation matrix used on species density, and densities pooled into feeding guild; and (4) canonical correspondence analysis (CCA) optimizing on mesohabitat units. PC-ORD v.5 was used to conduct the cluster analysis, PCA, and CCA (McCune and Mefford, 1999; McCune and Grace, 2002). Ordination objects were the mesohabitat units and attributes were fish unit abundances by species and adult/YOY, as densities per sampled area. In the CCA, habitat attributes included maximum water depth and bed slope.

RESULTS

Physical habitat structure

Pool-type units were distinguished by their physical characteristics of length, width, maximum depth, and by bed slope characteristics (Table 2). Pool-mid units were generally longer than the other pool units, averaging 8.3 m compared with 2.7–3.1 m for pool-front, -rear, and -scour units. Pool-mid units were generally deeper as would be expected, with pool-averaged depths equal to 0.43 m compared with the other pool units approximately equal to 0.3 m. Maximum depths for pool-mid units ranged from 0.46–1.07 m. Bed slope was the physical characteristic that distinctly differentiated the full channel pool units with the pool-front unit averaging 0.0702, the pool-rear unit averaging −0.0591, and the pool-mid unit nearly zero.

Glide units were distinguished by water depth characteristics (Table 2). Unit average depth was 0.25 m. Maximum depth was 0.32 m, differing from the average by only 0.07 m and implying a uniform bed structure. In addition, depth coefficient of variance (CV) was 0.15, a generally low value compared with more complex bed structure found in riffles with depth CVs above 0.27 ($P < 0.01$). Bed slopes ranged from −0.0018–0.0047, averaging 0.0005. Bed slopes for glides were similar to riffle-simple units, but tended to be positive rather than negative ($P = 0.40$).

Simple and complex riffles were distinguished by length, depth CV, and bed slope (Table 2). Riffle-simple units were much shorter than riffle-complex units, averaging 6.3 m compared with 21.3 m for complex riffles. Average water depths for simple riffles were only slightly greater than complex riffles, averaging 0.17 m and 0.14 m, respectively ($P = 0.04$). However, depth CV was significantly different between these

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Table 2. Physical characteristics of mesohabitat units from the July/August 2001 field survey, upper Embarras River, Illinois

Mesohabitat unit metric	Meoshabitat unit type								
	Pool-front	Pool-mid	Pool-rear	Pool-scour	Glide	Riffle-simple	Riffle-complex	Submerged point bar	Marginal deadwater
Unit length (m)									
Average	2.7	8.3	3.6	3.1	6.9	6.3	21.3	11.7	6.5
Minimum	1.0	3.2	1.2	1.6	3.9	4.3	13.2	10.3	1.9
Maximum	5.2	17.8	6.9	4.2	9.6	9.6	29.3	12.5	10.9
Unit width (m)									
Average	3.6	4.8	4.4	1.7	3.9	3.3	2.2	1.3	1.5
Minimum	2.3	2.7	3.1	1.2	2.7	1.9	1.7	1.0	1.3
Maximum	5.2	7.3	6.0	2.2	4.8	4.2	2.6	1.6	2.4
Average depth (m)									
Average	0.32	0.43	0.31	0.30	0.25	0.17	0.14	0.17	0.15
Minimum	0.22	0.30	0.23	0.25	0.17	0.12	0.10	0.11	0.12
Maximum	0.46	0.68	0.42	0.36	0.30	0.22	0.18	0.29	0.18
Average depth (CV)	0.16	0.17	0.15	0.27	0.15	0.27	0.43	0.32	0.15
Maximum depth (m)									
Average	0.51	0.64	0.52	0.43	0.32	0.24	0.20	0.21	0.23
Minimum	0.43	0.46	0.37	0.30	0.20	0.18	0.15	0.15	0.18
Maximum	0.82	1.07	0.91	0.58	0.46	0.30	0.23	0.27	0.34
Unit slope									
Average	0.0702	<0.00	−0.0591	—	0.0005	−0.0003	0.0030	—	—
Minimum	0.0307	<0.00	−0.0037	—	−0.0018	−0.0039	−0.0007	—	—
Maximum	0.1329	<0.00	−0.1253	—	0.0047	0.0036	0.0092	—	—
No. of sampled units	13	14	12	8	10	6	12	7	4

riffle units averaging 0.27 and 0.43, respectively, indicating a much more heterogeneous bed structure for complex riffles ($P<0.01$). Average bed slope for riffle-simple units of −0.0003 was significantly different from riffle-complex units of 0.0030 ($P=0.01$).

Lateral mesohabitats consisting of pool-scour, submerged point bar, and marginal deadwater units did not comprise the full channel width, typically averaging 2.2–4.8 m in length (Table 2). Average width for these units was less than 1.7 m. Bed slopes were not reported because they represented lateral units. Submerged point bar and marginal deadwater units were shallow, averaging less than 0.17 m.

