## HABITAT VARIATION DUE TO SEASONAL FLOODING OF THE LOWER FRASER

### **RIVER AND THE INFLUENCE ON THE MACROINVERTEBRATE COMMUNITY**

By

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### Abstract

Most large rivers of the world are of exceptional importance to many human uses but the ecosystems they support are often neglected in ecological research. The Fraser River, British Columbia, is a large river characterized by a regularly recurring flood cycle driven by snowmelt which seasonally inundates an extensive lateral shore zone. This study investigated the importance of the shore zone as a flow refugium to the macroinvertebrate community of the lower Fraser River during flooding, and the physical variations to the benthic habitat associated with flooding. Measures of hydraulic forces and substrate mobility were significantly higher at water depths of 1.5 and 3.0 m in the active channel during flooding of the Fraser River in 1995, than depths of 0.2 and 0.5 m within the shore zone where the substrate remained immobile. This variation produced a lateral gradient of increasing hydraulic stress from shallow to deep water depths along which the benthic community of the Fraser River appeared to be organized. The spatial distribution of invertebrate taxa generally reflected an organism's morphological and trophic suitability to particular hydraulic conditions which varied laterally between the shore zone and active channel.

Shallow water depths of the shore zone satisfied the physical criteria of flow refugia by maintaining substrate stability and low hydraulic stress during flooding. Demonstrating the provision of flow refugia in the shore zone was the first of two steps to determining the ecological importance of the lateral shore zone for the persistence of the macroinvertebrate community during flooding in the Fraser River. The extent to which organisms used the shore zone during high flows was also necessary to confirm its refuge potential. On the rising limb of the flood hydrograph, total density and species richness remained stable while the wetted area of the channel increased significantly. The persistence of the invertebrate community appears to have been facilitated by a shift in the distribution of a major proportion of organisms from depths

of 1.5 and 3.0 m in the active channel to the lateral shore zone during months of peak discharge. The ecological importance of this zone was demonstrated by the broad diversity of taxa with varying feeding behaviours and morphologies which concentrated in the shore zone.

# **Table of Contents**

Abstract	ii
List of Tables	vi
List of Figures	vi11
Acknowledgments	xii

# Chapter 1: Background and Statement of Research

Introduction	1
Overview of Large Rivers	2
Impacts of Flooding	3
Research Statement	6

# Chapter 2: Physical Habitat Characterization of the Fraser River and Variations through Freshet

10
13
18
18
21
23
26
27
29
31
39
48

Fraser River	
Introduction	
Study Area and Methods	
Data Collection - Macroinvertebrates	
Data Collection - Organic Matter	
Shipek and Surber Test Samples	
Data Analysis	61
Results	
Physical Habitat Data	63
Organic Matter	
Macroinvertebrate Data	72
Discussion	

# Chapter 3: Physical Habitat Parameters and Benthic Invertebrate Distributions in the

# Chapter 4: The influence of seasonal flooding of the Fraser River on the Benthic

# Invertebrate Community: the Importance of the Lateral Shore Margin

Introduction	
Study Area and Methods	
Organic Matter	
Data Analysis	
Results	
Community-Level Data	
Species-Level Data	
Organic Matter	
Discussion	

# Chapter 5: Study Limitations and Recommendations for Future Research

Арр	endix	148
Ittit	T CRCCS	
Refe	STANCAS	139
	Recommendations	134
	Limitations	132

List of Tables

Table 2-1. Hydrological measurements for the Fraser River at Hope, 35 km upstream of the study area, on each sampling date of this study. (Source: Water Resources Branch, Environment Canada)
Table 2-2. Summary of ANOVA results for sedimentary variables [transformed by $\log_{10}(x + 1)$ for S <sub>0</sub> , $\tau_{\bullet}$ , and proportion < 2 mm]. NS: p > 0.05
Table 2-3. Summary of ANOVA results (General Linear Model, SAS 1990) for hydraulic variables $[log_{10}(x + 1)]$ . The tests were for the effects of sampling date, water depth, and study site on measures of each variable. The analyses did not include interaction terms for the effect of site, see text for details
Table 3-1. Summary of physical variables measured in this study. Refer to text for further details
Table 3-2. Structure coefficients of variables measured in this study for the first four principal components of the PCA. Structure coefficients were calculated as the correlation between the original variable and the principal component (* = $p < 0.05$ ; ** = $p < 0.01$ ; *** = $p < 0.0001$ )
Table 3-3. Mean periphyton chlorophyll $a$ (± standard error) from each study site in the Fraser River. Values are the concentration (mg cm <sup>-2</sup> ) of chlorophyll $a$ collected from 3 cobbles in August, 1995. Differences between sites were not significant (p = 0.1)3-19
Table 3-4. Structure coefficients of macroinvertebrate taxa collected in this study for the first four principal components of the PCA using presence/absence data from all sampling dates. Structure coefficients were calculated as the correlation between the original variable and the principal component (* = $p < 0.05$ ; ** = $p < 0.01$ ; *** = $p < 0.001$ )
Table 3-5. Semi-partial correlations between the sedimentary and hydraulic variables measured in this study and each macroinvertebrate taxon. Only those variables with significant coefficients are listed where the correlation coefficient is $r_{0.1(2),112} = 0.155$ and df = (136  observations - 24  physical and taxon variables) = 112 (* = p < 0.05; ** = p < 0.01; *** = p < 0.0001). Refer to Table 3-1 for meaning of symbols
Table 3-6. Partial Correlations between the sedimentary and hydraulic variables measured in this study and each macroinvertebrate group. Only those variables with significant ( $p < 0.05$ ) coefficients are listed where the correlation coefficient is $r_{0.1(2), 115} = 0.153$ and df = (136 observations - 21 physical and taxon variables) = 115. Refer to Table 3-1 for meaning of symbols. (* = $p < 0.05$ ; ** = $p < 0.01$ ; *** = $p < 0.001$ )
Table 3-7. Results of stepwise multiple regression analyses. Only dependent variables with $adj-r^2 > 0.20$ are listed and only independent variables that entered at p < 0.10 were included in the regression model. PC = Principal Component Variable; (-) indicates negative effect of independent variable on dependent variable, (+) indicates positive effect. Refer to Table 3–2 for the relation of PC variables to the original hydraulic and sedimentary variables3-33

Table 4-1. Summary of ANOVA results for functional feeding groups  $[log_{10}(x + 1)]$ . The tests were for the effects of sampling date, water depth, and study site on measures of each

variable. The analyses did not include interaction terms for the effect of site, see text for
details. NS: p > 0.05
Table 4-2. Summary of ANOVA results for invertebrate taxa $[log_{10}(x + 1)]$ . The tests were for
the effects of sampling date, water depth, and study site on measures of each variable. The
analyses and not include interaction terms for the effect of site, see text for details. No. $p > 0.05$
0.00.
Fable 4-3. Distance (m) from the lower limit of terrestrial vegetation to the river margin at low
flow conditions in April, 1995, prior to flooding. The river margin extended over this
distance to the vegetation boundary at peak discharge in June. Measurements were made
along 3 transects that subdivided each study site4-22

•

# List of Figures

۲.

Figure 2-1. Location map of the gravel reach of the lower Fraser River where the present study was conducted. The Agassiz gauge station is located near the town of Agassiz and sites were situated within 10 km of the station
Figure 2-2. Grain size distribution of paired sediment samples collected by the Shipek grab and Scoop dredge from (A) unarmoured and (B) armoured surface substrates. Comparisons between sampling methods of mean grain size, $D$ , and the proportion of material < 2 mm in paried samples found no significant difference between sampling methods (paired t-test, $p > 0.05$ )
Figure 2-3. Patterns of discharge, temperature, and turbidity in the Fraser River during 1995. Data were collected from the gauge station at Hope, 35 km upstream of the study sites. Values of discharge are the daily mean while turbidity and temperature were measured 3 times per month. Shaded circles indicate dates on which sampling occurred2-21
Figure 2-4. Mean grain size of sediment samples collected from 3 study sites, listed in downstream order, in the Fraser River. Values represent the mean ( $\pm$ standard error) of samples taken on (A) 5 sampling dates and (B) 4 water depths through the flood cycle of 1995. Depth-wise contrasts of <i>D</i> are based on the average of values made through the study, and date-specific contrasts are the average of measures taken at multiple water depths. This served to isolate the desired spatial and temporal pattern of <i>D</i> , however, the standard error of each mean value therefore encompass systematic variation because differences in <i>D</i> between sampling dates and water depths were significant
Figure 2-5. The proportion, by weight of sediment samples < 2 mm collected from 3 study sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected at 4 water depths through the flood cycle of 19952-26
Figure 2-6. Nikuradse's bed roughness measured at 3 study sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected from (A) 4 water depths and (B) on 5 dates through the flood cycle of 1995
Figure 2-7. Trask's index of substrate heterogeneity measured at 3 study sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of sediment samples collected on (A) 5 dates and (B) from 4 water depths through the flood cycle of 19952-29
Figure 2-8. Depth-averaged measures of (A) mean velocity and (B) Froude number measured at 4 water depths through the flood cycle in the Fraser River. Values are the mean (± standard error) of measures taken at 3 study sites. For each variable, differences between water depths were significant. See text for further details of ANOVA results
Figure 2-9. Shear velocity at 4 water depths measured through the flood cycle of 1995 in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of measures collected from 3 study sites. Differences between sites were not significant while water depths and dates differed significantly from one another. Missing values in April were due to mechanical failure of the current meters

Figure 2-10. Turbulence intensity measured at 3 sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected from (A) 4 water depths and (B) on 5 sampling dates through the flood cycle of 1995......2-35

Figure 2-12. Shields entrainment function measured through the flood cycle, 1995, in the gravel
reach of the lower Fraser River. Values are the mean (± standard error) of samples collected
from (A) 4 water depths and (B) 3 study sites. $\tau_{*c}$ is the critical value of Shields above
which mobile bed conditions are likely. No measures from 0.2 and 0.5 m were collected in
April (B)

Figure 3-2. Ordination of samples by Principal Component Analysis along Principal Component
axes 1 and 3. The water depth of each sample is designated by the appropriate symbol.
Values represent a sample collected at a particular site, depth, and date in the Fraser River
in 1995

Figure 3-4. Dry weight of (A) FPOM and (B) CPOM at 4 water depths in the Fraser River.
Samples were collected from 3 study sites and data are presented as the mean (± standard
error) of samples from 5 sampling dates through the study. Note the scale of y-axes differ

Figure 3-8. Ordination of invertebrate samples collected (A) in all months and (B) in April only by Principal Component Analysis along axes 1 and 3. Presence/absence data were used in the analysis and the variance explained by each axis is indicated. Taxa with significant Figure 3-9. Ordination of invertebrate data with physical habitat variables by Canonical Correlation Analysis along Vectors 1 and 2. Data from all months were included in the analysis and 55% of the total variation in the data was explained by the vectors. "Fines" refers to the % sediment < 2 mm in sediment samples. Refer to Table 3-1 for meaning of Figure 3-10. Ordination of invertebrate data with physical habitat variables by Canonical Correlation Analysis along Vectors 1 and 2. Data from all months were included in the analysis and 63% of the total variation in the data was explained by the vectors. "Fines" Figure 3-11. Relation of (A, B, C) 3 common taxa and (D, E, F) 3 functional groups with Principal Component 1, representing a gradient of increasing hydraulic conditions. Only those taxa and groups whose density  $(\log_{10}(x+1))$  was significantly related to Principal Component 1 are presented. Regression results are summarized in Table 3-7. See text for Figure 4-1. Total invertebrate density in relation to (A) shear velocity and (B) Shields Entrainment Function in the gravel reach of the lower Fraser River. Shields Entrainment Function,  $\tau_{\star}$ , is a measure of substrate mobility and gravel substrate is likely to become Figure 4-2. Invertebrate taxonomic richness in relation to (A) shear velocity and (B) Shields Entrainment Function in the gravel reach of the lower Fraser River. Shields Entrainment Function. $\tau_{\star}$  is a measure of substrate mobility and gravel substrate is likely to become Figure 4-3. Total invertebrate density (mean  $\pm$  standard error) at (A) 4 water depths and (B) 3 study sites through the flood cycle in the Fraser River. Line graph (A) indicates the sum of densities from all depths in a given month. Total density in August and September was Figure 4-4. Taxonomic richness (mean ± standard error) at (A) 4 water depths and (B) 3 study Figure 4-5. Distribution of functional feeding groups at 4 water depths through the flood cycle, 1995, in the Fraser River. Values are the mean density (± standard error) of samples Figure 4-6. Densities of collector-gatherer invertebrates at 4 water depths during the flood cycle in the Fraser River, 1995. Values represent the mean (± standard error) of samples collected 

Figure 4-7. Densities of (A) a collector-gatherer and (B) a collector-filterer at 4 water depths during the flood cycle in the Fraser River. Values represent the mean (± standard error) of samples collected from 3 study sites. See Table 4-2 for ANOVA results	)f  -20
Figure 4-8. Density of (A) FPOM and (B) CPOM at 3 sites along a lateral gradient from the lower limit of terrestrial vegetation into the active river channel for April, 1995. Values refer to the water depth (m) of samples in the active channel, and "Mid-Shore" and "Vegetation" samples are taken from the shore zone which is the area between the river margin and vegetation at low flow. Note the scale of y-axes differ and the x-axes are not representative of the relative position of each sample location	L-21

Figure 5-1. Velocity collected at 1.5 m water depth over 4 min in May, 1995, at Agassiz.	
Measurements were made 3 cm above the channel bed	5-6

.

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### **Chapter 1 : Background and Statement of Research**

### Introduction

It is widely acknowledged that the physical habitat exerts a major influence on the structure and function of macroinvertebrate communities in lotic systems of all sizes (Power et al. 1988). The habitat has been inextricably linked to the abundances and distributions of populations, and often limits the range of life history strategies and ecological traits that it suits (Wetmore et al. 1990; Robinson et al. 1992). On this theme, Southwood (1977, 1988) proposed that the habitat is a templet that imposes restrictions on the life history strategies and ecological traits of resident organisms. Numerous studies have presented evidence in support of the habitat templet concept and suggest that benthic community structure is primarily governed by the physical conditions of the habitat (Power et al. 1988; Scarsbrook and Townsend 1993). Moreover, an organism's ability to colonize and persist in a given habitat is influenced by the frequency and intensity of change that the habitat undergoes (Scarsbrook and Townsend 1993; Flecker and Feifarek 1994). Detailed information on the physical conditions impinging on the biota, measured at a temporal and spatial scale relevant to the organisms, is therefore important to the mechanistic understanding of lotic communities.

Significant efforts have been made to understand the relation between the physical habitat and benthic community structure in small streams (Cobb et al. 1992; Lancaster and Hildrew 1993b). Rubber boots are usually adequate for field work in small streams and intense sampling over their entire length is manageable for an individual or small team (Hynes 1989). Similar investigations, however, have rarely been conducted on intermediate and large river systems (Thorp et al. 1992; see BioScience v. 45(3) 1995). Ecological studies of large systems are uncommon as they clearly require a much greater effort for adequate sampling (Minshall

1988), as well as specialized equipment and sampling gear (Hynes 1989; Stalnaker et al. 1989). Large European rivers have received some attention (see Arch. Hydrobiol. Suppl. v. 113(10) 1996), although extensive channelization, impoundments, and dredging have severely modified their ecosystems. For systems in a relatively unaltered state it is hypothesized that the main channel of large rivers is hostile relative to the channel margins, and high flow velocity and sediment transport produce a sterile environment that places great energetic demands on benthic organisms to maintain themselves (Church 1992).

### **Overview of Large Rivers**

In large rivers fluvial processes and geological constraints are the main governers of channel morphology (Church 1992), and thus construct the habitat templet for benthic organisms. This property makes them ideal systems for ecological studies of habitat-biota relations as the factors governing habitat structure are mainly limited to those of fluvial nature. This is in contrast to smaller systems where non-fluvial factors, such as large organic material accumulations and non-alluvial sediment that is derived from hillslope processes and terrain instability within the watershed are also significant (Church 1992).

According to a morphological classification by Church (1992), large rivers usually exceed 20 to 30 m in channel width and have a bankfull discharge exceeding 20 - 50 m<sup>3</sup> s<sup>-1</sup>. The ratio of mean grain diameter to water depth is typically less than 0.1 and flow is characterized by a well-defined vertical velocity profile. This property implies a multi-dimensional aspect of the physical habitat wherein both water depth and flow velocity interact to determine the sedimentary and hydraulic characteristics of the benthic habitat. Along with the geology of the channel substrate, patterns of flow also determine the ability of the river to move sediment (referred to as flow competence), and thus govern the morphology and stability of the entire river channel (Leopold 1994). The influence of flow on the physical habitat therefore operates at many spatial scales, and the habitat of a river channel is a product of all previous flows that have occurred over an extended period of time.

Major alterations in channel morphology may be ongoing for many years, with the developing channel pattern being associated with the long-term flow regime rather than an individual flood event. For example, the flow-controlled sequence of erosion, transport, and deposition of sediment in the Fraser River near Agassiz has led to significant morphological changes along a major length of channel over a time period of several decades (Church and McLean 1994). These changes are a product of many individual flood events and have implications for the physical habitat of the benthic community. The spatial and temporal scale of these long-term morphological changes, however, may be less relevant to a generation of benthic organisms than are changes associated with individual flood events. Increasing water depth and hydraulic stress due to flooding produce immediate, point-specific changes to the physical habitat that directly affect the benthic community (Giberson and Hall 1988; Cobb et al. 1992; Lancaster and Hildrew 1993b). Moreover, the time scale of individual flood events, particularly seasonal flooding, is comparable to the life cycle duration of many benthic species (Sweeney 1984; Power et al. 1988), whereas the long-term morphological evolution of a river will have greater influence on species abundances and the persistence of successive generations (Poff 1992).

### **Impacts of Flooding**

In an ecological context, flooding is often referred to as a hydrologic "disturbance", of which the impact on the benthic community is related to the frequency, regularity, and

magnitude of the disturbance (Resh et al. 1988). Resh et al. (1988) referred to systems with regularly recurring flood regimes as being hydrologically "predictable", and unpredictable floods will typically have much greater impact on the benthic community than predictable ones of similar magnitude. This is because a predictable flood regime influences benthic community composition over evolutionary time and filters out species with unsuitable life history strategies, behaviours, and morphology (Scarsbrook and Townsend 1993). In predictable systems, it is expected that the generation time of species, as well as the timing of life history events such as emergence and reproduction should correspond to the temporal flood regime (Robinson et al. 1992). Moreover, such traits are indicative of the community's suitability to the system and resilience to disturbance (Butler 1984).

Systems characterized by a flashy flood regime may impose different ecological constraints than those with a predictable frequency of flooding. In flashy systems, short generation times and ecological traits such as high mobility, small body size, and early and rapid colonization should be most successful for population persistence (Poff and Ward 1989). Regardless of the long-term influence of the flood regime on community structure, there are ecological consequences of single flood events to the benthic community of all lotic systems, with both predictable and flashy disturbance regimes: population densities are reduced, habitat instability is induced, and resources are exported (Gurtz and Wallace 1984; Lancaster and Hildrew 1993b). Hence, subsequent discussion will focus on the impact of single flood events on the benthic community and physical habitat of lotic systems.

Flooding produces immediate, point-specific changes to the physical habitat that directly affect the benthic community and pose a general threat of loss to animals by displacement or mortality (Lancaster and Hildrew 1993a). Increasing water depth and hydraulic stress due to flooding can erode macroinvertebrates from the substrate, particularly when sediment is

mobilized from the channel bed. However, many benthic communities are persistent over the duration of multiple flood events in that species composition and relative abundances remain generally stable (Boulton et al. 1992). This stability is believed to result from the availability of flow refugia that are defined by Lancaster and Hildrew (1993b) as places not subjected to severe hydraulic stresses during hydrologic disturbances and thus likely to reduce density-independent mortality of macroinvertebrates. The provision of flow refugia depends on spatial heterogeneity within the river channel, such that channel features are differentially influenced by the physical impacts of flooding. The recognition of channel features that provide refugia during flooding is important to studies of benthic community structure and function, and also of processes that maintain diversity or influence the productivity of lotic communities (Power et al. 1988).

There are three commonly cited areas of flow refugia. Firstly, the hyporheic zone has been thought to provide temporary refuge from flooding, as well as chemical disturbances (Giberson and Hall 1988). The spatial extent of the hyporheos is difficult to define, but has been known to extend up to 2 km from the main channel of the Flathead River, Montana, where high densities of both lotic insects and subterranean crustaceans have been collected (Stanford and Ward 1988). The ecological viability of the hyporheic zone generally depends on hydraulic conductivity of the sediment layers and the porosity, or storage capacity of the sediment (Brunke and Gonser 1997). A second area of flow refugia is in-stream channel features that can maintain low hydraulic stress during flooding (Lancaster and Hildrew, 1993b). For example, large particles protruding above the channel bed can provide localized hydraulic "dead zones" on their downstream side. Lastly, lateral flow refugia may be provided in the near-shore margins and floodplain habitats of rivers. Extensive floodplain habitats are known to provide refugia, as well as nursery areas and spawning grounds for fishes in lowland rivers (Schlosser 1991; Sparks

1995), but the importance of lateral habitats as flow refugia to benthic organisms is relatively unstudied.

Large rivers often consist of an extensive floodplain area that becomes inundated during flooding, and may persist as smaller, isolated habitats during periods of low flow. Unfortunately, many of the world's large rivers have been engineered so that the main channel has been irreversibly cut off from the floodplain by dykes. Large rivers that have so far escaped major alterations provide an exceptional opportunity to examine the ecological importance of lateral habitats as flow refugia to benthic organisms. The Fraser River, British Columbia, is one such large river where the mainstem channel has remained unregulated over its entire course and where channel alterations by dyking have been mostly restricted to the lower-most reaches (Northcote and Larkin 1989). As is the case for most large, northern temperate rivers, physiographic confinement has limited floodplain development on the Fraser River in comparison to lowland, tropical rivers. However, the pronounced seasonal flood hydrograph has developed an expansive channel zone that includes near-shore margins, side-channels, and in some places floodplain habitats that may be, to an extent, functionally similar to extensive floodplain areas of other large rivers.

### **Research Statement**

The purpose of this study is to investigate the influence of seasonal flooding on the macroinvertebrate community of the Agassiz gravel reach of the lower Fraser River, and the physical changes to the benthic habitat associated with flooding. Such changes occur at a temporal and spatial scale relevant to a generation of benthic organisms and have direct impact on community structure (Lancaster and Hildrew 1993b; Growns and Davis 1994), and the

persistence of populations through time (Giberson and Hall 1988; Cobb et al. 1992). Characterizing the benthic habitat of the Fraser River and the physical variations associated with the seasonal flow regime was therefore an essential first step of this study. The two main components of the benthic habitat were examined, namely the sedimentary and hydraulic components. Measures to address each component were selected on the basis of their ecological relevance and capacity to characterize the benthic habitat through freshet.

The sedimentary variables measured in this study were mean grain size (*D*), Trask's coefficient of sorting (S<sub>o</sub>), substrate roughness ( $k_s$ ), and the truncated mean grain size of fine sediment  $\leq 2$  mm. Together, they captured the structural diversity of the habitat at the appropriate scale of benthic organisms, and thus the diversity of niches available for the macroinvertebrate community to exploit. As well, they characterized the local topographic variation in the bed which may influence near-bed flow patterns (Davis and Barmuta 1989) and provide in-stream refugia to macroinvertebrates from hydraulic stress (Lancaster and Hildrew 1993b).

