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The relationships among three habitat scales and stream benthic invertebrate community structure

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SUMMARY

1. The relationships between three habitat scales and lotic invertebrate species composition were investigated for the 15 540 km^2 Yakima River basin in south-central Washington, U.S.A.
2. The three spatial scales were sample (the sampled riffle), reach (a length of ten–twenty stream widths) and segment (a length of stream of nearly uniform slope and valley form having no change in stream order).
3. Physical variables were highly correlated between scales and expressed a relationship between altitude, basin form and small-scale physical structure.
4. Multiple discriminant function analyses indicated that segment- and reach-scale variables discriminated among species-defined groups better than sample-scale variables.
5. Species composition varied along a complex altitudinal gradient of changing basin form and resultant land use.
6. There was no clear relationship between species richness and altitude on a site basis. However, when viewed at the basin scale, maximum richness was observed at the transition between montane and valley sites.

Introduction

Hynes (1975) presented the importance of viewing stream components and processes as part of a larger, interrelated system. This concept included not only in-stream components but the valleys (basins) through which streams flow. Since that seminal paper a more integrated and consequently larger scale view of stream ecosystems has developed (Vannote *et al.*, 1980; Statzner & Higler, 1986; Whittier, Hughes & Larsen, 1988; Corkum, 1989). One aspect of this larger view of the connectiveness of stream to valley has been a greater appreciation for the influence of geomorphology on lotic communities.

Physical aspects of lotic systems are strongly dependent on geomorphological structure (Strahler, 1957; Leopold, Wolman & Miller, 1964; Lotspeich, 1980; Frissell *et al.*, 1986), and characteristics of the stream valley establish limits on both the function and structure of the contained lotic communities. For instance, channel slope affects sediment size distribution in small (metres and less) habitat units (Frissell *et al.*, 1986). In turn, sediment composition has a strong influence on benthic invertebrate composition at the scale of commonly used benthic samplers (0.09 m^2) (Minshall & Minshall, 1977; Lamberti & Resh, 1979). At a larger scale, changes in channel slope influence habitat complexity, causing longitudinal variations in reach-level species richness (Statzner & Higler, 1986; Ormerod *et al.*, 1994).

Over the last several decades there has been increasing use of benthic invertebrates as indicators of the quality of lotic habitats (Hellawell, 1986; Lenat, 1988; Metcalfe, 1989; Plafkin *et al.*, 1989; Rutt, Weatherley & Ormerod, 1990; Rosenberg & Resh, 1993), specifically for the study of the chemical quality of surface waters (Winner, Boesel & Farrell, 1980; Clements, Cherry & Carins, 1988; Leland *et al.*, 1989). The sensitivity of community structure as an indicator of anthropogenically induced change in aquatic systems has been shown by long-term, large-scale field manipulations (Leland & Carter, 1985; Schindler, 1987). However, methods to accurately define and interpret the effects of natural *v* anthropogenic impacts on non-experimental aquatic communities are needed (Carins, 1981; Luoma & Carter, 1991; Rossaro & Pietrangelo, 1993). Even though techniques have been developed to predict community composition based on the influences of a few environmental factors (Wright *et al.*, 1984), the continuing loss of habitat and the lack of pristine areas (reference sites) (Sweeney, 1993) severely limits our ability to determine whether locations are impacted. Refining our understanding of the geomorphological influences on richness and composition seems an important component in both invertebrate ecology and impact assessment.

The purpose of this study was to explore the relationships among different scales of geomorphological structure and invertebrate species composition in a large river basin. Previous work has shown geomorphological influences to be scale dependent (Corkum, 1989, 1992; Quinn & Hickey, 1990; Brussock & Brown, 1991). As a result, the interpretation of these influences and their parameterization for modelling benthic community structure will also be scale dependent. To this end, three levels of scale were considered: site (sample), reach and segment. The significance of these scales to the study of stream community composition has already been demonstrated by research on geomorphological influences on fish distributions and production (Lanka, Hubert & Wesche, 1987) and studies on the life histories of aquatic insects (Resh & Rosenberg, 1989).

Study location

This study took place in the Yakima River basin in south–central Washington, U.S.A. (Fig. 1). The Yakima basin is bordered on the north and west by the Cascade Range with altitudes reaching 2495 m. Altitude decreases to 104 m at the confluence of the Yakima and Columbia Rivers. Mean annual precipitation ranges from 356 cm yr^{-1} in the Cascade Range to less than 25 cm yr^{-1} near the mouth of the basin (Rinella, McKenzie & Fuhrer, 1992). The majority of stream riffles in the basin contain basalt cobble–pebble substrates.

Land use in the Yakima basin varies with the physical setting. The north-western and western mountains, heavily forested in spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), and at lower altitudes pines (*Pinus ponderosa*), are generally used for timber production. The valleys are used for the cultivation of fruits, grains, alfalfa and hops. Livestock grazing occurs throughout the middle and lower basin. As a result of these extensive agricultural practices in the lower, more arid portions, the Yakima is one of the most heavily irrigated basins in the U.S.A. (Rinella *et al.*, 1992). Irrigation practices have changed historic water flow patterns. In the agricultural areas, valley streams are channelized into drains that transport irrigation water from the fields to the mainstem streams.

Stream water in the basin is neutral to slightly alkaline. Specific conductivities increase from a low of 75 µS cm^{-1} in the mountains to a high of 300 µS cm^{-1} in the lower valleys. Total phosphorus increases from up to 0.04 mg l^{-1} in the mountains to 0.1 mg l^{-1} or more in the agricultural drains. Nitrite/nitrate nitrogen increases from 0.13 mg l^{-1} in the mountains to 1.0 mg l^{-1} or more in the drains (Rinella *et al.*, 1992).

Materials and methods

Sixty sites were sampled on permanent second to sixth order streams over two contiguous weeks during the low flow period of October and November 1990. Sampling was done at northern, higher elevation sites before southern, lower sites to avoid winter weather conditions and thereby increase equality of effort among sites.

Physical variables

Physical measurements of sample, reach and segment were taken in the field and from topographic maps (Table 1). Field physical measurements were taken at two levels of resolution: the location where the biological sample was taken (the sampled riffle) and over the reach (ten–twenty stream widths) that included the sample location. In general, sample variables were measured along two–three transects per riffle at sites on fourth or lower order streams. On higher order streams two–three transects extended perpendicularly from the margin to near the middle of the stream. The transects were placed at both ends

