

THE UNIVERSITY OF CALGARY

Scale mismatch confounds generality of the river continuum concept:
bridging the gap through explicit resource modelling.

by

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ABSTRACT

Mean drainage geomorphology is a predictable function of stream size. Since stream biota and resource gradients exist within these geomorphic constraints, Vannote *et al.* (1980) argue that stream size generally explains patterns of benthic macroinvertebrate composition. Although some studies support this argument, a number of studies find stream size to be a poor predictor of invertebrate composition. The confusion appears to lie in the incongruent spatial and temporal scales of mean drainage geomorphology and the focal scale of benthic macroinvertebrate composition data. To confirm this, the present study demonstrates that stream size is unable to explain the major trends in invertebrate composition among reaches in a Canadian Rocky Mountain drainage system. Further, stream size correlates highly with mean drainage geomorphology, but inconsistently captures geomorphic conditions at the scale of the invertebrate community. Finally, a water temperature model demonstrates that explicitly addressing resources is essential to correcting the scale problem.

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INTRODUCTION

The river continuum concept and its proponents argue that benthic macroinvertebrate abundances and resource gradient levels are attuned to changes in mean channel morphology with increasing stream size (e.g. Vannote *et al.* 1980; Bruns *et al.* 1982; Minshall *et al.* 1982; Minshall *et al.* 1983; Ward and Stanford 1983; Bruns *et al.* 1984; Minshall *et al.* 1985a, b; Statzner and Higler 1986; Naiman *et al.* 1987; Meyer and Edwards 1990). Fluvial geomorphologists have demonstrated that mean channel morphology is a predictable function of stream order, drainage area and/or discharge (e.g. Leopold and Maddock 1953; Leopold and Langbein 1962; Langbein and Leopold 1964; Leopold *et al.* 1964; Langbein and Leopold 1966; Schumm 1977). Since benthic macroinvertebrates in streams respond by their occurrences and relative abundances to resource gradients (e.g. O'Connell and Campbell 1953; Illies and Botosaneanu 1963; Minshall and Minshall 1977; Rabeni and Minshall 1977; Vannote *et al.* 1980; Statzner 1981; Cummins *et al.* 1983a; Minshall *et al.* 1983; Statzner and Higler 1986; Power *et al.* 1988; Statzner *et al.* 1988; Tate and Heiny 1995; Wohl *et al.* 1995; Richards *et al.* 1996), and since physical stream morphology provides the template upon which stream biota and resources are placed (Minshall 1988; Pringle *et al.* 1988; Resh *et al.* 1988; Poff and Ward 1989; Townsend and Hildrew 1994; Nolan *et al.* 1995), compositional patterns are argued to be attuned to the mean physical state of the drainage system. This perspective is further supported by the overwhelming visual image of stream flow, which compellingly suggests that longitudinal changes involved with unidirectional increases in fluid volume must dominate resource gradients and patterns of invertebrate composition (e.g. Statzner and Higler 1986).

Although the river continuum concept is generally accepted in the aquatic literature, surprisingly few studies have attempted to empirically test the relationship between stream size and patterns of benthic macroinvertebrate composition (Statzner and Higler 1985). In fact, a number of studies present circumstantial evidence indicating stream size poorly predicts invertebrate compositional patterns (Winterbourn *et al.* 1981; Huryn and Wallace 1987; Brussock and Brown 1991; Rundle *et al.* 1993; Brewin *et al.* 1995). Clearly some confusion exists with regards to the general application of this theory.

The purpose of the present paper is to address this confusion by showing the contrasting results of past studies is due to an inconsistent match between the spatial and temporal scale of the processes of stream size and the scale of benthic macroinvertebrate community data. Explicit resource-based modelling overcomes this scale problem, providing a more general framework for explaining patterns of benthic macroinvertebrate composition in streams. Before proceeding, however, a brief fluvial geomorphic review will clarify the difficulty in linking the scale of mean drainage geomorphology to the scale of benthic macroinvertebrate community compositions.

The mean geomorphology of drainage networks represents an interaction between geology and precipitation. Stream network (Horton 1945; as modified by Strahler 1957), hydraulic geometry and allometric analyses of drainage basins have revealed relationships between mean drainage geomorphology and stream size common to all drainage basins (Leopold and Maddock 1953; Bull 1975; Williams 1978; Osterkamp 1979; Morisawa 1985). For example, longitudinal stream profiles are usually concave upward and described by an exponential or logarithmic function (Shulits 1941; Yatsu 1955; Hack 1957; Woodford 1961). Stream length and drainage area are commonly related by a power function with an exponent between 0.5-0.7,

indicating that drainage basins tend to elongate as they erode (Hack 1957; Gray 1961; Leopold *et al.* 1964). Bankfull width and depth tend to increase as power functions of increasing drainage area, with bankfull width generally increasing at a faster rate than depth (Hack 1957). Substrate particle size is a combined function of stream slope and drainage area, where particle size decreases with increasing drainage area for streams of equal slope and decreases with decreasing slope for streams of equal area (Hack 1957). Channel slope generally decreases as a power function of increasing drainage area (Hack 1957). Finally, the sequential distance between bed structures, commonly identified as pools or riffles, is found to be a consistent proportion of 5 to 7 times the bankfull width. This means that as stream size increases the absolute distance between riffles (or pools) increases, while the distance relative to stream size remains the same (Leopold *et al.* 1964; Yang 1971a; Gregory *et al.* 1994).

These characteristic relationships derive from a dynamic balance between the channel processes of erosion and deposition *averaged over spatial and temporal scales of 10^3 - 10^5 meters and 10^1 - 10^4 years* (Leopold *et al.* 1964; Schumm 1977; Frissell *et al.* 1986; Tarboton *et al.* 1989; Petts and Amoros 1996). Expressed in terms of energy, regularities in mean river form are achieved by the spatially and temporally averaged adjustment between the tendency to maximize the efficiency of energy utilization (minimum work) and the tendency toward a uniform rate of energy expenditure (minimum variance) (e.g. Mackin 1948; Leopold and Maddock 1953; Leopold and Wolman 1957; Langbein 1964; Leopold *et al.* 1964; Langbein and Leopold 1966; Yang 1971a, b; Gregory and Walling 1973; Yang and Stall 1973; Yang *et al.* 1981). In other words, stream size captures the spatially and temporally averaged geomorphic properties of a drainage system.

On the other hand, studies examining invertebrate compositions among stream reaches within a drainage have a consistent *focal scale of 10^1 - 10^2 meters and 10^1 - $10^{0.5}$ years* (Frissell *et al.* 1986; Huryn and Wallace 1987). This focal scale has proven the most useful for studying continuous changes in invertebrate assemblages and habitat characteristics (Illies and Botosaneanu 1963; Pennak 1971; Carter *et al.* 1996). The physical processes operating at this focal scale however, produce geomorphic characteristics that can vary widely from the characteristics described by mean drainage scale relationships. For example, the presence of large remnant glacial deposits and/or large vegetative debris can cause unexpected and unpredictable convexities in the longitudinal stream profile, disrupting relationships between stream length and slope versus drainage area (Knighton 1976, 1983). More importantly, these materials can block and divert flow, creating arhythmically placed step-pool bed structures that are formed largely independent of the general processes driving channel geomorphology (Heede 1972a, 1972b; Keller and Swanson 1979; Keller and Tally 1979; Newson 1981; Marston 1982; Whittaker and Jaeggi 1982; Gerrard 1990; Grant *et al.* 1990; De Jong and Ergenzinger 1995; Keller *et al.* 1995). Under these conditions, channel slope becomes highly variable and the relative spacing between steps or pools becomes considerably less than 5-7 times the bankfull width (Grant *et al.* 1990; Keller *et al.* 1995).

Consequently, in this type of reach the abiotic template upon which stream biota and resources are assembled is more locally variable and is no longer a completely predictable function of stream size. Systems where drainage scale geomorphic relationships have been found to be inconsistent measures of reach scale geomorphology include high gradient mountain systems, humid systems and arid desert systems (Miller 1958; Wertz 1966; O'Loughlin 1969; Ponton 1972; Hack 1973; Newson and Harrison 1978;

Hayward 1980; Clark and Hansen 1988; Chin 1989). A mountain drainage is therefore an ideal system in which to test the general ability of stream size to explain patterns of benthic invertebrate community composition and instream resource gradients.

The objectives of the present study are three fold. The first objective is to determine the major trends in variation in benthic macroinvertebrate community composition and instream environmental characteristics in a Canadian Rocky Mountain drainage system and test the ability of stream size to account for these trends. The second objective is to demonstrate that stream size consistently accounts for mean drainage scale geomorphology, but is inconsistent in accounting for geomorphic conditions at the scale of the invertebrate community. The third objective is to construct a simple, explicit resource model that explains a significant portion of the variation in benthic macroinvertebrate compositional patterns, thereby correcting for the inconsistency in scale.

METHODS

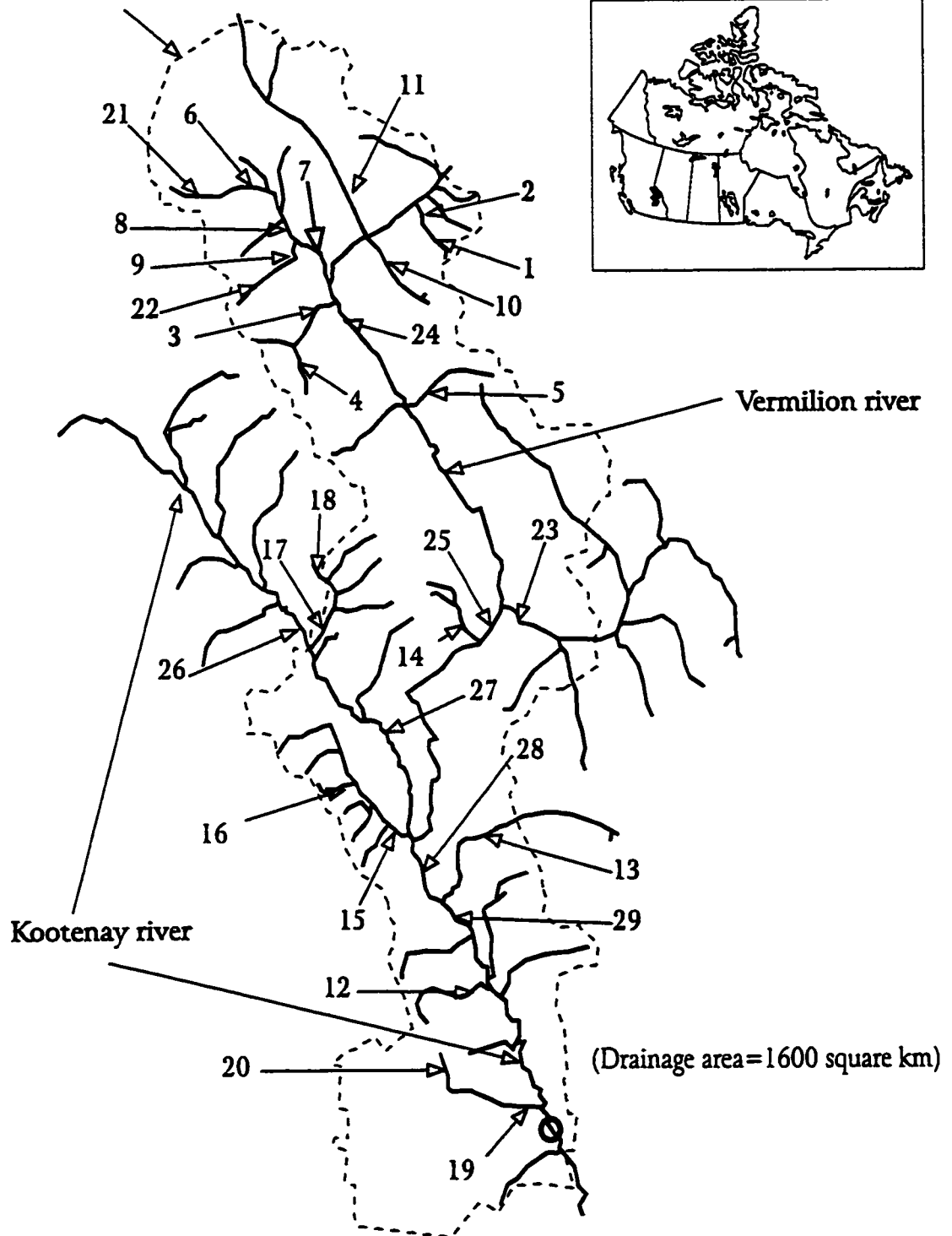
Study Area and Site Selection

The study was conducted in the 1600 km² headwaters of the Kootenay river system, located in Kootenay National Park in the Rocky Mountains of southeastern British Columbia (50° 34' to 51° 19' N, and 115° 48' to 116° 22' W) (Figure 1). Since the Park was established in 1919 it has experienced no major boundary changes or human alteration (Masters 1990). Streams of the Kootenay drainage are therefore largely considered pristine.

The study streams in the Kootenay drainage are underlain by the geology of the Chancellor Formation and two of its subgroups, the Cathedral formation and the Mackay group (Geol. Surv. Can {no date}; Price and

FIGURE 1: Map of the Kootenay river system showing the location of sampling sites. Site numbers and names are listed in Table 1. Open circle represents the endpoint for longitudinal profile measurements (see methods).

Kootenay Park Boundary



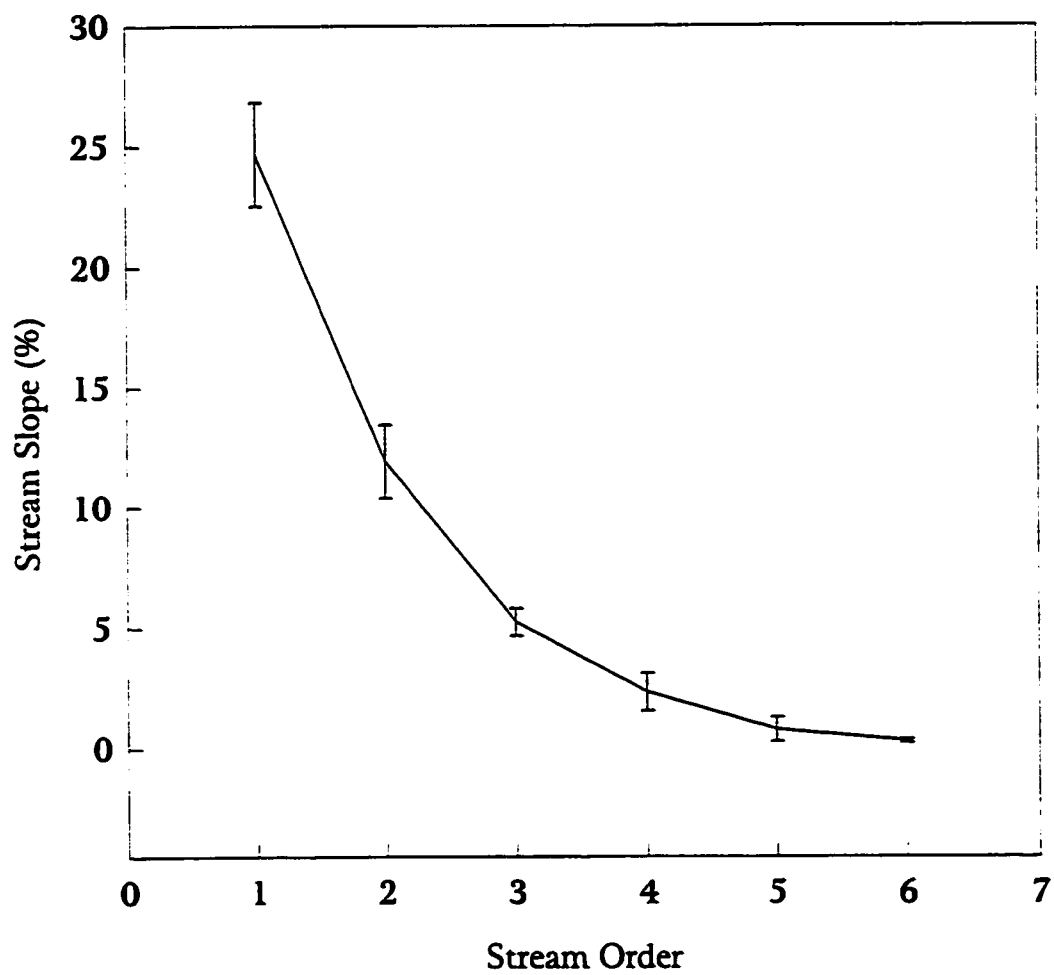
Mountjoy 1972; Reesor 1973; Cook 1975; Price *et al.* 1978; Price *et al.* 1980). All of these formations consist of a mixture of limestone, slate and dolomite. Stanley creek is underlain partially by geology of the Gog group, which also contains sandstone deposits.