Fish community structure

Fish density averages for the main channel pool units ranged from 73.6/100 m^2 to 147.0/100 m^2, while density averaged 218.6/100 m^2 for the scour pool unit (Table 3). Fish densities in pool-front units were significantly greater than those found in the pool-rear units ($P=0.072$); however, they were not significantly greater than those found in the pool-mid units ($P=0.665$). Fish densities in scour pool units were significantly greater than in pool-front, -mid, and rear units ($P=0.001$, 0.011, <0.001, respectively). Fish biomass averages among all the pool units ranged between 11.82 g m^{-2} and 48.83 g m^{-2}, and varied widely between 0.69 g m^{-2} and 190.86 g m^{-2}. Biomass in rear-pool units was significantly less than in the pool-front and -mid units ($P<0.001$, 0.036, respectively), but not significantly different from scour pool units ($P=0.281$). Biomass in front-pool units was significantly greater than in scour pool units ($P=0.009$). The presence of large fish greatly influenced these metrics. Larger fish species generally occupied pool-mid units as evidenced by the moderate average density and high average biomass observed. In contrast, smaller fish generally occupied pool-scour units as evidenced by high average density and low average biomass. Adult fish richness in the main channel pool units was between 20 and 23 species, greater than all other mesohabitat units. Fish diversity averages in the pool units ranged between 2.55 and 2.91.

Fish density averages in glide, riffle-simple, and riffle-complex units were 131.0/100 m^2, 99.9/100 m^2, and 236.3/100 m^2, respectively (Table 3). Fish densities in the glide units were significantly greater than in pool-rear units ($P=0.007$), significantly less than in scour pool units ($P=0.020$), and not significantly different from pool-front and -mid units ($P=0.146$, 0.568, respectively). However, biomass in glides was significantly less than in all pool-type units ($P<0.001$ pool-front, $P=0.005$ pool-mid, $P=0.046$ pool-rear, and $P=0.005$ scour pool). Fish densities in glide units were significantly less than found in riffle-complex units

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Table 3. Fish measurements per mesohabitat unit type, sampled in July/August 2001 on the upper Embarras River, Illinois. Young-of-the-year fish is indicated by YOY

Fish metric	Meoshabitat unit type								
	Pool-front	Pool-mid	Pool-rear	Pool-scour	Glide	Riffle-simple	Riffle-complex	Submerged point bar	Marginal deadwater
Density (no. per 100m^2)									
Average	147.0	91.9	73.6	218.6	131.0	99.9	236.3	4.9	33.5
Minimum	25.9	18.5	30.3	36.9	44.0	42.3	103.9	0.0	0.0
Maximum	272.7	188.4	153.3	807.7	317.5	250.0	504.2	11.4	85.7
Biomass (g m^{-2})									
Average	48.83	33.51	11.82	21.12	4.98	15.07	2.95	0.02	16.33
Minimum	2.02	1.38	0.69	1.05	0.50	0.20	0.34	0.00	0.00
Maximum	162.25	190.86	74.83	92.57	15.14	48.44	4.96	0.11	55.99
Species richness									
Adult fish	20	23	21	18	15	11	12	1	4
YOY fish	10	10	8	8	8	5	11	4	4
Diversity (H)									
Average	2.62	2.91	2.55	2.55	2.44	2.17	2.34	0.41	1.42
Minimum	1.78	2.04	1.91	1.97	1.61	1.24	1.22	0.00	0.00
Maximum	3.32	3.73	3.41	3.14	3.18	3.04	3.22	2.89	2.73
No. of sampled units	13	14	12	8	10	6	12	7	4

($P = 0.100$), but not significantly different from pool-simple units ($P = 0.223$). Fish densities in the riffle-complex units were significantly greater than found in the riffle-simple units ($P = 0.037$). However, biomass in the riffle-complex units was significantly less than in the riffle-simple units ($P < 0.001$). The riffle-complex unit had the greatest density/biomass ratio of all units with the highest average density of 236.3/100 m^2 and low biomass of 2.96 g m^{-2}, indicating that small fish generally occupied this unit. Fish diversity averages in glide and riffle units ranged from 2.17–2.44, slightly lower than diversities found among the pool units.

Fish densities, biomass, and diversities were generally lower in submerged bar and marginal deadwater units compared with all other mesohabitat units (Table 3). Fish densities in submerged point bar and marginal deadwater units were 4.9/100 m^2 and 33.5/100 m^2, respectively. Only small fish occupied point bar units as observed by a unit average biomass of 0.02 g m^{-2}, whereas an occasional large fish would occupy the deadwater unit as evidenced by the biomass range of 0.00–55.99 g m^{-2}. Adult and YOY fish richness did not exceed four species in these units, and was lower than all other mesohabitat units.

Fish habitat use

Fish assemblages per mesohabitat unit were significantly different based on a two-way frequency table analysis (df = 192; $\chi^2 = 225.3$; $P < 0.01$). Observations with expected frequency values less than 1 were not used (Legendre and Legendre, 1998). Dissimilarity of fish assemblages among mesohabitat units suggested that fish community structure was unique among units classified. Dissimilarities of fish assemblages among mesohabitat units were further explored with ordination statistics.

