

Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river

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SUMMARY

1. The spatial distribution of macroinvertebrate species was examined in relation to hydraulic and sedimentary conditions in a large gravel-bed river, the Fraser River, Canada. Mean annual discharge in the Fraser River is $2900 \text{ m}^3 \text{ s}^{-1}$ and annual flood discharge, due to snowmelt in May and June, averages $8760 \text{ m}^3 \text{ s}^{-1}$.
2. Invertebrates were sampled from four water depths (0.2, 0.5, 1.5, 3.0 m) at various levels of discharge that together captured the spatial and temporal variability of the physical habitat. Several hydraulic (near-bed shear velocity, Boundary Reynolds number, turbulence intensity, depth-averaged velocity, Froude number, Reynolds number) and substratum variables (mean grain size, Trask's sorting coefficient, Nikuradse's roughness, percentage of fine sediment, and Shields entrainment function) were measured for each sample of macroinvertebrates. Concentrations of fine and coarse particulate organic matter were also assessed.
3. The physical habitat was characterized by a major gradient of hydraulic conditions that corresponded positively with increasing water depth and accounted for 52% of the total variation in the habitat data. Substratum conditions and the concentration of organic matter explained 24% of the total variation in the habitat data.
4. The distribution of invertebrates was correlated significantly with hydraulic variables and suggests that hydraulic conditions represent a major physical gradient along which the benthic community is organized. The distribution of organic matter and substratum texture were also important for some species. The spatial distribution of most species reflected morphological and trophic suitability to particular habitat conditions.
5. Hydraulic stress associated with foraging and maintaining position, as well as organic matter retention in coarse substrata, are probable mechanisms affecting the spatial distribution of macroinvertebrates.

Introduction

The fluvial environment is characterized by many interacting physical factors that produce spatial and temporal heterogeneity and may exert a major influence on benthic invertebrates. Many studies have examined the relative importance of different physical factors in structuring the benthic community (e.g.

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Culp, Walde & Davies, 1983; Gowns & Davis, 1994; Quinn and Hickey, 1994; Robertson, Lancaster & Hildrew, 1995). Hydraulic and substratum conditions have been identified as two factors that affect community composition, and the abundance and distribution of the constituent populations (Statzner, Gore & Resh, 1988; Cobb, Galloway & Flannagan, 1992; Quinn & Hickey, 1994). Other factors including resource availability (Richardson, 1993), water chemistry (Giberson & Hall, 1988), temperature (Bournaud, Tachet & Roux, 1987) and light (Robinson & Minshall, 1986) have also been shown to play important roles.

The complex interactions between many physical factors makes distinguishing their individual effects on benthic organisms difficult. The interrelation of hydraulics and substratum is particularly problematic because each in part depends on the other. For example, grain size composition of the channel substratum influences the distribution of many benthic taxa (e.g. Gurtz & Wallace, 1984), and is largely determined by the competence of past and present flows (Leopold, 1994). Grain size composition determines the heterogeneity and surface roughness of the substratum which, in turn, creates fine-scale patterns of near-bed flow that influence organic matter retention and the distribution of benthic organisms (e.g. Culp *et al.*, 1983; Hart, Clark & Jasentuliyana, 1996). Surface roughness has also been shown to influence the biotic interactions of competition and predation (Fuller & Rand, 1990; Lancaster, Hildrew & Townsend, 1990), in addition to providing in-stream flow refugia to invertebrates from hydraulic stress (Lancaster & Hildrew, 1993; Robertson *et al.*, 1995). A stable substratum, potentially providing flow refugia, is a product of grain size composition and hydraulic stress exerted on the channel bed.

Elevated hydraulic stress can reduce substratum stability, as well as requiring more energy from organisms to maintain position and prevent accidental loss from the substratum (Ciborowski, 1983). Many stream-dwelling organisms possess specialized traits, such as claws, ventrally positioned gills and streamlining or dorso-ventral flattening of the body, which may reduce lift and drag forces (Statzner & Holm, 1982, 1989; Statzner, 1988). Others have a morphology suited to burrowing, which minimizes flow exposure, while some taxa concentrate along the lateral margins of river channels, where hydraulic forces are

reduced (Rempel, Richardson & Healey, 1999). Additionally, synchrony between emergence and seasonal flooding enables organisms to escape predictable hydrologic fluctuations (Hayden & Clifford, 1974; Gibbs & Mingo, 1986).

Overall, morphology, behaviour and physiology influence tolerance of particular hydraulic and sedimentary conditions, which vary spatially within the fluvial environment. If habitat selection is based on hydraulic and substratum suitability, the spatial distribution of species should correspond to the spatial pattern of physical conditions. Hydraulic and substratum conditions would therefore represent major physical gradients along which the benthic community is organized. Differential use of the habitat by invertebrate species based on hydraulic conditions has been demonstrated under laboratory conditions (Horne, Bennison & Davis, 1992) and in the field, where the spatial scale of the study was individual stones (Hart *et al.*, 1996). The association of taxa with a particular grain size or degree of substratum roughness has also been shown (Fuller & Rand, 1990; Holmuzki & Messier, 1993; Quinn & Hickey, 1994; but see also Culp *et al.*, 1983).

Our purpose was to examine the spatial distribution of benthic invertebrates in relation to hydraulic and sedimentary conditions in a large, non-regulated, gravel-bed river. Large rivers, particularly deep-water habitats, are relatively unstudied in ecological research. It has been suggested that deep water in large rivers is a hostile habitat, relative to the channel margins, because high velocity and sediment transport place high energetic demands on benthic organisms (Church, 1992). This study encompassed several water depths, at several sites, and at various levels of discharge in order, first, to define the major environmental gradients of the benthic habitat and determine their spatial and temporal characteristics. Second, we evaluated the importance of these physical gradients as determinants of benthic community structure by contrasting invertebrate distribution between shallow and deep water in the main channel. The range of sample locations and sample dates together captured the spatial and temporal heterogeneity of the benthic habitat. It was hypothesized that pronounced hydraulic and sedimentary characteristics of the river may represent major physical gradients along which the benthic community is organized.

Methods

Study area

The study was carried out along a 10 km reach of the Fraser River, British Columbia, 125 km upstream from the city of Vancouver (49°13'N, 121°49'W). The Fraser River has a drainage area of 233 000 km² and the mainstem is unregulated over its 1350 km length. The study reach has a mean annual discharge of approximately 2900 m³ s⁻¹ (McLean, 1990) and is characterized by a wandering channel with wooded islands and mid-channel gravel bars. While some dikes exist within the study reach, they have been placed well beyond the main channel to maintain relatively natural river processes and morphology. Annual flooding is predictable and long lasting. Mean annual flood discharge in the study reach is 8760 m³ s⁻¹ and the flood cycle is driven by snowmelt and peaks in June. Average channel velocity ranges from 1.4 m s⁻¹ at low flow to 3.2 m s⁻¹, and the associated range in mean channel depth is from 4.1 m at low flow to 7.9 m during flooding (McLean, 1990).