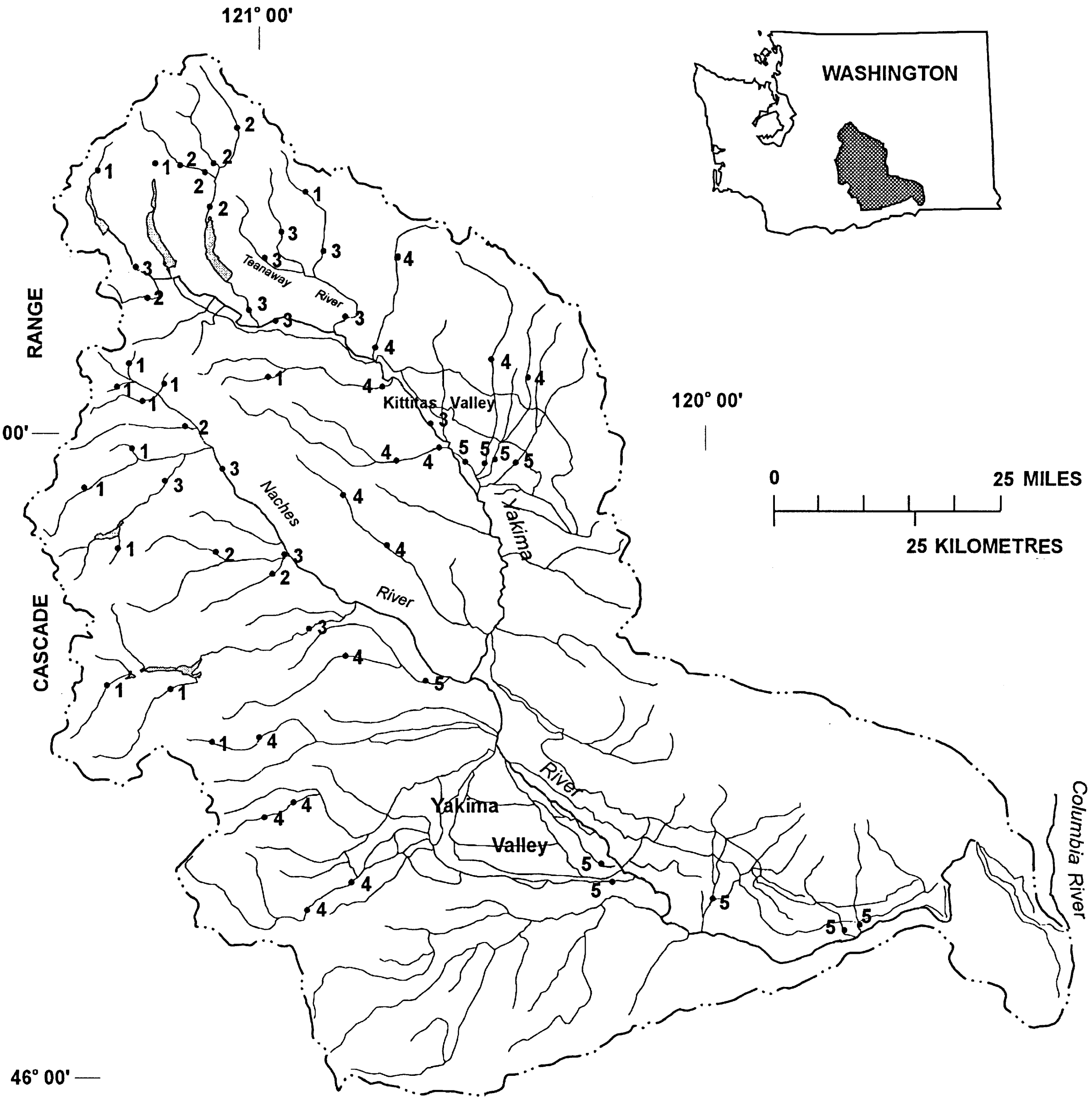

Fig. 1 Yakima River basin. Sites are shown as filled circles. Numbers associated with circles indicate the TWINSPAN group to which the site belongs.

and the middle of the portion of the riffle sampled for invertebrates. Measurements were taken at 0.2, 0.4, 0.6 and 0.8 of transect length. Velocity was measured with a Pigmy- current meter at 0.6 of the water depth. Substratum particle size was determined for each transect by estimating dominant and largest particle size with an underwater viewing box. Particles were categorized on the phi-scale as: boulder (> 256 mm), large cobble (> 128 mm), small cobble (> 64 mm), pebble (> 32 mm), gravel (> 2 mm) and sand (Cummins, 1962). Mean embeddedness was estimated by picking, at random, a minimum of three particles (pebble or larger) along each transect and recording percentage depth of embeddedness. Consolidation of the sediment (resistance to displacement) was estimated on a 4-point scale from 1 = moves easily under foot (rounded, well-sorted sediments) to 4 = very difficult to displace. Water-surface gradient was measured over the area sampled for benthic invertebrates with a water level ≈ 10 m in length. Canopy cover

Table 1 Acronyms, transformations and definitions of measured physical variables. Transformations: a = arcsin, l = $\log_{10}$ and s = square root

Sample variables		
AVGDPTH	l	Mean sampled riffle depth (m)
CVDPTH		Coefficient of variation of depth
AVGVEL		Mean sampled riffle velocity ($\mathrm{m\ s^{-1}}$)
CVVEL		Coefficient of variation of velocity
EMBED	s	Percentage embeddedness to nearest 10%
CANJUN	a	Percentage shading in June
CANOCT	a	Percentage shading in October
CONSOLID		Consolidation: 1 = least, 4 = most
SFCGRAD		Sampled riffle water-surface gradient (%)
SAMDPS		Dominant particle size (phi)
SAMLPS		Largest particle size (phi)
Reach variables		
RIF%	a	Percentage of riffle in reach
RUN%	a	Percentage of run in reach
POOL%	a	Percentage of pool in reach
RIFDPTH		Median riffle depth (1 < 0.15 m, 2 < 0.3 m, 3 < 0.6 m, 4 < 1.2 m, 5 > 1.2 m)
POOLDPTH		Median pool depth (1 < 0.15 m, 2 < 0.3 m, 3 < 0.6 m, 4 < 1.2 m, 5 > 1.2 m)
RIFSED	a	Riffle dominant particle size (phi)
POOLSED		Pool dominant particle size (phi)
ALGAE	a	Riffle cover (0 = 0%, 1 < 10%, 2 = 11–30%, 3 = 31–70%, 4 = 70–100%)
MACROPH	a	Riffle cover (0 = 0%, 1 < 10%, 2 = 11–30%, 3 = 31–70%, 4 = 70–100%)
MOSS	a	Riffle cover (0 = 0%, 1 < 10%, 2 = 11–30%, 3 = 31–70%, 4 = 70–100%)
WIDTH	l	Wetted width at sampled riffle (m)
RHSLP	l	Map-derived reach slope (%)
Segment variables		
SGLGTH	l	Segment length (m)
SGSLP	s	Segment slope (%)
SGORDER		2–6
SGSIN	l	Ratio of stream length to valley length
ALT		Altitude of site (m)
VALWDTH	l	Valley width (m)
VALSSMN	s	Minimum valley side slope (%)
VALSSMX	s	Maximum valley side slope (%)
AREA	l	Basin area ($\mathrm{km^2}$)
Land-use variables		
FOREST%	a	Percentage of basin as forest
RANGE%	a	Percentage of basin as rangeland
AGRI%	a	Percentage of basin as agriculture
URBAN%	a	Percentage of basin as urban
COND		Specific conductivity ($\mathrm{\mu S\ cm^{-1}}$)

was measured with a Solar Pathfinder™ as percentage of total daily insolation that was blocked (Platts *et al.*, 1987).

Reach variables were measured either on site or determined from topographic maps. On-site reach variables were linear lengths of riffles, pools and runs measured with a range finder over ten–twenty stream widths and converted to percentage of reach. Median depth categories of the riffles and pools also were estimated. Aquatic macrophyte, moss and algal cover was estimated as percentage cover. Dominant substratum particle sizes were estimated for riffles and pools as was done for site variables. Reach slope was determined from 1 : 24 000 scale topographic maps over a length of uniform slope which included the site. The minimum length (≈ 610 m) was limited by that which could be measured with a map wheel.

All segment variables were obtained from 1 : 24 000 scale topographic map data unless otherwise stated. Segment length was determined by measuring the length of stream that had a reasonably consistent slope, similar valley shape and no change in stream order (Frissell *et al.*, 1986). Segment slope was segment elevation drop divided by segment length. Sinuosity was determined by dividing segment stream length by straight valley length. Valley width was measured at the first 12.2 m topographic map contour and valley side slopes were measured perpendicular to the valley bottom over a 304 m distance from the channel (Cupp, 1989). Stream order (Strahler, 1957) was determined by occurrence of solid stream lines. Drainage area upstream of the site was determined with a planimeter by moving perpendicularly from the site to the appropriate topographic divide and following it on a 1 : 100 000 scale map. Percentage land use estimates were taken from a 1974 1 : 250 000 scale map.

In addition to the above measurements, water samples were taken for assessing specific conductivity.

Biological samples

Benthic invertebrates were collected at each site in riffle habitat. Two separate 3 × 0.3 m travelling kicknet samples were taken. Mesh size was 425 μm. In small streams, samples were taken to include as much of the presumed riffle variability as possible (Godbout & Hynes, 1982). In larger streams, samples were taken from near mid-channel and from areas near the margin. Samples were preserved with 10% formalin in the field, washed and transferred to 75% ethanol in the laboratory and identified to the lowest practicable taxonomic level, normally species. Operational taxonomic units (such as *Hydropsyche* sp. 1) were employed when necessary.

Numerical techniques

Jaccard coefficients were calculated between all pairs of sites. These coefficients are based on presence/absence species data and were evaluated to assess species turnover across the basin.

Species-by-sample data were classified by the hierarchical divisive method, TWINSPAN (Hill, 1979). Abundance values were used with pseudospecies cut levels of 0, 10, 100, 1000. All taxa collected and identified were used in the analysis.

Site groups defined by TWINSPAN were used in multiple discriminant function analyses (MDFA) to determine the relationship between the measured physical variables and the species-defined site groups. We chose normal instead of stepwise MDFA, thereby avoiding the possibility of the numerical method randomly choosing significant variables from a suite of highly correlated physical variables (Green, 1979; Williams, 1983).