The hydraulic variables included in this study were shear velocity (U<sub>\*</sub>), turbulence intensity (T<sub>\*</sub>), Reynolds roughness number (Re<sub>\*</sub>), Shields Entrainment Function ( $\tau_*$ ), mean velocity (U), Froude number (Fr), and Reynolds number (Re). The latter three are depthaveraged parameters whereas the former are measures of near-bed conditions. Both types of measures were included in this study because the more easily obtainable depth-averaged measures have been commonly used in benthic studies to infer near-bed hydraulic conditions. By including both depth-averaged and near-bed parameters, this study compared the usefulness of each as predictors of macroinvertebrate community structure. The Fraser River is a large, gravel-bed river with a seasonal flood cycle that is highly predictable in both its timing and duration. This study extends the limited benthological research conducted on the Fraser River to gravel-substrate habitats since the only previous study was restricted to fine-gravel sediment associated with depositional habitats such as backwater areas and side-channels (Northcote et al. 1976). By sampling through the flood cycle in both shallow and deep water habitats, the physical changes induced by freshet were investigated. This provided a spatio-temporal characterization of habitat change under a regularly recurring flow regime to which macroinvertebrate community structure data were related. It also provided the basis for a habitat templet of large rivers from which to evaluate ecological predictions derived from small streams, and determine the extent to which information gained from small stream research can be extended to larger systems. Not only is this study unique to ecology, but geomorphic field studies have also rarely extended into deep water. Physical changes due to flooding have been more commonly inferred from sediment sampling of dry gravel bars as flood discharge decreases, and from flume experiments that examine near-bed sediment transport and velocity patterns over various substrate conditions.

The results of this study are presented in the following format. Chapter 2 provides a detailed characterization of the benthic habitat of the Agassiz gravel reach of the lower Fraser River and the physical changes induced by flooding. This characterization serves as the basis for Chapter 3 which investigates the relation between sedimentary and hydraulic conditions of the habitat and benthic community structure. Because the macroinvertebrate community of the Fraser River and other rivers of similar size and morphology have been relatively unstudied, the emphasis of Chapter 3 is restricted to the relation between habitat characteristics and the benthic community without specific attention to variations in community structure through the flood cycle. Chapter 4 focuses on spatial and seasonal variations in macroinvertebrate distributions and

# Chapter 2 : Physical Habitat Characterization of the Fraser River and Variations through Freshet

### Introduction

River systems of all sizes are characterized by a heterogeneous and temporally dynamic physical habitat. Many interacting factors and processes contribute to the nature of the habitat, the most important of which are flow regime and the supply of sediment (Kellerhals and Church 1989). Secondary factors such as local geologic history, climate, vegetation, and riparian land use are also important. Clearly, most of these factors are subject to change both in time and space, and thus introduce significant variability to the habitat of a river system. This variability exerts powerful influence over the distribution and abundances of benthic organisms, and their ability to persist in a given habitat through time (Growns and Davis 1994; Quinn and Hickey 1994). A detailed study on the spatio-temporal variability in a river system was designed so as to understand and explain the patterns of distribution and abundance of organisms.

Temporal variation is represented by fluctuations in flow that can range from individual storm events to seasonal climate variations. These fluctuations are mainly a function of the regional climate and geological setting (Poff 1996). For example, British Columbia's coastal regions are usually characterized by synoptically flashy discharges associated with rain storm events while rivers of the interior plateau have a seasonally predictable flood hydrograph corresponding to annual spring snowmelt. The frequency and intensity of flow fluctuations constitutes the flow regime of a river, and is the major source of geomorphic and hydraulic change in lotic systems (Carling 1992). For example, changes in flow directly alter near-bed hydraulic characteristics such as turbulence intensity and the shear stress exerted on the channel substrate. An increase in flow may induce substrate instability and increased sediment transport which has consequences for channel form and geometry.

The temporal flow regime of a river also has ecological implications for aquatic organisms. Fluctuations in flow may enhance community diversity by maintaining an intermediate level of disturbance which prevents competitively superior species from becoming dominant (Resh et al. 1988). Along with combinations of light and temperature, a river's flow regime may also serve as a cue for life history events of some aquatic organisms (Sweeney 1984; Robinson et al. 1992). Moreover, temporal fluctuations in flow are an important mechanism for resource cycling in rivers where, for example, seasonal flooding causes temporary inundation of floodplain habitats in which accumulations of organic matter are suspended and transported downstream (Grubaugh and Anderson 1989). Most importantly, flow fluctuations impart a high degree of spatial variability to the habitat of a lotic system.

Spatial variability may be observed in many forms along a reach of river, from largescale shifts in channel morphology to punctuated changes in substrate grain size associated with channel bed structure. Complex spatial patterns of flow velocity can also be found both within the water column and at the water-substrate interface. Features such as vortices and turbulent eddies developing over rough substrates, and gradients of turbulence with increasing water depth create a diverse hydraulic environment that may vary considerably within a given area (Davis and Barmuta 1989).

Spatial variability in rivers creates a myriad of habitats that will be differentially influenced by temporal fluctuations in flow. This can result in the formation of flow refugia for benthic organisms during periods of high flow in areas not subject to increased hydraulic stress (Lancaster and Hildrew 1993b). For example, in-stream habitat patches can maintain low and/or invariable hydraulic stress with increasing discharge (Davis and Barmuta 1989). These patches are often associated with large substrate particles protruding above the bed whose upstream side is exposed to high shear forces and whose downstream side provides a localized hydraulic "dead zone" (cf. Lancaster and Hildrew 1993a). At a larger scale, the upstream heads of islands and bars in a braided river channel are subject to higher velocity than the downstream tails which remain predominantly benign and thus offer hydraulic refuge to benthic organisms (Vogel 1981). A similar contrast in hydraulic conditions exists along a cross-section of channel, where the near-shore margins may maintain relatively low velocity in comparison to the main channel, thus providing lateral flow refuge to macroinvertebrates. In some river systems, however, the occurrence of low velocity habitats and hydraulic dead zones can also lead to significant fine sediment deposition that may limit productivity and produce unsuitable habitat conditions for some invertebrate species (Gurtz and Wallace 1984; Culp et al. 1986). Fine sediments may also have significant variation in surface chemistry, with the tendency to adsorb heavy metals and organic contaminants from the ambient aquatic environment, which may be deleterious to benthic organisms (Hall et al. 1976).

The fact that some habitats undergo greater geomorphic and hydraulic change than others over the duration of a single flow event poses difficulties for field research and data collection (Minshall 1988). Extensive field sampling over a time period encompassing physical changes to the habitat due to varying flow is essential so that the inherent variability of the habitat is captured. The purpose of this study is to investigate the sedimentary and hydraulic characteristics of the gravel reach of the lower Fraser River, and the physical variation associated with seasonal flooding. This study was the first step to investigating the influence of flooding on the macroinvertebrate community. The Fraser River was chosen in part due to its predictable flow regime and extended freshet that corresponds with annual spring flooding. Sampling was conducted 5 times through the river's flow hydrograph to encompass the period of annual flooding, and at several sites and water depths that together captured the inherent geomorphic variability of one reach of the river.

#### **Study Area**

The Fraser River, British Columbia, has a drainage area of 233 000 km<sup>2</sup> and a mean annual discharge of 3 700 m<sup>3</sup> s<sup>-1</sup> at its outlet to the Strait of Georgia. The mainstem of the river is unregulated over its 1 350 km length and passes through 11 biogeoclimatic zones (Northcote and Larkin 1989). Spring flooding, commonly referred to as "freshet", is a major hydrological event that is highly predictable and long-lasting. Mean annual flood discharge near the town of Agassiz at the Agassiz gauge station is 8 760 m<sup>3</sup> s<sup>-1</sup> (McLean 1990), and the Fraser River flood cycle is characterized by a unimodal hydrograph driven by snowmelt and peaking in June. Channel width and depth increase significantly for up to 4 months of the year, particularly in the Agassiz reach downstream of Hope where the river emerges from the physiographic confinement of the Coast and Cascade Mountains (Fig. 2-1). A 10-km stretch of the Agassiz reach was selected for this study.

Many physical characteristics of the reach are well-known due to a long-term sampling program conducted by the Water Survey of Canada (Water Resources Branch, Environment Canada) that included regular measurements of discharge, suspended and bedload sediment transport, water quality, stage level, and temperature. Detailed studies of sediment transport and channel instability in this reach have also been conducted (McLean and Church 1986; McLean 1990).



Figure 2-1. Location map of the gravel reach of the lower Fraser River where the present study was conducted. The Agassiz gauge station is located near the town of Agassiz (indicated by the arrow) and sites were situated within 10 km of the station.

The Agassiz reach has a mean annual discharge of approximately 2 900 m<sup>3</sup> s<sup>-1</sup> (Mannerström and McLean 1985) and is characterized by a wandering, laterally unstable channel with wooded islands and mid-channel gravel bars. This regime persists until Mission where a sharp reduction in channel slope, accompanied by increased dyking, confines the channel until its confluence with the Strait of Georgia at Vancouver. While some dykes exist within the Agassiz reach, they have been placed well beyond the main channel to maintain a relatively natural river morphology. Along the Agassiz reach of river, average width of the main channel is 527 m and the water surface slope at mean flood discharge is 0.00047 (McLean 1990). Mean velocity at Agassiz is 1.4 m s<sup>-1</sup> at low flow and increases to 3.2 m s<sup>-1</sup> during freshet, and the associated variation in mean channel depth is from 4.1 m at low flow to 7.9 m during freshet (McLean 1990).

Considerable volumes of sediment transport and deposition are characteristic of the Agassiz reach where an average of 100 000 m<sup>3</sup> of bedload gravel is mobilized each year (Church and McLean 1994). The vast majority of sediment load, however, is in the form of suspended sediment and greatest volumes of transport correspond with the timing and magnitude of flood discharge. Up to 2 m of channel bed scour has been recorded in the thalweg at exceptionally high discharge (McLean 1990), while large quantities of suspended sediment are seasonally deposited in low velocity areas such as side channels and the distal ends of gravel bars. Consequently, this reach is laterally unstable with intermittent shifts of the channel that lead to a changing hydraulic geometry and flow behaviour (McLean 1990). Overall, there is net deposition of sediment in the Agassiz reach which averages 1.8 cm yr<sup>-1</sup> of bed aggradation over several decades (Church and McLean 1994).

Three gravel bars within a 10 km stretch of the Agassiz reach were selected as sites for this study. The design was to sample several water depths through freshet to enable

representation of both the active river channel and floodplain habitats. A relatively low flood discharge in 1995, however, did not inundate most floodplain areas and thus limited the extent of sampling to the near-shore channel margins. The shore zone refers to the area adjacent to the active channel that has developed from sediment deposition during lateral shifting and seasonal expansion of the river channel. It generally extends to, but not beyond the lower limit of perennial terrestrial vegetation where the geomorphic floodplain habitat begins. Site selection took place before the onset of freshet in early April 1995, when river stage level was relatively low and the physical characteristics of each site could be visually assessed. Each site was selected on the basis of visual similarity in substrate composition, bank slope, flow velocity and orientation to the river bank, and riparian vegetation. The laterally unstable nature of the channel has, however, produced highly variable channel geomorphology which made the selection of similar sites difficult. Consequently, each of the three sites differed slightly in physical character and together captured the natural variability within this reach of river.

The most upstream site, referred to as *Hope*, was a large gravel bar on the south side of the Fraser River (49°13'10 N, 121°44'80 W). Mature cottonwood dominated the riparian vegetation which was separated from the river margin by over 100 m during low flow in April. The gravel bar substrate resembled a "framework gravel bed" as described by Church et al. (1987), with large gravels on the surface and the interstitial spaces partially filled with finer sediment. The main channel of the Fraser River has incised deeply into this coarse alluvial substrate to develop a steeply sloped channel bank. The seasonally inundated near-shore habitat, however, was relatively flat. While bank slope was not measured in this study, the main channel bank at *Hope* was the steepest of the three sites.

The second site, *Agassiz*, was 2 km downstream from *Hope* and situated on the north side of the main river channel (49°13'15 N, 121°49'10 W). A bedrock outcrop extended to the

channel edge just upstream of the site, but along the length of the site approximately 30 m of gravel bar separated the riparian vegetation of poplars and shrubs from the channel edge at low flow. Bank slope was very shallow and the site had a slight back-eddy character in shallow water. The substrate at *Agassiz* was characteristic of an armoured bed (cf. Parker and Klingeman 1982), where the fine sediment has been selectively entrained and transported from the bed over time to produce a coarse surface layer of relatively immobile sediment. Presumably, the armoured layer was a product of historical flow conditions that have since become more depositional due to lateral shifting of the channel because the surface gravels at *Agassiz* had a thick layer of fine sediment and periphyton that persisted through the duration of this study.

The most downstream site, *Deer*, was a large gravel bar situated on the south side of the river (49°13'87 N, 121°51'43 W). The exposed shore-zone habitat at low flow was slightly concave in nature where a back-eddy flow pattern developed at high flow during freshet. River bank slope was also steeper than at *Agassiz*, and a short bank of sand elevated the riparian habitat above the shore zone gravel bar. Mature poplars and some larger coniferous trees composed the riparian vegetation which was approximately 40 m from the river margin at low flow in April. The surface substrate resembled a "matrix-supported gravel bed" (Church et al. 1987) wherein large cobbles are not always in contact with each other and fine sediment makes up a significant portion of the bed material.

The length of each study site was defined by the distance along which flow orientation was parallel to shore with no major erosional or depositional features. Each site was sub-divided by 3 sampling transects perpendicular to the river bank and four sampling depths of 0.2, 0.5, 1.5, and 3 m were designated along each transect. At these sites, macroinvertebrate and sediment samples were collected along with measurements of several hydraulic variables described in detail below. The sites were sampled 5 times in 1995, both before and after freshet in April and

September, and three times during flooding in May, June, and August. A total of 180 samples and physical measurements (5 dates x 3 sites x 3 transects/site x 4 depths/transect) were collected for this study. Transect locations, marked with flagging tape, were fixed during the study whereas the location of sampling sites on the channel bed shifted laterally as water depth increased and decreased through freshet. This sampling design allowed contrasts to be made between the active channel at low flow and the shore zone at high flow conditions since water level in the Fraser River increased < 1.5 m during flooding while samples were collected over 3.0 m water depth. Samples therefore extended into the active channel even during months of high flow when 1.5 m samples were roughly matched to the location of shallow samples from April and September.

### Methods

#### Data Collection

Grabs of channel bed sediment and flow velocity measurements were collected at each sampling location. For sediment samples, a weighted Shipek grab sampler (Wildco: Wildlife Supply Company) consisting of 2 concentric half cylinders was used at depths of 1.5 and 3 m. The removable inner semi-cylinder, or sample scoop, was rotated at high torque to become nested within the outer cylinder. The Shipek was deployed by power-operated winch from the side of a power boat and, upon impact with the channel bottom, the scoop automatically released to collect a bottom sample. The cylindrical configuration of the Shipek protected the sample from washout as it was retrieved from the river bottom. While the depth of penetration into the channel bed varied with sedimentary conditions, the Shipek generally penetrated 6 - 10 cm into the bed which is roughly the depth of the surface sediment layer in coarse gravel-beds (Church et al. 1987).

The winch returned the Shipek to the boat where the scoop containing the sediment sample was drained through a 4 mm and 63  $\mu$ m sieve. Material greater than 4 mm was washed to remove all invertebrates and retained for sediment analysis. Sediment finer than 63  $\mu$ m was allowed to settle out in a plastic tub and also kept for analysis. The fraction greater than 63  $\mu$ m was preserved in 4% formaldehyde for sorting of the invertebrates from the substrate. Once sorted, the preserved material was washed and recombined with the other fractions for grain size analysis. Five casts of the Shipek, totaling 0.2 m<sup>2</sup> of channel bed area, were taken for each sample. A sonar mounted to the power boat enabled sampling depths of 1.5 and 3.0 m to be located. Because the boat could not safely maneuver in shallow water, a hand-held scoop dredge was used to collect grab samples of sediment from 0.2 and 0.5 m sampling depths. An approximately equal area of 0.2 m<sup>2</sup> was sampled by deep and shallow sampling methods, and sample penetration at shallow depths was also restricted to the surface layer of the substrate. A comparative test between the Shipek and scoop dredge indicated a similar sampling behaviour in various substrate conditions (see below).

To adequately represent the size distribution of channel bed sediment, samples were truncated prior to grain size analysis. A truncation point of 64 mm was used and was based on bulk sample standards developed for river gravels (Church et al. 1987) to determine the total sample weight necessary to adequately represent all grain size fractions. The standards are based on the proportion, by weight, that the largest stone represents of the total sample where, ideally, no individual stone should exceed 0.1% of the sample. This criterion may be relaxed depending on the goal of the sampling program (Rood and Church 1994). For example, representative sampling to 64 mm requires a 365 kg sample to meet the 0.1% criterion in contrast to 33 and

18 kg for the 1 and 2% criteria, respectively. The average sample weight in this study was 3.3 kg and samples were collected from 3 transects at each gravel bar site for a given date and water depth. Sediment samples from the 3 transects collectively totaled 9.9 kg and given the relative proximity of transects along the length of a given site, were considered to roughly meet a 4% criterion for grain size representation.

Sediment samples from *Agassiz*, and all samples in September required washing prior to analysis to remove a layer of fine sediment and periphyton that had adhered to the surface of larger gravels. Efforts were made to retain all fine material during the washing procedure for grain size analysis. Samples were oven-dried at 190°C, weighed, and sieved at standard  $\frac{1}{2} \phi$ intervals to determine the grain size distribution. Phi ( $\phi$ ) units and millimeters are referred to in this study as measures of grain size (*D*), and the relation between them is:

$$\phi = -\log_2 D \,(\text{mm}) = -3.3219 \,\log_{10} D \,(\text{mm}) \tag{1}$$

Samples in which the fraction less than 8 mm was exceptionally large were split into a more manageable weight of 400 - 700 g for sieving. The sieved fractions were then ashed in a muffle furnace (500°C, 8 h) to determine the ash free dry mass of organic matter and mineral substrate in each  $\frac{1}{2} \phi$  fraction.

Velocity was measured using a rod stacked with 3 current meters to obtain near-bed vertical velocity profiles at each site. A Marsh-McBirney electromagnetic current meter (20 Hz) and 2 rotational Ott meters were fixed at heights of 3, 10, and 30 cm above the bed. At each location, velocity readings were collected over 2 intervals of 60 s. Accurate velocity measurements close to the bed surface were difficult to collect in this study for the following reasons: (i) High turbidity in the Fraser River made placement of the velocity meter directly

adjacent to the bed difficult to verify; (ii) depths of 1.5 and 3 m were sampled from a boat which was required to hold steady position against the river current over the 120 s period of data collection; (iii) the Agassiz reach of the Fraser River consists of coarse, poorly-sorted gravel substrate. Roughness elements protruding above the bed can produce localized distortions in the near-bed flow; and (iv) the rotational Ott meters were prone to mechanical problems. Several attempts at data collection were often necessary before velocity measurements over 120 s were successfully gathered, particularly in deep water with the boat. Consequently, velocity data for some samples through the study are lacking.

An Interocean S4 oceanographic sampler provided a second source of velocity measurements at deep depths. The S4 was deployed from the power boat and velocity at 0.6 of the depth below the water surface was obtained for samples at 1.5 and 3 m depths on each of the 5 sample dates. At shallow depths, the equivalent measure of velocity at 0.6 of the depth was provided by a rotational Ott meter stacked on the rod. The S4 was chosen over an Ott meter for measures at deep water depths because of the difficulty in changing the height configuration of current meters stacked on the rod.

### Sedimentary Measures

Several descriptive measures of grain size composition were calculated for all sediment samples. Each was selected for its capacity to characterize the substrate texture and relative stability of the physical habitat through freshet. Mean (D) grain size of the sample was calculated following Folk (1965) as:

$$D = (D_{84} + D_{50} + D_{16}) / 3 \tag{2}$$

where  $D_x$  is the grain diameter (mm) at which x percent of the sample by weight is finer. Percentile diameters  $D_{16}$ ,  $D_{50}$ , and  $D_{84}$  were obtained from cumulative frequency curves of the grain size distribution of each sediment sample and in this study, the relation between D and  $D_{50}$  was approximately linear ( $r^2 = 0.97$ ).

Trask's coefficient of sorting (S<sub>o</sub>) measures grain size homogeneity of a sediment sample (Inman 1952). It was measured as:

$$S_{o} = \sqrt{D_{84} / D_{16}}$$
 (3)

which was modified for gravel-bed rivers (M. Church, Univ. of British Columbia, pers. comm.). A homogeneous grain size distribution yields a value of  $S_0 = 1$  and sample heterogeneity increases with increasing  $S_0$ .

Channel bed roughness was also calculated to capture the local topographic variation in the bed which can influence near-bed flow patterns. Nikuradse's roughness, modified for gravelbed rivers after Church et al. (1990), was calculated as:

$$k_s = 3.5 D_{84}$$
 (4)

where  $D_{84}$  was obtained from cumulative frequency curves of grain size distributions prior to truncation at 64 mm. In contrast to measures of *D* and S<sub>o</sub>, a non-truncated percentile diameter was used to most closely represent the true roughness of the bed and not bias measures of k<sub>s</sub>. Seventy out of 180 sediment samples had stones exceeding the truncation limit of 64 mm and were affected by this. In these samples, the maximum stone size collected was less than 128 mm.

A sub-analysis was performed on the sediment data to isolate the fraction of the bed most likely to be entrained by flow during freshet. A truncation point of 2 mm was selected for the sub-analysis which corresponds with the geomorphic break between gravel and sand size classes, and also corresponds with the upper end of the fine mode in the typically bimodal size distribution of gravel-river sediments. All sediment samples were included in the sub-analysis and the proportion (%) of fine material < 2 mm making up the total sample weight was calculated.

### Hydraulic Measures

Velocity data were used to characterize hydraulic conditions associated with each sediment sample based on variables described by Carling (1992). The near-bed variables selected for this study were shear velocity, turbulence intensity, boundary Reynolds number, and sediment mobility. Each is briefly described below.

Near-bed shear velocity, U, was derived from the slope of the vertical velocity profiles obtained from measurements with the 3 stacked current meters. The velocity profile was plotted as velocity vs log depth and was inspected to ensure a log-normal relation between the variables. The slope was measured as:

$$\tan \alpha = (U_1 - U_2) / (\log Z_1 - \log Z_2)$$
(5)

where  $U_1$  = velocity at depth  $Z_1$  and  $U_2$  = velocity at depth  $Z_2$ . Shear velocity was then calculated as:

$$U_{\star} = \frac{5.75}{\tan \alpha} \tag{6}$$

Further information on the derivation of this relation is provided in Smith (1975) and Vogel (1981).
Turbulence intensity, T., was expressed as the coefficient of variation of near-bed velocity readings collected over 2 intervals of 60 s from a Marsh-McBirney electromagnetic current meter (Carling 1992). It should be noted that the height of this meter above the bed varied between months. In April, it was placed at 30 cm above the bed at water depths of 1.5 and 3.0 m, and at 3 cm above the bed at depths of 0.2 and 0.5 m. All readings in May, August, and September were collected at 3 cm height, and measurements in June were at 10 cm height from the bed. The consequences of varying placement of the electromagnetic meter between months on T. should be negligible as it is strictly a measure of variation about the mean. This should also be insignificant to measures of U. since 3 current meters were consistently placed at heights of 3, 10, and 30 cm above the bed in all months.

Boundary Reynolds number describes the nature of flow close to the bed and is commonly used as an indicator of near-bed turbulence (Carling 1992). It was calculated as:

$$\operatorname{Re}_{*} = \operatorname{U}_{*} \operatorname{k}_{s} / \operatorname{v} \tag{7}$$

where v is the kinematic viscosity of water (0.01 cm<sup>2</sup> s<sup>-1</sup> at 20°C). Smooth-turbulent flow exists at Re. < 3.5 when a near-bed laminar sublayer within the boundary layer is present. Rough-turbulent flow persists when Re. > 68 and turbulent flow disrupts the laminar layer.