Three gravel bars within the study reach were selected on the basis of similarity in substratum composition, bank slope, flow velocity and orientation to the river bank. Riparian vegetation consisted of black cottonwood (*Populus trichocarpa* Torr. & Gray), red alder (*Alnus rubra* Bong.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Western redcedar (*Thuja plicata* Donn). Mean grain size at each gravel bar was 30.6 ± 0.9, 35.7 ± 0.9 and 24.1 ± 0.9 mm. Gravel bars were divided by three transects perpendicular to the river bank and four depths of water (0.2, 0.5, 1.5 and 3.0 m) were sampled along each transect. At these locations, macroinvertebrate samples and measurements of several hydraulic and sedimentary variables were collected. The sites were sampled five times in 1995 through the annual flood cycle, totalling 180

macroinvertebrate samples and physical measurements (five dates × three sites × three transects/site × four depths/transect). Transect locations were fixed during the study while the location of sampling depths within the channel shifted laterally between months with changing levels of discharge. Hydrological measurements over the duration of the study are summarized in Table 1.

Macroinvertebrate samples

Benthic invertebrate samples were collected at depths of 1.5 and 3.0 m with a Shipek grab sampler. The Shipek is a weighted bottom sampler that was deployed by a power-operated winch from the side of a boat. A sonar mounted to the boat was used to locate sampling depths of 1.5 and 3.0 m. Five casts of the Shipek, totalling 0.2 m² of channel bed area, were pooled together for each sample. Benthic samples were passed through a series of sieves and material greater than 500 µm was preserved in 4% formaldehyde for sorting of the invertebrates from the sediment. Larger gravels and cobbles were first separated from this material, washed to remove any invertebrates, and combined with fractions less than 500 µm for grain size analysis. Once sorted, invertebrates were transferred to 70% ethanol for storage. The sorted sediment was then washed and recombined with the other sediment fractions for grain size analysis.

A Surber sampler (0.09 m², 500 µm mesh) was used to collect benthic samples at depths of 0.2 and 0.5 m because the boat could not safely manoeuvre in shallow water. A comparison of the sampling performance between the Shipek and Surber samplers was made prior to the study. Paired samples were collected at 50 cm water depth from two gravel bars in the study reach. The bars differed slightly in sediment texture, having mean grain sizes of 18.9 and

Table 1 Hydrologic measurements for the study reach of the Fraser River on each sampling date of this study. (Source: Water Resources Branch, Environment Canada)

Date (1995)	Discharge (Q) (m ³ s ⁻¹)	Temperature (°C)	Turbidity (NTUs)	Change in water level (m)
April	2216	9.5	15	0
May	5397	13.5	33.5	+1.5
June	5025	13	23	+1.4
August	4160	19	44	+1.0
September	1830	18	6.5	-0.2

33.1 mm, respectively. The total density of invertebrates did not differ statistically between samples collected by the Shipek and Surber samplers (paired *t*-test, $t = 1.54$, $P = 0.15$, 15 d.f.).

Invertebrates were identified to the lowest possible taxonomic classification, which was usually genus because species-level identification has not been determined for most taxa in the Fraser River basin. Taxa were assigned to the following functional feeding group (FFG) categories after Merritt & Cummins (1996) and Thorp & Covich (1991): collector-gatherers, collector-filterers, predators, grazers and shredders. Taxa were also classified according to flow exposure groups (FEG), proposed by Growns & Davis (1994), to examine invertebrate distributions with respect to near-bed flow conditions. The flow exposure category (obligate, facultative and avoider) assigned to each taxa was based on *a priori* assessments of morphology and feeding behaviour, as suggested by Growns & Davis (1994).

Physical measurements

Grabs of channel bed sediment and flow velocity measurements were collected with each sample of benthic invertebrates to characterize the hydraulic and substratum conditions. Sediment from 1.5 and 3.0 m was gathered by the Shipek grab and a scoop dredge was used at depths of 0.2 and 0.5 m. Each method provided a roughly equivalent volume of bed material. A comparative test conducted between the Shipek and scoop dredge determined that the grain size distribution of surface sediment collected by the two methods was similar (paired *t*-test, $t = -2.05$, $P = 0.13$, 3 d.f.). Sediment samples were oven-dried at 190 °C, weighed and sieved to determine the grain size distribution. Particles larger than 64 mm were omitted to avoid disproportionate representation by weight of large grain size fractions (Church, McLean & Wolcott, 1987).

The sieved fractions were ashed in a muffle furnace (500 °C, 8 h) to determine the ash-free dry mass of organic matter and mineral substratum in each size fraction. The organic component of substratum samples was expressed as the weight of coarse particulate organic matter (≤ 1 mm, CPOM) and fine particulate organic matter (< 1 mm, FPOM) per unit area. Several descriptive measures of grain size composition were calculated for all sediment samples: mean grain

size (Folk, 1965), Trask's coefficient of sorting which measures grain size homogeneity (Inman, 1952), and channel bed roughness (Church, Wolcott & Maizels, 1990; Table 2). Each was selected for its ecological relevance and capacity to characterize substratum composition and texture.

Near-bed flow velocity and velocity at 0.6 of the depth (depth-averaged velocity) were measured. Both variables were included in the study because the latter is more easily measured and has been commonly used to infer near-bed hydraulic conditions. Davis & Barmuta (1989) suggested that the importance of depth-averaged and near-bed measures may differ between large rivers and small streams; with greater water depth in large rivers, near-bed flow patterns may be more closely related to substratum characteristics than mean velocity. This study, therefore, served to compare inferred near-bed parameters with directly measured values and to evaluate the relation between them.

A rod stacked with three current meters was used to collect near-bed velocity measurements over two intervals of 60 s. The current meters used were a Marsh-McBirney electromagnetic meter (20 Hz) and two Ott impeller meters fixed at heights of 3, 10, and 30 cm above the bed, respectively. Depth-averaged velocity measurements at depths of 1.5 and 3.0 m were made using an Interocean S4 oceanographic sampler deployed from the boat. The S4 took continuous velocity readings over 120 s and depth-averaged velocity was expressed as the average of the readings. In shallow water, the equivalent measure of velocity at 0.6 of the depth was measured using an Ott meter. Velocity data were used to characterize hydraulic conditions associated with each invertebrate sample based on equations of Carling (1992) and others where specified. The near-bed variables measured were shear velocity, turbulence intensity, Boundary Reynolds number and substratum mobility determined by Shields entrainment function (Shields, 1936). Depth-averaged variables were mean velocity, Froude number and Reynolds number (Table 2).