Lithology and topographic structure show extensive evidence of glaciation. Glacial history of the area is long and complex with the last major advance and retreat around 10 000-19 000 years before present (Clague 1975; Luckman 1981). Glaciers and icefields are still found in the Main ranges at the north end of the drainage, runoff from which enters the Kootenay river system through tributaries of the Vermilion river.

The Park receives a mean annual precipitation between 450 mm to 1000 mm, with Park areas west of the continental divide receiving somewhat more moisture on average than areas to the east (Achuff *et al.* 1984). The moist climate is reflected in the vegetation and soil conditions in the Park, delineating broad ecological regions. Montane regions (<1800 m a.s.l.) are dominated by Douglas fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). Sub-alpine regions (1800 -2300 m a.s.l.) are dominated by Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*) and subalpine larch (*Larix lyallii*). Alpine regions (>2300 m a.s.l.) are largely treeless.

Streams in the Kootenay drainage have steep gradients (Figure 2), high water velocity and high turbulence which generally classify the Kootenay drainage as mountainous (Winterbourn *et al.* 1981; Ward 1992, 1994). Unlike temperate woodland streams, which rarely exceed a maximum slope of 0.2% (Jarrett 1990; Tate and Heiny 1995), stream slopes in the Kootenay drainage are rarely less than 2%, with some streams reaching upwards of 30% slope at their headwaters (Alger and Donald 1984). Streams range from 1st to

FIGURE 2: Mean slope (± 1 se) of 84 stream sections of the Kootenay drainage, grouped by stream order. Data from Alger and Donald (1984).



6th order (*sensu* Strahler 1964) and vary between 800 to 3000 meters in elevation (Alger and Donald 1984). Flow data gathered at regular intervals at Kootenay Crossing shows a maximum discharge of about 20 m³/s occurs between June and July, with a flow minimum of less than 1 m³/s occurring from December to February (Figure 3).

A total of 29 sites or sections of stream were selected for study with the intention of sampling as many different habitats within the Kootenay drainage as possible (Figure 1, Table 1). The sites were relatively accessible and suffered minimal impact or disturbance by humans (e.g. by road construction).

Benthic Macroinvertebrate Sampling

A stream reach, equivalent to 12 times the average bankfull width of the stream, was defined at each site for sampling benthic macroinvertebrates. This distance theoretically covers one full meander of the system (Leopold *et al.* 1964; Newbury and Gaboury 1993; Gregory *et al.* 1994). Three riffle sections were selected within each reach for invertebrate sampling. Pool areas were excluded from the sampling program to reduce within reach variability in taxonomic composition (Benke *et al.* 1984; Plafkin *et al.* 1989; Richards *et al.* 1993).

Benthic macroinvertebrates were sampled over a short period between September 15 and October 6. Fall was chosen as the sampling period in order to avoid the midsummer flood peak (Figure 3). Benthic invertebrate abundance and distribution can fluctuate dramatically during flood events, but stabilize rapidly to pre-flood levels as discharge declines in late summer (Tikkanen *et al.* 1994). This single season sampling strategy avoids confounding temporal variability with spatial patterns. Thus, differences in the pattern of invertebrate community composition among sites were assumed

FIGURE 3: Annual hydrograph of the Kootenay river at Kootenay crossing, Kootenay National Park, British Columbia. Water Survey of Canada data for mean (± 1 se) monthly discharge (m^3/s) from 1939-1990 (Environment Canada 1996).

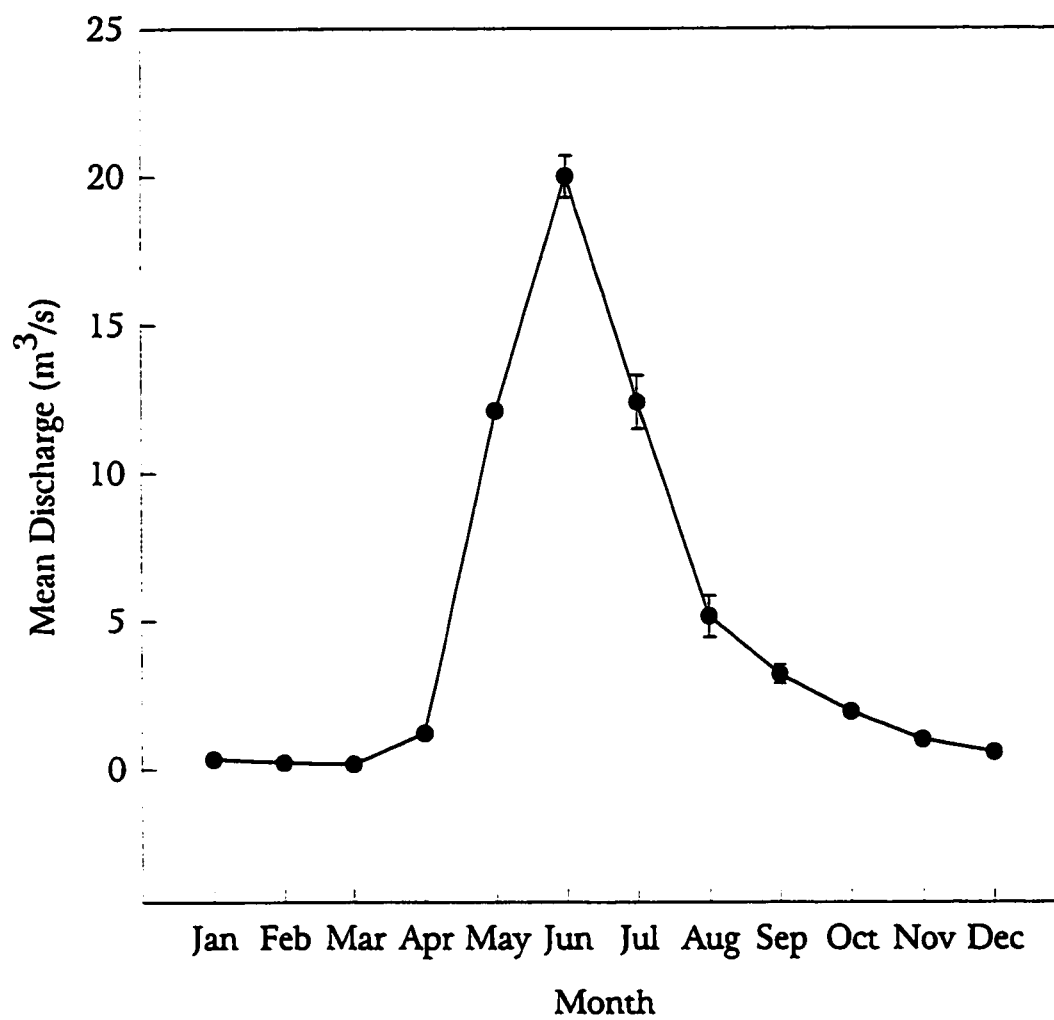


TABLE 1: Ecoregion, drainage area, stream order and site number for stream sites sampled in the Kootenay drainage. Ecoregion classification from Achuff *et al.* (1984).

Site name	Site no.	Site abbrev.	Drainage area (km ²)	Stream Order	Ecoregion
Stanley Tributary 1	1	ST1	1.5	2	Alpine
Stanley	2	ST	8.5	2	Sub-alpine
Numa	3	NUMA	39.6	3	Sub-alpine
Numa Tributary 4	4	NUMAT4	3.3	1	Sub-alpine
Hawk	5	HAWK	22.9	3	Sub-alpine
Helmet	6	HELM	34.5	3	Sub-alpine
Ochre	7	OCH	98.1	4	Sub-alpine
Ochre Tributary 2	8	OCHT2	7.9	2	Sub-alpine
Tumbling	9	TUMB	21.5	2	Sub-alpine
Haffner	10	HAFF	23.6	3	Sub-alpine
Tokkum	11	TOKK	77.3	3	Sub-alpine
Nixon	12	NIX	15.5	2	Sub-alpine
Daer	13	DAER	55.7	4	Montane
Wardle	14	WARD	18.5	3	Montane
Dolly Varden	15	DV	40.7	4	Montane
Dolly Varden Tributary 7	16	DVT7	4.9	1	Montane
Whitetail	17	WT	42.7	4	Montane
Whitetail Tributary 1	18	WTT1	3.9	1	Montane
Lower Swede	19	LSW	12.1	3	Montane
Upper Swede	20	USW	2.4	1	Montane
Helmet Tributary 9	21	HELMT9	3.5	2	Alpine
Tumbling Tributary 6	22	TUMBT6	5.9	1	Alpine
Simpson	23	SIMP	323	5	Montane
Vermillion 1	24	VERM1	367	5	Montane
Vermillion 2	25	VERM2	538.7	6	Montane

TABLE 1 continued.

Site name	Site no.	Site abbrev.	Drainage area (km ²)	Stream Order	Ecoregion
Kootenay 1	26	KOOT1	313.5	4	Montane
Kootenay 2	27	KOOT2	433.6	5	Montane
Main 1	28	MAIN1	1483.2	6	Montane
Main 2	29	MAIN2	1608.4	6	Montane

to represent ecological differences as a result of spatial, and not temporal, changes in environmental gradients.

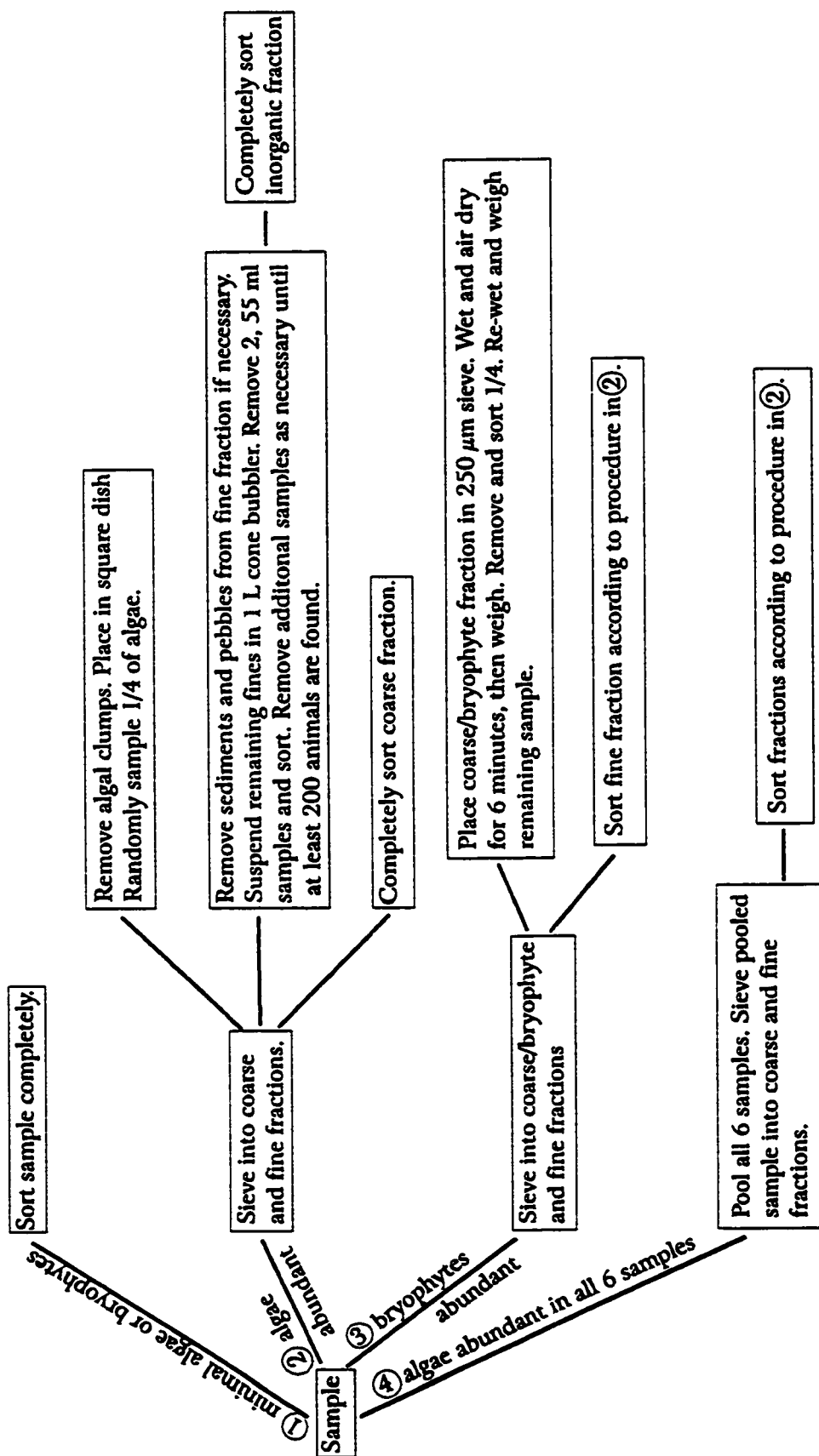
Quantitative samples of invertebrates were taken with a U-net that designates a known area of stream bottom (Scrimgeour *et al.* 1993) (125 μm mesh, 530 cm^2 area). Two sampling areas were randomly selected in each of the 3 riffles for invertebrate collection, for a total of 6 samples per reach. Six smaller, randomly allocated samples were chosen as these predictably yield greater precision in density estimates than fewer, larger samples (Downing 1979; Sheldon 1984).

Sampling for invertebrates started in the riffle furthest downstream and proceeded in an upstream direction, minimizing contamination of the samples by drifting invertebrates. Stones contained within the delineated area of the net were scrubbed within the mouth of the net to dislodge and collect attached invertebrates. Following the removal of large stones, substrate within the net were disturbed by hand to a depth of 5 cm in an effort to dislodge and gather the maximum number of benthic invertebrates from the delineated area. All invertebrates collected were stored in 10% formalin for later identification.

Invertebrates were separated from the detritus and inorganic material in the sample using a standardized sorting procedure diagrammed in Figure 4. Each sample was assessed visually to determine the appropriate procedure to follow. For quality control/quality assurance of the sorting procedure, one of the six samples from each reach was randomly selected and re-sorted. If the number of invertebrates found in the re-sort was $>10\%$ of the total number of invertebrates originally found, all six samples were re-sorted.

All invertebrates were identified to family level and enumerated. Family-level determination is sufficient for assessing important ecological patterns at the community level (i.e. Furse *et al.* 1984; Corkum 1989; Ferraro

FIGURE 4: Procedure for sorting benthic macroinvertebrate samples from the Kootenay drainage (derived from Wrona *et al.* 1982; Sebastien *et al.* 1988).



and Cole 1995; Bournaud *et al.* 1996; Bowman and Bailey 1997). The abundance of each taxon from each of the six samples in each reach was summed and divided by the total stream bottom area sampled to estimate taxa densities in the reach.

Taxa biomass at each reach was estimated by drying all individuals of each taxon at 60° C until constant weight was achieved. Dry mass was used as an estimate of taxon biomass at each site. The biomass of each taxon from each of the six samples in each reach was summed and divided by the total stream bottom area sampled to estimate taxon biomass per unit area in the reach.

