

Are River Styles ecologically meaningful? A test of the ecological significance of a geomorphic river characterization scheme

JAMES R. THOMSON*, MARK P. TAYLOR and GARY J. BRIERLEY

Department of Physical Geography, Macquarie University, North Ryde, Australia

ABSTRACT

1. Classification is a useful tool for researchers and managers wishing to group functionally similar sites or to identify unique or threatened habitats. A process-based river classification scheme that successfully integrates physical and biological aspects of lotic form and function would enhance conservation and restoration efforts by allowing more meaningful comparisons among sites, and improving functional understanding of lotic ecosystems.

2. The River Styles framework provides a geomorphological river characterization scheme in which assemblages of geomorphic units vary for differing River Styles, presenting differing arrays of aquatic habitat diversity for each style.

3. The ecological significance of the River Styles framework is tested by comparing the macroinvertebrate assemblages and habitat characteristics of pool and run geomorphic units for three different River Styles on the north coast of New South Wales, Australia.

4. Multivariate ordinations and analysis of similarity (ANOSIM) revealed that macroinvertebrate community structure differed between Bedrock-Controlled Discontinuous Floodplain rivers and Gorge rivers, and between Bedrock-Controlled Discontinuous Floodplain and Meandering Gravel Bed rivers, especially in pools. Differences between Gorge and Meandering Gravel Bed rivers were less apparent, largely due to variations within the Meandering Gravel Bed rivers group.

5. The variability in macroinvertebrate assemblage structure among geomorphic units was most strongly related to variability in substrate and hydraulic variables. Substrate composition differed significantly among all River Styles and geomorphic units, but other habitat variables showed few consistent differences among River Style groups.

6. These results suggest that the ecological similarity of macroinvertebrate communities within River Styles may presently be limited because some important large-scale drivers of local habitat conditions are not included in River Styles designations. Integrating River Styles classification with other large-scale variables reflecting stream size, temperature and hydrological regime may produce a process-based physical classification capable of identifying river reaches with similar ecological structure and function.

Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: physical habitat; habitat assessment; geomorphology; River Styles; river health; macroinvertebrates

*Correspondence to: J.R. Thomson, School of Biological Sciences, Monash University, Victoria 3800, Australia.

INTRODUCTION

Natural river systems exhibit an enormous variety of physical and biological forms and processes. Managers and researchers need to be able to order this variability so that they can prioritize conservation efforts, and be confident about extrapolating research or management outcomes to functionally similar systems. While both physical and biological criteria have been used to classify lotic systems (see Montgomery and Buffington (1998) and Naiman (1998) for reviews), successful integration of these related aspects into a single, process-based framework that encompasses a range of spatio-temporal scales remains a considerable challenge. A meaningful 'bio-physical' classification scheme would aid in prioritizing conservation and restoration efforts, improve selection of comparable sampling sites for ecological research and monitoring, allow identification of appropriate reference conditions for biological and physical assessments and restoration projects, and improve predictions about the effects of management actions and land-use changes through reference to their effects in functionally similar systems (Frissell *et al.*, 1986; Newson *et al.*, 1998; Bain *et al.*, 1999).

Because the structure and dynamics of physical habitat are believed to set the template on which biological organisms evolve and communities are organized (Southwood, 1977, 1988; Townsend and Hildrew, 1994), physical (or geomorphic) frameworks are generally considered the logical basis for developing classifications that are both physically and ecologically meaningful (Frissell *et al.*, 1986; Jowett, 1993; Padmore, 1998; Maddock, 1999; Newson and Newson, 2000). In particular, nested hierarchical models, in which habitat features at a given spatio-temporal scale are nested within the context of larger-scale, longer-term factors that ultimately constrain their behaviour, have received much attention (Frissell *et al.*, 1986; Naiman *et al.*, 1992; Hawkins *et al.*, 1993; Newbury and Gaboury, 1993). The ecological relevance of such physical classification schemes has rarely been tested explicitly, however.

For any geomorphologically based classification scheme to be useful in ecological applications, it must be ecologically meaningful. At the very minimum, this means that the relationships between geomorphic structures, functional habitats (*sensu* Harper *et al.*, 1992) and biotic communities must be understood. Ideally, biotic communities within geomorphic classes would be relatively distinct and exhibit similar dynamics. While this is unlikely to be the case across a wide range of geomorphic features and scales, hierarchical schemes do provide an opportunity to find spatial scales that are both ecologically and physically important, and to link these to physical processes operating at multiple scales. The physical and biological similarity of physical units (e.g. mesohabitats) may be enhanced by nesting them within the context of larger scale, constraining physical classes. The goal of this study was to examine the ecological significance of River Styles, a geomorphological characterization scheme, by comparing the similarity of macroinvertebrate communities within and among geomorphic classes.

River Styles and its potential for integrating geomorphology and ecology

The River Styles framework is a hierarchical procedure for geomorphic river characterization whereby reach-scale processes are explained within a catchment context (Brierley and Fryirs, 2000). Catchment conditions dictate the type of landscape units (i.e. topography) that in turn control the range of River Styles formed along river courses. The primary controls on the variability in river character and behaviour are induced by the valley-setting, measured in terms of the slope, valley shape and degree of valley confinement (Brierley *et al.*, 2002). In differentiating between River Styles, the relationship between channel and floodplain processes is the first level of identification. Distinction is made among confined (no floodplain), partly confined (discontinuous floodplain) and alluvial (continuous floodplain) valley settings. Nested within these valley settings, different River Styles are defined at the river reach scale (*sensu* Kellerhals *et al.*, 1976), whereby boundary conditions are sufficiently uniform along a stretch of river (i.e. there is no

significant change in the imposed discharge or sediment load) such that the river maintains a near-consistent geomorphic structure.

Individual River Styles are characterized by a distinct set of attributes, measured in terms of channel planform, channel geometry and the assemblage of geomorphic units (Brierley and Fryirs, 2000). The form and assemblage of geomorphic units are used to interpret process associations along river courses. For example, the distribution of floodplain geomorphic units records the propensity for sedimentation or reworking of deposits, with profound differences evident among features such as slow-flowing or standing water bodies (such as backswamps, billabongs, etc). The geo-ecological functioning and degree of connectivity beyond the channel is commonly dictated by the nature of geomorphic units at channel margins. For example, levees determine the character and extent of water/sediment inundation on floodplains, while crevasse splays indicate breaches of the levee and transfer of sediment from the channel to the floodplain zone. Instream geomorphic units are largely determined by discharge, slope and bed material texture, ranging from bedrock-controlled forms through to boulder steps to near-continuous pools (i.e. along a stream power gradient; *cf.* Grant *et al.*, 1990; Wadeson, 1994; Montgomery and Buffington, 1998). Although Brierley *et al.* (2002) have identified more than 20 River Styles in coastal catchments of New South Wales, the framework is generic and open-ended, allowing additional variants of River Styles to be added as the procedure is applied to new geographical areas.

There is considerable evidence that different geomorphic units (e.g. pools, runs, riffles, cascades, floodplains) support relatively distinct biotic assemblages, particularly for macroinvertebrates (e.g. Lium, 1974; Logan and Brooker, 1983; Pridmore and Roper, 1985; Brown and Brussock, 1991; Braaten and Berry, 1997). Since individual River Styles comprise distinct assemblages of geomorphic units, it is reasonable to infer that particular River Styles should have characteristic assemblages of habitat and biota (at least within climatic and biogeographic limits) at the reach scale (Taylor *et al.*, 2000; Thomson *et al.*, 2001). For example, geo-ecological differentiation of an upland swamp and a gorge, or a braided river with no floodplain and an anastomosing channel network with multiple backchannels and a network of wetlands on its floodplain, is self-evident, as the assemblages of geomorphic units, their formative relationship to different flow regimes, and vegetation associations are so distinct that the range of habitats differs notably among these different fluvial settings. Equally, the presence/absence of geomorphic units along a reach constrains habitat diversity. For example, the reach-scale assemblage of biota will differ between reaches that contain riffles and those that do not, because certain biota are specifically adapted to riffle habitats.

Furthermore, because the local physical structure of geomorphic units is influenced by hydrological and geomorphological processes which are controlled by larger-scale factors (e.g. valley setting, regional geology, discharge regime, hydraulic controls), geomorphic units of a given type may be physically, and therefore biologically, more similar within River Styles than between them. That is, if reach-scale morphology influences physical processes operating at the geomorphic unit and smaller scales, then particular geomorphic unit types (e.g. pools) should be physically more similar among reaches with similar reach-scale morphology compared with morphologically different reaches. If regional (reach scale) habitat factors influence local biotic communities through biotic processes (e.g. dispersal), then the ecological similarity of mesohabitats (geomorphic units and smaller scales) within River Styles may be further enhanced.

If geomorphic units are physically and biologically more similar within River Styles, then the scheme should provide a useful framework for ecological management. For example, rapid biomonitoring techniques often involve macroinvertebrate sampling in pools and/or riffles (e.g. Barbour *et al.*, 1999; Coysh *et al.*, 2000), so if these units are more similar within than between River Styles, then stratifying sampling programmes by River Style classes may help to reduce (or explain) natural variability. Similarly, habitat assessment procedures often lack an appropriate means with which to establish appropriate reference conditions for appraisal of habitat diversity and condition (Maddock, 1999; Davies *et al.*, 2000). River Styles classification provides a means of identifying the range of geomorphic units that should be

present in a reach (Brierley and Fryirs, 2000; Brierley *et al.*, 2002), and may also allow determination of the micro-habitat characteristics (e.g. particle size distributions, hydraulic characteristics) expected within particular geomorphic unit types for particular River Styles. If reaches of a particular River Style support distinctive biotic communities, then River Styles classification would enhance preliminary biodiversity assessments (assuming habitat diversity as a surrogate for biodiversity), and setting of conservation and restoration priorities (e.g. by identifying styles that are rare within a catchment and/or region).

The question posed herein is whether geomorphic units common to different River Styles are physically and or ecologically distinct to those River Styles (i.e. can habitat and biotic characteristics of geomorphic units be predicted from River Styles classification?). Specifically, the following questions were addressed:

- Are particular geomorphic unit types (e.g. pools, runs) physically more similar within than among different River Styles?
- Are macroinvertebrate assemblages within particular geomorphic unit types more similar within than among different River Styles?

