IMPORTANCE OF DETRITUS, SUBSTRATE AND FLOW TO MACROINVERTEBRATE DISTRIBUTION IN SECTIONS OF THE WEST RIVER

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ABSTRACT

The importance of near-bed flow and other types of environmental variables to macroinvertebrate distribution was examined within sections of a stream in Prince Edward Island. To carry out this part of the study, different methods of measuring near-bed flow were tested. The methods were tested at 5 sites on 3 streams, to choose the most practical and reliable methods for evaluating shear velocity and roughness to compare near-bed flow among patches where macroinvertebrates were later sampled. Therefore, results from the standard, but very time-consuming, method of measuring shear velocity using velocity profiles were compared to results obtained using alternative methods. The alternative methods tested included the use of FST hemispheres, and the prediction of shear velocity from more easily measured hydraulic variables (near-bed velocity, mean velocity, depth and roughness). The test results showed that mean velocity gave a good indication of shear velocity in most cases, but that the use of both mean velocity and velocity profiles was needed to cover the range of conditions at study sites on the West River. Determination of roughness based on substrate particle width was selected as a practical and reliable method of evaluating the roughness of near-bed flow. Values obtained with this method were correlated to those obtained with a more standard method of evaluating roughness based on streambed form.

Spatial variation in macroinvertebrate density was related to variation in flow conditions, streambed substrate and detritus within sections of the West River.

Macroinvertebrates were sampled in August and November of 2001 in patches set in a regular arrangement at two sites, a "run site" and a nearby small "riffle site". The densities of macroinvertebrate taxa at the run site were compared to patch substrate size composition, algal cover, different size fractions of detritus and various hydraulic variables (shear velocity, mean velocity, roughness, Froude number, depth and the vertical hydraulic gradient of subsurface flow). At this site, the densities of most dominant taxa were more closely related to detritus and substrate characteristics than to hydraulic variables. However, taxa densities were also related to variation that was shared between the substrate and detritus characteristics as well as the flow conditions. This observation is consistent with flow affecting macroinvertebrate distribution indirectly through movement of streambed material. The measured environmental variables explained 37 to 50% of the variation in macroinvertebrate densities within the run site, and the patterns were similar for samples taken in August and November. In contrast, the relationships from the run site did not necessarily apply to the smaller number of samples collected from the riffle site, possibly due to differences in environmental conditions and macroinvertebrate responses between sites.

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LIST OF COMMONLY USED ABBREVIATIONS

FST=Fliesswasserstammtisch (word derived from the German words for river, water and table)

POM=particulate organic matter

FPOM= fine particulate organic matter

CPOM= coarse particulate organic matter

FFG=functional feeding group

VHG=vertical hydraulic gradient

RDA= redundancy analysis

1. Introduction and Review of the Relevant Literature

INTRODUCTION

In streams, the abundance of benthic macroinvertebrates (those inhabiting the streambed) often varies considerably at an intermediate spatial scale (e.g. among locations a few metres apart; Merritt *et al.,* 1996). Relating macroinvertebrate distribution to spatial variation in benthic environments has long been a focus of research in stream ecology (Cummins, 1992). Many studies have found that the abundance of benthic macroinvertebrates is related to characteristics of the streambed material such as substrate (sediment) size and the amount of detritus (substrate/detritus; reviewed in Minshall, 1984). This study focusses on deposit-feeding detritivores (macroinvertebrates that feed on detritus deposited on the streambed), which often increase in density with the amount of detritus (Drake, 1984; Holomuzki and Messier, 1993; Graça, 2001). However, until the 1980s, very few studies examined whether or not stream macroinvertebrate distribution was related to spatial variation in near-bed flow (i.e. the movement of water close to the streambed) because of the lack of suitable methods for measuring near-bed flow (Davis and Barmuta, 1989). Therefore, relatively few studies have examined the relationship of macroinvertebrate distribution to both substrate/detritus and near-bed flow. Aspects of this relationship that are not yet well-understood include which methods of flow measurement are appropriate for such studies; how substrate/detritus and flow are inter-related; and how both these factors contribute to patterns of spatial variation in macroinvertebrate abundance. Furthermore, it is important to consider how the relationship of macroinvertebrates to their environment varies among different groups of macroinvertebrates and among different locations and seasons.

To describe near-bed flow, it is important to evaluate shear velocity (a measure of the force of flow acting parallel to the streamed) and roughness (the frictional resistance of the streambed to flow). However, there are no ideal methods for measuring these two variables at an intermediate spatial scale in streams (Davis and Barmuta, 1989; Nikora *et al.*, 1998). The standard method of evaluating shear velocity in streams is to use velocity profiles, which are determined from velocities measured at a range of heights above a point on the streambed (Gordon *et al.*, 1992). However, this method has practical limitations. For example, shear velocity at one point may not reflect shear velocity values at locations only centimetres away, particularly in areas of high roughness where flow is often highly variable (Frutiger and Schib, 1993). There are alternative methods for measuring shear velocity that offer certain advantages over the use of velocity profiles (see Statzner *et al.*, 1988; Statzner and Müller, 1989; Ackerman and Hoover, 2001 for examples). However, there is still considerable uncertainty about the appropriateness of these alternative methods. For example, certain methods of evaluating shear velocity may be appropriate for use in some rivers, but not others, since they do not perform consistently among rivers with different flow conditions (Lancaster and Hildrew, 1993, Quinn and Hickey, 1994; Dittrich and Schmedtje, 1995).

In streams, roughness is typically estimated from the unevenness of the height of the streambed (Gordon *et al.*, 1992). However, this method is not always suitable for studies of benthic macroinvertebrates because it is relatively time-consuming and usually involves contact with the streambed (Statzner *et al.*, 1988; Gibson *et al.*, 1998) which disturbs macroinvertebrates. A more practical alternative for measuring roughness involves using the width of substrate particles as an indicator of the unevenness of streambed height (Statzner *et al.*, 1988). The few studies that have tested such width-based methods (e.g. Statzner *et al.*, 1988; Quinn and Hickey, 1994) have found that these methods gave similar results to height-based methods. However, it is not yet known if width-based methods are widely applicable to different streams which may have different characteristics of streambed form.

Despite the difficulties with measuring near-bed flow, researchers have established that the distribution of some macroinvertebrates can be related to near-bed flow (Statzner *et al.*, 1988) as well as other characteristics of flow. For example, many taxa that feed by filtering particles from the water column (collector-filterers) prefer specific flow conditions such as high velocities (e.g. Wetmore *et al.*, 19990; Hart *et al.*, 1996). In contrast, the density of collector-gatherers (which feed on fine deposited detritus) is often negatively related to the velocity, force and turbulence of flow (Quinn and Hickey, 1994; Rempel *et al.*, 2000; Doisy and Rabeni, 2001). Macroinvertebrate densities can also be related to other characteristics of streamflow, including average properties of flow such as mean velocity (e.g. Doisy and Rabeni, 2001) and flow in the interstices of the streambed (subsurface flow; e.g. Pepin and Hauer, 2002).

Flow and substrate/detritus are known to have inter-related effects on macroinvertebrate distribution (Statzner *et al.*, 1988), but not all aspects of this relationship are well-understood. For one, the relative importance of flow *versus* substrate/detritus to macroinvertebrate distribution is still unclear. The distribution of macroinvertebrate communities in some studies was better predicted by flow variables (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001) than substrate/detritus, whereas the opposite trend was found in other studies (e.g. Drake, 1984; Miyake and Nakano, 2002). The inter-relationship of both these factors is of particular interest for deposit-feeding detritivore distribution, which can be affected directly or indirectly by flow.

Flow affects macroinvertebrates directly when individuals are influenced by the physical properties of flow. For example, strong forces of near-bed flow may limit an individual macroinvertebrate's ability to move and increase the energetic cost of feeding and other activities (Hart and Finelli, 1999). Flow can also affect macroinvertebrate distribution indirectly by influencing the accumulation of both detritus (Hildrew *et al.*, 1991) and substrate particles (Carling, 1992b). This indirect effect of flow may be especially important to the distribution of deposit-feeding detritivores. For example, the potential importance of indirect effects of flow is supported by the observation that collector-gatherers often increase in density with the amount of detritus, but decrease in density with increasing mean velocity or shear velocity (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001).

Flow, substrate/detritus and other factors can all contribute to commonly observed non-random, aggregated patterns of spatial variation in macroinvertebrate distribution (Ulfstrand, 1967; Cummins, 1992). Several researchers have stressed the importance of examining the spatial structure of macroinvertebrate and enviromental data (Borcard *et al.*, 1992; Downes *et al.*, 1993; Palmer *et al.*, 2000) to better understand the factors controlling macroinvertebrate distribution. For example, spatial variation in macroinvertebrate densities that is not related to spatial variation in abiotic factors such as flow may be related to biotic interactions affected by proximity such as predation or reproduction (Ulfstrand, 1967; Borcard *et al.*, 1992).

Finally, the relationship of macroinvertebrates to substrate/detritus and flow can vary among different categories of macroinvertebrates and with the season or location of sampling. Associations of macroinvertebrates with certain environmental characteristics (habitat associations) can vary among different functional feeding groups (modes of feeding such as collector-filters and collector-gatherers), as well as among different taxa, habits (types of locomotion and streambed attachment) and body sizes (e.g. Wetmore *et al.*, 1990; Rempel *et al.*, 2000; Snook and Milner, 2002). For example, macroinvertebrate body size can affect relationships to both flow and detritus, since smaller individuals experience less force of flow due to a smaller surface area (Vogel, 1994) and may consume smaller size fractions of detritus than larger individuals (Cummins and Merritt, 1996). The response of macroinvertebrates to detritus can also vary with the season or location of sampling, possibly due to changes in the availability of detritus (Corkum, 1992) or the portion of macroinvertebrate diet composed of detritus (Chapman and Demory, 1963).

The main objective of this study was to assess the relative importance of flow *versus* detritus and substrate composition to the distribution of macroinvertebrates at sites on the West River of Prince Edward Island, Canada. This thesis will report on two major components of the study. In the methodology component, different methods of evaluating near-bed flow were tested to select the most appropriate method for use at the study site. To test which of several alternative methods of evaluating shear velocity gave accurate results, values obtained from the alternative methods were compared with those obtained from the standard method of velocity profiles. To determine whether the use of velocity profiles would be limited by small-scale spatial variation in shear velocity, I tested the hypothesis that variation in shear velocity within patches would increase with patch roughness. Finally, I tested the hypothesis that values of roughness based on substrate particle width would be good indicators of values obtained using a more standard method based on streambed height unevenness at the study sites.

In the macroinvertebrate component, spatial variation in macroinvertebrate abundance was related to different aspects of the environment including near-bed flow, average properties of surface flow, subsurface flow, substrate size, and detritus. Macroinvertebrate densities and environmental variables were measured in patches in sections of the West River that had a range of substrate, detritus and flow characteristics. The analysis of the macroinvertebrate data was focussed on deposit-feeding detritivores, since the importance of flow and direct *versus* indirect effects of flow on the distribution of this group is not yet well-understood. Results from previous studies (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001; Miyake and Nakano, 2002), suggested that the densities of most deposit-feeding detritivores would be correlated to both flow and substrate/detritus variables. Evidence of indirect effects of flow was expected to be observed in the form of correlations between flow and substrate/detritus as well as between macroinvertebrate density and both flow and substrate/detritus. Other functional-feeding groups were also examined in this study to determine if some taxa in these groups had different relationships with environmental variables than deposit-feeding detritivores. For example, unlike deposit-feeding detritivores, collector-filterers were expected to have higher densities in areas of faster flow.

The habitat associations of macroinvertebrates were also expected to vary among different taxa, habits and body sizes. For example, smaller individuals of deposit-feeding detritivore taxa may be more closely correlated to fine detritus and more abundant in areas of high shear velocity than larger individuals. I expected to find some different relationships between macroinvertebrate densities and environmental variables in different seasons and locations if there were large differences in environmental conditions such as detritus availability.

The spatial variation of macroinvertebrate density within sections of the stream at the study sites was expected to be non-random and aggregated, and to be related to the pattern of spatial variation in flow and substrate/detritus. To test this hypothesis, benthic samples were taken in a regular arrangement in each section of the study sites.

LITERATURE REVIEW

The purpose of this literature review (chapter 1) is to provide background on the topics addressed in the research project of this thesis (chapters 2 and 3). In the literature review, background information is provided on general properties and types of stream flow, methods of near-bed flow measurement, and the relationship of macroinvertebrates to flow, detritus, and substrate composition.

1.1 Flow in the environment of stream macroinvertebrates

Benthic macroinvertebrates experience very different types of flow depending on whether they are positioned at the surface of the streambed, in the interstices of subsurface streambed material, or in the water column (Vogel, 1994; Plénet *et al.*, 1995; Boulton *et al.*, 1998). Macroinvertebrates may inhabit the surface of the streambed, substrate interstices of the subsurface layer, or both (Minshall, 1984; Williams, 1984). By definition, benthic macroinvertebrates do not inhabit the water column, however, they may be found in the water column after accidental dislodgement or during movement between different locations on the streambed (Allan, 1995).

Since this study focusses on methods of measuring near-bed flow and relationships between surface flow and macroinvertebrate distribution, the following discussion will focus mainly on surface flow. Surface flow is considered to include flow extending from the water surface to the streambed surface and to include the properties of the bulk flow region and the near-bed flow region. Subsurface flow, which occurs through the interstitial spaces among the streambed material will be addressed only briefly.

1.1.1 Classification of surface flow

Characterizing surface flow can be difficult since the appropriate variables and methods to use depend on the type (or category) of flow (Nowell and Jumars, 1984; Gordon *et al.*, 1992). Therefore, in order to describe the spatial variation in stream flow and to relate this variation to macroinvertebrate distribution, the type of flow must first be determined.

Hydraulic rough versus hydraulically smooth

Stream flow can be classified as hydraulically rough or hydraulically smooth according to properties of the boundary layer (the layer of water above the streambed where the velocity is affected by the presence of the surface of the streambed). Surface flow in streams is heavily influenced by the interaction of flowing water with the form of the streambed, and the boundary layer typically encompasses the entire depth of the water column (Gordon *et al.*, 1992).

With very few exceptions, the average condition of surface flow in any area of a stream is turbulent (flow that follows irregular paths; Davis and Barmuta, 1989; Gordon *et al.*, 1992). However, even in areas of turbulent flow there is a very thin layer of laminar flow (flow in parallel layers) along the streambed in the lowest portion of the boundary layer (called the laminar sublayer; Fig. 1.1). Note that the terms "boundary layer" and "laminar sublayer" are not equivalent in this discussion although certain

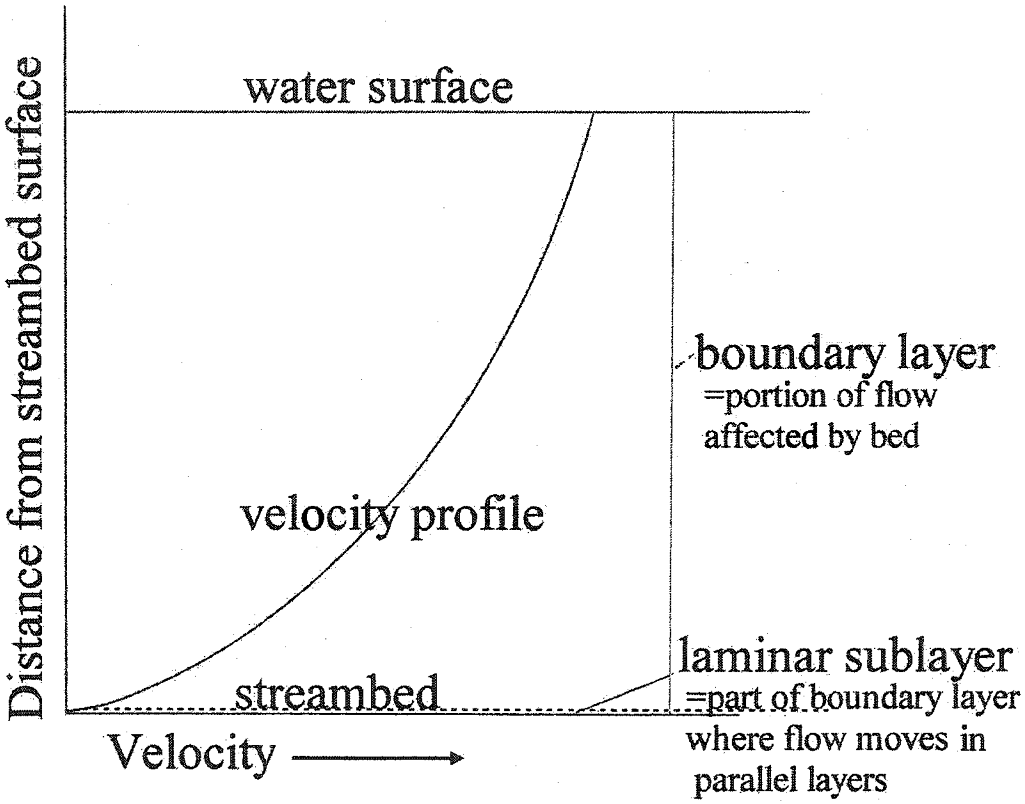


Fig 1.1. Diagram showing an example of how velocity changes with vertical position in the water column in a stream (velocity profile). In many areas of streams, the boundary layer region extends to the water surface and the laminar sublayer is broken up by streambed projections such as rocks.

ecology texts use the two terms interchangeably. The laminar sublayer exists because the motion of water molecules stops at the streambed surface when molecules directly in contact with the bed stick to the solid surface (no-slip condition). Thus, the velocity at where the water meets the streambed is zero. Velocity increases above the streambed, but the velocity immediately above the surface of the streambed is still slow enough to allow laminar flow (Gordon *et al.*, 1992).

In hydraulically smooth boundary layer flow, the laminar sublayer forms an intact (fully developed) layer over the streambed surface, whereas in hydraulically rough flow, it is broken up by roughness elements (forms of the streambed surface that project upwards, such as individual stones). Hydraulic roughness depends on the height of these roughness elements relative to the thickness of the laminar sublayer (which is affected by both the form of the streambed and the nature of the overlying flow). Stream flow is usually hydraulically rough (Nowell and Jumars, 1984) except in slow-flow areas such as pools that have a relatively thick laminar sublayer over surfaces with low roughness element height (Smith, 1975; Gordon *et al.*, 1992).

This means that in most areas of streams, the laminar sublayer is not intact. This is contrary to the belief held by many ecologists in the past that macroinvertebrates were "sheltered" within a laminar sublayer on the rock surfaces. In actuality, macroinvertebrates living on the streambed surface in most areas are subject to the variable hydraulic stresses of turbulent flow (Nowell and Jumars, 1984). Therefore, the remainder of this discussion will be limited to hydraulically rough flow.

Other types of classification for measurement of flow

Flow can also be classified based on how much boundary layer thickness, depth and velocity vary over time or distance (Table 1.1). Conventionally, hydraulically rough flow is classified as: "fully developed or growing" (based on variation of boundary layer thickness over distance); "steady or unsteady" (based on variation of depth and velocity over time) and "uniform, gradually varied, or varied" (based on variation of depth and velocity over distance; Table 1.1). All these types of flow can be seen in streams at different spatial and temporal scales (see Table 1.1. for examples).

Characterization of flow is the simplest in areas where flow patterns are relatively simple because flow is fully developed (i.e. the boundary layer thickness is constant over distance), steady (the depth and velocity are constant over a given time interval), and uniform (the depth and velocity are constant over a given distance; Nowell and Jumars, 1984). These types of relatively simple flow occur in some areas of streams, particularly at larger scales of measurement. For example, for the purposes of practical measurement, gradually varied stream flow in which velocity and depth change slowly over a section of the river, can be treated as uniform. Also, fluctuating stream flow can be treated as steady if the average values of velocity and depth are relatively constant over the time period of interest (Smith, 1975; Gordon *et al.*, 1992). Surface flow in streams is considered to be fully developed since the boundary layer of the streambed typically extends to the water surface in most areas, meaning that all the flow is affected by the streambed. However, at the smaller spatial scale of near-bed flow over individual stones, growing boundary layers can occur over stone surfaces within the larger fully developed boundary layer of the water column. Therefore, greater numbers and types of measurements are often needed to evaluate flow at smaller scales such as flow over

Table 1.1. Classifications of flow that are used to select appropriate methods of flow measurement

Classification[a]	Describes	Definition of type	Examples
fully developed or growing	thickness of the boundary layer[1]	fully developed: the thickness of the boundary is constant over distance[1]	the bulk flow in most sections of streams[1]
		growing: not as above	within the larger boundary region of bulk flow in streams, smaller growing boundary layers can occur over individual rocks[1]
steady or unsteady	whether velocity and depth are constant over a given time interval[1]	steady: velocity and depth are constant over time at a given location[1]	flow below a reservoir with constant discharge release[2]
		unsteady: not as above	during period of rapidly increasing discharge[2]
uniform, gradually varied or varied	whether velocity and depth are constant over distance[1]	uniform: velocity and depth are constant over distance in a given period of time[1]	flow in man-made rectangular channels[1]
		gradually varied: approximately uniform flow that can be considered uniform for the purposes of measurement[2]	flow in natural stream channels where the area of the wetted-cross section is nearly constant and the water surface is parallel to the streambed[2]
		varied: not as above	flow where the stream channel bends sharply[2]

a Classifications are not necessarily mutually exclusive, for example, flow can be either uniform and steady or varied and steady [4]

REFERENCES
[1]Gordon *et al.*, 1992; [2]Carling, 1992b; [3]Nowell and Jumars, 1984

individual stones (e.g. Hart *et al.*, 1996; Hoover, 2001) than over entire sections of streams (Nowell and Jumars, 1984; Gordon *et al.*, 1992).

1.1.2 Evaluation of stream flow

The evaluation of stream flow is based on hydraulics, the study of the physical properties of water in motion, such as velocity, acceleration, and force (Franzini and Finnemore, 1997). In this thesis, the terms "flow" and "hydraulics" are used interchangeably in some cases since it is the physical properties of flow that are of interest. Flow can be characterized using different hydraulic variables. The measurement of hydraulic variables to describe patterns of bulk flow, such as mean velocity and depth, can be accomplished using relatively simple and standard methods (Statzner *et al.*, 1988; Gordon *et al.*, 1992). In contrast, the selection and application of methods to characterize near-bed flow can involve more complicated considerations, starting with the selection of the relevant variables to be measured.

Selection of variables to be measured for evaluating near-bed flow

In this discussion of near-bed flow, the near-bed region is considered to be located a few centimetres or less from the streambed. Near-bed flow can be evaluated using hydraulic variables such as near-bed velocity, shear velocity and Froude number and with the variable of roughness.

Near-bed velocity

The velocity of near-bed flow often varies considerably in both horizontal and vertical directions among locations less than a centimetre apart (e.g. Hart *et al.*, 1996).

Therefore, a single measurement of velocity in the bottom few centimetres of flow (i.e. "near-bed velocity") is insufficient to describe the pattern of near-bed flow in that area (Nowell and Jumars, 1984) unless the spatial variation in flow follows a constant and predictable pattern. In contrast, other variables such as shear velocity and roughness provide more complete characterizations of near-bed flow than the near-bed velocity at a given point, since they are related to the overall pattern of spatial variation in flow (Nowell and Jumars, 1984).