Each taxon was also classified according to functional feeding group. Functional feeding group designations distinguish insect taxa that perform different functions within aquatic ecosystems with respect to processing of nutritional resource categories (Merritt and Cummins 1996). Although designations are made based on direct observation of feeding mechanisms and structures, rather than on the specific food source ingested, they do reflect broad categories of food sources (i.e. stone surface organic layers, fine particulate material) (Cummins and Klug 1979). In this respect, the functional group classifications are analogous to guilds, where sets of organisms using a particular resource class in a similar manner are grouped (Root 1967; Merritt and Cummins 1996). Insect taxa were classified as shredders, collector-gatherers, scrapers or predators, according to Merritt and Cummins (1996). Other invertebrates were classified according to the information provided by Pennak (1989).

Characterization of Resource Gradients

Detrital material, primarily allochthonous in origin, was collected and

stored along with each benthic invertebrate sample. The organic material from each sample was divided into fine ($125\ \mu\text{m} \leq \text{FPOM} < 1\ \text{mm}$), coarse ($1\ \text{mm} \leq \text{CPOM} < 2\ \text{mm}$) and extra coarse ($+\text{CPOM} > 2\ \text{mm}$) fractions, after complete removal of insects from each sample (Boulton and Lake 1992). Fractions were oven dried at 104°C for approximately 48 hrs, or until constant weight was achieved. Fractions were then ashed in a muffle oven at 550°C for 3-4 hours and reweighed. The ash-free dry mass (AFDM) measurement of each fraction from each of the six samples per reach was summed and divided by the total stream bottom area sampled to estimate mass per unit area of each detrital fraction in the reach.

Algal samples were collected from a randomly selected stone taken from the immediate area around each benthic sample. Stones selected were always greater than 10 cm in diameter. A $9.6\ \text{cm}^2$ template was used to mark an area on the surface of the stone and all algal material removed from within this area with a scalpel. Algal samples were frozen for later analysis. Samples were analyzed for Chlorophyll *a* (Turner Designs 10-AU fluorometer) and AFDM following the methods of Marker *et al.* (1980), Nusch (1980), Sartory and Grobbelaar (1984), and Aloï (1990). Values are expressed per unit area of stone surface.

A water sample was collected at each reach and transported at 0°C the same day to the University of Alberta limnology laboratory. Each sample was analyzed for nitrate-nitrite (NO_3^- , NO_2^-), ammonia (NH_4^+), soluble reactive phosphorus, total dissolved phosphorus, total phosphorus, total dissolved solids, dissolved organic carbon, bicarbonate (HCO_3^-) and alkalinity. A fraction of water was also collected from each reach and refrigerated for later turbidity analysis using a Hach Chemical Company Turbidimeter (model 2100A). Spot temperature and pH measurements were taken with a Fisher

Scientific accumet 1000 series handheld meter (model 1001), and pH readings later converted to estimates of hydrogen ion concentration. Conductivity was measured at each reach with a Horizon Ecology Co. meter (model 1484-10).

Reach surface slope was measured using a hand level and Bushnell laser-rangefinder binoculars (Lytespeed 400). Since reaches with very gradual slopes were difficult to measure accurately with these methods, slopes were instead estimated from 1:50 000 topographic maps. Bankfull width and bankfull depth were estimated for each reach at 3 separate transects according to the methods of Newbury and Gaboury (1993).

Present stream width was measured at three transects for each reach, along with approximately 10 depth and velocity measurements at regular intervals across each transect. Spot velocity measurements were taken at 0.6 times the depth below the surface of the stream (Chow 1959; Newbury and Gaboury 1993) using a Marsh/McBirney portable water current meter (Model 201) or a Price 1205 mini current meter. Mean stream velocity multiplied by mean cross-sectional area gave an estimate of present discharge for each reach.

Average flow conditions were estimated by calculating tractive force at each reach. Tractive force is a generalized measure of shear stress, the force exerted by the overlying flow on the streambed. It is fundamentally related to both the Manning and Chezy equations for estimating mean water velocity in an open channel (Gilvear and Bravard 1996), and is calculated by assuming that the downslope component of the gravitational force that causes flow equals the resisting shear force exerted by the streambed (Carlston 1969; Newbury and Gaboury 1993):

$$\tau = (g)(\rho)(R)(S) \quad (1)$$

where τ is the tractive force (N/m^2), g is the acceleration due to gravity (9.81

m/s^2), ρ is the density of water (1000 kg/m^3), R is the hydraulic radius (cross-sectional area of flow/wetted perimeter; m) and S is reach slope (m/m).

Bed paving materials were characterized at each reach by sampling 60 stones (20 per riffle) by the random walk method (Harrelson *et al.* 1994) and measuring each stone in 3 dimensions. The mean size of each stone was calculated, ranked and a cumulative frequency curve derived for each reach. Using the tractive force calculations and the substrate cumulative frequency curves, the percent of substrate stable at bankfull flows was calculated by assuming the tractive force (kg/m^2) is equal to the diameter of bed paving material at incipient motion (Newbury 1984; Cobb *et al.* 1992; Newbury and Gaboury 1993).

Roughness of the stream bottom was measured using a substrate profiler (Gore 1978; Statzner *et al.* 1988), consisting of 24 aluminum dowels protruding through a 50 cm x 50 cm square PVC plate, about 2 cm thick. Substrate roughness was estimated in 6 random locations in each reach by placing the profiler plate level to the stream surface and sliding each dowel up or down until it touched the stream bottom. The distance from the tip of each dowel to the plate was measured and the standard deviation of all 24 measurements calculated and multiplied by 2. This was called the substrate roughness coefficient (Statzner *et al.* 1988). The mean of the substrate roughness coefficient for all 6 samples provides an estimate of the roughness or variation in the stream bottom for each reach.

Seasonal trends in water temperature were estimated using optic stowaway, submersible thermographs (Onset computer corp. model WTS6-8K). These were deployed in mid-April 1996 and collected at the beginning of October 1996. Spot temperature readings were recorded at each reach every 60 minutes throughout the period of deployment. These data were used to

estimate minimum, maximum and average temperatures, as well as degree day accumulations. Degree days are a measure of the thermal units available to the organisms for development and are calculated by summing the daily mean temperatures above the 0° C threshold over the period of sampling (e.g. Arnold 1960; Wagner *et al.* 1984).

*Trends in Benthic Macroinvertebrate Composition and Resource
Gradients with Stream Size*

An ordination and a functional group analysis were performed to determine the general ability of stream size to account for trends in benthic macroinvertebrate community composition and resource gradients in the Kootenay drainage.

The purpose of the ordination analysis was, 1) to organize reaches according to the major trends in invertebrate composition, 2) identify the primary resource gradients influencing invertebrate abundance, and 3) compare the major trends of invertebrate composition to the pattern derived from organizing the reaches according to drainage area. Using the program PC-ORD (McCune and Mefford 1995), a principal components analysis (PCA) was performed to define the major trends in variation in benthic macroinvertebrate community composition. PCA is an objective and well understood indirect ordination technique that reduces the dimensionality of a multivariate data set while maximizing the variance explained (Gauch 1982).

A taxa abundance index incorporating density and biomass was calculated using the equation:

$$I_{ik} = \frac{(D_{ik} + B_{ik})}{2} \quad (2)$$

where I_{ik} is the abundance of taxa i in site k , and D_{ik} and B_{ik} are the relative density and relative biomass of taxa i in site k respectively. The utility of using indices to quantify the importance of taxa in community studies is discussed by Goff and Cottam (1967) in the context of vegetation studies.

Taxa with abnormally high abundances can potentially skew the ordination output (Noy-meir *et al.* 1975). To avoid the overwhelming effect of taxa with high abundances, benthic macroinvertebrate abundances were divided by the total abundance in each reach to standardize the range of the data.

Rare taxa tend to alter ordination output and mask ecological information because large numbers of zeros affect the algorithms (Swan 1970; Beals 1984). Also, it is generally preferable to have fewer descriptors (taxa) than sites, as an ordination cannot validly be calculated from a number of sites smaller than the number of taxa (Legendre and Legendre 1983). Taxa that were present in less than 50% of the sites were therefore eliminated from the site by taxa matrix. This resulted in a matrix with 16% empty cells (i.e. cells containing zeros), and 17 invertebrate families, or approximately half the number of taxa than sites in the ordination. Species standardization was avoided, as it tends to emphasize rare or "characteristic" species as opposed to overall site composition (Noy-meir *et al.* 1975).

PCA assumes species response curves to be linear in nature. When they are not, the ordination pattern from PCA can become distorted and difficult to interpret (Ter Braak 1988; Ter Braak and Prentice 1988). Reciprocal averaging (RA) was therefore applied to the data set as well, as it is an indirect ordination technique that is not restricted to linear species response curves (Jongman *et al.* 1987; Ter Braak 1988; Ter Braak and Prentice 1988). No

significant difference was found between the outputs of the PCA and RA analyses ($p < 0.005$; Spearman rank correlation), indicating the gradients being dealt with are short enough to be essentially linear. Therefore, only the PCA output is reported.

Using the program CANOCO (Ter Braak 1988), a redundancy analysis (RDA) was performed to determine the resource gradients that explain the most variation in community composition. This direct ordination technique attempts to explain species responses by producing ordination axes that are constrained to be linear combinations of the supplied environmental variables (Table 2; Ter Braak and Prentice 1988). Environmental variables were standardized by the maximum value for each column such that all values were scaled between zero and one (Legendre and Legendre 1983). A forward selection technique was used in CANOCO to select the ten environmental variables that explain the most variance in the data set. The correspondence between the RDA and PCA outputs were compared using Spearman rank correlations.

For both the PCA and RDA, the relative magnitude of eigenvalues for each axis is an expression of the relative importance of the axis, and indicate the amount of variance explained by that axis (Gauch 1982). Eigenvalues of each axis were compared to eigenvalues derived from a random distribution of eigenvalues with the same total variance, called the broken-stick method, to determine the significance of each axis (Legendre and Legendre 1983; Jackson 1993).

The ability of stream size to account for the major trends in invertebrate composition and resource gradients, as defined by ordination analysis, was tested by regressing the scores of the 29 reaches on PCA axis 1 and 2 against the drainage area of each reach. Drainage area measures continuous change in

TABLE 2: Physical, chemical and biotic environmental variables included in direct ordination analysis.

	Variable	Abbreviation	Unit of measurement
Physical	Slope	SLOPE	m/m
	Bankfull width	BFWDTH	m
	Bankfull depth	BFDPTH	m
	Present width	WIDTH	m
	Present depth	DEPTH	m
	Spot Discharge	DISCHRG	m ³ /s
	Bottom current	BOTTOM	m/s
	Current at 60% of the total depth from the surface	60%	m/s
	Minimum temperature	MINTEMP	°C
	Maximum temperature	MAXTEMP	°C
	Average temperature	AVTEMP	°C
	Degree Days	DEGDAY	°C
	Spot temperature	SPTEMP	°C
	Substrate Roughness coefficient	SUBRGH	cm
	Percent of substrate stable at bankfull flows	%STBL	%
	Tractive force	TFORCE	N/m ²
Biotic	Algae-chlorophyll a	ALGCHL	µg/cm ²
	Algae-ash free dry mass	ALGAFDM	g/cm ²
	Extra-coarse particulate organic material (>2mm)	+CPOM	g/m ²
	Coarse particulate organic material (1mm≤CPOM<2mm)	CPOM	g/m ²

TABLE 2 continued.

	Variable	Abbreviation	Unit of measurement
Biotic	Fine particulate organic material ($125\mu\text{m} \leq \text{FPOM} < 1\text{mm}$)	FPOM	g/m^2
Chemical	Nitrate + Nitrite ($\text{NO}_3^- + \text{NO}_2^-$)	NO3	$\mu\text{g/L}$
	Ammonia (NH_4^+)	NH4	$\mu\text{g/L}$
	Total dissolved solids	TDS	mg/L
	Soluble reactive phosphorus	SRP	$\mu\text{g/L}$
	Total phosphorus	TP	$\mu\text{g/L}$
	Total dissolved phosphorus	TDP	$\mu\text{g/L}$
	Alkalinity	ALK	mg/L as CaCO_3
	Bicarbonate (HCO_3^-)	HCO3	mg/L
	Carbonate (CO_3^{2-})	CO3	mg/L
	Dissolved organic carbon	DOC	mg/L
	Conductivity	COND	$\mu\text{mhos/cm}$
	Turbidity	TURB	NTU
	Hydrogen ion concentration	[H]	mmol/L

stream size and is the appropriate variable in this analysis for comparison to continuous changes in invertebrate composition. As compositional trends are assessed independent of stream size trends, this analysis represents an objective test of the correspondence between patterns of invertebrate composition and stream size.

In the **functional group** analysis, reaches were grouped according to stream order and trends in functional group composition examined for predictable patterns along a stream order axis. Reaches ranged from 1st to 6th order, with each group containing at least three reaches of each order (Table 1). For each group, the mean and standard error of the relative abundance of collector-gatherers, scrapers, shredders and predators were calculated, along with the mean and standard error for total invertebrate density, total invertebrate biomass and the abundance of coarse, fine and the ratio of coarse to fine particulate organic material. Since organic material is one of the more commonly identified environmental influences on community composition, it was selected for visual assessment (Cummins 1974; Cummins 1975; Cummins and Klug 1979; Vannote *et al.* 1980).

Although stream order is a categorical rather than a continuous measure of stream size, it is strongly correlated to drainage area (Leopold *et al.* 1964; Hughes and Omernik 1981). Assembling functional group data along a stream order, rather than a drainage area axis, simplifies the interpretation of trends. Furthermore, although the functional group analysis is a more subjective interpretation of compositional trends with stream size, it is the most common method used by supporters of the river continuum concept and is a valuable analysis (e.g. Minshall *et al.* 1983).

Fluvial Geomorphic Relationships

Drainage scale geomorphic properties of the Kootenay drainage were examined to demonstrate the existence of similar relationships between mean drainage geomorphology and stream size observed in drainages worldwide. Longitudinal profiles of 19 streams in the Kootenay drainage were plotted from 1:50 000 topographic maps. The profile for each stream was measured from the uppermost point of its headwaters to an arbitrarily selected endpoint on the mainstem of the Kootenay river just before it exits Kootenay National Park (Figure 1) (Hack 1957). Elevation was converted to fall by dividing each measurement by the total elevational drop. Profiles were plotted on a semi-logarithmic scale and the fit of a linear regression to the data used to assess profile smoothness.

Allometric relationships were derived between measured channel characteristics and drainage area. Drainage area for each of the 29 reaches was estimated from 1:50 000 topographic maps using a planimeter. Reach slope, bankfull width and depth, and bed paving materials were characterized according to the procedures outlined earlier. For bed paving materials, mean particle size was calculated for each stone, ranked and the median diameter of bed material for each site determined. Relationships between mean channel characteristics and drainage area were plotted on a double log scale, and the fit assessed using simple linear regression.

Geomorphic properties in the Kootenay drainage were also examined at the reach scale to demonstrate the highly variable geomorphology at the scale of the invertebrate community relative to the mean geomorphic properties of the Kootenay drainage. Local variation in reach slope and distance between pools and riffles was assessed for six reaches of different drainage area. At each break in the water surface profile, a slope measurement was taken using a hand

level and measuring tape until 5 to 10 measurements were made. Starting at the downstream end of each of the six reaches, pools and riffles were also identified and distances measured from the top of each pool (or riffle) area to the top of the next pool (or riffle) upstream of it. Distances between 5 pools (or riffles) were measured for each stream. Distances were converted to a multiple of bankfull width by dividing each distance by the mean bankfull width for the entire reach.

Explicit Modelling of Resource Gradients

A process-based model of water temperature was constructed to demonstrate that the inconsistent match between mean drainage geomorphic conditions and reach scale geomorphic conditions can be overcome by explicitly addressing the processes driving resource gradients at a scale appropriate to the invertebrate data. Water temperature was modelled as it is one of the important resources explaining the major trends in benthic macroinvertebrate composition in the Kootenay drainage (see results).