Mesohabitat units, as classified in this study, were organized distinctly by species abundance per habitat unit type, as observed by the cluster analysis dendrogram (Figure 2). The pool-front, scour pool, and glide units grouped with approximately 77% information remaining. The pool-front and scour pool units were dissimilar by approximately 55% information remaining from the pool-mid and pool-rear units, along with riffle-simple, submerged point bar, and marginal deadwater units. The pool-mid and pool-rear units were similar in fish community structure. Likewise, submerged point bar and marginal deadwater units were similar. Pool-mid and pool-rear units grouped separately from submerged point bar and marginal deadwater units with approximately 95% information remaining, and riffle-simple grouped separately among these units with approximately 87% information remaining. The riffle-complex unit was uniquely separated from all other units. In ordination space, the Euclidean distances among mesohabitat units (objects) in the PCA bi-plot organized similarly to the object partitioning observed by the hierarchical agglomerative clusters (Figures 2 and 3). A dominance of species oriented among eigenvectors for the pool-front, pool-mid, scour pool, and riffle complex units (Figure 3).

Mesohabitat units primarily aligned along the depth axis as observed by a CCA consisting of a habitat–species matrix and a second matrix of physical habitat attributes unit maximum depth and bed slope (Figure 4). Pool-front

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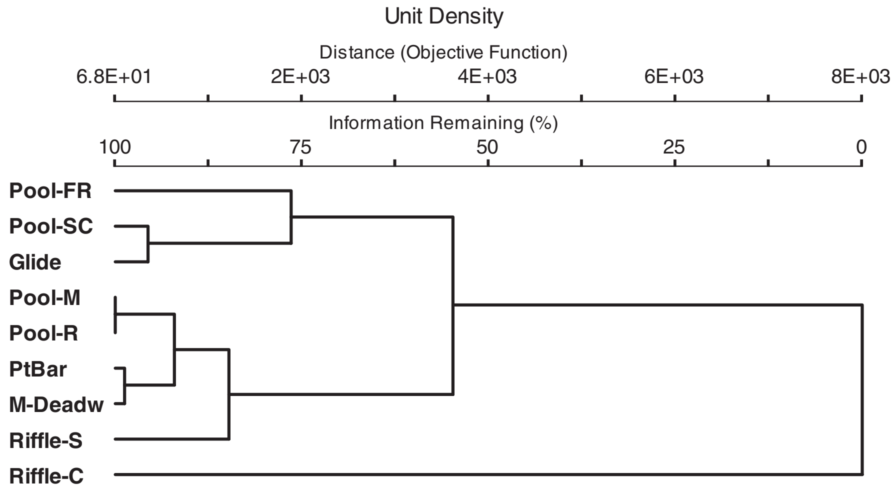

Figure 2. Hierarchical cluster analysis of mesohabitat units based on species density per mesohabitat unit.

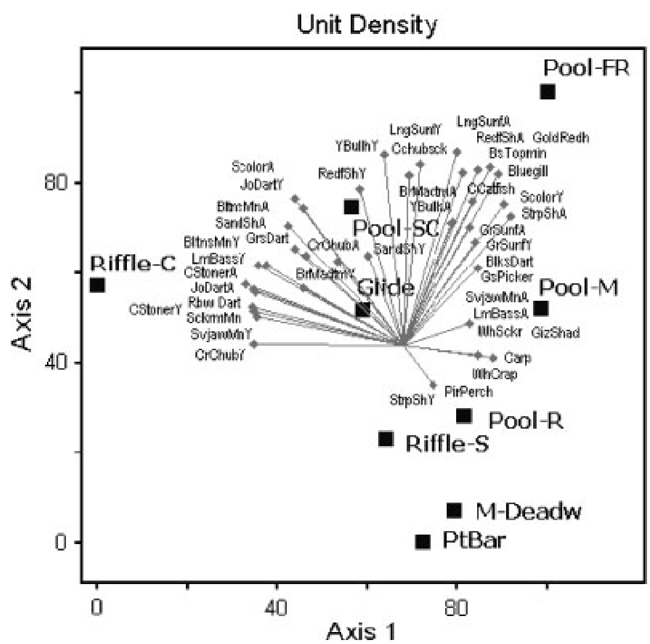

Figure 3. Principal components analysis of mesohabitat units based on species abundance per unit. Species codes are in Appendix A. PCA axes 1 and 2 explained 54.5% of the variance.

and pool-rear units also aligned with a slope axis. Unit fish densities significantly correlated with unit bed slope ($P = 0.06$, 0.04, respectively), but not with unit fish biomass (Table 4). However, fish biomass significantly correlated with unit maximum depths ($P = 0.09$).