Shear velocity and roughness

Two key variables for describing near-bed flow are shear velocity and roughness. The combination of these two variables fully describes near-bed flow in areas of relatively simple flow (uniform, steady, fully developed; Nowell and Jumars, 1984). Shear velocity is a measure of the "shearing" force of flow acting parallel to the streambed, and roughness characterizes the frictional resistance of the streambed to flow.

The value of shear velocity is related to the values of shear stress and skin friction (a type of drag). Shear stress is the force of flow per unit area parallel to the streambed. Skin friction is the force of shear stress acting on a defined area that is exposed to flow such as the surface of a rock or a macroinvertebrate (Smith, 1975; Gordon *et al.*, 1992). Skin friction can be thought of as being analogous to the force we feel on our thumb during the parallel motion of snapping our fingers. Shear velocity can be determined directly from shear stress using the value of water density as follows (Gordon *et al.*, 1992):

$$u^* = \sqrt{(\tau/\rho)} \tag{1.1}$$

where: u* = shear velocity (m/s), τ = shear stress (N/m^2; N (Newtons) = $kg{\cdot}m/s^2$) and ρ = water density (kg/m^3). Water density is constant for a given temperature of freshwater, assuming that solute concentrations are not high. Both flow velocity (e.g. mean velocity) and shear velocity are expressed in the same units, however "shear velocity" is a measure of force, not velocity.

Measures of both shear stress and shear velocity are considered redundant in studies of streams in which the water temperature varies by only a few degrees (Statzner *et al.*, 1988). This is because the relationship between shear velocity and shear stress is constant at a given water temperature since the density of the water is constant (see Gordon *et al.*, 1992 for details). In this discussion, I have followed the convention of many hydraulic references (e.g. Smith, 1975; Nowell and Jumars, 1984; Davis and Barmuata, 1989) by discussing shear in terms of shear velocity where appropriate.

Roughness characterizes the physical form of the streambed which contributes to the frictional resistance experienced by the overlying flow. The form of the streambed surface influences the development of velocity gradients above the streambed and recirculating currents around rocks (Vogel, 1994). The unevenness of the form of the streambed is important in determining the roughness of this surface (see p. 26). For example, a streambed with large rocks that project upwards into the flow has high roughness. There are various technical terms and specific definitions associated with different methods of evaluating roughness (see Bray, 1991 and Carling, 1992a for details). However, for the sake of simplicity, I have used the general term roughness for all values describing the resistance of the streambed to flow. Technically, roughness is not a hydraulic variable since it describes the form of the streambed and does not describe properties of flow directly. However, roughness is referred to as a hydraulic variable in this discussion since it is used to predict physical properties of flow (Nowell and Jumars, 1984).

Dimensionless hydraulic variables

Simple hydraulic variables such as roughness and mean velocity are difficult to compare in systems of different sizes. However, these variables can be used to calculate complex dimensionless hydraulic variables (variables without units) to compare hydraulic properties over a wide range of conditions. For example, dimensionless hydraulic variables are appropriate for comparing flow in flumes, small rivers and large rivers (Smith, 1975). Dimensionless hydraulic variables that are also appropriate for describing the properties of near-bed flow experienced by benthic organisms include Froude number and roughness Reynolds number (Statzner *et al.*, 1988; Davis and Barmuta, 1989).

Froude number is a particularly useful hydraulic variable for describing spatial variation of flow in shallow areas where velocity and depth are strongly affected by changes in streambed form (Newbury, 1984). Froude number is determined from the relationship of mean velocity to depth, and is related to the acceleration and direction of flow (Wetmore *et al.*, 1990). Rapid changes in Froude number (Fr) can be observed in streams where flow accelerates and the streamlines converge as water drops over the shallow surface of an obstacle such as a boulder (Wetmore *et al.*, 1990; Fig 1.2). The Froude number of an area within a section of a stream (local Froude number) is determined using the following formula (Gordon *et al.*, 1992):

$$Fr = U/\sqrt{(gd)} \qquad (1.2)$$

where Fr = local Froude number, U = mean velocity (m/s), g = gravitational acceleration

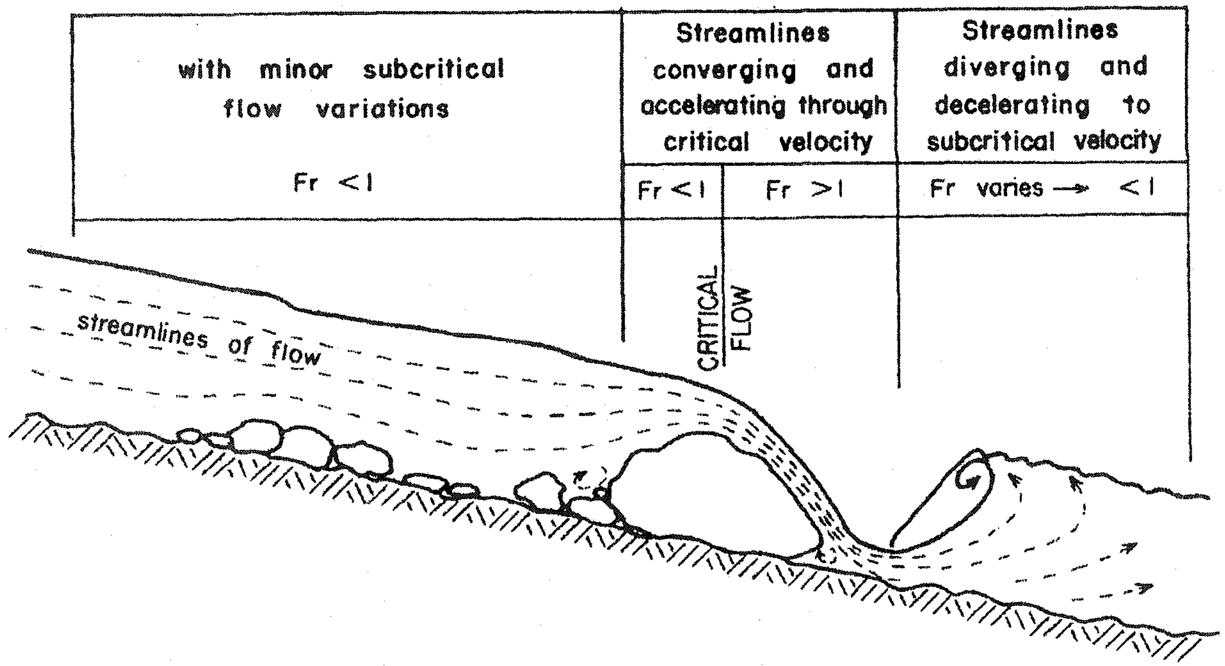


Fig. 1.2. Diagram of a longitudinal section of a stream area with variation in local Froude number (Fr; adapted from Wetmore *et al.*, 1990). "Streamlines" or average paths of flow are shown. Names for categories of Fr (subcritical, critical and supercritical) are listed above the corresponding Fr value.

constant (9.8 m/s^2) and d = depth (m). Froude number is considered appropriate for the evaluation of both bulk flow and near-bed flow (Davis and Barmuta, 1989; Wetmore *et al.*, 1990; Gordon *et al.*, 1992).

Roughness Reynolds number increases with the level of near-bed turbulence, and is used to describe near-bed flow in some studies of benthic macroinvertebrates (see section 1.3, p.39 for examples). The value of this hydraulic variable increases with both shear velocity and roughness (Gordon *et al.*, 1992).

1.1.3 Methods of evaluating near-bed hydraulic variables

Near-bed hydraulic variables can be evaluated using direct or indirect methods of measurement. Direct methods involve directly measuring velocity or other properties of flow at the location of interest using specialized tools that can take measurements over very small areas close to the streambed (described in Hart and Finelli, 1999; Ackerman and Hoover, 2001). However, tools for direct measurement of near-bed hydraulic variables are rarely used in studies of stream ecology for several reasons including expense, limited availability, and difficulty of operation in natural streams (Newbury, 1996; Hart and Finelli, 1999; Ackerman and Hoover, 2001).

Indirect determination of near-bed hydraulic variables

Most studies of stream ecology, including this one, use indirect methods to determine near-bed flow (Newbury, 1996). Indirect methods are based on measurements of flow above the location of interest, the form of the streambed, or both, and require making assumptions about the structure of flow. Hydraulic variables that can be measured using indirect methods include shear velocity and roughness. In the following section, standard methods for measuring shear velocity and roughness will be discussed, as well as alternative methods that offer practical advantages for studies of stream ecology such as speed and non-invasiveness.

Many of the methods commonly used in stream ecology are only appropriate for relatively simple patterns of flow. Therefore, the following discussion focusses on evaluating the appropriateness of alternative methods for use in sections of streams that have flow that is fully developed and can be treated as uniform and steady (as discussed in "other types of classification"; p.12). Indirect methods are considered appropriate for evaluation of flow within such sections at an intermediate spatial scale (i.e. in areas that range in size between a point and entire sections of streams; Statzner *et al.*, 1988).

Measurement of shear velocity

The traditional method of evaluating shear velocity in streams is to measure flow velocities at a range of heights above a point on the streambed to construct a velocity profile (Carling, 1992a; Gordon *et al.*, 1992; also see Fig 1.1, p.10) . Shear velocity is then calculated from the rate at which velocity decreases over depth (expressed as log depth). An important limitation of the velocity profile method is that the profile shape must be logarithmic over the depth of measurement (Carling, 1992a). The velocity profile method is time-consuming and difficult to apply in certain conditions, such as areas of shallow depth (Biron *et al.*, 1998). Therefore, the simpler alternative methods reviewed in the following section have been proposed for evaluating shear velocity at intermediate spatial scales in streams (Table 1.2).

Table 1.2. Comparison of methods for measuring shear velocity on an intermediate spatial scale in streams. The reliability of results from each method are addressed in terms of precision, results from field-testing of accuracy, and theoretical considerations related to accuracy. Practical considerations such as speed and invasiveness of measurement are listed for each method

Method	**Description**	**Reliability**	**Practical considerations**
Velocity profiles	Velocity measurements at different heights from the bed in the bottom layer of flow used to calculate shear velocity[1]: $u^* = \text{slope}/5.75 \quad (1.3)$ where u^* = shear velocity, slope = slope of plot of velocity *versus* log depth	• Standard for accuracy in field work[1] • Results consistent with direct measurements of shear velocity if flow conditions are "relatively simple[2,3] • Shear velocity measured at a point may not reflect shear velocity in surrounding area where near-bed flow is highly variable over small distances[1,4] • Velocity measurement with traditional flow meters limits accuracy because of coarse spatial resolution[5,6] • Difficult to orientate tools for velocity measurement properly because of cross-currents near the bed[7] • Results not always precisely replicable due to uncertainty in determining exact slope from velocity profile[8]	• Near-bed profile must be logarithmic[1] • Difficult to obtain enough velocity measurements at different heights close to the bed in areas where the logarithmic portion of profile is very thin (e.g. shallow water, strongly accelerating flow)[2,6,7] • Relatively time-consuming
FST hemispheres	Hemispheres of different densities that slide along a smooth plate placed level on the streambed; hemispheres move at known values of shear stress[7]	• Moderately[7] to weakly[4] correlated with values from velocity profiles • Relationship between FST hemisphere movement and shear velocity constant over different roughnesses in tests by designers[7] but not in an independent study[9] • FST hemisphere movement affected by properties of near-bed flow other than shear velocity (e.g. lift)[7] • Resolution of measurement limited to 24 different values (number of different hemispheres in a set)	• Restricted to shallow depth[7] • Requires moving streambed substrate to level the plate[7,a] • Relatively time-consuming

continued...

Table 1.2., continued

Method	Description	Reliability	Practical considerations
Mean velocity[d]	If mean velocity is correlated to shear velocity, mean velocity values can be used as an indicator of shear velocity Mean velocity is often estimated from velocity measurement at one or a few depths[10]	• Moderately correlated to values determined with velocity profiles [11,12e] and direct measurement of near-bed flow[2] • Ratio of mean velocity to shear velocity expected to vary with relative roughness[13] •Estimation of mean velocity from measurements at one or a few depths assumes predictable change in velocity over depth [10]	
Near-bed velocity	If near-bed velocity is correlated to shear velocity, near-bed velocity values can be used as an indicator of shear velocity	• Can be closely related to values determined using direct measurement of near-bed flow even if near-bed profile is not strictly log-normal[2] • Ratio of near-bed velocity to shear velocity expected to vary with roughness[14] • Velocity measured at a point may not reflect velocity in the surrounding area where near-bed flow is highly variable over small distances • Difficult to orientate tools for velocity measurement properly because of cross-currents near the bed[7]	
Calculation from mean velocity, depth and roughness	Shear velocity is calculated using the Keulegan equation[15]: $u^* = \frac{U}{5.75 \log_{10}(12d/k)}$ (1.4) where u* = shear velocity (m/s),U = mean velocity (m/s), d = [b]depth (m),k = roughness (m)	• Moderately correlated to values determined with velocity profiles[11] • Accuracy may be limited by accuracy of roughness measurements (see Table 3 for details) • Developed for use at reach-scale, may not be appropriate for intermediate spatial scales[1] • Results can be replicated with good precision[8]	• Disturbance to the streambed and time required for measurement depends on method used to measure roughness (see Table # for details)

continued...

Table 1.2., continued

Method	Description	Reliability	Practical limitations
Calculated from the factors related to the weight of water and the downward force of water on the streambed	Shear stress calculated using the following equation [15]: $$\tau = \rho g DS \qquad (1.5)$$ where τ = shear stress (N/m^2) g = gravitational acceleration constant ($9.8 m/s^2$), S = slope of water surface, ρ = water density (kg/m^3), d = [b] depth(m)	• [c]Results consistent with values determined from velocity profiles[7] • Slope of water surface difficult to measure accurately[1] • Developed for use in entire sections of streams, may not be appropriate for intermediate spatial scales[1]	• Measurement of slope generally involves contact with the streambed

[a] Uniform, fully developed, velocity profile has a regular shape

[b] The appropriate measure of depth depends on the scale of measurement and desired precision. For work in entire sections of streams, hydraulic radius (definition in [10]) is used as a measure of depth, which can be approximated by mean depth for wider streams. Depth at the sampling location is sometimes used in place of hydraulic radius for work at intermediate scales [14,15]

[c] My interpretation of results based on close relationship of both shear stress values calculated from slope and depth and values determined using FST hemispheres to velocity profile results

[d] Where mean velocity is the mean of the velocity of flow from the water surface to the bed

[e] My interpretation of results based on data analysis presented in publication

REFERENCES

[1]Carling, 1992a; [2]Hoover, 2001; [3]Ackerman and Hoover, 2001; [4]Frutiger and Schib,1993; [5]Hart *et al.*, 996; [6]Biron *et al.*,1998; [7]Statzner and Müller, 1989; [8]Wilcock,1996; [9]Dittrich and Schmedtje, 1995; [10]Gordon *et al.*, 1992; [11]Quinn and Hickey, 1994; [12]Rempel *et al.*, 2000; [13]Smith, 1975; [14]Nowell and Jumars, 1984; [15]Statzner *et al.*, 1988

Alternative methods of evaluating shear velocity

Alternative methods for evaluating shear velocity include the use of FST (Fliesswasserstammtisch) hemispheres, the use of other hydraulic variables as indicators of relative shear velocity, and the calculation of shear velocity from other hydraulic variables (Table 1.2). The word "Fliesswasserstammtisch" is derived from the German words for river, water and table. FST hemispheres are hemispheres of different densities that are used in combination with a smooth level plate placed on the streambed. Hemispheres of different densities will move along the plate in response to proportional levels of shear stress as determined by calibration in flumes and streams (Statzner and Müller, 1989). Shear velocity can then be calculated from the determined shear stress using equation 1.1., p.15. In addition, other hydraulic variables can be used as indicators of areas where shear velocity is relatively low or high, because in many streams there is a correlation between shear velocity and certain hydraulic variables that are easier to measure, such as near-bed velocity or mean velocity (Statzner *et al.*, 1988; Lancaster and Hildrew 1993; Quinn and Hickey, 1994). Finally, methods that have been used to calculate average values of shear velocity for entire sections of streams have been adapted for use at intermediate spatial scales, including calculation of shear velocity from values of mean velocity, depth and roughness or from values of water slope and depth (Table 1.2).

Some alternative methods are more practical than others for use in stream ecology studies (Table 1.2). For example, mean velocity and near-bed velocity can be measured quickly with little disturbance to the streambed, while measurement of shear velocity using FST hemispheres is relatively time-consuming and invasive. Invasive measurement techniques can be inappropriate for use in studies of stream macroinvertebrates, since contacting or moving streambed material may disturb macroinvertebrates.

Reliability of methods for determining shear velocity

There is often disagreement among researchers about which alternative methods of measuring shear velocity are most appropriate for work at intermediate spatial scales. This disagreement stems from the fact that results and conclusions from different field tests do not always agree (Table 1.2) due to differences in either the comparison of methods or the hydraulic properties of flow present at the study location. For example, in some studies, results from alternative methods are compared to those from velocity profiles (e.g. Frutiger and Schib, 1993; Quinn and Hickey, 1994), while in other studies, results from alternative methods are compared to results from other alternative methods (e.g. Statzner *et al.*, 1988; Lancaster and Hildrew, 1993). However, results from comparisons among the same methods can also vary among studies (Table 1.2) and even between different rivers in the same study (Lancaster and Hildrew, 1993; Quinn and Hickey, 1994). This suggests that the appropriateness of a particular method depends on the hydraulic properties of flow in the area of interest.

In addition, not all researchers believe that methods developed for smaller or larger spatial scales are appropriate for use at an intermediate spatial scale. For example, it may be inappropriate to use point measurements such as velocity profiles and near-bed velocity to characterize the force or velocity of near-bed flow over areas greater than a few centimetres in diameter where flow is highly variable, such as areas with high roughness (Carling, 1992a; Frutiger and Schib, 1993). This may mean that the use of single velocity profiles to evaluate shear velocity over larger areas in many studies of benthic macroinvertebrates (e.g. Quinn and Hickey, 1994; Rempel *et al.*, 2000) is problematic. This is the reason why some researchers argue that calculation of shear velocity from other hydraulic variables (Statzner *et al.*, 1988; Quinn and Hickey, 1994) may produce values that better reflect average shear velocity over an area than a velocity profile at a single point. However, other experts argue that these equations, which were developed to measure shear velocity at a reach scale (i.e. in entire sections of streams), are not necessarily appropriate for use at intermediate spatial scales (Carling, 1992a). In conclusion, further field testing is required to clarify which methods of measuring shear velocity are appropriate for different hydraulic conditions and scales of study (Statzner *et al.*, 1988)

Measurement of roughness

Roughness can be evaluated based on a change in velocity above the streambed or measured directly from the form of the streambed (Table 1.3). As with shear velocity, the standard method for accurate evaluation of roughness in streams is to calculate roughness from a velocity profile (Carling, 1992a, Gordon *et al.*, 1992; see Table 1.3 for method of calculation). However, it is often difficult to apply this method reliably in streams. The major source of error is determining the position of zero depth for the profile in areas where the streambed surface is highly uneven (reviewed in Bray, 1991; Quinn and Hickey, 1994, Biron *et al.*, 1998).

Due to the difficulty of accurately measuring roughness in natural channels using velocity profiles, roughness in streams is typically estimated directly from the form of the streambed (Gordon *et al.*, 1992). This method is based on results from experimental work in flumes that placed roughness elements with simple shapes in regular

Table 1.3. Comparison of approaches for evaluating roughness on an intermediate spatial scale in streams. Roughness can be quantified from velocity profiles or various methods based on streambed form. The potential accuracy and precision of each approach is addressed based on theoretical considerations.

Method	**Description**	**Potential accuracy/precision**
Velocity profiles	Velocity measurements at different heights from the bed used to determine roughness based on value of roughness length Roughness length is determined from plot of velocity *versus* log depth where roughness length is the value of the intercept on the depth axis[1]	• Some experts feel this is the most accurate method for streams[1] • Determining position of zero depth is difficult in areas with highly uneven bed height and affects values of roughness[2]
Evaluation from streambed form (specific examples below):	(See examples below)	Considerations that apply to all examples below: • Difficult to relate complex topography of natural streambeds to regular surfaces used in flume experiments[3] • One field study found that topography of gravel beds is complex and cannot be well-described without using several parameters to describe 3-dimensional form[3] •The effects of larger roughness elements located upstream of the area of interest[4,5] are not accounted for by most methods
Particle diameter	Roughness calculated from characteristic particle size diameter (e.g. median particle size diameter) and a constant chosen to reflect large differences in other factors affecting roughness[a4]	•Basing roughness values mostly on a characteristic particle size is considered reasonably accurate by some experts, but not by others[3,4] •Does not adequately account for effect of substrate particle arrangement on roughness[3]
Particle width	Roughness is calculated from portion of patch area covered by substrates of different widths, where width is measured in a downstream direction from an overhead view[7]	• Based on assumption that substrate particle diameter is proportional to streambed projection height[6] (points listed above for particle diameter also apply here)
Unevenness of height	Roughness is calculated from variation in streambed height in a downstream direction[7]	

[a]e.g. substrate particle arrangement[8]

REFERENCES

[1]Carling, 1992a; [2]Biron *et al.*, 1998; [3]Nikora *et al.*, 1998; [4]Nelson *et al.*, 1995; [5]Hart *et al.*, 1996; [6]Davis and Barmuta, 1989; [7]Statzner *et al.*, 1988; [8] Chow, 1981 cited in Carling, 1992a

arrangements to determine how the form of these elements affected near-bed flow. These studies established that the height of roughness elements on the bottom affected roughness, but that this relationship varied with the spacing of the elements (early work reviewed in Morris (1955), recent work summarized in Coleman *et al.* (1984); Davis and Barmuta (1989)). For example, if roughness elements are widely spaced, the value of roughness is related directly to the shape of individual projections. However, if roughness elements are closely spaced, their effect on the resistance of the surface to flow is interactive (Nowell and Church, 1979). Accordingly, much less is known about quantifying the effect of streambed projection spacing than streambed projection height on roughness (Davis and Barmuta, 1989). Methods of measuring roughness from streambed form quantify roughness based on either the diameter of substrate particles as determined by sieving, the unevenness of streambed height, or the width of substrate particles as measured from overhead (Table 1.3).

The practical advantages and disadvantages of different approaches to measuring roughness depend on the equipment used to collect measurements of streambed form (Table 1.4). For example, substrate particle diameter is typically determined by sieving, which is highly invasive since it requires removing material from the streambed. Collecting information on streambed height unevenness can be relatively time-consuming and most methods involve contact with the streambed (Table 1.4). Measuring roughness based on substrate particle width as viewed from overhead offers important practical advantages such as non-invasiveness and speed, but can only be applied if the streambed is visible through the water (Table 1.4).

Table 1.4. Comparison of methods for measuring streambed form to evaluate roughness on an intermediate spatial scale in streams. Each method is described, including the type of information it provides about streambed form. Practical considerations such as speed and invasiveness of measurement are listed for each method.