Stream temperature has been theoretically and empirically modelled numerous times (e.g. Edinger *et al.* 1968; Brown 1969; Johnson 1971; Sinokrot and Stefan 1994; Kim and Chapra 1997). Therefore, the various processes driving instream temperatures are well understood and an index of instream temperature can be derived by substituting simple surrogate measures for these processes. The result of these substitutions is a model that is not dimensionally equivalent to temperature, but is a correlate that changes in a fashion consistent with instream temperature.

Models of instream temperature generally have two components. The meteorological component describes incoming solar radiation as a function of variables such as air temperature, cloud cover and humidity (atmospheric emissivity), sunshine duration and reflectance from the earth surface (Raphael

1962; Delay and Seaders 1966; Bristow and Campbell 1984; Hostetler 1991; Sinokrot and Stefan 1993, 1994). Air temperature alone captures 70-90% of the variation in solar energy, making it a powerful surrogate measure of this component of instream temperature (Smith and Lavis 1975; Bristow and Campbell 1984; Aubinet 1994). Summer and fall air temperature also explain a fair amount of the variation directly in instream water temperature; however, the relationship tends to overestimate water temperature at the lower air temperature range, especially for small mountain streams (Brown 1969; Smith and Lavis 1975; Crisp and Howson 1982).

The topological and hydrological component of these models describes the transfer and storage of heat from solar energy in the water column as a function of processes such as conduction, convection, evaporation, bed absorption and sensible heat loss (Raphael 1962; Delay and Seaders 1966; Bowles *et al.* 1977; Jobson 1977; Gulliver and Stefan 1986; Sinokrot and Stefan 1993). These processes are correlated to stream size. For example, conduction of heat into and out of the stream is mainly a function of water volume, occurring more rapidly in smaller streams as a result of the lower volume of water and thus lower total capacity for heat storage (Smith and Lavis 1975; Jobson 1977). Similarly, the lower total capacity for heat storage in small streams also means a greater sensitivity to cold groundwater and glacial inputs, which have less measureable effect on instream temperatures as water volume increases (Sinokrot and Stefan 1993). Furthermore, the increase in average size of bed paving material in smaller streams may also decrease bed absorption by shading the surrounding material and increasing scatter (Brown 1969; Smith and Lavis 1975). Finally, the processes of convection and evaporation occur more readily as streams widen, canopy cover decreases, and the water surface becomes more directly exposed to solar energy and air

movement (Gulliver and Stefan 1986). Overall, this indicates that characteristic topological and hydrological changes that occur with stream size can account for the tendency of smaller streams to be colder than expected, given the solar energy available, as well as for the increasingly stronger fit between incoming solar energy and instream temperature for larger streams.

Knowing that air temperature, as a surrogate measure of solar energy, is a strong correlate of water temperature and assuming that air temperature increasingly overestimates the temperature of smaller streams as a result of characteristic topological and hydrological changes with decreasing stream size, the following index of stream temperature was constructed:

$$T_w = T_{air}(1 - 1/DA) \quad (3)$$

where T_w is the water temperature index, T_{air} is the air temperature (°C) and DA is the drainage area (km²) for each reach. The water temperature index is modelled as a direct function of the air temperature, minus a proportion of the air temperature that is dependent on the size of the reach. For large reaches, the proportion of the air temperature that is subtracted is very small and the model predicts a close correspondence between air temperature and water temperature. As drainage area decreases, the proportion of the air temperature that is subtracted linearly increases, and the model predicts much lower water temperatures.

Mean maximum July air temperatures in Kootenay National Park were empirically predicted from elevation data according to the equation:

$$T_{air} = 17.83 - 0.00674(E) \quad (4)$$

where T_{air} is the mean maximum July air temperature and E is elevation (m) (Janz and Storr 1977). The relationship is highly significant ($p < 0.01$,

$r^2=0.97$). The water temperature index was calculated for each of the 29 sites after substituting equation (4) into (3) and the results regressed against the maximum July water temperatures measured in each reach using the submersible thermographs (see earlier methods).

The ability of the stream temperature index to explain the major trends in benthic invertebrate composition at the reach scale was tested by regressing the water temperature index against the reach scores on PCA axis 1 and 2.

RESULTS

Trends in Benthic Macroinvertebrate Composition and Resource Gradients with Stream Size

The ordination analysis shows that 1) aquatic insect larvae dominate the major trends in benthic macroinvertebrate composition in the Kootenay drainage 2) these trends correlate highly with reach water temperature, organic matter abundance and nutrient levels and 3) drainage area is unable to explain the major trends in benthic macroinvertebrate community composition and resource gradients identified by PCA and RDA .

A comparison of the eigenvalues of the first four dimensions of the PCA to broken-stick eigenvalues indicates axis 1 and 2 represent significant compositional trends (Figure 5; Table 3). A continuous gradient of reach separation based on benthic macroinvertebrate composition is observed in these 2 dimensions, with axis 1 accounting for 59% of the total variance in composition and axis 2 accounting for 16% (Figure 5). PCA axis 1 represents a transition in community composition from high positive loadings of the families Chironomidae, Nematoda, Perlodidae and Ameletidae, to high negative loadings of the families Heptageniidae, Taeniopterygidae and Chloroperlidae (Figure 5). The families Baetidae, Hydracarina, Tipulidae,

FIGURE 5: Site scores and taxa loadings on the principal components analysis of the benthic macroinvertebrate abundance data. Open circles represent the 29 reaches sampled. Each line represents an invertebrate taxa, where the length and angle of the line indicate the strength and direction of the relationship (Jongman *et al.* 1987). For full taxa names see Appendix A.

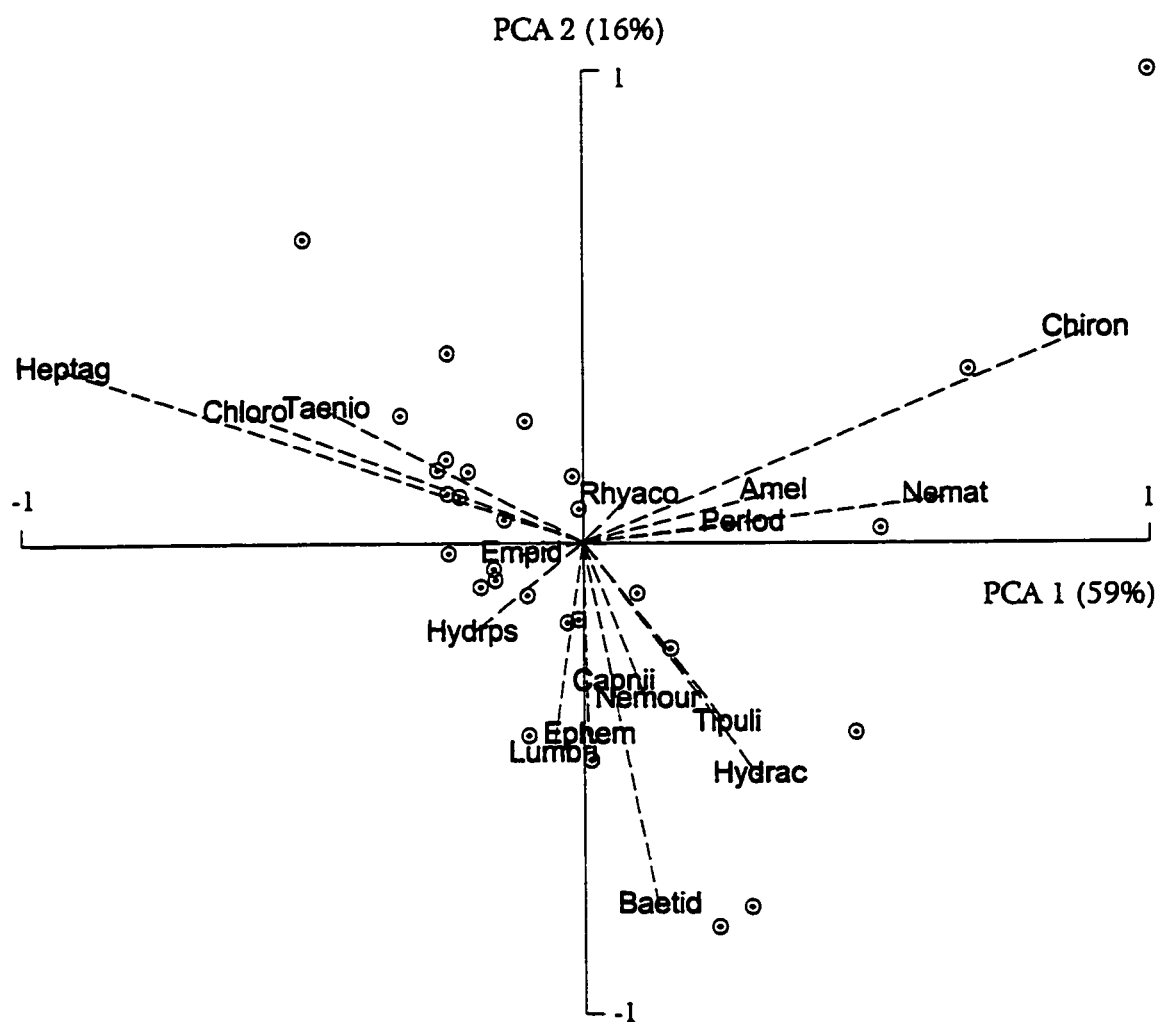


TABLE 3: Comparison of eigenvalues calculated for each PCA axis to eigenvalues from random data. The * indicates the axis contains more information than would be expected by chance and is therefore considered for interpretation (Legendre and Legendre 1983; Jackson 1993).

	eigenvalue	broken-stick eigenvalue (of Jackson 1993)
PCA axis 1	1.608*	0.550
PCA axis 2	0.446*	0.390
PCA axis 3	0.205	0.310
PCA axis 4	0.150	0.257

Nemouridae, Ephemerellidae, Lumbriculidae and Capniidae have high negative loadings on PCA axis 2 (Figure 5).

Similar to the PCA, the RDA ordination pattern demonstrates a continuous gradient of site separation with RDA axis 1 accounting for 51% and RDA axis 2 accounting for 14% of the total variance in composition (Figure 6). RDA axis 1 represents a transition in environmental characteristics from high positive loadings of coarse particulate organic material, algal abundance and total phosphorus to high negative loadings of maximum water temperature and nitrate concentration. Alkalinity, dissolved organic carbon and to a lesser extent, maximum water temperature, soluble reactive phosphorus concentration, algal abundance and hydrogen ion concentration have high negative loadings on RDA axis 2 (Figure 6). Also, the relative positions of the 29 reaches in ordination space are very similar between the PCA and RDA (axis 1 $r^2=0.84$, axis 2 $r^2=0.82$; Spearman rank correlation). Major changes in invertebrate composition identified by the PCA therefore occur in conjunction with major transitions in resource gradients identified by the RDA. Overall, shifts in maximum water temperature, organic matter abundance and nitrate concentration are the strongest determinants of benthic macroinvertebrate community composition in reaches of the Kootenay drainage (Figure 6).

A comparison of compositional patterns in the Kootenay drainage relative to drainage area indicates that drainage area cannot account for the major trends in benthic macroinvertebrate community composition and resource gradients defined by the ordination analysis. Linear regressions between the scores of each reach on PCA axis 1 and PCA axis 2 versus the drainage area of each reach are non-significant (Figure 7).

The **functional group** analysis demonstrates similar results to the

FIGURE 6: Site scores and environmental variable loadings on the redundancy analysis. Axes are constrained to be linear combinations of environmental variables. The 10 variables with the highest correlations with benthic macroinvertebrate abundances are illustrated, where the length and angle of the line represent the strength and direction of the relationship (Jongman *et al.* 1987). Open circles represent the 29 reaches sampled. For full description of environmental variables see Table 2.

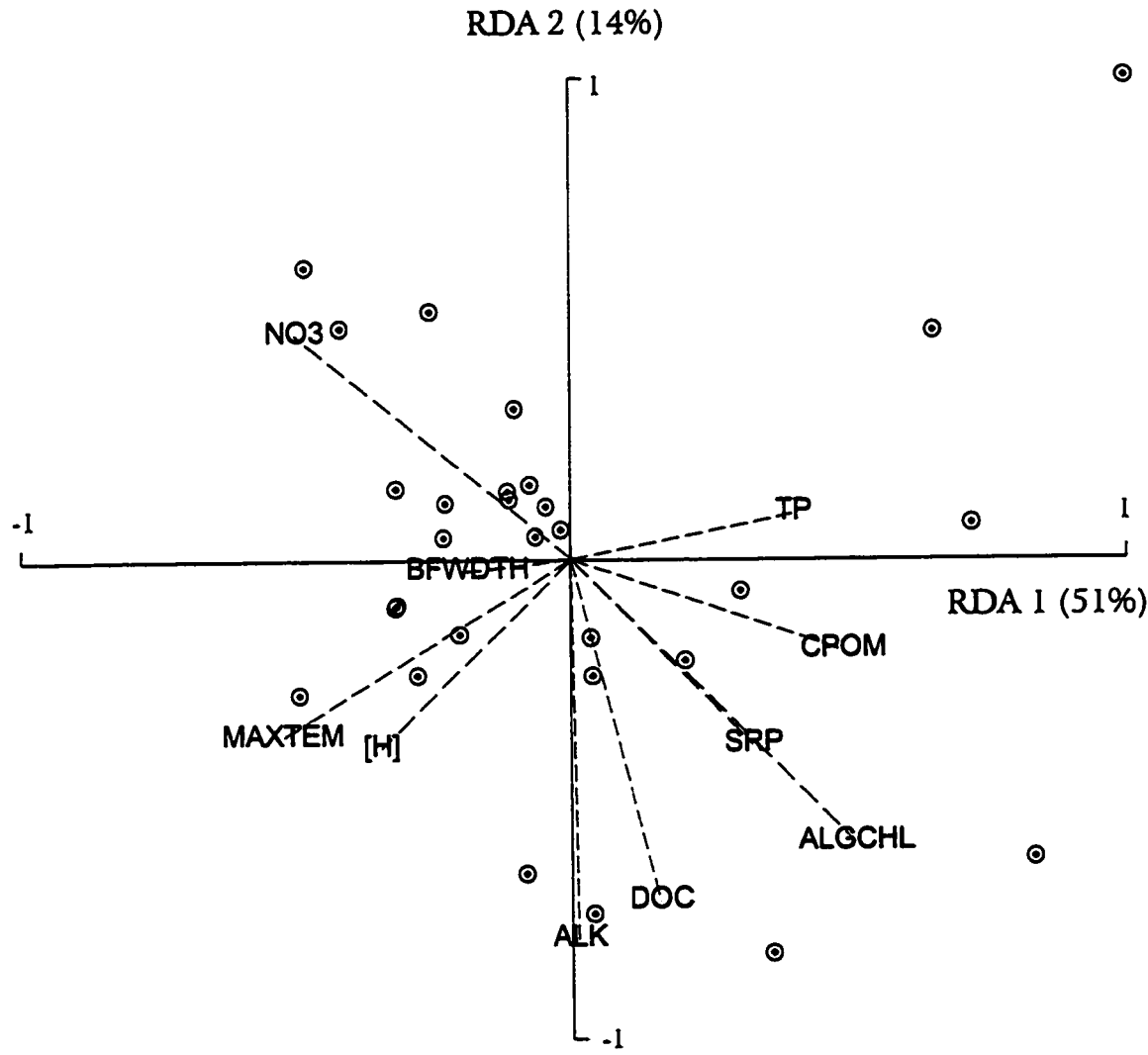
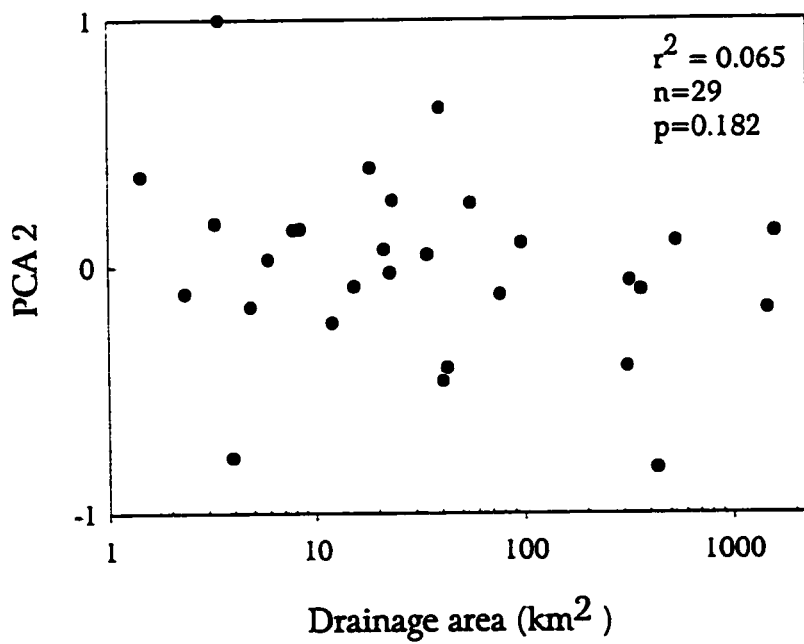
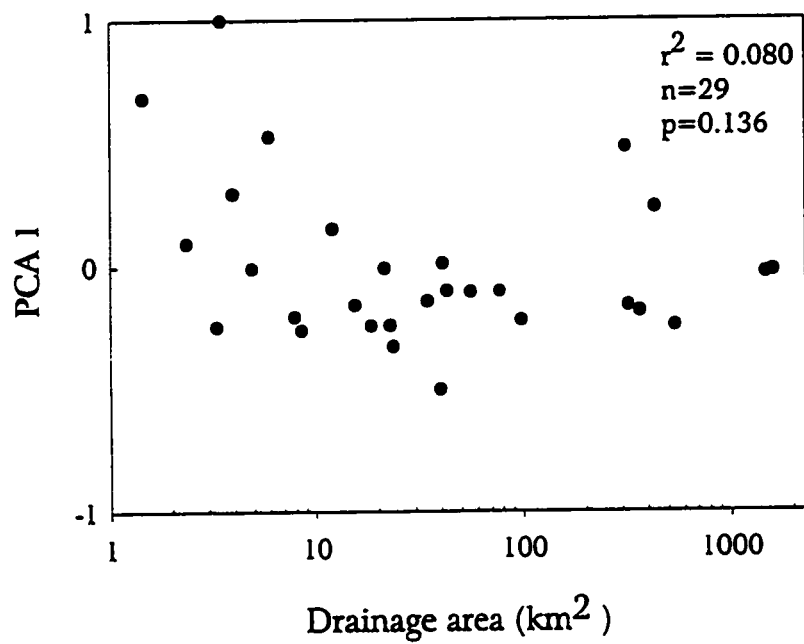