The relation between flow and substrate stability was assessed using Shields (1936) entrainment function:

$$\tau_* = \rho U_*^2 / g D_{50} (\rho_s / \rho - 1)$$
(8)

where g is the acceleration due to gravity (980 cm s<sup>-1</sup>), and  $\rho_s$  and  $\rho$  are the density of the grain material and of water, respectively (2.65 g cm<sup>-3</sup> for quartz, 0.998 g cm<sup>-3</sup> for water at 20°C). While the original application of  $\tau_*$  was for uniform, homogeneous sediment, it is been widely applied

as a relevant measure of stability in natural rivers (Wilcock 1993). For relatively loose gravel sediments, the critical value of  $\tau_* > 0.045$  induces substrate movement (M. Church, pers. comm.). However, the relative roughness and packing characteristics of natural river sediment may improve the stability of the grains such that the critical value of  $\tau_*$ , i.e.  $\tau_*c$ , increases to values in the range of 0.06 - 0.075 (Church 1978).

Depth-averaged hydraulic variables were also calculated and differ from the near-bed measures described above by incorporating water depth and mean flow velocity at 0.6 depth below the water surface (U) rather than near-bed hydraulic conditions. Both types of measures were included in this study because the more easily obtainable measure of mean velocity has been commonly used in studies to infer near-bed hydraulic conditions. This study therefore serves to compare commonly inferred near-bed variables with directly measured values, and to evaluate the relation between them. Depth-averaged variables included in this study were Froude number and Reynolds number.

Froude number is a dimensionless measure that describes the ratio of inertial to gravitational forces:

$$Fr = \sqrt{U^2 / g d}$$
(9)

where U is the mean velocity measured at 0.6 water depth below the surface and d is water depth. If Fr < 1, the flow is regarded as subcritical. Supercritical flow occurs when Fr > 1, and is characterized by standing waves and broken, white water on the surface.

The ratio of inertial to viscous forces acting on the flow, or the turbulence level of free flow, is referred to as the Reynolds number. It is a dimensionless number that characterizes the total flow depth, and was calculated as:

$$\text{Re} = \text{U} \text{d} / \text{v}$$

Laminar flow exists when Re < 500 and fully turbulent flow exists when Re > 2500. Flow in rivers and streams is usually turbulent except at very shallow depths or at low velocity, in which case viscous forces may be significant.

 $\sim 2$ 

Additional environmental variables included in this study were water temperature, turbidity, and discharge. These data were obtained from the Water Survey of Canada gauge station at Hope which is 35 km upstream of Agassiz. A previous comparison of annual historic data between Agassiz and Hope found a high degree of similarity (McLean and Mannerström 1985) which is expected since there are no major tributaries along the Fraser River between Hope and Agassiz, and the travel time of flow between locations is only a few hours.

## Shipek Test Samples

A comparison was made between the Shipek and scoop dredge to determine the similarity of sampling behaviour in the surface layer of an armoured and unarmoured substrate. Sediment samples were collected from the surface layer of 2 gravel bar sites in the Agassiz reach where the power boat could safely maneuver in shallow water. One site was unarmoured while the armoured site consisted of a gravel framework draped with medium-grained sand and periphyton. At each site, 2 paired samples were collected by the Shipek and scoop method at 50 cm water depth. This was the maximum water depth that could be safely sampled by the scoop method and was chosen to test the ability of each method to retain fine material during sample retrieval through the water column.

A statistical comparison between paired samples showed no significant difference between methods in measures of mean grain size (paired t-test, t = -2.05, p = 0.13, df = 3), mean

(10)

grain size truncated at 2 mm (t = 1.33, p = 0.29, df = 3), and the proportion of material finer than 2 mm (t = 1.20, p=0.32, df = 3). The grain size distribution of sediment samples collected from unarmoured substrate by the Shipek and scoop methods was highly similar (Fig. 2-2). In armoured substrate, however, the sampling behaviour of the 2 methods was less comparable and samples from the Shipek appeared to contain a greater percentage of fine sediment than scoop samples. Shipek samples from armoured substrate. Subsequent use of the Shipek in this study confirmed that it did not consistently penetrate the surface layer of armoured substrates, thus accounting for the greater percentage of fine sediment in samples. This tendency was easily recognized by the small volume of sediment collected, and was only observed at the *Agassiz* site that is heavily armoured. Surprisingly, invertebrates were commonly seen in these samples which supports the ability of the Shipek to retain fine material from sampling depths up to 3 m. In such cases, the sample was discarded and the Shipek re-deployed until 5 complete surface samples were obtained. Overall, the average weight of sediment samples collected by 5 Shipek casts (3472.2  $\pm$  286.5 g) and one scoop sample (3123.6  $\pm$  178.1 g) was similar.

#### Data Analysis

A combination of descriptive and statistical methods of data analysis were used to investigate the sedimentary and hydraulic characteristics of the gravel reach of the lower Fraser River, and the physical variation associated with flooding. For statistical analyses, all variables were first tested for violation of the assumption of normality using normal probability plots and the Shapiro-Wilk test for normality which is considered a highly conservative test (Zar 1984). To achieve normality, a  $log_{10}$  (x + 1) transformation was applied to the following variables: S<sub>0</sub>, % fine sediment, U., T., Re., U, Re, and  $\tau$ . While the arcsine transformation is recommended for percentage data (Zar 1984), the distribution of fine sediment was lognormal and therefore a



Grain Size (mm)

Figure 2-2. Grain size distribution of paired sediment samples collected by the Shipek grab and Scoop dredge from (A) unarmoured and (B) armoured surface substrates. Comparisons between sampling methods of mean grain size, D, and the proportion of material < 2 mm in paired samples found no significant difference between sampling methods (paired t-test, p > 0.05).

 $log_{10}$  (x + 1) transformation was appropriate. No transformation was required for Fr, D, and k<sub>s</sub>. All results are presented as untransformed means and standard errors of the mean, while it is recognized that the untransformed values are not exactly comparable with the transformed equivalents to which statistical analyses were applied.

Differences in sedimentary and hydraulic variables were tested using a three-way analysis of variance (ANOVA) incorporating the fixed effects of study site, water depth, and sampling date. The General Linear Models procedure of SAS (SAS Institute 1990) was used which is suited to the unbalanced sample design of this study with occasional missing velocity measurements. Least-squares estimates of means were calculated and compared using Tukey's Studentized Range Test that controls for the type I experimentwise error rate with a critical value of  $\alpha = 0.05$ . For the intent of identifying interesting trends in the data, results of ANOVAs where p exceeded the critical value are also presented and appropriately labeled as non-significant.

All 2-way and 3-way interaction terms were included in the ANOVA of sediment data. For hydraulic variables, only the interaction of date x depth was evaluated because hydraulic conditions are primarily a product of flow and, given the level of precision of velocity measurements for this study, are not expected to differ significantly between study sites along the 10 km reach of river.

# Results

River discharge followed a predominantly unimodal regime, with maximum discharge reaching 6 840 m<sup>3</sup> s<sup>-1</sup> on June 9, 1995 (Fig. 2-3). Significant amounts of rain in August, during the 4<sup>th</sup> sampling period of the study, increased discharge on the declining limb of the hydrograph.



Figure 2-3. Patterns of discharge, temperature, and turbidity in the Fraser River during 1995. Data were collected from the gauge station at Hope, 35 km upstream of the study sites. Values of discharge are the daily mean while turbidity and temperature were measured 3 times per month. Shaded circles indicate dates on which sampling occurred.

In comparison with the mean annual flood discharge of 8 760 m<sup>3</sup> s<sup>-1</sup> recorded at Agassiz (McLean 1990), freshet in 1995 was a relatively small event. At peak flow, the wetted channel area extended into the terrestrial vegetation by up to 5 m at *Agassiz* and *Deer*, but remained below the limit of vegetation at *Hope*. Similar to discharge, water temperature in the Fraser River followed a unimodal pattern with a temporal regime that generally corresponded to that of air temperature rather than flow (Fig. 2-3). Between April and July, values of turbidity showed several peaks including one that corresponded with maximum discharge in early June. Turbidity significantly increased in mid-July which roughly corresponded with the early onset of rain. Measures of turbidity and temperature were taken less frequently than discharge which allowed only approximate contrasts between variables to be made. Hydrological measurements for each of the five sample dates are summarized in Table 2-1.

Date	Discharge (Q) m <sup>3</sup> s <sup>-1</sup>	Temperature °C	Turbidity (NTUs)
April	2216	9.5	15
May	5397	13.5	33.5
June	5025	13	23
August	4160	19	44
September	1830	18	6.5

**Table 2-1**. Hydrological measurements for the Fraser River at Hope, 35 km upstream of the study area, on each sampling date of this study. (Source: Water Resources Branch, Environment Canada)

# Sedimentary Variables

Sediment samples collected from the gravel reach of the lower Fraser River exhibit a bimodal grain size distribution that is characteristic of framework gravel beds (Church et al. 1987). Modes of grain size, averaged over all samples were 0.25 and 45 mm. Spatial variability

Effect	df	MS	F	p
Mean Grain Size, D			-	
Date	4	294.59	8.30	< 0.0001
Depth	3	93.49	2.63	0.05
Site	2	1687.12	47.52	< 0.0001
Date x Depth	12	58.25	1.64	0.09
Date x Site	8	45.14	1.27	NS
Depth x Site	6	71.62	2.01	0.07
Date x Depth x Site	23	36.74	1.03	NS
Error	104	35.51		
Proportion < 2 mm, %				
Date	4	587.46	20.23	< 0.0001
Depth	3	350.84	12.08	< 0.0001
Site	2	382.81	13.18	< 0.0001
Date x Depth	12	65.02	2.24	0.02
Date x Site	8	51.92	1.79	0.09
Depth x Site	6	78.11	2.69	0.027
Date x Depth x Site	23	49.64	1.71	0.04
Error	105	29.05		
Nikuradse's Roughness, k <sub>s</sub>				
Date	4	6377.88	1.58	NS
Depth	3	4937.85	1.22	NS
Site	2	120187.04	29.75	< 0.0001
Date x Depth	12	1560.81	0.39	NS
Date x Site	8	15082.08	3.73	< 0.001
Depth x Site	6	19922.23	4.93	< 0.001
Date x Depth x Site	23	5494.21	1.36	NS
Error	104	4039.62		
Trask's Index of Homogeneity, S <sub>o</sub>				
Date	4	0.09	4.95	< 0.001
Depth	3	0.23	12.39	< 0.0001
Site	2	0.13	6.98	< 0.001
Date x Depth	12	0.04	2.15	0.02
Date x Site	8	0.01	0.62	NS
Depth x Site	6	0.05	2.87	0.01
Date x Depth x Site	24	0.02	1.25	NS
Error	119	0.02		
Shields Entrainment Function, τ.				
Date	4	0.01	7.27	< 0.0001
Depth	3	0.03	39.79	< 0.0001
Site	2	0.001	1.81	NS
Date x Depth	10	0.004	4.64	< 0.0001
Date x Site	8	0.001	1.65	NS
Depth x Site	6	0.0009	1.06	NS
Date x Depth x Site	19	0.002	1.79	0.04
Error	89	0.0009		

**Table 2-2.** Summary of ANOVA results for sedimentary variables [transformed by  $log_{10}(x + 1)$ for S<sub>0</sub>,  $\tau_*$ , and proportion < 2 mm]. NS: p > 0.05.

in channel sediment was observed throughout the study, and notable differences in substrate characteristics were found between study sites (Table 2-2). Mean grain size, D, was significantly higher at *Agassiz* than at *Hope* and *Deer* in all months and at all water depths (Fig. 2-4). While differences between water depths were only marginally significant (p = 0.05), *Hope* showed greatest variability in D, being comparable to sediment samples from *Agassiz* at shallow depths while showing more similarity with *Deer* at depths of 1.5 and 3.0 m (Fig. 2-4b). At all sites, measures of D significantly decreased during the months of freshet when sampling locations were laterally shifted toward the shore margin of the active channel.

A decrease in mean grain size during freshet corresponded with an increasing proportion of sediment < 2 mm in substrate samples (Fig. 2-5). The proportion of fine sediment increased and then decreased through the flood cycle at all sites, hence the non-significant date x site interaction (Table 2-2), although site-specific differences were noted. The greatest increase in fine sediment was at *Deer* which had the highest proportion of fines at all sampling dates and water depths. This is consistent with visual observations of *Deer* during low flow conditions when predominantly fine sediment was seen in the shore-zone and floodplain habitats of the site. It is also consistent with the possibility of *Deer* being a matrix-supported bed wherein fine sediment makes up a significant portion of the bed material. However, the proportion of fine material comprising a matrix-supported bed is between 22 and 32% (Church et al. 1987) and *Deer* only approaches this range of values in June, suggesting the bed may instead be a tightly-filled framework gravel. The proportion of fine sediment in samples collected from *Agassiz* and *Deer* increased between April and June and then steadily declined from June to September. Highest values at *Hope*, however, were in May after which time the proportion of fines decreased through to September. At all sites, the proportion of fines in sediment samples



Figure 2-4. Mean grain size of sediment samples collected from 3 study sites, listed in downstream order, in the Fraser River. Values represent the mean ( $\pm$  standard error) of samples taken on (A) 5 sampling dates and (B) 4 water depths through the flood cycle of 1995. Depth-wise contrasts of *D* are based on the average of values made through the study, and date-specific contrasts are the average of measures taken at multiple water depths. This isolated the desired spatial and temporal pattern of *D*, however, the standard error of each mean value therefore encompasses systematic variation because differences in *D* between sampling dates and water depths were significant.



**Figure 2-5**. The proportion, by weight, of sediment samples < 2 mm collected from 3 study sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected at 4 water depths through the flood cycle of 1995.

exhibited a high degree of contingency between April and September, representing conditions before and after freshet in 1995 (p = 0.1, ANOVA).

The differences in surface roughness,  $k_s$ , between study sites were significant with *Agassiz* and *Hope* being significantly higher in  $k_s$  than *Deer*. Overall differences between sampling dates and water depths were not significant, however, sites exhibited significantly different variation in  $k_s$  between dates and depths (Fig. 2-6) and produced significant date x site and depth x site interactions (Table 2-2). *Agassiz* showed little change in roughness between water depths while surface roughness increased at *Deer* between 0.2 and 3.0 m. At both sites,  $k_s$  was lowest in May and June during freshet while roughness increased slightly at *Hope* over the same period (Fig. 2-6b). The seasonal increase in roughness at *Hope* was matched with significantly higher values of  $k_s$  at shallow depths, however, these temporal and spatial patterns in roughness may be biased by the lateral shift in sample locations to the near-shore margin during freshet in May and June. Substrate roughness was also highly contingent as values of  $k_s$  in April and September, before and after freshet, were similar at all sites (p = 0.15, ANOVA).

The seasonal decrease in D and  $k_s$  observed at *Agassiz* and *Deer* corresponded with increased substrate heterogeneity at both sites (Fig. 2-7a). *Deer* was most heterogeneous and showed greatest variability in S<sub>o</sub> between shallow and deep depths, as well as between low-flow and freshet conditions. In contrast, measures of heterogeneity at *Agassiz* were relatively similar at all water depths, hence the significant depth x site interaction (Table 2-2). Measures of heterogeneity at *Agassiz* were also relatively similar in all months of sampling except June when S<sub>o</sub> increased. At *Hope*, the change in S<sub>o</sub> during the months of freshet was unique as samples showed increasing homogeneity between May and June. Other sites were least homogeneous in June, and all sites decreased in S<sub>o</sub> after freshet. Overall, sediment samples from the Fraser River were heterogeneous in sediment texture and the deviation was greatest at water depths of 3.0 m.







Figure 2-7. Trask's index of substrate heterogeneity measured at 3 study sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of sediment samples collected on (A) 5 dates and (B) from 4 water depths through the flood cycle of 1995.

#### Hydraulic Variables

While significant differences in substrate characteristics were found between sites, hydraulic variables showed greatest variation between water depths (Table 2-3). In addition, the non-significant date x depth interaction for most variables suggested that while river discharge varied between sampling dates, hydraulic conditions at a given water depth were relatively unchanged. Mean velocity, U, measured at 0.6 depth below the water surface, increased significantly with increasing water depth on all sampling dates (Fig. 2-8a). All sites had similar U and at each water depth, there was no significant variation between April and September.

The depth-averaged measure of Reynolds number showed virtually identical trends to those of U presented in Fig. 2-8a. Reynolds number is the ratio of inertial to viscous forces acting on the flow and given that viscosity, a function of water temperature, changed only slightly from April to September, the similarity in Re from April to September is not surprising. *Agassiz* and *Hope* had higher Re, and thus greater inertial forces acting on the flow than at *Deer*. Values of Re exceeded 2500 at all sampling locations through the study, which characterized flow conditions as fully turbulent.

Froude number also increased with depth, and characterized the flow conditions of the gravel reach of the lower Fraser River as subcritical (i.e. Fr < 1). Fr measures the ratio of inertial to gravitational forces acting on the flow, with inertial forces increasing with water velocity and gravity forces being primarily a function of changing water depth. Depths of 1.5 and 3.0 m were significantly higher in Fr than shallow depths in all sampling months, although differences between depths of 1.5 and 3.0 m, and between depths of 0.2 and 0.5 m were mostly non-significant (Fig. 2-8b). This implies that inertial forces dominated in deep water where water velocity was highest, but were relatively similar between 1.5 and 3.0 m. Dominant gravitational

Effect	df	MS	F	p
Mean Velocity, U				
Date	4	0.004	1.24	NS
Depth	3	1.16	372.31	< 0.0001
Site	2	0.005	1.53	NS
Date x Depth	12	0.001	0.39	NS
Error	153	0.003		
Reynolds Number, Re				
Date	4	0.07	0.98	NS
Depth	3	39.87	568.83	< 0.0001
Site	2	0.26	3.75	0.03
Date x Depth	12	0.04	0.52	NS
Error	153	0.07		
Froude Number, Fr				
Date	4	0.03	4.62	0.002
Depth	3	0.34	57.73	< 0.0001
Site	2	0.02	2.71	NS
Date x Depth	12	0.004	0.65	NS
Error	158	0.006		
Shear Velocity, U.				
Date	4	0.28	5.08	< 0.001
Depth	3	3.19	70.82	< 0.0001
Site	2	0.002	0.04	NS
Date x Depth	10	0.36	6.58	< 0.0001
Error	138	0.06		
Boundary Reynolds Number, Re.				
Date	4	0.94	1.61	NS
Depth	3	10.17	17.49	< 0.0001
Site	2	4.52	7.77	< 0.001
Date x Depth	10	1.26	2.16	0.02
Error	138	0.98		
Turbulence, T.				
Date	4	0.02	4.71	< 0.001
Depth	3	0.02	3.68	0.01
Site	2	0.004	0.87	NS
Date x Depth	12	0.006	1.26	NS
Frror	151	0.004		

**Table 2-3.** Summary of ANOVA results (General Linear Model, SAS 1990) for hydraulicvariables  $[log_{10}(x + 1)]$ . The tests were for the effects of sampling date, water depth, andstudy site on measures of each variable. The analyses did not include interaction termsfor the effect of site, see text for details. NS: p > 0.05.



Figure 2-8. Depth-averaged measures of (A) mean velocity and (B) Froude number measured at 4 water depths through the flood cycle in the Fraser River. Values are the mean (± standard error) of measures taken at 3 study sites. For each variable, differences between water depths were significant. See text for further details of ANOVA results.

forces at shallow depths were comparable between 0.2 and 0.5 m. Fr also showed a significant increase from April to August, and the pattern of variation between dates was similar for all water depths (date x depth interaction, p = 0.79).

The near-bed measure of shear velocity, U<sub>•</sub>, also increased with depth and revealed that hydraulic conditions within a few centimeters of the channel bed were significantly more variable between depths and at varying levels of discharge than were depth-averaged conditions (Table 2-3). Greatest temporal variability occurred in deep water (Fig. 2-9). At depths of 3.0 m, U<sub>•</sub> increased significantly during peak discharge in June but was relatively constant between other sampling dates. Measures of U<sub>•</sub> at 1.5 m depth were most variable through the duration of the study, being highest in April and June and having low values similar to shallow depths in the months of May, August, and September. At depths of 0.2 and 0.5 m, U<sub>•</sub> was relatively constant between April and September, with lowest values in June and highest values of U<sub>•</sub> in August. The difference in U<sub>•</sub> between study sites was not significant. Data in April for shallow depths are lacking due to mechanical failure of the Ott current meters.

Measures of turbulence intensity, T., showed variability both between sampling dates and water depths that was site-specific. A steady increase in T. from shallow to deep depths was found at *Agassiz* while turbulence was highest at 0.5 m at *Deer* and *Hope* (Fig. 2-10a). A comparison between sample dates suggests that T. was negatively related to river discharge at *Agassiz* and *Hope* as lowest values occurred in June during peak flow (Fig. 2-10b). In contrast, the seasonal pattern at *Deer* showed significantly higher T. in June over all other months. Measures of T. in April and September, representing conditions before and after freshet, were comparable at *Deer* and *Hope* but were lower at *Agassiz* in September.



**Figure 2-9**. Shear velocity at 4 water depths measured through the flood cycle of 1995 in the lower Fraser River. Values are the mean (± standard error) of measures collected from 3 study sites. Differences between sites were not significant while water depths and dates differed significantly from one another. Missing values in April were due to mechanical failure of the current meters.



Figure 2-10. Turbulence intensity measured at 3 sites in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected from (A) 4 water depths and (B) on 5 sampling dates through the flood cycle of 1995.

Boundary Reynolds number showed comparable depth-specific patterns through the flood cycle as U<sub>\*</sub>, and all values of Re. through the study greatly exceeded 68 which designated the flow as turbulent and having no laminar layer present. An examination of seasonal variation in Re. revealed contrasting patterns between study sites (Fig. 2-11), with *Hope* having considerably higher Re. than other sites in the months of May and June. Moreover, *Hope* showed the greatest variability in boundary Reynolds number through the study and mean values during freshet were 3-fold higher than in September. Given that Re. is derived from U<sub>\*</sub> and k<sub>s</sub> which both showed an increase at *Hope* during freshet, this is not surprising as a relatively rough substrate surface will experience greater Re. compared with a surface of lower k<sub>s</sub>. Measures of Re. at *Agassiz* were least variable through the study but still indicated a slight increase in Re. from May to June. Interestingly, both *Agassiz* and *Deer* showed an increase in Re. from August to September while at *Hope*, Re. decreased. This variation is also likely related to changes in the relative roughness of the bed surface as sample locations laterally shifted back into the active channel zone in September.

Shields entrainment function includes information about the near-bed hydraulic and sedimentary characteristics of the sample site to provide a measure of substrate mobility. Where  $\tau_{*} > 0.06 (\tau_{*c})$ , mobile sediment conditions in gravel-bed rivers are likely to occur. The substrate was significantly more mobile at 3.0 m depth in all months except May when conditions at 1.5 and 3.0 m were similar (Fig. 2-12a). Values of  $\tau_{*}$  were highest in June and lowest in September for all water depths and shallow depths of 0.2 and 0.5 m never exceeded the critical value of  $\tau_{*}$  throughout the duration of the study. This concurs with earlier results showing that greatest hydraulic forces were at deep depths, particularly in June, and that smallest mean grain size corresponded with June samples. *Agassiz*, with coarsest mean grain size and an armoured substrate surface was least mobile of the 3 sites but did exceed  $\tau_{*c}$  in June (Fig. 2-12b). Despite



**Figure 2-11**. Boundary Reynolds number measured at 3 sites through the flood cycle in the Fraser River. Values are the mean (± standard error) of measures collected from multiple water depths. Missing values in April were due to mechanical failure of the current meters.



Figure 2-12. Shields entrainment function measured through the flood cycle of 1995 in the gravel reach of the lower Fraser River. Values are the mean (± standard error) of samples collected from (A) 4 water depths and (B) 3 study sites. τ<sub>\*c</sub> is the critical value of Shields above which mobile bed conditions are likely. No measures from 0.2 and 0.5 m were collected in April (B).

major differences in the substrate characteristics of *Deer* and *Hope*, measures of  $\tau$ . were similar in most months of the study. This similarity reflects the interacting influence of both hydraulic and sedimentary conditions on  $\tau$ .; *Deer* had a relatively low *D* in all months as compared with *Hope* but hydraulic conditions at the two sites differed such that U. was sufficiently high at *Hope* to create equally mobile conditions at both sites during freshet.