Method	Description	Information obtained	Practical limitations
Sieving	Sample of streambed collected, particle sizes separated by sieving, each size fraction quantified	• Size distribution of particles in surface layer of streambed	• Requires removing material from the streambed
Profiling device	Sliding rods pressed into streambed, fixed in place, then measured or traced[2]	•Streambed projection height and spacing	• Profiler contacts the streambed • Relatively time-consuming[2,3]
Visual estimation from overhead	Estimation of portion of streambed area covered by substrate with different particle widths[3]	• Area covered by particles of different widths • Subjective, but trained observers can produce very similar results[2]	• Bed must be visible through water
Photograph taken from overhead	As above, using photograph to measure areas and particle widths	• Area covered by substrate of different widths	• Bed must be visible through water

REFERENCES

[1]Ziser, 1985; [2]Statzner *et al.*, 1988; [3]Gibson *et al.*, 1998

Reliability of methods of measuring roughness based on streambed form

It is difficult to evaluate how accurately roughness measurements based on streambed form reflect the actual resistance of the streambed to flow. One serious problem in evaluating these methods at an intermediate spatial scale is that the recommended standard method of calculating roughness from velocity profiles is often unreliable under field conditions. Furthermore, it is difficult to apply the relationships between surface form and roughness that have come from flume studies to the complex geometry of natural streambeds. Therefore, formulas used for determining roughness from streambed form are approximate solutions because they do not reflect many aspects of streambed form known to affect roughness (Table 1.3, p.27). Roughness calculated from streambed height unevenness is considered more reliable than roughness calculated from other substrate dimensions such as particle diameter or width. However, measures of diameter and width may give reliable estimates of roughness if they are good indicators of changes in streambed height (Statzner *et al.*, 1988). Only a few studies have compared width or diameter based roughness estimates with height-based roughness measurements (e.g. Statzner *et al.*, 1988; Quinn and Hickey, 1994). More studies are need to determine if width or diameter based methods can be applied to other streams that may have different characteristics of streambed form.

Another problem with methods of determining roughness based on streambed form is that roughness values calculated with some formulas have no units (e.g. width-based roughness in Winget, 1985) or are not comparable to values calculated with other formulas (e.g. the roughness measures in Statzner *et al.*, 1988). Measurements of roughness that do not have a well-defined scale can be used in a relative way to identify areas that have higher or lower roughness. However, the use of various scales of measurement in aquatic ecology literature is a source of potential confusion when roughness values are used to make comparisons between studies, or to calculate complex hydraulic variables (Carling, 1992a).

1.1.4 Spatial variation in surface flow

The hydraulic properties of both bulk surface flow and near-bed flow vary within sections of a stream as channel topography and streambed roughness vary (Gordon *et al.*, 1992). Spatial variation in bulk flow can be easily observed from the bank of a stream. For example, mean velocity and depth are often obviously lower near the banks than in the centre of the channel. A change in Froude number can be seen in areas where the mean velocity of flow increases and depth decreases as water moves over the tops of rocks that are close to the water surface (Gordon *et al.*, 1992; Newbury, 1996; also see Fig. 1.2, p.18).

Near-bed flow in streams varies over intermediate (Statzner *et al.*, 1988) and finer spatial scales (Hart and Finelli, 1999). For example, at an intermediate spatial scale, shear velocity can vary by 6-fold or more within sections of small streams (Lancaster and Hildrew 1993; Ackerman and Hoover, 2001). At a finer spatial scale, near-bed velocity can vary by several orders of magnitude in different locations at the same depth over individual stones (Hart *et al.*, 1996). There can also be a marked change in near-bed flow between the tops and crevices of rocks (Nowell and Jumars, 1984). For example, a zone of high shear velocity can occur around the tops of rocks positioned close together (observed in Biron *et al.*, 1998) in a characteristic three-dimensional pattern of near-bed flow known as skimming flow (Morris, 1955). Variation of near-bed flow at these fine spatial scales is important to consider when working at larger spatial scales since it can affect our ability to accurately characterize the average flow (Hart and Finelli, 1999). For example, a point measurement of shear velocity calculated from a velocity profile may be different from the value of shear velocity only a few centimetres away (Carling, 1992a).

1.1.5 Variation in surface flow with increasing discharge

As discharge (the volume of water that passes a point per unit time) increases during run-off events, changes occur in patterns of bulk flow and near-bed flow. For example, the depth, mean velocity, and wetted width of bulk flow generally increase with discharge, but the relative increase of each measure varies with channel form (Power *et al.*, 1995). As discharge increases, near-bed flow changes more in some locations than others. If the streambed is relatively stable, the change in shear velocity over discharge may follow a predictable trend with greater increases occurring in some locations than others (Lancaster and Hildrew, 1993). For example, shear velocity typically increases less along sloping channel margins than farther out from shore (e.g. gravel bars in Rempel *et al.*, 1999) since discharge tends to become concentrated closer to the centre of the channel (Gordon *et al.*, 1992).

1.1.6 Subsurface flow

In areas where the streambed is permeable, water flows beneath the surface of the streambed in the interstices of streambed material (Packman and Bencala, 2000). Although the velocity of subsurface flow is generally much lower than that of surface flow (Rabeni and Minshall, 1977; Boulton *et al.*, 1998), the rate of subsurface flow can be important to macroinvertebrates in interstitial or streambed surface habitats (see sections 1.5, p. 46 and 1.7.3, p. 54).

Water moving through streambed interstices can consist of surface water that passes through the streambed before returning to the surface (connective flow) and also water that moves between surface water and groundwater (Packman and Bencala, 2000). Connective flow can occur when turbulent flow penetrates the streambed or when changes in channel topography cause spatial variation in the pressure of surface flow (Packman and Bencala, 2000). For example, surface water often moves into the streambed in areas of decreasing stream water depth and emerges from the streambed in areas of increasing depth (White, 1990). Surface water-groundwater exchange occurs in streams in upwelling zones where groundwater is discharged into the stream and in downwelling zones where surface water recharges into the groundwater table (Hynes, 1973).

Patterns of subsurface flow are controlled by hydraulic gradient, which is a pressure differential related to direction and strength of flow, and hydraulic conductivity (the permeability of the streambed to flow; Lee and Cherry, 1978; Boulton *et al.*, 1998). Hydraulic conductivity is closely related to substrate size composition, and tends to increase with average substrate size composition, but is also affected by the proportion of smaller substrate particles (Pfannkuch, H.O. and R. Paulson, 1998, University of Minnesota, Minneapolis, USA, Grain size distribution and hydraulic properties).

Vertical hydraulic gradient

Many studies of stream ecology use measurements of vertical hydraulic gradient (VHG) to describe patterns of vertical flow (e.g. Valett *et al.*, 1994; Boulton and Foster, 1998, Pepin and Hauer, 2002). If the streambed substrate is permeable, positive VHG indicates upwelling zones and negative VHG indicates downwelling zones (Lee and Cherry, 1978). Upwelling zones can result from either connective flow or groundwater discharge (Alexander and Caissie, 2003).

In streams, VHG can vary by as much as several orders of magnitude between locations only metres apart (Valett *et al.,* 1994). The discharge level of the stream can affect VHG, since VHG is influenced by the height of the stream water surface relative to the groundwater table (Hynes, 1973). Before considering how spatial variation in surface and subsurface flow affects macroinvertebrates, it is important to understand how macroinvertebrate communities in streams are described.

1.2 Categories and measures used to describe macroinvertebrate communities

Stream benthic macroinvertebrates are invertebrates such as insect larvae, worms and snails that inhabit the streambed and are >1 mm in length as mature larvae or aquatic adults. In studies relating macroinvertebrates to environmental variables, macroinvertebrates are often categorized according to taxon, habit, functional feeding group and stage of development or body size (Cummins, 1992) because of differences in how certain categories of macroinvertebrates relate to their environment. Macroinvertebrates that belong to related groups of species, but may not have been identified to the level of species, are referred to as "taxa".

The category of habit describes taxa according to their mobility, method of locomotion, and typical position within the benthic environment (Table 1.5). For example, taxa categorized as "swimmers" cling to submerged objects and move by short bursts of swimming. Less mobile "burrowers" are often found burrowed in

Table 1.5. Definition of selected macroinvertebrate habits[1]

Habit	Description
Swimmers	Move through short bursts of "fishlike" swimming. Individuals usually cling to objects such as rocks when not swimming
Clingers	Adapted for attachment to streambed surfaces
Sprawlers	Inhabit the surface of fine sediments, have modifications for staying on top of soft substrate and are tolerant of fine sediment
Burrowers	Burrow into substrate sediment or plant material. Often inhabit areas of fine sediment in pools of streams

REFERENCES
[1]table after Cummins and Merritt, 1996

streambed substrate or plant material. Macroinvertebrate habit is expected to influence the relationship between macroinvertebrate distribution and stream environmental conditions. For example, highly mobile species are probably less influenced by small-scale environmental patchiness than species with limited mobility (Downes *et al.*, 1993). Also, the vertical position of an individual in the stream environment is important in determining the environmental conditions that are experienced. For example, by hiding in substrate interstices, burrowers can avoid the high velocity and forces of flow experienced by swimmers in the water column or clingers on the streambed (summarized in Vogel, 1994).

The category of functional feeding group (FFG) describes the mode of feeding and the dominant food in the diet of macroinvertebrate taxa (Table 1.6; Cummins and Merritt, 1996). For example, scrapers which feed on attached algae often have mandibles with blade-like inner margins for removing algae. The term "deposit-feeding detritivores" as used in this study includes the detritus-feeding shredders (which feed predominately on deposited coarse particulate organic matter; particles > 1mm; CPOM) and collector-gatherers (which feed predominately on deposited fine particulate organic matter; particles < 1mm; FPOM). Another common FFG that includes detritivores is the collector-filterer group which feeds on FPOM carried in the water column.

Macroinvertebrate FFGs are often assigned at the genus-level of identification (identification of groups of very closely related species, e.g. FFG guide in Merritt and Cummins, 1996), partly because of the difficulty in identifying aquatic invertebrates beyond genus. However, the actual mode of feeding and diet of macroinvertebrates can vary considerably among species in the same genus, among individuals of different ages and with season or location (Hawkins, 1985; Cummins and Merritt, 1996). Therefore,

Table 1.6. Definition of selected macroinvertebrate functional feeding groups (FFG)[1]

FFG	Dominant food in diet	Mode of feeding
Shredders	Coarse particulate organic matter > 1mm (CPOM), CPOM may be of terrestrial origin (e.g. leaves and wood) or aquatic origin (e.g. aquatic macrophytes)	Chewing or mining of leaf pieces or aquatic macrophytes or gouging of wood
Collector-Filterers	Fine particulate organic matter < 1mm (FPOM)	Filtering material from water column
Collector-Gatherers	Fine particulate organic matter < 1mm (FPOM)	Browsing surface deposits or mining sediment
Scrapers	Periphyton (attached algae) and associated material	Grazing or scraping of surfaces on objects such as rocks and plants
Predators	Other animals	Ingest whole animal or parts or pierce tissues and suck fluids

REFERENCES
[1]table after Cummins and Merritt, 1996

although FFG categorization is a useful tool for examining relationships between macroinvertebrates and food resources (Cummins and Merritt, 1996) it cannot be used with high certainty to predict what a macroinvertebrate is eating.

The stage of development and body size of macroinvertebrates can also influence their relationship with the stream environment (Wetmore *et al.*, 1990; Lloyd and Sites, 2000; Snook and Milner, 2002). Although macroinvertebrates generally grow as they age, the specific relationship between body size and age for a given taxon is not fixed since growth is affected by other factors, such as temperature and the sex of an individual (Butler, 1984). The behaviour of macroinvertebrates often changes with both growth and development. For example, the youngest larvae of many aquatic insect species (early instars) usually feed on fine particles of detritus and/or living material that is also tiny (e.g. diatoms) although mature larvae may feed other food resources (Cummins and Merritt, 1996). In addition, some macroinvertebrate taxa switch from subsurface to surface habitats of the streambed over the course of their life cycle (Williams, 1984).

To describe macroinvertebrate communities, the number of macroinvertebrates in each category of interest is often evaluated in terms of density, relative abundance, or measures of community structure. Density is the number of individuals per area where area is the surface area of streambed unless otherwise specified. The relative abundance of macroinvertebrates is the percentage of total individuals in a sample represented by a given category. Community composition of macroinvertebrates can be described by the relative abundance of different groups or by measures of community structure such as number of taxa or diversity indices. The subsequent discussion focuses on the relationship between environmental conditions and benthic macroinvertebrate density, since the macroinvertebrate community in this study was analysed primarily according to the density of different taxa.

1.3 Observations from field studies relating surface flow and macroinvertebrate distribution

Field studies that explore the relationship of macroinvertebrates to flow provide valuable information by identifying relationships between flow and macroinvertebrate distribution. It is rarely possible to determine the force of flow on an individual macroinvertebrate in the field due to the difficulty of directly measuring flow velocities around an individual on the streambed and the difficulty of working with live invertebrates (Statzner and Holm, 1989). However, hydraulic variables determined through indirect measurement of flow can be used to compare the magnitude and variability of force experienced by macroinvertebrates in different areas of a streambed (Statzner *et al.*, 1988). Many surveys of macroinvertebrate distribution have found that the density of some taxa, but not others, is related to hydraulic variables such as mean velocity, depth, shear velocity (or shear stress), near-bed velocity and three-dimensional patterns of flow (Gore, 1978; Gore and Judy, 1981; Wetmore *et al.*, 1990; Quinn and Hickey, 1994; Bouckaert and Davis, 1998; Rempel *et al.*, 2000; Doisy and Rabeni, 2001; Wellnitz *et al.*, 2001).

Relationships of macroinvertebrate distribution to surface flow can vary among different categories of macroinvertebrates such as different functional-feeding groups. For example, the density of collector-gatherers is often negatively related to mean velocity, depth, Froude number, and roughness Reynolds number (e.g. Quinn and Hickey, 1994; Rempel *et al.*, 2000; Doisy and Rabeni, 2001). The relationship of shredders to surface flow is not as well characterised, since in many streams, shredders are much less abundant than collector-gatherers (e.g. Minshall *et al.*, 1982; Parker, 1989; Rempel *et al.*, 2000). In contrast, many collector-filterers prefer specific flow conditions such as high flow velocities because they use the water current to feed. Therefore, they have distributions that are associated with very fine-scale spatial variation in near-bed flow (e.g. Wetmore *et al.*, 1990; Hart *et al.*, 1996). Although it may be possible to make generalizations about the relationship of certain function-feeding groups to flow, more research is needed to determine if such generalizations can be made for other groups including shredders.

Relationships with surface flow can also vary with macroinvertebrate habit, body size or taxon. For example, Snook and Milner (2002) found that most individuals in areas with high roughness Reynolds number (high near-bed turbulence) had small body size and clinger habit (see Table 1.5, p. 35 for definition of habits). In contrast, individuals in their study with swimmer habits were generally restricted to stream sections with low roughness Reynolds number. In addition, the relationship between surface flow and macroinvertebrate density can vary with the larval size or instar of a given species (Statzner, 1981; Wetmore *et al.*, 1990). Although some groups of taxa are generally associated with certain hydraulic conditions, there can also be variation in surface flow relationships among different taxa, including those in the same FFG (Wetmore *et al.*, 1990) and species in the same genus (see results in Gore and Judy, 1981). Finally, the relationship of macroinvertebrate density to hydraulic conditions can vary between different seasons or locations (Quinn and Hickey, 1994; Doisy and Rabeni, 2001). All of these factors make it difficult to make generalizations about how flow affects macroinvertebrates. These factors also emphasize the need to examine habitat associations separately for different groups such as different taxa and body sizes (rather than grouping all individuals in a functional-feeding group together) and the need to compare results among different seasons and locations.

1.3.1 Methods of analysis for relating surface flow to macroinvertebrate distribution

A variety of different hydraulic variables and methods of data analysis have been used in studies relating stream macroinvertebrate distribution to flow. The appropriate choice of hydraulic variables for a study depends in part on the macroinvertebrate parameters of interest and the hydraulic conditions of the study location (see sections 1.3 above and p. 20 of section 1.1.3 for details). For example, a few simple hydraulic variables may be enough to examine how flow in a riffle of constant depth is related to the distribution of macroinvertebrate taxa with well-understood flow preferences (e.g. Wellnitz *et al.*, 2001). In contrast, several hydraulic variables (including measures of turbulence) may be more appropriate for studies that are performed in areas of complex flow (e.g. Bouckaert and Davis, 1998) or ones that relate flow to a variety of macroinvertebrate taxa and functional feeding groups (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001).

There are definite disadvantages and advantages to the use of simple hydraulic variables that describe bulk flow, such as mean velocity, compared to the use of variables that describe near-bed flow, such as shear velocity. Simple hydraulic variables such as mean velocity are difficult to compare between different systems (see p.17 of section 1.1.2) and do not necessarily reflect the force or velocity of near-bed flow experienced by benthic macroinvertebrates (Statzner *et al.*, 1988). However, unlike near-bed flow, properties of bulk flow can be measured easily and accurately with standard methods (section 1.1.2, p.14). More importantly, mean velocity or depth is often at least as closely related to macroinvertebrate data as measures of near-bed flow such as shear velocity, Froude number and roughness Reynolds number (see correlations with mean velocity in Statzner *et al.*, 1988; Matthäi, 1991; Quinn and Hickey, 1994; Doisy and Rabeni, 2001; and relationship with depth in Rempel *et al.*, 2000). The relationship of mean velocity and depth to macroinvertebrate distribution may be related to the fact that these simple hydraulic variables that describe near-bed flow are related to other hydraulic variables at many study sites (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001).

There are different methods of data analysis that can be used to relate hydraulic variables to macroinvertebrate data. Hydraulic variables can be individually related to macroinvertebrate data, for example by using correlation matrices to relate the densities of different taxa to the values of each hydraulic variable (e.g.Quinn and Hickey, 1994). Alternatively, statistical analysis can be used to determine the mathematical combination of hydraulic variables most closely related to macroinvertebrate data. Statistical methods applied in this approach include multiple regression (e.g. Lloyd and Sites, 2000; Quinn and Hickey, 1994); gradient analysis (which can be used to relate multiple hydraulic and macroinvertebrate community variables simultaneously; e.g. Doisy and Rabeni (2001)); and the Joint Preference Factor method (e.g. Gore and Judy, 1981; Orth and Maughan, 1983). The Joint Preference Factor method develops statistical models to predict invertebrate data based on the values of certain hydraulic variables at which the peak values of macroinvertebrate measures (e.g. density or diversity) occur (Gore, 1978; Gore and Judy, 1981).

The use of hydraulic variables in statistically pre-determined combinations can often predict macroinvertebrate densities with greater certainty than either simple or dimensionless hydraulic variables on their own (Orth and Maughan, 1983; Quinn and Hickey, 1994; Statzner *et al.*, 1988). However, models developed using these approaches can involve complex data analysis and can be difficult to interpret and use. For example, models developed in one stream may not predict macroinvertebrate densities with high certainty in other streams with different environmental conditions (Statzner et *al.*, 1988; Quinn and Hickey, 1994; Statzner *et al.*, 1998).

1.4 Direct effects of surface flow on macroinvertebrates

Relationships between macroinvertebrate distribution and flow conditions can be caused by direct effects of flow, indirect effects of flow (discussed in section 1.7, p. 51) or by spurious correlation of flow with other factors that affect habitat selection. Flow is considered to affect macroinvertebrates directly when individuals are influenced by the physical properties of flow (Hart and Finelli, 1999).

1.4.1 Forces of near-bed flow experienced by macroinvertebrates

Macroinvertebrates living on the surface of the streambed in hydraulically rough flow experience different forces, including lift (a force directed away from the streambed), and drag (a force directed downstream that is related to shear stress on a defined area, see section 1.1.2, p.15; Statzner and Holm, 1989). The drag on an individual macroinvertebrate consists of two components, skin friction, which imposes a shearing force over the entire body surface area, and pressure drag, which pushes body surfaces facing upstream in a downstream direction (Vogel, 1994).

The values of lift, skin friction, and pressure drag acting on the individual are affected by several factors. Each force increases with the velocity of flow and the body size of the individual, and is also influenced by the macroinvertebrate's shape and orientation compared to the main direction of flow. However, the exact nature of this relationship varies with the type of force (Vogel, 1994; Statzner and Holm, 1989). For example, most stream macroinvertebrates are thought to experience much more drag than lift, and may need to expend more energy to avoid being pushed downstream than to avoid being swept upwards off the substrate surface. However, individuals with large, dorsoventrally flattened bodies, that hold themselves positioned parallel to the substrate, may be strongly affected by lift. Overall, the direct effects of near-bed flow should vary the most among macroinvertebrates as body size changes during growth, but may also vary with other factors including body shape (Statzner *et al.*, 1988).

1.4.2 Potential mechanisms for direct effects of flow on macroinvertebrate distribution

Flow can influence macroinvertebrate distribution directly by affecting habitat suitability and the movement of individuals between different patches of streambed (streambed areas smaller than entire sections of a stream). Near-bed flow can influence the suitability of streambed surface habitats by affecting the macroinvertebrate's ability to move and feed and the energetic costs of these activities (review in Hart and Finelli, 1999). For example, Bournaud (1975) found that as velocity in an experimental flume was increased, the upstream walking of a cased-caddisfly slowed and took more energy to accomplish. High energetic costs may lead the macroinvertebrates to change their behaviour, for example, to move upstream or to drift (to be transported downstream in the water column) to seek more suitable habitat (Gore, 1994; Lancaster and Mole, 1999). Subsequently, the paths travelled by drifting macroinvertebrates can be influenced by the pattern of bulk flow. For example, macroinvertebrate drift can be affected by mean velocity since velocity can influence the distance that macroinvertebrates travel before returning to the substrate (Allan, 1995; Lancaster *et al.*, 1996).

The direct effects of flow on macroinvertebrate distribution are expected to vary among different categories of macroinvertebrates. For example, some taxa are better adapted to inhabit areas with faster velocities and stronger forces of near-bed flow (Vogel, 1994) than others. Also, certain macroinvertebrates are able to reduce the distance they drift by actively swimming towards the substrate (Lancaster, 1999).

1.4.3 Evidence supporting direct effects of flow on macroinvertebrate distribution

Experimental studies carried out in flumes or artificial channels or that use artificial substrate in natural channels, allow researchers to examine the effects of flow by controlling variation in different types of environmental characteristics. These studies have provided strong evidence that spatial or temporal variation in flow can cause variation in macroinvertebrate density and community composition (Beckett and Miller, 1982; Corrarino and Brusven, 1983; Irvine, 1985; Osborne and Herricks, 1987; LaCoursiere, 1991;Winterbottom *et al.*, 1997; Lancaster, 1999; Lancaster and Mole, 1999). Results from such experimental studies can then help researchers to interpret field patterns. For example, in one study, the relationship of macroinvertebrate density to spatial variation in near-bed velocity observed in streams was found to be consistent with the pattern observed in flumes that had little variation in other environmental factors (Lancaster, 1999).

1.5 Relationship of subsurface flow to macroinvertebrate distribution

The distribution of macroinvertebrates in the surface layer of the streambed can also be related to characteristics of subsurface flow, including the direction and velocity of interstitial flow. Few studies have examined the effects of vertical flow on surface-dwelling macroinvertebrates (Stanford and Ward, 1993; Plénet *et al.*, 1995; Boulton *et al.,* 1998). However, one study that did, found that certain macroinvertebrate taxa inhabiting the surface layer of a riffle were more abundant in upwelling zones than in downwelling zones (Pepin and Hauer, 2002). In addition, in several field experiments that evaluated interstitial flow, many macroinvertebrate taxa had higher densities in patches with smaller substrate particles where flow velocity was slower than in those with larger substrate particles (e.g. Rabeni and Minshall, 1977; Parker, 1989). These findings suggest that more study should be done to determine whether the distribution of macroinvertebrates in the surface layer of streambeds is often related to subsurface flow patterns.