Fish community structure was analysed by feeding guild, in which herbivores and insectivores were found more commonly compared with omnivores and piscivores (Figure 5). Herbivores mainly consisted of YOY and the central stoneroller. Herbivores commonly occurred in the

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riffle-complex unit, and in general were found in varying frequencies among all units. In addition, herbivore density oriented along the eigenvector for the riffle complex unit (Figure 6). As shown in Figure 5, large omnivores such as the carp and white sucker occurred mostly in the pool-mid unit, and the only small omnivore, the bluntnose minnow, occupied pool, glide, and riffle units. Omnivores appeared to be resource generalists as expected; however, group densities oriented along the scour pool unit eigenvector, as observed in Figure 6. Insectivores were found in all main channel units, and their use of different units was species-specific (Figure 5). Insectivores were frequently found in pool-front units and dominated by centrarchid species and several other species, including redfin shiner, blackside topminnow, golden redhorse, channel catfish, adult brindled madtom, yellow bullhead, and adult striped shiner (Figure 3). Several insectivore species also oriented along the riffle-complex unit eigenvector including: central stoneroller, suckermouth minnow, greenside darter, adult johnny darter, YOY largemouth bass, and other YOY. As observed in Figure 6, insectivores oriented among the pool-front and scour pool unit eigenvectors. Piscivores were found in pool units, where the largemouth bass was found more frequently in mid pool units, and they oriented along the pool-front and -mid unit eigenvectors (Figures 5 and 6). Glide units weakly oriented with any particular species assemblage, and pool-rear, riffle-simple, submerged bar, and marginal deadwater units were poorly oriented by any particular species assemblage (Figures 3 and 6).

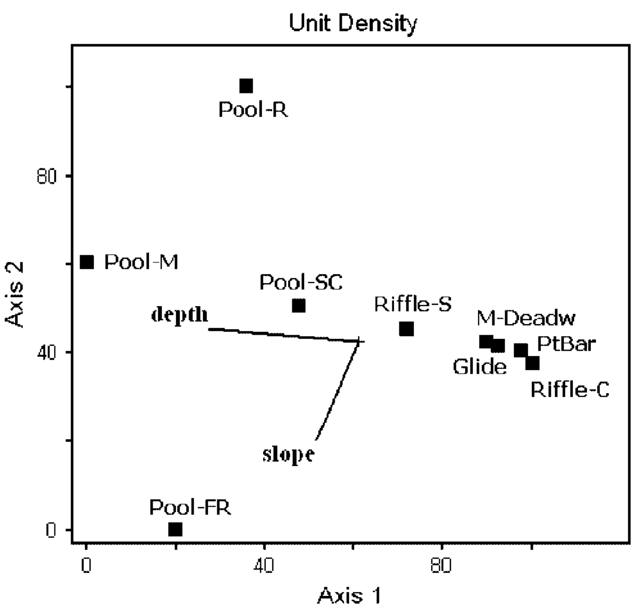

Figure 4. Canonical correspondence analysis of mesohabitat units based on species abundance per unit with environmental factors maximum depth and bed slope.

DISCUSSION

Distinct patterns of fish use were observed within mesohabitat units classified by this study's ecohydraulic-based classification scheme. This scheme viewed each mesohabitat unit type as a hydraulic habitat patch with unique 3D flow structures and geomorphic characteristics. Most importantly, fish community structure among the mesohabitat units could be distinguished by feeding guild (Figure 6). This suggests that during the summer low-flow period when feeding is a dominant activity for fish survival, species occupied the mesohabitats with flow and geomorphic environments conducive to food gathering. Others similarly found fish habitat use organized by dietary needs, but compared pool and riffle units only (Angermeier, 1982; Schlosser, 1985, 1987; Aadland, 1993). Because this study's mesohabitat units were linked to a basic biological need, these units can be considered as 'functional habitats' for summer low-flow. Functional habitats were defined as ecologically relevant habitat units, in which patterns of biota use are related to species requirements (Newson *et al.*, 1998; Kemp

Table 4. Statistical correlations between physical habitat characteristics (maximum depth and slope) and unit fish density (no. per $100m^2$) and biomass (g m^{-2}) for pool-type units on the upper Embarras River, Illinois

Mesohabitat unit	Fish density		Fish biomass		No. of sampled units
	Max. depth	Slope	Max. depth	Slope	
Pool-front	0.09 (0.37)	0.42 (0.06)*	0.41 (0.06)*	0.18 (0.26)	13
Pool-mid	−0.09 (0.38)	—	0.38 (0.09)	—	14
Pool-rear	−0.30 (0.18)	−0.54 (0.04)*	0.36 (0.13)	−0.04 (0.46)	12
Pool-scour	0.33 (0.18)	—	−0.02 (0.49)	—	8

Pearson *r* values reported, with statistical significance in parentheses (*P*).
*Indicates a significance level less than 0.1.