## Discussion

Sedimentary conditions in the gravel reach of the lower Fraser River exhibited tremendous spatial variability that is characteristic of alluvial rivers (Church 1992). This variability was expressed along a gradient of water depths ranging from 0.2 to 3.0 m, as well between the active channel and near-shore channel margins, and most notably between study sites. Three gravel bar sites within a 10 km length of the Agassiz reach were selected for study and the sedimentary characteristics at each were found to be highly divergent. The most upstream site, *Hope*, had a relatively homogeneous and coarse substrate surface that is typical of framework gravel beds with only a small fraction of sediment material < 2 mm. *Agassiz* was similar to *Hope* in mean grain size and the small proportion of fine sediment in the substrate, however, the surface of *Agassiz* was heavily armoured with a layer of fine sediment and periphyton draping the stone surfaces. Lastly, *Deer* appeared to feature a matrix-supported bed surface with fine sediment comprising a significant portion of the substrate which contributed to low measures of bed roughness and grain size, and highest substrate heterogeneity of the 3 sites.

At each site, sedimentary properties exhibited spatial variation across water depths as well as seasonal variation between months of low flow and freshet. This spatio-temporal variability, however, is confounded by the shift in sample locations from the active channel in April and September to the near-shore margin habitat in May, June, and August. Hence, depthwise comparisons that examine the average value of measures collected on all dates at a specified water depth must be made with caution. For most sedimentary variables, the effect of depth was secondary to the site-specific and seasonal sources of variation in the data. Study sites differed in all sedimentary variables except  $\tau$ . and seasonal variation exhibited a high degree of contingency between measures made in April and September when river discharge was roughly equal. Contingency refers to the degree to which time determines state (Colwell 1974) and, in this study, discharge is a function of time of year and had significant influence on the sedimentary properties of study sites. Freshet therefore induced physical variation in the benthic habitat of the Fraser River as opposed to permanent change and the variation was related to shifting sample locations between the active channel at low flow and the shore margin during freshet.

At high discharge, the proportion of sediment < 2 mm collected in sediment samples increased due to lateral expansion of the active channel into near-shore areas that act as an accumulation zone for fine material in natural river systems (Church 1992). In the shore zone, sediment is only seasonally worked by fluvial processes during periods of high flow and significant deposition of fine material on the falling limb of freshet can occur (Church and McLean 1994). Consequently, this may lead to higher substrate heterogeneity and often lower mean grain size in the shore zone than in the active channel. This was observed at all sites in this study although the clarity of such seasonal patterns can become obscured in a laterally unstable channel such as the gravel reach of the lower Fraser River where previously active channel surfaces become shore zone areas due to changing channel geometry and patterns of flow.

The seasonal working of fluvial processes in the near-shore margin also leads to differences in the packing characteristics of the bed between the shore and main channel zones.

Bed materials in the active channel are usually structured and closely packed in comparison to the 'loose' conditions (cf. Church 1978) of the shore zone such that the value of  $\tau_{\bullet}$  necessary to initiate bed mobility may exceed  $\tau_{\bullet} > 0.06$  in the main channel. Even with this adjustment, however, results presented above are unchanged and shallow water depths of 0.2 and 0.5 m consistently provided stable bed conditions at all levels of river discharge in contrast to depths of 1.5 and 3.0 m. Despite the possibly 'loose' packing conditions of most near-shore areas, these habitats are recognized to have low  $\tau_{\bullet}$  as a result of bank resistance and a lateral velocity gradient from the active channel to the shore-zone that results in low shear stress at the river banks (Parker 1978). Bank resistance becomes increasingly important in determining  $\tau_{\bullet}$  as the steepness, or curvature, of the bank increases.  $\tau_{\bullet}$  is also reduced as the protrusion of particles above the bed relative to water depth increases (Carling 1983). In this study, low sediment mobility at shallow depths was likely due to low shear velocity and secondarily flow resistance from the curved banks while moderate mobility was found across the mid-channel where flow velocity was higher and resistance was primarily from bottom drag.

Site-specific differences in  $\tau$ . are likely related to multiple factors including the relative roughness, size distribution, and packing characteristics of the grains, varying bank cohesion and bank steepness, as well as hydraulic conditions at a site. Highest values of  $\tau$ . were during freshet at *Hope* which had a moderate mean grain size and was subject to relatively high hydraulic stress. Corresponding with the increased  $\tau$ . in June was a decrease in the proportion of sediment < 2 mm in substrate samples from *Hope* and an increase in k<sub>s</sub>. Together, these patterns suggest that *Hope* becomes depleted of fine material early in the flood cycle in contrast to *Agassiz* and *Deer* that have relatively high proportions of fine sediment in June, and that hydraulic conditions at *Hope* may be degrading the substrate surface to develop a highly coarse, surface pavement.

Hydraulic conditions in this study followed a gradient of increasing water depth from 0.2 to 3.0 m. The lateral velocity gradient was detected by both depth-averaged and near-bed hydraulic variables at all study sites and through the flood cycle of 1995. Depth-averaged variables, however, generally failed to capture seasonal and depth-specific variability that near-bed measures of U, Re, and T, detected. Measures of U, and Re, indicated that hydraulic forces at water depths of 0.2 and 0.5 m were consistently weaker than at 1.5 and 3.0 m on all sampling dates, and did not change significantly through the study. Relatively constant hydraulic conditions prevailed at 0.2 and 0.5 m as the position of the shallow sampling locations shifted laterally into the shore zone during high flow. In contrast, 1.5 and 3.0 m depths showed significant differences between sampling dates for all hydraulic variables.

At shallow depths, several complex factors affect the hydraulic conditions of the habitat. For example, the relative protrusion of stones above the bed increases with decreasing water depth and the diameter of large cobbles can often approximate the height of the water column. This was observed at *Agassiz* and *Hope*, and under these conditions the hydraulic relation of the velocity profile (Eq. 5) ceases to apply (Church and Gilbert 1975). Measures of U<sub>\*</sub> become dominated by the turbulent wakes of individual roughness elements that have greatly augmented flow resistance over smaller stones and U<sub>\*</sub> serves only to characterize the average hydraulic gradient through the water column. With increasing surface roughness, shallow depths become increasingly complex hydraulic environments with jetting flow between roughness elements and turbulent wakes developing in association with projecting elements.

A second factor contributing to hydraulic conditions in shallow water is that flow resistance originates from two sources, namely bottom drag and lateral drag from the channel banks (Parker 1978). The effect of lateral drag is generally dependent on the steepness and curvature of the river banks and in this study, was therefore not likely consistent between sampling dates or study sites. Bottom and lateral drag together produce flow conditions in the near-shore margin that are decoupled from those of the main channel and hence are insensitive to seasonal variation in river discharge. This hydraulic constancy at various levels of discharge was observed at 0.2 and 0.5 m water depths in the present study. In contrast to shallow habitats, deep depths experienced seasonal variation in hydraulic conditions based on conventional hydraulics due to a tighter coupling with the main flow. Only where major bottom topography produces irregular flow patterns that project into the water column will the velocity profile at deep depths show an inner profile that is decoupled from that of the main flow. This may be the case at 1.5 m depth where greatest variability in measures of U. were observed through the study.

In conclusion, discharge in the Fraser River at Agassiz ranged from 1 830 m<sup>3</sup> s<sup>-1</sup> at low flow to 6 840 m<sup>3</sup> s<sup>-1</sup> during freshet and was accompanied by tremendous variation in the hydraulic and sedimentary conditions of the habitat. The substrate was coarser and more homogeneous in the active channel at low flow than in the shore zone during freshet where a significantly greater proportion of fine sediment was observed. Study sites also exhibited spatial variability in substrate conditions with *Hope* being most coarse and relatively homogeneous while *Agassiz* was heavily armoured, and *Deer* featured a framework gravel tightly filled with fine sediment that comprised a significant portion of the substrate. Hydraulic conditions at each site were generally similar and exhibited a major lateral gradient of increasing velocity with water depth that persisted through the flood cycle in the lower Fraser River. In addition to having lower hydraulic stress, the substrate at shallow depths remained relatively immobile during the months of peak flood discharge while mobile conditions were probable at deep depths. Shallow depths therefore satisfied the physical criteria of flow refugia by maintaining substrate stability and low hydraulic stress during flooding. Subsequent chapters will examine the characteristics of the physical habitat in relation to the distribution and abundances of macroinvertebrates (Chapter 3), and seasonal variation in invertebrate distributions through the flood cycle with particular emphasis on the extent to which organisms use the shallow, near-shore zone during high discharge as a flow refugium (Chapter 4).

# Chapter 3 : Physical Habitat Parameters and Benthic Invertebrate Distributions in the Fraser River

## Introduction

The fluvial environment is characterized by many interacting physical factors that exert a major influence on benthic invertebrates (Power et al. 1988). Together, these factors produce spatial and temporal heterogeneity in the fluvial environment that in turn elicits variability in benthic community patterns (Palmer and Poff 1997). The focus of many studies has been to examine the relative importance of different physical factors in structuring the benthic community (Culp et al. 1983; Growns and Davis 1994; Quinn and Hickey 1994; Robertson et al. 1995). Hydraulic and substrate conditions have been consistently identified as two dominant factors that affect community composition and the abundances and distributions of the constituent populations (Statzner et al. 1988; Wetmore et al. 1990; Cobb et al. 1992; Quinn and Hickey 1994). Other factors including resource availability (Culp et al. 1983; Richardson 1993), water chemistry (Giberson and Hall 1988), temperature (Bournaud et al. 1987), and light (Robinson and Minshall 1986) have also been shown to play important roles.

The complex interactions between many of these factors make separating out the individual effects of each on benthic organisms difficult. The interrelation of hydraulics and substrate is particularly difficult to separate because each is in part functionally dependent on the other. For example, grain size composition of the channel substrate influences the distribution of many benthic taxa (Gurtz and Wallace 1984), and is largely determined by the competence of past and present flow conditions (Leopold 1994). Grain size composition determines the heterogeneity and surface roughness of the substrate which in turn creates fine-scale patterns of

near-bed flow variation that influence the distributions of some benthic organisms (Hart et al. 1996). Substrate stability, often equated to benthic habitat stability (Malmqvist and Otto 1987), is a product of grain size and shear stress exerted on the bed and will largely determine the risk to an organism of being crushed or dislodged from the substrate, and thus its ability to persist in a habitat through time (Cobb et al. 1992). At a larger scale, variations in flow competence along a length of channel result in distinct erosional and depositional habitats that can selectively influence the distribution of organisms based on suitable morphological and ecological traits (Thorp 1992).

The ecological importance of both substrate and hydraulic characteristics to benthic macroinvertebrates is well-documented. For example, a rough surface substrate has high retentive ability to store allochthonous organic matter which is an important source of nutrients, food, and microhabitat for many organisms (Culp et al. 1983; Richardson 1992). Substrate roughness and heterogeneity have also been shown to influence the biotic interactions of competition and predation (Fuller and Rand 1990; Lancaster et al. 1990), in addition to providing in-stream refugia to invertebrates from hydraulic stress (Lancaster and Hildrew 1993b; Robertson et al. 1995). And while hydraulic forces may place energetic demands on resident organisms to maintain position and prevent accidental drift from the substrate (Ciborowski 1983), near-bed flow velocity is also important for oxygen and nutrient cycling as well as the delivery of fine particulate matter to filter-feeding organisms.

Previous research has speculated that many stream-dwelling organisms possess specialized traits to deal with hydraulic forces that are a constant feature of fluvial environments. Streamlining or dorso-ventral flattening of the body is a morphological trait which is considered to reduce lift and drag forces on an organism (Statzner and Holm 1982, 1989; Statzner 1988). Additional examples of flow-resistant morphologies include anal claws of caddisflies that cling to the substrate and ventrally-positioned gills of some mayflies that provide suction to the substrate surface and reduce the risk of accidental drift. Of course, not all benthic species possess such morphological traits but may instead show avoidance of hydraulic forces with feeding or microhabitat preferences that restrict their distribution to unexposed habitats, often away from the substrate surface. Such behavioural adjustments to flow are possessed by many dipterans and oligochaetes whose morphologies are suited to burrowing into the substrate, and as well by taxa with distributions concentrated along the lateral margins of river channels. The synchronous timing of life history stages such as emergence with increasing discharge due to flooding is a physiological adjustment to flow which enables organisms to escape the fluvial environment during predictable hydrologic fluctuations (Hayden and Clifford 1974; Gibbs and Mingo 1986).

These examples demonstrate that the morphology, behaviour, and physiology of an organism will influence its tolerance to particular hydraulic and sedimentary conditions which vary spatially within the benthic environment. If organisms are selecting a given location based on hydraulic and substrate suitability, the spatial distribution of species should correspond to the spatial pattern of similar physical conditions within the habitat. Hydraulic and substrate 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 which limit the distribution of organisms has been demonstrated both under laboratory conditions (Horne et al. 1992) and most recently 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 roughness of the substrate has also been shown, although to a lesser extent (Holomuzki and Messier 1993; Quinn and Hickey 1994; but see also Culp et al. 1983).

The purpose of this study is to examine the spatial distribution of benthic invertebrates in relation to hydraulic and sedimentary conditions in a large, gravel-bed river. The study was

conducted at multiple water depths and under various flow conditions to capture spatial and temporal habitat heterogeneity which are likely to be significant, large-scale factors directly influencing the benthic environment. It is hypothesized that the pronounced hydraulic and sedimentary characteristics of the river may represent major physical gradients along which the benthic community is organized. This study is unique in that large rivers are relatively unstudied in benthic ecological research. Deep water habitats of large rivers, in particular, have been entirely ignored and it is suggested that such habitats are hostile relative to the channel margins because high velocities and sediment transport create a sterile environment that places great energetic demands on benthic organisms to maintain themselves (Church 1992). Four water depths were selected in this study to contrast between the active main channel and the near-shore channel margin, and to evaluate the importance of physical habitat conditions as a determinant of benthic community structure in a large river.

#### **Study Area and Methods**

The study area and methods for data collection of hydraulic and sedimentary variables have been described in Chapter 2. A summary of hydraulic and sedimentary variables relevant to this chapter is presented in Table 3-1, and only those methods not described above are outlined here.

#### Data Collection - Macroinvertebrates

Benthic samples of invertebrates were collected at depths of 1.5 and 3.0 m with a Shipek grab sampler. The Shipek is a weighted bottom sampler and was deployed by a power-operated winch from the side of a power boat. A sonar mounted on the boat enabled the sampling depths

Name	Symbol	Units	Formula	Description	
Sedimentary Measures					
Mean Grain Size	D	mm	$(D_{84} + D_{50} + D_{16})$	mean grain size of the sample	
			3		
Trask's Sorting Coefficient	So	none	$\sqrt{\mathrm{D}_{84} \ / \ \mathrm{D}_{16}}$	grain size homogeneity of the sample (heterogeneity > 1)	
Nikuradse's Roughness	k <sub>s</sub>	mm	3.5 * D <sub>84</sub>	bed roughness, topographic variation	
% Fines	n/a	%	$\frac{\text{weight} < 2 \text{mm}}{\text{total weight}} * 100$	proportion by weight of the total sample less than 2 mm	
			3	· ·	
Hydraulic Measures: Near-bed					
Shear velocity	U.	cm s <sup>-1</sup>	1	slope of vertical velocity log profile	
			slope * 5.75		
Turbulence Intensity	T∗	none	direct measure	coefficient of variation of near-bed velocity	
Boundary Reynolds Number	Re₊	none	$\frac{U_* k_s}{v}$	nature of flow close to the bed, near- bed turbulence ( $v = 0.01 \text{ cm}^2 \text{ s}^{-1}$ )	
Shields Entrainment	τ.	none	$0 \text{ IL}^2$	non-dimensional measure of substrate	
Function				stability ( $\rho = 0.998 \text{ g cm}^{-3}$ ; $g = 980$	
			$g D_{50} \left(\frac{1}{\rho} - 1\right)$	cm s <sup>-1</sup> ; $\rho_s = 2.65 \text{ g cm}^{-3}$ )	
······································					
Hydraulic Meas	ures: Dep	th-Averag	ged		
Mean Velocity	U	cm s <sup>-1</sup>	direct measure	velocity measured at 0.6 depth below water surface	
Froude Number	Fr	none	$\sqrt{U^2/\mathrm{gd}}$	turbulence close to the water surface	
Reynolds Number	Re	none	$\frac{U d}{V}$	turbulence of free flow ( $v = 0.01 \text{ cm}^2 \text{ s}^{-1}$ )	

**Table 3-1**. Summary of physical variables measured in this study. Refer to text for further details.

of 1.5 and 3.0 m to be located. Once retrieved from the river bottom, benthic samples were passed through a series of sieves and material greater than 500  $\mu$ m was preserved in 4% formaldehyde for sorting of the invertebrates from the sediment. The sediment fraction less than 500  $\mu$ m was retained for grain size analysis. Larger gravels and cobbles were separated from the preserved material, washed to remove any invertebrates, and combined with the fraction less than 500  $\mu$ m for analysis. Preserved samples were sorted with a dissecting microscope and the invertebrates were transferred to 70% ethanol for storage. The sorted sediment was then washed and recombined with the other sediment fractions for analysis. Five casts of the Shipek, totaling 0.2 m<sup>2</sup> of channel bed area were taken for each sample. Because the boat could not safely maneuver in shallow water, a Surber sampler (0.09 m<sup>2</sup>, 500  $\mu$ m mesh) was used at depths of 0.2 and 0.5 m to collect benthic samples. A comparative test between the Shipek and Surber samplers was conducted prior to this study and showed that the sampling performance of the two methods was similar (see below).

Invertebrates were identified to the lowest possible taxonomic classification according to Merritt and Cummins (1996). Invertebrates from the Fraser River were noticeably small in body size and identification beyond family level was difficult for some taxa, particularly stoneflies. Taxa were assigned to the following functional feeding group categories after Merritt and Cummins (1996): collector-gatherers, collector-filterers, predators, grazers, and shredders. Taxa were also classified according to flow exposure groups of Growns and Davis (1994) to examine the distribution of invertebrates with respect to near-bed flow conditions. The three categories of flow exposure, obligate, facultative, and avoider, were based on *a priori* assessments of morphology and feeding behaviour as specified by Growns and Davis (1994).

Data Collection - Organic Matter
Sediment samples were oven-dried at 190 °C, weighed, and sieved to determine the grain size distribution. The sieved fractions were then ashed in a muffle furnace (500 °C, 8 h) to determine the ash free dry mass of organic matter and mineral substrate in each size fraction. The organic component of substrate samples was expressed as the weight of organic matter  $\geq$  and < 1 mm per unit area. Each size fraction is hereafter referred to as coarse particulate (CPOM) and fine particulate organic matter (FPOM), respectively.

The influence of water depth on the standing crop of periphyton was estimated during the August sampling period, on the declining limb of the discharge hydrograph. Periphyton samples were collected at each site from water depths of 20, 40, and 60 cm. Three cobbles were selected at each of the water depths that were of similar size and shape. An area of 11.3 cm<sup>2</sup> was sampled from each of the 3 cobbles, equaling a total area of 34 cm<sup>2</sup> sampled from the 3 water depths at each study site. A cylindrical plastic template was attached to the upper surface of each cobble by suction and the area cleaned using an electric drill and toothbrush and river water. Several cleanings were often required before the water-periphyton mixture was collected from the template using a syringe. The water-periphyton mixtures from the 3 cobbles at each water depth were pooled and stored on ice in the dark until analysis. Chlorophyll *a* pigment was extracted in 90% acetone and the concentration (mg cm<sup>-2</sup>) measured using a fluorometer.

# Shipek and Surber Test Samples

A comparison was made prior to the study to determine if the sampling performance of the Shipek differed from that of the Surber sampler. Benthic samples were collected from 2 gravel bar sites in the Agassiz reach where the power boat could successfully maneuver in shallow water. At each site, paired samples were collected by the Shipek and Surber sampler at 50 cm water depth. The sites differed slightly in sediment texture, having mean grain sizes of 18.9 and 33.1 mm, respectively. A total of 16 paired samples using each method was collected from the sites and sorted to determine the invertebrate density in each sample. On average, the density of organisms in Surber samples exceeded that of Shipek samples by 1.5, although densities of paired samples did not statistically differ between each method of invertebrate sampling (t = 1.54, p = 0.15, df = 15).

# Data Analysis

Multivariate ordination of the physical data was used to summarize total variation in the data and identify major environmental gradients. Ordination is a mathematical technique designed to reveal major patterns among samples when a large number of quantitative variables have been measured. It is particularly useful when variables are highly correlated and univariate tests may fail to detect inter-variable relations and significant effects (Anholt 1990). The ordination techniques used in this study were Principal Components Analysis (PCA) and Canonical Discriminant Analysis (CDA). The PCA was used to summarize total variation in the physical data set using a covariance matrix that required transformation of all variables [ $log_{10}$  (x + 1)] prior to multivariate analyses to standardize the data and conform with assumptions of multivariate normality (Gauch 1982). CDA is related to PCA in that it is also a data reduction technique that summarizes variation between levels of a main effect. A distinct gradient in physical variables with respect to water depth (main effect) was evident from results of the PCA, thus CDA was used to summarize variation between water depths and identify variables that discriminate between levels of depth.

The densities of FPOM and CPOM between water depths and sampling dates were examined using an analysis of covariance (ANCOVA) to statistically control for substrate and hydraulic conditions. Both substrate texture (Maridet et al. 1995) and flow conditions (Grubaugh and Anderson 1989) have been shown to influence the distribution of organic matter in previous studies. Where no significant interaction was found between the covariate and effect, the slopes were assumed to be equal for the analysis and least-squares estimates of means were used to compare differences between depths and dates (SAS Institute 1990).

A PCA was applied to the invertebrate data in an attempt to identify a gradient of community compositional change from which an environmental gradient could be inferred. A total of 30,068 invertebrates representing 34 taxa was collected in this study (Appendix 1), however, many taxa were represented by only a few specimens. Only those taxa representing greater than 1% of the total were included in the PCA. Furthermore, only presence/absence data were used in the analysis because of the considerable number of zeros in the data set. Both of these steps were necessary to avoid problems of non-linearity. A significant number of zeros in a data set can create non-linearity in the species response where PCA assumes a linear response curve for all species (Gauch 1982). The use of presence/absence data in multivariate analyses is an approach that provides distributional and community composition information while minimizing the influence of changes in taxon abundances due to non-measurable factors such as demographic fluctuations due to life history patterns.

Canonical Correlation Analysis (CCoA) was used to examine the relation between the invertebrate and physical habitat data. CCoA is a direct gradient analysis that examines species' distributions along known environmental gradients. It is less prone to the non-linearity problems of PCA since the statistical significance of CCoA is determined by multiple correlations between data sets (Pimentel 1979). For this reason, abundance data for taxa representing greater than 1% of the total invertebrates were used in the analysis and all invertebrate and physical habitat data were  $log_{10}$  (x + 1) transformed to meet assumptions of multivariate normality and reduce the influence of numerically dominant taxa (Gauch 1982). A CCoA was also applied to invertebrate

62

data classified according to functional feeding groups and flow exposure groups. Multiple regression and correlation analysis options of the Cancorr procedure of SAS (SAS Institute 1990) were used to assist in interpreting 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.

In addition to CCoA, step-wise multiple regression was used to determine which physical variables might be significant predictors of taxon distributions. Step-wise multiple regression analyses were performed by backward elimination using the STEPWISE procedure of SAS (SAS Institute 1990), and the abundances of individual taxa, as well as those of functional feeding groups and flow exposure groups were examined. Rather than use the original hydraulic and sedimentary variables measured in this study, principal component variables resulting from the PCA were used as they are not intercorrelated and summarized significant variation in the physical data. Collinearity among regressor variables can otherwise lead to spurious conclusions regarding the significance of the variables to the regression model (Zar 1984). The first 4 principal component variables were entered as independent variables in the analysis along with sampling date, water depth, and study site. Only variables that entered at p < 0.10 were retained in the final regression model. This analysis differed from the CCoA by using physical variables derived independently from the invertebrate data to examine patterns of taxon distributions and abundances.