All physical variables were first analysed by a non-parametric ANOVA (Kruskal–Wallis) using TWINSPAN group membership as the factor variable (Leach, 1979). In general, physical variables that showed significant differences ($P < 0.05$) among TWINSPAN groups were chosen for further analyses. A second analysis was done using only four of the five TWINSPAN groups, as one group was very different from the remaining four. Physical variables were transformed to approximate normality prior to MDFA. Differences in the percentage of sites correctly classified by the MDFA using scale-specific physical variables and relative site group separations were used as measures of the ability of the scales to discriminate among the TWINSPAN species groups.

Smaller scale geomorphological variables tend to be a function of larger scale structure (Strahler, 1957; Frissell *et al.*, 1986). As a result, canonical correlation analyses (CCAs) were used to assess the correlation and redundancy among sets of physical variables (Ebisemiju, 1988).

Results

Total richness of the basin was 300 species as measured during the autumn 1990 sampling period. Richness among sites ranged from twenty to sixty-nine species. As an indication of species turnover across the basin, Jaccard coefficients ranged from 0.0 (no species in common) to 0.57 (1.0 represents two samples with identical species present). Of the 1770 possible site pairs, only eight Jaccard coefficients equalled 0.0, indicating there were few site comparisons with completely different species composition.

Five different site groups were derived using TWINSPAN (Hill, 1979) (Fig. 1). Group 5, valley sites, separated at the first division. These ten sites had similar species composition and lacked many species present in the remaining sites. The fifty remaining sites were divided at the second and third division in the TWINSPAN classification, producing a total of five groups. Differences in taxon richness were significant among

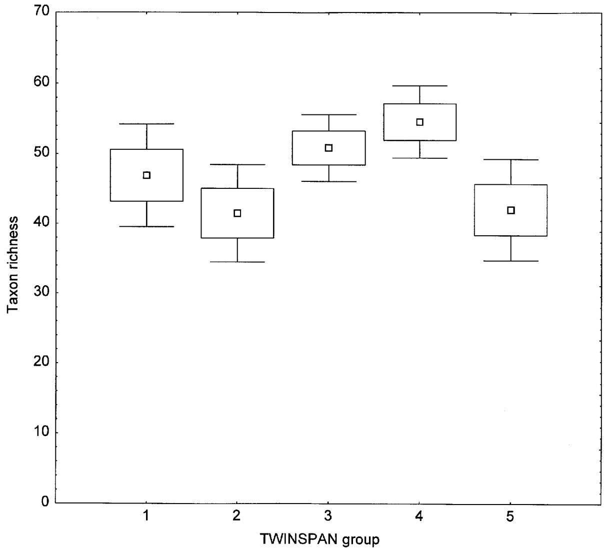

Fig. 2 Mean taxon richness of TWINSPAN groups. Central box is the mean, large box is ± 1 SE, end of whisker is ± 1.96 SE. *n* for groups 1–5 is 14, 9, 12, 15 and 10, respectively.

the five groups ($P < 0.05$, ANOVA) (Fig. 2). *Post-hoc* comparisons showed that differences between groups 4 and 5 ($P < 0.05$, Newman–Keuls) contributed to the significant differences in richness among the five groups. Although richness varied only slightly among the defined groups, the taxa within each group changed markedly (Table 2). Abundance varied greatly among groups ($P < 0.001$, Kruskal–Wallis) and had a general trend of increasing from group 1 to group 5 (Fig. 3).

Description of groups

Many physical characteristics varied among the groups for each level of resolution (Table 3). Most variables showed significant differences among the five groups (Table 4), although when group 5 was eliminated from the analyses, fewer significant differences in the physical variables existed among the remaining four groups (Table 4).

Group 1 sites were small, high-gradient streams in narrow, steep-sided valleys. They had a mean altitude of 1009 m, were heavily forested (95%) and had the highest canopy cover (72%). Taxa most frequently found at many group 1 sites but rarely in other groups were *Zapada columbiana*, *Z. frigida* Claassen, *Parapsyche elsis*, *Rhyachophila* nr *blarina* Ross, *R. vocala* and *R. valuma*. The most abundant taxa were *Polycelis coronata*, *Mesenchytraeus* sp. 1, *Baetis tricaudatus*, *Rhithrogena* nr *robusta*, *Drunella doddsi*, *Cinygmula* sp. and nr *Doddsia occidentalis*.

Group 2 sites had the second highest mean altitude (781 m) and were located in sub-basins ≈ 3 times larger than group 1 sites. Their basins were 94% forested but mean site canopy cover declined to 65% due to greater stream widths. Unlike group 1, there were no taxa found exclusively in group 2. However, several taxa present in the group 2 and lower elevation sites were absent or very rare in group 1 sites, such as *Nais behningi*, *N. communis*, *Hydrophsyche* nr *amblis* and *Rheotanytarsus* sp. Taxa that were exceptionally abundant in group 2 sites were *Mesenchytraeus* sp. 1, *Baetis tricaudatus*, *Diphetor hageni*, *Cinygmula* sp., *Zapada cinctipes* and *Sweltsa* sp.

Group 3 sites included the highest stream order sites sampled in the upper half of the basin, including all upstream mainstem sites. Mean altitude of these sites was 669 m. Although 96% of their basin area was forested, site canopy cover decreased to one-third (23%) of group 1 and group 2 sites due to widening of the channel and differences in riparian vegetation. Taxa with the highest abundances at these sites were *Mesenchytraeus* sp. 1, *Nais behningi*, *Baetis tricaudatus*, *Cinygmula* sp., *Ephemerella* nr *infrequens*, *Zapada cinctipes*, *Sweltsa* sp. and *Antocha* sp. As in group 2, there were no taxa found exclusively in group 3, although the following were quite rare in the higher elevation groups but abundant in group 3: *Acentrella turbida*, *Osobenus yakimae*, *Orthocladius appersoni*, *Optioservus seriatus* and *Atherix* sp.

Group 4 sites were on lower elevation tributaries and had a mean altitude of 656 m, approximately the same as group 3. These sites were similar to group 1 sites in having high mean water-surface gradient (2.38%) and similar channel depths. They also were similar to group 2, having similar widths and reach slopes. The basins these streams drained were still heavily forested (90%) but the mean canopy cover was only 48%. Biologically, group 4 was the transition between the higher elevation sites and valley sites. This group had slightly higher mean richness but ≈ 30% higher total richness than any of the other four groups. It was the lower altitudinal limit for many species, such as *Epeorus (Ironopsis)* sp., *Cinygmula* sp., *Drunella doddsi*, nr *Doddsia occidentalis* and *Sweltsa* sp. Major taxa absent or rare from groups 1–3, first appearing in group 4 were *Cheumatopsyche* sp., *Aulod-*

Table 2 Taxonomic components of TWINSPAN groups representing a constancy (defined as the frequency of a taxon in a group) of ⩾ 50% within any group. Values are $\log_{10}(x + 1)$. Designation of nr indicates near, e.i. indicates early instar and imm indicates immature