Data analysis

Principal Components Analysis (PCA) of the physical variables was used to summarize total variation in the data and identify major environmental gradients. Variables were logarithmically transformed

Table 2 Summary of physical variables measured in the study

Name	Symbol	Units	Formula	Description
<i>Sedimentary measures</i>				
Mean grain size	D	mm	$\frac{(D_{84} + D_{50} + D_{16})}{3}$	Mean grain size of the sample
Trask's sorting coefficient	S _o	None	$\sqrt{D_{84}/D_{16}}$	Grain size homogeneity of the sample (heterogeneity > 1)
Bed roughness	k _s	mm	3.5 × D ₈₄	Bed roughness, topographic variation
% Fines		%	$\frac{\text{weight} < 2 \text{ mm}}{\text{total weight}} \times 100$	Proportion by weight of the total sample less than 2 mm
<i>Hydraulic measures: near-bed</i>				
Shear velocity	U _*	Cm s ⁻¹	$\frac{1}{\text{slope} \times 5.75}$	Slope of vertical velocity log profile
Turbulence intensity	T _*	None	Direct measure	Coefficient of variation of near-bed velocity
Boundary Reynolds number	Re _*	None	$\frac{U_* k_s}{\nu}$	Nature of flow close to the bed, near-bed turbulence ($\nu = 0.01 \text{ cm}^2 \text{ s}^{-1}$)
Shields Entrainment Function	τ _*	None	$\frac{g D_{50} (\frac{\rho_s}{\rho} - 1)}{\rho U_*^2}$	Non-dimensional measure of substrate mobility ($\rho = 0.998 \text{ g cm}^{-3}$; $g = 980 \text{ cm s}^{-1}$; $\rho_s = 2.65 \text{ g cm}^{-3}$)
<i>Hydraulic measures: depth-averaged</i>				
Mean velocity	U	Cm s ⁻¹	Direct measure	Velocity measured at 0.6 depth below water surface
Froude number	Fr	None	$\frac{\sqrt{U^2 / g d}}{U d}$	Turbulence close to the water surface
Reynolds number	Re	None	$\frac{U d}{\nu}$	Turbulence of free flow ($\nu = 0.01 \text{ cm}^2 \text{ s}^{-1}$)

D_x, grain diameter (mm) at which x percent of the sample by weight is finer; ν, kinematic viscosity of water; g, acceleration due to gravity; ρ_s and ρ are the density of the grain material and water, respectively; d, water depth.

[log₁₀(x + 1)] and a covariance matrix was used to standardize the data and minimize variation caused by the different scale of the variables. Correlation analysis determined the loading of each variable on the eigenvectors. Significance was determined using the Bonferroni correction for the total number of contrasts made ($P = 0.05/14$ variables = 0.0036) to reduce the likelihood of a significant correlation due to chance and to reduce over-interpretation of the data (Rice, 1989). Multivariate analysis of variance (MANOVA) was used to determine the effect of water depth, sampling date and site on the environmental gradients corresponding to the first two eigenvectors. The MANOVA differentiated how much of the variation in the physical gradients was attributable to each of these three factors.

Canonical Correlation Analysis (COR) was used to examine the relation between the invertebrate and physical habitat data. COR is a direct gradient analysis that determines coefficients (scores) for taxa and coefficients for physical variables in order to maximize the species-habitat correlation (Jongman, Ter

Braak & Van Tongeren, 1995). Only those taxa representing greater than 1% of the total invertebrates collected in the study were used in the analysis (11 of 34 taxa). All invertebrate and habitat data were log₁₀(x + 1) transformed to reduce the influence of numerically dominant taxa and standardize the scales of the physical data. Multiple regression and correlation analysis options of the CANCELL procedure of SAS (SAS Institute Inc., 1990) were used to interpret the canonical correlation analyses and isolate the effect of physical variables on individual taxa. The least-square criterion of the linear regression analysis was applied. A COR was also applied to invertebrate data classified according to functional feeding groups and flow exposure groups.

Results

Physical habitat data

An ordination by PCA of the hydraulic and sedimentary variables explained 87% of the variance in the

data by the first three principal component axes. Axis 1 (eigenvalue = 0.90) accounted for 52.0% of the variance and all of the hydraulic variables (U_* , Re_* , T_* , U , Fr , and Re) had significantly positive loadings on the axis (Table 3). The variance explained by axis 2 (eigenvalue = 0.42) and axis 3 (eigenvalue = 0.19) was 24.1% and 11.0%, respectively. Significant loadings on axis 2 represented a positive gradient of increasing FPOM, CPOM, % fine sediment and substratum homogeneity, S_o . Negative loadings represented an increasing gradient of mean grain size, D .

An analysis of principal component scores for axes 1 and 2 found that samples were clustered in order of increasing water depth along the hydraulic gradient of axis 1 (Fig. 1). Water depth accounted for 97.4% of the explained variance in axis 1 ($F_{3,126} = 358.25$, $P < 0.0001$, MANOVA), while sampling date and site explained relatively little variance along the axis (2.0 and 0.6%, respectively). There was considerable variation along axis 2 for all water depths, which suggests there was significant within-depth variation in substratum characteristics and the concentration of organic matter. Water depth accounted for only 5.1% of the explained variance in axis 2, whereas site explained 13.9% and sampling date accounted for 81.0% of the explained variance (date: $F_{4,126} = 11.37$, $P < 0.0001$, MANOVA). Organic matter and sedimentary variables, therefore, did not exhibit a depth-related gradient, as did the hydraulic variables along axis 1, but rather showed a temporal pattern of

change. Refer to Table 3 of Rempel *et al.* (1999) for details of the distribution of organic matter.

Macroinvertebrate data

Mean macroinvertebrate density in the Fraser River was 168 m^{-2} (Appendix 1). Total invertebrate density was highest at depths of 0.2 and 0.5 m (Fig. 2). Taxonomic richness, defined as the number of taxa in the community, was highest in samples from 1.5 m depth. Values of richness were first corrected using the rarefaction method (Krebs, 1989) to adjust for unequal sample areas of the Shipek grab and Surber sampler. The statistical breakdown on the effects of water depth, sampling date and site on total density, taxon richness, and densities of FFG and FEG are presented in Rempel *et al.* (1999).

Collector-gatherers were the predominant FFG in benthic samples, comprising 91.4% of the total fauna. The distribution of gatherers was primarily at depths of 0.2 and 0.5 m (Fig. 3). Predators, filterers, grazers and shredders were all relatively uncommon and represented 3.4, 3.1, 1.4, and 0.7% of the total fauna, respectively. Filterers were most common at 1.5 m, shredders appeared to be distributed evenly between water depths, and predators and grazers were uncommon in deeper water.

According to the flow exposure classification, avoiders were predominant in the study (67.5%) and were most common at depths of 0.2 and 0.5 m (Fig.