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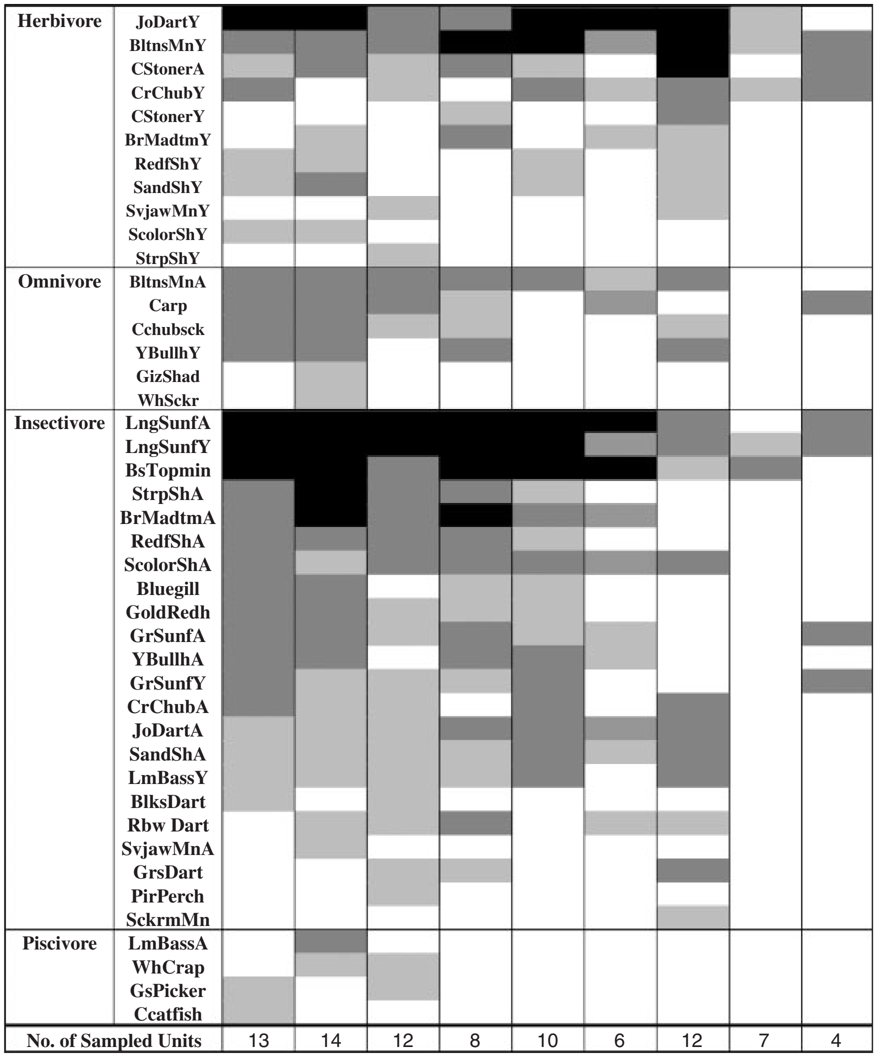

Figure 5. Fish species use of mesohabitat units organized by feeding guild, in which use is shown by percentage occurrence per unit type. Percentages shown as: white 0%, light grey 1–20%; dark grey 20–60%, black >60%. Species codes are in Appendix A.

et al., 1999). Use of PAEDs to collect fish undisturbed by samplers in specific unit volumes played a key role in linking flow patches with fish occupancy (Schwartz and Herricks, 2004).

Patterns of fish use among the different pool units (i.e. pool-front, -mid, and -rear, and scour pool units) were most noteworthy. Fish densities were generally greater in the pool-front and scour pool units compared with the pool-mid and -rear units. Based on fish density, insectivores occupied pool-front and scour pool units dominantly (Figure 6). It can be suggested from this study that these two units provide key feeding locations, where food items are more readily available to insectivores, perhaps controlled by the hydraulics at pool entrance slope. Several studies indirectly suggest that the pool entrance is a principal fish feeding location (Litvak and Hansell, 1990; Tyler and Clapp, 1995). Because fish density was significantly correlated with bed slope of pool-front units, this suggests that steeper pool entrance slopes that form strong downward-directed currents followed by decelerating flow may concentrate food items. Large adult insectivores, omnivores, and piscivores occupied pool-mid units. While, insectivores typically feed near submerged vegetated bank areas, and

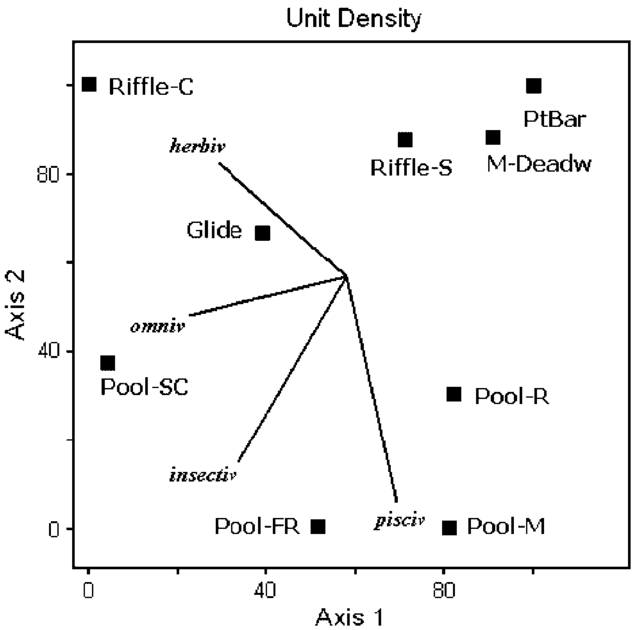

Figure 6. Principal components analysis of mesohabitat units based on species abundance per unit pooled into feeding guild groups consisting of herbivores, omnivores, insectivores, and piscivores. PCA axes 1 and 2 explained 85.1% of the variance.

capture terrestrial insects that drop in the open water (i.e. longear sunfish, green sunfish, striped shiner), omnivores bottom feed (i.e. carp, white sucker, brindled madtom), and piscivores (i.e. largemouth bass, white crappie) seek prey in open waters (Smith, 1979; Schlosser, 1982, 1987; Aadland, 1993). Because the maximum depth for pool-mid units was significantly correlated with fish biomass in this study, this suggests that depth and relatively low velocities provide the preferred habitat patch for large fish. In the pool-rear unit, fish density and biomass were lower than found in pool-front and -mid units. It may be that food items are less abundant or less accessable in this mesohabitat unit, or flow conditions are not optimal for fish to position themselves in advantageous feeding locations.