Both surface and subsurface flow can be related to macroinvertebrate distribution, however the two kinds of flow may affect macroinvertebrates in different ways. Surface flow may affect macroinvertebrate distribution directly, whereas subsurface flow is thought to affect macroinvertebrate distribution mainly through indirect mechanisms related to water temperature and chemistry (discussed in section 1.7.3, p.54). However, Plénet *et al.* (1995) suggested that in areas with strong upwelling or downwelling, the force of vertical currents may be sufficient to move small interstitial invertebrates towards or away from the surface of the streambed.

1.6 Relationship of detritus and substrate to macroinvertebrate distribution

Macroinvertebrate distribution can also be related to characteristics of streambed substrate and detritus, but these factors can be difficult to distinguish. At an intermediate spatial scale, densities of certain categories of macroinvertebrates are often, but not always, positively correlated to amounts of detritus. Positive relationships between detritus and macroinvertebrate density have been observed for the total density of macroinvertebrates (Corkum, 1992; Friberg and Larsen, 1998; Doisy and Rabeni, 2001), deposit-feeding detritivores (e.g. Rempel *et al.*, 2000, review in Graça, 2001) and, in some cases, for taxa that do not feed on deposited detritus (e.g. Drake, 1984). The density of shredders which feed on coarse detritus tends to be closely related to the abundance of this food resource (e.g. Friberg and Larsen, 1998; Rempel *et al.*, 2000, review in Graça, 2001). The abundance of collector-gatherer taxa is often positively related to quantities of deposited detritus (e.g. Drake, 1984; Holomuzki and Messier, 1993), but can also be unrelated (e.g. Rempel *et al.*, 1999) or negatively related (e.g. Drake, 1984) to detritus.

The relationship of deposit-feeding detritivores to detritus is variable and can change with macroinvertebrate body size, detritus composition (Dobson, 1999, Graça, 2001), detritus particle size (Minshall *et al.*, 1982; Drake, 1984), and the season (Minshall *et al.*, 1982) and location (Drake, 1984; Corkum, 1992; Doisy and Rabeni, 2001) of observation. Therefore, relationships between deposit-feeding detritivores and detritus may be described more precisely by analysing different macroinvertebrate body sizes and types of detritus separately than by analysing them together. For example, Holomuzki and Messier (1993) found that the average body size of the collector-gatherer mayfly *Paraleptophlebia guttata* was larger in leaf litter deposits than on most particle sizes of bare mineral substrate. Minshall *et al.* (1982) found that the distribution of collector-gatherers among different areas of a stream (i.e. at a larger than intermediate spatial scale) was most strongly correlated with ultrafine particulate organic matter in the winter and coarse detritus in the summer .

Reasons for the difficulty in distinguishing the responses of macroinvertebrates to detritus or substrate (Culp *et al.*, 1983) include the fact that substrate size and the abundance of fine detritus are often confounded in both experimental (e.g. Rabeni and Minshall, 1977) and observational studies (e.g. Rempel *et al.,* 1999). Furthermore, macroinvertebrate distribution is often related to substrate characteristics including average substrate size, heterogeneity of substrate size, the amount of fine sediment, and the abundance of algal mats (Minshall, 1984). For example, de March (1976) found that macroinvertebrate community composition within a section of a stream was closely related to spatial variation in average substrate size and whether the interstices of coarser substrates were filled with fine sediment. Vegetation such as algal mats increase the structural complexity and surface area of streambed habitats and can harbour high total densities of macroinvertebrates and be the preferred habitat of certain taxa (review in Minshall, 1984; see algal mats in Dudley *et al.*, 1986).

1.6.1 Explanations for relationship of substrate/detritus to macroinvertebrate distribution

There are several possible explanations for associations between macroinvertebrate distribution and substrate/detritus characteristics. For one, macroinvertebrates are often attracted to areas with a high abundance of detritus because they are feeding directly on the detritus (Dobson *et al.*, 1992; Dobson, 1999). Detritus is an important food resource for stream macroinvertebrates, especially in small woodland streams (Cummins, 1992).

Predators may also be more abundant in areas with high detritus if these areas also have a high abundance of detritivore prey (see predator-prey associations in Williams and Smith, 1996).

Observed variation in detritivore-detritus relationships with characteristics of detritus, macroinvertebrate body size, and sampling season or location can also be explained by the use of detritus as a food resource. For example, shredder density may be more closely correlated to certain types of detritus since shredders prefer certain species of leaves and leaves that have been microbially conditioned (have altered nutritional value due to the action of aquatic fungus; see review in Graça, 2001). The relationship between detritivores and detritus may change with macroinvertebrate body size and sampling season or location because of changes in the portion of macroinvertebrate diets composed of detritus. Such changes can occur with larval growth or with the abundance of detritus at the time and location of sampling (Chapman and Demory, 1963; Hawkins, 1985). Also, the aggregation of macroinvertebrates to detrital food resources is expected to be the strongest when detritus is a limiting resource (review in Minshall, 1984). For instance, shredder populations and coarse detritus are thought to be closely related because leaf litter is often a limiting resource for shredders (Hildrew *et al.*, 1991; Dobson and Hildrew, 1992; Dobson, 1999).

Macroinvertebrates can also be associated with detritus for reasons that are not related to feeding. For example, macroinvertebrates can be attracted to detritus because detritus such as leaf litter or wood is being used as habitat or because detritus is being used as material to build macroinvertebrate cases or tubes (review in Minshall, 1984). Also, very fine size fractions of detritus and macroinvertebrate abundance may be correlated because the macroinvertebrates themselves produce very fine particles of detritus by defecation (Minshall *et al.*, 1982).

Relationships between macroinvertebrate density and substrate structure may be caused by habitat selection based on substrate characteristics or through the interaction between substrate and other environmental factors (review in Minshall, 1984). For example, burrowers may be unable to inhabit areas with large substrate particles such as boulders where burrows cannot be created (review in Minshall, 1984). In contrast, the presence of fine substrate decreases the abundance of many other macroinvertebrate habits by impairing important life functions. For example, fine sediment can reduce oxygen uptake by clogging gills or by reducing the availability of open interstices for habitation in coarse substrate (review in Waters, 1995). Algal mats can affect the density of different macroinvertebrate taxa negatively by reducing the area of bare mineral substrate available for collector-filterer attachment or positively by providing potential points of attachment for macroinvertebrates on algal filaments (Dudley *et al.*, 1986). Algal mats and substrate composition can also affect macroinvertebrates through interaction with other properties of the environment. For example, algal mats can enhance the accumulation of attached algal food resources and detritus (Dudley *et al.*, 1986). Substrate stability can also influence macroinvertebrate distribution (Miyake and Nakano, 2002) since many macroinvertebrates can't tolerate shifting substrates. Stability is affected by the interaction of flow with substrate size (see section 1.7.1, p. 51).

Evidence for direct effects of substrate size and detritus

Field experiments have shown that correlations between macroinvertebrate abundance and substrate/detritus can be attributed in part to the direct effects of these factors. For example, some experimental studies have found that detritus (Dobson *et al.*,

1992) or detritus and/or substrate size (e.g. Rabeni and Minshall, 1977; Reice, 1980; Parker, 1989) influenced macroinvertebrate distribution more than measured hydraulic variables. The relative importance of substrate size *versus* detritus to macroinvertebrate distribution has varied among experiments. For example, in one experiment using subsurface enclosures, the abundance of most macroinvertebrate taxa varied little with substrate size when the amount of interstitial detritus was similar among enclosures (Culp *et al.*, 1983). However, Reice (1980) found that many macroinvertebrate taxa showed preferences for certain substrate sizes regardless of the presence or absence of surface leaf litter. Finally, Barber and Kevern (1973) found that the density of some macroinvertebrate taxa such as mayflies varied with both substrate size and detritus, while other taxa such as oligochaete worms did not respond to either substrate or detritus manipulations.

1.7 Indirect effects of flow on macroinvertebrate distribution

Since characteristics of substrate and detritus can affect macroinvertebrate distribution directly, flow can affect macroinvertebrate distribution indirectly by influencing the distribution of these streambed materials. This aspect of the relationship between macroinvertebrate distribution and substrate/detritus can be better understood by examining the relationship between flow and substrate/detritus as well as that between macroinvertebrates and both flow and substrate/detritus.

1.7.1 Relationship between flow, detritus, and substrate structure

The movement of streambed material is heavily influenced by the properties of flow such as shear stress (the force acting parallel to the streambed per unit area). However, the relationship varies among different types of material. For example, lower shear stress is needed to move organic particles than mineral particles of similar size, since organic matter has lower density (Peterson, 1999). The shear stress required to erode substrate material tends to increase with particle size for size fractions coarser than sand, but is also influenced by substrate size composition and particle arrangement (see review of Shields curve in Gordon *et al.*, 1992).

Although the composition of the streambed substrate at any given time has some relationship to flow at that time, it may be more closely related to hydraulic conditions during past high discharge events when large amounts of material may have been transported and redeposited (Gordon *et al.*, 1992). Other features of the streambed such as algal mats are also affected by surface flow hydraulics (Statzner *et al.*, 1988). For example, algal mats can be greatly reduced by scouring during high discharge events (Dudley *et al.*, 1986). Also, there is often a lower proportion of fine substrate in riffles and other areas with high shear stress than in slower areas (Gordon *et al.*, 1992). Similarly, detritus often collects in areas that typically have slow average velocity (Minshall *et al.*, 1982; Jones, 1997) or maintain low shear stress during high discharge events (Hildrew *et al.*, 1991).

However, the accumulation of detritus is also affected by the interaction of flow with substrate particles. In areas with high velocities, coarser size fractions of detritus (e.g. greater than a few millimetres in diameter) can become pinned against obstacles such as rocks, and be retained despite high shear stress (Parker, 1989; Scarsbrook and Townsend, 1993). Thus, in some streams, the amount of coarse detritus is greater in riffles than in pools (e.g. Scarsbrook and Townsend, 1993). Below the surface of the streambed, fine detritus is most efficiently captured in the interstices of smaller substrate particles (e.g. gravel) where subsurface flow is relatively slow (Rabeni and Minshall, 1977; Parker, 1989). Therefore, measures of flow, detritus and substrate size composition are often confounded in streams, since substrate size affects the accumulation of detritus and the accumulation of both types of material is influenced by flow patterns.

Although the relationship between flow and the movement of large particles is relatively well understood, the relationship between surface flow hydraulics and the accumulation of very fine detritus and sediment is not. Minshall *et al.* (2000) found that the transport and deposition of very fine detritus (<0.1 mm) was poorly predicted by surface flow properties such as mean velocity, water surface slope and shear stress which work well to predict the movement of larger particles. Similarly, it is more reliable to predict substrate accumulation from hydraulic measurements such as shear stress for larger particles such as sand or gravel than for smaller particles such as silt (Carling, 1992b).

Factors such as fine-scale turbulence (Carling, 1992b) and subsurface vertical flow (Minshall *et al.*, 2000) may have an important influence on the accumulation of very fine material. For instance, fine material may be efficiently retained in downwelling zones where downwards flow draws suspended fines into the streambed (Lee, D.R. 2000, Waterloo Educational Services, Waterloo, Ontario, course notes for The Waterloo Stream Course). This hypothesis has not been tested in enough studies to draw any definite conclusions. Pusch (1996, cited in Franken *et al.*, 2001) found that the amount of fine organic matter "loosely associated" with substrate material was significantly higher in downwelling zones than in upwelling zones, whereas Boulton and Foster (1998) found that silt did not vary significantly between upwelling and downwelling zones.

1.7.2 Evidence of indirect effects of flow through modification of substrate/detritus

Descriptive field studies have shown associations between the abundance of macroinvertebrates and both flow and detritus characteristics (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001; Miyake and Nakano, 2002). These observations suggest that indirect effects of flow through modification of substrate/detritus could have an important influence on macroinvertebrate distribution. Several studies have provided evidence that the effects of flow on substrate/detritus can cause variation in macroinvertebrate distribution. For example, Hildrew *et al.*, (1991) used a combination of descriptive and experimental approaches to demonstrate that the frequency of high shear stress flows over streambed patches could affect shredder density by influencing quantities of leaf litter. Peckarsky and Penton (1990) found that experimental enclosures that reduced interstitial flow rates resulted in an increase of detritus and fine sediment as well as in the relative abundance of shredders. Finally, the erosion and deposition of substrate particles during floods can have an effect on local macroinvertebrate distribution. This effect can persist longer than the time required for macroinvertebrate density to recover from the direct physical effects of flow during floods, supporting the potential for flow to affect macroinvertebrates indirectly through modifying substrate structure (Matthaei and Townsend, 2000).

1.7.3 Other indirect effects of flow on macroinvertebrate distribution

Flow conditions can also affect macroinvertebrate distribution indirectly through modification of important habitat characteristics other than substrate and detritus. For example, surface flow can affect macroinvertebrate distribution indirectly by influencing dissolved oxygen levels (Eriksen *et al.*, 1996); the presence of odour cues in the water (reviewed in Hart and Finelli, 1999), scouring by suspended fine sediment (Culp *et al.*, 1986), rates of predation, the efficiency of filter-feeding, and the outcome of competitive interactions (reviewed in Hart and Finelli, 1999). The direction and discharge rate of vertical flow can affect macroinvertebrates indirectly due to differences in water temperature or chemistry between surface and subsurface water which can lead to corresponding differences in water quality between upwelling and downwelling zones (review in Boulton *et al.* 1998; Franken *et al.*, 2001; Pepin and Hauer, 2002). For example, algal biomass on the streambed surface can be more abundant in nitrogen-rich upwelling zones than in downwelling zones (Valett *et al.* 1994; Pepin and Hauer, 2001). This can lead to high abundances of certain grazing macroinvertebrate taxa in upwelling zones (Pepin and Hauer, 2001) because of differences in the abundance of food.

1.8 Importance of spatial structure in studies of stream macroinvertebrates

Spatial structure describes patterns of spatial variation for example, correlation of values of a given variable among nearby locations (auto-correlation; Legendre and Legendre, 1984) or whether distribution is random, sparse, or aggregated (i.e. clumped; Downing, 1991). Macroinvertebrate communities often have non-random spatial structure, such as the aggregated distribution of macroinvertebrate abundance over sections of a stream (Ulfstrand, 1967; Downing, 1991, Cummins, 1992; also see references in Downes *et al.*, 1993). Stream environments also have non-random spatial structure, since for example, nearby patch locations tend to have similar depth and substrate characteristics.

Insight into the relationships of macroinvertebrates with their environment can be gained by considering the locations at which samples were collected. For example, stream invertebrates at a given location may be related not only to environmental characteristics at that location, but also to the environmental characteristics in locations centimetres to metres away (macroinvertebrates in Lancaster and Mole, 1999; Beisel *et al.*, 2000; smaller invertebrates in Palmer *et al.*, 2000). Examining spatial structure can also help to elucidate the possible causes of unexplained variation in community data. For example, spatial variation in community data that is not related to spatial variation in abiotic variables such as flow, substrate and detritus, may be related to biotic interactions affected by proximity such as predation or reproduction (Ulfstrand, 1967; Borcard *et al.*, 1992). For example, macroinvertebrate prey may aggregate to help avoid predation (Rasmussen and Downing, 1988) and groups of recently hatched macroinvertebrates can be found close to egg cases (discussed in Ulfstrand, 1967).

1.9 Review of descriptive field studies similar to this study

Several previous studies similar to this study have compared macroinvertebrate distribution at an intermediate spatial scale to both hydraulic variables and detritus and/or substrate size. Overall, these studies have suggested that hydraulic variables are better predictors of macroinvertebrate community composition and of the densities of some taxa than detritus or substrate composition For example, in a study of macroinvertebrate distribution along gravel bars in the Fraser river (Rempel *et al.*, 2000), a depth-related gradient in hydraulic variables such as shear velocity was more closely associated than detritus or substrate size to community taxonomic composition. In their study, the density of taxa that typically inhabited the streambed surface or did not feed predominantly on deposited detritus was also most closely associated with hydraulic variables (Rempel *et al.*, 2000). Similarly, Doisy and Rabeni (2001) concluded that mean velocity was the best overall predictor of macroinvertebrate community composition in a gravel-bed river, and Orth and Maughan (1983) concluded that hydraulic variables (such as mean velocity, depth and Froude number) were better predictors of the densities of most taxa found in riffles of a warm-water stream than substrate size.

In contrast, other studies have found that macroinvertebrate densities were more closely related to detritus or substrate than to hydraulic variables. For example, Drake (1984) and Miyake and Nakano (2002) found that the variation in densities of macroinvertebrate taxa at an intermediate spatial scale was better predicted by detritus than by flow velocity (mean velocity in Drake, 1984: Dr. J. Drake, 2003, Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, USA Personal Communication; velocity measured at a constant depth in Miyake and Nakano, 2002). Also, Lloyd and Sites (2000) found that the distribution of riffle beetle larvae (Elmidae) was more closely related to measures of substrate size than to hydraulic variables.

However, it is difficult to draw any definite conclusions about the relative importance of flow *versus* substrate/detritus to macroinvertebrate distribution from a limited number of studies. For example, the relationship of macroinvertebrate distribution to each type of environmental variable is difficult to distinguish in streams where flow and substrate/detritus characteristics are closely correlated (Rempel *et al.*, 2000; Doisy and Rabeni, 20001). Also, the use of different methodologies among studies means that the results from these studies are not strictly comparable. For example, unlike Doisy and Rabeni (2001), Drake (1984) measured only one hydraulic variable and collected benthic samples to a much greater depth below the surface of the streambed. Therefore, additional studies are needed that relate macroinvertebrate distribution to environmental characteristics using standard or commonly used methods to evaluate both flow and substrate/detritus in detail.

1.10 Role of descriptive field studies in stream ecology

Descriptive field studies play an important role in relating macroinvertebrate distribution to flow, substrate and detritus. They allow us to find patterns and to test hypotheses about these patterns using controlled observations (Cox, 1996). In addition, field studies are crucial for identifying stream ecosystem properties that result from the interaction of different components ("emergent properties"; Odum, 1977). For example, the indirect effect of flow on macroinvertebrate distribution through modification of streambed substrate and detritus would not be apparent in studies performed in flumes that do not contain both moveable streambed material and macroinvertebrates.

However, descriptive studies relating macroinvertebrate distribution to environmental characteristics such as flow have certain limitations including the problem of disentangling effects of inter-correlated environmental variables (see discussions in Minshall, 1984; Statzner, 1981). In descriptive studies, it is often difficult to distinguish between the *active selection* of habitat characteristics by macroinvertebrates and the *association* (i.e. correlation) of macroinvertebrates with habitat characteristics for other reasons (Olabarria *et al.*, 2002).

Thus, experimental studies are often performed after descriptive studies to establish whether or not observed patterns reflect cause and effect (Cox, 1996). For example, some studies relating macroinvertebrate distribution to flow and substrate or detritus have successfully combined descriptive and experimental approaches to establish both the nature and cause of relationships between macroinvertebrates and environmental conditions (e.g. Holomuzki and Messier, 1993; Hildrew *et al.*, 1991). In conclusion, although experimental studies are often needed to establish the cause of relationships between stream macroinvertebrates and environmental conditions, descriptive field studies are needed to discover relationships that are relevant.

2. Evaluation of methods to characterize near-bed flow

2.1 Introduction

Near-bed flow has a strong influence on streambed environments since it affects both substrate composition and the distribution of benthic organisms (Hart and Finelli, 1999). Two key hydraulic variables for characterizing near-bed flow are shear velocity and roughness (Nowell and Jumars, 1984). Shear velocity and roughness are interrelated but not redundant since shear velocity should increase with roughness, but is also expected to increase with mean velocity and decrease with depth (Smith, 1975).

Shear velocity and roughness are rarely measured in studies of stream ecology because there are no ideal methods of measurement for the intermediate spatial scales that are often of interest (Nowell and Jumars, 1984; Ackerman and Hoover, 2001). Methods of measurement that are practical enough to be used by stream ecologists, such as those that have low cost and invasiveness, perform better in some streams than others (Lancaster and Hildrew 1993; Quinn and Hickey, 1994) and are considered unreliable by some experts (Carling, 1992a; Nikora *et al.*, 1998).

The standard method of determining shear velocity in streams, through calculation from velocity profile measurements, is time-consuming and difficult to apply in certain conditions such as shallow depths (Statzner and Müller, 1989; Carling, 1992a). In addition, since velocity profiles are measured at a single point over the streambed, they may not reflect shear velocity within an entire patch (areas larger than a point but smaller than entire sections of a stream; Hart *et al.*, 1996), especially in areas of coarse substrate with high roughness (Frutiger and Schib, 1993). This can be problematic in studies where point measurements of shear velocity are to be compared with measurements or samples taken over a larger area, such as benthic samples.

The alternative methods proposed for evaluating shear velocity in streams to overcome the limitations of velocity profiles (e.g. FST hemispheres and using other hydraulic variables as indicators of shear velocity; described in section 1.1.3, p. 19) also have potential disadvantages. For example, FST hemispheres are difficult and time-consuming to use, and disrupt the stream bottom. The use of other hydraulic variables as indicators of shear velocity is a simple and practical method but relies on the close correlation of shear velocity to the measured hydraulic variables (e.g. Statzner *et al.*, 1988; Lancaster and Hildrew, 1993; Quinn and Hickey, 1994). Also, some equations that are used to predict shear velocity from the values of these variables may not work well at intermediate spatial scales (Carling, 1992a).

Two common methods for evaluating roughness in studies of stream ecology are to look at how the height of the streambed surface varies within a patch or to look at the overhead width (diameter) of substrate particles within a patch. Roughness values determined from the overhead width of substrate particles can be obtained more quickly and with less disturbance to the streambed than those obtained from streambed height (Statzner *et al.*, 1988). The few studies that have compared values of width-based and height-based roughness measurements on an intermediate spatial scale (e.g. Statzner *et al.*, 1988, Quinn and Hickey, 1994) have found that the values were correlated. However, it is not yet known if roughness measurement based on substrate particle width can be applied to streams with different characteristics of streambed form.

The objective of this methodology component of the study was to select methods for characterizing spatial variation of shear velocity and roughness among patches (circles of 0.06 m^2) of streambed at the West River sites where macroinvertebrates would later be sampled. The main focus was to select methods that give reliable results but be as simple and noninvasive as possible. The reliability of alternative methods of measuring shear velocity will therefore be evaluated by comparing the results to results obtained from the standard method of calculation from velocity profiles. Based on previous studies, I expect the values of shear velocity from velocity profiles to be correlated to results from the most widely used alternative methods tested in this study (FST hemispheres and the use of mean velocity or a combination of mean velocity and roughness as shear velocity indicators). This study will also examine the applicability of the velocity profile method to an entire patch by exploring the spatial variation of shear velocity determined from profiles within patches. Specifically, the hypothesis that variation in shear velocity within a patch increases with patch roughness will be tested since it is expected that this factor will limit the usefulness of the velocity profile method. There is no reliable standard method for accurate measurement of roughness in natural channels. Therefore, the decision of whether to measure roughness based on streambed height or substrate particle width will be made by testing the hypothesis that width-based measurements will give similar results to height-based measurements, and by testing if either measure of roughness would be more useful for predicting shear velocity from values of mean velocity, depth and roughness.