METHODS

Study area

Habitat and macroinvertebrate assemblages were sampled for three replicate reaches of three different River Styles. Individual reaches were sampled from separate rivers to ensure sites were truly independent. The three styles selected for comparison were Gorge (a confined style), Bedrock-Controlled Discontinuous Floodplain (hereafter referred to as BCDF, a partly confined style), and Meandering Gravel Bed (an alluvial style, hereafter referred to as MGB). Rivers were selected principally from the Manning Catchment, on the north coast of New South Wales, Australia (Figure 1). Due to the difficulty of finding meandering gravel bed sites in good condition in the Manning catchment, the Stars Creek site, situated within 30 km of the nearest site in the Manning catchment (Dingo River, Figure 1), was included in the study. Given its proximity to the Manning catchment, differences associated with climatic, vegetative or biogeographic factors are considered to be minimal.

Catchment geology

The Manning and Hastings catchments occur within the New England Fold Belt, which exhibits complex geology and faulting of Devonian, Carboniferous and Permian aged rocks (Gilligan and Brownlow, 1987). The predominant lithologies within the catchments are sandstone, siltstone, mudstone, slate, limestone, porphyry, basalt, dolerite, chert, jasper, schist and phyllite. Most rivers in the two catchments rise on meta-sediments with the lower parts of the Hastings Basin being dominated by Devonian and Carboniferous sedimentary rocks (e.g. siltstones, sandstones, conglomerates). The lower parts of the Manning catchment are dominated by similar sequences with the additional presence of volcanic tuffs and tuffaceous sandstone.

Study site selection

Given that the aim of this study was to determine whether River Style *per se* affects macroinvertebrate assemblages, selected reaches of each River Style were located at similar catchment positions, so that factors such as altitude and stream size, which have been shown to influence macroinvertebrate community composition (e.g. Wright *et al.*, 1984; Marchant *et al.*, 1997), but which are not direct determinants of River Style, were as consistent as was practicable (see Table 1). Good condition reaches were selected by consulting recent River Styles reports (Cohen and Brierley, 1999; Ferguson *et al.*, 1999) along with visual

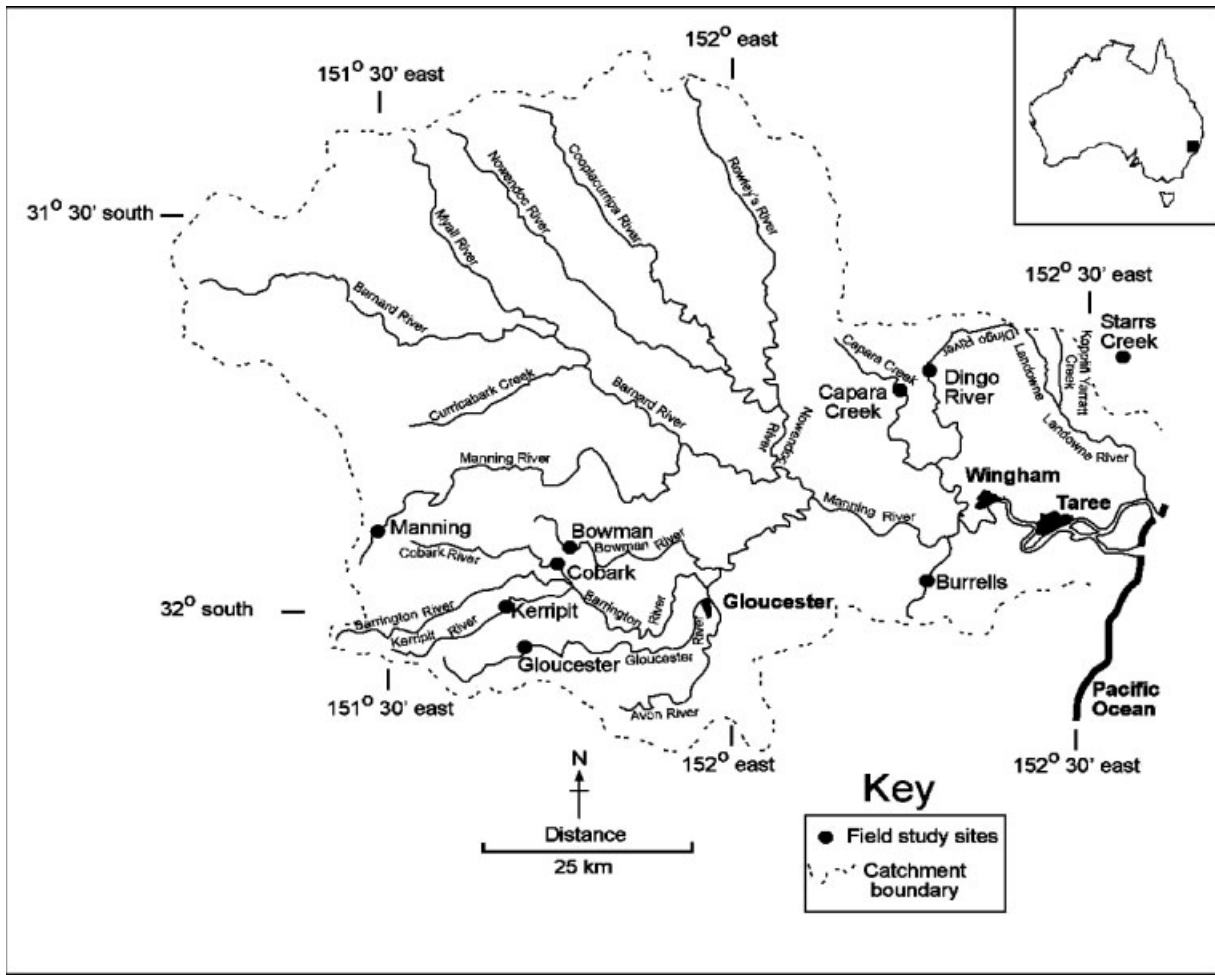


Figure 1. Study site map showing the locations of the field sites examined in this study.

assessment of local habitat condition, riparian condition, local land use, potential upstream impacts, and basic water quality tests — dissolved oxygen (DO), conductivity, pH, turbidity and temperature. The names and locations of the nine study reaches are shown in Table 1 and Figure 1, along with altitude, slope, catchment area, distance from source and estimated discharge at time of measurement.

Gorge reaches comprise bedrock-controlled pools and extensive runs, separated by riffles and occasional boulder/gravel bars. Reaches of BCDF River Style have occasional to semi-regular (alternating) floodplain pockets. Instream zones comprise pool-riffle sequences with cascades, runs and glides. Bedrock boundaries are common. Lateral and point bars form transient sediment stores. Channel margins often have benches adjacent to floodplain pockets. Relative to some other reaches of this River Style in coastal valleys of New South Wales, levees are relatively subdued in this river system (*cf.*, Ferguson and Brierley, 1999), and most floodplain pockets are relatively flat-topped (*i.e.* proximal-distal variability is not pronounced). However, whenever pockets are sheltered by bedrock spurs, local ponding may be evident at floodplain margins. Finally, selected MGB reaches have fully self-adjusting pool-riffle sequences, as bedrock is only locally evident. Glides and runs characterize the transitional zones between pools and riffles. Point bars are common, and continuous areas of floodplain may have significant heterogeneity, including some cut-offs

Table 1. Summary details for the reaches examined in this study. MGB — Meandering Gravel Bed, BCDF — Bedrock-Controlled Discontinuous Floodplain. Cond. = conductivity, DO = Dissolved Oxygen

| Reach / catchment | River style | pH | Cond $\mu\text{S cm}^{-1}$ | DO (mg L ⁻¹) | Mean phi | Slope m m ⁻¹ | Elevation (m) | Catchment area (km ²) | Discharge (m ³ s ⁻¹) | Distance from source (km) | Latitude | Longitude |
|-------------------|-------------|------|----------------------------|--------------------------|----------|-------------------------|---------------|-----------------------------------|---|---------------------------|----------|-----------|
| Manning Catchment | | | | | | | | | | | | |
| Dingo River | BCDF | 7.84 | 150.3 | 10.5 | -5.98 | 0.005 | 120 | 61 | 0.24 | 24.5 | 152.30 | -31.68 |
| Capara Creek | BCDF | 7.4 | 110 | 10.15 | -5.63 | 0.006 | 130 | 46 | 0.16 | 17 | 152.23 | -31.72 |
| Gloucester River | BCDF | 6.29 | 54.6 | 10.1 | -6.62 | 0.025 | 330 | 64 | 0.5 | 18 | 151.69 | -32.05 |
| Kerritpit River | Gorge | 7.16 | 65 | 11.1 | -7.60 | 0.006 | 290 | 62.5 | 1 | 28 | 151.67 | -32.00 |
| Manning River | Gorge | 7.47 | 46.9 | 9.8 | -6.77 | 0.015 | 1150 | 24 | 0.5 | 11 | 151.49 | -31.88 |
| Bowman River | Gorge | 7.9 | 195.2 | 10.9 | -9.13 | 0.020 | 320 | 36.5 | 0.163 | 19 | 151.77 | -31.92 |
| Burrell Creek | MGB | 8.11 | 456 | 10.4 | -5.02 | 0.001 | 50 | 61 | 0.1 | 9.5 | 152.26 | -32.03 |
| Cobark River | MGB | 7.92 | 131.2 | 10.2 | -5.37 | 0.001 | 250 | 78 | 0.79 | 35.5 | 151.71 | -31.95 |
| Hasting catchment | | | | | | | | | | | | |
| Starrs Creek | MGB | 7.23 | 89.9 | 8.9 | -3.49 | 0.001 | 40 | 15 | 0.15 | 7.5 | 152.56 | -31.67 |

(billabongs), flood channels and occasional backswamps. Overall, the range of geomorphic units increases from confined through partly confined to the alluvial River Styles. However, in this study, a test of the ecological significance of the River Styles framework focuses on common units to the three selected River Styles, namely pools and runs.

Habitat and macroinvertebrate sampling

All sites were sampled once within a two week period in May 2000 at base flow discharge, after a period of negligible rainfall.

Habitat mapping

Instream habitat characteristics of each reach were assessed and mapped using the habitat mapping procedure outlined by Thomson *et al.* (2001). A geomorphic unit map of each reach was drawn at a scale of *ca* 1:5000 identifying the spatial distribution of pools, runs, riffles, cascades, bars, etc. (see Brierley and Fryirs, 2000). Each geomorphic unit within the reach was then further divided into hydraulic units — patches of homogeneous surface flow type and substrate composition (Thomson *et al.*, 2001). A range of habitat variables was measured or estimated within each hydraulic unit, thus allowing a range of microhabitat features such as woody debris and macrophytes to be placed within an hydraulic context, such that specific combinations of habitat variables (e.g. woody debris in fast flowing versus slow flowing patches) could be identified (*cf.*, Armitage and Cannan, 1998). Because the size of each hydraulic unit is recorded, the data collected using this procedure can be easily aggregated to give geomorphic unit or even reach-scale estimates of variables if required (e.g. length of bank edge with trailing vegetation). The parameters recorded for each hydraulic unit are listed in Table 2. Hydraulic variables (depth, roughness values and velocity) were measured at three randomly selected points within each hydraulic unit. For the analyses reported here, all habitat variables were aggregated to give weighted (by hydraulic unit area) averages for each geomorphic unit.