	Group				
	1	2	3	4	5
Rhyacophila vocala Milne	1.7	0.3	0.3	0.3	
Rhyacophila valuma Milne	1.7	0.8	0.3		
Prionocypris longiforma Dobbin	2.2	1.9		0.3	
Parapsyche elsis (Milne)	1.8	0.3			
Zapada columbiana Claassen	2.3	1.5			
Zapada oregonensis Claassen	2.5	2.1	2.0	1.5	
Epeorus (*Ironopsis*) sp.	2.6	2.1	1.1	1.1	
nr *Doddsia occidentalis* (Banks)	3.5	2.3	0.8	2.5	
Stempellinella sp.	1.6	1.1			
Neophylax sp.	0.9	2.2	0.3	1.0	
Brillia retifinis Saether	1.9	1.6		1.7	1.3
Megarcys sp.	1.7	1.0	1.4		
Hexatoma sp.	1.4	0.6	1.1	0.6	
Polycelis coronata (Girard)	2.7	2.6	2.2	2.3	0.9
Caudatella hystrix Traver	1.9	1.7	1.7	0.5	
Rhithrogena nr *robusta* Dodds	2.7	2.0	2.0	1.4	
Limnephilidae e.i.	1.8	0.3	1.5	1.0	
Rhyacophila betteni gr.	2.3	1.5	1.0	1.4	
Ameletus nr *sparsatus* McDunnough	1.9	2.1	1.4	1.3	
Drunella doddsi Needham	2.4	2.0	2.4	2.0	
Arctopsyche grandis (Banks)	1.9	2.0	1.4	1.4	
Doroneuria sp.	1.8	1.3	0.8	0.9	
Ephemerellidae e.i.	2.3	1.3	2.1	0.8	
Eucapnopsis brevicauda (Claassen)	1.4	1.9	2.0	1.1	
Perlodidae tp2 e.i.	2.4	1.9	2.2	2.4	
Micrasema sp.	1.7	1.7	0.3	2.3	
Rhyacophila narvae Navas	1.9	1.1		1.5	
nr *Capnia* e.i.	2.8	2.5	1.5	2.3	0.8
Dicranota sp.	1.8	0.5	1.0	1.8	1.2
Rhyacophila acropedes gr.	2.2	1.8	1.6	2.6	0.5
Drunella grandis (Eaton)	2.0	1.5	1.8	1.8	
Mesenchytraeus sp. 1	3.6	3.1	3.8	3.3	
Rhithrogena nr *hageni* Eaton	2.8	2.1	3.2	3.2	1.9
Cinygmula sp.	3.6	3.3	3.4	3.8	
Calineuria californica (Banks)	1.7	1.7	2.1	2.0	
Zapada cinctipes Banks	2.4	2.9	2.6	3.0	
Cricotopus (*Nostococladius*) sp.	1.9	1.5	3.3	2.8	
Lepidostoma e.i.	1.8	1.7	3.5	2.4	
Sweltsa sp.	2.5	2.4	3.2	2.7	
nr *Pericoma*	1.4	1.6	1.9	2.8	
Epeorus sp.	2.5	2.4	2.7	3.3	1.7
Simulium tuberosum complex (Lundstrom)	0.8	1.5	2.2	2.2	
Claassenia sabulosa (Banks)		1.2	1.6	1.3	
Orthocladius frigidus Zetterstedt	1.4	0.3	2.2	0.3	
Brachycentrus americanus (Banks)	0.5	1.8	2.5	1.9	
Hesperoperla pacifica Banks		1.1	1.5	1.8	
nr *Cryptolabis*			2.7		
Orthocladius appersoni Soponis		1.3	2.2	1.6	
Acentrella turbida (McDunnough)	0.3	1.0	2.4	1.0	
Cricotopus sp. 2		1.0	2.0	1.6	

Table 2 *Cont.*

	Group				
	1	2	3	4	5
Petrophila sp.				1.0	
Brychius sp.				0.3	
Atractides sp.	0.8		1.5	2.0	
Osobenus yakimae (Hoppe)		0.5	1.9	1.8	
Skwala sp.	0.7	1.2	1.9	2.4	1.3
Polypedilum nr *aviceps* Townes		1.3	2.8	2.1	0.8
Lebertia sp.	1.2	1.3	2.0	2.3	1.2
Optioservus quadrimaculatus (Horn)	1.1	0.6	1.5	2.3	1.1
Simulium canadense Hearle	1.1			4.0	2.0
Perlodidae tp1 e.i.	0.7		2.5	2.9	1.7
Diphetor hageni (Eaton)	1.6	2.2	1.3	2.9	1.5
Parametriocnemus sp.	1.7	0.8		2.4	1.5
Glossosoma sp.	2.5	1.4	2.2	2.3	2.0
Micropsectra sp.	2.5	1.2	2.2	2.1	2.2
Tvetenia bavarica gr. sp.	1.7	2.5	2.2	2.2	2.0
Baetis tricaudatus Dodds	3.5	3.5	3.4	4.2	4.2
Ephemerella nr *infrequens* e.i. McDunnough	2.3	2.9	3.4	3.7	3.1
Paraleptophlebia sp.	2.7	2.6	2.5	3.6	2.5
Antocha sp.	1.5	1.3	3.0	2.8	2.2
Hydropsyche nr *amblis* Ross		2.7	3.3	3.4	2.6
Nais behningi (Michaelsen)	0.8	2.0	3.4	2.9	2.4
Eukiefferiella brehmi gr. sp.	1.7	1.0	2.5	1.9	1.5
Optioservus seriatus (LeConte)			1.9	2.3	1.8
Cricotopus tremulus gr. sp.			1.9	2.1	1.8
Optioservus spp. (larvae)			2.7	3.1	2.8
Zaitzevia parvula (Horn)	0.5	1.0	1.6	2.7	2.7
Eiseniella tetraedra (Savigny)			1.1	1.7	1.6
Nais variabilis (Piguet)			1.1	1.9	1.8
Rheotanytarsus sp.		2.1	2.0	2.7	3.0
Hydropsychinae e.i.		2.0	2.8	2.9	3.1
Nais communis (Piguet)		2.0	2.4	2.5	2.6
Hydropsyche cockerelli Banks		1.3	1.9	0.3	2.4
Mermithidae	0.5	0.7	1.7		2.0
Cheumatopsyche sp.			2.6	2.8	3.2
Eukiefferiella claripennis gr. sp.			1.3	2.4	3.0
Aulodrilus pluriseta (Piguet)				1.6	2.3
Simulium vittatum complex Zetterstedt	0.5			2.0	3.4
Crangonyx obliquus-richmondiensis gr.					2.4
Diamesa sp.			2.0	1.5	2.5
Tricorythodes sp.					2.4
Hydropsyche nr *californica* Banks				0.3	3.3
Tubificidae tp1 imm					3.0
Nais simplex (Piguet)				0.7	1.8
Dugesia sp.					2.9
Thienemanniella sp.	0.3		1.1	1.3	2.2
Tubificidae tp2 imm				0.5	2.0
Cricotopus bicinctus gr. sp.			1.2	1.6	2.3
Bothrioneurum vejdovskyanum Stolc				1.1	3.1
Cricotopus trifascia gr. sp.				0.3	2.6
Caecidotea racovitzai (Williams)					3.3
Pisidium sp.		0.8	1.0	1.6	2.1

Table 3 Physicochemical characteristics per TWINSPAN group. Subscript a = mean (with standard deviation). Subscript m = median (with 25–75% range)