Fish assemblages were distinctly different in complex riffle units compared with all other mesohabitat units. This unit contained the highest overall density of fish, and while it was dominated by herbivores, insectivores were also abundant. Shallow waters support primary production, providing food resources for herbivores, while interspersed deeper water pockets and gravel substrates provide ideal feeding locations for insectivores. As found in other studies, fish assemblages in complex riffles included YOY (i.e. bluntnose minnow, creek chub, redfin shiner), darters (i.e. greenside darter, rainbow darter), stonerollers, and sand shiners (Aadland, 1993, Vadas and Orth, 2000). Ecologically, complex riffles are important because during low flow they prevent predator migration and provide safe areas for YOY and other small fish (Schlosser, 1987; Schaefer, 2001). It can be suggested that simple riffles with greater water depths and shorter lengths, which are comparatively lower in fish density, do not provide the food or protection from predation. Likewise, submerged point bar and marginal deadwater units were least occupied among all the nine units, and it follows that they may also be poor in food resources and susceptible to predation.

This study portrays the stream as a mosaic of hydraulic habitat patches supporting specific biotic resource needs, and provides a basis by which ecological information may be incorporated into the stream restoration design process. Although this study focuses on the summer low-flow period, it was part of a larger study of species–habitat relationships and patch concepts at multiple flow stages and seasons (Schwartz, 2002), and it illustrates how useful ecological information can be obtained through sampling and analysis of ecohydraulic data. For example, these ideas were successfully applied to restoration of an urban Illinois stream (Wade *et al.*, 2002; Schwartz and Herricks, 2007). In general, the ecological information derived from this study can be integrated with physical-hydraulic protocols and applied to stream restoration design as follows:

1. Entrance slope to a main channel pool should direct flow downward along the bed, to provide feeding positions for insectivores.
2. Depth in the main channel pool should be deep, relative to other stream locations, to provide feeding positions for insectivores, bottom-feeding omnivores, and piscivores.
3. Scour pools provide feeding positions for insectivores, and typically occur next to instream structural elements that deflect flows.
4. Complex-riffles should be shallow with relatively deep pockets interspaced along the thalweg, which provide feeding positions for herbivores, some insectivores, and YOY fish.
5. Each fish species showed a distinctive pattern of mesohabitat unit occupancy (Figure 5), illustrating variability in unit use and expression of biological needs, and the need for hydraulic habitat diversity.

Future research coordinating PAED samples with detailed 3D hydraulic measurements by an ADV would further strengthen relationships of fish use of hydraulic habitat patches. In addition, research on how juxtaposition of mesohabitat units influences reach-scale fish community structure would also provide important ecological information for stream restoration design. This mesohabitat classification scheme provides the ecohydraulic framework to underpin such research.

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REFERENCES

Aadland LP. 1993. Stream habitat types: their assemblages and relationship to flow. *North American Journal of Fisheries Management* **13**: 790–806.

Allan JD. 1995. *Stream Ecology, Structure and Function of Running Waters*. Chapman & Hall: London.

Angermeier PL. 1982. Resource seasonality and fish diets in an Illinois stream. *Environmental Biology of Fishes* **7**: 251–264.

Bain MB, Finn JT, Brooke HE. 1988. Streamflow regulations and fish community structure. *Ecology* **69**: 382–392.

Bain MB, Stevenson NJ. 1999. *Aquatic Habitat Assessment, Common Methods*. American Fisheries Society: Bethesda, ML.

Barbour MT, Gerritsen J, Synder BD, Stribling JB. 1999. *Rapid Bioassessment Protocols for Use in Wadable Streams and Rivers: Periphyton, Benthic Macroinvertebrates, and Fish*. EPA 841-B-99-002. US Environmental Protection Agency: Washington, DC.

Bisson PA, Montgomery DR. 1996. Valley segments, stream reaches, and channel units. In *Methods in Stream Ecology*, Hauer RF, Lambert GA (eds). Academic Press: San Diego, CA; 23–42.

Bisson PA, Sullivan K, Nielsen JL. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society* **117**: 262–273.

Bovee KD, Lamb BL, Bartholow JM, Stalnaker CB, Taylor J, Henroksen J. 1998. Stream habitat analysis using the instream flow incremental methodology. US Geological Survey, Biological Resources Division Information and Technology Report. USGS/BRD-1998-0004.

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

Clarke SJ, Bruce-Burgess L, Wharton G. 2003. Linking form and function: towards an ecohydromorphic approach to sustainable river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **13**: 439–450.