Depth-averaged velocity was measured with a propeller current meter (Hydrological Services Pty. Ltd., model CMC-200) at 0.4 depth for 30 s. Roughness height, spacing and groove width (Davis and Barmuta, 1989; Young, 1992) were measured *in situ* with a ruler for all roughness elements within a 25 cm radius of the point at which velocity was measured and these values averaged for each flow point. Derived hydraulic indices (Froude number, Reynolds number, roughness Reynolds number and shear velocity) were then calculated for each flow point, before hydraulic unit and weighted geomorphic unit scale averages were calculated. The proportion of substrate particles falling into each of seven size categories (Table 2) within each hydraulic unit was visually estimated.

Habitat mapping was conducted prior to macroinvertebrate sampling because the use of kick nets (see below) alters roughness characteristics of the stream bed. Care was taken to make habitat estimates/measurements from the bank wherever possible, or to make minimal disturbance to the stream bed and vegetative habitats in pools and runs that were to be sampled. Basic water quality parameters (DO, conductivity, pH, turbidity, temperature) were also measured on site prior to habitat mapping (Table 1).

Macroinvertebrate sampling

At each site, two pools and two runs were sampled for macroinvertebrates. Pools and runs are identified on the basis of bed morphology and substrate characteristics. Pools typically have concave beds, and accumulate fine-grained sediment and organic materials at base flows. In contrast, runs have relatively flat beds and are zones of fine sediment transport at base flows, so that fine grained materials are rarely present.

A semi-quantitative sample was collected for each geomorphic unit using sweep and kick nets. Hydraulic unit patches were sampled in proportion to their relative size within each geomorphic unit, such that a total

Table 2. A list of the variables measured as part of the geo-ecological mapping exercise

| | |
|---------------------|---|
| Hydraulic variables | Flow type ^a velocity ^b (m s ⁻¹) depth ^b (m) roughness ^b (m) vertical spacing ^b (m) horiz. spacing ^b (m) groove width ^b (m) |
| Substrate | Mean phi ^c Sorting Packing ^d (1–5) |
| Aquatic vegetation | Emergent (%) Floating (%) Submerged (%) Filamentous algae (%) Moss (%) |
| Organic matter | Multiple logs Single logs Twigs and leaves Detritus |
| Bank morphology | LHB RHB LHB bank slope RHB bank slope |
| Riparian vegetation | LHB ^e RHB ^e LHB trailing RHB trailing LHB shading ^f RHB shading ^f Total shading ^g |
| Dimensions | Max. length (m) Max. width (m) |
| Derived indices | Mean Froude Mean Reynolds Mean shear Mean roughness Re |

^a Refer to Thomson et al. (2001).

^b Means of three random measurements within each hydraulic unit.

^c Calculated from proportion of bedrock, boulder, cobble, pebble, gravel, sand, and silt.

^d After Anderson (1993) 1 = packed, armoured, 2 = packed, not armoured, 3 = moderate compaction, 4 = low compaction, 5 = no packing.

^e Specht (1970) vegetation classification.

^f Proportion of bank length for which riparian vegetation overhangs stream.

^g Proportion of total stream area shaded by riparian vegetation. LHB/RHB = Left-hand bank/right-hand bank.

of 3 min sampling effort was made for each geomorphic unit. Within each hydraulic unit, microhabitat features (logs, macrophytes, bare substrate, etc.) were also sampled in proportion to their relative abundance within that unit. Logs were sampled by holding a net downstream of the log and vigorously

rubbing the log by hand. Bare substrate and patches of leaf litter (or other organic matter) were sampled by disturbing the bottom with feet while holding a kick net downstream. Macrophytes and trailing vegetation were sampled by passing a sweep net through vegetation. Each sample was preserved on site with 70% alcohol solution and returned to the laboratory for processing.

Laboratory procedures

Macroinvertebrate samples were sub-sampled to the greater of 10% or 300 individuals with a Marchant (1989) sub-sampler and identified to family level by professional taxonomists. Total abundances were estimated by dividing the number of each family per sub-sample by the sub-sample fraction.

Analysis

Ordinations were used to explore the similarity of macroinvertebrate assemblages between samples. Two ordination techniques were used initially; Non-metric Multi Dimensional Scaling (NMDS, Kruskal, 1964) and Detrended Correspondence Analysis (DCA, ter Braak, 1995). In addition, unimodal canonical correspondence analysis (CCA: ter Braak, 1995) was used to relate environmental variables to macroinvertebrate patterns. NMDS was based on Bray-Curtis similarity matrix derived from $\sqrt[4]{}$ transformed data. Macroinvertebrate data were $\sqrt[2]{}$ transformed for DCA and CCA analysis.

Differences in macroinvertebrate assemblages between River Styles were tested for significance using a two-factor nested Analysis of Similarity (ANOSIM, Clarke and Warwick, 1994), with rivers nested within River Style. Separate analyses were performed for pool, run and combined samples. ANOSIM derives a test statistic, R , which contrasts the similarities among samples within treatments (i.e. River Styles) with the similarities among samples between treatments (Clarke and Warwick, 1994). In nested ANOSIM, samples within a level of the nested factor (in this case samples within a river) are treated as a single sample for comparisons between main treatment groups (i.e. between River Styles). The significance of R is calculated by a permutation test: R statistics are calculated for arbitrarily arranged samples and compared with the R statistic derived from the true sample arrangement. The probability of obtaining an R statistic greater than or equal to the 'true' R with randomly arranged samples is then calculated. Five thousand random permutations were used in calculating the significance of tests for differences between rivers, and 280 (all possible) permutations for tests for differences between River Styles. Significance levels were set at $P < 0.05$ for these tests. For pair-wise comparisons between River Style groups following a significant River Style effect, only 10 permutations are possible (i.e. there are 10 ways that six rivers can be arranged into two groups of three). Significance levels for these tests were therefore set at $P = 0.1$ (i.e. tests were considered significant if grouping rivers according to River Style produced a higher R statistic than any other possible combination of rivers into groups of three). The similarity matrices used for ANOSIM were derived using the Bray-Curtis similarity measure with $\sqrt[4]{}$ transformed data.

Variation in biological data was compared with environmental variables by unimodal canonical correspondence analysis (CCA). In CCA the ordering of taxa is modified through the addition of a multiple linear regression with environmental variables (ter Braak, 1995). To ensure that the sample order was not inappropriately distorted from that produced in unconstrained ordination, sample scores for NMDS, DCA and CCA axes were compared by correlation. Environmental variables were range standardized (0–1) for use in CCA.

CCA was initially performed using all local habitat variables to explore relationships among all habitat variables and macroinvertebrate assemblages. A second CCA was performed using forward stepwise regression to identify those habitat variables that 'best explained' the pattern in the macroinvertebrate data. Variables were selected in turn and those that significantly added to the explained variation were retained. Significance was tested by monte-carlo permutation tests (ter Braak, 1995).

Site-scale environmental variables (catchment area, distance from source, etc.) were excluded from the initial CCAs because all (four) samples from the same site have the same values for these variables, such that strong relationships could be obtained simply due to spatial autocorrelation in the biological data rather than actual habitat effects. Samples from the same site are likely to have similar biotic assemblages simply because they are close to each other, not necessarily because they are at the same altitude, etc. A separate CCA was conducted with the site-based variables included (without selection of variables through stepwise regression), and vectors for these variables are shown to indicate possible relationships. However, because of the low sample size ($n=9$), it is difficult to make sound conclusions about the effects of these variables on the observed pattern in the macroinvertebrate data.

Selected habitat variables, specifically mean phi, mean velocity, mean depth and those variables shown to be significantly related to the pattern in macroinvertebrate data through CCA, were tested for differences between River Styles with three-factor mixed model ANOVA. River Style and Geomorphic Unit were fixed factors and River was a random factor nested within River Style but crossed with Geomorphic Unit. Assumptions of ANOVA were checked by examination of box and residual plots, and transformations (log or arcsine) made to homogenize variances where necessary. Following significant River Style effects or River Style \times Geomorphic Unit interactions, the Student-Newman-Keuls (SNK) procedure (Winer *et al.*, 1991) was used to compare treatment means.

ANOSIM and NMDS analyses were performed with the Primer software package (Clarke and Warwick, 1994), CCA and DCA with the Canoco package (version 4, ter Braak and Smilauer, 1998), and ANOVA with Systat (v.10).

RESULTS

Ordinations

Ordinations by NMDS, DCA and CCA showed similar patterns, and sample scores for axes from all ordinations were highly correlated (Table 3). Thus the pattern in the data is robust to the ordination method, and is not distorted by constraining with environmental data. For simplicity, only the CCA ordination is presented here.

As noted from Figure 2, samples from BCDF reaches tended to group together in the ordination, and to separate from other samples. Gorge samples also tended to be grouped together (though less tightly), but the MGB samples are widely scattered. MGB samples from the same river grouped together but the three rivers are widely separated. Differences between pools and runs were small, and generally not as great as differences between rivers or River Styles.

These results are supported by ANOSIM results (Table 4). When pools and runs were analysed together, a significant ($P=0.046$) River Style effect was obtained (Global $R=0.325$), with the greatest difference being between BCDF and Gorge sites ($R=0.741$, $P=0.1$). BCDF and MGB sites were also different ($R=0.370$, $P=0.1$), but Gorge and MGB sites were not ($R=-0.037$, $P=0.7$).

When pools were analysed separately, the global R for the test of the River Style effect was larger ($R=0.465$, $P=0.004$) and all pair-wise comparisons were significant at the $P=0.1$ level (there is no possible way of combining the sites into groups of three that produces an equivalent or larger R statistic). The greatest differences were again between BCDF and Gorge sites ($R=0.667$, $P=0.1$), then between BCDF and MGB sites ($R=0.407$, $P=0.1$), followed by Gorge and MGB sites ($R=0.370$, $P=0.1$). When runs were analysed separately, large between-river differences were evident ($R=0.926$, $P<0.001$), but there were no consistent differences between any River Styles (Global $R=0.148$, $P=0.204$).