FIGURE 7: Log-linear regression of site scores on principal component analysis axis 1 and 2 against drainage area.

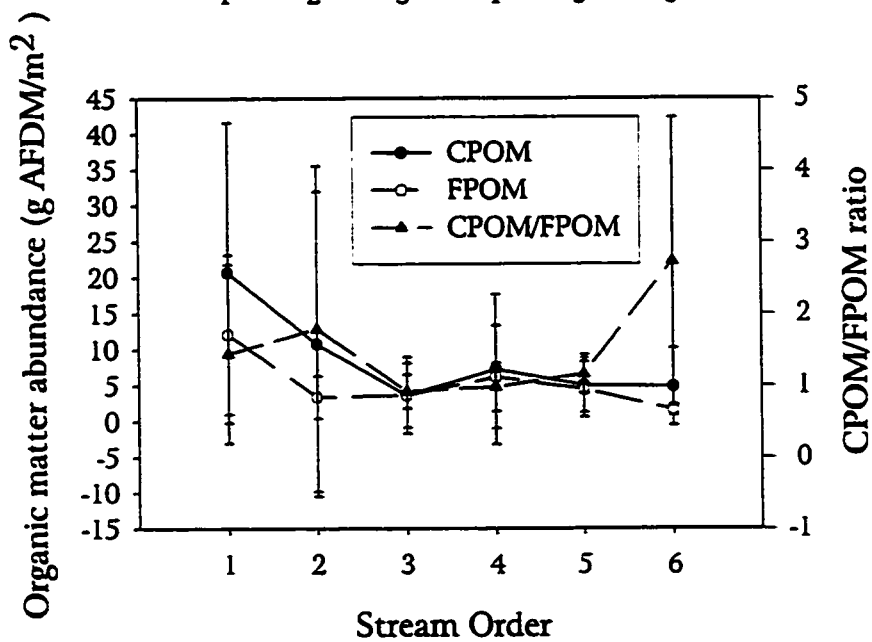
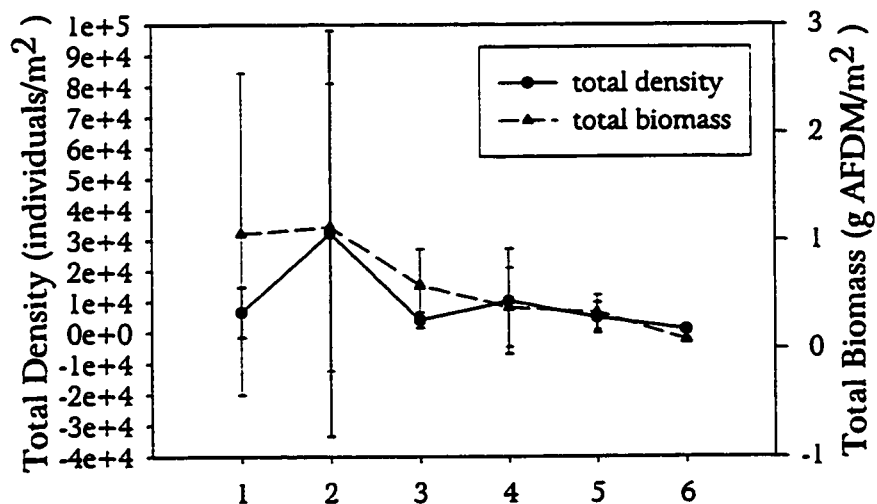
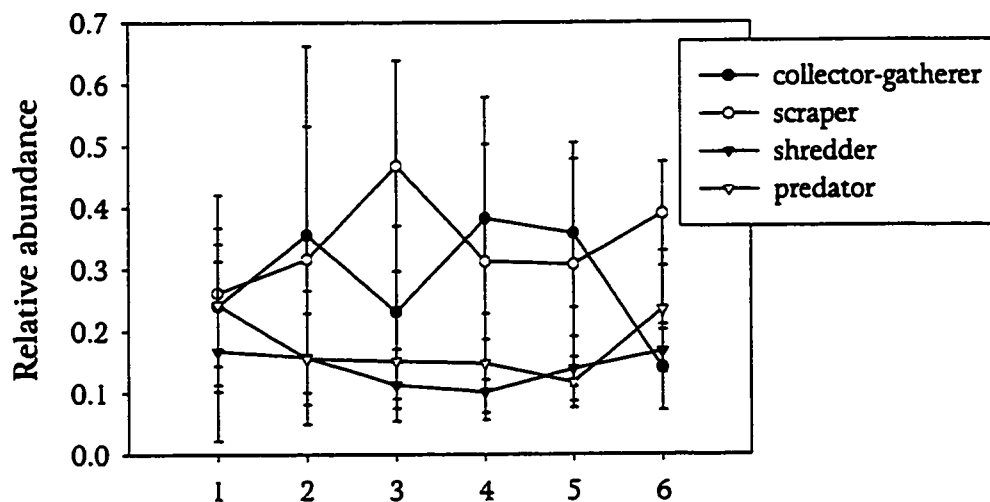


ordination analysis. No predictable changes or shifts in benthic invertebrate community composition or organic matter abundance are evident along an increasing stream order gradient (Figure 8). The relative abundance of collector-gatherers and scrapers fluctuates widely on average with increasing stream order, demonstrating no apparent predictable pattern (Figure 8). On the other hand, shredders and predators constitute a relatively stable proportion of the community on average regardless of stream order. Variance from the mean however, is large for all functional groups (Figure 8). Total invertebrate biomass shows a slight decrease on average with increasing stream order; however, variance from the mean is high, especially for smaller order reaches (Figure 8). Total invertebrate density tends to remain relatively stable with increasing stream order, although again, low order reaches show large variance from the mean (Figure 8). Finally, both coarse and fine particulate organic material show a slight decrease in abundance with increasing order, with coarse particulate organic material 1-3 times as abundant as fine particulate organic material on average (Figure 8). Organic matter abundance shows large variance from the mean for most orders (Figure 8). In summary, benthic invertebrate community composition and organic material abundances vary widely both within and among stream orders and demonstrate no predictable pattern along a stream order gradient.

Fluvial Geomorphic Relationships

Drainage scale fluvial geomorphic relationships in the Kootenay drainage are similar to drainages worldwide, demonstrating predictable trends with increasing stream size. The longitudinal profiles of 19 streams all show a significantly smooth concave upward profile, with an exponential decline in channel gradient with increasing distance from headwaters ($p < 0.005$ for all 19

FIGURE 8: Mean (± 1 se) relative functional group abundance, total taxa density, total taxa biomass and organic matter abundance along a stream order axis. Data from at least three reaches were included in the calculations for each stream order (see Table 1). Functional groups were classified using Merritt and Cummins (1996) and Pennak (1989).



linear regressions; lowest $r^2=0.92$). Distance from headwaters is a positive power function of drainage area, with the exponent of 0.58 indicating that the Kootenay drainage is elongating as it erodes ($r^2=0.93$; Figure 9a). Also, both bankfull width and bankfull depth are positive power functions of drainage area, with width increasing at a greater rate than depth ($r^2=0.85$ and 0.74 respectively; Figure 9b). Channel slope is a positive power function of the ratio of median diameter of bed paving material to drainage area ($r^2=0.87$; Figure 9c). This indicates that for a given drainage area, size of bed paving material decreases predictably with decreasing slope, and that for a given slope, bed material size decreases with increasing drainage area. Channel slope is a negative power function of drainage area ($r^2=0.86$; Figure 9d).

Reach scale geomorphic characteristics on the other hand, can vary substantially from the mean drainage scale geomorphic conditions of the Kootenay river system. Although reach slope on average follows the same decreasing trend with increasing drainage area that was observed for mean channel slope measurements, variance from the mean is extremely high for smaller drainage area reaches (Figure 10). Within the smallest reaches, slope varies from 35% to horizontal and completely overlaps the slope conditions found in reaches that are 2 orders of magnitude larger in drainage area. As drainage area increases, variance in reach slope decreases and mean channel slope becomes a stronger measure of reach slope conditions.

Similarly, the distance between pools or riffles relative to the bankfull width of a reach increases with increasing drainage area (Figure 11). For reaches small in drainage area, the distance between pools or riffles is relatively short, averaging between 1-2 bankfull widths. As drainage area increases, the relative pool or riffle spacing increases until pools and riffles eventually become spaced a predictable 5-7 bankfulls widths apart. The transition between bed

FIGURE 9: Allometric relationships between mean drainage geomorphic characteristics and drainage area for the Kootenay system: a) distance from headwaters versus drainage area, b) bankfull width (●) and depth (O) versus drainage area, c) slope versus the ratio of median diameter of bed paving material to drainage area, d) slope versus drainage area.

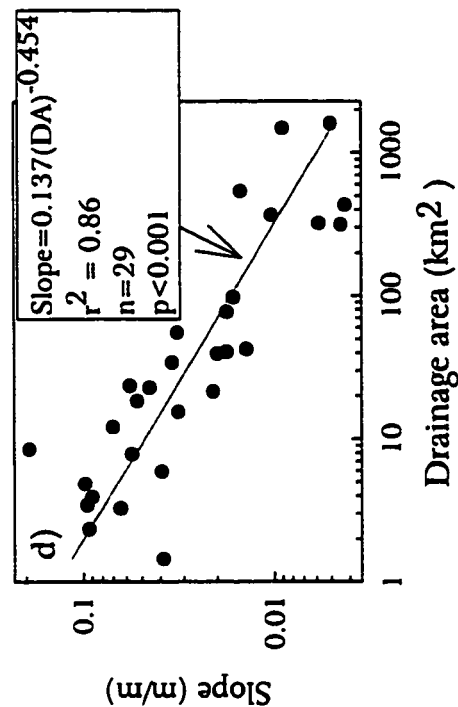
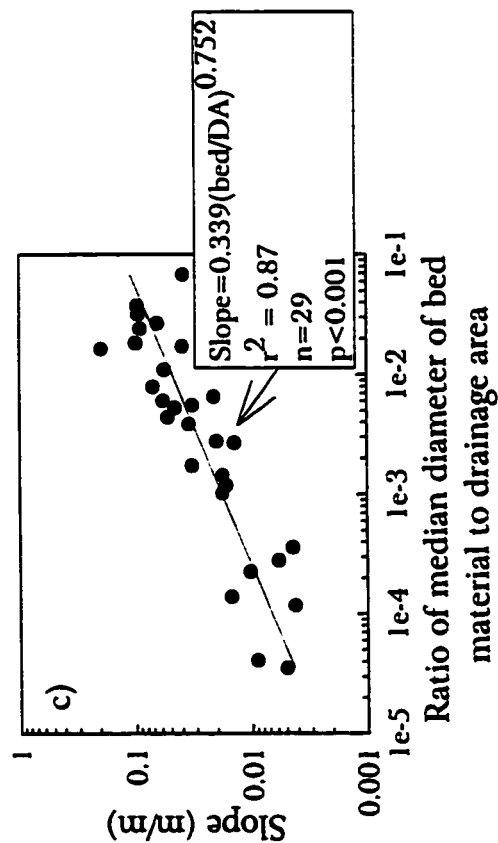
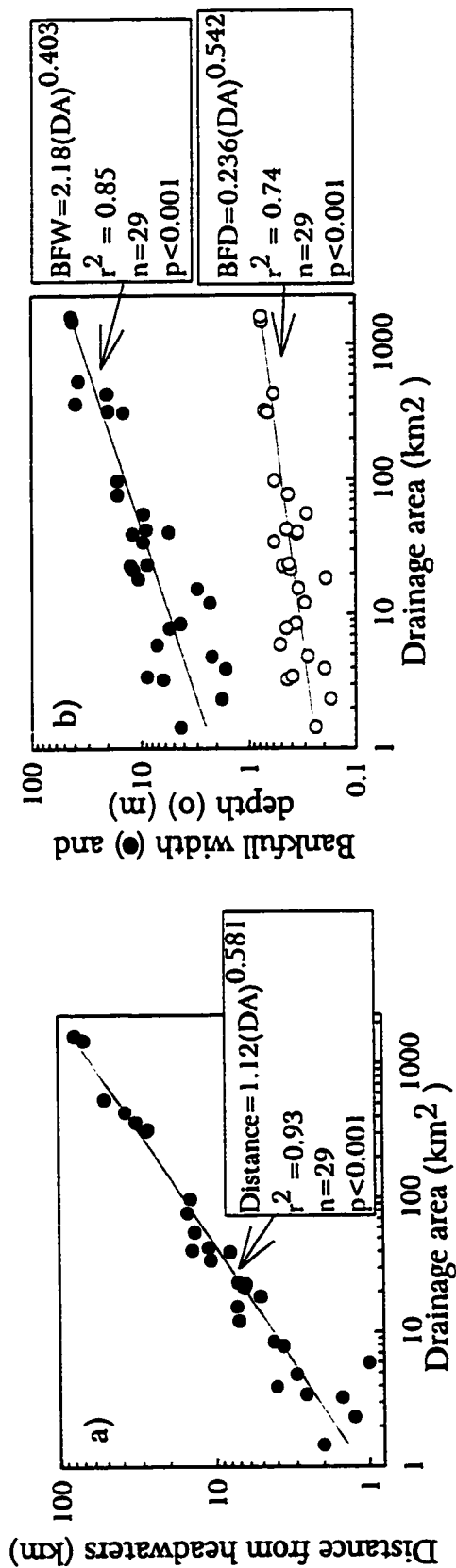


FIGURE 10: Relationship between the mean (± 1 sd) reach slope versus drainage area for 6 of the 29 reaches sampled in the Kootenay drainage. Site names are listed on the upper portion of the figure. For full names see Table 1. The dotted line represents the predicted slope using the equation from Figure 9d.