	Group 1 (*n* = 14)	Group 2 (*n* = 9)	Group 3 (*n* = 12)	Group 4 (*n* = 15)	Group 5 (*n* = 10)	All groups (*n* = 60)
Sample						
AVGDPTH$_a$ (m)	0.25 ± 0.074	0.41 ± 0.236	0.31 ± 0.100	0.17 ± 0.046	0.25 ± 0.183	0.26 ± 0.149
CVDPTH$_a$	18.1	13.8	17.0	23.3	13.6	17.8
AVGVEL$_a$ (m s^{-1})	0.76 ± 0.28	0.76 ± 0.23	0.72 ± 0.18	0.59 ± 0.13	0.55 ± 0.20	0.68 ± 0.22
CVVEL$_a$	29.79	29.11	24.83	35.57	27.30	29.73
EMBED$_m$ (%)	23.5 (15.5)	16.0 (5.5)	22.0 (16.5)	11.0 (14.0)	37.0 (23.0)	20.0 (20.0)
CANJUN$_a$ (%)	49 ± 24	46 ± 30	9 ± 11	41 ± 29	6 ± 12	31 ± 29
CANOCT$_a$ (%)	72 ± 25	65 ± 29	23 ± 18	48 ± 29	10 ± 14	45 ± 33
CONSOLID$_m$ (1–4)	3.0 (0.5)	3.0 (1.3)	2.8 (1.0)	2.0 (1.0)	3.0 (1.0)	3.0 (1.0)
SFCGRAD$_a$ (%)	2.01 ± 0.86	1.73 ± 1.18	1.37 ± 0.77	2.38 ± 1.02	1.29 ± 0.68	1.81 ± 0.98
SAMDPS$_m$ (phi)	–7 (0)	–7 (1)	–7 (1)	–7 (0)	–6 (1)	–7 (0)
SAMDPS$_m$ (phi)	–7 (1)	–8 (0.5)	–8 (0.5)	–7 (1)	–7 (2)	–7 (1)
Reach						
RIF%$_a$ (%)	77 ± 22	78 ± 31	78 ± 25	71 ± 19	38 ± 34	69 ± 29
RUN%$_a$ (%)	7 ± 11	5 ± 16	10 ± 16	8 ± 12	55 ± 35	15 ± 25
POOL%$_a$ (%)	15 ± 12	16 ± 16	10 ± 10	20 ± 15	6 ± 7	14 ± 13
RIFDPTH$_m$ (1–5)	2.5 (1.25)	3.0 (1.2)	2.75 (0.5)	2.0 (0.5)	2.0 (1.0)	2.5 (1.25)
POOLDPTH$_m$ (1–5)	4.0 (0.5)	4.5 (1.5)	4.0 (1.0)	3.25 (1.0)	3.75 (1.5)	4.0 (1.0)
RIFSED$_m$ (phi)	–8 (1)	–8 (1)	–8 (0.5)	–7 (1)	–6.5 (2)	–8 (1)
POOLSED$_m$ (phi)	–7 (1)	–7 (2)	–7.5 (1.5)	–7 (1.25)	–7 (1)	–7 (2)
ALGAE$_m$ (0–4)	1.0 (1.0)	0.5 (1.0)	1.5 (1.0)	1.0 (1.0)	2.25 (2.0)	1.0 (1.5)
MACROPH$_m$ (0–4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (2.75)	0.0 (0.0)
MOSS$_m$ (0–4)	1.0 (1.0)	1.0 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (1.0)
WIDTH$_a$ (m)	7.5 ± 4.0	18.2 ± 17.1	25.3 ± 15.2	6.3 ± 2.3	4.6 ± 2.9	11.9 ± 12.4
RHSLP$_a$ (%)	3.4 ± 2.6	2.2 ± 1.5	0.9 ± 0.5	2.2 ± 1.0	0.9 ± 0.8	2.0 ± 1.8
Segment						
SGLGTH$_a$ (m)	4994 (± 3024)	4402 (± 1348)	11 465 (± 3899)	7071 (± 2087)	5004 (± 2592)	6720 (± 3713)
SGSLP$_a$ (%)	2.9 (± 2.0)	2.0 (± 1.4)	0.9 (± 0.5)	2.2 (± 0.9)	0.8 (± 0.6)	1.8 (± 1.5)
SGORDER$_m$ (2–6)	3.0 (0.5)	4.0 (1.0)	5.0 (1.5)	4.0 (1.0)	4.0 (1.0)	4.0 (1.0)
SGSIN$_a$ (D)	1.14 (± 0.11)	1.14 (± 0.12)	1.20 (± 0.13)	1.09 (± 0.06)	1.14 (± 0.20)	1.14 (± 0.13)
ALT$_a$ (m)	1009 (± 161)	781 (± 92)	669 (± 116)	656 (± 154)	321 (± 135)	704 (± 258)
VALWDTH$_a$ (m)	212 (± 160)	231 (± 196)	553 (± 444)	247 (± 137)	5442 (± 3507)	1164 (± 2381)
AREA$_a$ (km^2)	41 (± 33)	121 (± 116)	631 (± 673)	154 (± 95)	115 (± 141)	211 (± 371)et
VALSSMN$_a$ (%)	15.9 (± 10.2)	18.7 (± 14.1)	5.8 (± 5.6)	16.8 (± 11.7)	3.6 (± 8.0)	12.4 (± 11.6)
VALSSMX$_a$ (%)	41.4 (± 11.3)	42.0 (± 7.7)	33.1 (± 18.9)	30.9 (± 14.4)	5.2 (± 12.3)	31.2 (± 18.2)
FOREST%$_a$ (%)	95 (± 8)	94 (± 5)	96 (± 4)	90 (± 12)	4 (± 12)	79 (± 35)
RANGE%$_a$ (%)	4 (± 6)	1 (± 2)	1 (± 2)	8 (± 11)	11 (± 13)	5 (± 9)
AGRI%$_a$ (%)	0 (0)	0 (0)	1 (± 1)	2 (± 4)	76 (± 23)	13 (± 30)
URBAN%$_a$ (%)	0 (0)	0 (0)	1 (± 1)	0.2 (± 0.8)	8 (± 13)	1.6 (± 5.9)
COND$_a$ (μs cm^{-2})	57 (± 37.0)	40 (± 16.6)	75 (± 27.9)	127 (± 51.3)	282 (± 71.6)	115 (± 94.6)

rilus pluriseta and *Eukiefferiella claripennis* gr. The most abundant taxa in group 4 were *Mesenchytraeus* sp. 1, *Baetis tricaudatus*, *Cinygmula* sp., *Epeorus* sp., *Rhithrogena* nr *hageni*, *Ephemerella* nr *infrequens*, *Paraleptophlebia* sp., *Zapada cinctipes*, *Skwala* sp., *Hydropsyche* nr *amblis*, *Optioservus* larvae, *Antocha* sp. and *Rheotanytarsus* sp.

Group 5 consisted of the sites that the TWINSPAN analysis separated from the previous four groups on the first division. They were all in valley agricultural areas and most were partially channelized. Mean altitude was 321 m. The standard deviation of the elevation was high because some group 5 sites were in the Kittitas Valley and others in the lower Yakima Valley (Fig. 1). Land use for the sites averaged 76% agriculture, 11% range and 8% urban (Table 3). This contrasts sharply with the other four groups. Group

Table 4 Non-parametric ANOVA (Kruskal–Wallis) of physical variables among TWINSPAN groups within each scale. Left columns are the analyses with all sites, right columns are the analyses excluding group 5 (the valley sites). †Variable was not used in MFDA or CCA. Significant levels are $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

	Groups			Groups			Groups	
Sample	1–5	1–4	Reach	1–5	1–4	Segment	1–5	1–4
AVGDPTH	**	***	WIDTH	***	***	SGLGTH†	***	***
CVDPTH†			RIF%	*		SGSLP	***	**
AVGVEL			RUN%	***		SGORDER†	***	***
CVVEL†			POOL%†			SGSIN	*	*
EMBED	**	*	RIFDPTH	**	**	ALT	***	***
CANJUN†	***	***	POOLDPTH	*	*	VALWDTH	**	*
CANOCT	***	***	RIFSED	*		AREA	***	***
CONSOLID			POOLSED			VALSSMN	***	*
SFCGRAD	*	*	ALGAE	***	**	VALSSMX	***	
SAMDPS†	*		MACROPH	*				
SAMLPS	*		MOSS	**	***			
			RHSLP	***	**			

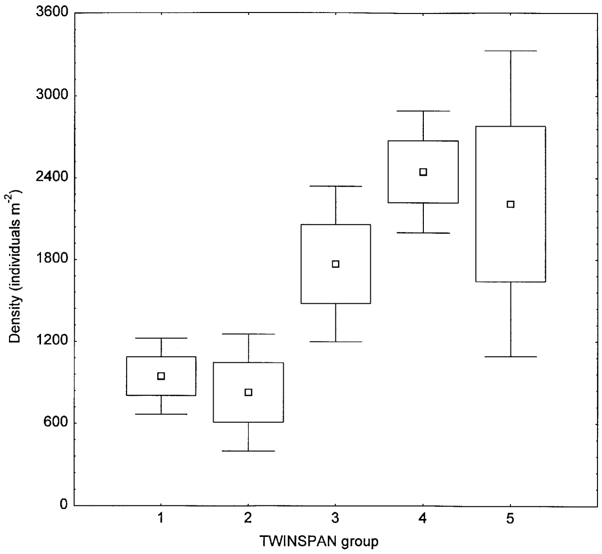

Fig. 3 Mean density (ind. m^{-2}) of TWINSPAN groups. Central box is the mean, large box is ± 1 SE, end of whisker is ± 1.96 SE. *n* for groups 1–5 is 14, 9, 12, 15 and 10, respectively.

Fig. 4 Taxon richness of major taxonomic categories within TWINSPAN groups. TWINSPAN division hierarchy is diagrammed below.

	grp1	grp2	grp3	grp4	grp5
Oligochaeta	3	5	10	21	25
Crustacea	1	1	0	2	13
Ephemeroptera	24	20	17	21	12
Plecoptera	28	24	20	27	4
Trichoptera	27	25	24	27	9
Coleoptera	4	6	5	9	6
Chironomidae	27	22	40	52	43
Mollusca	0	1	1	5	6
Total richness	114	104	117	164	118

5 sites had a characteristic fauna with very low overlap with groups 1–3 and was most similar to group 4. The most numerous taxa were *Baetis tricaudatus*, *Ephemerella* nr *infrequens*, *Eukiefferiella claripennis* gr., *Dugesia* sp., *Hydropsyche* nr *californica*, *Diamesa* sp., *Cricotopus trifascia* gr. sp., *Thienemanniella* sp. *and Polypedilum* nr *convictum* Walker.