Overall differences in macroinvertebrate assemblages between River Styles were relatively small, and appeared to be mostly related to differences in relative abundances of families rather than their presence or

Table 3. Pearson correlation coefficients between ordination axis scores. Asterisks indicate significance at the * $P < 0.05$ or ** $P < 0.01$ level. *CCA**n* refers to CCA axes derived from local habitat variables only, *CCAB**n* to axes derived using all environmental variables (*n* refers to the axis number)

| | DCA1 | DCA2 | DCA3 | DCA4 | MDS1 | MDS2 | CCAB1 | CCAB2 | CCAB3 | CCAB4 |
|------|----------|----------|---------|---------|----------|----------|---------|---------|----------|----------|
| CCA1 | -0.871** | -0.09 | 0.053 | 0.229 | 0.121 | -0.749** | 0.853** | 0.212 | 0.125 | -0.115 |
| CCA2 | 0.128 | -0.862** | -0.089 | 0.259 | -0.877** | -0.188 | -0.185 | 0.906** | -0.132 | -0.206 |
| CCA3 | -0.025 | -0.324 | 0.172 | -0.57** | -0.232 | -0.1 | 0.043 | -0.046 | -0.631** | -0.629** |
| CCA4 | 0.067 | 0.043 | 0.538** | 0.124 | -0.121 | 0.028 | -0.031 | 0.066 | 0.354* | -0.513** |

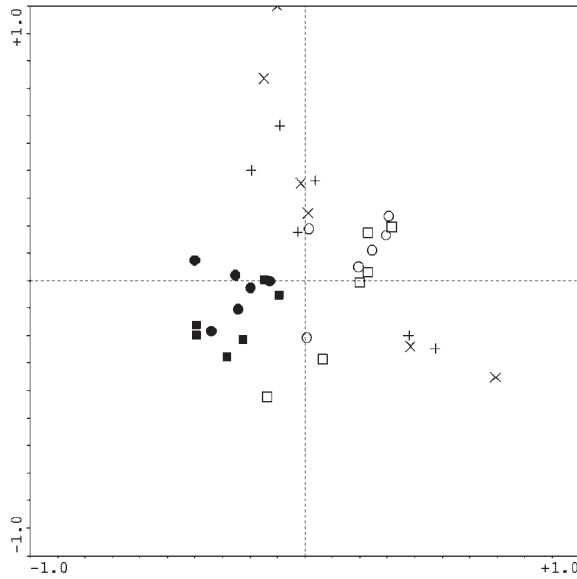


Figure 2. Distribution of macroinvertebrate samples in CCA ordination space. ● BCDF pools, ■ BCDF runs, ○ Gorge pools, □ Gorge runs, × MGB pools, + MGB runs.

Table 4. Results of nested ANOSIM comparing similarities of macroinvertebrate assemblages within and between River Styles

| | Between Rivers | | Between River Styles | | BCDF vs Gorge | | BCDF vs MGB | | Gorge vs MGB | |
|-------|----------------|-----------------------|----------------------|-----------------------|---------------|-----------------------|-------------|-----------------------|--------------|-----------------------|
| | <i>R</i> | <i>P</i> ^a | <i>R</i> | <i>P</i> ^b | <i>R</i> | <i>P</i> ^c | <i>R</i> | <i>P</i> ^c | <i>R</i> | <i>P</i> ^c |
| All | 0.773 | <0.001 | 0.325 | 0.046 | 0.741 | 0.100 | 0.370 | 0.100 | -0.037 | 0.700 |
| Pools | 0.704 | 0.002 | 0.465 | 0.004 | 0.667 | 0.100 | 0.407 | 0.100 | 0.370 | 0.100 |
| Runs | 0.926 | <0.001 | 0.148 | 0.204 | | | | | | |

^aProbability calculated from 5000 random permutations.

^bProbability calculated from 280 (all possible) random permutations.

^cProbability calculated from 10 (all possible) random permutations.

absence. Of 73 families found, none was unique to one River Style, and only five were present in at least two rivers of one style and completely absent from all rivers of another style (Table 5).

Relationships between habitat variables and macroinvertebrate data

The arrangement of the 36 macroinvertebrate samples, 74 macroinvertebrate taxa and environmental variables along the first two CCA axes are presented in Figures 2, 3 and 4, respectively. The lengths and

Table 5. Summary of invertebrate taxa found in each river and River style. Row entries show the number of rivers in each category in which each taxon was found

| Taxa | Code | Total Rivers | BCDF Rivers | Gorge Rivers | MGB Rivers |
|-----------------|------|--------------|-------------|--------------|------------|
| Ancylidae | Anc | 4 | 2 | 1 | 1 |
| Anthericidae | Ant | 5 | 1 | 1 | 3 |
| Aphroteniinae | Aph | 7 | 3 | 1 | 3 |
| Atriplectides | Atr | 2 | 0 | 1 | 1 |
| Atyidae | Aty | 8 | 3 | 2 | 3 |
| Baetidae | Btd | 9 | 3 | 3 | 3 |
| Blephacerae | Ble | 4 | 1 | 2 | 1 |
| Caenidae | Cae | 9 | 3 | 3 | 3 |
| Cal/Hel | CH | 6 | 2 | 3 | 1 |
| Calamoceridae | Cal | 8 | 3 | 3 | 2 |
| Carculionodae | Car | 1 | 0 | 0 | 1 |
| Ceinidae | Cei | 1 | 1 | 0 | 0 |
| Ceratopogonidae | Cer | 7 | 3 | 1 | 3 |
| Chironominae | Ch | 9 | 3 | 3 | 3 |
| Coenagrionidae | Coe | 1 | 0 | 0 | 1 |
| Conoesucidae | Con | 8 | 3 | 3 | 2 |
| Corixidae | Cor | 1 | 1 | 0 | 0 |
| Corydalidae | Cy | 6 | 3 | 2 | 1 |
| Culicidae | Cul | 2 | 0 | 1 | 1 |
| Diamesinae | Dia | 1 | 0 | 1 | 0 |
| Dixidae | Dix | 3 | 0 | 2 | 1 |
| Dugessidae | Dug | 4 | 3 | 1 | 0 |
| Dytiscidae | Dyt | 5 | 2 | 1 | 2 |
| Ecnomidae | Ecn | 6 | 1 | 2 | 3 |
| Elmidae | El | 9 | 3 | 3 | 3 |
| Empididae | Emp | 9 | 3 | 3 | 3 |
| Eusiridae | Eus | 1 | 0 | 1 | 0 |
| Gerridae | Ger | 4 | 2 | 0 | 2 |
| Glossosomatidae | Glo | 8 | 3 | 3 | 2 |
| Gomphidae | Go | 3 | 1 | 0 | 2 |
| Gripopterygidae | Gri | 9 | 3 | 3 | 3 |
| Gyrnidae | Gyr | 2 | 1 | 0 | 1 |
| Helicophidae | Hel | 5 | 2 | 2 | 1 |
| Helicopsychidae | Hls | 9 | 3 | 3 | 3 |
| Hydraenidae | Hyd | 3 | 1 | 1 | 1 |
| Hydrobiidae | Hbi | 4 | 2 | 1 | 1 |
| Hydrobiosidae | Hbd | 9 | 3 | 3 | 3 |
| Hydrophilidae | Hpl | 7 | 3 | 1 | 3 |
| Hydropsychidae | Hs | 8 | 3 | 3 | 2 |
| Hydroptilidae | Hpt | 9 | 3 | 3 | 3 |
| Kokiridae | Ko | 1 | 0 | 1 | 0 |
| Leptoceridae | Lcd | 9 | 3 | 3 | 3 |
| Leptophlebiidae | Lep | 9 | 3 | 3 | 3 |
| Lymnaeidae | Lym | 1 | 0 | 1 | 0 |
| Mesoveliidae | Mes | 1 | 0 | 1 | 0 |
| Mite | Mit | 9 | 3 | 3 | 3 |
| Muscidae | Mus | 1 | 0 | 0 | 1 |
| Nannochonsidae | Nan | 1 | 0 | 1 | 0 |
| Nematoda | Nem | 3 | 2 | 1 | 0 |
| Nematomorpha | Np | 2 | 1 | 1 | 0 |
| Odontoceridae | Od | 1 | 0 | 1 | 0 |
| Oligochaeta | Oli | 9 | 3 | 3 | 3 |
| Orthocladinae | Ort | 9 | 3 | 3 | 3 |

Table 5 (continued)

| Taxa | Code | Total Rivers | BCDF Rivers | Gorge Rivers | MGB Rivers |
|-----------------|------|--------------|-------------|--------------|------------|
| Philopotamidae | Phi | 5 | 3 | 1 | 1 |
| Physidae | Phy | 1 | 0 | 0 | 1 |
| Planorbidae | Pla | 4 | 1 | 2 | 1 |
| Podonomopsis | Pod | 4 | 1 | 1 | 2 |
| Polycentropidae | Pol | 1 | 0 | 1 | 0 |
| Psephenidae | Pse | 8 | 3 | 3 | 2 |
| Psychodidae | Psy | 1 | 0 | 0 | 1 |
| Pyalidae | Pyr | 2 | 1 | 1 | 0 |
| Scirtidae | Sci | 9 | 3 | 3 | 3 |
| Simuliidae | Si | 9 | 3 | 3 | 3 |
| Sphaeridae | Sph | 3 | 1 | 1 | 1 |
| Staphlyinidae | Sta | 1 | 0 | 1 | 0 |
| Stratiomyidae | Str | 1 | 0 | 1 | 0 |
| Synlestidae | Syn | 1 | 1 | 0 | 0 |
| Tanypodinae | Tan | 9 | 3 | 3 | 3 |
| Tasimiidae | Tas | 5 | 1 | 2 | 2 |
| Temnocephala | Tem | 1 | 0 | 0 | 1 |
| Tipulidae | Tip | 9 | 3 | 3 | 3 |
| Veliidae | Ve | 1 | 0 | 1 | 0 |
| Zygoptera imm | Zy | 2 | 1 | 0 | 1 |

directions of environmental arrows (Figure 3) are related to their importance in 'explaining' variation in macroinvertebrate taxa and direction of taxa compositional changes across samples. Mean velocity, mean Froude number and mean Reynolds number were highly correlated with each other, and therefore only Froude number (which was most strongly correlated with the ordination axes) is included in the CCA plot. The first two axes account for 27.4% and 34.8% of variation in the family data and family-environment relationship respectively (Table 6). Individual habitat variables were generally only weakly correlated with the first two ordination axes. The separation of BCDF and Gorge samples seems to be along a gradient reflecting substrate composition (especially % cobbles), the number of logs and, less strongly, instream vegetation (macrophytes and filamentous algae).