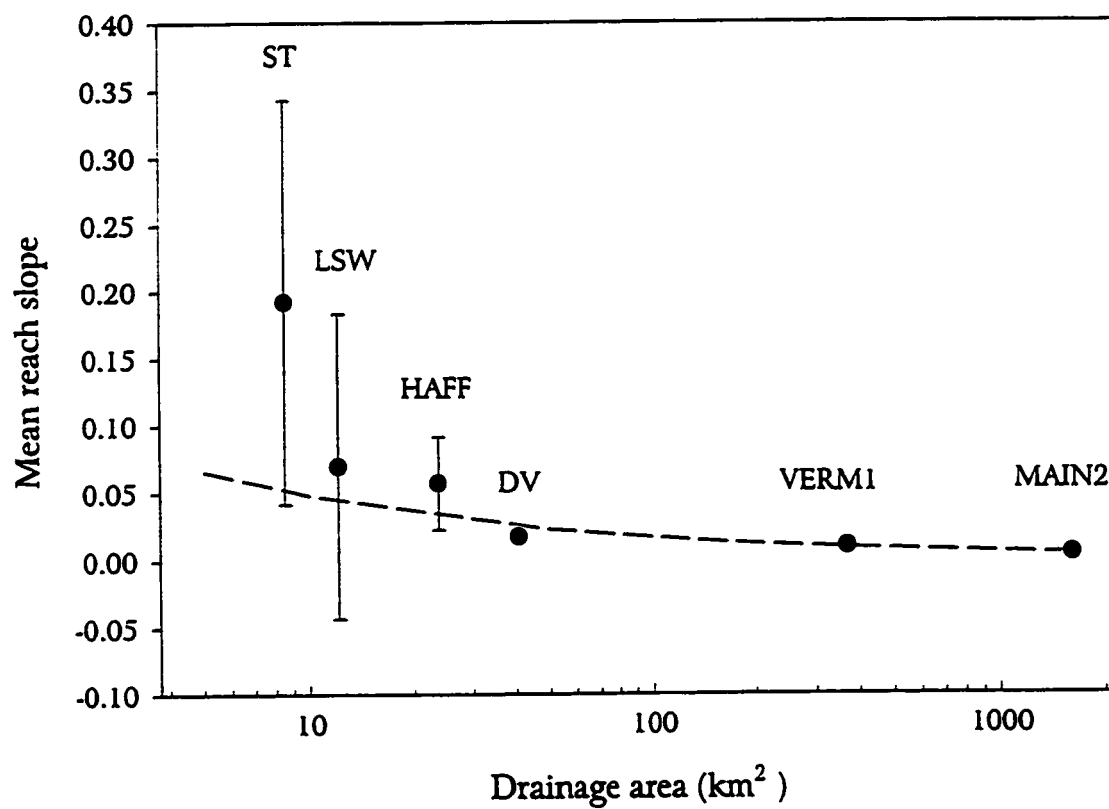
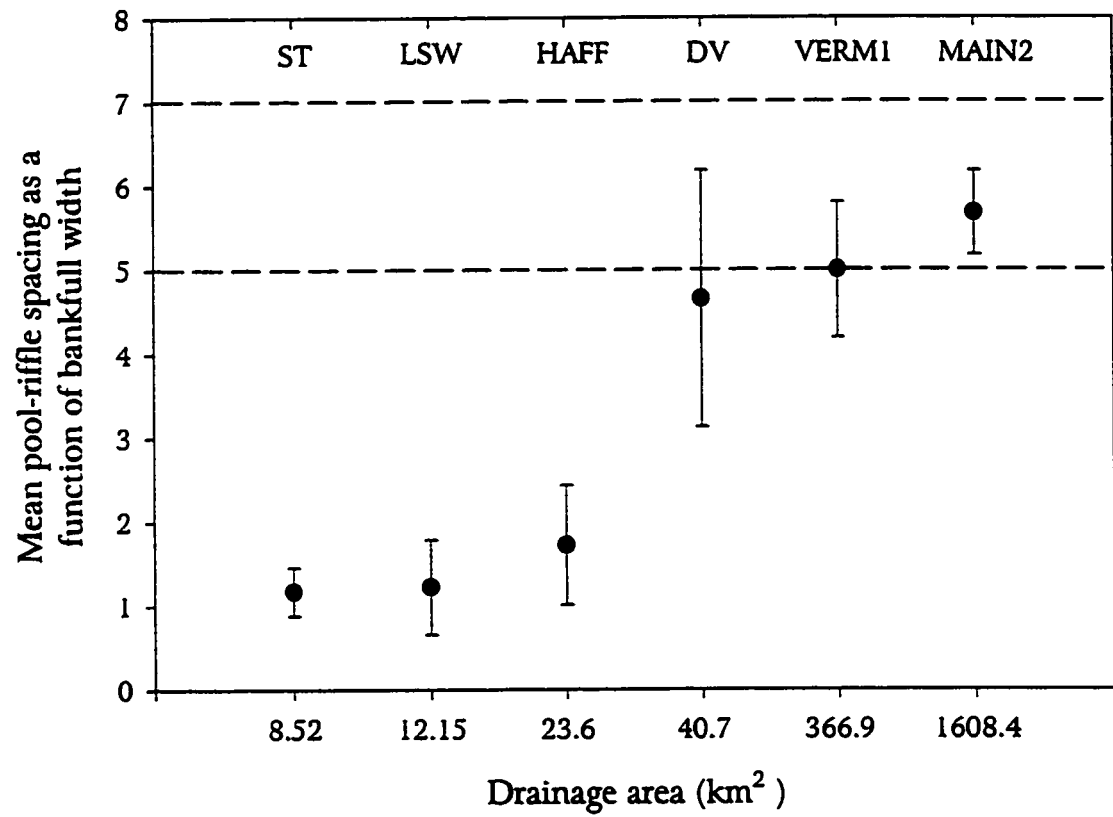


FIGURE 11: The mean (± 1 sd) distance between successive pools or riffles, relative to mean bankfull width of the reach, versus drainage area. A relative spacing of 5-7 bankfull widths between successive pools or riffles signifies a state of dynamic equilibrium at the reach scale (Leopold *et al.* 1964). This zone is marked by two horizontal dotted lines.



structures whose spacing is more locally derived to bed structures whose spacing reflects a state of mean dynamic equilibrium occurs at a drainage area of approximately 40 km² (Figure 11). This is the same point in which variability in reach slope decreases dramatically and begins to more closely match drainage scale mean channel slope measurements (Figure 10).

Explicit Modelling of Resource Gradients

The explicit temperature model successfully explains a significant amount of the variation in the major trends in benthic macroinvertebrate composition at the reach scale in the Kootenay drainage. A linear regression between the water temperature index and the maximum July water temperature measured in each reach is highly significant ($p < 0.001$), indicating the water temperature index is a strong correlate of reach scale water temperature (Figure 12). Furthermore, a linear regression between the water temperature index and the PCA site loadings is highly significant for axis 1 ($p < 0.01$) but is not significant for axis 2 ($p = 0.06$) (Figure 13).

DISCUSSION

The river continuum concept argues that stream size represents the mean geomorphic state of drainage networks and as such provides a general organizational framework to explain patterns of benthic macroinvertebrate abundances (Vannote *et al.* 1980). Since its conception, the river continuum perspective of stream organization has permeated the aquatic literature and is prominent in recent stream ecology and fluvial geomorphology texts (Allan 1995; Petts and Amoros 1996). Contrary to the predictions of the river continuum concept however, the results of the ordination and functional group analysis in the present study clearly show that stream size does not explain a

FIGURE 12: Linear regression between mean maximum July water temperature, measured in each of the 29 reaches of the Kootenay drainage using submersible thermographs (see methods), and the water temperature index.

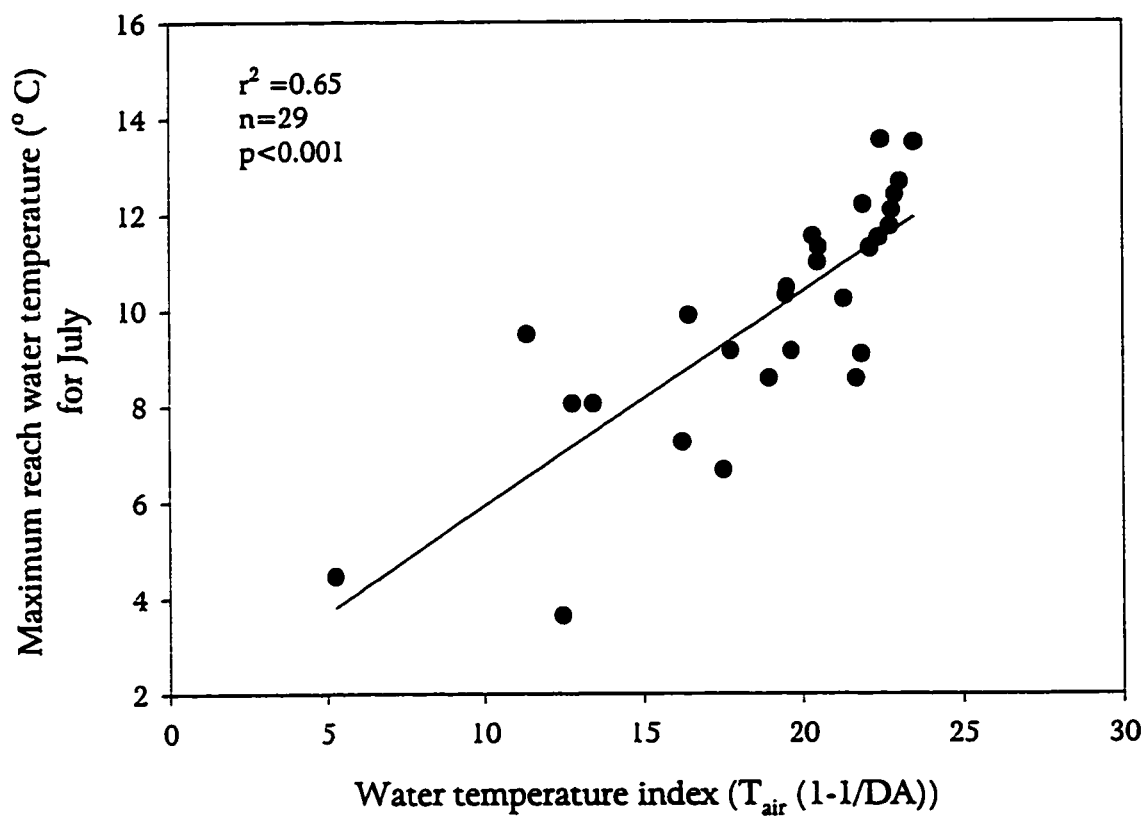
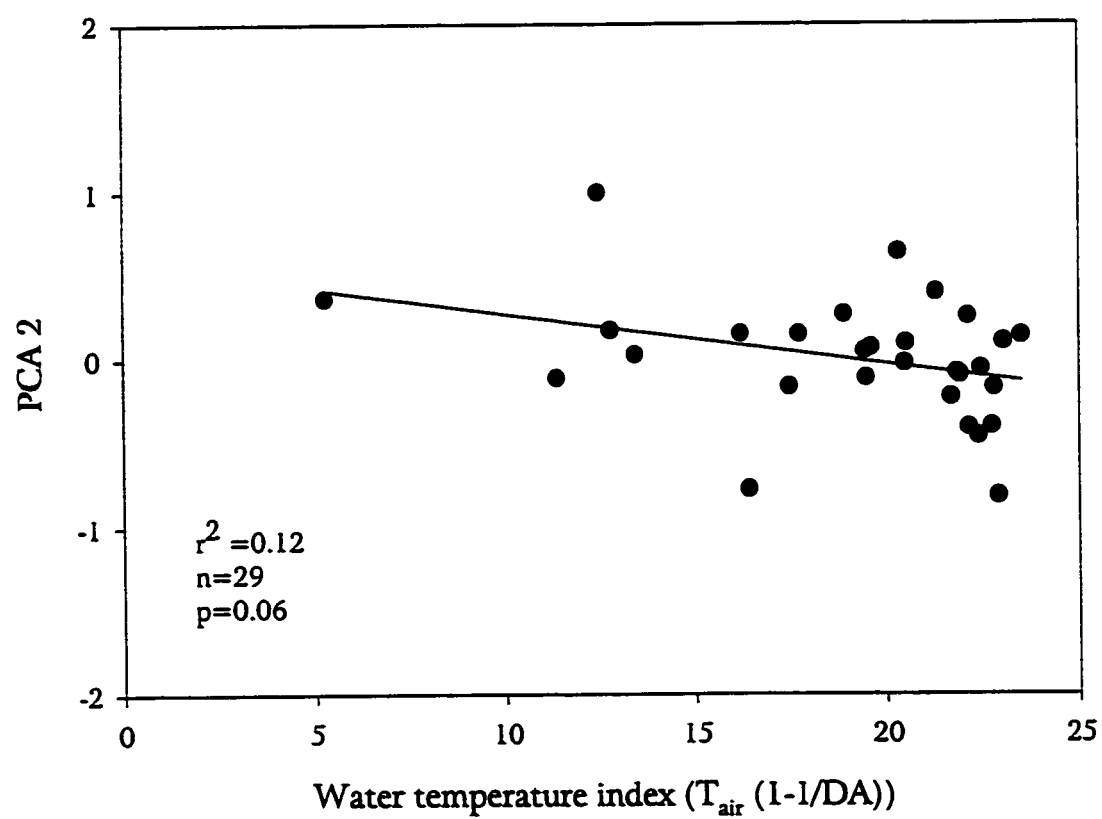
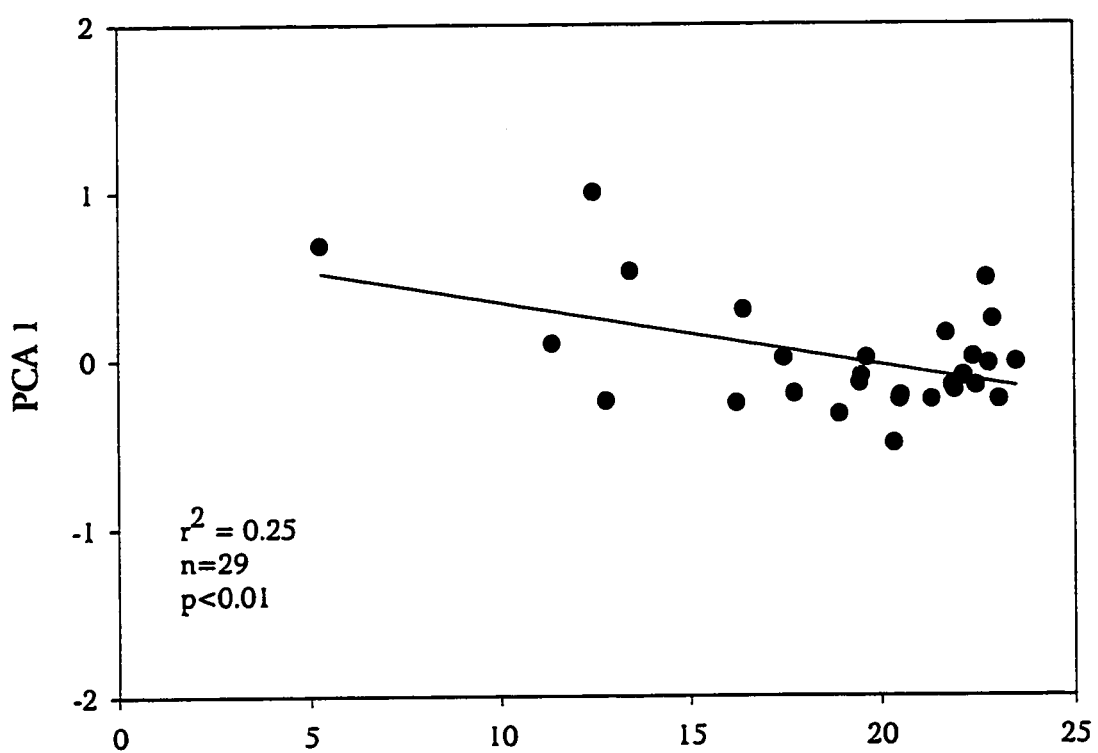


FIGURE 13: Linear regression of site scores on principal component axis 1 and 2 versus the water temperature index.



significant amount of the variation in the major trends in benthic macroinvertebrate community composition in the Kootenay drainage (Figure 7 and 8). These results empirically support the circumstantial evidence of past studies, revealing the poor correspondence between stream size and patterns of benthic invertebrate abundance in certain drainages (Winterbourn *et al.* 1981; Huryn and Wallace 1987; Brussock and Brown 1991; Rundle *et al.* 1993; Brewin *et al.* 1995).