Oligochaete, crustacean, chironomid and molluscan richness generally increased from group 1, high elevation sites to the lower elevation group 5 valley sites (Fig. 4). Mayfly, stonefly and caddisfly richness was rather similar among groups 1–4 but decreased markedly in group 5 (Fig. 4).

Multiple discriminant function analyses

Variables used in the MDFA at the different levels of resolution are listed in Table 4. Sample variables SAMDPS and CANJUN were highly correlated with two other variables, SAMLPS ($r = 0.76$, $P < 0.001$, Spearman r) and CANOCT ($r = 0.88$, $P < 0.001$, Spearman r), respectively. Reach variable POOL% was not used because it is linearly dependent on RIF% and RUN%. Segment variable SGORDER also was not used because it was highly correlated with AREA ($r =$

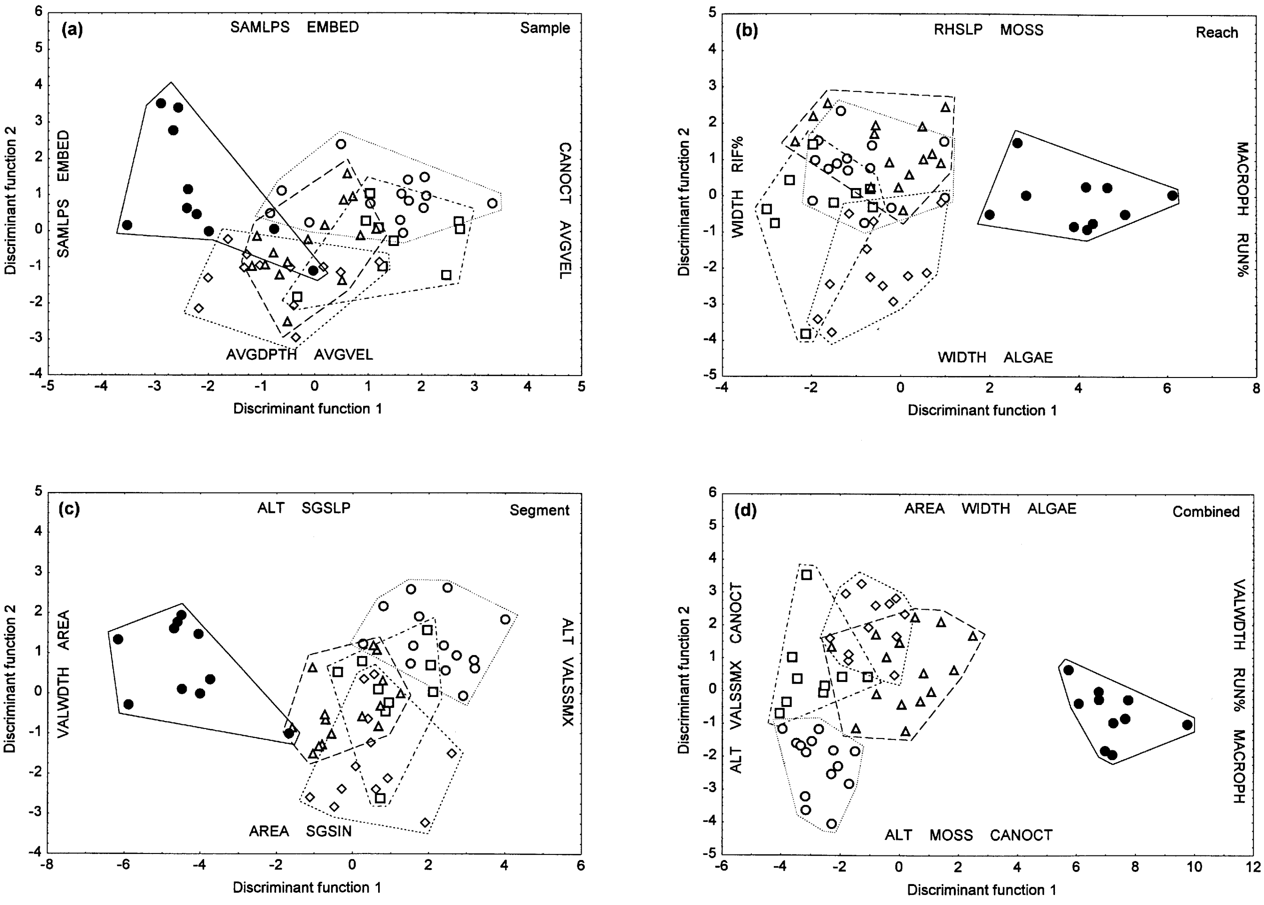

Fig. 5 TWINSPAN group discrimination in relationship to the first and second discrimiant functions from scale-specific MDFA. Variables most highly correlated with the discrimiant functions are listed on the plots. (a) Sample-scale variables; (b) reach scale; (c) segment scale; (d) all variables combined. TWINSPAN groups are: open circles, group 1; open squares, group 2; open diamonds, group 3; open triangles, group 4; filled circles, group 5.

Table 5 Percentage of variance explained by the significant discriminant functions ($P < 0.05$, chi-squared). NS, not significant

	Discriminant functions		
	1	2	3
Sample	55	26	14
Reach	60	25	12
Segment	76	18	NS
Combined	72	13	9

Table 6 Percentage of sites classified into the anticipated TWINSPAN group by the MFDA using the scale-specific physical variables

	Group					
	1	2	3	4	5	Mean
Sample	86	67	83	47	80	72
Reach	79	67	92	87	100	85
Segment	85	44	75	93	90	80
Combined	100	89	93	100	100	97

0.80, $P < 0.001$, Spearman r). Lastly, although segment length (SGLGTH) was needed for the calculation of segment slope, it is a rather subjective measure and was not used in further analyses.

The analysis of the sample variables produced three significant discriminant functions (DF) (Table 5), but only the first appeared to distinguish groups (Fig. 5a). Sites with high canopy cover were separated from sites with lower canopy cover having generally smaller substratum sizes and higher substratum embeddedness. Group discrimination was low, with only 72% of the sites classified into the respective TWINSPAN groups (Table 6).

Reach variables also produced three significant DFs,

Table 7 Scale-specific variables most highly correlated to the significant ($P < 0.05$, chi-square) discriminant functions

	Discriminant functions		
	1	2	3
Sample	–SAMLPS –EMBED +CANOCT +AVGVEL	–AVGDPTH –AVGVEL +SAMLPS +EMBED	–AVGDPTH –EMBED +SFCGRAD +CANOCT
Reach	–WIDTH –RIF% +MACROPH +RUN%	–WIDTH –ALGAE +RHSLP +MOSS	–WIDTH –RIF% +MOSS +RIFDPTH
Segment	–VALWDTH –AREA +ALT +VALSSMX	–AREA –SGSIN +ALT +SGSLP	
Combined	–ALT –VALSSMX –CANOCT +VALWDTH +RUN% +MACROPH	–ALT –MOSS –CANOCT +AREA +WIDTH +ALGAE	–WIDTH –RIFDPTH –AVGDPTH +SFCGRAD +SGSLP +VALSSMN

all of which distinguished site groups (Fig. 5b). DF 1 represented the separation of all valley sites (group 5) from upland sites along a gradient of high aquatic macrophyte cover and reduced percentage riffle to high percentage riffle. The second DF separated the high order group 3 sites, with stream order represented by increased width, from the smaller, lower order sites in groups 1, 2 and 4. The third DF ordered the montane groups along an altitudinal gradient similar to the second DF of the segment scale (see below) (Table 7). Reach variables classified the highest percentage (85%) of sites into the anticipated TWINSPAN groups (Table 6).

The influence of altitude was very evident on the two significant DFs in the segment level analysis (Fig. 5c). Altitude was highly correlated with the first DF, separating upland sites from lowland sites located in broad valleys. The second DF separated the upland sites based principally on sub-basin size, going from high elevation, smaller, higher gradient stream basins to lower elevation, mainstem basins. Segment variables classified 80% of the sites into the anticipated TWINSPAN groups.