Forward stepwise regression identified eight local habitat variables that significantly 'explained' biological variation using CCA. Three of these were substrate variables (proportion of boulder, cobbles and sand), two were hydraulic variables (mean Froude number and mean shear velocity), and three related to vegetation (number of logs, % filamentous algae and % moss). The first two axes of the CCA ordination using only these variables accounted for 53.2% of the family environment relationship (Table 7). The ordination of macroinvertebrate samples constrained only by these habitat variables was very similar to the original CCA ordination and NMDS ordination (Table 3), although the first two axes accounted for only 19% of variation in the macroinvertebrate data (compared with 27% for original CCA). Three factor ANOVA was used to compare the eight selected variables, in addition to mean phi, mean velocity and mean depth, between River Styles.

The largest and most consistent habitat difference between River Styles was in substrate composition (Figure 5). Mean phi in pools was significantly different for all three River Styles, and in runs was significantly greater in gorge than in BCDF and MGB reaches (Table 8). Substrate differences would be even more apparent at the reach scale because of the presence of bedrock and boulder steps/cascades in Gorge reaches. ANOVA results indicate that of the eight variables that apparently had most influence on macroinvertebrates, % cobble, % moss and mean Froude number differed significantly between two River Styles in some geomorphic units, but none differed between all three River Styles. The proportion of

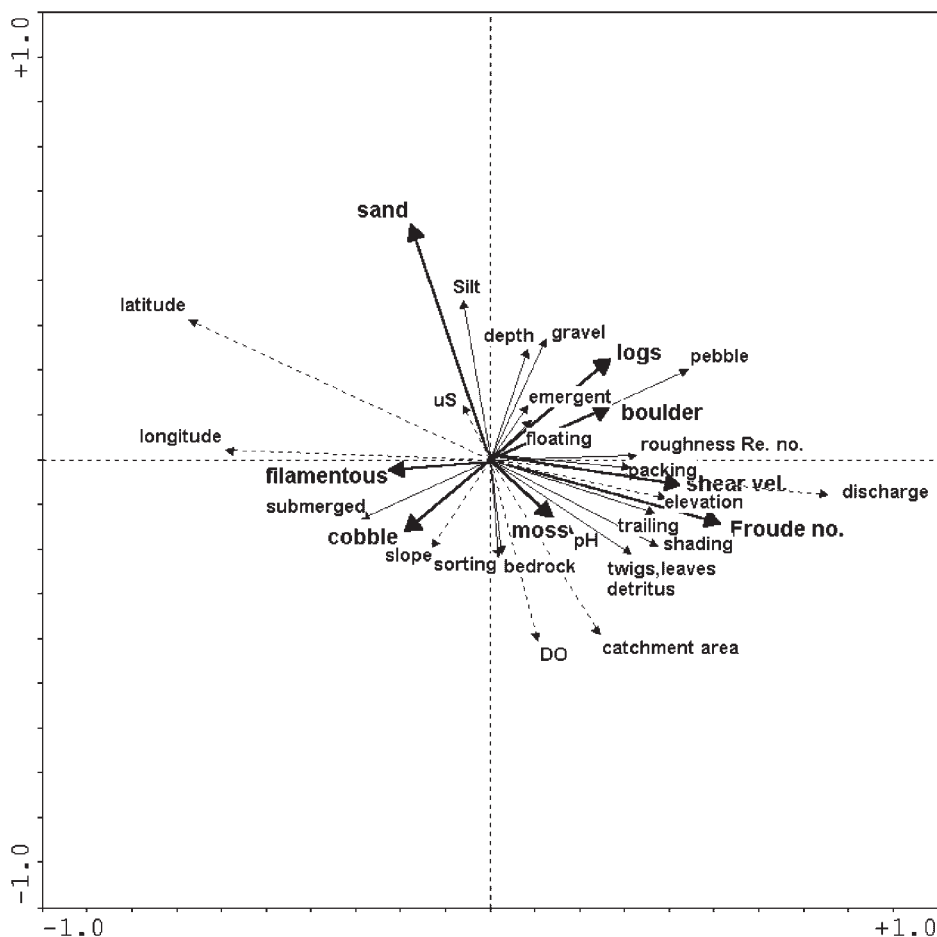


Figure 3. Relationship between habitat variables and first two axes of CCA ordination. Solid lines indicate variables selected by forward stepwise regression as significantly 'explaining' variation in macroinvertebrate data.

cobbles was significantly greater in BCDF pools than in MGB or Gorge pools (Figure 5, Table 8). MGB runs also had less cobble than BCDF runs, but Gorge runs had equivalent cobble to BCDF runs (and therefore more than MGB). Mean Froude number was significantly lower in BCDF runs than in MGB or Gorge runs, with no differences in pools (Table 9). This result reflects higher velocities in MGB and Gorge runs (Figure 6, Table 9). Moss was significantly more abundant in Gorge runs than MGB or BCDF runs (Figure 6, Table 10). Other habitat variables that were important in the CCA were highly variable within River Styles groups, although some showed non-significant trends for differences between River Styles. For example, the number of logs was generally lower in BCDF pools than MGB or Gorge pools (Figure 6).

Important habitat variables (cobble, Froude number, logs) were often more similar between MGB and Gorge reaches than between either of these styles and BCDF (Figures 5 and 6). This is consistent with the pattern observed in the macroinvertebrate data (biggest differences between BCDF and other River Styles), and suggests that those patterns may be largely driven by local habitat differences.

Macrophytes were rare at all sites at the time of sampling and consequently showed little relationship to macroinvertebrate data, and differences between River Styles were not observed.

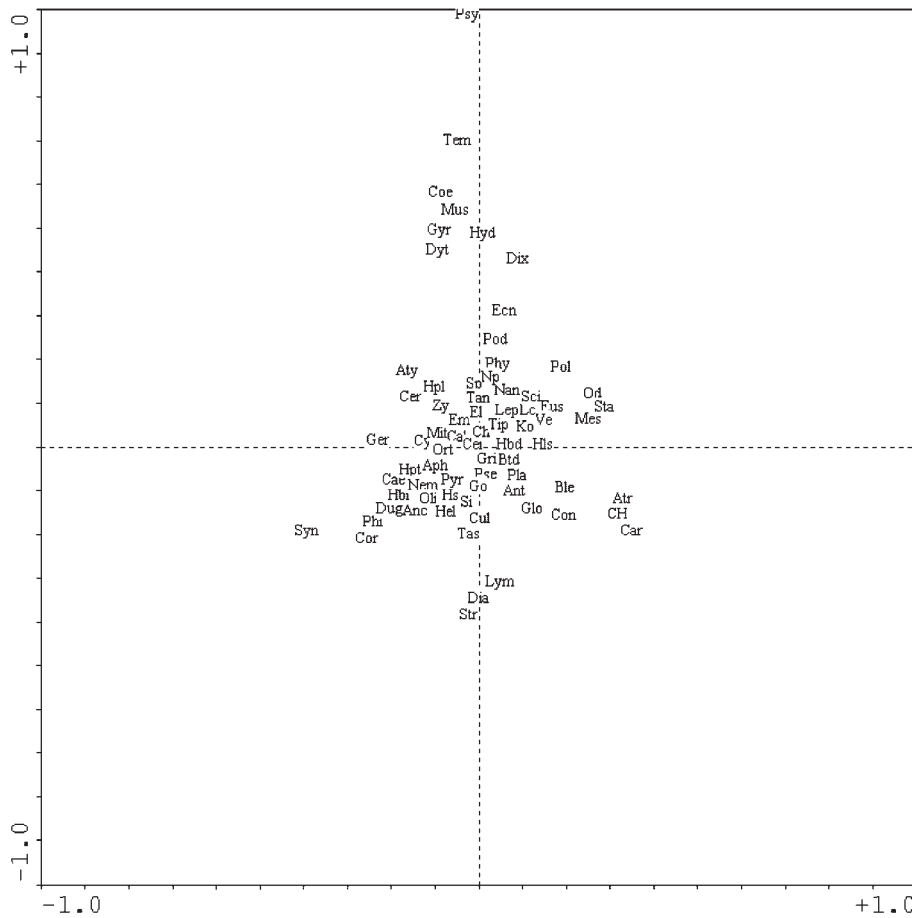


Figure 4. Distribution of macroinvertebrate families in CCA ordination space. Family names are coded according to Table 5.

Table 6. Summary of CCA results using all local habitat variables

| Axes | 1 | 2 | 3 | 4 |
|---|-------------------|-------|---------|---------|
| Eigenvalues | 0.148 | 0.110 | 0.082 | 0.061 |
| Family-environment correlations | 0.972 | 0.951 | 0.966 | 0.873 |
| Cumulative percentage variance of family data | 15.7 | 27.4 | 36.1 | 42.6 |
| Cumulative percentage variance of family-environment relationship | 20.0 | 34.8 | 45.6 | 54.2 |
| | Eigen value/trace | | F ratio | P-value |
| First canonical axis | 0.148 | | 1.676 | 0.030 |
| all canonical axes | 0.742 | | 1.274 | 0.025 |

DISCUSSION

Despite numerous geomorphological river classification schemes being developed and advocated as useful for ecological applications (e.g. Frissell *et al.*, 1986; Rosgen, 1994), there have been few attempts to test explicitly whether biotic communities are consistently different between different geomorphological classes.