Table 3 Structure coefficients of variables measured in the study for the first three principal components of the PCA. Structure coefficients are the correlation between the original variable and the principal component (* $P < 0.004$, Bonferroni correction). Refer to Table 2 for meaning of symbols

Variable	Principal component 1	Principal component 2	Principal component 3
D	-0.179	-0.517*	0.173
S_o	0.219	0.610*	-0.168
k_s	-0.138	-0.142	0.161
% Fines	0.308*	0.792*	-0.165
U	0.947*	0.019	-0.207
U_*	0.836*	0.044	0.523*
T_*	0.331*	-0.143	0.156
Re_*	0.781*	-0.025	0.618*
τ_*	0.630*	0.224*	0.360*
Fr	0.702*	-0.006	-0.183
Re	0.959*	0.045	-0.264*
CPOM	-0.201	0.741*	0.097
FPOM	-0.197	0.898*	0.085
Total variance explained:	52.0%	24.1%	11.0%

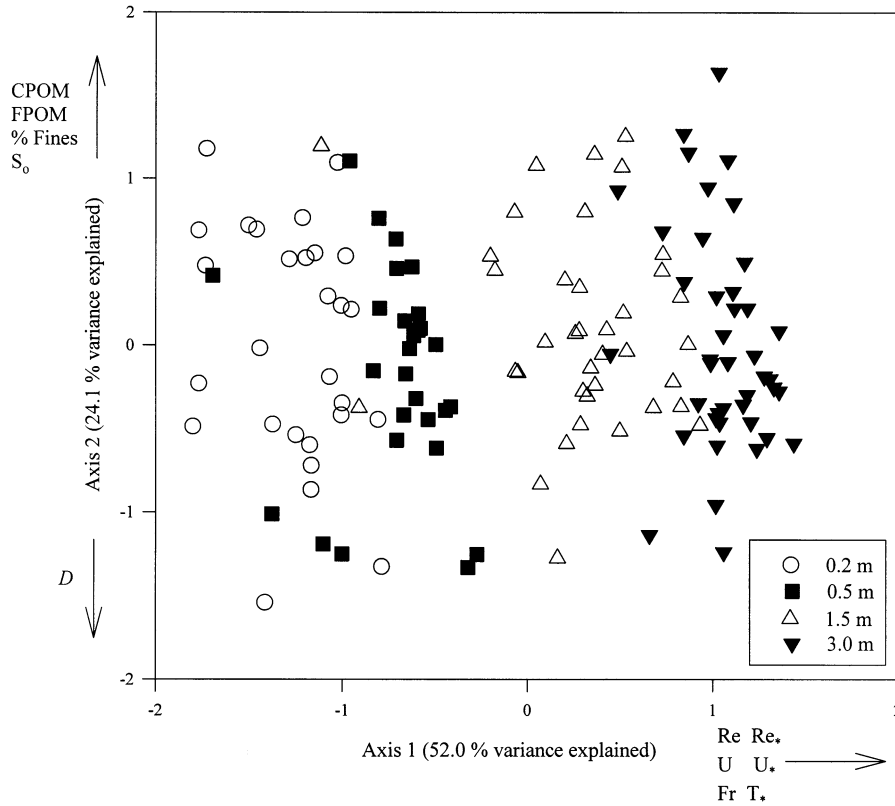


Fig. 1 Plot of sample scores from Principal Component Analysis of physical measures along principal component axes 1 and 2. Values represent a sample collected at a particular site, water depth and date in the Fraser River.

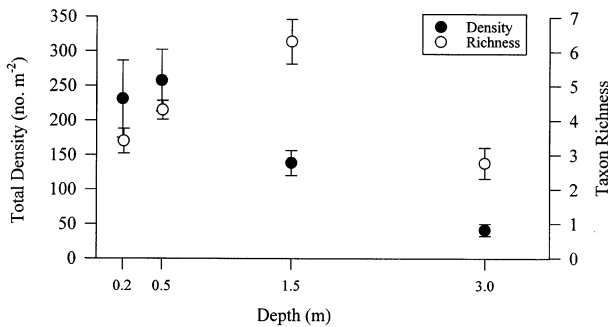


Fig. 2 Density of total taxa and taxonomic richness between water depths in the Fraser River. Means (± 1 SE) are given for samples collected from three sites on five sampling dates. Note the scale of y-axes differ.

4). Facultative invertebrates, those with distributions on both the upper surface and within interstitial spaces of the substratum, represented 17.5% of the total fauna and had highest density in shallow water. Obligate taxa representing 15% of the fauna were most numerous at 1.5 m depth.

Of the 34 taxonomic groups identified, 11 repre-

sented greater than 1% of the total invertebrates collected and were included in multivariate analyses: *Rhithrogena*, *Ephemerella*, *Heptagenia*, *Baetis*, *Hydropsyche morosa* group, Tanyptodinae, Tanytarsini, *Robackia* nr. *demeijerei*, Chironomini sp. B, Orthoclaadiinae, and Oligochaeta. Direct gradient analysis using COR of the physical habitat data with the invertebrate data captured 74.8% of the total variance in the first three canonical variables. A strong physical gradient of hydraulic and sedimentary conditions was identified along the first canonical variable (eigenvalue = 1.22), which alone accounted for 36.4% of the variance (Fig. 5). The sedimentary variable *D* had the highest negative loading and the hydraulic variables *Re*, *U*, *Fr* and *U** had the highest positive loadings on the axis. Vectors of all invertebrate taxa except *R. nr. demeijerei*, *Rhithrogena* and Chironomini sp. B had negative loadings on axis 1, thus being negatively related to the hydraulic gradient of axis 1. *Robackia nr. demeijerei* had the highest positive correlation with axis 1.

A positive gradient of CPOM and FPOM was identified along canonical variable 2 (eigenvalue = 0.78),