2.2 Methods

Both the comparison of methods of measuring near-bed flow and the exploration of potential variation of shear velocity within patches were performed in two phases involving different locations. In the first phase, measurements were taken at three "test" sites in three different test streams so that a wide range of flow conditions could be evaluated. Data from the first phase were used to help determine data collection in the second phase. For example, results from the first phase were used to refine measurement procedures and to select a method of measuring shear velocity for further testing.

In the second phase, the selected method of measuring shear velocity was tested at the West River riffle and run study sites during different seasons to see if results there would be similar to those from the test streams. In addition, the second phase included a second survey to further explore the extent of spatial variation in shear velocity (from profiles) in patches with different levels of roughness.

2.2.1 Site Description

The test stream sites surveyed during the first phase (Clyde River site, Westmoreland River site and the test site on the West River) and the main study sites, which are on a branch of the West River upstream of the test site, are all located in the south-central region of Prince Edward Island, Canada (Table 2.1, Fig 2.1). The test sites and study sites were wadeable riffles or runs in channels with wetted widths from 5 to 19 m (Table 2.1). At most sites, the substrate ranged in size from fine sand to boulders (see Table 2.2 for definition of substrate size categories used in this chapter). Within all sites, hydraulic measurements were restricted to areas with relatively simple flow structure in order to satisfy the assumptions of certain methods and to avoid complex flow patterns which are difficult to model. Flow structure was considered to be relatively simple if the channel shape favoured uniform or approximately uniform flow (i.e. the banks were approximately parallel and the channel did not bend sharply; Carling, 1992a), and if the depth was greater than three times the average height of streambed projections. The latter criterion was used because streambed projections that are high relative to the water depth increase the complexity of flow, especially in areas

Table 2.1. Location and channel width of test sites on test streams and main study sites on the West River.

River/site	**Geographical co-ordinates**	**Stream order[a]**	**Wetted width (m)**	**Number of patches**
Clyde River	63 15'57" W, 46 14'35" N	2nd	5 to 9	16
Westmoreland River, East Branch	63 28'46" W, 46 14'14" N	3rd	6	3
West River/test site	63 21'12" W, 46 12'23" N	4th	15 to 19	10
West River/riffle site of main study sites	63 21'03" W, 46 13'52" N	4th	4 to 5	10
West River/run site of main study sites	63 20'59" W, 46 13'48" N	4th	7 to 9	54

[a] *sensu* Strahler from 1:50,000 scale map[1]

REFERENCES
[1]Gordon *et al.*, 1992

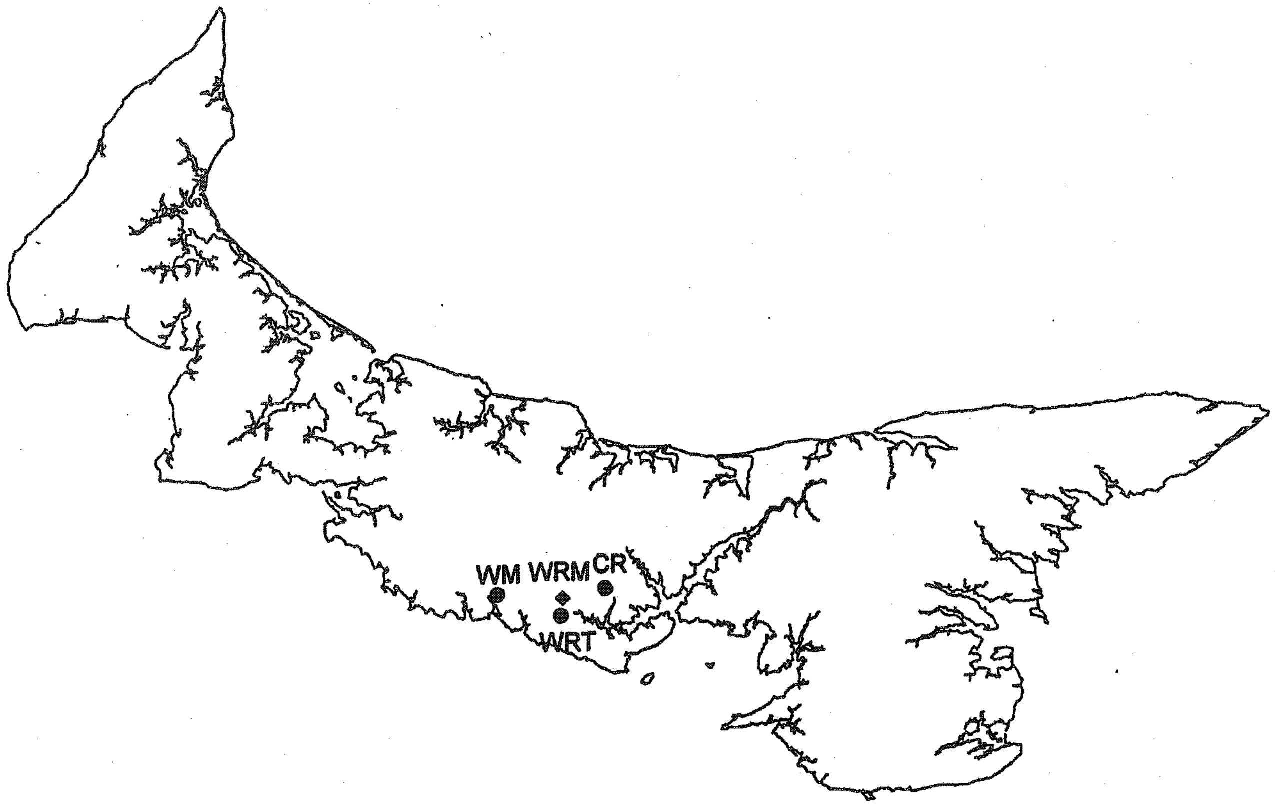


Fig. 2.1. Prince Edward Island, showing the location of study sites. WM = Westmoreland site, WRM = West River main study sites (riffle and run sites), WRT = West River test site, and CR = Clyde River.

Table 2.2. Substrate size classes used in this thesis. Size class names are used in chapters 2 and 3, and the phi value scale is used in chapter 3.

Diameter (mm)	Phi value [a]	Size class name [1]
>256	≤ -8	Boulder
128-256	-7 to -8	Large cobble
64-128	-6 to -7	Small cobble
32-64	-5 to -6	Large pebble
16-32	-4 to -5	Small pebble
8-16	-3 to -4	Coarse gravel
4-8	-2 to -3	Medium gravel
2-4	-1 to -2	Fine gravel
1-2	0 to -1	Very coarse sand
0.250-1	2 to 0	Coarse-medium sand
0.250-0.063	4 to 2	Very fine-fine sand
0.063-0.00075	≥4	Silt and clay

[a]Phi value = $-\log_2$ (diameter in mm) [see2]

RERERENCES
[1]Gordon *et al.,* 1992; [2]Rempel *et al.*, 1999

of fast flow (Davis and Barmuta, 1989).

The main study sites on the West River were a fast upstream section of the river located to one side of an island (riffle site) and a large slower section (run site) downstream from the riffle site (Fig 2.2). The riffle site contained areas with higher mean velocity than any area of the run site, so was included in this study to extend the range of flow velocities characterized. The substrate size ranged from sand to small cobbles in the riffle site and from silt to boulders in the run site and the run site had a more gradual water surface slope then the riffle (Table 2.3). Each site was divided roughly in half transversely to create downstream areas which were surveyed in the summer ("summer downstream areas") before benthic samples were collected in these areas and the upstream areas which were surveyed in the fall ("fall upstream areas"; Fig 2.2), also before benthic sampling. The two areas of each site had similar channel geomorphology except that in the fall upstream area of the run site the boulders were flatter and median substrate size was larger than in the summer downstream area (Table 2.3). However, discharge was much higher when the summer downstream surveys were carried out than when the fall upstream surveys were performed (Table 2.4).

Measurement of characteristics for site description of main study sites

Slope and substrate size composition of the West River riffle and run sites were determined in August, 2002. Water surface slope was measured using a rod and a surveyor's transit set on a tripod to determine the change in elevation over a horizontal distance. Median substrate size was determined for each section from measurements of 98 substrate particles using the random walk method (Wolman, 1954; Newbury and Gaboury, 1993).

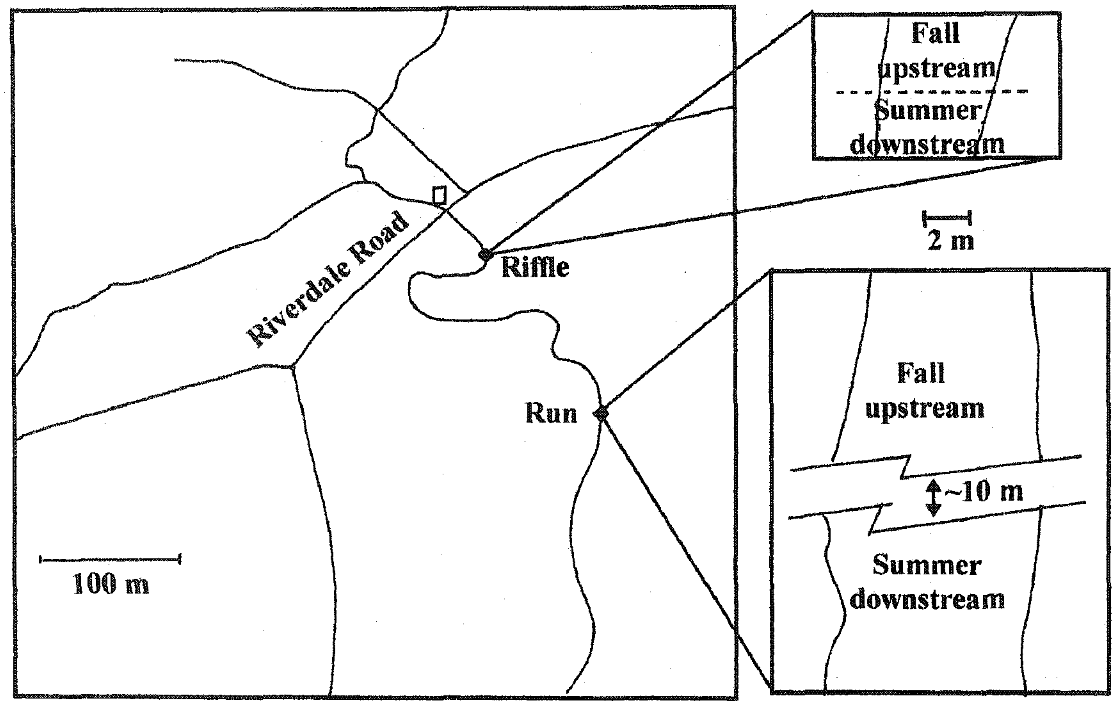


Fig 2.2. The main study site locations on the West River. (See Fig. 2.1, p. 66 for location of these sites in Prince Edward Island). The location of fall upstream and summer downstream areas is shown for both the riffle and run sites. The open rectangle indicates the location of the Environment Canada guaging station.

Table 2.3. Selected characteristics of channels at the riffle site and at each area/season of the run site on the West River.

	Riffle site	**Summer downstream/run site**	**Fall upstream/run site**
slope of water surface	1.4%	0.7%	0.8%
size range of substrate	sand to small cobble (0.25 to 128 mm)	silt to boulder (< 0.06 mm to > 256 mm)	silt to boulder (< 0.06 mm to > 256 mm)
median substrate size (cm)	2.5	2.7	6.3

Table 2.4. Surveys for comparison of values of mean velocity and shear velocity (from profiles) at main study sites (riffle and run sites) on the West River. On each survey date, measurements were taken in all patches of either the summer downstream or fall upstream areas of both sites. Location and discharge are listed for both sites on each survey date.

Date in 2001	Season/area	Site	Discharge (m^3/s) [a]
Jul. 3	summer downstream	run	1.08
Jul. 3	summer downstream	riffle	n/a
Jul. 31	summer downstream	run	0.79
Jul. 31	summer downstream	riffle	n/a
Sep. 21	fall upstream	run	0.54[b]
Sep. 21	fall upstream	riffle	0.59[b]
Oct. 31	fall upstream	run	0.55
Oct. 31	fall upstream	riffle	0.50

[a] Discharges at run site from[1], riffle site discharges from measurements taken in this study
[b] Note that the riffle site is expected to have lower discharge than the run site since it only channels part of the discharge from the run site.

REFERENCES

[1]Environment Canada, 2001

Continuous records of discharge levels were provided by an Environment Canada gauging station upstream of the riffle site at the Riverdale bridge (Fig. 2.2). Discharge levels for the riffle site, (which channelled only part of the stream water that passed the guaging station) were determined from mean velocity and depth measurements taken at regular intervals along a transect (Gordon *et al.*, 1992).

2.2.2 Comparison of methods of evaluating shear velocity and roughness at test sites

To evaluate methods of measuring roughness and shear velocity, results from standard methods were compared to those from simpler alternative methods. In the first phase, hydraulic measurements were taken at the test sites from May 22 to June 8 of 2001. All measurements were taken in patches that were circles of 0.063 m^2, which approximated the area of the benthic samples that would later be collected.

The choice of patch locations was restricted to depths of 5 to 40 cm due to the practical difficulties of taking measurements in shallower or deeper water. The location of patches at test sites was selected systematically to cover a matrix of combinations of mean velocity (0 to 0.5 m/s, 0.5-1 m/s and >1m/s) and roughness (visually estimated median particle diameter of 0-3 cm, 3-10 cm, and >10 cm). This selection system, based on Quinn and Hickey (1994), ensured that measurements were taken in a wide range of near-bed flow conditions and over a wide range of shear velocity values. At least three patches were measured for each combination of mean velocity and roughness except for the combination of the highest mean velocity and lowest roughness, for which only one patch could be found. Each patch was temporarily marked by placing coloured weights at the upstream and downstream patch edges while measurements were being taken.

Comparison of methods of measuring roughness

Two methods were tested for determining roughness values based on streambed shape. Although it is also possible to determine roughness values from velocity profiles, this method was not tested since previous studies have indicated that it is often unreliable in areas with large substrate size and high roughness (reviewed in Bray, 1991; Quinn and Hickey, 1994).

The first method of measuring roughness in this study was based on the more standard criterion of substrate height uneveness (height-based roughness; Davis and Barmuta, 1989) whereas the other simpler method was based on using substrate width as an indicator of streambed height (width-based roughness). To calculate height-based roughness, a profile was made of the streambed along the diameter of each patch in the direction of flow. This profile was constructed using a profiler based on a design by Ziser (1985), consisting of a row of sliding rods held between two pieces of wood (Fig. 2.3). The resulting profile was used to calculate height-based roughness using the following equation (Statzner *et al.*, 1988):

$$k_h = SD \times 2 \tag{2.1}$$

where k_h = height-based roughness (m), SD = standard deviation of streambed heights.

To determine width-based roughness, the streambed in each patch was photographed with a digital camera through a clear-bottomed plexiglass box. Widths of substrate particles (measured in the main direction of flow) and particle surface areas were evaluated from the photos with the software imaging package SCION®, using the patch markers to determine photograph scale (Fig 2.4). Two equations were used to calculate width-based roughness for each patch based on the portion of the patch area covered by substrate in different size classes. The first equation (the "simple equation",

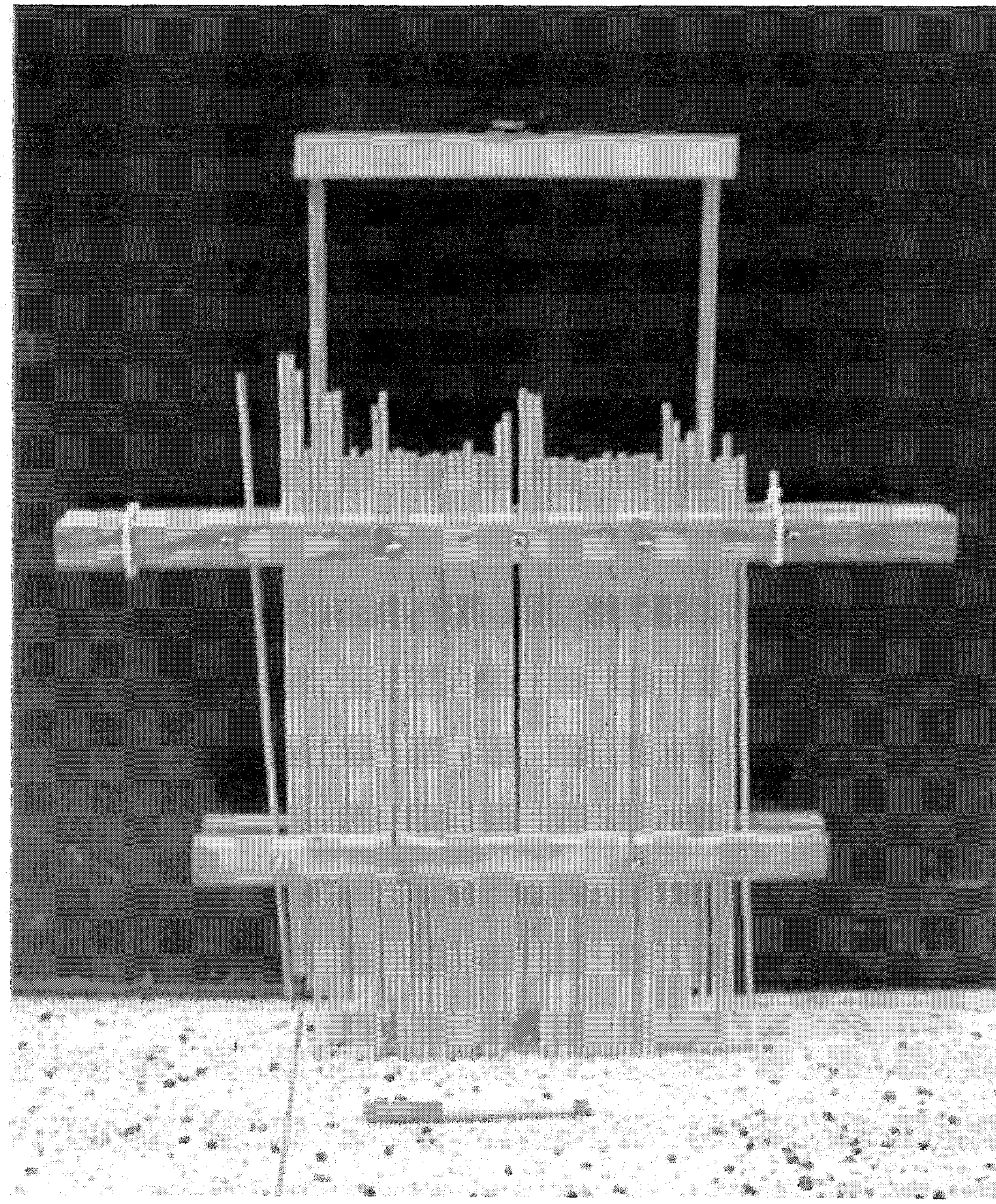


Fig. 2.3. Profiler used for height-based roughness measurements of the study patches. To obtain a profile of a patch, the bolts in the profiler boards were loosened, then the wooden dowel rods were allowed to slide downwards to trace the form of the streambed.

Fig 2.4. Example of digital photograph used in the determination of width-based roughness values. Temporary markers placed at the patch boundaries provided a scale for measurement and indicated the main direction of flow.

equation 2.2.; Winget,1985) was evaluated using approximate measurements to rank roughness on an ordinal scale. The second equation (the "complex equation", equation 2.3; Gibson *et al.*, 1998) provided a more detailed evaluation of roughness. Roughness values calculated using both these equations do not have units, and thus indicate relative rather than absolute values of roughness. The "simple" equation for width-based roughness (k_{w1}) is:

$$k_{w1} = (5 \times C_1) + (3 \times C_2) + C_3 / 9 \quad (2.2)$$

where k_{w1} = width-based roughness (simple), C_n (C_1, C_2 or C_3) = values determined from which substrate size classes covered the largest portion of the patch area, and the substrate size of those respective classes. The substrate size class represented by C is C_1 = most area covered, C_2 = second most area, C_3 = third most area. If there are only 2 size classes of substrate particles present in a patch, $C_2 = C_3$. If there is only one size class present, $C_1 = C_2 = C_3$. The value of C_n is C = 4 for substrate particle widths > 30.5 cm, C = 3 for 30.5-7.6 cm, C = 2 for 7.6-2.5 cm, C = 1 for < 2.5 cm. For example, if most of the patch area is covered by substrate particles > 30.5 cm in width, $C_1 = 4$.

The complex equation for determination of width-based roughness (k_{w2}) is:

$$k_{w2} = \sum (P_n \times C_n) \quad (2.3)$$

where k_{w2} = width-based roughness (complex), P_n = proportion of the patch covered by substrate particle size class C_n, and C_n = substrate particle size class values assigned based on substrate particle widths: C = 6 for substrate particle widths 400-25.5 cm, C = 5 for 25.0-15.5 cm, C = 4 for 15-6.5 cm, C = 3 for 6.0-2.5 cm, C = 2 for 2.5 - 2cm, C = 1 for <2 cm. For example, if 90% of the patch surface area is covered by substrate particle 400-25.5 cm and the remaining 10% of the patch is covered by substrate particles 25.0-15.5 cm, $k_{w2} = (0.9 \times 6) + (0.1 \times 5)$.

Comparison of methods of evaluating shear velocity at test sites

To compare different methods of evaluating shear velocity, results from alternative methods of measuring shear velocity were compared to values obtained using the standard method of velocity profiles. The alternative methods that were tested were the direct measurement of shear velocity using FST hemispheres, or the prediction of values of shear velocity from mean velocity, near-bed velocity, or the combination of mean velocity, depth and roughness.

Before velocity measurements were taken, the main direction of flow was determined by suspending a piece of flagging tape underwater. Then velocities were measured (time-averaged over 20 seconds) in the main direction of flow at a range of depths in the centre of each patch. Velocity measurements were taken with a Marsh-McBirney® electromagnetic flow meter which was set on a top-setting wading rod and attached to a Flo-Mate® computer with a digital display (Marsh-McBirney Inc., 4539 Metropolitan Court, Frederick, Maryland, 21704-9452, USA). To improve the precision of depth-settings, the wading rod was equipped with spirit levels to ensure that the rod was held perpendicular to the streambed. Except where the circular base of the wading rod was needed to prevent the rod from sinking into soft sediment, the base was removed to allow the lower part of the rod to fit into crevices between rocks. To increase the consistency of measurement technique among patches, the flow meter sensor was never positioned above the tops of large rocks.

Mean velocity was measured at 0.4 of the depth from the bed and near-bed velocity was measured at 2.5-3 cm from the bed. To construct the velocity profiles that were used to calculate shear velocity, velocity was measured at the near-bed velocity point then at 7 points taken at 0.8 or 1 cm intervals above the near-bed velocity point, followed by measurements taken at 1.6 or 3.2 cm intervals up to the water surface. Velocity was plotted against log depth and the relationship was examined for each profile. Shear velocity was calculated from the measurements closest to the bed for those patches for which a good log-linear relationship was evident (Pearson $r^2>0.5$) using equation 1.3, Table 1.2, p. 21.