Table 7. Summary of CCA results using only habitat variables forward stepwise regression as significantly ($P < 0.005$) explaining variation in macroinvertebrate data

| Axes | 1 | 2 | 3 | 4 |
|---|-------------------|----------------|-----------------|-------|
| Eigenvalues | 0.113 | 0.073 | 0.051 | 0.040 |
| Family-environment correlation | 0.865 | 0.831 | 0.776 | 0.903 |
| Cumulative Percentage variance of family data | 12.0 | 19.7 | 25.1 | 29.3 |
| Cumulative Percentage variance of family-environment relationship | 32.4 | 53.2 | 67.9 | 79.4 |
| | Eigen value/trace | <i>F</i> ratio | <i>P</i> -value | |
| First canonical axis | 0.113 | 3.667 | 0.005 | |
| all canonical axes | 0.348 | 1.977 | 0.005 | |

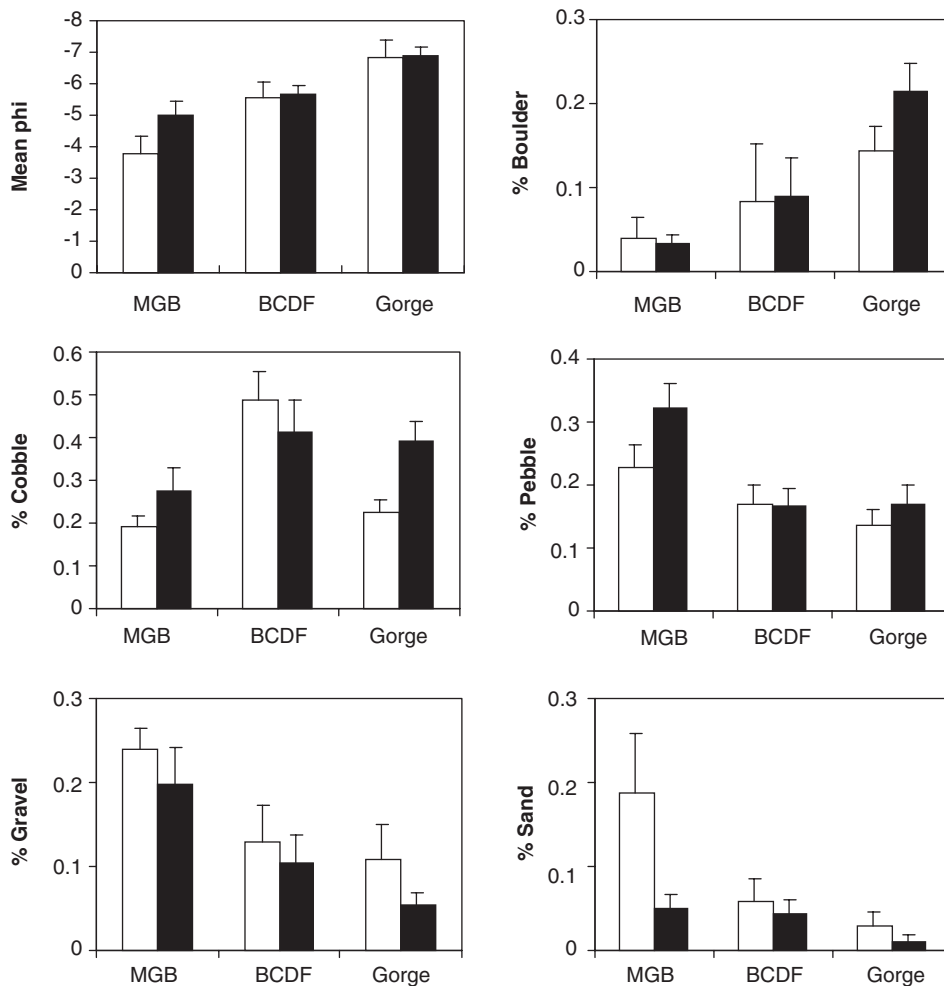
Figure 5. Means (± 1 S.E.) of selected substrate variables in pools (open bars) and runs (grey bars) in MGB, BCDF and Gorge River Styles. $n = 6$ for all bars.

Table 8. Results of ANOVA comparing selected substrate variables between River Styles and geomorphic units

| df | Mean Phi | | | Boulder | | | Cobble | | | Sand | | |
|--------------------------|------------------|--------|--------|---------|-------|-------|--------|--------|-------|-------|--------|-------|
| | SS | F | P | SS | F | P | SS | F | P | SS | F | P |
| | River Style (RS) | 2 | 33.096 | 5.479 | 0.044 | 0.303 | 0.272 | 0.216 | 3.129 | 0.177 | 0.222 | 1.836 |
| Geomorphic unit | 1 | 4.037 | 46.414 | 0.000 | 0.001 | 0.124 | 0.737 | 9.595 | 0.021 | 0.123 | 11.303 | 0.015 |
| RS × Geounit | 2 | 1.753 | 10.078 | 0.012 | 0.012 | 1.245 | 0.353 | 11.870 | 0.008 | 0.061 | 2.806 | 0.138 |
| River (RS) | 6 | 18.123 | 3.382 | 0.016 | 0.557 | 7.000 | 0.001 | 1.557 | 0.223 | 0.363 | 3.928 | 0.013 |
| Geounit × River (RS) | 6 | 0.522 | 0.097 | 0.996 | 0.029 | 0.371 | 0.887 | 0.096 | 0.996 | 0.066 | 0.709 | 0.647 |
| Residual | 16 | 19.646 | | 0.212 | | | 0.354 | | | 0.246 | | |
| SNK comparisons | | | | | | | | | | | | |
| Pools:MGB < BCDF < Gorge | | | | | | | | | | | | |
| Runs:MGB = BCDF < Gorge | | | | | | | | | | | | |
| SNK comparisons | | | | | | | | | | | | |
| Pools:BCDF > MGB = Gorge | | | | | | | | | | | | |
| Runs:MGB = BCDF = Gorge | | | | | | | | | | | | |

Table 9. Results of ANOVA comparing hydraulic variables between River Styles and geomorphic units

| df | Velocity | | | Depth | | | Froude | | | Reynolds | | |
|--------------------------|------------------|-------|--------|-------|-------|--------|--------|-------|--------|----------|--------|--------|
| | SS | F | P | SS | F | P | SS | F | P | SS | F | P |
| | River Style (RS) | 2 | 0.022 | 0.386 | 0.696 | 0.020 | 1.011 | 0.418 | 0.010 | 0.553 | 0.602 | 3.065 |
| Geomorphic unit | 1 | 0.110 | 61.536 | 0.000 | 0.132 | 19.432 | 0.005 | 0.053 | 51.045 | 0.000 | 4.080 | 7.366 |
| RS × Geounit | 2 | 0.024 | 6.614 | 0.030 | 0.015 | 1.071 | 0.400 | 0.015 | 6.974 | 0.027 | 2.641 | 2.384 |
| River(RS) | 6 | 0.173 | 4.269 | 0.009 | 0.058 | 0.499 | 0.800 | 0.054 | 2.291 | 0.087 | 19.974 | 15.494 |
| Geounit × River(RS) | 6 | 0.011 | 0.264 | 0.946 | 0.041 | 0.349 | 0.900 | 0.006 | 0.266 | 0.945 | 3.324 | 2.578 |
| Residual | 16 | 0.108 | | 0.310 | | | 0.063 | | | 3.438 | | |
| SNK comparisons | | | | | | | | | | | | |
| Pools:MGB = BCDF = Gorge | | | | | | | | | | | | |
| Runs:BCDF < MGB = Gorge | | | | | | | | | | | | |
| SNK comparisons | | | | | | | | | | | | |
| Pools:MGB = BCDF = Gorge | | | | | | | | | | | | |
| Runs:BCDF < MGB = Gorge | | | | | | | | | | | | |

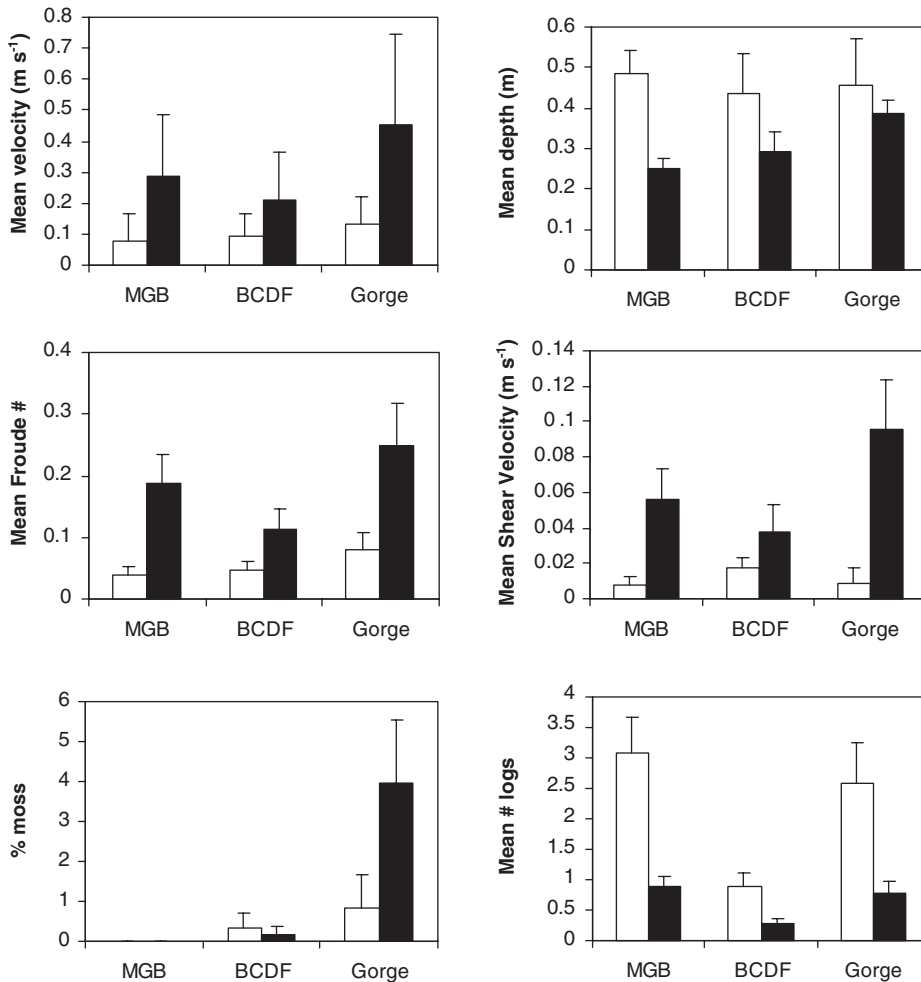


Figure 6. Means (± 1 S.E.) of selected hydraulic and organic matter variables in pools (open bars) and runs (grey bars) in MGB, BCDF and Gorge River Styles. $n=6$ for all bars.

Table 10. Results of ANOVA comparing organic variables between River Styles and geomorphic units

| | df | Moss | | | Filamentous algae | | | Logs | | |
|-----------------------------|----|-------|----------|----------|-------------------|----------|----------|--------|----------|----------|
| | | SS | <i>F</i> | <i>P</i> | SS | <i>F</i> | <i>P</i> | SS | <i>F</i> | <i>P</i> |
| River Style (RS) | 2 | 0.097 | 7.775 | 0.022 | 0.150 | 0.220 | 0.809 | 5.488 | 2.427 | 0.169 |
| Geomorphic unit | 1 | 0.029 | 7.770 | 0.032 | 0.008 | 0.375 | 0.563 | 0.084 | 0.646 | 0.557 |
| RS \times Geomunit | 2 | 0.061 | 8.273 | 0.019 | 0.069 | 1.683 | 0.263 | 0.670 | 0.646 | 0.557 |
| River(RS) | 6 | 0.038 | 2.160 | 0.102 | 2.048 | 9.490 | 0.000 | 6.785 | 1.444 | 0.241 |
| Geomunit \times River(RS) | 6 | 0.022 | 1.270 | 0.325 | 0.122 | 0.566 | 0.751 | 3.109 | 0.662 | 0.681 |
| Residual | 16 | 0.046 | | | 0.576 | | | 18.012 | | |

SNK comparisons
Pools: MGB = BCDF = Gorge
Runs: MGB = BCDF < Gorge

The results of this study suggest that River Styles reach-scale classification has some ecological relevance at the scale of geomorphic units. In the geomorphic units examined for the three River Styles, macroinvertebrate communities were more similar within some River Styles than between them. However, there was considerable between-river biotic variability within the MGB style, such that the pools and runs in sampled rivers could not readily be separated from the Gorge style in terms of macroinvertebrate community structure. Furthermore, differences between macroinvertebrate communities in the pools and runs of all River Styles were relatively small, and related more to the relative abundances of families than to their presence or absence. Some important habitat variables differed between styles, most notably substrate composition, but others did not. As such, River Styles classification alone may be insufficient to group sites with ecologically similar pools and runs.