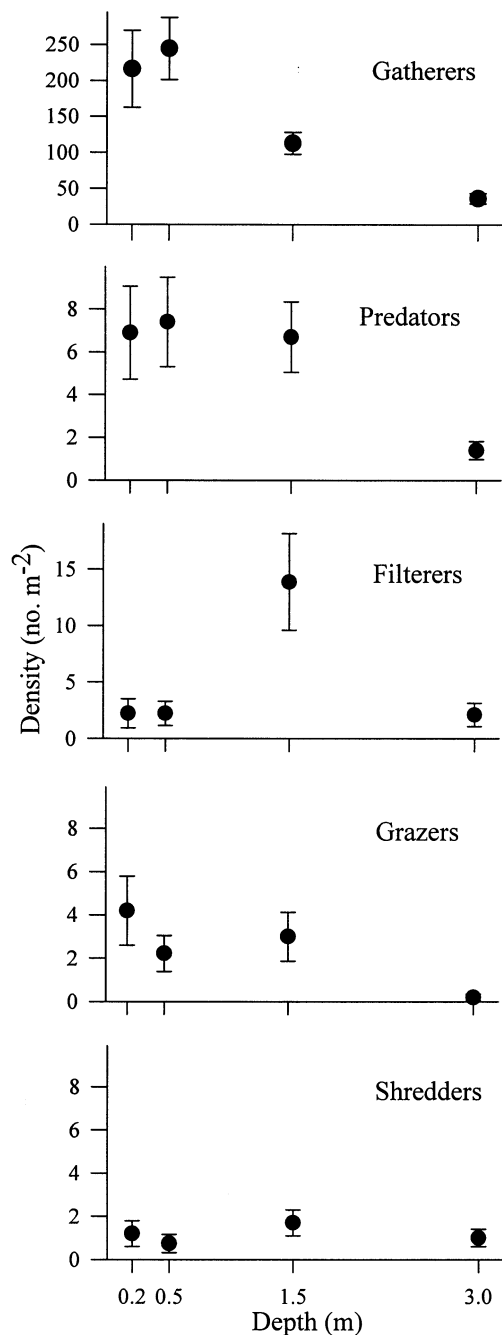


Fig. 3 Density of invertebrates classified into functional feeding groups between water depths in the Fraser River. Means (± 1 SE) are given for samples collected from three sites on five sampling dates. Note the scale of y-axes differ.

which accounted for 23.2% of the variation. Vectors of *R. nr. demejerei* and Chironomini sp. B also had significant positive loadings on axis 2. An environmental gradient of canonical variable 3 (eigenvalue = 0.51, 15.2% variance) was less interpretable, with the

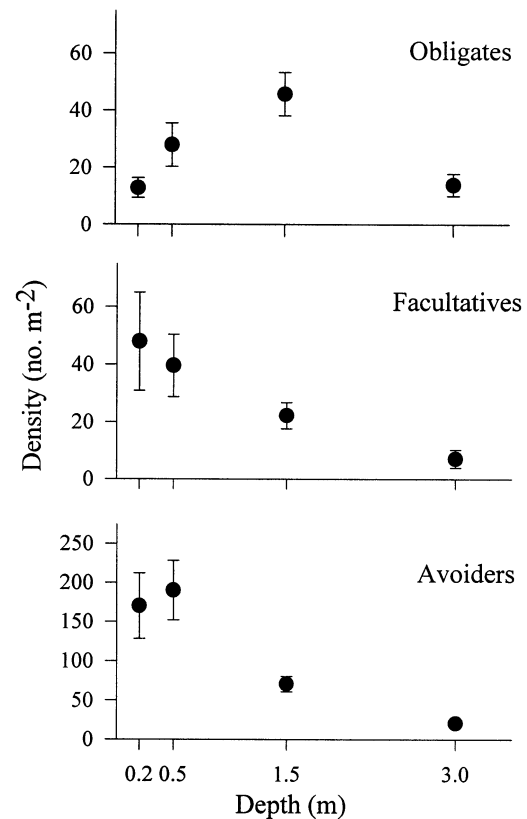


Fig. 4 Density of invertebrates classified into flow exposure groups between water depths in the Fraser River. Means (± 1 SE) are given for samples collected from three sites on five sampling dates. Note the scale of y-axes differ.

highest positive loading from turbulence intensity and highest negative loading from substratum homogeneity.

The association of invertebrate data with canonical variables was taxon-specific and the correlation options of COR were used to identify the relative importance of physical variables to the distribution of each taxon (Table 4). Despite the high loading of *D* on variable 1, mean grain size did not affect taxa when the effects of all other physical variables were held constant ($P > 0.05$). Substratum roughness, k_s , was positively correlated with *Rhithrogena* and *Hydropsyche morosa* gp., and both *H. morosa* gp. and Oligochaeta were negatively correlated with substratum homogeneity. CPOM was positively correlated with *Ephemera*, Tanypodinae, Tanytarsini, *R. nr. demejerei* and Chironomini sp. B, while FPOM had a positive relation with Chironomini sp. B only. *Rhithrogena* had a positive correlation with turbulence intensity, despite its relatively small loading on vari-

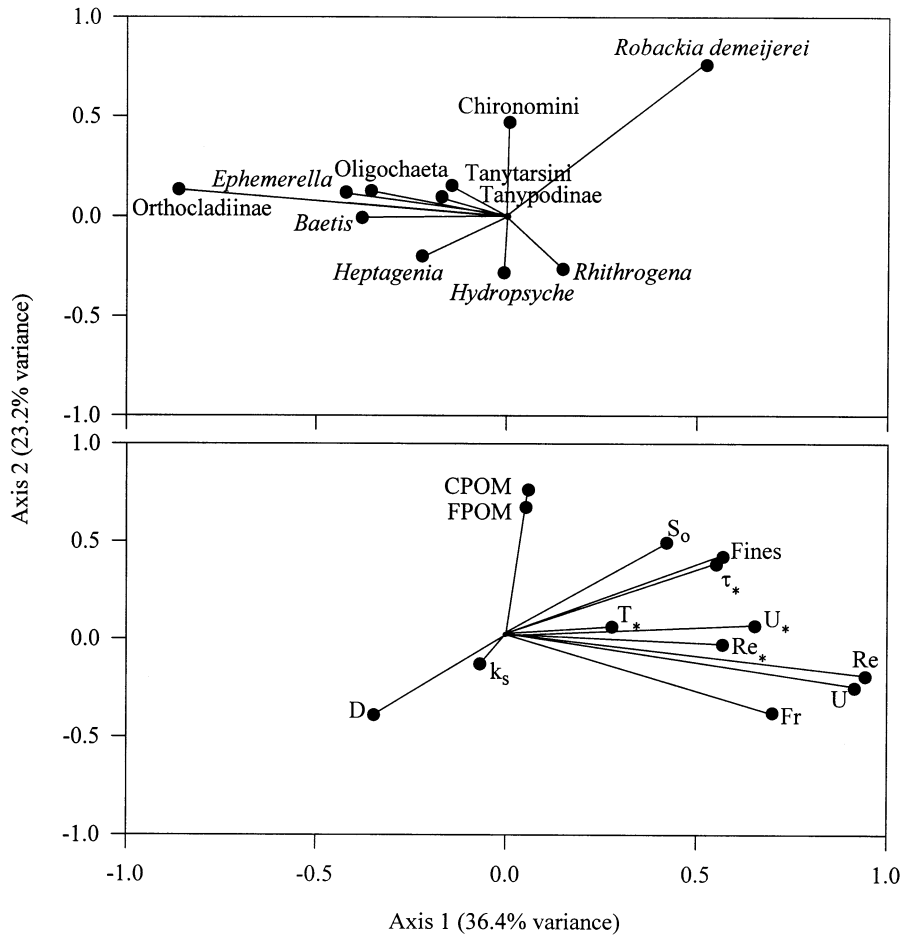


Fig. 5 Bi-plot of invertebrate data with physical habitat variables by Canonical Correlation Analysis along axes 1 and 2. Data from all months were included in the analysis and the two axes explained 59.6% of the total variation in the data. 'Fines' refers to the % sediment < 2 mm in sediment samples. Refer to Table 2 for meaning of symbols.