Shear velocity was calculated from shear stress measured with FST hemispheres (KC Denmark, Holmbladsvej 19, DK-8600 Silkeborg, Denmark). The FST hemisphere readings were taken according to the instructions by Statzner and Müller (1989; Fig 2.5). Then, shear stress was determined based on the heaviest hemisphere that could be moved by the force of flow in that patch, using the table in Statzner *et al.* (1991). Shear stress values from FST readings were converted to values of shear velocity using equation 1.1 (p.15) and water temperatures that were measured on each survey date.

Hydraulic measurements were taken in a specific order to minimize disturbance to each patch. Velocity measurements were taken first because they caused little disturbance to the streambed, followed by roughness profiles, and photographs, then FST hemisphere measurements.

2.2.3 Testing of mean velocity as an indicator of shear velocity at the main study sites

Results from the first phase of the study indicated that mean velocity was a good indicator of shear velocity at the test sites, so further testing carried out at the main study sites on the West River focussed on this method without further testing of other

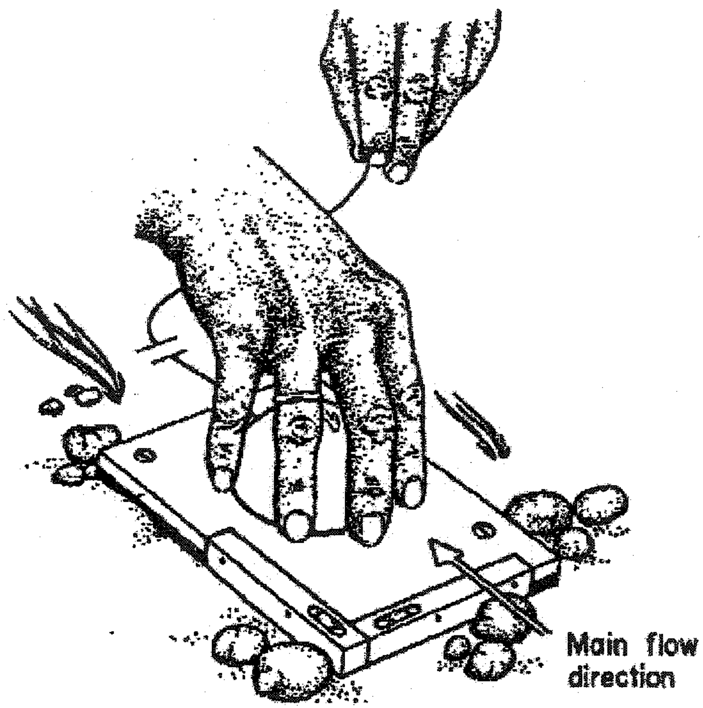


Fig 2.5. Positioning of FST hemispheres for determination of shear velocity (reproduced from Statzner and Müller, 1989).

alternative methods for evaluating shear velocity. In the second phase, mean velocity and velocity profiles were measured in the summer downstream areas of the riffle and run sites on Jul. 3, and Jul. 31, then in the fall upstream areas of both sites on Sep. 21 and Oct. 31 of 2001 (Table 2.4, p.71).

Unlike the selection of patch locations at the test sites (which were set up to cover a range of mean velocity and roughness), patch locations at the main study sites were set in a staggered grid design with patch centres set 1.3 m apart across transects placed at 2 m intervals along the river (Fig 2.6). Patches were located on each survey date by triangulating from stakes placed at the ends of each transect.

Hydraulic variables were measured as in the test rivers, except for two modifications in measurement procedure which were made based on results from the first phase. First, the procedure for mean velocity measurement was modified to improve accuracy. The method of measuring mean velocity at 0.4 of the depth is based on the assumption that the velocity profile of the entire water column has a logarithmic shape (Gordon *et al.*, 1992). Since this was not true in all test patches, mean velocity in all patches with water depth > 10 cm was calculated by averaging velocity measurements at 0.2 and 0.8 of the depth (Gordon *et. al.*, 1992):

$$U = 0.5\,(V_{0.2} + V_{0.8}) \tag{2.4}$$

where U = mean velocity (m/s), and V_n = velocity at n × depth from the streambed

The second modification involved the portion of the velocity profile used to calculate shear velocity. Shear velocity must be calculated from the bottom logarithmic portion of the velocity profile. Therefore, in the second phase, velocity profile measurements were taken at the lowest 5 points at 0.8 cm intervals (starting at 2.5-3 cm

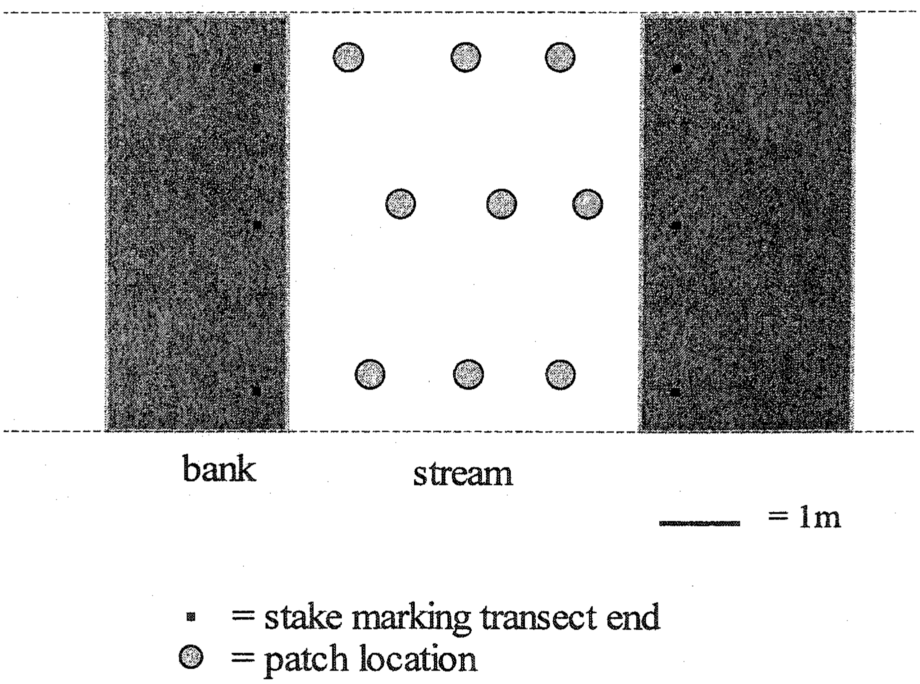


Fig. 2.6. Example of typical arrangement of patches at the riffle and run sites on the West River.

from the bed) where the profile had a logarithmic shape (Carling 1992a; and based on results from the first phase of the study).

2.2.4 Variation of shear velocity within patches

The variation of shear velocity within patches was explored during both phases of this study component by measuring velocity profiles at different points within a subset of the patches used for the comparison of different methods of evaluating near-bed flow. In the first phase (i.e. surveys in the 3 test streams) shear velocity was determined at three points in each of 10 test patches that were selected to cover a range of roughness and mean velocity in each patch. Velocity profile measurements were taken at the centre of each patch and at two other points arranged diagonally relative to the main direction of flow, so that the outside two points were located 10-15 cm from the centre point.

Results from the first phase resulted in the hypothesis that variation in shear velocity would be higher in patches with high roughness than in patches with low roughness. This hypothesis was tested in the second phase by taking velocity profile measurements in patches with contrasting levels of roughness in the summer downstream patches of the West River run site on July 9, 2001. Five "rough" patches (most of the area within a patch covered by rocks > 10 cm wide) and 5 "smooth" patches (most of the area within a patch covered by rocks < 10 cm wide) were selected with relatively homogeneous substrate size and velocity profiles were taken at 3 points in each patch as previously described. However, additional measurement points for velocity profiles were included in each patch in this second set of trials to examine how shear velocity varied with vertical position. Three points were positioned in crevices between larger rocks and the additional three measurement points were positioned at rock tops as close as possible to each crevice point (Fig 2.7).

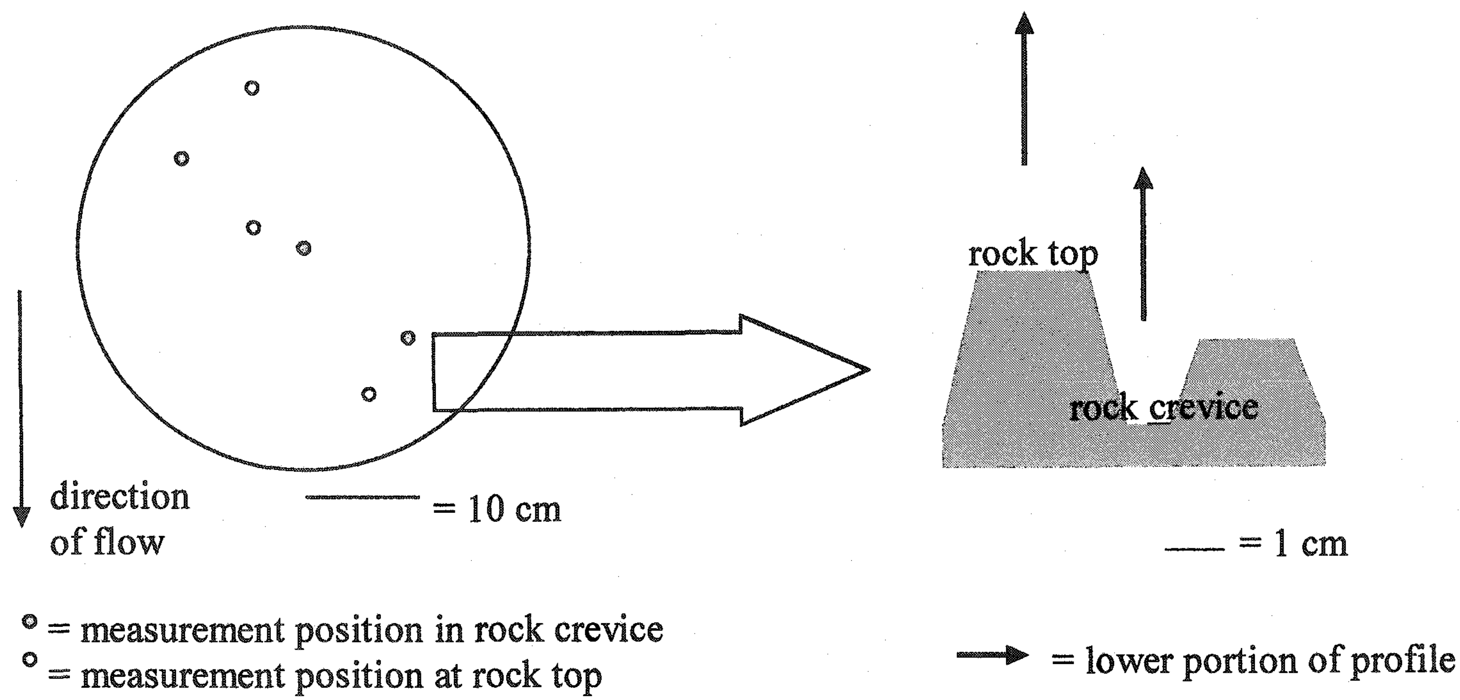
2.2.5 Variation of mean velocity within patches

The variation of mean velocity within patches was also examined in the same test patches used to explore the variation of shear velocity (from profiles), since like shear velocity, mean velocity is measured at a point. To compare the extent of variation in mean velocity and shear velocity within patches, mean velocity was measured at the same three locations as shear velocity in this subset of test patches.

2.2.6 Data Analysis

Selection of methods for comparing near-bed flow among patches

To select methods of measuring near-bed flow, the values of standard hydraulic measurements were compared to values from alternative methods using correlation. In the first phase, data from the different test streams were combined for analysis since patterns did not appear to differ among streams when the data were plotted. The relationship between shear velocity from profiles and mean velocity, roughness and depth was evaluated by stepwise linear regression. Mean velocity, roughness and depth can also be used to calculate values of shear velocity with the Keulegan equation (equation 1.4, Table 1.2, p.22). However, this approach was not appropriate for the measures of roughness tested in this study since width-based roughness values do not have units, and height-based roughness values are not equivalent to the measure of roughness used to develop the Keulegan equation (see Bray, 1991 and Carling, 1992a for details). In the second phase (i.e. testing at the 2 sites on the West River) data from



A. Horizontal positions of velocity profiles within a patch **B.** Vertical positions of velocity profiles

Fig. 2.7. Example of typical measurement positions within a patch for survey of spatial variation of shear velocity (from profiles). This survey was carried out in rough and smooth patches during the second phase of this study. A . Measurement positions within the patches varied slightly among patches, depending on the location of rocks. B. Measurements were taken at both crevices and tops of rocks.

riffle and run sites were pooled since patterns did not differ between sites. For correlation and regression analysis, variables were transformed if necessary to satisfy assumptions of linearity, error normality, and equal variance. Spearman correlation was used for variables that had non-normal distributions. For consistency, coefficients of determination (r^2 or r_s^2 values) are given for both Spearman and Pearson correlation in the results of this chapter (section 2.3, p. 86). Coefficients of determination obtained using Spearman and Pearson correlation are comparable for large sample sizes (e.g. sample sizes of >20 in this study) since they have similar values (Milton, 1999).

Variation of shear velocity within patches

For data examining the extent of spatial variation of shear velocity (from profiles) within the 10 test site patches, the range in shear velocity among the three measurement points in each patch was examined graphically. To explore whether the spatial variation in shear velocity increased with patch roughness or mean velocity, patches were plotted in order of their measured width-based roughness (complex equation; equation 2.3, p.76) as well as in order of measured mean velocity values.

For data collected in the second phase (measuring 6 points in each patch) patterns of spatial variation in shear velocity (from profiles) were examined using 2-way ANOVA to test for differences in "rough" *versus* "smooth" patches, among different patches of the same roughness type, and with vertical position (rock crevices *versus* tops). For analyses comparing the extent of spatial variation in shear velocity across patches, the coefficient of variation (CV) was calculated for the 3 measurements taken at the same vertical position in each patch. The appropriate statistical assumptions were checked for 2-way ANOVA, however groups in which n<5 were not tested for normality or equal variance prior to analysis, and 2-way ANOVA was assumed to be robust to mild departures from group normality if n was large and group sizes were close to equal (Zar, 1999). All statistical analyses were done with the software package SPSS® version 10.

Missing values

In some data sets, values were missing for certain hydraulic variables because measurements were missed by accident; the measuring equipment could not be positioned properly in the patch (for example, the flow meter sensor could not be lowered close enough to the uneven substrate surface); or, in the case of velocity profiles, there was not a good log-linear relationship between velocity and depth. For data analysis examining the variation of shear velocity within patches, the range and CV of shear velocity (from profiles) was not calculated unless values could be obtained for all three measurement points. All values of n are listed in the Results section.

2.3 Results

2.3.1 Comparison methods for evaluating near-bed flow

Roughness

A comparison of different types of roughness measurements taken at the test sites showed that both width-based roughness values calculated with the simple equation and width-based roughness values calculated with the complex equation were correlated to height-based roughness measurements (Pearson correlation, $r^2 = 0.57$ (same r^2 value for both), $P<0.01$, $n = 29$). The values calculated with the simple and complex equation were also closely correlated to each other (Pearson correlation, $r^2 = 0.90$, $P< 0.001$, $n = 29$).

Shear velocity

Some of the alternative methods of measuring shear velocity produced values that were moderately correlated to shear velocity determined from the standard method of calculation from velocity profiles. Shear velocity (from profiles) was most strongly correlated with mean velocity values and shear velocity values obtained using FST hemispheres (Table 2.5). Mean velocity and shear velocity values from FST hemispheres were also strongly correlated to each other ($r_s^2 = 0.83$, $P<0.01$, $n = 27$ for log shear velocity (from FST) and mean velocity). Near-bed velocity, width-based roughness (calculated with either equation), and height-based roughness were weakly or not significantly correlated to shear velocity from profiles (Table 2.5).

The use of a combination of mean velocity, depth and roughness values to predict shear velocity was tested using stepwise multiple regression. Mean velocity was the only variable that contributed significantly to the model predicting shear velocity from profiles (Fig. 2.8). The addition of depth or roughness (width-based roughness (simple equation), width-based roughness (complex equation), or height-based roughness) did not provide a significantly better model for predicting shear velocity than mean velocity alone ($P> 0.05$).

At the main study site, the pattern of correlation between mean velocity and shear velocity in patches varied between the two seasons/areas, which had different discharge levels. The correlation between mean velocity and shear velocity was similar to the test sites in the fall upstream surveys ($r_s^2 = 0.42, 0.51$ for Sept.21 and Oct.31 surveys), but

Table 2.5. Strength of relationships (Spearman's r) between shear velocity determined from velocity profiles and other hydraulic variables at test sites (n = 27).

Variable	[c]r_s^2
[a]shear velocity (from FST)	[b]0.51**
[a]mean velocity	0.55**
near-bed velocity	0.21*
[a]height-based roughness	0.13
width-based roughness (complex equation)	0.14
width-based roughness (simple equation)	0.13

[a] values of this variable log-transformed
[b] n = 26
[c] all correlations were positive, all values of shear velocity log-transformed, * = P<0.05, ** = P<0.01.

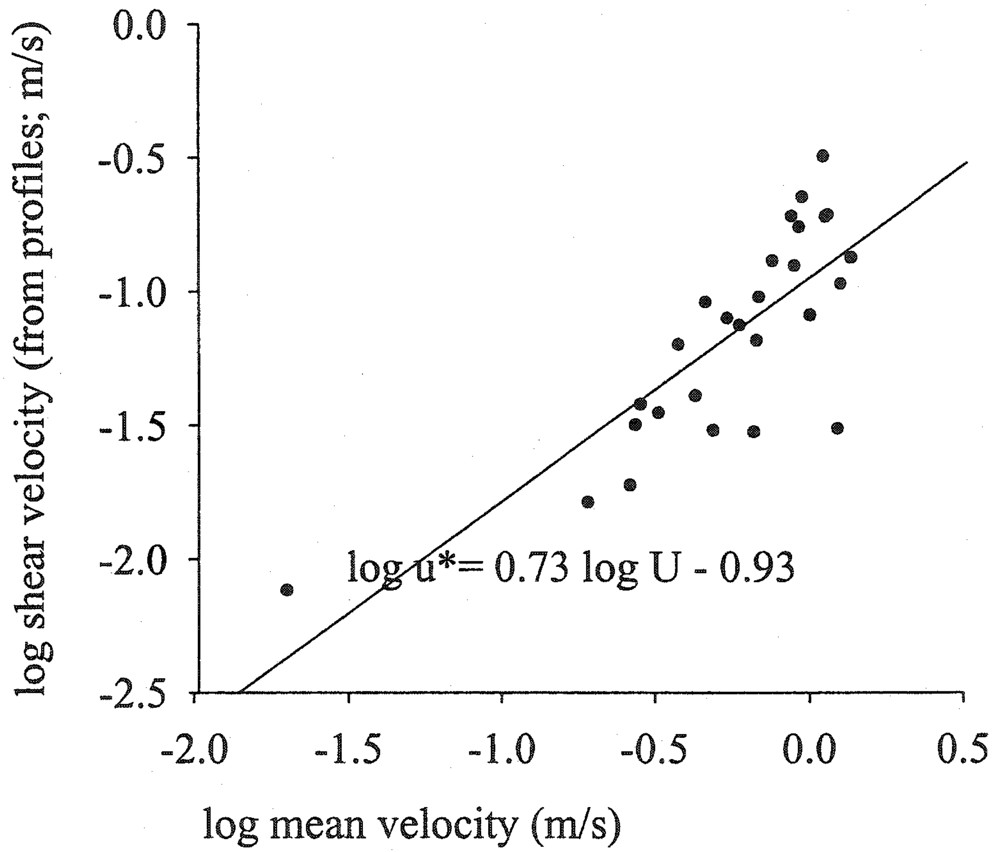


Fig. 2.8. Relationship of shear velocity (from profiles) to mean velocity in test patches ($P<0.001$, $n = 27$), u* = shear velocity (from profiles), U = mean velocity. (This regression model is still significant ($P<0.001$) if the outlying point with the lowest values of shear velocity and mean velocity is excluded).

was much weaker in the summer downstream surveys (r_s^2 = 019,0.25 for Jul.3 and Jul.31 surveys). In summer downstream surveys, which were taken when discharge levels were higher (Table 2.4, p.71), the average values of mean velocity and shear velocity in patches were higher than in fall upstream surveys (Table 2.6).

2.3.2 Variation of shear velocity (from profiles) within patches

The extent of spatial variation in shear velocity increased with patch roughness, as seen in data collected from test patches and patches at the main study site. The extent of spatial variation in shear velocity was considerable in at least some test patches with high roughness (maximum CV = 105%, Table 2.7, Fig 2.9), and did not appear to be related to mean velocity measured at the centre of each patch. For patches examined at the main study site, variation of shear velocity across patches (expressed as CV) was significantly higher in rough than smooth patches (2-way ANOVA, $P<0.05$, Fig 2.10). Values of shear velocity measured in one smooth patch were very low compared to values in other smooth patches (2-way ANOVA of patch × vertical position, $P< 0.05$ for patch, $P<0.05$ for difference of one patch with others in Tukey's HSD post-hoc test). Therefore, shear velocity measurements from that patch were excluded from the analysis of variation with vertical position so that these measurements would not dominate the observed relationships. The difference in shear velocity between rock tops and crevices was still greater in rough than smooth patches after data from this patch was excluded (2-way ANOVA, $P<0.05$, Fig 2.11).

Coefficients of variation were calculated to determine the relative magnitudes of the variation in mean velocity and shear velocity in each patch. Mean velocity varied much less than shear velocity (from profiles) within test patches (Table 2.7).

Table 2.6. Comparison of median values of hydraulic variables in summer downstream *versus* fall upstream surveys of main study sites on the West River (n=32, except where noted).

Hydraulic variable	**Survey date in 2001/Season/area of sites**			
	Jul.3/Summer downstream	Jul. 31/Summer downstream	Sep. 21/Fall upstream	Oct. 31/Fall upstream
depth (m)	0.24	0.20	0.22	0.23
mean velocity (m/s)	0.75	0.62	0.38	0.39
shear velocity from profiles (m/s)	0.094[a]	0.086[b]	0.065[c]	0.073[d]
width-based roughness	n/a	2.22	n/a	2.22

[a] n=28, [b] n =28, [c] n=30, [d] n=28

Table 2.7. Variation within patches of shear velocity (from profiles) *versus* mean velocity. Variation of each measure is expressed as the coefficient of variation (CV) among measurements taken at 3 points in each of 9 test site patches. Patches are listed in order of CV of shear velocity.