With all scales combined, most sites (97%) were classified into the anticipated TWINSPAN groups. The first DF separated the lower altitude, high percentage run and aquatic macrophyte cover valley sites from the high altitude sites with greater canopy cover and steep valleys (Fig. 5d). The second DF produced a continuum from narrow, high elevation sites through lower elevation, higher order (wider) mainstem sites containing less canopy cover and higher algal cover. The third DF separated group 4 sites from the other montane sites because of the greater channel slopes and decreased widths (Table 7).

As anticipated, all between-scale CCAs were highly significant ($P < 0.001$, chi-squared). Segment-to-reach had an $R_C = 0.97$ and segment-to-site had an $R_C = 0.87$. Total redundancy of the reach variables, given the segment variables, was 45%, whereas total redundancy of the site variables, given the segment variables, was only 33%. The highest redundancy (57%) was that of the site variables, given the reach variables.

Discussion

Our goals were to investigate the relationship between physical variables and benthic community structure in a large river basin. We viewed these influences at three separate spatial scales shown to have utility in biological and geomorphological studies (Frissell *et al.*, 1986; Resh & Rosenberg, 1989). The CCA results were consistent with the concept that large-scale variables exhibit hierarchical influence on smaller scale variables (Allen & Starr, 1982). Although the high between-scale canonical correlations may have been a function of the high similarity of a few variables (e.g. segment slope and reach slope) (Cooley & Lohnes, 1971; Cooke & Doornkamp, 1974), the redundancy values indicated unique influences represented by the different scales.

The first discriminant function of all scales detected the major biological gradient by separating the valley from the montane sites. Segment and reach scales recovered the complete species classification on the second and third DFs, respectively. However, the sample scale did not correspond as well to our biological classification. There was little similarity between the species classification and the separation of montane sites by the second or third DFs of the sample scale. This indicates a poor relationship between these small-scale variables and large-scale variation in species composition. In contrast, the ability of segment and reach scales to recover the biological classification indicates the importance of large-scale variables on predicting benthic species composition in this basin.

The differences in the ability to reproduce the species classification with variables measured at different scales leads to several important considerations in the design of large-scale bioassessments. First, sample-scale variables appear to be inadequate predictors of community structure when considered over larger geographical areas (Corkum, 1989), although this deficiency may indicate the need to increase measurement resolution of small-scale variables. We used rather coarse ordinal measures of many variables, a practice common to large-scale studies and bioassessments (Plafkin *et al.*, 1989). Secondly, although the reach scale correctly classified the highest percentage of sites (85%), this percentage was not substantially better than the segment scale (80%). Additionally, on-site reach-scale variables were the most time demanding to acquire.

Altitude, which represents a very complex gradient, had the strongest influence on the species composition in the basin and had the highest correlation with the first two discriminant functions when all scales were combined. Altitude covaries with many geomorphological variables at the basin scale; it also covaries with climate-related variables, including temperature (Culp & Davies, 1982; Growns & Davis, 1994 [see Table 2]). Temperature regime influences many aspects of aquatic insect life history (Ward, 1992) and therefore must influence community composition. This is particularly true over larger spatial scales and in regions of high basin relief such as the Yakima basin (Vannote & Sweeny, 1980; although see Statzner & Higler, 1986). Unfortunately, temperature is rarely measured in a biologically meaningful fashion in large-scale surveys (normally only point samples), consequently its influence is difficult to assess. That our results are not directly attributable to altitude is suggested by comparison with Ward (1986) where similar relationships between land form and benthic composition were obtained at very different altitudes.

We found a substantial change in benthic composition and a significant decrease in taxa richness at the valley sites. This change in community structure could be a function of changes in geomorphological structure and/or changes induced by land use influences. Land use is principally a function of climate and land form and can be largely predicted by altitude within large river basins of the western U.S.A. Agricultural and urban land use frequently lead to modified flow regimes, channel form, riparian vegetation and water chemistry, all factors known to influence community composition (Newbold, Erman & Roby, 1980; Hawkins, Murphy & Anderson, 1982; Ormerod *et al.*, 1993; Richards, Host & Arthur, 1993). However, other physical variables also change longitudinally in the absence of land use influences (Vannote *et al.*, 1980), therefore natural changes in community structure should be anticipated (Rundle, Jenkins & Ormerod, 1993; Ormerod *et al.*, 1994). For example, large valleys have naturally lower slope and higher sinuosities leading to reduced stream power and smaller substratum size (Rosgen, 1994). This leads to abrupt changes in the habitat available to invertebrates. Taxa dominant at our valley sites (e.g. oligochaetes, chironomids) are often associated with impacted sites (Plafkin *et al.*, 1989) but also are common components of low gradient reaches (Ward, 1986). Consequently, it is difficult to separate the influences of land use and natural longitudinal changes in stream habitat (Ormerod *et al.*, 1994; Suren, 1994) on benthic composition, particularly at a coarse level of taxonomic resolution.

There was no clear relationship between either mean group richness or individual site richness and altitude as has been shown elsewhere (Ormerod *et al.*, 1994; Suren, 1994). However, by calculating total richness per group, maximum richness was observed in group 4. These sites contained high richness of mayflies, stoneflies and caddisflies found in the higher elevation groups, as well as high richness of oligochaetes, chironomids and molluscs, taxa associated with the valley sites.

Two current hypotheses that address benthic richness over larger geographical areas are the river continuum concept (RCC) (Vannote *et al.*, 1980) and the study of Statzner & Higler (1986). The RCC predicts maximum richness in mid-order reaches containing high environmental variability. Alternatively, Statzner & Higler (1986) show maximum richness where major changes in stream slope create areas of high in-stream hydraulic variability. Either hypothesis would predict maximum richness at group 4 sites, which were mid-order sites with the highest mean water surface gradient and high segment valley slope (i.e. high hydraulic variability). By observing richness at the basin scale *v* longitudinally a different view of large-scale patterns in stream benthic richness may be seen (Corkum, 1989). For example, short spatial distances between geomorphologically and taxonomically dissimilar valley and montane sites also may contribute to the high richness of this group.

Establishing relationships between physical variables and biological variables is dependent on the choice and measurement of the physical variables as well as the efficacy of the biological classification. In our study, 22% of the sites 'misclassified' by MDFA were TWINSPAN borderline sites (Hill, 1979). Borderline decisions occur whenever continuous data are forced into discrete groups (van Groenewoud, 1992; Belbin & McDonald, 1993). This leads to less than optimal relationships being established between physical and biological variables.

Although covariances were normally very high among physical variables, some misclassified sites had uncommon (relative to the sample set) geomorphological characteristics. For example, a few high elevation, low gradient sites in glaciated valleys were difficult to classify with any scale. As a result the present classification would not be expected to be a good predictor of communities in a basin dominated by glaciated valleys. Refinement of the classification is dependent on evaluating these misclassifications.

High correlations between variables within and among scales complicate the determination of which variables are most important in controlling benthic structure. Nevertheless, there are important consequences of these hierarchical relationships. First, benthic community structure is not just a function of site-specific conditions but also larger scale influences (Minshall, 1988; Corkum, 1989). Secondly, from a practical standpoint, large-scale variables may be used in place of small-scale variables to predict benthic community structure. This is an important consideration if large-scale variables can be measured with greater ease or accuracy. These relationships also emphasize the utility of pre-existing large-scale physical data for the design of sampling programmes. Lastly, hierarchical relationships can provide explanations for community structure that are less basin specific. This allows more realistic comparisons of community structure to be made among basins (Culp & Davies, 1982; Ward, 1989).

Using different scales of geomorphological descriptors may help us better understand the relationships between the landscape and stream benthic communities. Whether the goal is to describe natural factors that influence species distributions or determine the effects of anthropogenic disturbances, controls imposed by geomorphological structure should be considered. Without an understanding of the physical template that constrains species composition, identification of human-induced chemical and physical stresses on these assemblages will be difficult (Rossaro & Pietrangelo, 1993). This is particularly true for larger geographical areas with a diversity of geomorphological structure.

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References

Allen T.F.H. & Starr T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity.* University of Chicago Press, Chicago.

Belbin L. & McDonald C. (1993) Comparing three classification strategies for use in ecology. *Journal of Vegetation Science*, **4**, 341–348.

Brussock P.P. & Brown A.V. (1991) Riffle–pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia*, **220**, 109–117.