A number of authors have suggested that geomorphic anomalies may account for weak relationships between stream size and patterns of invertebrate composition (Winterbourn *et al.* 1981; Minshall *et al.* 1983; Statzner and Higler 1985). In other words, it is thought that these drainage systems are in a poorly developed state of dynamic equilibrium, and as such represent exceptions to the general river continuum model. Clearly however, this is not the case for the Kootenay drainage, where mean drainage scale geomorphic conditions reflect a developed state of dynamic equilibrium (Figure 9a-d; Mackin 1948; Leopold and Maddock 1953; Langbein 1964; Leopold *et al.* 1964; Langbein and Leopold 1966; Yang 1971a, b; Yang *et al.* 1981). The Kootenay drainage therefore, clearly meets the mean drainage geomorphic requirements of the river continuum concept and is in fact quite similar geomorphologically to the systems in which supporting evidence for the river continuum concept has been gathered (e.g. Naiman *et al.* 1987). Thus, the disagreement between the predictions of the river continuum concept and the results of the present study cannot be accounted for by geomorphic anomalies in the Kootenay drainage. Another explanation for the discrepancy between stream size and patterns of benthic macroinvertebrate composition in the Kootenay drainage must exist.

The explanation for the disagreement lies in the discrepancy between

the spatial and temporal scale at which mean drainage geomorphic conditions are characterized using stream size, and the environmental conditions at the scale of the invertebrate community in studies of compositional change among streams. In other words, the assumption of the river continuum concept that the mean geomorphic characteristics at the drainage scale can be consistently substituted for the geomorphic characteristics at the reach scale, does not generally hold for all stream systems.

A simple scale comparison theoretically supports this statement. For example, the present study focuses on benthic macroinvertebrate compositions at a spatial and temporal scale of 10^1 - 10^2 meters and 10^{-1} - $10^{-0.5}$ years. The spatial scale is representative of the reach, defined as 12 times the mean bankfull width in accordance with established hydrological relationships (Leopold *et al.* 1964), and the temporal scale is representative of the short, 1-2 month period between September and October. In contrast, mean geomorphic relationships with stream size reflect erosional and depositional processes that operate over spatial and temporal scales of 10^3 - 10^5 meters and 10^1 - 10^4 years (Leopold *et al.* 1964; Schumm 1977; Frissell *et al.* 1986; Tarboton *et al.* 1989; Petts and Amoros 1996). At this spatial scale, relating the geomorphic template of a stream to stream order (Strahler 1957, 1964) reveals relationships that apply to the entire section of stream of equal order. The distance between streams of consecutive order may include numerous reaches as defined in this study. Similarly, relating the geomorphic template of a stream to drainage area reveals relationships that derive from the sorting and distribution of material over years or decades (Leopold *et al.* 1964). During this time span, benthic macroinvertebrate compositions characterized over the 2 month window of this study may have undergone numerous changes as a result of shorter scale variations in physical conditions in the reach. The mean

physical state of a drainage system therefore exists at a spatial and temporal scale several orders of magnitude larger than the focal scale of stream composition studies. The author is unaware of any studies that compare faunal compositions among streams of different order by actually sampling and characterizing the community along the entire length of stream of equal order, or for that matter of studies that pool samples taken over long time periods in order to characterize the "typical" long term community in a section of stream. In doing so, most of the processes relevant to the dynamics of the invertebrate community would be overlooked.

Subsequently, if the theory is sound and stream size is a poor predictor of patterns of benthic macroinvertebrate composition in the Kootenay drainage due to an inconsistent match in scale, then differences between the geomorphic characteristics of the reach compared to the mean geomorphic characteristics of the drainage should be evident. As expected, the results of the present study show that mean drainage geomorphic conditions in the Kootenay drainage do not always reflect reach scale physical characteristics. Reach scale slopes are highly variable in drainages less than 40 km², and can potentially deviate widely from the predicted average (Figure 10). Similarly, pool and riffles are spaced short distances apart in smaller streams, and only in streams larger than 40 km² does the spacing match the 5-7 bankfull widths distance that signifies a mean state of dynamic equilibrium (Figure 11). Like many other mountainous systems, the presence of large glacial deposits and/or vegetative debris within the reach can serve to locally disrupt predictable drainage scale geomorphic relationships (e.g. Heede, 1972a, b; Keller and Swanson 1979; Keller and Tally 1979; Newson 1981; Marston 1982; Whittaker and Jaeggi 1982; Gerrard 1990; Grant *et al.* 1990; De Jong and Ergenzinger 1995; Keller *et al.* 1995). In the Kootenay drainage, a drainage

area of 40 km² represents the transition point between small streams whose physical characteristics are largely locally controlled to larger streams whose physical characteristics are a function of mean erosional and depositional forces. The fact that mean geomorphic characteristics at the drainage scale cannot be consistently substituted for the geomorphic characteristics at the reach scale in this system, explains the poor correlation between stream size and patterns of benthic macroinvertebrate composition.

Clearly, in order to understand the general pattern of benthic macroinvertebrate composition in streams then, the stream size axis used in the river continuum concept must be replaced by an explicit model of the processes influencing composition at the reach scale. In the Kootenay drainage, redundancy analysis (RDA) shows that the major trends in variation in invertebrate composition at the reach scale are explained primarily by stream temperature and organic matter abundance (Figure 6). This is consistent with the results of many other studies (e.g. Minshall *et al.* 1983; Wright *et al.* 1984; Naiman *et al.* 1987; Ormerod and Edwards 1987; Power *et al.* 1988; Quinn and Hickey 1990; Malmqvist and Mäki 1994; Marchant *et al.* 1994; Tate and Heiny 1995; Richards *et al.* 1996).

Numerous field and experimental studies have demonstrated the importance of water temperature on invertebrate distributions. For example, many aquatic invertebrate taxa require fairly specific temperature regimes for efficient growth, reproduction and emergence (e.g. Dodds and Hisaw 1925; Illies and Botosaneanu 1963; Sweeny 1978; Sweeny and Vannote 1978; Hildrew and Edington 1979; Ward and Stanford 1982; Vannote and Sweeny 1980). From an evolutionary perspective, stream temperature is thought to have played a major role in the invasion and spread of invertebrates in flowing water systems, which may account for the specific thermal tolerances of many

taxa (Ross 1963; Ross 1967; Hynes 1970a, b; Vannote and Sweeny 1980; Olsson 1981; Ward and Stanford 1982; Hynes 1988; Irons *et al.* 1993).

Similarly, the distribution and abundance of allochthonous and autochthonous organic material has a strong influence on the distribution and abundance of aquatic invertebrates (Cummins 1974; Cummins 1975; Anderson and Sedell 1979; Cummins and Klug 1979; Hawkins *et al.* 1982; Wallace and Gurtz 1986; Richards and Minshall 1988; Cummins *et al.* 1989; Boulton and Lake 1992; Dudgeon 1994). Experimental manipulations of allochthonous organic material abundance have demonstrated significant effects on species abundances and overall compositions in streams (Rabeni and Minshall 1977; Culp 1982; Culp *et al.* 1983; Culp and Davies 1985). Nutrient addition and enrichment experiments have also shown severe bottom-up effects on the invertebrate community by altering algal abundances (Fairchild and Lowe 1984; Fairchild *et al.* 1985; Hershey *et al.* 1988; Ogilvie 1988; Hinterleitner-Anderson *et al.* 1992; Peterson *et al.* 1993). In fact, the high correlation of nutrient levels with compositional trends in the RDA may likely represent the influence of these variables on organic matter abundance rather than a direct effect on the benthic invertebrates (Figure 6).

Patterns of benthic macroinvertebrate community composition in the Kootenay drainage can be explained by explicitly modelling the processes driving water temperature. The energy from incoming solar radiation was estimated using an empirical air temperature versus elevation relationship for the approximate period of sampling. This was combined with an estimate of the energy transfer and sensitivity to groundwater input of each reach using the approximate volume of water present in each reach, and an index of water temperature created that explains a significant amount of the variation in the actual water temperature measured in each reach over the same period of time

(Figure 12).

Although this model is not an actual estimate of water temperature, as it is not dimensionally correct, it is a correlate of water temperature derived from an understanding of the processes influencing water temperature. As such, the model successfully explains a significant amount of the variation in the major trends in benthic invertebrate composition in the Kootenay drainage (Figure 13). In other words, this simple explicit model of instream temperature provides an organizational framework for understanding patterns of invertebrate composition in the Kootenay drainage. This suggests that a general understanding of patterns of invertebrate composition in streams requires that the important resources are identified and explicitly modelled at the appropriate focal scale.

A weakness of the stream temperature model may be that it is overly simplistic. The simplicity of the model however, is also one of its most appealing aspects. An increasingly complex resource model requires increasingly greater amounts of time to gather the relevant data to run the model. The success of the present model in explaining compositional patterns in the Kootenay drainage indicates that compositional similarities among reaches can be assessed by simply measuring the elevation and the area draining into each reach. The ease of applying the model is a great asset, although a more realistic model may explain a larger portion of the variation in the data.

Ideally, a larger portion of the variation in composition in the Kootenay drainage would have been explained by creating a model of coarse particulate organic material abundance (CPOM), to be used in conjunction with the temperature model. An attempt to do this however, met with limited success due to the difficulty in estimating a few key components. Previous work

suggests the abundance of CPOM in a reach is primarily a function of the amount of terrestrially derived litter entering the reach, the proportion of this litter that is retained versus transported out of the reach, the amount of CPOM already present in the reach and/or entering the reach from upstream, and the rate at which this material degrades into finer particulates by both physical and biological means (Short and Ward 1980; Short *et al.* 1980; Cummins *et al.* 1983b). Combining these components into a simple model is obviously difficult; however, some of these components have been previously studied in detail such that a simpler surrogate measure of the process may be substituted. For example, the transport of material from a reach has been linked to discharge levels with some success (e.g. Fisher and Likens 1973; Fisher 1977; Bilby and Likens 1979; Schlesinger and Melack 1981). Similarly, the biological breakdown of organic material is known to be strongly related to temperature, and the retentive properties of streams more fundamentally related to hydrologic and substrate related features (e.g. Boling *et al.* 1975; Speaker *et al.* 1984).

For terrestrially derived litter inputs however, no general process models exist in the literature that allow the substitution of simpler variables. A number of papers suggest a relationship exists between stream size and litter input, due to differences in canopy cover over the stream (Cummins *et al.* 1989; McClain and Richey 1996). However, the results of two other papers relating litter input to stream order contradict this argument (Connors and Naiman 1984; Benfield 1997). Without actual litter-trap data therefore, this component of the model cannot be estimated. Combined with the difficulty in estimating contributions of CPOM from reaches upstream and the amount remaining in a reach from previous litter infusions, the prediction of CPOM abundances in reaches of the Kootenay drainage was limited. A more

thorough study of the various components of CPOM dynamics in streams could provide a stronger, more general explanation for invertebrate distributional patterns in stream systems.

The stream temperature model also illustrates that not all the processes driving resource levels are related to the geomorphic characteristics of the stream. This suggests that, even when drainage scale geomorphology corresponds to reach scale geomorphology, drainage scale geomorphology would still not capture all the processes driving resource gradient levels. For example, the total energy from solar radiation projected onto a stream surface is a function of geographical location and large scale climatic processes, both of which are largely independent of drainage scale geomorphic characteristics (Crisp and Howson 1982; Bristow and Campbell 1984; Sinokrot and Stefan 1993; Aubinet 1994). Only when this solar energy actually interacts with the water column of the stream do the processes of absorption, reflection, conduction and so on become modified by stream geomorphic characteristics (Bowles *et al.* 1977; Jobson 1977; Sinokrot and Stefan 1993). Characterizing reaches according to geomorphic characteristics alone is therefore not sufficient for explaining benthic macroinvertebrate compositional patterns. This requires characterizing the processes driving the important resources that occur within the stream itself, as well as those that occur external to the stream.

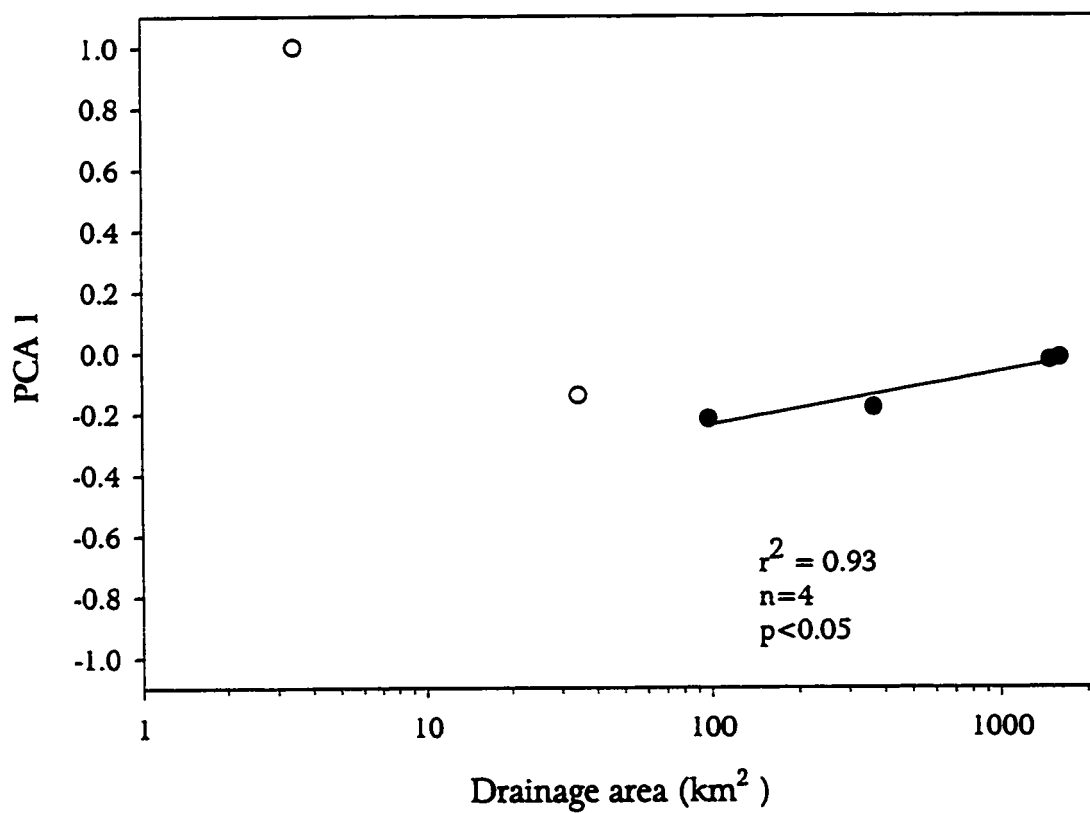
It still remains to be explained why stream size is able to account for patterns of benthic macroinvertebrate composition in some systems. The research leading to and supporting the river continuum concept focused on temperate woodland systems, where the characteristic mean geomorphic relationships denoting dynamic equilibrium and the predictable relationship between pool-riffle spacing and mean stream width were first recognized (Leopold *et al.* 1964). The river continuum concept was therefore developed in

drainages where drainage scale and reach scale geomorphic characteristics coincide. In the present study, drainage scale estimates of physical characteristics only coincide with reach scale conditions in streams greater than 40 km².