Table 1. *Heptagenia* was negatively correlated with U and *Baetis* was negatively correlated with U_* .

A COR of environmental data with invertebrate data classified according to FFG explained 93.8% of the total variance in the first three canonical variables. Canonical variable 1 (eigenvalue = 0.95) captured 54.6% of the variance and the positive vector represented an increasing gradient of depth-averaged hydraulic variables Fr , Re and U . Highest negative loadings on axis 1 were of CPOM, FPOM, D and k_s . On canonical variable 2 (eigenvalue = 0.42), highest positive loadings were of the sedimentary variables k_s and D and negative loadings were of the near-bed hydraulic variables Re_* and U_* . A bi-plot of invertebrate data with variables 1 and 2 revealed a negative loading of all faunal groups except collector-filterers on variable 1, thus being negatively associated with

depth-averaged hydraulic variables (Fig. 6). Collector-gatherers had the highest negative loading on axis 1. Partial correlations of FFG with each of the physical variables identified a positive association of Re with collector-filterers, grazers and predators (Table 5). The numerically dominant collector-gatherers were positively associated with CPOM and negatively associated with U . Shredders were also correlated significantly with CPOM.

Similar results were obtained with a COR of environmental data with FEG. Canonical variable 1 (eigenvalue = 1.20) captured 61.3% of the variance and the negative vector represented an increasing gradient of both depth-averaged and near-bed hydraulic variables (Fig. 7). Positive loadings on canonical variable 2 (eigenvalue = 0.56) were of D , k_s and T_{*r} , while negative loadings were of FPOM. All faunal groups

Table 4 Partial correlations between the sedimentary and hydraulic variables measured in the study and each macroinvertebrate taxon from Canonical Correlation Analysis. Only those variables with a correlation coefficient greater than $r_{0.1(2),111} = 0.156$ are listed

Taxon	Positive correlation coefficients	Negative correlation coefficients
<i>Rhithrogena</i>	T* k _s †	---
<i>Heptagenia</i>	---	U†
<i>Ephemera</i>	CPOM*	---
<i>Baetis</i>	---	U*
<i>Hydropsyche morosa</i> gp.	k _s * Re†	S _o †
Orthoclaadiinae	---	---
Tanyptodinae	CPOM*	---
Tanytarsini	CPOM*	---
<i>Robackia</i> nr. <i>Demeijerei</i>	CPOM*	---
Chironomini sp. B	CPOM* FPOM†	---
Oligochaeta	Fr†	S _o †

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$). Refer to Table 2 for meaning of symbols.

had positive loadings on variable 1, thus being negatively associated with hydraulic conditions. Avoiders had the highest positive loading on axis 1 and obligates had the highest positive loading on axis 2. Partial correlations of FEG with each of the physical variables identified a positive association of facultatives and avoiders with CPOM (Table 6). Obligate taxa were positively correlated with substratum roughness and Re.

Discussion

The Fraser River features a hydraulic gradient, corresponding to increasing water depth, which captured greater than 50% of the variance in the physical habitat data. In contrast, sedimentary conditions and the distribution of organic matter were significantly variable at a given water depth and showed a temporal gradient of change through the study. The strong association of invertebrate data with hydraulic conditions supports the hypothesis that flow patterns represent a major physical gradient along which benthic invertebrates are distributed. The greatest variation in benthic community data was captured by a gradient of hydraulic variables, which is consistent with previ-

ous studies showing the distribution of benthic organisms to be strongly influenced by hydraulic conditions (Wetmore, Mackay & Newbury, 1990; Lancaster & Hildrew, 1993; Hart *et al.*, 1996; Quinn & Hickey, 1994). In several of these studies, changes in the hydraulic conditions of a habitat due to changing discharge were accompanied by shifts in the distribution of species, which further supports the relation of benthic community structure to hydraulics (Lancaster & Hildrew, 1993; Robertson *et al.*, 1995). While this study did not examine taxon-specific changes in distribution with changing river discharge (see Rempel *et al.*, 1999), the association between benthic invertebrate distributions and the nature of the ambient flow environment was consistently strong through the study.

The increasing hydraulic gradient from shallow to deep water appeared to be an important determinant of the abundance of benthic invertebrates in the Fraser River. Highest total density corresponded with depths of 0.2 and 0.5 m where hydraulic stress was lowest. The density of collector-gatherers also sharply declined with increasing water depth. Average density exceeded 200 individuals m^{-2} at depths of 0.2 and 0.5 m and gatherers had a significant negative relation with water velocity. All gatherers except *Rhithrogena* were classified as either facultative or flow-avoider taxa which, not surprisingly, showed a similar relation. Each of these classes was also positively correlated with CPOM and positively associated with mean grain size.

Both organic matter and substrate composition can influence the distribution of benthic invertebrates, but the individual effect of each is often difficult to separate. We found most invertebrate taxa, as well as collector-gatherers and shredders, to be positively associated with a vector of increasing D . Invertebrate density, however, was found not to be related to mean grain size, but was positively correlated with organic matter when both variables entered the model simultaneously. This is consistent with Culp *et al.* (1983), where the distribution of many gatherer taxa was influenced by detrital matter, but not substratum conditions that ranged from large gravel to small pebbles. Large substratum material with a rough surface topography can facilitate the retention of organic matter and create microhabitats of reduced hydraulic stress for foraging (Holomuzki & Messier, 1993). The benefits of improved detrital retention and