Clifford NJ, Harmar OP, Harvey G, Petts GE. 2006. Physical habitat, ecohydraulics and river design: a review and re-evaluation of some popular concepts and methods. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**: 389–408.

Dietrich WE. 1987. Mechanics of flow and sediment transport in river bends. In *River Channel Environment and Process*, Richards K (ed.). Blackwell Press: Oxford; 179–227.

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.

Frothingham KM. 2000. Function follows form: relating riverine aquatic habitat to three-dimensional flow and geomorphological form. PhD dissertation, University of Illinois at Champaign-Urbana.

Frothingham KM, Rhoads BL. 2003. Three-dimensional flow structure and channel change in an asymmetrical compound meander loop, Embarras River, Illinois. *Earth Surface Processes & Landforms* **28**: 625–644.

Frothingham KM, Rhoads BL, Herricks EE. 2002. A multiscale conceptual framework for integrated eco-geomorphological research to support stream naturalization in the agricultural Midwest. *Environmental Management* **29**: 16–23.

Gregory SV, Swanson FJ, McKee WA, Cummins KW. 1991. An ecosystem perspective of riparian zones. *BioScience* **41**: 540–551.

Hawkins CP, Kershner JL, Bisson PA, Bryant MD, Decker LM, Gregory SV, McCullough DA, Overton CK, Reeves GH, Steedman RJ, Young MK. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* **18**: 3–12.

Howard AD. 1992. Modeling channel migration and floodplain sedimentation in meandering streams. In *Lowland Floodplain Rivers: Geomorphological Perspectives*, Carling PA, Petts GE (eds). John Wiley: Chichester; 1–41.

Jackson DA, Peres-Neto PR, Olden JD. 2001. What controls who is where in freshwater fish communities — the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 157–170.

Kaufmann PR, Levine P, Robinson EG, Seeliger C, Peck DV. 1999. *Quantifying Physical Habitat in Wadable Streams*. EPA/620/R-99/003. US Environmental Protection Agency, Office of Research and Development: Washington, DC.

Kemp JL, Harper DM, Cross-Giuseppe A. 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 159–178.

Knighton D. 1998. *Fluvial Forms and Processes*. Edward Arnold: London.

Legendre P, Legendre L. 1998. *Numerical Ecology*. Elsevier.

Litvak MK, Hansell RIC. 1990. Investigation of food habit and niche relationships in a cyprinid community. *Canadian Journal of Zoology* **68**: 1873–1897.

Maddock I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* **41**: 373–391.

McCune B, Grace JB. 2002. *Analysis of Ecological Communities*. MjM Software Design: Gleneden Beach, Oregon, USA.

DOI: 10.1002/aqc

McCune B, Mefford MJ. 1999. *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Gleneden Beach, Oregon, USA.

Newson MD, Harper DM, Padmore CL, Kemp JK, Vogel B. 1998. A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 431–446.

Newson MD, Newson CL. 2000. Geomorphology, ecology and river channel habitat: mesoscale approaches to basin-scale challenges. *Progress in Physical Geography* **24**: 195–217.

Padmore CL. 1998. The role of physical biotopes in determining the conservation status and flow requirements of British rivers. *Aquatic Ecosystem Health and Management* **1**: 25–35.

Palmer MA, Bernhardt ES, Allan JD, Lake PS, Alexander G, Brooks S, Carr J, Clayton S, Dahm CN, Follstad Shah J *et al*. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* **42**: 208–217.

Parasiewicz P. 2001. MesoHABSIM: a concept for application of instream flow models in river restoration. *Fisheries* **26**: 6–13.

Poff NL. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**: 391–409.

Rabeni CF, Jacobson JB. 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. *Freshwater Biology* **29**: 211–220.

Rabeni CF, Sowa SP. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. *Canadian Journal of Fisheries and Aquatic Sciences* **53**(Suppl. 1): 252–259.

Rashleigh B, Parmar R, Johnston JM, Barber MC. 2005. Predictive habitat models for the occurrence of stream fishes in the Mid-Atlantic Highlands. *North American Journal of Fisheries Management* **25**: 1353–1366.

Raven PJ, Boon PJ, Dawson FH, Ferguson AJD. 1998. Towards an integrated approach to classifying and evaluating rivers in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 383–393.

Rhoads BL, Schwartz JS, Porter S. 2003. Stream geomorphology, bank vegetation, and three-dimensional habitat hydraulics for fish in Midwestern agricultural streams. *Water Resources Research* **39**: 1218–1230. DOI: 10.1029/2003WR002294.

Rodríguez JF. 2003. Mean flow and turbulence characteristics of pool-riffle structures in low-gradient streams. PhD dissertation, University of Illinois at Urbana-Champaign.

Rodriguez JF, Bombardelli FA, Garcia MH, Frothingham KM, Rhoads BL, Abad JD. 2004. High-resolution numerical simulation of flow through a highly sinuous river reach. *Water Resources Management* **18**: 177–199.

Schaefer J. 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum*, and *Cyprinella venusta*). *Freshwater Biology* **46**: 379–388.

Schlosser IJ. 1982. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* **52**: 395–414.

Schlosser IJ. 1985. Flow regime, juvenile abundance, and the assemblage structure on stream fishes. *Ecology* **66**: 1484–1490.