Carins Jr.J. (1981) Biological monitoring. Part VI—Future needs. *Water Research*, **15**, 941–952.

Clements W.H., Cherry D.S. & Carins Jr.J. (1988) Structural alterations in aquatic insect communities exposed to copper in laboratory streams. *Environmental Toxicology and Chemistry*, **7**, 715–722.

Cooke R.U. & Doornkamp J.C. (1974) *Geomorphology in Environmental Management: An Introduction*. Clarendon Press, Oxford.

Cooley W.W. & Lohnes P.R. (1971) *Multivariate Data Analysis*. John Wiley & Sons, New York.

Corkum L.D. (1989) Patterns of benthic invertebrate assemblages in rivers of northwestern North America. *Freshwater Biology*, **21**, 191–205.

Corkum L.D. (1992) Spatial distributional patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia*, **239**, 101–114.

Culp J.M. & Davies R.W. (1982) Analysis of longitudinal zonation and the River Continuum Concept in the Oldman–South Saskatchewan River system. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 1258–1266.

Cummins K.W. (1962) An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist*, **67**, 477–503.

Cupp C.E. (1989) *Stream Corridor Classification for Forested Lands of Washington*. Washington Forest Protection Associates, Olympia, Washington.

Ebisemiju F.S. (1988) Canonical correlation analysis in geomorphology with particular reference to drainage basin characteristics. *Geomorphology*, **1**, 331–342.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Godbout L. & Hynes H.B.N. (1982) The three dimensional distribution of the fauna in a single riffle in a stream in Ontario. *Hydrobiologia*, **97**, 87–96.

Green R.H. (1979) *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley & Sons, New York.

Growns I.O. & Davis J.A. (1994) Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. *Journal of the North American Benthological Society*, **13**, 417–438.

Hawkins C.P., Murphy M.L. & Anderson N.H. (1982) Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology*, **63**, 1840–1856.

Hellawell J.M. (1986) *Biological Indicators of Freshwater Pollution and Environmental Management*. Elsevier Applied Science, London.

Hill M.O. (1979) *TWINSPAN—A FORTRAN Program for Arranging Multivariate Date in an Ordered Two-way Table by Classification of the Individuals and Attributes*. Ecology and Systematics, Cornell University, Ithaca, NY.

Hynes H.B.N. (1975) The stream and its valley: Edgardo Baldi Memorial Lecture. *Verhandlungen Internationale Vereinigung der Limnologie*, **19**, 1–15.

Lamberti G.A. & Resh V.H. (1979) Substrate relationships, spatial distribution patterns, and sampling variablility in a stream caddisfly population. *Environmental Entomology*, **8**, 561–567.

Lanka R.P., Hubert W.A. & Wesche T.A. (1987) Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. *Transactions of the American Fisheries Society*, **116**, 21–28.

Leach C. (1979) *Introduction to Statistics: A Nonparametric Approach for the Social Sciences*. John Wiley & Sons, Chichester.

Leland H.V. & Carter J.L. (1985) Effects of copper on species composition of periphyton in a Sierra Nevada, California, stream. *Freshwater Biology*, **14**, 281–296.

Leland H.V., Fend S.V., Dudley T.L. & Carter J.L. (1989) Effects of copper on species composition of benthic insects in a Sierra Nevada, California, stream. *Freshwater Biology*, **21**, 163–179.

Lenat D.R. (1988) Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society*, **7**, 222–233.

Leopold L.B., Wolman M.G. & Miller J.P. (1964) *Fluvial Processes in Geomorphology*. W.H. Freeman, San Francisco.

Lotspeich F.B. (1980) Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. *Water Resources Bulletin*, **16**, 581–586.

Luoma S.N. & Carter J.L. (1991) Effects of trace metals on aquatic benthos. *Metal Ecotoxicology: Concepts and Applications* (eds M.C. Newman and A.W. McIntosh), pp. 261–300. Lewis Publishers, Chelsea, MI.

Metcalfe J.L. (1989) Biological water quality assessment of running waters based on macroinvertebrate communities: history and present status in Europe. *Environmental Pollution*, **60**, 101–139.

Minshall G.W. (1988) Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263–288.

Minshall G.W. & Minshall J.N. (1977) Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. *Hydrobiologia*, **55**, 231–249.

Newbold J.D., Erman D.C. & Roby K.B. (1980) Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1076–1085.

Ormerod S.J., Rundle S.D., Lloyd E.C. & Douglas A.A. (1993) The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. *Journal of Applied Ecology*, **30**, 13–24.

Ormerod S.J., Rundle S.D., Wilkinson S.M., Daly G.P., Dale K.M. & Juttner I. (1994) Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biology*, **32**, 309–322.

Plafkin J.L., Barbour M.T., Porter K.D., Gross S.K. & Hughes R.M. (1989) *Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish*. Report no. 444/4–89–001, Office of Water, U.S. Environmental Protection Agency, Washington, DC.

Platts W.S., Armour C., Booth G.D., Bryant M., Bufford J.L., Cuplin P., Jensen S., Lienkamper G.W., Minshall G.W., Monsen S.B., Nelson R.L., Sedell J.R. & Tuhy J.S. (1987) *Methods for evaluating riparian habitats with applications to management*. U.S. Department of

Agriculture, Forest Service, Intermountain Research Station.

Quinn J.M. & Hickey C.W. (1990) Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research*, **24**, 387–409.

Resh V.H. & Rosenberg D.M. (1989) Spatial–temporal variability and the study of aquatic insects. *Canadian Entomologist*, **121**, 941–963.

Richards C., Host G.E. & Arthur J.W. (1993) Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. *Freshwater Biology*, **29**, 285–294.

Rinella J.F., McKenzie S.W. & Fuhrer G.J. (1992) *Surface-water-quality assessment of the Yakima River Basin, Washington: analysis of available water-quality data yhrough 1985 water year.* U.S. Geological Survey Open-File Report 91–453.

Rosenberg D.M. & Resh V.H. (1993) *Freshwater Biomonitoring and Benthic Macroinvertebrates*. Chapman & Hall, New York.

Rosgen D.L. (1994) A classification of natural rivers. *Catena*, **22**, 169–199.

Rossaro B. & Pietrangelo A. (1993) Macroinvertebrate distribution in streams: a comparison of CA ordination with biotic indices. *Hydrobiologia*, **263**, 109–118.

Rundle S.D., Jenkins A. & Ormerod S.J. (1993) Macroinvertebrate communities in streams in the Himalaya, Nepal. *Freshwater Biology*, **30**, 169–180.

Rutt G.P., Weatherley N.S. & Ormerod S.J. (1990) Relationships between the physicochemistry and macroinvertebrates of British upland streams: the development of modelling and indicator systems for predicting fauna and detecting acidity. *Freshwater Biology*, **24**, 463–480.

Schindler D.W. (1987) Detecting ecosystem response to anthropogenic stress. *Canadian Journal of Fisheries and Aquatic Sciences*, **44** Suppl. 1, 6–25.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology*, **16**, 127–139.

Strahler A.N. (1957), Quantitative analysis of watershed geomorphology. *Transactions, American Geophysical Union*, **38**, 913–920.

Suren A.M. (1994) Macroinvertebrate communities of streams in western Nepal: effects of altitude and land use. *Freshwater Biology*, **32**, 323–336.

Sweeney B.W. (1993) Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **144**, 291–340.

van Groenewoud H. (1992) The robustness of correspondence, detrended correspondence, and TWINSPAN analysis. *Journal of Vegetation Science*, **3**, 239–246.

Vannote R.L. & Sweeny B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, **115**, 667–695.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Ward J.V. (1986) Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hydrobiologie, Supplementum*, **74**, 133–199.

Ward J.V. (1989) The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, **8**, 2–8.

Ward J.V. (1992) *Aquatic Insect Ecology: 1. Biology and Habitat*. John Wiley & Sons, New York.

Whittier T.R., Hughes R.M. & Larsen D.P. (1988) Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Science*, **45**, 1264–1278.

Williams B.K. (1983) Some observations on the use of discriminant analysis in ecology. *Ecology*, **64**, 1283–1291, .

Winner R.W., Boesel M.W. & Farrell M.P. (1980) Insect community structure as an index of heavy-metal pollution in lotic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 647–655.

Wright J.F., Moss D., Armitage P.D. & Furse M.T. (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.

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