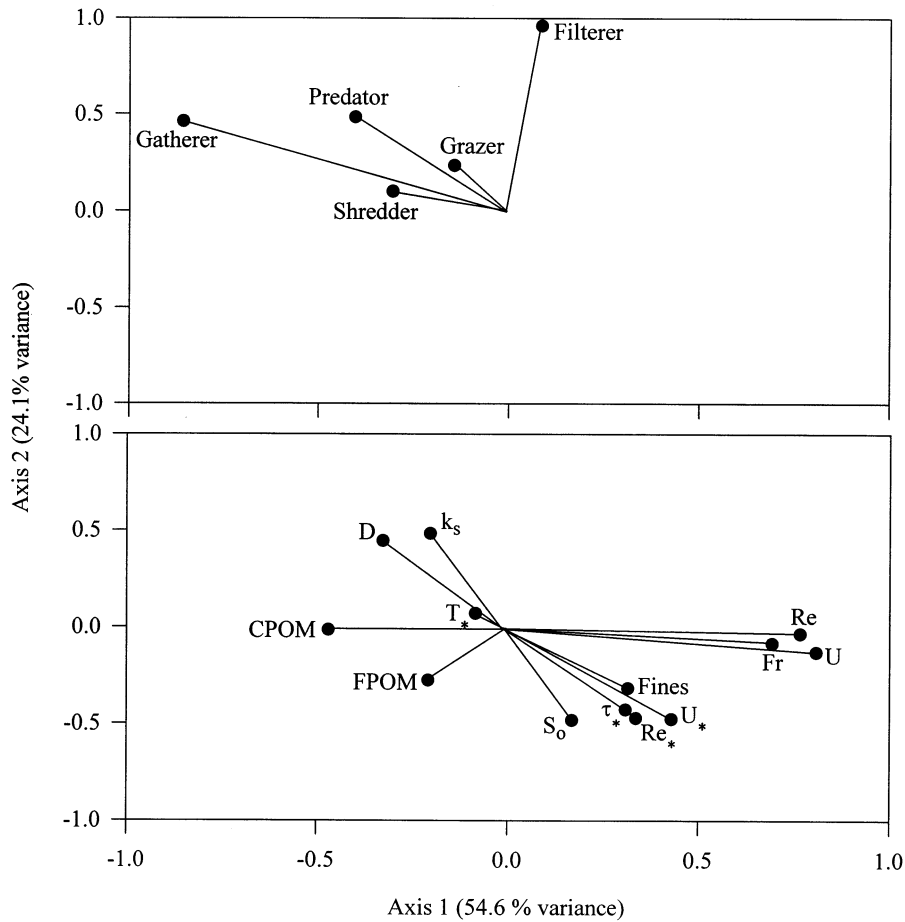


Fig. 6 Bi-plot of functional feeding group data with physical habitat variables by Canonical Correlation Analysis along axes 1 and 2. Data from all months were included in the analysis and the two axes explained 78.7% of the total variation in the data. 'Fines' refers to the % sediment < 2 mm in sediment samples. Refer to Table 2 for meaning of symbols.

reduced hydraulic stress due to coarse substrata probably influenced the distribution of collector-gatherers and shredders in the Fraser River. Substratum topography may have allowed CPOM to accumulate in localized areas of reduced hydraulic stress even in deep water because shredders were slightly more abundant at 1.5 m.

The benefits of reduced hydraulic stress for some invertebrates may be counteracted by the negative effects of fine sediment deposition. Sediment deposition results from low velocity conditions and can cause algae and organic matter to become covered by fine sediment. Characteristically high turbidity and sedimentation in the Fraser River probably limit algal and grazer productivity and account for the low representation of grazers in the benthic community. Grazers were uncommon in the Fraser River and the concentration of chlorophyll *a* was extremely low,

Table 5 Partial correlations between functional feeding groups and the sedimentary and hydraulic variables measured in the study from Canonical Correlation Analysis. Only those variables with a correlation coefficient greater than $r_{0.1(2), 117} = 0.152$ are listed

Group	Positive correlation coefficients	Negative correlation coefficients
Gatherers	CPOM*	U^*
Filterers	k_s^{**} Re^*	S_o^*
Grazers	Re^*	---
Predators	Re^{**}	---
Shredders	CPOM* $T^* \dagger$ $Re_* \dagger$	---

$\dagger P < 0.1$; * $P < 0.05$; ** $P < 0.01$). Refer to Table 2 for meaning of symbols.

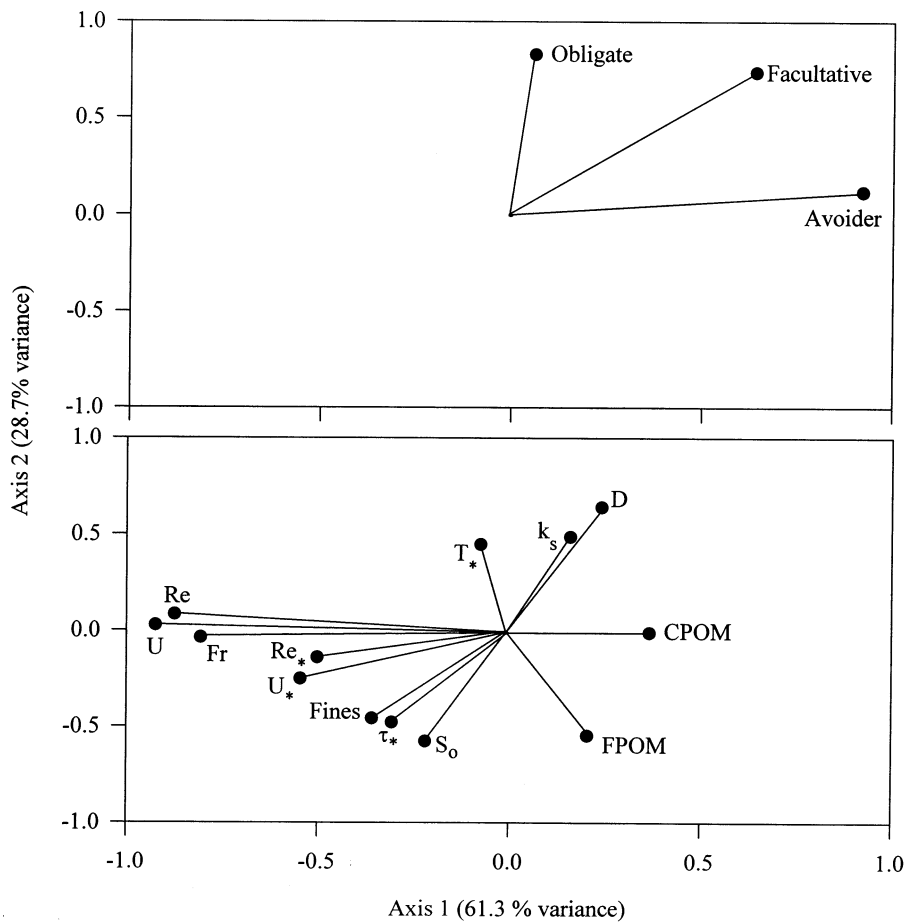


Fig. 7 Bi-plot of flow exposure group data with physical habitat variables by Canonical Correlation Analysis along axes 1 and 2. Data from all months were included in the analysis and the two axes explained 90.0% of the total variation in the data. 'Fines' refers to the % sediment < 2 mm in sediment samples. Refer to Table 2 for meaning of symbols.

averaging $0.0016 \text{ mg cm}^{-2}$ over water depths of 0.2, 0.4 and 0.6 m.