#### Results

Physical Habitat Data

63

An ordination by PCA of the sedimentary and hydraulic variables explained 94.0% of the variance in the data by the first 4 principal component axes. Axis 1 accounted for 52.0% of the variance and all of the hydraulic variables (U<sub>\*</sub>, Re<sub>\*</sub>, T<sub>\*</sub>, U, Fr, and Re) had significantly positive loadings on the axis (p < 0.0001; Table 3-2). The variance explained by axis 2 and axis 3 was 24.1% and 11.0%, respectively. Significant loadings on axis 2 represented a positive gradient of increasing FPOM, CPOM, % fine sediment, and S<sub>o</sub>, and negative loadings represented an increasing gradient of *D*. An ordination of principal component variables 1 and 2 found that samples were distinctly clustered in order of increasing water depth along the hydraulic gradient of axis 1 (Fig. 3-1). Along axis 2 there was a high degree of spread in samples that was similar for all water depths. This suggests that there was significant variation in substrate characteristics and the density of organic matter within samples from all water depths. Sedimentary variables therefore did not exhibit a depth-related gradient as did the hydraulic variables along axis 1. This is consistent with ANOVA results of sedimentary variables in which more significant variation was accounted for in differences between study sites and sampling dates than between water depths (Chapter 2).

Axis 3 represented a positive gradient of the near-bed hydraulic variables Re. and U. A plot of Principal Component axes 1 and 3 indicated that samples from 0.2, 0.5, and 3.0 m were more tightly clustered than samples from 1.5 m along axis 3 (Fig. 3-2). The variation in near-bed hydraulic conditions within samples from shallow depths and 3.0 m was therefore small relative to the variation within samples from 1.5 m depth. This is again consistent with results from three-way analyses of variance of hydraulic variables such as shear velocity in which differences between water depths were always significant and differences between sampling dates were primarily at 1.5 m, thus producing a significant date x depth interaction term (Chapter 2).

Variable	Principal	Principal	Principal	Principal
	Component 1	Component 2	Component 3	Component 4
D	-0.179*	-0.517***	0.173*	0.232**
So	0.219*	0.610***	-0.168	-0.328***
k <sub>s</sub>	-0.138	-0.142	0.161	0.083
% Fines	0.308**	0.792***	-0.165	-0.317**
U	0.947***	0.019	-0.207*	0.035
U₊	0.836***	0.044	0.523***	-0.050
T*	0.331***	-0.143	0.156	0.337***
Re.	0.781***	-0.025	0.618***	-0.019
τ.	0.630***	0.224**	0.360***	-0.120
Fr	0.702***	-0.006	-0.183*	0.049
Re	0.959***	0.045	-0.264**	0.068
СРОМ	-0.201*	0.741***	0.097	0.630***
FPOM	-0.197*	0.898***	0.085	-0.254**
Total Variance Explained:	52.0%	24.1%	11.0%	7.1%

**Table 3-2**. Structure coefficients of variables measured in this study for the first four principal components of the PCA. Structure coefficients are the correlation between the original variable and the principal component (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001).



Figure 3-1. Ordination of samples by Principal Component Analysis along Principal Component axes 1 and 2. The water depth of each sample is designated by the appropriate symbol. Values represent a sample collected at a particular site, depth, and date in the Fraser River in 1995.



**Figure 3-2**. Ordination of samples by Principal Component Analysis along Principal Component axes 1 and 3. The water depth of each sample is designated by the appropriate symbol. Values represent a sample collected at a particular site, depth, and date in the Fraser River in 1995.

Results of the CDA supported PCA results of a strong hydraulic gradient from shallow to deep water depths (Fig. 3-3). Samples from each water depth were discretely clustered along Canonical Variable 1 which captured variation in hydraulic measurements and explained over 99% of the total variance in physical data. Specifically, the variables Re, U, and U. had significant loadings on variable 1, implying that the depth-averaged measures of Re and U in combination with U. have exceptionally high discriminating power between water depths. Canonical Variable 2 explained 0.5% of the total variation and discriminated between depths based on positive loadings of U. and  $\tau$ ., and the negative loading of *D*. The clusters of samples from 0.5 m depth was positioned at a greater distance along the vector of *D* on Variable 2 than other water depths which suggests that mean substrate grain size is coarser at this depth. The relatively small portion of variation explained by Variable 2, however, reflects the minimal power of *D* to discriminate between levels of water depth relative to hydraulic variables. This is supported by ANOVA results (Chapter 2) in which *D* did not significantly differ between depths and by PCA results in which the variation in *D* was similar at all water depths.

### Organic Matter

The fraction of FPOM accounted for a much greater proportion of total organic matter than CPOM in Fraser River samples, averaging 6 times more weight than CPOM in most samples. Densities of FPOM were significantly higher at depths of 0.2, 0.5, and 1.5 m than at 3.0 m, and were generally highest at *Deer* (Fig 3-4a). Of the 3 sites, Agassiz had the lowest densities of FPOM, and shallow depths had higher densities than deep depths. Densities at *Deer* were highest in all months and at most water depths, with 0.2, 0.5, and 1.5 m depths being similar, but significantly higher than densities at 3.0 m. At *Hope*, densities of FPOM were similar at all water depths. When mean substrate grain size was included as a covariate, differences in FPOM between depths were insignificant which suggests that FPOM density is related to substrate grain



**Figure 3-3**. Ordination of samples by Canonical Discriminant Analysis along Canonical Variables 1 and 2. Water depth is designated by the appropriate symbol. Values represent a particular combination of water depth, sampling date, and study site in the gravel reach of the lower Fraser River.

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**Figure 3-4**. Dry weight of (A) FPOM and (B) CPOM at 4 water depths in the Fraser River. Samples were collected from 3 study sites, listed in downstream order, and data are presented as the mean (± standard error) of samples from 5 sampling dates through the study. Note the scale of y-axes differ.

size ( $F_{3,139} = 0.72$ , p = 0.54, ANCOVA). While FPOM has been shown to vary with hydraulic conditions (Grubaugh and Anderson 1989), an ANCOVA using different hydraulic measures as covariates did not statistically add to the explained variation in FPOM between depths in this study.

Similar to the FPOM fraction, densities of CPOM differed between water depths and were site-specific. While *Agassiz* showed little variation in CPOM density between water depths, densities at *Deer* were highest at 1.5 and 3.0 m (Fig. 3-4b). This sharply contrasts with the distribution of FPOM which was generally most abundant at shallow water depths. Densities of CPOM at *Hope* were similarily high at 0.2, 1.5, and 3.0 m. A covariance analysis on the distribution of CPOM found that substrate roughness,  $k_s$ , accounted for the significant difference in CPOM between water depths (depth:  $F_{3,139} = 1.77$ , p = 0.14, ANCOVA with  $k_s$  as covariate). The variation in CPOM between depths was not further explained when different hydraulic measures were used as a covariate in an ANCOVA.

Concentrations of periphyton chlorophyll *a* were similar between water depths of 20, 40, and 60 cm (p > 0.5, ANOVA). Differences in chlorophyll *a* between sites were not statistically significant, although samples from *Agassiz* were on average 3 times higher in measured concentrations than at *Deer*, and 8 times higher than at *Hope* (Table 3-3). This confirmed visual observations made at *Agassiz* of a layer of periphyton draping the surface of most stones. The average chlorophyll *a* concentration from all periphyton samples was 0.0016 mg cm<sup>-2</sup> which is extremely low relative to other studies that have used similar sampling and pigment extraction methods (e.g., Quinn and Hickey 1994; P. F. Dymond, Univ. of British Columbia, unpubl. data).

**Table 3-3**. Mean periphyton chlorophyll a (± standard error) from each study site in the Fraser River. Values are the concentration (mg cm<sup>-2</sup>) of chlorophyll a collected from 3 cobbles in August, 1995. Differences between sites were not significant (p = 0.1).

Site	Chlorophyll a	-
Agassiz	0.0031 ± .001	-
Deer	$0.0012 \pm .0002$	
Hope	$0.0004 \pm .00003$	

#### Macroinvertebrate Data

Benthic samples collected from the gravel reach of the lower Fraser River had an average macroinvertebrate density of 168 m<sup>-2</sup>. Invertebrates were classified into 34 taxonomic groups and the level of classification differed between groups depending on the size of the organisms and reliability of the identification (Appendix 1). Invertebrates from the Fraser River were notably small in body size relative to tributaries within the Fraser basin (P. F. Dymond, unpubl. data) which made identification beyond the family level difficult. Mayflies and caddisflies were identified to genus, stoneflies to family, dipterans to either family or subfamily (Chironomidae only), oligochaetes, leeches, and mites to order, and nematodes only to phylum. Of the 34 taxonomic groups identified, 11 represented greater than 1% of the total organisms collected and were included in multivariate analyses: *Rhithrogena, Ephemerella, Heptagenia, Baetis, Hydropsyche*, Tanypodinae, Tanytarsini sp. A, Tanytarsini sp. B, Chironomini, Orthocladiinae, and Oligochaeta. A summary of distributional data for the remaining taxa is provided in Appendix 1.

Total fauna density decreased significantly with water depth (p < 0.0001; Fig. 3-5a), where the critical value was adjusted by the Bonferroni correction to account for the number of taxa in the community (i.e.  $\alpha = 0.05 / 34 = 0.0015$ ). Differences between study sites were not statistically significant (p < 0.01), although total densities at *Deer* and *Hope* were similar but



Figure 3-5. Density of (A) total taxa and (B) taxonomic richness between water depths in the gravel reach of the lower Fraser River. Means (± standard error) are given for samples collected from 3 sites on 5 sampling dates in 1995. Note the scale of y-axes differ.

greater than at *Agassiz*. Taxonomic richness, defined as the number of taxa in a benthic sample, was also lowest at *Deer* while *Agassiz* and *Hope* had similar values (p < 0.0005). Richness was highest in samples from 1.5 m depth (p < 0.0001; Fig. 3-5b) and differences between depths of 0.2, 0.5 m, and 3.0 m were not significant.

Collector-gatherers were the predominant functional feeding group in samples from the lower Fraser River, comprising 91.4% of the total fauna. The distribution of gatherers was primarily at shallow depths of 0.2 and 0.5 m (Fig. 3-6). 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 significantly more abundant at 1.5 m (p < 0.0001) and depths of 0.2, 0.5, and 3.0 m were similar. Shredders appeared to be distributed evenly between water depths while predators and grazers were less abundant with increasing water depth.

According to the flow exposure classification, avoiders were predominant in the Fraser River (67.5%) and had highest densities at shallow water depths of 0.2 and 0.5 m (Fig. 3-7). Facultative invertebrates, those with distributions that include both the upper surface and interstitial spaces of the substrate represented 17.5% of the total fauna and had highest densities at shallow depths. Obligate taxa representing 15% of the fauna showed highest densities at 1.5 m water depth.

An ordination by PCA of presence/absence data for the 11 most common macroinvertebrate taxa accounted for 62.4% of the total variance in the first four principal components. Table 3-4 summarizes the contribution of the original taxa to each principal component. A compositional gradient of fauna from shallow to deep depths was evident along the axis of principal component 3 which clustered deep depths with high occurrences of Tanytarsini sp. B and *Rhithrogena*, and shallow depths with Orthocladiinae, Tanytarsini sp. A,



**Figure 3-6**. Density of invertebrates classified into functional feeding groups between water depths in the gravel reach of the lower Fraser River. Means (± standard error) are given for samples collected from 3 sites on 5 sampling dates in 1995. Note the scale of y-axes differ.



**Figure 3-7**. Density of invertebrates classified into flow exposure groups between water depths in the gravel reach of the lower Fraser River. Means (± standard error) are given for samples collected from 3 sites on 5 sampling dates in 1995. Note the scale of y-axes differ.

**Table 3-4**. Structure coefficients of macroinvertebrate taxa collected in this study for the first four principal components of the PCA using presence/absence data from all sampling dates. Structure coefficients are the correlation between the original variable and the principal component (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.0001).

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Taxon	Principal	Principal	Principal	Principal
	Component 1	Component 2	Component 3	Component 4
Rhithrogena	0.655***	-0.187*	0.420***	-0.365***
Heptagenia	0.641***	-0.203**	-0.019	-0.233**
Ephemerella	0.788***	0.017	-0.001	-0.063
Baetis	0.565***	-0.466***	-0.019	-0.458***
Hydropsyche	0.572***	-0.105	0.027	-0.236**
Orthocladiinae	0.636***	0.111	-0.250**	0.426***
Tanypodinae	0.407***	0.103	0.076	-0.122
Chironomini	0.048	0.478***	-0.069	0.045
Tanytarsini sp. A	0.385***	0.722***	-0.159*	-0.236**
Tanytarsini sp. B	-0.033	0.302***	0.868***	0.365***
Oligochaeta	0.637***	0.285***	-0.099	0.174*
Total Variance Explained:	31.0%	11.6%	10.8%	9.0%

and Oligochaeta (Fig. 3-8a). A clustering pattern of invertebrate samples by sampling date or study site was not evident in plots of any of the principal components. A PCA of presence/absence faunal data collected in April revealed an even clearer taxonomic distinction between shallow to deep water depths (Fig. 3-8b). Deep depths were clustered with significant loadings of Tanytarsini sp. B, *Rhithrogena*, and *Ephemerella*, and shallow depths had high occurrences of Orthocladiinae and *Baetis*. Similar results were obtained when data from any of the 5 sampling dates were analyzed separately by PCA. Changes in community composition between April and September due to taxon-specific life history patterns likely contributed to the amount of scatter in the ordination of samples from all dates (Fig. 3-8a) since spring and summer are the seasons of active growth and development for most invertebrates in the northern hemisphere. This would have minimal influence on community data from only one sampling date and thus identify community compositional gradients related mainly to environmental conditions.

Direct gradient analysis using CCoA of the physical habitat data with the invertebrate data captured 83.7% of the total variance in the first 4 canonical variables. A strong physical gradient of sedimentary and hydraulic conditions was identified along the first canonical variable which alone accounted for 37.5% of the variance (Fig. 3-9). The sedimentary variable *D* had a significantly negative loading and the hydraulic variables Re, U, Fr, U, and Re, had highest positive loadings on the axis. Vectors of all invertebrate taxa except *Rhithrogena* and Tanytarsini sp. B had negative loadings on axis 1, thus being positively related to increasing mean grain size and having a negative relation with the hydraulic gradient of axis 1. This hydraulic gradient was previously found to correspond with a lateral gradient of increasing water depth from PCA and CDA results reported above. Tanytarsini sp. B had the highest positive correlation with the hydraulic gradient of axis 1, and together with *Rhithrogena* had been previously associated with



**Figure 3-8**. Ordination of invertebrate samples collected (**A**) in all months and (**B**) in April only by Principal Component Analysis along axes 1 and 3. Presence/absence data were used in the analysis and the variance explained by each axis is indicated. Taxa with significant positive and negative loadings on each axis are indicated. (**A**: n=180; **B**: n=36)



Vector 1 (37.5% variance)

**Figure 3-9**. Ordination of invertebrate data with physical habitat variables by Canonical Correlation Analysis along Vectors 1 and 2. Data from all months were included in the analysis and 55% of the total variation in the data was explained by the vectors. "Fines" refers to the % sediment < 2 mm in sediment samples. Refer to Table 3-1 for meaning of symbols.

deep water samples by PCA. Environmental gradients represented by canonical variables 2 and 3 were less interpretable, but generally had highest loadings from CPOM, FPOM,  $S_o$ , and D.

The association of invertebrate data with variables 2 and 3 was highly taxon-specific and the correlation options of CCoA were used to identify the relative importance of physical variables to the distribution of each taxon (Table 3-5). Despite the high loading of *D* on variable 1, mean grain size was a non-significant factor affecting each of the benthic taxa when the effects of all other physical variables were held constant (p > 0.05). Substrate roughness, k<sub>s</sub>, was positively correlated with *Rhithrogena* and *Hydropsyche*, and both *Hydropsyche* and Oligochaeta were negatively correlated with substrate heterogeneity. CPOM had significantly positive correlations with *Ephemerella*, Tanypodinae, Tanytarsini sp. A, Tanytarsini sp. B, and Chironomini while FPOM had a positive relation with Chironomini only. Several taxa were positively correlated with turbulence intensity, T, despite its relatively small loading on variable 1 and the predominantly negative correlation between most taxa and other hydraulic variables. Specifically, *Rhithrogena*, *Heptagenia*, *Ephemerella*, *Baetis*, and Tanypodinae had positive correlations with T. Also of significance was the negative correlation of Chironomini with the % fine sediment in substrate samples.

A CCoA of physical data with invertebrate data classified according to functional feeding groups and flow exposure groups explained 87.0% of the total variance in the first 4 canonical variables. Canonical variable 1 captured 35.4% of the variance and the negative vector represented an increasing gradient of the % fine sediment < 2 mm in the substrate and of depth-averaged hydraulic variables Fr, Re, and U. Highest loadings on the positive vector of canonical variable 2 were of FPOM, CPOM, and the sedimentary variables  $k_s$ ,  $S_o$ , and the % fine sediment. A scatterplot of invertebrate data with variables 1 and 2 revealed a positive loading of all faunal groups on variable 1 (Fig. 3-10). Collector-gatherers, facultative, and avoider taxa had highest

**Table 3-5**. Partial correlations between the sedimentary and hydraulic variables measured in this study and each macroinvertebrate taxon. Only those variables with significant coefficients are listed where the correlation coefficient is  $r_{0.1(2),112} = 0.155$  and df = (136 observations - 24 physical and taxon variables) = 112 (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.0001). Refer to Table 3-1 for meaning of symbols.

Taxon	Positive Correlation	Negative Correlation
	Coefficients	Coefficients
Rhithrogena	T. **	
	k <sub>s</sub> *	
	Re *	
Heptagenia	T* *	U *
Ephemerella	T* *	
	CPOM *	
Baetis	Fr *	U *
	T* *	
Hydropsyche	k <sub>s</sub> **	S <sub>o</sub> *
	Re *	
Orthocladiinae		
Tanypodinae	CPOM *	
	T. *	
Chironomini	CPOM *	% Fines *
	FPOM *	
Tanytarsini sp. A	CPOM *	
Tanytarsini sp. B	CPOM **	
• •	Re *	
Oligochaeta		Fr *
Ŭ		S. *



Axis 1 (38.5 % variance)

**Figure 3-10**. Ordination of invertebrate data with physical habitat variables by Canonical Correlation Analysis along Vectors 1 and 2. Data from all months were included in the analysis, 63% of the total variation in the data was explained by the vectors. "Fines" refers to the % sediment < 2 mm in sediment samples.

positive loadings, thus being negatively associated with fine sediment and depth-averaged hydraulic conditions, and positively related to T.

Partial correlations of faunal groups with each of the physical variables confirmed the relative importance of T. to patterns of gatherers, shredders, and facultative and avoider taxa (Table 3-6). Interestingly, only gatherers were significantly correlated with CPOM despite its recognized importance as a food and microhabitat resource to benthic organisms in other studies (e.g., Richardson 1992). Gatherers, and obligate and facultative taxa were positively correlated with densities of FPOM. All flow exposure groups as well as gatherers were negatively correlated with the % fine sediment in substrate samples which had the highest negative loading on canonical variable 1. While not statistically significant, grazers were also negatively related to fine sediment (p < 0.1). Only collector-filterers and obligate taxa were positively correlated with hydraulic variables and predators were not significantly correlated with any physical variable.

Step-wise multiple regression analyses indicated that the independent variables included in the regression model were generally poor predictors for many of the invertebrate taxa. Of the 11 taxa representing greater than 1% of the invertebrates collected in the study, only 5 had model adjusted-r<sup>2</sup> values exceeding 0.2 after backwards elimination of the independent variables (Table 3-7). Regression results for functional feeding and flow exposure groups were similar, and gatherers as well as facultative and avoider taxa had greater than 20% of the variance in density explained by the regression model. *Ephemerella*, Orthocladiinae, Oligochaeta, gatherers, and facultative and avoider taxa had a significant negative relation with Principal Component 1 which represented a gradient of increasing hydraulic conditions (Fig. 3-11). Except for *Ephemerella* and Oligochaeta, PC 1 explained the largest proportion of the total variation in the density of these taxa. *Ephemerella* and Oligochaeta were each positively related to PC 4 which described increasing CPOM, mean grain size, and turbulence intensity. Sampling date was a

84

**Table 3-6**. Partial Correlations between the sedimentary and hydraulic variables measured in this study and each macroinvertebrate group. Only those variables with significant (p < 0.05) coefficients are listed where the correlation coefficient is  $r_{0.1(2), 115} = 0.153$  and df = (136 observations - 21 physical and taxon variables) = 115. Refer to Table 3-1 for meaning of symbols. (\* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.0001).

Group	Positive Correlation	Negative Correlation	
	Coefficients	Coefficients	
Gatherers	FPOM **	% Fines ***	
	CPOM *	Fr *	
	T <sub>*</sub> *		
Filterers	U *		
Grazers		Re *	
Predators			
Shredders	T• **		
	S.*		
Obligates	FPOM ** 11 **	% Fines *	
	8		
Facultatives	T* **	% Fines ***	
	FPOM *	Fr *	
Avoiders	T <b>.</b> *	% Fines ***	

**Table 3-7.** Results of stepwise multiple regression analyses. Only dependent variables with<br/>adj-r² > 0.20 are listed and only independent variables that entered at p < 0.10 were<br/>included in the regression model. PC = Principal Component Variable; (-) indicates<br/>negative effect of independent variable on dependent variable, (+) indicates positive<br/>effect. Refer to Table 3–2 for the relation of PC variables to the original hydraulic and<br/>sedimentary variables.

Dependent Variable	model adj-r <sup>2</sup>	Independent Variable	F	р
Fnhamaralla	0.23	(-) PC 1	14.18	0.0002
Epnemerellu	0.25	(-) PC 2	17.68	0.0002
		(-) PC 4	16.08	0.0003
		(+) rC 4	10.98	0.0001
Hydropsyche	0.20	(+) Date	19.06	0.0001
		(-) Site	6.71	0.01
		(-) PC 3	3.95	0.05
		(+) PC 4	4.05	0.05
Orthocladiinae	0.46	(-) Site	5 76	0.02
	0110	(-) PC 1	98.00	0.0001
		(-) PC 2	7 04	0.009
		(+) PC 3	3 88	0.05
		(+) PC 4	2.00 4 77	0.03
		(1)104		0.05
Tanytarsini sp. B	0.28	(+) PC 1	14.61	0.0002
		(+) PC 2	38.90	0.0001
Oligochaeta	0.21	(-) Site	19.25	0.0001
		(-) PC 1	9.19	0.003
		(-) PC 2	3.35	0.07
		(+) PC 4	9.52	0.003
Collector Cathorors	0.27	() PC 1	41.05	0.0001
Conector - Gatherers	0.27	() PC 2	41.05	0.0001
v		(-) PC 2	4.11	0.03
Facultatives	0.31	(-) PC 1	11.79	0.0008
		(-) PC 2	28.87	0.0001
		(+) PC 3	3.88	0.05
Avoiders	0.37	(-) PC 1	63 48	0.0001
	0.57	(+) PC 3	6.61	0.0001
		(1)103	0.01	0.01



**Figure 3-11**. Relation of 3 common taxa (**A**, **B**, **C**) and 3 functional groups (**D**, **E**, **F**) with Principal Component 1, representing a gradient of increasing hydraulic conditions. Only those taxa and groups whose density  $(\log_{10}(x+1))$  was significantly related to Principal Component 1 are presented. Regression results are summarized in Table 3-7. See text for further details.

significant predictor of *Hydropsyche* density, indicating that density increased between April and September, 1995. The density of *Hydropsyche*, as well as Orthocladiinae and Oligochaeta decreased between study sites of *Agassiz*, *Deer*, and *Hope*. Orthocladiinae, Oligochaeta, collector-gatherers, and facultative taxa were significantly related to the negative vector of PC 2 which represented increasing mean grain size. The density of Tanytarsini sp. B had a positive relation with PC 1 and PC 2 where the positive vector of PC 2 described conditions of increasing organic matter, substrate homogeneity, and fine sediment in the substrate.