Of the various environmental attributes considered here, only substrate composition, as indicated by mean phi classes, showed significant differences between all three River Styles, and these differences were evident in all geomorphic units. Substrate is a primary determinant of the abundance and diversity of many aquatic organisms, especially macroinvertebrates (e.g. Ormerod and Edwards, 1987; Jowett and Richardson, 1990; Beisel *et al.*, 1998), macrophytes (Power, 1996) and algae (Bergey, 1999; Niyogi *et al.*, 1999; Downes *et al.*, 2000). In general, substrate particle size is a function of stream power and particle size decreases from steep headwater reaches (high power) to low gradient lowland rivers (Knighton, 1998). However, the differences in substrate composition observed in this study are not solely a function of distance from source, stream size, or even of slope. Reaches with virtually identical slope, catchment area, and discharge had different substrate composition. This is because valley confinement is also a determinant of unit stream power, and confined rivers have greater power per unit width of channel for a given discharge and slope than unconfined rivers. Unit power varies with the cube of velocity, and velocity decreases as cross-sectional area increases. Confined channels therefore have greater capacity to transport sediment under high flows. Thus valley confinement, the primary large-scale determinant of River Styles (Ferguson and Brierley, 1999; Brierley and Fryirs, 2000; Brierley *et al.*, 2002), has important consequences for a fundamental local habitat variable — substrate.

Other habitat variables showed some differences between pools and runs in the three River Styles examined. For example, the cover of moss was greater in Gorge reaches than either BCDF or MGB reaches. This probably reflects the larger, and therefore more stable, substrate elements in these reaches, combined with greater shading from steep valley sides. This again demonstrates how valley setting can directly (via shading) and indirectly (via stream power) influence local habitat features.

Several habitat variables were unexpectedly similar between pools and runs in Gorge and MGB reaches but different to BCDF reaches. In particular, mean velocity, and therefore Froude number, was greater in pools in MGB and Gorge reaches than in BCDF reaches, but overall discharges were not different between the River Styles. While faster currents in Gorge pools are expected (steep slopes and often downstream of fast-flowing cascades/bedrock steps), there is no obvious explanation why stream currents should also be fast in MGB pools relative to BCDF pools at similar discharge stages.

Other habitat variables are clearly not influenced by River Style. Macrophyte and algal growth showed no pattern of differences between River Styles. While substrate may influence habitat for plants, other factors that are independent of River Style will also be important (temperature, aspect, nutrient availability, etc.). Many physico-chemical factors known to be important determinants of ecological habitat will be independent of River Style (e.g. water temperature). This means that even within a catchment, two reaches of the same River Style will not necessarily have equivalent habitat and biotic assemblages, despite physical similarities.

The large-scale variables that have most often been found to be useful in predicting macroinvertebrate community composition include: catchment area, distance from source, mean annual discharge (all indicative of stream size), conductivity, alkalinity (a surrogate for geology), and altitude (which broadly indicates temperature regime) (e.g. Wright *et al.*, 1984; Moss *et al.*, 1987; Marchant *et al.*, 1997;

Newson and Newson, 2000). None of these factors are direct determinants of River Style, although many influence geomorphological processes. There is often a predictable downstream sequence of River Styles (as slope and valley shape change) such that certain River Styles are generally found at certain positions within a catchment (and therefore may be of similar size), but this is not always the case. Adjacent sub-catchments can have extremely contrasting downstream patterns of River Style (Brierley and Fryirs, 2000), and particular styles may occur in various catchment positions irrespective of stream size. As a consequence, some fundamental habitat variables (temperature, hydraulics), and therefore biotic assemblages, may vary significantly within any given River Style, even within an individual catchment.

Variability in reach-scale morphology and dynamics at similar catchment positions also means that general large-scale variables may not always be good predictors of local habitat conditions. For example, although Davies *et al.* (2000) found catchment-scale variables (catchment area, stream length, relief ratio, alkalinity, % volcanic rocks, % metasediments, dominant geology and dominant soil type) to be reasonably good predictors of local habitat conditions, their empirical model using these variables misclassified 31% of sites into groups previously classified on the basis of local habitat characteristics. River Styles classification could potentially add to these commonly used large-scale factors in grouping similar sites. Two rivers of the same style and in similar catchment positions (of similar size) are more likely to be physically and ecologically similar than are two rivers of different style in the same catchment positions, or two rivers of the same style but in different catchment positions. Including River Styles in such classifications would have the advantage of incorporating a process-based element to the classification, such that sites grouped together could be expected to exhibit similar dynamics and functional responses to catchment-scale changes. Incorporating hydrological variables into physical classifications is also likely to improve their ecological relevance, because the interaction of hydrology and morphology dictates disturbance regimes (frequency and predictability of flooding and drying, degree of substrate movement during floods, refuge availability during floods and droughts), which can have significant influence on lotic community structure and function (Lake, 2001).

The pattern of (dis)similarities within and between River Styles evident in the macroinvertebrate data presented here (pools and runs in MGB and Gorge reaches were similar to each other and contrast with BCDF reaches) was reflected in many important habitat variables, and several local habitat variables were significantly correlated with variation in the macroinvertebrate data. This suggests that macroinvertebrates are responding to local (geomorphic unit scale and smaller) habitat variables rather than to larger scale factors. This is consistent with other studies of macroinvertebrate community structure that suggest that local factors are more important than regional factors (e.g. Robson and Barmuta, 1998; Robson and Chester, 1999). Hence the relevance of hierarchical schemes for classifying macroinvertebrate habitats may only lie in the degree to which large-scale factors influence local habitat features, such that local habitat characteristics, and therefore biotic assemblages, may be predicted from larger-scale variables. If local habitat characteristics of a habitat unit (e.g. a pool) are known, placing that unit within a larger-scale context (e.g. within a River Style) may not improve the ability to predict the macroinvertebrate assemblage within it. This does not necessarily diminish the potential usefulness of hierarchical classification schemes in ecological management, provided that local habitat conditions can be accurately predicted from larger-scale factors. The reach-scale assemblage of geomorphic units will undoubtedly be more relevant to fish and other biota that move over larger spatial scales and have a greater range of habitat requirements. For example, different geomorphic units may act as feeding (runs), resting (backwater) and spawning (gravel bars) sites for fish, such that the composition of fish assemblages may be influenced by the reach-scale assemblage of geomorphic units.

The similarity of pool and run fauna is somewhat surprising, given that pools are generally slow, deep flowing habitats relative to runs. However, key habitat variables including mean phi, logs, filamentous algae, macrophytes, etc. did not differ between geomorphic units, or differed between geomorphic units

only in some River Styles (e.g. velocity and Froude number were equivalent in pools and runs in BCDF reaches). Furthermore, because all microhabitats within each geomorphic unit were sampled as part of a composite sample, expected differences due to differences in depth, velocity, etc., (where they existed, such as in Gorge reaches) may have been partially obscured by taxa found in common microhabitats such as woody debris, macrophytes, trailing vegetation, slow-flowing stream margins, etc. It is also important to note that pools and runs were defined by geomorphic factors (principally bed morphology) rather than hydraulic characteristics, hence some pools had areas of fast-flowing water and, conversely, areas of slow-flowing water were common along the margins of runs. The physical and biological similarity of pools and runs is somewhat counter to our initial hypothesis that geomorphic units comprise distinct habitats, and therefore reaches with different assemblages of geomorphic units should have different habitat characteristics. However, pools and runs are very similar geomorphic units. Indeed some geomorphologists contend that a run is merely a type, extension or part of a pool (particularly during high flows) and thus may not justify classification as a separate unit (Rowntree and Wadeson, 1999). Pools and runs were selected for this study because they were the only geomorphic units common to all three River Styles. Nevertheless, these results highlight the need for care when assigning names to habitat units, ensuring that their transitional nature is recognized explicitly. To maximize their ecological relevance, geomorphological classifications of rivers must be tied to hydraulic criteria in order to define habitat units objectively (Jowett, 1993). Thomson *et al.* (2001) have described how the addition of hydraulic units to the River Styles hierarchy provides a means of collecting habitat data (including hydraulic and vegetative characteristics) at ecologically relevant spatial scales within a geomorphic framework.

Geomorphic processes are clearly of ecological importance to river ecosystems because they are primarily responsible for determining channel and floodplain morphology and substrate composition. In turn, these factors interact with hydrology to influence disturbance regimes, flow hydraulics, riparian and instream vegetation, and fluxes of inorganic and organic materials. However, the complex interaction of geomorphological, hydrological and biotic feedbacks operating over multiple spatio-temporal scales means that there may be considerable natural variation in the range of habitats found within particular geomorphic river types. Furthermore, ecological processes are influenced by many factors that are largely independent of morphology (climate, biogeography, biotic interactions, nutrients). A classification scheme based on geomorphology alone can never provide a means of ordering ecological variability, and any scheme that groups functionally similar rivers will need to combine geomorphic and non-geomorphic features. This is routinely done at very broad scales, but ordering the enormous range and variation of geomorphic and non-geomorphic features that exist at scales most relevant to management (catchments, reaches, and habitats) remains a considerable challenge. Incorporation of factors such as stream size, altitude and hydrology into classification procedures such as the River Styles framework may enable identification of relatively discrete ranges of habitat variables, and therefore biotic communities, within particular classes.

Classification is a useful tool for researchers and managers wishing to identify functionally similar sites or to identify unique or threatened habitats. However, no single scheme is likely to have universal application. The complex interactions between geomorphology, hydrology and ecology mean that some, or even many, river systems will be unique, at least in terms of certain attributes (Kershner *et al.*, 1992; Townsend and Riley, 1999). The overarching philosophy of the River Styles framework is 'know your catchment', and the characterization methodology is principally designed to assist catchment managers develop a process-orientated, physical, understanding of particular river systems (Brierley *et al.*, 2002). Without appropriate understanding of geomorphological processes it is difficult, if not impossible, to develop effective management plans to rehabilitate or even maintain river structure and functioning. River Styles designations may form a useful basis for habitat classification and assessment, and other ecological and conservation applications, provided other biologically important factors are incorporated into the classifications.