In contrast to the pattern of density of most invertebrate taxa, taxonomic richness was highest at 1.5 m where intermediate hydraulic stress was encountered. The concentration of CPOM and FPOM was similar at 1.5 m as at lesser depth, suggesting that the supply of organic matter for food and as a microhabitat (Richardson, 1992) did not represent a trade-off for invertebrates in deep water. Filter-feeders, including *Hydropsyche morosa* gp., were virtually absent except at 1.5 m depth, and were positively correlated with Re and substratum roughness. The distribution of *Hydropsyche* is consistent with other studies, where its highly retentive capture net and anal claws allowed it to occupy high velocity microhabitats for effective filter-feeding (Fuller & Mackay, 1980; Wet-

more *et al.*, 1990). A topographically rough substratum may further assist with feeding by enabling *Hydropsyche* to protrude into the flow and intercept a significant portion of suspended material.

Table 6 Partial correlations between flow exposure groups and the sedimentary and hydraulic variables measured in the study from Canonical Correlation Analysis. Only those variables with a correlation coefficient greater than $r_{0.1(2), 119} = 0.150$ are listed

Group	Positive correlation coefficients	Negative correlation coefficients
Obligates	k_s^{**} Re^{**}	---
Facultatives	CPOM*	---
Avoiders	CPOM*	U**

+ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$). Refer to Table 2 for meaning of symbols.

The positive correlation of filterers with Re , a depth-averaged velocity measure, rather than near-bed conditions was surprising given the suggestion that near-bed flow patterns in deep water may be more closely related to substratum characteristics than mean velocity (Davis and Barmuta, 1989). We believe that in deep water, where filterers and obligate flow exposure taxa were most common, near-bed hydraulic conditions are tightly coupled with the main flow profile because flow resistance results only from bottom drag. In contrast, near-shore flow conditions are chaotic due to a combination of channel bottom drag and lateral drag from the bank. Measures of near-bed and depth-averaged velocity, therefore, may not differ much in deep water and thus serve equally well as predictors of distribution in large rivers.

In deep water, where hydraulic stress is greatest, the gatherer taxa *Rhithrogena* and *Robackia* nr. *demeijerei* were most common. The morphology and feeding behaviour of these taxa are very different despite having similar depth and habitat associations. *Robackia* has a very thin and elongate body with reduced prolegs. In comparison, *Rhithrogena* is a dorso-ventrally flattened gatherer with specialized ventral gills that provide suction to the substratum and thereby reduce the risk of erosion from the channel bed. In large, coarse substrata, *Rhithrogena* is known to forage within the interstices and on the lower surfaces of cobbles, where additional protection from hydraulic stress is provided (Glozier & Culp, 1989). *Rhithrogena* was positively correlated with k_s , reflecting the importance of substratum topography in high velocity habitats both for detrital retention and to create microhabitats of reduced hydraulic stress for foraging.

Functional feeding group classification was useful in this study for examining ecologically relevant community-level associations with the physical habitat. The usefulness of invertebrate classification by flow exposure groups was, however, questionable. Most taxa of one functional feeding group belong to the same flow exposure group (e.g., most grazers are obligates), which suggests that the information gained by the two classification systems may be redundant. Moreover, classification of facultative taxa presents a problem in that some taxa may conform to the definition of facultative flow exposure while others have uncertain exposure to flow such that only

the obligate and avoider groupings may contain ecological information. The usefulness of flow exposure classification probably depends on detailed information on the microhabitat of each taxon and the ability to characterize the benthic habitat at a fine-scale.

Large gravel-bed rivers are relatively unstudied in aquatic ecology and the results of our study suggest that hydraulic conditions, as well as substratum texture and the distribution of organic matter, represent major gradients along which benthic invertebrates in the Fraser River are distributed. The greatest variation in benthic community data was captured by hydraulic conditions, which corresponded to a lateral gradient of increasing water depth. While the highest density of invertebrates was found in shallow water, where hydraulic stress was lowest, several abundant taxa such as *Rhithrogena* and *Robackia* nr. *demeijerei* were most common in deep water. The spatial distribution of taxa generally reflected their morphological and trophic suitability to particular hydraulic and sedimentary conditions of the benthic habitat.

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Appendix 1: Macroinvertebrate taxa collected from three study sites in the gravel reach of the Fraser River

	Functional feeding group	Flow exposure group	Average density (nos. m ⁻²)
Nematoda	CG	A	0.66
Annelida			
Oligochaeta			
Naididae	CG	A	3.6
Tubificidae	CG	A	3.1
Hirudinea	P	A	0.09
Arthropoda			
Arachnida			
Hydracarina	P	F	0.3
Insecta			
Ephemeroptera			
Baetidae			
<i>Baetis</i> sp.	CG	A	8.7
Ephemerellidae			
<i>Caudatella</i> sp.	CG	F	0.06
<i>Ephemerella</i> sp.	CG	F	18.4
<i>Serratella tibialis</i> McDunnough	CG	F	1.6
<i>Drunella doddsi</i> Needham	Gr	O	0.2
Heptageniidae			
<i>Cinygmula</i> sp.	Gr	F	0.8
<i>Epeorus</i> sp.	Gr	F	0.03
<i>Heptagenia</i> sp.	CG	F	5.5
<i>Rhithrogena</i> sp.	CG	O	16.6
Ameletidae			
<i>Ameletus</i> sp.	Gr	F	0.8
Plecoptera			
Perlodidae	P	O	1.5
Chloroperlidae	P	F	0.2
Nemouridae	Sh	F	0.1
Capniidae	Sh	F	0.5
Trichoptera			
Glossosomatidae			
<i>Glossosoma</i> sp.	Gr	O	0.4
Hydropsychidae			
<i>Hydropsyche</i> nr. <i>Morosa</i> group	CF	O	4.4
<i>Cheumatopsyche</i> sp.	CF	O	0.6
Lepitostomatidae			
<i>Lepidostoma</i> sp.	Sh	O	0.5
Hydroptilidae			
<i>Hydroptila</i> sp.	Gr	O	0.2
Diptera			
Tipulidae			
<i>Hesperoconopa</i> sp.	Sh	A	0.06

Appendix 1: Macroinvertebrate taxa collected from three study sites in the gravel reach of the Fraser River

	Functional feeding group	Flow exposure group	Average density (nos. m ⁻²)
Chironomidae			
Orthocladiinae	CG	A	70.8
Tanypodinae	P	A	2.0
Chironominae			
Chironomini sp. A	CG	A	6.3
Chironomini sp. B	CG	A	8.3
<i>Robackia</i> nr <i>demeijerei</i> kruseman	CG	A	9.8
Ceratopognidae	P	A	0.09
Simuliidae			
<i>Prosimulium</i> sp.	CF	O	0.06
Empididae			
<i>Hemerodromia</i> sp.	P	O	0.6
Dolichopodidae	P	F	0.8

Abbreviations for functional feeding groups are: CG = collector gatherer; CF = collector filterer; Gr = grazer; P = predator; Sh = shredder. Flow exposure group abbreviations are: A = avoider; F = facultative; O = obligate.