The present study has also shown that water temperatures and organic matter abundances are both partially influenced by processes that occur independent of changes in channel geomorphology. Reaches that are in every way physically similar are found to harbour very different communities and resource levels due to differences in the processes not related to channel morphology. That this was not apparent in earlier examinations of the river continuum concept, suggests that there was little or no replication of sampling among various stream sizes. In other words, samples were effectively taken and compared successively along a single tributary, with one measure of invertebrate composition for each stream size. A brief examination of the small number of papers confirming the relationship between stream size and compositional patterns shows this to be the case (e.g. Sedell *et al.* 1978; Hawkins and Sedell 1981; Culp and Davies 1982; Minshall *et al.* 1983; Minshall 1985b; Naiman *et al.* 1987; Meyer and Edwards 1990).

Applying the above conditions to streams in the Kootenay drainage demonstrates the specific application of the river continuum concept. Six reaches located along one continuous length of stream were selected in the Kootenay drainage, four of which were greater than 40 km² in drainage area and two of which were smaller. A regression of the major trend in variation in invertebrate composition, represented by the PCA axis 1 site scores, against drainage area shows that drainage area explains a significant amount of the variation in composition for the 4 sites greater than 40 km² ($p < 0.05$; Figure 14). This result is consistent with the predictions of the river continuum

FIGURE 14: Linear regression of site scores on principal component axis 1 for 6 reaches located successively downstream of each other in the Kootenay drainage, versus drainage area. The solid line represents the significant relationship found between drainage area and the 4 reaches greater than 40 km² in drainage area, shown with solid circles. Including in the regression the remaining 2 sites, which are less than 40 km² in drainage area and represented by open circles, results in a relationship that is non-significant. A drainage area of 40 km² represents the approximate transition between reaches whose geomorphic characteristics are locally derived and highly variable from reach to reach, to reaches whose geomorphic characteristics coincide with mean drainage geomorphic characteristics.



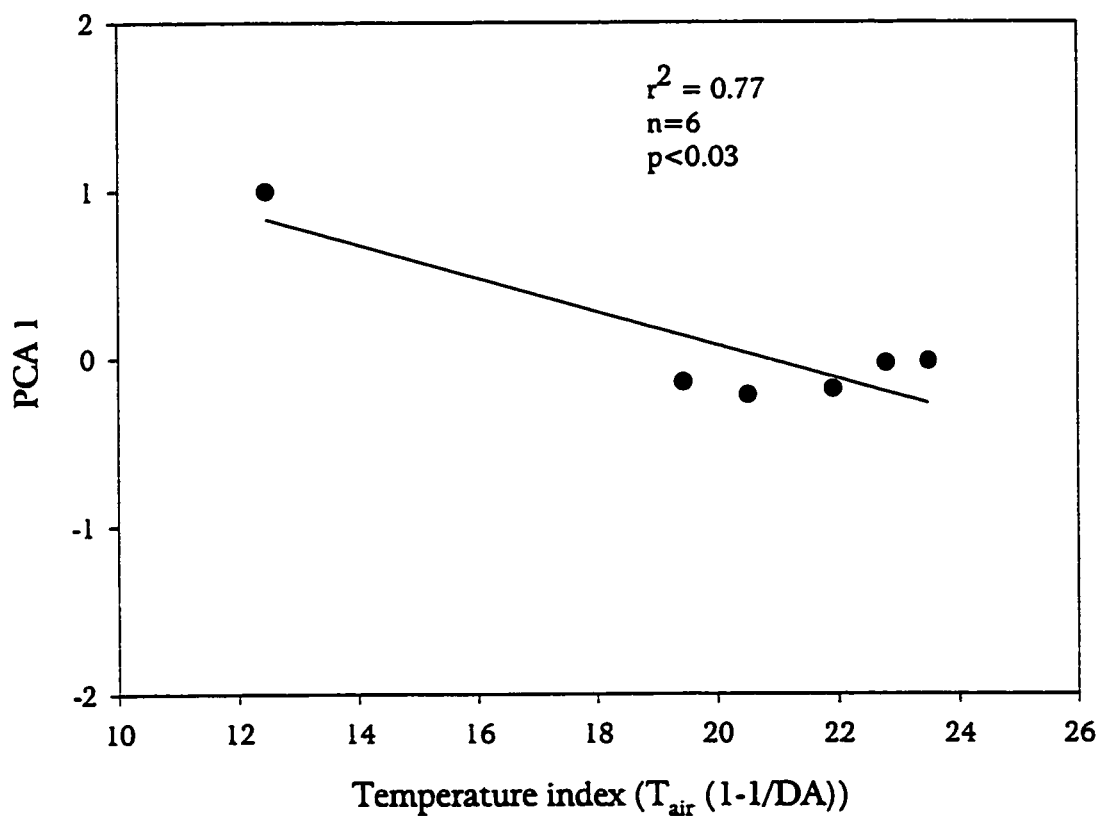
concept. However, as soon as these very specific conditions are violated by including in the regression the 2 remaining sites that are smaller than 40 km², the relationship is no longer significant ($r^2 = 0.4$, $p = 0.14$). Stream size variables therefore explain patterns of composition only when the differing geomorphic scales coincide and when samples are collected along a single tributary. However, they do not provide an organizational framework for patterns of benthic macroinvertebrate composition that is general to all stream systems.

A general understanding of compositional patterns requires an explicit understanding of the processes driving composition at the correct focal scale. As such, the regression of the PCA 1 site loadings for all six sites against the results of the instream temperature model shows that the model accounts for a significant amount of the variation in composition of all 6 reaches ($p < 0.03$; Figure 15).

CONCLUSION

The results of this study indicate that the prevailing paradigm that stream communities and resource gradients are organized in a general fashion consistent with unidirectional increases in water flow needs to be re-examined. The failure of stream size variables to explain the major trends in variation in benthic macroinvertebrate community composition in the Kootenay drainage is primarily due to the discrepancy between the observed reach scale compositional patterns and the implied drainage scale processes. An explicit awareness of scale is an essential component of future research in stream ecology in order to properly link pattern and process (Carter *et al.* 1996; Allan *et al.* 1997; Johnson and Covich 1997; Johnson *et al.* 1997; Richards *et al.* 1997; Townsend *et al.* 1997). This study has further demonstrated that the solution to explaining compositional patterns in streams lies in an explicit

FIGURE 15: Linear regression of site scores on principal component axis 1 for 6 reaches located successively downstream of each other in the Kootenay drainage, versus the water temperature index.



understanding of the processes underlying the important resources. This argument is strongly supported by the fact that stream size significantly explains benthic macroinvertebrate compositional patterns only when specific geomorphic conditions are met and that beyond these conditions the stream temperature model alone significantly accounts for the patterns. Other recent studies have also demonstrated that a general explanation for patterns of faunal organization in streams lies in process explicit modelling (e.g. D'Angelo *et al.* 1997). The next step of the present study is therefore to develop a process model of particulate organic material abundances. Most importantly this requires a better understanding of terrestrially derived litter inputs to streams. Lacking a scale explicit process argument for explaining patterns of benthic macroinvertebrate composition in streams, the river continuum perspective of stream organization represents a specific scenario rather than a general model for all stream systems.

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APPENDIX A: List of taxa identified in the Kootenay drainage along with functional group designations from Merritt and Cummins (1996) and Pennak (1989). Also included is a brief summary of the major trends in benthic macroinvertebrate abundance in the Kootenay drainage. Sh=shredder, C-G=collector-gatherer, Scr=scrapper, Pr=predator.

Order	Family	Abbreviation of Family	Functional Group
Ephemeroptera	Baetidae	BAETID	C-G
	Heptageniidae	HEPTAG	Scr
	Ephemerellidae	EPHEME	C-G
	Leptophlebiidae	LEPTOP	C-G
	Ameletidae	AMELET	Scr
Trichoptera	Hydropsychidae	HYDRPS	C-G
	Brachycentridae	BRACHY	C-G
	Rhyacophilidae	RHYACO	Pr
	Limnephilidae	LIMNEP	Sh
	Glossosomatidae	GLOSSO	Scr
	Hydroptilidae	HYDROP	Scr
Plecoptera	Perlidae	PERLID	Pr
	Perlodidae	PERLOD	Pr
	Peltoperlidae	PELTOP	Sh
	Taeniopterygidae	TAENIO	Sh
	Chloroperlidae	CHLORO	Pr
	Capniidae	CAPNII	Sh
	Nemouridae	NEMOUR	Sh

APPENDIX A continued

Plecoptera	Pteronarcyidae	PTERON	Sh
Diptera	Chironomidae	CHIRON	C-G
	Empididae	EMPIDI	Pr
	Ceratopogonidae	CERATO	Pr
	Psychodidae	PSYCHO	C-G
	Tipulidae	TIPULI	Sh
	Dixidae	DIXIDA	C-G
	Pelecorhyncidae	PELECO	Pr
	Simuliidae	SIMULI	C-G
	Pipunculidae	PIPUNC	?
	Blephariceridae	BLEPHA	Scr
Coleoptera	Elmidae	ELMIDA	C-G
Oligochaeta	Lumbriculidae	LUMBRI	C-G
Collembolla		COLLEM	C-G
Hydracarina		HYDRAC	Pr
Hirudinea		HIRUDI	C-G
Copepoda		COPEPO	C-G
Ostracoda		OSTRAC	C-G
Nematoda		NEMATO	C-G
Gastropoda		GASTRO	Scr

A total of 38 benthic macroinvertebrate taxa were identified in the Kootenay drainage in communities consisting predominantly of aquatic insect larvae. Dipterans of the family Chironomidae were the most abundant taxa, accounting for approximately 57% of the total number of invertebrates identified. Other abundant taxa included the mayflies Heptageniidae (14%) and Baetidae (8%), and the stonefly Nemouridae (5%). In terms of biomass, Heptageniidae was the dominant taxa, accounting for 21% of the total biomass measured in fall 1995. The stonefly Perlodidae (16%), the dipteran Chironomidae (10%) and the caddisfly Hydropsychidae (8%) also accounted for large portions of the total biomass. Total invertebrate densities ranged from 85 individuals/m² to 166 000 individuals/m², while total invertebrate biomass ranged from 0.02 g/m² to 3.7 g/m².

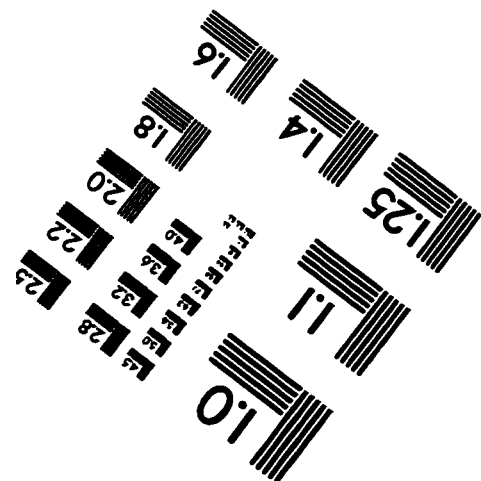
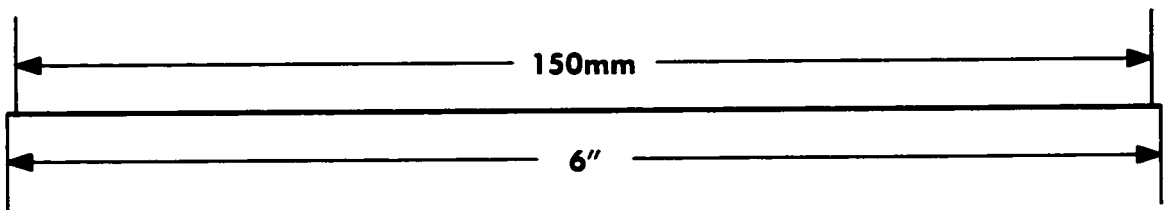
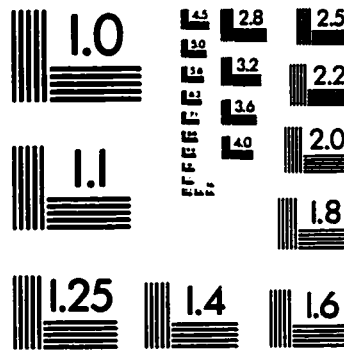
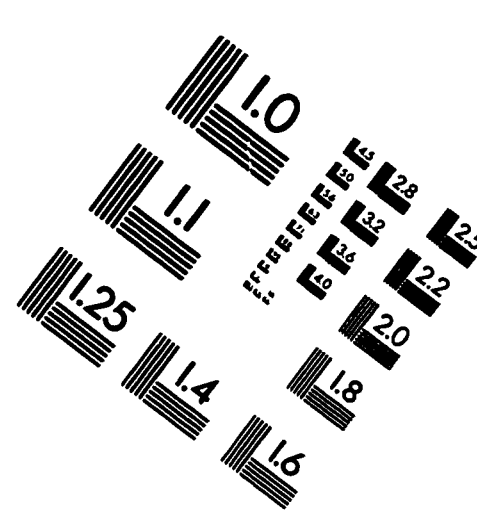
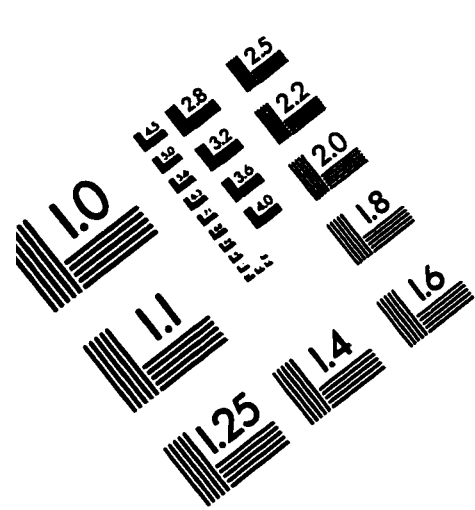
The families Chironomidae and Heptageniidae had the widest distribution in the Kootenay drainage, being identified in all 29 sites sampled. The family Nemouridae was identified in all sites except Helmet tributary 9. Chloroperlidae was identified in all sites except Helmet tributary 9 and Tumbling tributary 6, similar to Hydracarina which was absent only Tumbling tributary 6 and Tumbling creek. The families Baetidae and Ameletidae were absent in 3 of 29 sites, whereas Ephemerellidae, Perlodidae and Taeniopterygidae were absent in 4 sites.

The remaining taxa had more restricted ranges. On the extreme end of this, the family Leptophlebiidae was found only in Kootenay 1, the families Hydroptilidae and Perlidae found only in Kootenay 1 and Kootenay 2, the family Pteronarcidae found only in Main 1 and Main 2 and the family Blephariceridae found only in Vermilion 1 and Vermilion 2.

Overall, the invertebrate taxa identified in the Kootenay drainage are generally typical of rivers in the Rocky mountains (Ward 1975; Ward 1992;

Ward and Kondratieff 1992). Particularly strong transitions occur among reaches in the Kootenay drainage with respect to the abundances of Chironomidae, Heptageniidae and Baetidae. For example, the communities in glacially fed streams, such as Stanley Tributary 1 and Helmet Tributary 9 (Figure 1, Table 1), were largely dominated by chironomids. This pattern is consistent with other north temperate rivers (Minshall *et al.* 1985b).

IMAGE EVALUATION TEST TARGET (QA-3)



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