CV of shear velocity (from profiles)	**CV of mean velocity**
4%	2%
21%	3%
41%	3%
52%	18%
60%	8%
69%	5%
89%	11%
97%	26%
105%	9%

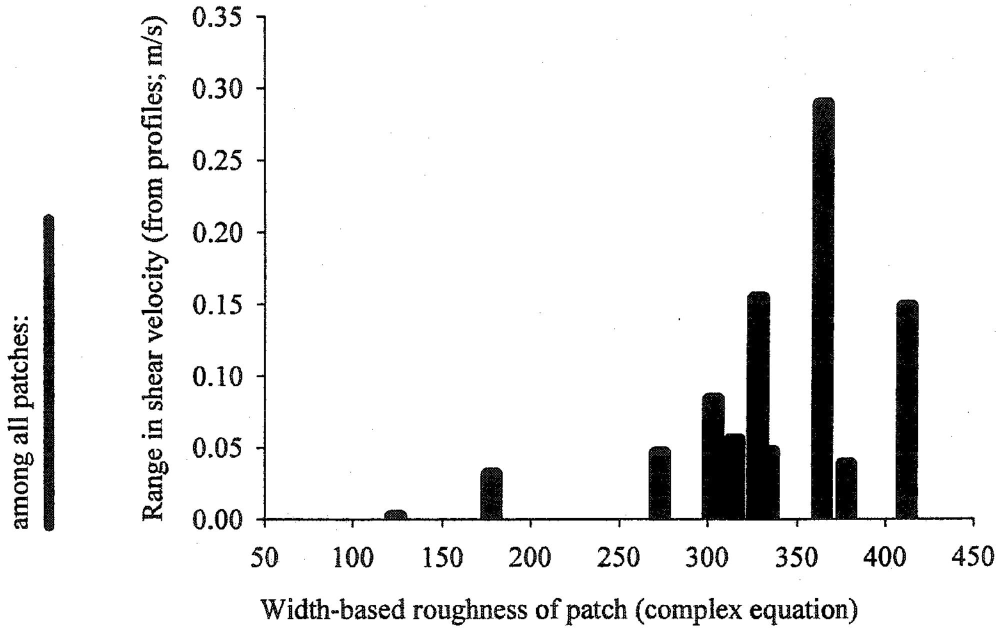


Fig 2.9. Spatial variation of shear velocity (from profiles) across test patches as related to patch roughness (width-based, complex equation; n=10). The range of shear velocity among the centre points in these patches is shown on the left for comparison.

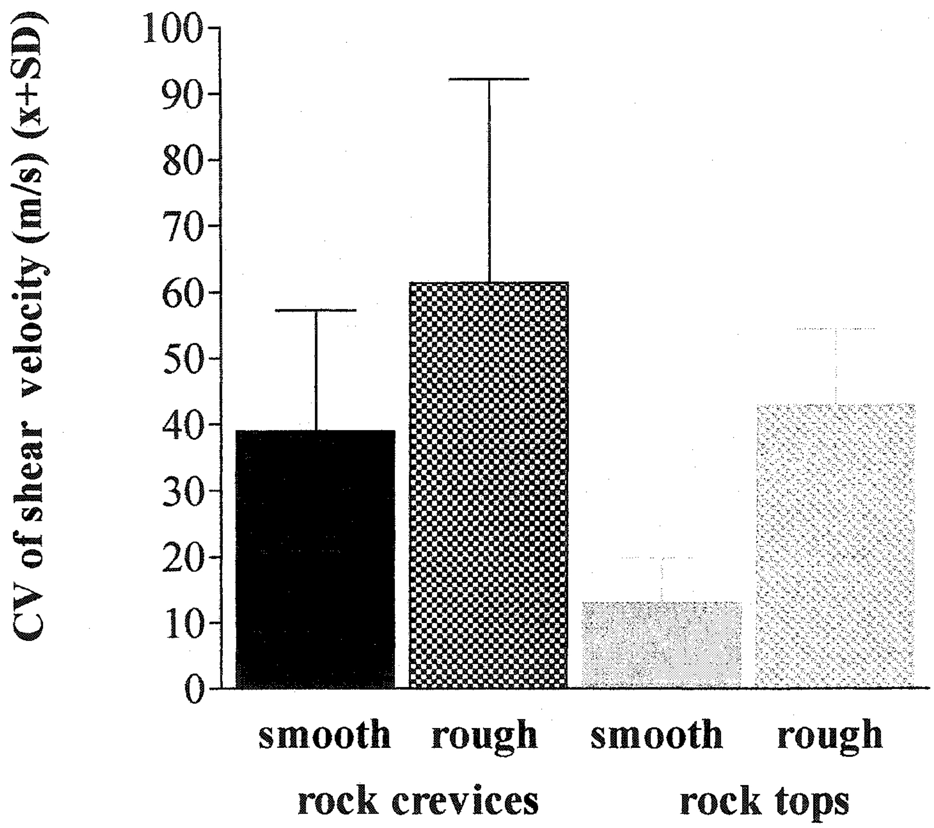


Fig. 2.10. Spatial variation of shear velocity (from profiles) across rough and smooth patches (expressed as coefficient of variation (CV) among 3 measurement points). The CV of shear is compared for measurements taken at either rock crevices or rock tops in patches of each type of roughness at the West River run site (2-way ANOVA, P<0.05 for patch roughness type, n = 5,5,4,2).

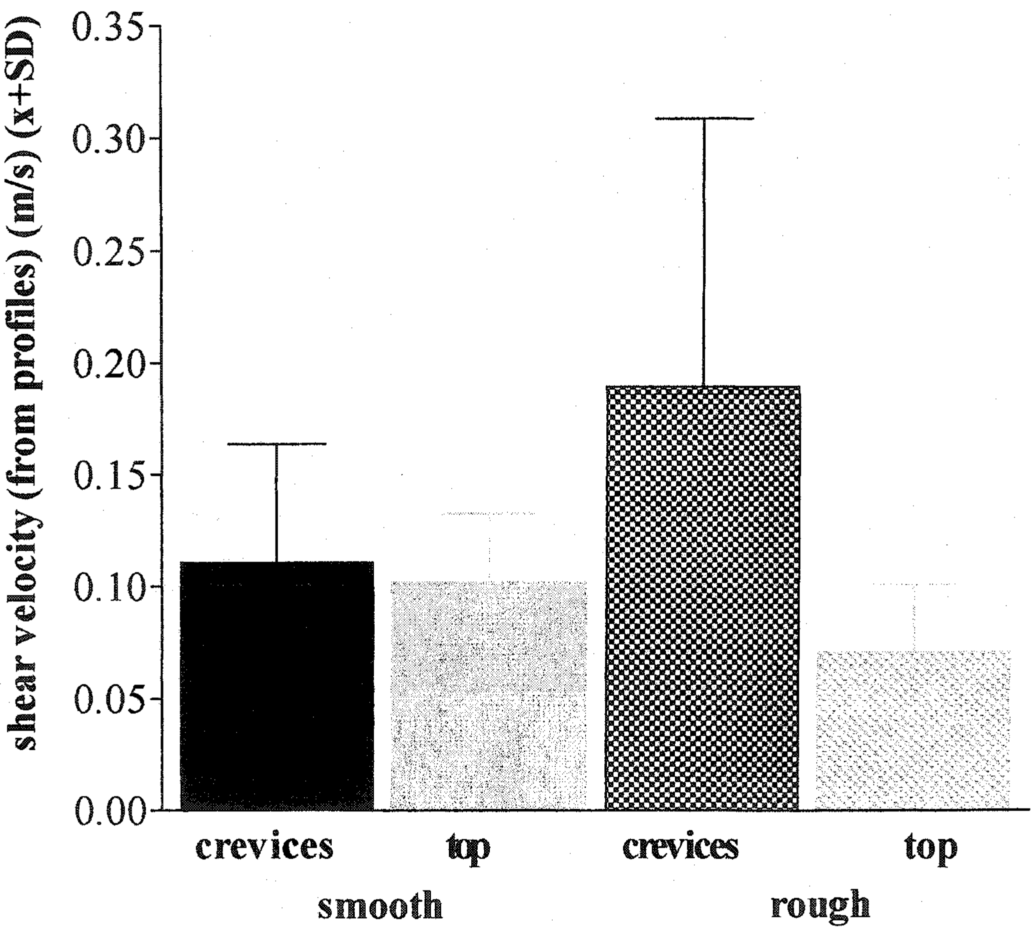


Fig. 2.11. Shear velocity values for crevices and tops of rocks in rough and smooth patches (2-way ANOVA, P<0.001 for vertical position, P<0.01 for vertical position*patch roughness type interaction n = 12,10,15,14). Patches were located in the West River run site.

2.4 Discussion

The focus of the methodology component of this study was to select the most appropriate methods for comparing near-bed flow among patches at the West River site in order to relate macroinvertebrate distribution to flow patterns. Some of the simpler methods of evaluating shear velocity and roughness were well correlated with more standard methods, suggesting that, at least in the West River, these methods provided good indicators of near-bed flow conditions.

2.4.1 Roughness

As hypothesized, width-based roughness determined using the simple equation of Winget (1985; equation 2.2, p.76) was a reliable and practical indicator of relative streambed height unevenness as determined from the profiler at the test sites. Other studies that compared width-based measurements of streambed patch roughness to height-based measurements using similar methods (Quinn and Hickey, 1994; Statzner *et al.*, 1988) also found significant correlations between the two measures. However, the correlations in those studies were weaker, suggesting that characteristics of streambed form and substrate particle arrangement at a given site can affect this relationship.

Width-based roughness had several practical advantages compared to height-based roughness determined with the profiler, including speed of measurement and lower disturbance of the streambed. Using the simple equation for width-based roughness greatly reduced the time required for the analysis of digital photos and gave results that were closely correlated to those obtained with the complex equation. However, width-based roughness calculated using the simple equation would not be appropriate for certain applications of roughness values. For example, in streams with similar substrate size composition among patches, the resolution of this method may be too coarse to compare roughness among patches, since resulting values of roughness could be identical for many patches. Also, since width-based roughness values are relative and do not have units, this method is not appropriate for comparison with roughness values calculated using different methods or for calculation of complex hydraulic variables, such as roughness Reynolds number.

2.4.2 Shear velocity

Mean velocity was a useful indicator of shear velocity in the test patches because it was correlated to the standard measurement of shear velocity from profiles and the measurement procedure was less time-consuming. Results from Quinn and Hickey (1994) also support using mean velocity as an indicator of relative shear velocity in streams. Surprisingly, when trials in the test streams were repeated at the main study sites, mean velocity was a good indicator of shear velocity (from profiles) in the fall upstream surveys, but not in the summer downstream surveys. The correlation between shear velocity (from profiles) and mean velocity may have been lower in the summer surveys due to the presence of more complex patterns of flow at the higher discharge levels present during the summer surveys.

Shear velocity values measured using FST hemispheres were closely related to shear velocity (from profiles) at the test sites, confirming the utility of the hemispheres in predicting shear velocity. However, compared to the measurement of mean velocity, the use of FST hemispheres is more time-consuming and causes greater disturbance to the streambed, which makes the hemispheres a less practical alternative. Also, results from this study and previous studies (Matthäi, 1991; Dittrich and Schmedtje, 1995) suggest that FST hemispheres may not provide a better indication of shear velocity values than mean velocity. Dittrich and Schmedtje (1995) propose several explanations for why FST hemisphere measurements may not be a better indicator of shear velocity than mean velocity. For example, like mean velocity, FST hemispheres may not reflect the effect of patch roughness on shear velocity, since the streambed is covered with a smooth level plate during measurement using FST hemispheres.

Since shear velocity is known to be affected by roughness and depth (Smith, 1975), the result that adding these variables to mean velocity did not improve the prediction of shear velocity (from profiles) was unexpected. However, this finding is consistent with results from Quinn and Hickey (1994), who found only a weak correlation between roughness and shear velocity among patches of streambed. For the surveys in this study, there are several possible explanations for this finding. For example, depth and roughness may not have been measured over a wide enough range to see any pattern related to the relative values of these variables (i.e. relative roughness). It is also possible that roughness measures in this study were not an accurate reflection of effect of the streambed form on near-bed flow within patches. For example, the methods used did not account for certain factors known to influence roughness such as large protruding rocks located upstream of the patch area (Nelson *et al.*, 1995). Probably the most important factor in this study, though, is that shear velocity measurements taken at a point could not be reliably compared to roughness values which were based on measurements taken over a transect of the patch or the whole patch area. This is because shear velocity (from profiles) varied considerably within at least some test patches with high roughness.

2.4.3 Variation of shear velocity within patches

Spatial variation of shear velocity within patches increased with patch roughness. The variation of near-bed flow is expected to increase with roughness, although this relationship can be modified by other factors such as average shear velocity (Nowell and Jumars, 1984). Results from other studies (which examined spatial variation of near-bed flow at larger spatial scales) found that variation in shear velocity (Biron *et al.*, 1998) and near-bed velocity (Palmer *et al.*, 1997) was higher in areas with coarser substrate than in areas with fine substrate.

Velocity profiles may not be a practical method of characterizing shear velocity in patches with high roughness. Results from this study indicate that velocity measured at a single point may not reflect average shear velocity in small patch areas even in sections of streams with relatively simple flow structure. However, velocity profile measurements taken at single points have been used to characterize shear velocity over patches of streambed in many studies comparing different methods of evaluating near-bed flow (e.g. Statzner and Müller, 1989; Quinn and Hickey, 1994) or examining the influence of near-bed flow on benthic macroinvertebrate distribution (e.g. Quinn and Hickey, 1994; Rempel *et al.*, 2000). Therefore, the use of single velocity profiles to characterize shear velocity within patches is probably an important source of error in many studies.

In this study, roughness measures based on substrate particle width were not useful for predicting average values of shear velocity, however, width-based roughness may be a useful as an indicator of small-scale variation in shear velocity. For example, values of width-based roughness could be used to help determine the number of velocity profiles measurements per area needed to accurately evaluate shear velocity in a patch. Also, while most studies of relationships between macroinvertebrates and near-bed flow focus on average conditions of near-bed flow in sampled patches, there is also a need for studies investigating how macroinvertebrates respond to spatial variation in near-bed flow (Palmer *et al.*, 1997, Hart and Finelli, 1999). In such studies, width-based roughness could provide a useful starting point for identifying patches with contrasting levels of small-scale spatial variation in near-bed flow.

2.4.4 Choice of methods for macroinvertebrate study component

One method of evaluating roughness and two methods of evaluating shear velocity were chosen for use in the macroinvertebrate component of this study. Width-based roughness determined from photographs of the streambed and calculated with the simple equation was chosen to compare roughness among patches because it was the most practical method tested and because values of width-based roughness were correlated to values from the height-based method.

Shear velocity determined from velocity profiles and mean velocity were chosen as measures for comparing shear velocity among patches. Since there are different advantages and disadvantages associated with each method, the use of both methods together may be complementary. Although the velocity profile method is considered more accurate for comparing shear velocity among points than measurements of mean velocity (Carling, 1992a), shear velocity (from profiles) may not have reflected average shear velocity in patches with high roughness. Measurement of velocity profiles at several points within each patch could be used to characterize shear velocity more accurately in patches with high roughness, however, this method was considered to be prohibitively time-consuming for use in this study. Therefore, although mean velocity was not as accurate an indicator of shear velocity (from profiles) in some summer downstream patches, mean velocity varied less within patches than shear velocity. Therefore, mean velocity may still provide a more accurate reflection of average shear velocity within patches with high roughness.

3. Relationship of stream macroinvertebrate distribution to detritus, substrate size and flow conditions in sections of the West River, PEI

3.1 Introduction

The distribution of benthic macroinvertebrates within a section of a stream is usually non-random and aggregated (Ulfstrand, 1967; Cummins, 1992). This variation in macroinvertebrate density can be related to spatial variation in environmental characteristics such as the amount of detritus and substrate composition (substrate/detritus) as well as flow (the physical properties of water in motion; Minshall, 1984; Statzner *et al.*, 1988). The interpretation of such relationships is complicated by different factors including the inter-relationship between substrate/detritus and flow, how macroinvertebrate response to environmental variables varies and the potential effects of biotic interactions on the spatial structure of macroinvertebrate distribution (Minshall, 1984; Borcard *et al.*, 1992; Rempel *et al.*, 2000; Doisy and Rabeni, 2001).

Substrate and detritus characteristics are often correlated with hydraulic variables since flow affects the distribution of these streambed materials (Hildrew *et al.*, 1991; Carling, 1992b; Gordon *et al.*, 1992). This inter-relationship makes it difficult to determine the relative importance of flow and substrate/detritus to macroinvertebrate distribution and whether flow is affecting macroinvertebrate distribution directly or indirectly (Hart and Finelli, 1999; Rempel *et al.*, 2000; Doisy and Rabeni, 2001). To begin with, variation in macroinvertebrate density can be related to different substrate, detritus and hydraulic variables (Minshall, 1984; Hart and Finelli, 1999). For example, macroinvertebrate densities in a patch of streambed can vary with the amount of detritus, substrate size composition, and the density of vegetation, such as algal mats (Drake, 1984; review in Minshall, 1984; Lloyd and Sites, 2000; and see discussion of algal mats in Dudley *et al.*, 1986). Spatial variation in macroinvertebrate densities can also be related to different hydraulic variables that describe near-bed or surface flow. Near-bed flow variables include shear velocity and roughness. Variables which describe the average properties of surface flow (bulk flow) include mean velocity, depth, and Froude number (e.g. Quinn and Hickey, 1994; Rempel *et al.*, 2000; Doisy and Rabeni, 2001). Patterns of subsurface flow, which can be described by vertical hydraulic gradient, may also be important to the distribution of macroinvertebrate density (Pepin and Hauer, 2002). In many cases, macroinvertebrate density is related to both substrate/detritus and hydraulic variables simultaneously. For example, collector-gatherers (which feed on deposited fine detritus) often increase in density with the amount of detritus, but decrease in density with increasing mean velocity or shear velocity (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001). In cases like these, density patterns could be caused by the direct effects of both substrate/detritus and flow on collector-gatherer density or reflect the indirect effect of flow through modification of substrate/detritus characteristics (Minshall, 1984; Hart and Finelli, 1999).

The relationship of macroinvertebrates to environmental conditions can vary among different categories of macroinvertebrates, including different functional feeding groups, taxa, body sizes, and habits (types of locomotion and streambed attachment; e.g. Wetmore *et al.*, 1990; Rempel *et al.*, 2000; Snook and Milner, 2002). For example, macroinvertebrate body size can affect relationships to both flow and detritus, since smaller individuals experience less drag (Vogel, 1994) and may consume smaller size fractions of detritus than larger individuals (Cummins and Merritt, 1996). The response of macroinvertebrates to detritus can also vary with the season or location of sampling, possibly due to changes in the availability of detritus (Corkum, 1992) or the portion of macroinvertebrate diet composed of detritus (Chapman and Demory, 1963).

Also, non-random patterns of macroinvertebrate distribution can be caused by biotic as well as abiotic (e.g. physical) factors. These biotic factors include predation, reproduction or competition (Borcard *et al.*, 1992). For example, recently hatched macroinvertebrates are usually found close to their egg case (discussed in Ulfstrand, 1967), but as they grow, they may move to avoid competition or predation. By examining the spatial structure of both the macroinvertebrate and the environmental data, it is possible to evaluate the relative importance of environmental conditions as compared to other factors in structuring macroinvertebrate distributions (Borcard *et al.*, 1992).

The main purpose of this component of the study is to describe the importance of hydraulic and substrate/detritus variables to spatial variation in the density of deposit-feeding detritivores in sections of the West River. Results from previous studies (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001; Miyake and Nakano, 2002), suggest that the densities of most deposit-feeding detritivores will be correlated to both hydraulic and substrate/detritus variables. I expect to find correlations between flow and substrate/detritus as well due to indirect effects of flow on deposit-feeding detritivore densities. For example, I expect both the density of collector-gatherers and the amount of fine detritus to decrease with shear velocity.

The secondary objectives of this study component include examining how relationships between macroinvertebrate density and environmental variables vary among different categories of macroinvertebrates, and whether the observed relationships are consistent between different locations and seasons. Certain groups of macroinvertebrates are expected to have different relationships with environmental characteristics. For example, unlike deposit-feeding detritivores, collector-filterers may have higher densities in areas of high velocity or shear velocity. Also, smaller individuals of deposit-feeding detritivore taxa may be more closely correlated to fine detritus and more abundant in areas of high shear velocity than larger individuals. I expect to find some different relationships between macroinvertebrate densities and environmental variables in different seasons and locations if there are large differences in environmental conditions such as detritus availability. Another secondary objective is to examine how location in the stream is related to the pattern of spatial variation in macroinvertebrate density and environmental variables. The distribution of macroinvertebrates in each stream section is expected to be non-random and aggregated, and this pattern is expected to be partly related to the pattern of spatial variation in flow and substrate/detritus.

3.2 Methods

3.2.1 Site Description

Macroinvertebrate habitat associations (i.e. correlations between macroinvertebrate density and environmental characteristics) were studied at two nearby sites on the West River (corresponding to the "main study sites" in chapter 2; Figs. 2.1 and 2.2, pp. 66, 69). The stream flow at the smaller upstream site had high velocities (riffle site; Fig 3.1) and the flow at larger downstream site had moderately high velocities (run site; Fig 3.2). These study sites were chosen partly because they were located close to each other so should have similar discharge patterns and because there were no dams upstream of the sites to alter natural fluctuations in discharge. Discharge in this section of the West River is typically highest during spring snowmelt and lowest from July to October, with an annual mean of 1.9 m^3/s (1989 to 1998 records, Environment Canada). Also, both

Fig 3.1. The riffle site of the main study sites on the West River, PEI.

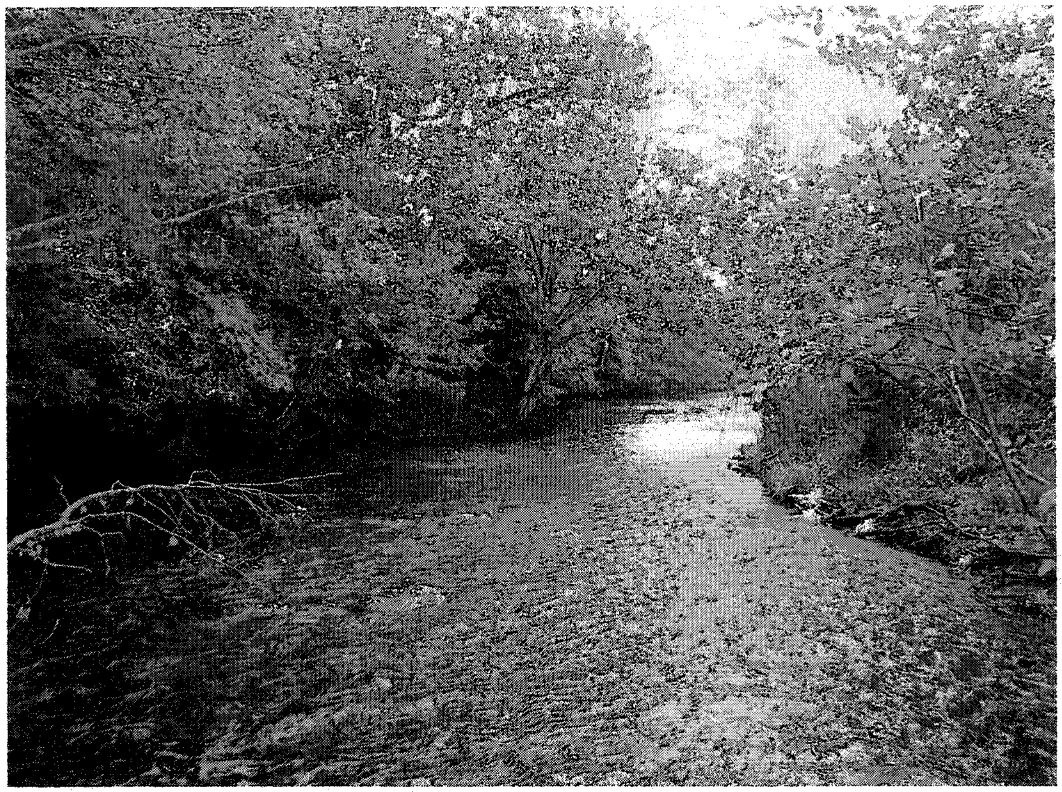


Fig 3.2. The run site of the main study sites on the West River, PEI. View of the summer downstream season/area extends from the foreground to the channel bend where the water surface appears smooth.

sites had a wide range of substrate/detritus and flow characteristics among different patches, unlike many pools and some other nearby riffles and runs in the West River. This made the study sites ideal for comparing the pattern of spatial variation of environmental characteristics with the spatial variation of macroinvertebrate densities within different sections of the stream..