# Discussion

The gravel reach of the lower Fraser River is characterized by a lateral hydraulic gradient that corresponds to increasing water depth. In contrast, sedimentary variables and the distribution of organic matter displayed significant variability between water depths as well as between sampling dates in this study. The highly significant correlation of invertebrate distributions with hydraulic conditions in the Fraser River supports the hypothesis that flow patterns represent a major physical gradient along which the benthic community is organized. The greatest variation in benthic community data was captured by a gradient of hydraulic variables which is consistent with previous studies showing the distribution of benthic organisms to be strongly influenced by hydraulic conditions (Wetmore et al. 1990; Lancaster and Hildrew 1993b; Hart et al. 1996; Quinn and Hickey 1996). In several of these studies, changes to the hydraulic conditions of a habitat due to high or fluctuating discharge were accompanied by shifts in the distribution of species which further supports the relation of benthic community structure to hydraulics (Lancaster and Hildrew 1993b; Robertson et al. 1995). While this study did not examine taxon-specific shifts in distribution with changing river discharge (see Chapter 4), the

association between benthic invertebrate distributions and the nature of the ambient flow environment was consistently strong through the study.

The lateral hydraulic gradient from shallow to deep water depths appeared to be an important determinant of taxa richness and the abundance of macroinvertebrates in the Fraser River. Total density was highest at shallow depths of 0.2 and 0.5 m where hydraulic stress was lowest but which represented temporally unstable aquatic habitat as sample locations moved from the active channel at low discharge to the shore zone during the period of high flow in May, June, and August. Taxonomic richness was highest at 1.5 m depth where hydraulic conditions were intermediate between shallow and 3.0 m depths, and where measures of near-bed shear velocity and boundary Reynolds number were most variable (Chapter 2). This supports the prediction of Statzner and Higler (1986) that highest species richness occurs where hydraulic heterogeneity is maximized. While the prediction was made for a longitudinal gradient along which maximum hydraulic heterogeneity is expected to occur in the mid-reaches of a river, the influence of a lateral hydraulic gradient on taxonomic richness in the Fraser River appears to be analogous. Habitat stability at 1.5 m depth relative to shallow depths may have also influenced taxonomic richness in the Fraser River. The risk of water levels dropping to expose the channel bed is relatively low at 1.5 m, and thus the risk to invertebrates of physical exposure is also low. Statzner and Higler (1986) did not address habitat stability in their study, however, conditions at 1.5 m depth may represent an optimum trade-off between physical exposure and hydraulic exposure such that the diversity of invertebrate species with various morphological and behavioural traits to cope with hydraulic stress can be maximized.

Classification of the macroinvertebrate taxa into functional feeding groups enabled the distribution of organisms with similar morphology and feeding preferences to be examined. Collector-gatherers represented 91% of the taxa and sharply declined in density with increasing

water depth. Average density exceeded 200 individuals m<sup>-2</sup> at depths of 0.2 and 0.5 m and gatherers had a significant negative relation to hydraulic stress. 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 FPOM which had highest densities at shallow depths, and was 6 times more abundant by weight than CPOM in the Fraser River.

FPOM was found to covary with mean grain size and coarse substrates are known to increase organic matter retention in fluvial systems (Culp et al. 1983). Both organic matter and substrate grain size composition influence the distribution of benthic invertebrates but the individual effect of each is often difficult to separate. Culp et al. (1983) found that the distribution of many gatherer taxa was influenced by the presence of detrital matter but not various substrate conditions that ranged from large gravel to small pebbles. This supports results of the present study where most invertebrate taxa were positively associated with a vector of increasing *D* by CCoA but were found to be non-significantly related to mean grain size and positively correlated with organic matter when the effect of grain size was held constant. The availability of organic matter may also be enhanced by low velocity conditions which allow particles to settle out of suspension rather than be transported downstream. The combination of large, coarse substrate and reduced hydraulic conditions at shallow depths likely facilitated the retention of organic matter and thereby influenced the distribution of collector-gatherers in the Fraser River.

Shredders were also expected to have a positive correlation with organic matter in this study. CPOM is the primary food resource and has been consistently linked to high densities of shredders in other studies (e.g., Quinn and Hickey 1994). In the gravel reach of the lower Fraser River, shredder taxa were uncommon and represented less than 1% of all organisms collected in

this study. No individual taxon was analyzed by CCoA or stepwise regression due to the very small sample size and therefore conclusions about the relation of shredders to the physical conditions of the benthic habitat are uncertain. However, mean grain size was positively correlated with shredders and the scatterplot of functional feeding groups with physical habitat variables (Fig. 3-10) associated shredders with the positive vectors of CPOM, mean grain size, and substrate roughness. As previously mentioned, a coarse substrate with a rough surface topography improves detrital retention in the channel bed and creates microhabitats of reduced hydraulic stress for foraging (Culp et al. 1983; Holomuzki and Messier 1993). In this study, substrate topography was likely an important factor allowing for greatest accumulations of CPOM at depths of 1.5 m where hydraulic stress is known to be relatively high. Shredders were slightly more abundant at 1.5 m depth which may have been facilitated by substrate roughness that created localized areas of reduced hydraulic stress for foraging.

The benefit to collector-gatherers and shredders of hydraulically benign areas for detrital retention may, however, also benefit their predators by aggregating a potential food resource and minimizing the energetic costs of foraging. While predators were not significantly correlated with any environmental variables, highest densities corresponded with the distribution of gatherers and filterers which made up almost 95% of the total benthic organisms in the Fraser River. Tanypodinae were the only common predator in the study and demonstrated a negative relation with hydraulic conditions by CCoA. Both the energetic costs of foraging at elevated levels of hydraulic stress and the limited prey resource in deep water may have influenced the distribution of predators in the Fraser River. It is possible that predators influenced the distribution of benthic invertebrates in the Fraser River, thereby accounting for some of the unexplained variation in regression analyses. Predation has been shown to be important to the distribution of species and community organization in some systems (Hart 1992; Sih and

91

Wooster 1994), however, the Fraser's pronounced hydraulic gradient and relatively mobile gravel substrate likely minimize the frequency of ecological interactions (Feminella and Resh 1990) and contribute to the low abundance of obligate predators in the benthic community.

The benefits of reduced hydraulic stress to many invertebrates for foraging may be counteracted by the negative effects of other factors. Significant fine sediment deposition can result from low velocity conditions and may limit primary productivity by reduced light penetration and produce unsuitable habitat conditions for some invertebrate species. Probable ecological consequences for fine sediment deposition include reduced foraging for most trophic groups as particulate organic matter and algae become draped by fine sediment. The proportion of fine sediment in substrate samples was a major environmental gradient identified by CCoA with which all flow exposure groups as well as gatherers and grazers were negatively correlated. Grazers were uncommon in the gravel reach of the lower Fraser River during the period of this study, and showed only a slight depth-related distribution with lowest densities at 3.0 m. This was not surprising as periphyton chlorophyll a did not differ between 0.2 and 0.6 m water depth and concentrations were extremely low in all samples. It is impossible to determine if concentrations of chlorophyll a measured in August, 1995 were representative of concentrations at other times of the year since the only previous study in the Agassiz reach of the Fraser River used sampling methods that are not comparable with the present study (Northcote et al. 1975). In studies where high periphyton biomass was recorded, water depth was shown to significantly limit chlorophyll *a* production and consequently limit the distribution of invertebrate grazers (Quinn and Hickey 1994). High volumes of suspended sediment in the Fraser River result in turbidity and significant deposition of fine sediment in near-shore areas, the majority of which is coincident with the timing of freshet between May and August (Northcote and Larkin 1989).

92

These factors likely limit algal and grazer productivity in the Fraser River and account for the insignificant representation of grazers in the benthic community.

Conditions of low near-bed velocity can also result in reduced oxygen transport into the channel substrate. Saturated oxygen conditions in the sediment are important to macroinvertebrate metabolism and the demand increases with water temperature since levels of saturated oxygen decrease. Areas of low flow can therefore become unfavorable for invertebrate respiration as temperature increases during summer months. The distribution of various invertebrate species has been shown to shift to areas of increased turbulence as temperature increases and oxygen concentrations decrease (Kovalak 1976; Wiley and Kohler 1980). In this study, no taxon was negatively associated with T. and 50% of the taxa examined by CCoA had significant positive correlations. T. was recognized as a major environmental gradient with which gatherers and shredders, as well as facultative and flow-avoider taxa, were positively correlated. Each of these groups was most abundant at shallow depths with low near-bed velocity and high T. may therefore have provided optimal conditions for foraging while maintaining oxygenated substrate conditions, particularly during the summer months of this study. Further study is required to evaluate this hypothesis as the relation between T<sub>•</sub> and sediment oxygen concentrations is poorly documented, and the tolerance of different species to low concentrations of oxygen is not well-known.

Turbulent flow patterns also influence the delivery of inorganic nutrients and suspended organic matter to benthic invertebrates (Shimeta and Jumars 1991). Turbulence intensity has been found to explain significant variation in the distribution of filter-feeding larval blackflies (Hart et al. 1996) and significantly alter the rates of food particle interception by blackflies (Shimeta and Jumars 1991). While filter-feeders have been positively associated with turbulence in previous community-level studies (e.g., Growns and Davis 1994), filterers in this study were only correlated with depth-averaged measures of U. Moreover, no filterer taxa were associated with FPOM and highest densities of filterers were predominantly at 1.5 m. At this water depth, densities of FPOM were moderately high and flow velocity would supply suspended material to filter-feeding organisms (Fuller and Mackay 1980). However, the association of depth-averaged velocity measures with filter-feeders rather than near-bed measures was surprising. It is believed that T<sub>\*</sub> is a good predictor of the distribution of taxa occupying shallow habitats such as gatherers and shredders because flow conditions in the near-shore margin are chaotic and dominated by complex bed topography (Hart et al. 1996). This is due to a combination of channel bottom drag and lateral drag from the bank which produces flow patterns that are decoupled from those of the main channel (Parker 1978). In this situation, measures of velocity may only serve to characterize the average hydraulic gradient through the water column while turbulence intensity provides a direct characterization of the near-bed flow environment. At deep depths where obligate taxa and filterers were most common, near-bed hydraulic conditions are more tightly coupled with the main flow profile because flow resistance is primarily a result of bottom drag. Measures of near-bed and depth-averaged velocity may therefore not differ as greatly at deep depths and thus serve as equally good predictors of taxa distributions.

Measures of near-bed turbulence are relatively uncommon in studies of stream ecology because the spatial and time scale required for these measures is quite fine. Turbulence intensity is a point-specific measure of fine-scale temporal variation in flow intended to characterize the hydrodynamic environment immediately adjacent to benthic organisms (Hart et al. 1996). Conventional techniques of averaging velocity measurements collected over a given period are relatively coarse and may not adequately characterize the flow conditions directly influencing insect behaviour and distributions. For instance, the flow that dislodges insects is unlikely to be described by mean shear velocity as drift is more conceivably induced by a high velocity burst of flow that comes over the substrate only periodically (Power et al. 1988). Fluctuating, or unsteady flow conditions are common in nature and contain accelerating currents that impose a hydraulic force in addition to that derived from bottom drag such that mean values of velocity likely underestimate the actual force experienced by organisms (Hart et al. 1996). It is not surprising, therefore, that T<sub>\*</sub> was a significant correlate with the distribution of many invertebrate taxa in the Fraser River since it characterizes the ambient flow environment inhabited by benthic organisms.

At deep depths where measures of hydraulic stress are greatest, the gatherer taxa *Rhithrogena* and Tanytarsini sp. B were most common. The morphology and feeding behaviour of these taxa are highly divergent despite the similar depth and habitat association. Little is known of the ecology of Tanytarsini species and the two species found in this study were markedly different both in distribution and morphology. Tanytarsini sp. B were the most positively correlated with hydraulic conditions of all taxa and feature a very thin and elongate body with reduced prolegs. In comparison, *Rhithrogena* are a dorso-ventrally flattened gatherer with highly specialized ventral gills which provide suction to substrate elements and thereby reduce the risk of erosion from the channel bed. In large, coarse substrate, *Rhithrogena* is known to forage both within the interstices and on the lower surfaces of cobbles which provides additional protection from elevated hydraulic stress at deep water depths (Glozier and Culp 1989). *Rhithrogena* was positively correlated with k<sub>s</sub> which reflects the importance of substrate topography to gatherers in high velocity habitats both for detrital retention and to create microhabitats of reduced hydraulic stress for foraging.

A contrast of these deep water taxa highlights the diversity of strategies apparently suitable for persistence in habitats of elevated hydraulic stress. *Rhithrogena* is morphologically streamlined to reduce hydraulic drag and remain attached to the substrate (Vogel 1981), while Tanytarsini sp. B is able to burrow within the sediment and somewhat escape the forces of
hydraulic drag. A third taxon known to inhabit high velocity areas is the filterer caddisfly *Hydropsyche* which, in this study, was correlated with k<sub>s</sub> and Re. This is consistent with other studies where the highly retentive capture net and specialized morphology of *Hydropsyche* allowed it to occupy high velocity microhabitats which provided effective positions for filter-feeding (Fuller and Mackay 1980; Wetmore et al. 1990). The flow-adapted morphology of *Hydropsyche* includes dexterous anal claws that cling to the substrate while feeding. A topographically rough substrate further assists in feeding by enabling *Hydropsyche* to protrude well into the flow and intercept a significant portion of suspended material.

In this study, functional feeding group classification was useful in identifying physical factors important to the distribution of taxa with similar morphology and foraging behaviour. Results suggest that the distribution of trophic groups corresponded to the spatial partitioning of similar physical conditions within the habitat. Classification of macroinvertebrates based on feeding preferences has received some criticism since species-specific information is lost to generalization and not all organisms are restricted to one prey type through the life cycle (e.g., Fuller and Mackay 1980). However, functional feeding group classification was useful in this study for the purpose of examining community-level associations with the physical habitat of a large gravel-bed river.

The usefulness of classification by flow exposure groups is 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 is redundant. Moreover, many studies suggest that benthic organisms undergo an ontogenetic shift in habitat distribution (Holomuzki and Messier 1993) and that hydraulic forces exerted on a young larva are radically different than those experienced at a larger body size (Statzner 1988; Statzner and Holm 1989). Also, many invertebrate species are relatively mobile and may

experience a wide variety of flow conditions as they move within and about the substrate seeking food. Furthermore, the 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. It is believed that the usefulness of flow exposure group classification will depend on the availability of detailed information on microhabitat use of a particular taxon and the ability of studies to characterize the benthic habitat at a fine-scale.

In conclusion, hydraulic conditions as well as substrate texture and the distribution of organic matter represent major gradients along which the benthic community of the lower Fraser River appears to be organized. The spatial distribution of taxa generally reflected an organism's morphological and trophic suitability to particular hydraulic conditions which varied along a lateral gradient from shallow to deep water depths. Large, gravel-bed rivers are relatively unstudied in aquatic ecology and these results were therefore an essential step prior to examining the response of the benthic community to variation in habitat conditions due to seasonal flooding (Chapter 4). This study detailed the association of physical habitat variables with common invertebrate taxa and trophic groups and provides the basis from which to assess variation in the distribution of organisms through the period of annual flooding in the Fraser River.

# Chapter 4 : The Influence of Seasonal Flooding of the Fraser River on the Benthic Invertebrate Community: the Importance of the Lateral Shore Margin

# Introduction

Flood events are commonly referred to as disturbances and the consequences of hydrologic disturbances to aquatic communities are well documented (e.g., Sousa 1984; Resh et al. 1988; Reice et al. 1990). Increased near-bed shear velocity, substrate instability, and scouring of the substrate surface are commonly associated with flood events and have been shown to deleteriously affect benthic organisms (Boulton et al. 1992; Cobb et al. 1992; Lancaster and Hildrew 1993b; Scarsbrook and Townsend 1993; Flecker and Feifarek 1994; Robertson et al. 1995). Both the downstream export of resources and the risk to organisms of being eroded from the substrate are common consequences of elevated hydraulic forces due to flooding, while substrate instability has been found to induce catastrophic drift of organisms to depths of 2.0 m below the substrate surface in the Rhône River, France (Dole-Olivier et al. 1997). It is not surprising, therefore, that the most significant negative impacts of flooding on benthic organisms are believed to occur in gravel-bed rivers due to the highly unstable nature of the channel substrate (Sagar 1986; Resh et al. 1988; Scrimgeour and Winterbourn 1989).

Proposed mechanisms by which populations persist in hydrologically disturbed environments include morphological, behavioural, and physiological traits (Statzner and Holm 1982, 1989; Waringer 1989), as well as flow refugia (Sedell et al. 1990; Lancaster and Hildrew 1993b; Robertson et al. 1995; Winterbottom et al. 1997). Many organisms have morphological traits that reduce the probability of being eroded from the channel bed by hydraulic forces such as anal claws, hooks, suckers, and stream-lined body shapes. Both observational and

experimental studies indicate that morphological traits are a fundamental mechanism by which benthic organisms persist in flowing water (Statzner and Holm 1989; Horne et al. 1992; Hart et al. 1996). Some organisms also show behavioural avoidance of hydraulic forces with feeding or microhabitat preferences that restrict their distribution to unexposed habitats, often beneath the substrate surface. Physiological traits may include life cycle synchrony with the timing of disturbance to escape the harsh conditions accompanying flood events (Hayden and Clifford 1974; Gibbs and Mingo 1986). In conjunction with the inherent spatial heterogeneity of lotic systems, morphological, behavioural, and physiological traits likely enhance an organism's ability to persist in flowing water and resist erosion from the substrate during flooding.

Flow refugia are a second class of mechanism by which populations are able to persist in hydrologically-disturbed environments. Flow refugia are defined as habitats that maintain substrate stability and low hydraulic stress at varying levels of discharge, and where density-independent losses of benthic animals are likely to be small (sensu Lancaster and Hildrew 1993a). The availability of refugia depends on spatial heterogeneity within the river channel, such that channel habitats are differentially influenced by the physical impacts of flooding. Refugia can be manifested at many spatial scales such as fine-scale patches of in-stream flow refugia (Lancaster and Hildrew 1993b; Robertson et al. 1995; Winterbottom et al. 1997), larger-scale woody debris dams (Palmer et al. 1996), and reach-scale floodplains and lateral river margins (Hayden and Clifford 1974; Gibbs and Mingo 1986; Thorp 1992; Smock 1994). At each spatial scale, flow refugia have been shown to accumulate organisms during flooding which are subsequently available to recruit or recolonize areas that have been subjected to more severe physical disturbance and in which the loss of individuals has occurred.

Empirical evidence strongly supports the role of refugia in the persistence of benthic populations through physical disturbance (Palmer et al. 1992, 1996; Lancaster and Hildrew

1993b; Robertson et al. 1995; Winterbottom et al. 1997). The majority of these studies have examined flow refugia occurring at a relatively fine spatial scale such as in-stream microhabitats, and have found significant shifts in the distribution of organisms to patches of reduced hydraulic stress during flood events. The importance of various types and spatial scales of flow refugia, however, are likely to differ among organisms as well as among disturbance regimes. For instance, highly mobile species may readily undergo shifts in microdistribution into fine-scale patches of flow refugia (Lancaster and Hildrew 1993b; Hart et al. 1996) while more sedentary species may passively redistribute to areas of reduced hydraulic stress such as lateral channel margins during flooding (Ciborowski 1987).

The disturbance regime may also limit the types of refugia available since smaller refugia become less resistant as disturbance intensity increases (Sedell et al. 1990; Townsend and Hildrew 1994). Where the substrate is relatively mobile or flood intensity is sufficiently high to induce substrate instability, fine-scale refugia such as in-stream patches may destabilize and thereby limit the availability of refugia to larger-scale channel features such as channel margins and floodplain habitats (Sedell et al. 1990). Thus, while fine-scale patches have been shown to be critical to the survival of lotic organisms in many streams, particularly those with stable substrate, these patches may be unavailable in more intensely or frequently disturbed systems. On this premise, the current study was conducted in a large, gravel-bed river subject to substrate instability during flooding where the lateral shore zone maintains relatively stable substrate conditions and may represent an important flow refuge to benthic invertebrates.

The purpose of this study is to investigate the response of a macroinvertebrate community to flooding of a large, gravel-bed river, and to determine the ecological importance of the lateral shore zone as a flow refuge. Extensive lateral margins are geomorphic features of many large rivers in northern latitudes where physiographic confinement or engineering modifications have limited floodplain development. It was predicted that elevated hydraulic stress during flooding and the physical instability of the active channel would result in a shift in distribution of organisms from the active channel to the shore zone during flooding. Within the active channel, increasing water depth and flow velocity result in high shear stress which can erode macroinvertebrates from the substrate, particularly where the sediment is mobilized (Lancaster and Hildrew 1993a; Cobb et al. 1992; Dole-Olivier et al. 1997). In contrast, the lateral shore zone is temporarily inundated during flood events and maintains low velocity and stable substrate conditions. According to Lancaster and Hildrew (1993a), habitats providing these conditions constitute refugia and knowledge of such habitats is of obvious importance to understanding ecological processes that maintain diversity or influence the productivity of lotic communities (Power et al. 1988). Determining the ecological importance of lateral margins is particularly important given that engineering modifications and anthropogenic impacts to large river systems often directly alter these habitats (Sparks 1995).

The study was carried out in the Fraser River, British Columbia, which is characterized by a seasonal flood cycle that is highly regular in its timing, magnitude, and duration. The spatial scale of the study was a 10 km reach of river with a coarse gravel-bed that is prone to channel instability and bedload transport during flooding (Mannerstrom and McLean 1985; McLean 1990). Sampling occurred at low flow conditions before and after flooding in April and September, as well as three times during the flood cycle. Samples were collected at fixed depths of 0.2, 0.5, 1.5, and 3.0 m which meant that sample locations shifted laterally from the active channel in months of low flow into the shore zone during months of flooding. Samples extended into the active channel even during months of high flow because water level in the Fraser River increased < 1.5 m during flooding while samples were collected over 3.0 m water depth. This sampling design was appropriate to contrast the distribution of invertebrates between the active channel and shore zone, and enabled a shift in the distribution of organisms between low and high flow conditions to be detected.

# **Study Area and Methods**

The study area and methods for data collection of hydraulic and sedimentary variables have been described in Chapter 2, and macroinvertebrate sampling techniques have been outlined in Chapter 3. Only those methods not described above are provided here.

#### Organic Matter

Organic matter samples were collected with each invertebrate sample, detailed in Chapter 3, as well as from the dry sediment of the shore zone before the onset of flooding in April, 1995. In conjunction with the April samples collected in the active channel at water depths of 0.2, 0.5, 1.5, and 3.0 m, it was possible to reconstruct a lateral gradient of organic matter from within the active channel to the outer limit of the shore zone. Each channel habitat was evaluated with respect to food resources to determine if flow refugia within the shore zone represented a trade-off of reduced foraging opportunities for benthic organisms. The shore zone boundary was set at the lower limit of terrestrial vegetation, based on aerial photographs from previous years which indicated the Fraser River generally expanded to the lower limit of vegetation in years of average flood discharge. The distance from the river margin in April to the vegetation boundary was measured at each of the 3 study sites along the designated transects. A sample was collected at the mid-point of this distance and directly adjacent to the vegetation boundary along the 3 transects at each site. Samples were analyzed for the density, by weight (g m<sup>-2</sup>), of CPOM and FPOM following methods described in Chapter 3.