ACKNOWLEDGEMENTS

This study was conducted as part of LWRRDC Project MQU6, funded as a collaborative grant by Land and Water Australia (LWA) and the NSW Department of Land and Water Conservation (DLWC). Fruitful discussions with Bruce Chessman, Glenda Orr and David Outhet (all at NSW DLWC) and Kirstie Fryirs (Macquarie University) greatly aided the development of this project. We are grateful to LWA and NSW DLWC for their financial support and to all the landowners who gave permission to access their land.

REFERENCES

- Anderson JR. 1993. State of the Rivers Project. Report 2. Implementation Manual. Department of Natural Resources: Queensland.
- Armitage PD, Cannan CE. 1998. Nested multi-scale surveys in lotic systems — tools for management. In *Advances in River Bottom Ecology*, Bretschko G, Helesic J (eds). Backhuys Publishers: Leiden, The Netherlands; 293–314.
- Bain MB, Hughes TC, Arend KK. 1999. Trends in methods for assessing freshwater habitats. *Fisheries* **24**: 16–21.
- Barbour MT, Gerritsen J, Snyder BD, Stribling JB. 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water: Washington, D.C.
- Beisel JN, Usseglio-Polatera P, Thomas S, Moreteau JC. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* **389**: 73–88.
- Bergey EA. 1999. Crevices as refugia for stream diatoms: effect of crevice size on abraded substrates. *Limnology and Oceanography* **44**: 1522–1529.
- Braaten PJ, Berry CR. 1997. Fish associations with four habitat types in a South Dakota prairie stream. *Journal of Freshwater Ecology* **12**: 477–489.
- Brierley GJ, Fryirs K. 2000. River styles, a geomorphic approach to catchment characterisation: implications for river rehabilitation in Bega Catchment, New South Wales, Australia. *Environmental Management* **25**: 661–679.
- Brierley GJ, 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.
- Brown AV, Brussock PP. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* **220**: 99–108.
- Clarke KR, Warwick RM. 1994. Change in marine communities: an approach to statistical analysis and interpretation. UK NERC and Plymouth Marine Laboratory: Plymouth.
- Cohen T, Brierley GJ. 1999. *River Styles in Hastings basin, mid North Coast, NSW*. Report for NSW Department of Land and Water Conservation, Department of Physical Geography, Division of Environmental and Life Sciences, Macquarie University: Sydney, NSW, Australia.
- Coys J, Nichols S, Simpson J, Norris R, Barmuta L, Chessman B, Blackman P. 2000. Ausrivas: National River Health Program predictive model manual. <http://ausrivas.canberra.edu.au/man/pred/>
- Davies NM, Norris RH, Thoms MC. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. *Freshwater Biology* **45**: 343–369.
- Davis JA, Barmuta LA. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology* **21**: 271–282.
- Downes BJ, Lake PS, Schreiber ESG, Glaister A. 2000. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia* **123**: 569–581
- Ferguson R, Brierley GJ. 1999. Downstream changes in valley confinement as a control on floodplain morphology, Lower Tuross River, New South Wales, Australia: a constructivist approach to floodplain analysis. In *Varieties of Fluvial Form*, Miller AJ, Gupta A (eds). John Wiley: Chichester; 377–407.
- Ferguson R, Brierley GJ, Reinfelds I. 1999. *River Styles in Manning Catchment, North Coast, NSW*. Project MQU1 report for Land and Water Resources Research and Development Corporation, Department of Physical Geography, Division of Environmental and Life Sciences, Macquarie University: Sydney, NSW, Australia.
- Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in watershed context. *Environmental Management* **10**: 199–214.
- Gilligan LB, Brownlow JW. 1987. Metallogenic study. In *Tamworth-Hastings 1:250 000 Metallogenic Map SH 56-13, SH 56-14, Mineral Deposit Data Sheets and Metallogenic Study*, Gilligan LB, Brownlow JW (eds), NSW Geological Survey: Sydney; 349–442.
- Harper DM, Smith CD, Barham PJ. 1992. Habitats as the building blocks for river conservation assessment. In *River Conservation and Management*, Boon PJ, Calow P, Petts GE (eds). John Wiley: Chichester; 311–319.

- Grant GE, Swanson FJ, Wolman MG. 1990. Pattern and origin of stepped-bed morphology in high gradient streams, Western Cascades, Oregon. *Geological Society of America Bulletin* **102**: 340–352.
- 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.
- Jowett IG. 1993. A method for objectively identifying pool, run and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research* **27**: 41–248.
- Jowett IG, Richardson J. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. *New Zealand Journal of Marine & Freshwater Research* **24**: 19–30.
- Kellerhals R, Church M, Bray DI. 1976. Classification and analysis of river processes. *Journal of the Hydraulics Division, American Society of Civil Engineers* **102**: 813–829.
- Kershner JL, Snider WM, Turner DM, Moyle PB. 1992. Distribution and sequencing of mesohabitats: are there differences at the reach scale? *Rivers* **3**: 179–190.
- Knighton D. 1998. *Fluvial Forms and Processes*. Arnold: London.
- Kruskal JB. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115–129.
- Lake PS. 2001. Disturbance, patchiness and diversity in streams. *Journal of the North American Benthological Society* **19**: 573–592.
- Lium BW. 1974. Some aspects of aquatic insect populations of pools and riffles in gravel bed streams in western United States. *Journal of Research, U.S. Geological Survey* **2**: 379–384.
- Logan P, Brooker MP. 1983. The macroinvertebrate faunas of riffles and pools. *Water Research* **17**: 263–270.
- Maddock I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* **41**: 373–391.
- Marchant R. 1989. A subsampler for samples of benthic invertebrates. *Bulletin of the Australian Society for Limnology* **12**: 49–52.
- Marchant R, Hirst A, Norris RH, Butcher R, Metzeling L, Tiller D. 1997. Classification and prediction of macroinvertebrate assemblages from running waters in Victoria Australia. *Journal of North American Benthological Society* **16**: 664–681.
- Montgomery DR, Buffington JM. 1998. Channel processes, classification, and response. In *River Ecology and Management*, Naiman RJ, Bilby RE (eds). Springer: New York; 13–42.
- Moss D, Furse MT, Wright JF, Armitage PD. 1987. The prediction of the macro-invertebrate fauna of unpolluted running water sites in Great Britain using environmental data. *Freshwater Biology* **17**: 41–25.
- Naiman RJ. 1998. Biotic stream classification. In *River Ecology and Management*, Naiman RJ, Bilby RE (eds). Springer: New York; 97–119.
- Naiman RJ, Lonzarich DG, Beechie TJ, Ralph SC. 1992. General principles of classification and the assessment of conservation potential of rivers. In *River Conservation and Management*, Boon PJ, Calow P, Petts GE (eds). John Wiley: Chichester; 93–123.
- Newbury R, Gaboury M. 1993. A field manual for stream habitat exploration and rehabilitation. Manitoba Habitat Heritage Corporation: Winnipeg.
- Newson MD, Harper DM, Padmore CL, Kemp JL, 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.
- Niyogi DK, McKnight DM, Lewis WM. 1999. Influences of water and substrate quality for periphyton in a montane stream affected by acid mine drainage. *Limnology and Oceanography* **44**: 804–809.
- Ormerod SJ, Edwards RW. 1987. The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye, Wales UK, in relation to environmental factors. *Freshwater Biology* **17**: 533–546.
- 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.
- Power P. 1996. Effects of current velocity and substrate composition on growth of Texas wildrice (*Zizania texana*). *Aquatic Botany* **55**: 199–204.
- Pridmore RD, Roper DS. 1985. Comparison of the macroinvertebrate faunas of runs and riffles in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research* **19**: 283–291.
- Robson BJ, Barmuta LA. 1998. The effect of two scales of habitat architecture on benthic grazing in a river. *Freshwater Biology* **39**: 207–220.
- Robson BJ, Chester ET. 1999. Spatial patterns of invertebrate species richness in a river: the relationship between riffles and microhabitats. *Australian Journal of Ecology* **24**: 599–607.
- Rosgen DL. 1994. A classification of natural rivers. *Catena* **22**: 169–199.

- Rowntree KM, Wadeson RA. 1999. A hierarchical geomorphological model for the classification of selected South African rivers. Final Report to the Water Research Commission, WRC Report No. 497/1/99, Pretoria: South Africa.
- Southwood TRE. 1977. Habitat, the templet for ecological strategies. *Journal of Animal Ecology* **46**: 357–365.
- Southwood TRE. 1988. Tactics, strategies and templets. *Oikos* **52**: 3–18.
- Specht RL. 1970. Vegetation. In *The Australian Environment*, 4th edn, Leeper GW (ed.). Commonwealth Scientific and Industrial Research Organisation and Melbourne University Press: Melbourne; 44–67.
- Taylor MP, Thomson JR, Fryirs K, Brierley GJ. 2000. Habitat mapping using the River Styles methodology. *Ecological Management and Restoration* **1**: 223–226.
- ter Braak CJF. 1995. Data analysis in community and landscape ecology. In *Ordination*, Jongman RH, ter Braak CJF, van Tongeren OFR (eds). Cambridge University Press: Cambridge, UK; 91–173.
- ter Braak CJF, Smilauer P. 1998. CANOCO Reference manual and users guide to Canoco for windows: software for Canonical Community Ordination (version 4). Microcomputer Power: Ithaca, NY, USA.
- Thomson JR, Taylor MP, Fryirs KA, Brierley GJ. 2001. A geomorphic framework for river characterization and habitat assessment. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 373–389.
- Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* **31**: 265–275.
- Townsend CR, Riley RH. 1999. Assessment of river health: accounting for perturbation pathways in physical and ecological space. *Freshwater Biology* **41**: 393–405.
- Wadeson RA. 1994. A geomorphological approach to the identification and classification of instream flow environments. *South African Journal of Aquatic Sciences* **20**: 1–24.
- Winer BJD, Brown DR, Michels KM. 1991. *Statistical Principles in Experimental Design*. McGraw-Hill: New York.
- Wright JF, Moss D, Armitage PD, Furse MT. 1984. A preliminary classification of running water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. *Freshwater Biology* **14**: 221–256.
- Young WJ. 1992. Clarification of the criteria used to identify near-bed flow regimes. *Freshwater Biology* **28**: 383–391.