Schlosser IJ. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* **68**: 651–659.

Schlosser IJ. 1988. Predation rates and the behavioral response of adult Brassy Minnows (*Hybognathus hankinsoni*) to Creek Chub and Smallmouth Bass predators. *Copeia* 691–697.

Schmidt JC, Rubin DM, Ikeda H. 1993. Flume simulation of recirculating flow and sedimentation. *Water Resources Research* **29**: 2925–2939.

Schwartz JS. 2002. Stream habitat characterized by stage-specific flows and three-dimensional geomorphological complexity: development of ecological criteria for stream restoration design. PhD dissertation, University of Illinois at Urbana-Champaign.

Schwartz JS, Herricks EE. 2004. Use of prepositioned areal electrofishing devices with rod electrodes in small streams. *North American Journal of Fisheries Management* **24**: 1320–1330.

Schwartz JS, Herricks EE. 2005. Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1540–1552.

Schwartz JS, Herricks EE. 2007. Evaluation of pool-riffle naturalization structures on habitat complexity and the fish community in an urban Illinois stream. *River Research and Applications* **23**: 451–466.

Smith PW. 1979. *The Fishes of Illinois*. University of Illinois Press: Urbana.

Thompson A. 1986. Secondary flows and the pool-riffle unit: a case study of the processes of meander development. *Earth Surface Processes and Landforms* **11**: 631–641.

Thompson DM, Wohl EE, Jarrett RD. 1999. Velocity reversals and sediment sorting in pools and riffles controlled by channel constrictions. *Geomorphology* **27**: 229–241.

Thomson JR, Taylor MP, Fryirs KA, Brierley GJ. 2001. A geomorphological framework for river characterization and habitat assessment. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 373–389.

Townsend CR, Doledec S, Scarbrook MR. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology* **37**: 367– 387.

Tyler JA, Clapp DP. 1995. Perceptual constraints on stream fish habitat selection: effects of food availability and water velocity. *Ecology of Freshwater Fish* **4**: 9–16.

Vadas RL, Orth DJ. 2000. Habitat use of fish communities in a Virginia stream system. *Environmental Biology of Fishes* **59**: 253–269.

Wade RJ, Rhoads BL, Rodriguez J, Newell M, Wilson D, Herricks EE, Bombardelli F, Garcia, M, Schwartz JS. 2002. Integrating science and technology to support stream naturalization near Chicago, Illinois. *Journal of the American Water Resources Association* **38**: 931–944.

Wadeson RA, Rowntree KM. 1998. Application of the hydraulic biotope concept to the classification of instream habitats. *Aquatic Ecosystem Health and Management* **1**: 143–157.

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APPENDIX A — FISH SPECIES LIST AND ORDINATION CODES

Ordination code	Fish common name	Fish species name
BlksDart	Blackside darter	*Percina maculata*
BsTopmin	Blackstripe topminnow	*Funduus notatus*
BltnsMnA; BltnsMnY;	Bluntnose minnow; adult, YOY	*Pimephales notatus*
BrMadtmA; BrMadtmY	Brindled madtom; adult, YOY	*Noturus miurus*
Bluegill	Bluegill	*Lepomis macrochirus*
CStonerA; CStonerY	Central stoneroller; adult, YOY	*Campostoma pullum*
Ccatfish	Channel catfish	*Ictalurus punctatus*
Carp	Common carp	*Cyprinus carpio*
CrChubA; CrChubY	Creek chub; adult, YOY	*Semotilus atromaculatus*
Cchubsck	Creekchub sucker	*Erimyzon oblongus*
GoldRedh	Golden redhorse	*Moxostoma erthrurum*
GrsDart	Greenside darter	*Etheostoma blennioides*
GrPicker	Grass pickerel	*Esox americanus*
GrSunfA; GrSunfY	Green sunfish; adult, YOY	*Lepomis cyanellus*
GizShad	Gizzard shad	*Dorosoma cepedianum*
JoDartA; JoDartY	Johnny darter	*Etheostoma nigrum*
LmBassA; LmBassY	Largemouth bass	*Micropterus salmoides*
LngSunfA; LngSunfY	Longear sunfish; adult, YOY	*Lepomis megalotis*
PirPerch	Pirate perch	*Aphredoderus sayanus*
RbwDart	Rainbow darter	*Etheostoma caeruleum*
RedfShA; RedfShY	Redfin shiner; adult, YOY	*Lythrurus umbratilis*
SandShA; SandShY	Sand shiner; adult, YOY	*Notropis ludibundus*
SvjawMnA; SvjawMnY	Silverjaw minnow; adult, YOY	*Notropis buccata*
ScolorA; ScolorY	Steelcolor shiner	*Cyprinella whippi*
StrpShA; StrpShY	Striped shiner; adult, YOY	*Luxilus chrysocephalus*
SckrmMn	Suckermouth minnow	*Phenacobius mirabilis*
WhCrap	White crappie	*Promoxis annularis*
WhSckr	White sucker	*Catostomus commersonnii*
YBullhA; YBullhY	Yellow bullhead; adult, YOY	*Ameirurs natalis*

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