# Data Analysis

All statistical analyses were carried out on  $\log_{10}(x+1)$  transformed data which met assumptions of normality and homogeneous variances in the data. The response of the macroinvertebrate community to seasonal flooding in the Fraser River was assessed by threeway analysis of variance (ANOVA) to compare differences in total density, taxonomic richness, and specific taxon densities between sampling dates, water depths, and study sites. The General Linear Models procedure of SAS (SAS Institute 1990) was used and least-squares estimates of means were compared using Tukey's Studentized Range Test which controls for the type I experimentwise error rate with a critical value of  $\infty = 0.05$ . For analyses of total density and taxonomic richness, the Bonferroni correction was applied to  $\infty$  to adjust for the number of taxa incorporated in the measures (i.e.,  $0.05 / 34 \tan = 0.001$ ). The effect of study site was excluded from interaction terms of the ANOVA and only the interaction of sampling date x water depth was evaluated. The reasons for this were two-fold. First, hydraulic conditions and substrate mobility were hypothesized to influence the distribution of organisms during flooding and each factor was shown to have similar patterns which were statistically similar between study sites (Chapter 2). Second, the statistical test was suited to evaluate the importance of the lateral shore margin to invertebrates during flooding by the date x depth interaction which, if significant, would indicate a depth-wise shift in distribution among dates. Such a distributional shift would result from either an individual changing position from deep to shallow water between sampling dates, or from its position remaining unchanged while the location of sample sites shifted laterally within the channel during flooding. Each possible outcome is differentiated by a distribution shift to shallower depths in the former case, or a shift to deeper depths in the latter case between low and high flow conditions. Alternatively, a non-significant date x depth

interaction would indicate a coincident shift in distribution to the shore zone with the lateral shift in sample locations during flooding.

#### Results

#### Community-Level Data

Total invertebrate density in the gravel reach of the lower Fraser River was negatively related to the physical habitat measures of shear velocity and substrate mobility (Fig. 4-1). A similar negative relation of invertebrate density was found with other measures of velocity (i.e., Re., U, Re, Fr), although shear velocity likely provides the most direct characterization of the near-bed hydraulic environment. The maximum sample density of 1 289 invertebrates m<sup>-2</sup> was collected from near-bed velocity conditions of 2.71 cm s<sup>-1</sup> and stable substrate ( $\tau_* = 0.001$ ). Total density sharply declined above a velocity of 20 cm s<sup>-1</sup> and  $\tau_* > 0.075$ , which designates the probable substrate conditions in a natural, gravel-bed river as unstable.

Taxonomic richness (Fig. 4-2) did not decline as sharply with U<sub>\*</sub> and  $\tau_*$  as did invertebrate density. The average value of richness (4.2 ± 3.2 taxa) was found at near-bed velocities ranging from 0 to > 50 cm s<sup>-1</sup> and in relatively mobile substrate conditions. The maximum richness of 17 taxa was found at a velocity of 1.97 cm s<sup>-1</sup> and in highly stable sediment ( $\tau_* = 0.0008$ ). Relative to smaller tributary streams, species richness in the Fraser River was low (P. F. Dymond, pers. comm.).

On the rising limb of the discharge hydrograph between April and June, 1995, total invertebrate density remained relatively unchanged (Fig. 4-3a). A significant decline was observed in August and was followed by a sharp increase in density in September when



Figure 4-1. Total invertebrate density in relation to (A) shear velocity and (B) Shields Entrainment Function in the gravel reach of the lower Fraser River. Shields Entrainment Function, τ<sub>\*</sub>, is a measure of substrate mobility and gravel substrate is likely to become mobilized at τ<sub>\*</sub> > 0.06.



**Figure 4-2.** Invertebrate taxonomic richness in relation to (A) shear velocity and (B) Shields Entrainment Function in the gravel reach of the lower Fraser River. Shields Entrainment Function,  $\tau_*$ , is a measure of substrate mobility and gravel substrate is likely to become mobilized at  $\tau_* > 0.06$ .



**Figure 4-3**. Total invertebrate density (mean  $\pm$  standard error) at (**A**) 4 water depths and (**B**) 3 study sites through the flood cycle in the Fraser River. Line graph (A) indicates the sum of densities from all depths in a given month. Total density in August and September was significantly different from other months (p < 0.0001).

discharge had returned to low flow conditions. Total density in the months of August and September was significantly different from other sampling dates of the study (p < 0.0001). In all months but April, lowest density was at 3.0 m water depth while highest total density changed from 1.5 m in April to shallow depths of 0.5 and 0.2 m in other months. Measures of shear velocity and Shields entrainment function significantly were previously found to increase between May and June at depths of 1.5 and 3.0 m while shallow depths showed little variation in near-bed hydraulic conditions and substrate mobility through freshet (Chapter 2).

Total invertebrate density differed between study sites (p < 0.01), with Deer and Hope being higher than Agassiz overall. Changes in density among dates were site-specific and while Agassiz was lowest of the 3 sites in April and June, it had a slightly higher total density than *Hope* and *Deer* in the months of August and September (Fig. 4-3b). Of the 3 study sites, total density was most stable at *Agassiz* between April and August, 1995. In contrast, a sharp reduction in total density was recorded at *Deer* between June and August.

Average species richness between April and June, and in the month of September was similar. Richness in August, however, was less than in other months (p < 0.01). Depths of 3.0 m had lowest species richness in all months except April when both 1.5 and 3.0 m samples had higher richness than at shallow depths (Fig. 4-4a). In the remaining months of the study, water depths of 0.2, 0.5, and 1.5 m did not significantly differ in species richness. Site-specific variation in richness was observed among sampling dates, with *Deer* showing the greatest variability through the study (Fig. 4-4b). At *Deer*, richness declined between April and May, and also between June and August while values at *Hope* and *Agassiz* were generally stable through time. Overall, *Deer* had significantly lower species richness than *Hope* and *Agassiz* (p < 0.0005).



Figure 4-4. Taxonomic richness (mean ± standard error) at (A) 4 water depths and (B) 3 study sites through the flood cycle in the Fraser River, 1995.

Collector-gatherers were the predominant functional feeding group in the Fraser River (91.4% of total fauna) and were most abundant at shallow depths of 0.2 and 0.5 m in all months except April (Fig. 4-5a). The density of gatherers in April was highest at 1.5 m depth, averaging 200 individuals m-2, and the equivalent number of animals was found at 0.5 m in May and June. The shift in abundance from 1.5 m in April to shallow depths through the flood cycle is reflected in the significant date x depth interaction (p < 0.0001; Table 4-1). Overall, the density of gatherers was significantly higher at Agassiz and Hope than at Deer. In previous studies, differences in the distribution of taxa between habitats have been attributed to contrasting modes of foraging behaviour, mobility, and morphology (see review by Mackay 1992). Gatherer taxa were therefore sub-classified into clingers/swimmers and burrowers, after Merritt and Cummins (1996), and an analysis of variance was used to determine if site differences were related to behaviour. Differences in gatherer density between study sites were not statistically accounted for in the analysis, although densities of burrowers were slightly higher at Deer and Agassiz in most months of the study. Burrowers made up a greater proportion of the total gatherers (60.0%).

The remaining functional feeding groups were relatively uncommon in this study. Predators, collector-filterers, grazers, and shredders each represented 3.4, 3.1, 1.4, and 0.7% of the total fauna, respectively. Predators were significantly higher at 1.5 m depth in April but were most common at shallow depths in other months (Fig. 4-5b). Highest densities of filterers were recorded in August and September, on the declining limb of the discharge hydrograph, and filterers were generally most abundant at water depths of 1.5 m (Fig. 4-5b). Densities were significantly higher at *Agassiz* than at *Hope* and *Deer*. Grazers were generally limited to depths not exceeding 1.5 m (Fig. 4-5d), and densities remained low from August to September while most other groups increased in abundance between the sampling dates. Shredders were significantly less abundant during the months of flooding in the Fraser River than in April and

Effect	df	MS	F	р
<b>Collector Gatherers</b>				
Date	4	5.97	19.09	< 0.0001
Depth	3	6.56	21.00	< 0.0001
Site	2	1.01	3.25	0.04
Date x Depth	12	1.34	4.28	< 0.0001
Error	158	0.31		
Collector Filterers				
Date	4	1.70	8.88	< 0.0001
Depth	3	2.33	12.15	< 0.0001
Site	2	1.36	7.08	0.001
Date x Depth	12	0.17	0.90	NS
Error	158	0.19		
Predators				
Date	4	0.94	3.52	0.009
Depth	3	1.13	4.23	0.007
Site	2	0.67	2.53	NS
Date x Depth	12	0.46	1.73	NS
Error	158	0.27		
Grazers				
Date	4	0.71	4.43	0.002
Depth	3	0.45	2.81	0.04
Site	2	0.01	0.09	NS
Date x Depth	12	0.24	1.51	NS
Error	158	0.16		
	-			
Shredders				
Date	4	0.45	4.45	0.002
Depth	3	0.13	1.34	NS
Site	2	0.20	2.03	NS
Date x Depth	12	0.10	1.03	NS
Error	158	0.10		

**Table 4-1.** Summary of ANOVA results for functional feeding groups  $[log_{10}(x + 1)]$ . The tests were for the effects of sampling date, water depth, and study site on measures of each variable. The analyses did not include interaction terms for the effect of site, see text for details. NS: p > 0.05.



**Figure 4-5**. Distribution of functional feeding groups at 4 water depths through the flood cycle, 1995, in the Fraser River. Values are the mean density (± standard error) of samples collected from 3 sites. Note the scale of y-axes differ.

September, and no significant depth or site association was detected (Fig. 4-5e). A nonsignificant date x depth interaction for predators, filterers, grazers, and shredders (Table 4-1) indicated that the depth-wise distribution of taxa was stable as the location of sample sites shifted laterally between the shore zone and active channel through the study.

#### Species-Level Data

Five taxa were selected for detailed examination of the response to seasonal flooding in the Fraser River. Together, the taxa represented the range of distributional patterns observed among all taxa in this study, and selection of taxa was based on relatively high abundances through the study and the availability of ecological information on the taxa. *Rhithrogena* is a common mayfly gatherer in the Fraser River, and highest densities shifted from 1.5 and 3.0 m in April to shallow water depths during the months of peak flooding (Fig. 4-6a). The change in distribution was reflected in the significant date x depth interaction of an ANOVA (Table 4-2). Densities in September were similar to those in April before flooding, and the depth-wise distribution of *Rhithrogena* was also highly similar before and after flooding in the Fraser River. Both *Hope* and *Agassiz* had significantly higher densities of *Rhithrogena* than *Deer*.

Another mayfly gatherer in the Fraser River, *Baetis*, showed a similar distribution to *Rhithrogena* through the flood cycle (Fig. 4-6b). Significantly higher densities were found at 1.5 m in April while densities in June and August were highest at shallow depths of 0.2 and 0.5 m (date x depth interaction, p < 0.0001; Table 4-2). At the return of low flow conditions in September, *Baetis* was distributed relatively evenly across water depths of 0.2, 0.5, and 1.5 m. Interestingly, *Baetis* was nearly absent from benthic samples in May, and totally absent from 3.0 m samples in May through August.



**Figure 4-6**. Densities of collector-gatherer invertebrates at 4 water depths during the flood cycle in the Fraser River, 1995. Values represent the mean (± standard error) of samples collected from 3 study sites. See Table 4-2 for ANOVA results.

Effect	df	MS	F	р
<i>Rhithrogena</i> sp.				
Date	4	3.69	10.32	< 0.0001
Depth	3	3.56	9.95	< 0.0001
Site	2	1.89	5.28	0.006
Date x Depth	12	0.99	2.78	0.002
Error	158	0.36		
<i>Baetis</i> sp.				
Date	4	1.62	5.22	0.0006
Depth	3	1.84	5.91	0.0008
Site	2	0.29	0.93	NS
Date x Depth	12	1.13	3.62	0.0001
Error	158	0.31		
Chironomini sp.				
Date	4	0.19	0.80	NS
Depth	3	0.73	3.01	0.03
Site	2	0.22	0.90	NS
Date x Depth	12	0.20	0.81	NS
Error	158	0.24	0101	
Tanytarsini sp. B				
Date	4	2.75	8.56	< 0.0001
Depth	3	3.51	10.92	< 0.0001
Site	2	1.20	3.72	0.03
Date x Depth	12	0.30	0.95	NS
Error	158	0.32		
Hydropsyche sp.				
Date	4	2.22	12.81	< 0.0001
Depth	3	1.07	6.15	0.0006
Site	2	1.22	7.02	0.001
Date x Depth	12	0.16	0.90	NS
Error	158	0.17		

**Table 4-2.** Summary of ANOVA results for invertebrate taxa  $[log_{10}(x + 1)]$ . The tests were for<br/>the effects of sampling date, water depth, and study site on measures of each variable.<br/>The analyses did not include interaction terms for the effect of site, see text for details.<br/>NS: p > 0.05.

Chironomini is also an abundant gatherer in the Fraser River and was found at similar levels of abundance at all study sites (p = 0.41). Densities were relatively similar among sampling dates and the depth-wise distribution of Chironomini did not change significantly between dates (Fig. 4-6c; Table 4-2). Chironomini was nearly absent from 3.0 m samples in all months while densities at water depths of 0.2, 0.5, and 1.5 m did not statistically differ. The taxon appeared to be most common, however, at shallow depths of 0.2 and 0.5 m in all months of the study.

Tanytarsini sp. B is a gatherer whose distribution in the gravel reach of the lower Fraser River sharply contrasted with that of most other gatherer taxa. Highest densities of Tanytarsini sp. B were at 1.5 and 3.0 m in all months of the study (Fig. 4-7a). In the months before and after flooding, Tanytarsini sp. B was nearly absent from shallow water samples. Highest densities were collected in June, at peak flooding, while densities in all other months were similar. Both *Deer* and *Hope* had higher densities of Tanytarsini sp. B than *Agassiz*. The filter-feeding caddisfly, *Hydropsyche*, was most abundant at 1.5 m water depth, and in the months of August and September (Fig. 4-7b). Densities in other months of the study were extremely low and restricted to depths of 1.5 and 3.0 m. The depth-wise distribution did not change significantly between sampling dates, as reflected in the non-significant date x depth interaction (Table 4-2), and significantly greater densities of *Hydropsyche* were collected at *Agassiz* and *Hope* than at *Deer* through the study (p < 0.001).

#### Organic Matter

Samples of organic matter collected before the onset of flooding in April, 1995, revealed a lateral gradient of increasing FPOM from the active channel to the shore zone (Fig. 4-8a). densities at the mid-point and outer boundary of the shore zone were on average 10 times higher



**Figure 4-7**. Densities of (**A**) a collector-gatherer and (**B**) a collector-filterer at 4 water depths during the flood cycle in the Fraser River. Values represent the mean (± standard error) of samples collected from 3 study sites. See Table 4-2 for ANOVA results.





Figure 4-8. Density of (A) FPOM and (B) CPOM at 3 sites along a lateral gradient from the lower limit of terrestrial vegetation into the active river channel for April, 1995. Values refer to the water depth (m) of samples in the active channel, and "Mid-Shore" and "Vegetation" samples are taken from the shore zone which is the area between the river margin and vegetation at low flow. Note the scale of y-axes differ and the x-axes are not representative of the relative position of each sample location.

by weight than in the active channel. The lateral distance over which these samples was collected, however, differed between study sites (Table 4-3). The width of the shore zone, representing the distance over which the river laterally expanded during flooding, was more than 3 times greater at Hope than the average width of roughly 30 m at Deer and Agassiz.

**Table 4-3.** Distance (m) from the lower limit of terrestrial vegetation to the river margin at lowflow conditions in April, 1995, prior to flooding. The river margin extended over thisdistance to the vegetation boundary at peak discharge in June. Measurements were madealong 3 transects that subdivided each study site.

Study Site	Transect 1	Transect 2	Transect 3	Average	
Agassiz	48.5	26.5	22.5	32.5	
Deer	43	37	10	30	
Hope	101.5	100	112	104.5	

FPOM was also more abundant than CPOM in samples of organic matter collected between April and September, 1995, which averaged 6 times more FPOM by weight. Densities of FPOM were significantly higher in May and June at all sites (Fig.4-9a) when the Fraser River had expanded into the shore zone due to flooding. Of the 3 sites, *Agassiz* had the lowest densities of FPOM, and shallow depths had higher densities than deep depths (Fig. 4-9b). Densities at *Deer* were highest in all months and at most water depths, while densities of FPOM at *Hope* were similar at all water depths. When mean substrate grain size was included as a covariate, differences in FPOM between depths were non-significant ( $F_{3,139} = 0.72$ , p = 0.54, ANCOVA) which indicates that FPOM density is negatively related to substrate grain size. While FPOM has been shown to vary with hydraulic conditions (Grubaugh and Anderson 1989), an ANCOVA using different hydraulic measures as covariates did not statistically add to the explained variation in FPOM between depths or sampling dates in this study. In contrast to FPOM, the distribution of CPOM was relatively similar between the shore zone and active channel of the Fraser River (Fig. 4-8b). Highest densities were in samples from the mid-point of the shore zone (p < 0.01) and lowest densities were at 0.5 m water depth within the active channel. Variation in CPOM between sample locations was site-specific, with *Hope* showing greatest variability among sample locations. Samples from the shore zone and deep water depths at *Agassiz* were relatively similar while the density of CPOM at 0.2 and 0.5 m was substantially lower. The fraction of CPOM at *Deer* was relatively similar between sample locations and was higher overall than at *Agassiz* and *Hope* (p < 0.03).

Densities of CPOM collected between April and September showed both seasonal trends and differences between water depths. Highest densities of CPOM were in May and June for most sites (Fig. 4-9c), although *Agassiz* did not change significantly through the duration of the study or between water depths (Fig. 4-9d). Values at *Hope* and *Deer* were significantly higher during freshet than in August and September, and at both sites, densities were highest at 1.5 m depth. Except at *Hope*, highest densities of CPOM were at deep depths of 1.5 and 3.0 m which contrasts with the distribution of FPOM. Adding k<sub>s</sub> as a covariate rendered differences in the distribution of CPOM between water depths as non-significant ( $F_{3,139} = 1.77$ , p = 0.14, ANCOVA).

# Discussion

Benthic community composition in the Agassiz gravel reach of the lower Fraser River was consistent with predictions made for lotic systems with pronounced disturbance regimes and those subject to substrate mobility during flooding (Poff and Ward 1989; Scarsbrook and Townsend 1993). Generalist gatherers made up a significant proportion of the community and



Figure 4-9. Dry weight of FPOM and CPOM at 3 study sites in the Fraser River. Data are presented as the mean (+/- standard error) of 4 water depths collected at 5 sampling dates through the flood cycle ( $\mathbf{A}$ ,  $\mathbf{C}$ ), and as the mean (+/- standard error) of 5 sampling dates collected at 4 water depths ( $\mathbf{B}$ ,  $\mathbf{D}$ ). Note the scale of y-axes differ.

specialist feeders such as shredders, grazers, filterers, and obligate predators were rare. The taxa were of notably small body size relative to tributaries of the Fraser River (P. F. Dymond, pers. comm.), and high mobility is a well-documented trait for many of the dominant taxa such as *Rhithrogena, Baetis*, and Orthocladiinae (Mackay 1992). Moreover, sedentary taxa and case-dwelling organisms such as some caddisflies were relatively uncommon, particularly at water depths of 1.5 and 3.0 m. These ecological traits have been suggested to facilitate the recolonization of aquatic habitats and allow the persistence of benthic populations through disturbances (Sagar 1986; Reice et al. 1990: Scarsbrook and Townsend 1993; Townsend and Hildrew 1994; Matthaei et al. 1996). In the Fraser River, these traits likely contributed to the persistence and stability of the benthic community during flooding, and may have enabled many species to shift laterally from the active channel to the hydraulically more benign shore zone at high discharge.

Total invertebrate density had a strong negative relation to near-bed shear velocity and substrate mobility which were previously shown to correspond to a well-defined lateral gradient of hydraulic stress from shallow to deep water depths. In contrast, species richness remained relatively high in habitats of elevated shear velocity and substrate mobility, and had similar values across water depths of 0.2, 0.5, and 1.5 m during the months of flooding. The discrepancy between patterns of density and richness suggests that factors other than species-specific traits may limit the distribution of the majority of individuals to hydraulically benign habitats. It is hypothesized that body size may have influenced the distribution of benthic organisms relative to hydraulic conditions since small individuals experience less hydraulic drag than larger ones of the same species (Vogel 1981; Statzner 1988). This would imply an ontogenetic shift in the distribution of benthic organisms in the Fraser River along the lateral hydraulic gradient,

although such a pattern is not well-documented in the literature. Body size measurements were not made in this study.

Several studies in which body size was examined provide support for an ontogenetic shift to habitats of reduced hydraulic stress. Different instars of caddisfly species have shown differential use of the benthic habitat based on hydraulic conditions (Fuller and Mackay 1980; Wetmore et al. 1990), and the distribution of final instar larvae of two simuliid species was found to shift to patches of slower near-bed velocity (Horne et al. 1992). The microdistribution of the stonefly *Leuctra nigra* also differed based on body size across patches of differing hydraulic stress, with smaller individuals being significantly more abundant in high velocity patches (Lancaster and Hildrew 1993b). Depending on the feeding behaviour and morphology of the species, an ontogenetic shift to habitats of reduced hydraulic stress may lead to more energy-efficient foraging and minimize the risk of accidental erosion from the substrate. While this study did not measure the body size of invertebrates, a pattern of smaller invertebrates at depths of 1.5 and 3.0 m was observed during the identification of organisms. Including body size measurements in future research of this nature would clarify the role of ontogeny in determining distribution patterns of benthic invertebrates.

While a majority of studies have documented immediate reductions in the densities of organisms as a consequence of flooding (e.g., Sagar 1986; Boulton et al. 1992, Flecker and Feifarek 1994), total density in the Fraser River remained stable on the rising limb of the flood hydrograph. This stability was observed at the 3 study sites within the 10 km reach of river which varied in both substrate conditions and densities of organic matter. Densities were also stable while the total wetted area of the channel markedly increased which could potentially result in an apparent decrease in density even without mortality. Average species richness was low overall, but also showed relative consistency through the flood cycle in comparison to other

studies (Sagar 1986; Scrimgeour and Winterbourn 1989; Scarsbrook and Townsend 1993). This contradicts predictions by Resh et al. (1988) and Townsend and Hildrew (1994), that flooding in gravel-bed rivers causes major reductions in richness and species densities. While the channel bed became mobilized during flooding which is typical of gravel-bed rivers, the lateral shore zone maintained substrate stability and low hydraulic stress during flooding and thereby satisfied the physical criteria of flow refugia (Lancaster and Hildrew 1993a). Shallow depths within the shore zone showed a significant increase in densities of organisms at the onset of flooding despite an overall increase in wetted channel area of the Fraser River, and likely contributed to the persistence of organisms through the flood cycle.

Stable total density during flooding was followed by a reduction in August, on the declining limb of the discharge hydrograph. Density reductions were primarily at shallow depths of 0.2 and 0.5 m and there are several hypotheses for this which this study is unable to refute or confirm. First, August sampling coincided with a small increase in discharge in the Fraser River due to unseasonal, heavy rainfall (Fig. 2-3). Measures of shear velocity increased from June to August, particularly at shallow depths, and may have resulted in the erosion of invertebrates from the shore zone. The sharpest reduction in density was seen at *Deer* which also had highest measures of substrate mobility in August. The smaller mean grain size of *Deer* is more readily mobilized at elevated levels of hydraulic stress which may have made *Deer* vulnerable to the loss of organisms in August. Species richness also declined between June and August at *Deer*. The site-specific patterns support the possibility that reductions in both density and richness were related to substrate instability due to an unexpected rise in discharge. This is also consistent with the hypothesis that substrate instability is a major factor limiting the persistence of organisms in gravel-bed rivers (Resh et al. 1988; Townsend and Hildrew 1994).

A second alternative for the reduction in density in August is that organisms which laterally shifted to the shore zone during flooding became stranded as water levels receded. Individuals with relatively poor locomotory abilities likely traveled to the shore zone by drift and Ciborowski (1987) determined that while drifting organisms, whether passive or active, would ultimately concentrate along the channel margin due to the spatial patterns of flow, animals required a complementary ability to actively travel back into the mid-channel. The significant horizontal distance over which the river margin shifted between low and high flow may have placed species with poor mobility at particularly high risk of becoming stranded between June and August. The risk of being lost from the channel may also serve to explain why densities at 0.5 m were higher than at 0.2 m during the months of flooding as 0.5 m water depth would provide relatively more stable and long-lasting aquatic habitat. Depths  $\geq$  0.5 m would therefore represent a favorable trade-off between the risk of being stranded by declining water levels and the risk of being dislodged or crushed due to hydraulic stress which increases with water depth.

A last hypothesis for the reduction in August densities is that a significant number of aquatic larvae emerged as terrestrial adults between June and August. While this hypothesis does not explain the site-specific reduction in densities, it accounts for the sharp increase in densities in September which would consist of new recruits to the system. The significant increase in abundance between August and September mainly occurred in 5 taxa, namely *Heptagenia*, *Ephemerella*, *Hydropsyche*, Orthocladiinae, and Naididae. No *Heptagenia* were collected in the month of June and a significant proportion collected in August were of small body size and had disproportionately small gills, indicating that they were in early instars. Orthocladiinae were the numerically dominant taxon collected in the Fraser River (43% of total invertebrates collected), and densities in September were more than 6 times those recorded in August. Notably, benthic

The relative abundances of these species in the Fraser River due to life cycle patterns may have confounded the seasonal pattern of total invertebrate density, thus accounting for the reduction in total density in August. Deciphering the life cycle patterns of aquatic organisms is extremely difficult due to the diversity in life history patterns both within and among invertebrate species which show remarkable plasticity with environmental factors such as temperature, latitude, and photoperiod (see review by Sweeney 1984). More information on the life cycles of Fraser River species, particularly whether recruitment is continuous or punctuated, and whether a species is univoltine or multivoltine would assist in clarifying temporal variations in species abundances.

On the rising limb of the discharge hydrograph, the distribution of a major proportion of invertebrates appeared to shift from the active channel to the shore zone. Collector-gatherers were the predominant functional feeding group in the Fraser River and highest densities showed a major shift from 1.5 m in April to shallow depths for the remaining months of the study. Gatherers feed on FPOM which was most abundant, by weight, at depths of 0.2 - 1.5 m in the shore zone. A lateral shift in distribution to the shore zone during flooding therefore provided gatherers a flow refuge as well as the opportunity to exploit an abundance of FPOM. The methods of this study were unable to decouple the interactive effects of organic matter and flow conditions on invertebrate distributions since some organisms may respond indirectly to hydraulic conditions through their direct response to the availability of food. In previous studies, food value was found to be of greater importance than substrate conditions to the distribution of invertebrates (Culp et al. 1983), and the food value of leaf packs was shown to be of greater importance than the provision of microhabitat to benthic organisms (Richardson 1992). However, given the relatively low mean density of organisms collected in the Fraser River (168  $m^{-2}$ ) and that FPOM was abundant to depths of 1.5 m, it is not believed that a limited food supply adequately accounts for the major distributional shift demonstrated by gatherers during flooding.

Rather, the strong lateral gradient in hydraulic conditions between the shore and active channel zone was likely most responsible for the shift.

The distribution of filter-feeders sharply contrasted that of gatherers in the Fraser River. Densities were highest at 1.5 m water depth in all months of the study, and did not show a shift in depth-wise distribution between months. This supports a synchronous shift in the distribution of filterers towards the shore zone with the lateral shift in sample locations during flooding. Given the nature of the feeding behaviour of filterers which relies on current velocity for the delivery of food, it is not unexpected that organisms appeared to track habitat conditions where current velocity was relatively high in all months of the study.

The lateral shore zone of the Fraser River appeared to be particularly important to the gatherer mayflies *Baetis* and *Rhithrogena*. Both these taxa showed marked shifts in distribution from 1.5 m at low flow in April to shallow depths within the shore zone during peak flooding. A similar, strong depth-wise distributional shift to the shore zone was also seen for *Ephemerella*, Orthocladiinae, Tanytarsini sp. A, Tubificidae, and Naididae (Appendix 1). The distribution of these taxa is consistent with the prediction that elevated hydraulic stress and the physical instability of the active channel resulted in a shift in the distribution of organisms to the shore zone during flooding. While some taxa are believed to migrate to shallow habitats for the mayfly taxa, most of which are known to swim directly to the water surface for emergence (J. Richardson, Univ. of British Columbia, pers. comm.).

The abundance of *Rhithrogena* and *Baetis* at shallow depths in the shore zone is consistent with suggestions that these taxa are rapid colonizers and early arrivals to new aquatic habitats (Mackay 1992; Matthaei et al. 1996). It is also consistent with previous observations of

*Baetis tricaudatus* that were found in high concentrations near-shore after flood episodes in the Pembina River, Alberta (Ciborowski and Clifford 1983). Both *Rhithrogena* and *Baetis* primarily forage on the upper surface of stones (Glozier and Culp 1989), and increased current velocity associated with flooding is known to inhibit the movement of many benthic invertebrates (Ciborowski 1987). Being directly exposed to elevated hydraulic stress related to flooding was therefore a probable stimulus to prompt a distributional shift of *Rhithrogena* and *Baetis* to more benign habitat within the shore zone.

The methods of this study were unable to determine the mode of travel used by these taxa to access the shore zone. Both *Rhithrogena* and *Baetis* are vigorous swimmers and crawlers (Mackay 1992) and *Rhithrogena* is not commonly found in stream drift (Mackay 1992; Matthaei et al. 1996). Whether the locomotory abilities of these taxa were adequate for travel over distances exceeding 30 m to the shore zone of the Fraser River is unknown, however, the upstream rate of active travel for the mayfly Leptophlebia cupida was averaged at 10 m hr<sup>-1</sup> (Hayden and Clifford 1974). The gradual rise in water level during flooding may have assisted an active distributional shift of *Rhithrogena* and *Baetis*. Secondary support for the active migration of *Rhithrogena* to the shore zone as a result of hydraulic conditions was the redistribution of many individuals to depths of 1.5 and 3.0 m in September. Rhithrogena does not likely recolonize areas by eggs (Matthaei et al. 1996) which suggests that it possessed a complementary ability to actively return to the active channel once hydraulic stress had receded. *Rhithrogena* is equipped with ventral gills that form a suction plate and is known to prefer large, rough substrate similar to Hope and Agassiz which provides stability for foraging. These traits may have enabled it to make an earlier shift back into the active channel than other taxa (Glozier and Culp 1989).

The lateral margin of the Fraser River was also an important habitat for Chironomini as highest densities were at 0.2 and 0.5 m depth in all months of the study. A similar pattern of distribution was also observed for Tanytarsini sp. A which were generally highest at shallow depths through the study and showed no marked difference in mean density between months. Relatively little is known about how Chironomini travel, how they orient themselves, and what stimulates them to move, but they are often recognized as a common component of stream drift (Oliver 1971). Unless the substrate becomes mobilized, however, it is unlikely that Chironomini will be accidentally eroded since they are known to penetrate a few centimeters into the substrate (Oliver 1971). Because dipterans such as Chironomini are thought to have relatively poor mobility (Mackay 1992), it is proposed that active drifting was the means by which individuals tracked the hydraulically benign shore zone through the flood cycle. The mode of return travel to the active channel, however, remains uncertain although the poor mobility of Chironomini suggests a more passive mode of recolonization.

The depth-wise distributions of Tanytarsini sp. B and *Hydropsyche* did not appear to change significantly through the flood cycle. Individuals were present in relatively high numbers at 1.5 m depth in all months of the study while the location of 1.5 m samples shifted laterally between the shore and active channel. The distribution of Tanytarsini sp. B and *Hydropsyche* therefore appeared to shift towards the shore zone coincident with the rise in water level. This maintains support for the prediction that elevated hydraulic stress would result in a lateral shift in distribution towards the shore zone. The restricted lateral shift of *Hydropsyche*, however, may relate to its foraging behaviour which requires current for filter-feeding. The hydraulically benign conditions at shallow depths may have represented a trade-off in foraging efficiency that would be unnecessary since *Hydropsyche* also demonstrate tremendous plasticity in net-

building behaviour relative to hydraulic conditions that is independent of instar (Fuller and Mackay 1980). The mesh size of net is positively correlated with velocity such that larger mesh sizes are spun at high velocities and allow larger food particles to be ingested (Fuller and Mackay 1980). Larvae of *Hydropsyche* have also been shown to have a broad diet which enables individuals to persist in a variety habitats and under variable flow conditions (Fuller and Mackay 1980).

The restricted lateral shift of Tanytarsini sp. B may be partially related to its small size and elongated body with reduced posterior prolegs that is suited to burrowing into the substrate to escape the forces of hydraulic drag. Its feeding behaviour also reduces the risk of erosion since it forages within interstitial crevices and burrows into the substrate for organic material where hydraulic forces are much reduced. This may account for lowest densities of Tanytarsini sp. B at *Agassiz* which had a heavily armoured bed in contrast to the substrate at *Deer* and *Hope* which may have provided more suitable burrowing habitat.

These data support the role of the lateral shore zone as an important flow refugia to invertebrates during flooding in the Fraser River. However, comment must be made in regards to the possibility of invertebrates collected in the lateral shore zone having originated from the hyporheos. No previous work has been conducted to confirm the existence, or possible extent of a hyporheic zone in the Fraser River and therefore only speculation can be made as to its probable contribution to the distributional patterns observed in this study. Hyporheic organisms are typically < 0.5 mm and have tubular-shaped bodies which facilitate foraging and movement within restricted interstitial spaces (Williams 1984). Organisms in this study were > 0.5 mm and while chironomids and oligochaetes were found at relatively high densities in the shore zone, other taxa that were also abundant in the shore zone are highly unlikely to occupy the hyporheos such as *Rhithrogena* and *Baetis*. For these taxa, arrival to the shore zone was most likely through

relocation from the active channel. The possibility that organisms sought refuge within the hyporheic zone of the active channel is also unlikely due to substrate instability in the active channel which has been shown to produce a "wash-out" effect of taxa from the sediment in gravel-bed rivers during flooding (Dole-Olivier 1997). Evidence for the active migration of invertebrates into the hyporheic zone during flood events is also lacking (Giberson and Hall 1988; Palmer et al. 1992).

In conclusion, observed patterns of distribution and abundances of invertebrates in the gravel reach of the Fraser River during flooding contradicted predictions made for gravel-bed rivers. Invertebrate densities and species richness in the Fraser River remained relatively stable through the flood cycle at 3 study sites which differed in substrate conditions. Most variation in the relative abundances of taxa could be explained by life cycle events. The persistence of the invertebrate community through flooding appears to have been facilitated by a shift in a large proportion of the total organisms from the active channel to the lateral shore zone during the months of peak discharge. Shallow water depths of 0.2 and 0.5 m within the shore zone satisfied the physical criteria of flow refugia by maintaining substrate stability and low hydraulic stress during flooding. The ecological importance of this zone as a flow refuge was demonstrated by the broad diversity of species with varying feeding behaviours and morphologies which concentrated in the shore zone and the overall stability of densities and species richness through flooding. Further studies are required to elucidate the mechanisms of lateral flow refugia use, and the factors directly influencing the distribution of taxa through flooding. It is nevertheless apparent that the lateral margin was a seasonally important habitat for a broad diversity of benthic invertebrates in the Fraser River.
## Chapter 5 : Study Limitations and Recommendations for Future Research

Examining the hydraulic and sedimentary conditions of a natural river system at a spatial scale relevant to benthic invertebrates is extremely difficult, and therefore seldom attempted in ecological research (Davis and Barmuta 1989). Such studies are particularly rare in large rivers where specialized sampling methods are usually required (Hynes 1989). The methods used in this research are not without their limitations but, for the purpose of the study, were effective at providing the necessary sedimentary, hydraulic, and invertebrate data. Several potential limitations are described below.

Methods for sediment and invertebrate sampling, as well as for measurements of nearbed current velocity, differed between shallow and deep water depths. This was not ideal for comparative analyses between the habitats, however, the methods used for sediment and invertebrate collection were evaluated prior to the study and confirmed that the sampling behaviour at shallow and deep depths was similar. Methods used for velocity measurements also differed between water depths as data were collected from a boat at 1.5 and 3.0 m. Turbid water conditions made it impossible to visually monitor the submerged current meters and ensure they remained properly oriented to the flow. However, each of the current meters was insensitive to horizontal variation in flow within 30° (M. Church, pers. comm.), and velocity measurements were collected over 120 s to offset slight variations in the data due to sampling procedures. Also, the graduated rod to which the current meters were mounted was equipped with a metal plate at its base and could be placed directly on the channel bed to ensure that velocity measurements were collected at the designated height. While these techniques are not conventional in stream ecological research, they effectively enabled samples of sediment and invertebrates, as well as measurements of near-bed velocity, to be obtained from a highly understudied habitats of fluvial systems.

It may be argued that velocity measurements from 3 cm above the channel bed were not at an adequately fine scale to be relevant to macroinvertebrates. Previous studies have found that the flow forces directly influencing the microdistribution of invertebrates are within millimeters of the channel bed (Statzner and Holm 1989; Hart et al. 1996). However, these studies focused on the microdistribution of invertebrates at spatial scales of a single stone and laboratory flumes, and over time periods of seconds to days. While fine-scale measurements of velocity may be appropriate for such a spatial and temporal scale of examination, flow patterns within millimeters of the bed are decoupled from the vertical flow profile of a natural river and are therefore not subject to seasonal variation. The purpose of this study was to examine the influence of seasonal flooding on the distribution of invertebrates and therefore measurements of velocity made within several centimeters of the channel bed that are more tightly coupled with the flow profile were appropriately scaled for this purpose.

Finally, a limitation of the study was the time period over which it was conducted. This study would have benefited from a second season of sampling, although previous studies that had extended data collection over several years have noted relatively slight variations in macroinvertebrate community patterns (e.g., Boulton et al. 1992). Because the intensity of flooding in the Fraser River in 1995 was below average, a second sampling period would determine the range of natural variability in community structure to the benefit of future benthic monitoring programs attempting to distinguish effects of perturbation. In years of higher peak flood discharge, the lateral gradient of hydraulic conditions between the shore zone and active channel would be even stronger and it is hypothesized that the distributional shift of benthic organisms from the active channel to flow refugia in the lateral shore zone would be increasingly

pronounced. The amount of variation in community structure that would result for higher flood discharge, however, is unknown.

## **Recommendations for Future Research**

Large, gravel-bed rivers have been relatively neglected in previous ecological research for reasons outlined in earlier chapters. The present study of the benthic ecology of the Agassiz gravel reach of the lower Fraser River therefore provides an important and necessary foundation on which future studies can be based. Suggested topics for future research in the Fraser River are described below, and most are also applicable to other fluvial systems where spatial and temporal flow patterns are significant factors influencing the benthic environment.

Future research is recommended to clarify the influence of life history events on distributional patterns and abundances of invertebrate populations. Total invertebrate density in the Fraser River remained stable between low flow conditions in April and peak flood discharge in June, but showed significant variation on the declining limb of the hydrograph. Several hypotheses were presented to explain the variation, the most probable of which was emergence of species between June and August, and hatching of new recruits between August and September. This hypothesis can be tested from body size measurements obtained by digitizing individuals to infer the timing of life history events of species. Measurements can be made in combination with taxonomic identification and therefore require minimal additional effort. Size measurements are a recommended component of future studies examining species distributions and abundances through time, and would clarify the influence of life cycle timing on variations in species densities during flooding of the Fraser River.

Size measurements of invertebrates distributed in a hydraulically heterogeneous environment would also serve to evaluate the influence of ontogeny on the distribution of organisms. It is hypothesized that populations should demonstrate differential habitat use based on hydraulic conditions since small individuals experience less hydraulic drag than larger ones of the same species (Vogel 1981; Statzner 1988). While such a pattern is poorly documented in the literature, body size is known to be an important factor determining habitat use for other organisms such as some fish species (Magnan and FitzGerald 1984; Osenberg et al. 1988). A system in which a hydraulic gradient is spatially well-defined such as the gravel reach of the lower Fraser River is best suited to future studies of this nature so that differential habitat use by organisms related to hydraulic conditions can be readily detected.

The extension of sampling beyond the main channel into other aquatic habitats such as side-channels is also recommended for future research. This study was restricted to the main channel of the Fraser River to contrast the ecological importance of the active channel and lateral shore zone during flooding. However, increasing discharge also tends to activate side-channels and back-eddy areas so that the low-flow conditions of the shore zone become spatially replicated and available for seasonal use by invertebrates. Side-channels may also present a qualitatively distinct habitat from that of the main channel since they often accumulate organic matter and exclude the coarser fraction of the sediment load traveling on or near the bed of the main channel (Church 1992). Side-channels therefore provide hydraulically benign conditions, in combination with reduced sediment transport and substrate instability, which may have a seasonal importance to the persistence of benthic populations in rivers such as the Fraser that experience regularly recurring floods. Wandering, braided, and anastomosed rivers are particularly suited to such research due to the heterogeneous geomorphology and diversity of habitat types within a typical reach of river that are available for sampling.

A further recommendation is made regarding the variables used to characterize the hydraulic habitat of streams and rivers. While measurements are commonly made at 0.6 water depth and averaged over some period of time, the hydraulic force likely to dislodge invertebrates from the substrate is a high velocity pulse that comes over the substrate only episodically (Power et al. 1988). Cyclic pulses in velocity were detected in the Fraser River when near-bed measurements were fortuitously collected continuously over several minutes. Plots of velocity measured at these locations show a pulse with a periodicity of  $\sim 60$  s (Fig. 5-1). Conceivably, velocity pulses have ecological implications for the ability of macroinvertebrates to persist in a habitat, but would go undetected if only average measures of velocity were made. Turbulence intensity, a measure of fine-scale temporal variation in velocity, captures the magnitude of change in velocity over time and characterizes the hydrodynamic environment immediately adjacent to benthic organisms (Hart et al. 1996). Turbulence was a significant correlate with the distribution of many invertebrate taxa in the Fraser River, and it is recommended that turbulence intensity be quantified in future research examining the ecology of benthic organisms in running water. Flow patterns in rivers are almost always turbulent and without such measures, the consequences of turbulence for benthic organisms will remain poorly understood.

A final recommendation for research concerns the use of flow refugia by invertebrates. While it appears the shore zone was a seasonally important habitat for a broad diversity of species in the Fraser River, many of the mechanisms of refugia use remain unclear. For instance, do animals within the shore zone actively relocated from the active channel during flooding, or do some inadvertently arrive by passive drift due to erosion? What is the active means by which animals return to the main channel on the declining limb of the flood hydrograph such as *Rhithrogena*? Are such lateral movements sufficient for population persistence, or do other flow refugia operating at different spatial and temporal scales that reduce population losses also exist?



**Figure 5-1**. Velocity collected at 1.5 m water depth over 4 min in May, 1995 at *Agassiz*. Measurements were made 3 cm from the channel bed.

For instance, side-channels or the hyporheos may have a seasonal importance to benthic invertebrates in the Fraser River. Refugia may also operate within populations on evolutionary and biogeographic scales and involve genotypic heterogeneity such as morphological traits and physiological synchronism of the timing of life history events with flooding. The mechanisms of the latter possible refugia are obviously more difficult to formalize, and an attempt has been recently made to define a hierarchical framework of classes of refugial mechanisms, operating at various spatial and temporal scales, by which populations may persist in environments subject to physical disturbance (Lancaster and Belyea 1997). This framework provides a base from which to formulate testable hypotheses of flow refugia use for future studies.

Results of this study support the importance of the lateral shore zone of the gravel reach of the lower Fraser River as a flow refugia to a broad diversity of macroinvertebrates during seasonal flooding. On the rising limb of the flood hydrograph, the distribution of a major proportion of organisms shifted from depths of 1.5 and 3.0 m to shallow depths within the shore zone where substrate stability and low hydraulic stress were maintained during flooding. The substrate within the shore zone was heterogeneous and generally finer in grain size than in the active channel, and also had greatest accumulations of FPOM. These habitat conditions were associated with highest densities of invertebrates that were numerically dominated by collector-gatherer taxa and whose distributions shifted from the active channel to the shore zone during flooding. In contrast, filter-feeders were most abundant at depths of 1.5 and 3.0 m in all months of the study and were associated with higher levels of hydraulic stress and relatively large, coarse substrate. Overall, the spatial distribution of taxa generally reflected an organism's morphology and feeding behaviour, and these traits appeared to influence the distributional shift of a major proportion of organisms from the active channel to the shore zone during flooding.

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**Appendix 1.** Macroinvertebrate taxa collected from 3 study sites in the gravel reach of the lower Fraser River. Abbreviations for functional feeding groups (FFG) are: CG - collector gatherer, CF - collector filterer, Gr - grazer, P - predator, Sh - shredder. Flow exposure group (FEG) abbreviations are: A - avoider, F - facultative, O - obligate. The depth-wise distribution of taxa among sampling dates in 1995 is indicated. "All" refers to the presence of the taxa at all sampling depths in a given month. Otherwise, numbers refer to the specific depths at which the taxa was collected (1 = 0.2 m, 2 = 0.5 m, 3 = 1.5 m, 4 = 3.0 m water depth).

	Functional	Flow Exposure	Average Density	April	May	June	August	Sept
	Feeding Group	Group	$(\# m^{-2})$					
Nematoda	CG	Α	0.06	3	-	-	-	4
Annelida								
Oligochaeta								
Naididae	CG	А	3.6	34	234	12	3	All
Tubificidae	CG	A	3.1	13	12	12	3	34
Hirudinea	Р	Α	0.09	-	-	3	-	2
Arthropoda								
Arachnida								
Hydracarina	Р	F	0.3	3	-	-	1	32
Insecta								
Ephemeroptera								
Baetidae								
Baetis sp.	CG	Α	8.7	All	13	123	123	All
Ephemerellidae							• •	
Caudatella sp.	CG	F	0.06	-	1	123	12	All
Ephemerella sp.	CG	F	18.4	All	123	123	1	All
Serratella tibialis	CG	F	1.6	-	2	-	-	124
Drunella doddsi	Gr	0	0.2	-	2	2	-	-
Heptageniidae								
Cinygmula sp.	Gr	F	0.8	All	-	-	13	-
Epeorus sp.	Gr	F	0.03	3	-	-	-	-
Heptagenia sp.	CG	F	5.5	All	23	-	All	All
Rhithrogena sp.	CG	0	16.6	All	123	All	123	All
Ameletidae								
Ameletus sp.	Gr	F	0.8	1	1 2	_	23	3

Appendix 1. Continued.											
	Functional Feeding Group	Flow Exposure Group	Average Density (# m <sup>-2</sup> )	April	May	June	Aug	Sept			
Insecta											
Plecoptera											
Perlodidae	Р	0	1.5	134	23	2	13	All			
Chloroperlidae	Р	F	0.2	14	3	-	-	-			
Nemouridae	Sh	F	0.1	14	-	-	-	-			
Capniidae	Sh	F	0.5	234	-	-	3	All			
Trichoptera											
Glossosomatidae											
Glossosoma sp.	Gr	0	0.4	3	-	1	-	-			
Hydropsychidae											
Hydropsyche sp.	CF	0	4.4	34	3	3	All	All			
Cheumatopsyche sp.	CF	0	0.6	34	3	-	3	3			
Lepidostomatidae											
Lepidostoma sp.	Sh	0	0.5	34	134	-	-	-			
Hydroptilidae											
Hydroptila sp.	Gr	0	0.2	3	-	-	-	134			
Diptera											
Tipulidae											
Hesperoconopa sp.	Sh	А	0.06	-	-	1	-	-			
Chironomidae											
Orthocladiinae	CG	А	70.8	All	All	All	All	All			
Tanypodinae	Р	Α	2.0	34	23	124	-	All			
Chironominae											
Chironomini	CG	А	6.3	123	All	All	123	123			
Tanytarsini sp. A	CG	А	8.3	All	All	123	All	All			
Tanytarsini sp. B	CG	А	9.8	34	All	All	234	34			
Ceratopogonidae	Р	А	0.09	3	2	-	-	-			
Simuliidae											
Prosimulium sp.	CF	0	0.06	-	-	3	-	-			
Empididae		-									
Hemerodromia sp	Р	0	0.6	3	123	23	23	23			
Dolichopodidae	P	F	0.8	2	_	23	3	-			