Land use in the area around the study sites was examined from the 2000 Corporate land use digital data layer (PEI Department of Agriculture and Forestry) and analyzed using the software program MapInfo® (version 7.0). Approximately half of the watershed upstream of the site is forested, with the remaining land used mostly for agriculture. The riparian zone of the West River was almost entirely forested between the study sites and for a distance of 4 km upstream of the riffle site. However, during heavy rainfalls the study sites received large inputs of sediment from sources including the dirt road of the Riverdale bridge and a potato field located on top of the hill on the east side of the stream (personal observation).

Location and season of data collection

The riffle and run sites had contrasting channel geomorphology and flow conditions. The riffle site had a narrower channel width and a steeper water surface slope than the run site (Table 2.3, p.70 and Table 2.1, p.65). Also, the riffle site had lower substrate stability than the run site due to high shear stress and small substrate size (Table 3.1). Therefore, including the riffle site as well as the run site allowed the evaluation of relationships between macroinvertebrates and the environment at different locations with contrasting environmental conditions.

Table 3.1. Comparison of substrate stability between riffle and run sites on the West River at the times of benthic sampling. Substrate stability of each area of the study sites was predicted from measurements of shear stress and substrate size taken over the entire area. The critical shear stress required to move a substrate particle was considered to be approximately the same value as the particle diameter in mm (Gordon *et al.*, 1992).

	Summer downstream		**Fall upstream**	
	riffle site	**run site**	**riffle site**	**run site**
shear stress (N/m^2)[a]	29	12	30	14
median substrate[b] size (cm)	2.5	2.7	2.5	6.3
predicted substrate stability	low	high	low	very high

[a]calculated using equation 1.5., p.23. The values of slope that were used in this calculation were taken from Table 2.3, p. 70. The measure of depth for each section was determined from the average hydraulic radius of the transects where patches were located. Hydraulic radius is the ratio of the wetted cross-section area to the wetted perimeter (Gordon *et al.*, 1992).

[b]taken from Table 2.3, p. 70

The riffle and run sites were similar in that both sites had forested riparian zones and most of the deposited POM on the surface of the streambed appeared to be fallen leaves. These fallen leaves were from several different species of deciduous trees including *Alnus rugosa* (speckled alder), *Betula alleghaniensis* (yellow birch), *Betula papyrifera* (white birch), *Acer rubrum* (red maple), *Salix* (willow), as well as from conifer trees.

Data were collected from downstream areas of the riffle and run site in the summer ("summer downstream" samples) and from upstream areas of both sites in the fall ("fall upstream" samples; Fig. 2.2, p.69). Since the method used for benthic sampling was destructive, the same area could not be sampled more than once during the study. Therefore, any expected seasonal patterns between samples collected in summer downstream and fall upstream areas might be confounded by location.

In both seasons/areas that were sampled, the channel geomorphology was similar but the flow conditions and leaf litter abundance were different. In both seasons/areas of the riffle and the run site, one side of the river had smaller substrate size and a gradually sloping bank while the other side of the river had larger substrate size and a steep bank. Substrate stability was also similar between the two seasons/areas of each site at the time of sampling (Table 3.1). When the summer downstream areas of both sites were sampled (August 1-2), there was visibly less leaf litter on the surface of the streambed at both sites than when the upstream fall samples were taken (November 1-2). The dates of sample collection were chosen partly to minimize the variation in discharge in the 2 weeks before sampling (Fig. 3.3). Discharge was higher when the summer downstream samples were collected then when upstream fall samples were collected (0.79 m^3/s *versus* 0.50 m^3/s; Fig. 3.3).

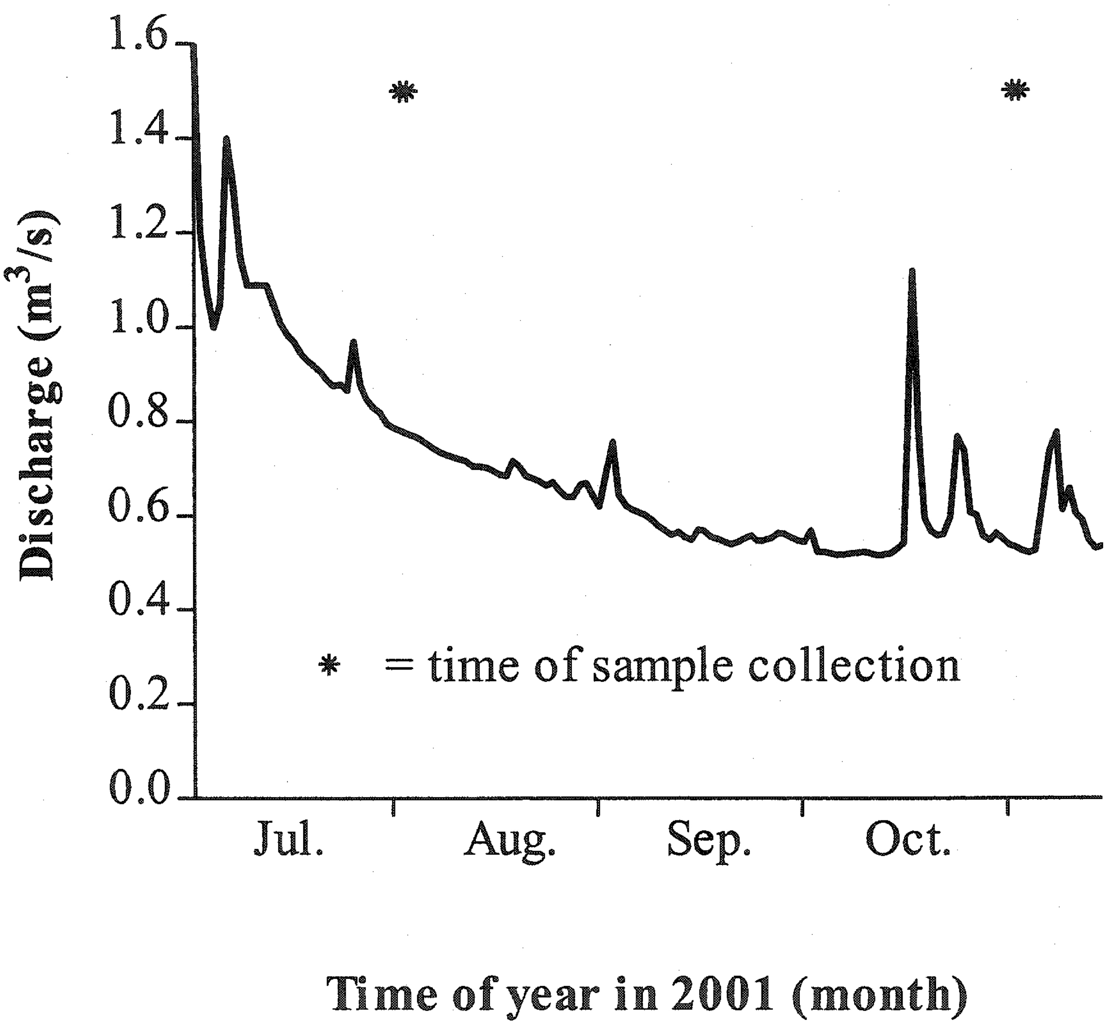


Fig 3.3. Hydrograph of the West River in summer and fall of 2001. The discharge measurements shown were taken at the Riverdale bridge just upstream of the main study sites (Environment Canada, 2001).

3.2.2 Comparison of environmental variables to macroinvertebrate data

The density of benthic macroinvertebrates was compared to substrate/detritus and hydraulic variables quantified in patches. At both sites, all measurements and samples were taken in circular patches (0.057 m^2) spaced in a regular arrangement (Fig. 2.6, p. 81) to explore how spatial variation in environmental variables was related to spatial variation in macroinvertebrate data. Of the 61 patches characterized in this study, 10 were in the riffle site, and 51 were in the run site.

Benthic sampling

Invertebrates, substrate and detritus in the top 5 cm layer of the streambed in each patch were sampled using a "box-type" sampler which enclosed 0.057 m^2 of the streambed (Fig. 3.4). Where possible, the sampler was driven at least 5 cm into the streambed. In areas of coarse substrate, the seal between the sampler bottom and the streambed was improved by attaching a ring-shaped foam base to the bottom of the sampler, and moving large rocks to one side if they interfered with sampler placement. After the sampler was placed, surface leaf litter (Table 3.2; detritus on the streambed surface > 32 mm in length) was removed and then the size of streambed rocks that were too heavy to collect was estimated by measuring the length of the B-axis (the shorter axis on the plane perpendicular to the shortest axis, Gordon *et al.*, 1992). The top 5 cm layer of the streambed was disturbed to suspend the fines (Wallace and Grubaugh, 1996) then a water sample containing the fines was collected. This water sample was a subsample of the total fines in the patch, so the total amount of fine material in the patch was estimated by comparing the volume of water collected to the volume measured in the sampler (before the sample was collected). The rest of the benthic sample was

Fig. 3.4. Collection of benthic sample using the box-type sampler without the foam base. A towel was used to improve the seal with the substrate in this and some other patches.

Table 3.2. Size classes of detritus measured in benthic samples.

Size class name	Abbreviation	Particle diameter (mm)	Composition
total particulate organic matter	total POM	all sizes (>0.0007)	sum of CPOM and FPOM described below
coarse particulate organic matter:	CPOM	>1	non-woody detritus
surface leaf litter	surf LL	>32	leaf material on the streambed surface
size classes of fine particulate organic matter:	FPOM	< 1	includes all FPOM as estimated from ash-free dry weight
fine particulate organic matter (1 to 0.5mm)	FPOM (1 - 0.5mm)	1- 0.5	
fine particulate organic matter (0.5 to 0.25mm)	FPOM (0.5 - 0.25mm)	0.5 to 0.25	
"very fine" fine particulate organic matter	VFPOM	0.25 to 0.125	
"very, very fine" fine particulate organic matter	VVFPOM	0.125 to 0.063	
"ultrafine" fine particulate organic matter	UFPOM	0.063 to 0.0007	

collected by removing the coarse streambed material by hand and pumping out the finer material with a hand-powered pump that fed into a net (200 µm mesh). Benthic samples were not obtained at 2 patch locations in each season/area of the run site where flow measurements were taken (in chapter 2) due to either the presence of large logs above the streambed surface or accidental loss of material during the collection of samples. After collection, sample material was preserved with 5% formalin. The subsamples of fine material in water were refrigerated and protected from light, then analysed to quantify fine organic and inorganic material as soon as possible (within 3 days following the start of sample collection).

Processing of benthic samples

Mineral substrates and detritus from the streambed were divided into size classes using different methods depending on the size of the material (Fig. 3.5). Size class divisions were made based on B-axis length measurements for rocks (>32mm), by dry-sieving for coarse substrate and detritus particles (32-0.25mm), and by size separation using fine sieves or glass microfiber filters under vacuum pressure (Wallace and Grubaugh, 1996) for very fine material (<0.25mm). Substrates were divided into one-phi size class interval beginning with >4 phi (<0.063mm). The phi scale is related to particle size diameter (mm) according to the following equation (Gordon *et al.*, 1992):

$$D_{phi} = -\log_2(D_{mm}). \qquad (3.1)$$

where: D_{phi} = diameter of particle (phi), and D_{mm} = diameter of particle (mm). Note that larger phi values of substrate size correspond to smaller values of substrate size in mm (Table 2.2, p.67). Detritus was divided into size classes corresponding to CPOM (>1mm diameter) and 5 categories of FPOM (<1mm diameter), the smallest of which was

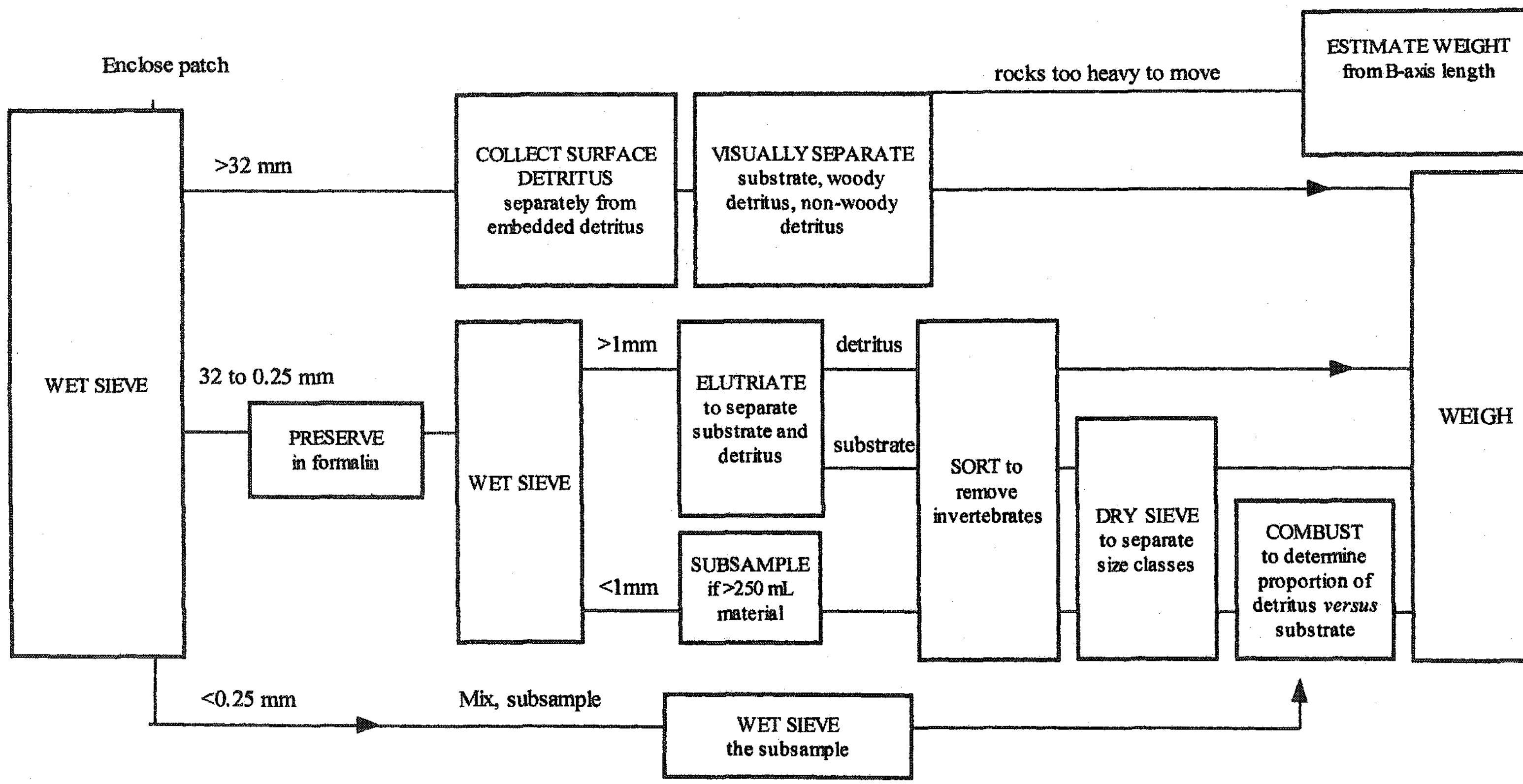


Fig. 3.5. Processing of benthic samples to measure weights of substrate and detritus particles in different size classes. For different sizes of material, different methods were used for size-separation and for separating detritus from mineral substrates.

<0.063-0.0007mm (UFPOM; Table 3.2).

The separation of detritus from mineral substrates was also performed using different methods for different sizes of material (Fig. 3.5). Large material (>32mm) was separated visually into mineral substrate or detritus components. Since few detritivore species feed on wood (Anderson and Cargill, 1987), detritus was further separated into "woody detritus" and "non-woody detritus". For the 32-1mm size fraction, detritus was separated from substrate particles by elutriation. The elutriated portion of some samples contained large amounts of algae, so the ratio of algae to detritus weight was estimated for each sample to find the approximate weight of detritus in a sample. After the invertebrates had been removed, material <1mm was combusted at 500 °C (Wallace and Grubaugh, 1996) for 1 to 2 hours (depending on the amount of material) to separate (mostly combustible) FPOM from inorganic (incombustible) substrate. Before combustion, material 1 to 0.25mm was subsampled if the sample contained >30mL of this size of material, by mixing it on a tray with 20 squares and randomly choosing squares until at least 15 mL of material was obtained from 2 or more squares. Fine material < 0.25mm was combusted following Wallace and Grubaugh (1996) using glass microfiber filters (Alhstrom, 0.7μm particle retention) to retain material during combustion. Values were not obtained for certain size fractions of detritus in a few samples due to the accidental loss of material during processing (see section 3.3., Results, p.128 for values of n).

The amount of detritus and substrate in each size class was quantified by weight for each sample. The median weight loss of detritus due to leaching during sample storage in preservatives was 12% with a maximum weight loss of 37%, and the final weights were not adjusted for this loss (see Appendix I for explanation). Detritus weight was determined by dividing the ash-free dry weights obtained from combustion by 0.9 (Pretty, 2000). The weights of rocks that were too heavy to collect were estimated from the relationship between rock size (B-axis length) and weight. This relationship was determined using regression analysis from measurements of 154 rocks collected from the West River ($r^2 = 0.91$, see Appendix II for details). For samples taken with the foam base, which reduced the area sampled, weights of substrates and detritus were adjusted to compensate for sample area using the following conversion factor:

$$\text{Foam factor} = \frac{\text{Surface area without foam}}{\text{Surface area with foam}} \qquad (3.2)$$

$$= 1.32$$

The substrate size composition in each patch was described using median particle size, amount of sand (-1 to 4 phi) and amount of silt (> 4 phi, including both organic and inorganic material), and the coefficient of uniformity, a measure of particle size heterogeneity (Table 3.3). The extent of algal mat growth in each patch was determined as the proportion of patch area covered with visible algae in digital photographs (see p. 73 of section 2.2.2 for photography methods).

Macroinvertebrates

Sorting and identification of invertebrates was carried out for each sample using a stereoscopic dissecting microscope (Olympus SZ-60). Sample material was passed through a 1mm mesh sieve, then invertebrates were removed from the material that was retained. If there was >250mL of material that was <1mm in a sample, this material was further subsampled, while those samples with less material were completely sorted. To subsample the material in the <1mm size class, it was spread out evenly on a tray marked with 20 squares, then 4 squares were randomly chosen for sorting. If <200

Table 3.3. Variables used to describe substrate composition of main study sites on the West River

Variable name	Abbreviation	Definition
median particle size	median	median size of substrate particles listed in phi values[a] note: smallest values indicate largest particle sizes
amount of sand	sand	weight of sediment in each patch from -1 to 4 phi or (1 to 0.063 mm)
amount of silt	silt	weight of inorganic and organic material in patch from >4 phi (or <0.063 mm)
coefficient of uniformity	CU	non-statistical measure of variation in substrate size appropriate for non-normal distributions, for which larger values reflect greater particle size heterogeneity Calculated using the following formula[1]: $CU = d_{60} / d_{10}$ (3.3) where d_{60} = grain diameter (mm) for which 60% of the sample by weight is finer than and d_{10} = corresponding grain diameter (mm) for 10% of the sample
algal cover	algal	proportion of patch surface area covered with visible algal mats

[a]see Table 2.2., p. 67 for relationship between phi values and particle diameter in mm

REFERENCES

[1] Pfannkuch and Paulson, 1998

invertebrates were found, additional squares were sampled until at least 200 individuals had been collected.

Aquatic insects were identified to genus where possible using the keys in Peckarsky *et al.*, 1990 and Merritt and Cummins (1996), except for chironomids which were classified as Chironominae, Tanypodinae or "other subfamilies" (mainly Orthocladiinae) based on eyespot and body shape characteristics as described in Oliver and Roussel (1983). Oligochaetes were classified as Tubificidae, Lumbriculidae, or "other families" based on body shape and size as described by Wetzel *et al.* (2000). Other non-insect taxa were identified to the lowest possible taxon using the keys in Thorp and Covich (2001). Macroinvertebrates were quantified separately for the 2 size categories of "large"(>1mm) and "small"(<1mm) individuals, which were determined by whether or not individuals were retained by the 1mm mesh sieve. Abundance (no./patch) and densities (no./m^2) of invertebrates in both size categories were adjusted for samples taken with the foam base as described for streambed material weights (equation 3.2, p.119).

Evaluation of flow

A set of hydraulic variables was chosen based on the results of the preliminary study (in chapter 2) and other studies similar to this one (reviewed in section 1.3, p. 39) to describe the variation in near-bed flow and bulk flow among patches. To describe near-bed flow, mean velocity and calculated shear velocity (determined from a velocity profile, equation 1.3, Table 1.2, p.21) were used to compare shear velocity among patches and a measure of roughness was used that was based on the width of substrate particles (equation 2.2, p.76). Bulk flow was described using the hydraulic variables of mean velocity, depth and Froude number (equation 1.2, p.17), which also describes near-bed flow. Hydraulic variables were all measured in patches on the day before benthic sampling began (see section 2.2.2, p. 72 and section 2.2.3, p. 78 for methods).

Vertical hydraulic gradient

The pattern of vertical flow in the streambed was evaluated by determining the vertical hydraulic gradient (VHG) in each patch using a mini-piezometer (based on design in Lee and Cherry, 1978) coupled with a manometer (based on design in Winter *et al.*, 1988; Fig. 3.6). Since measurements with the mini-piezometer disturbed the streambed, all VHG measurements were taken after sampling had been completed, on Aug. 21, 24, and 28 for summer downstream samples, and on Nov. 6, 9, and 12 for fall upstream samples.

The mini-piezometer was installed at a depth of 0.30 m below the surface of the streambed as close to the centre of the patch as possible, and at a depth of 0.30 to 0.10 m where large rocks prevented deeper installation. Measurements for VHG were not taken if the mini-piezometer could not be installed to a substrate depth of at least 10 cm, if it became clogged with silt, or if the time required for the differential hydraulic head to reach an equilibrium was greater than 30 minutes (see section 3.3, Results, p. 128 for values of n). In areas of fast flow, the mini-piezometer was surrounded by a stilling well (Fig. 3.6) to slow currents which would otherwise affect the accuracy of water level readings in the mini-piezometer (Maurice Valett, Department of Biology, Virginia Polytechnical Institute and State University, Blacksburg, Virginia, USA, Personal Communication, 2001).

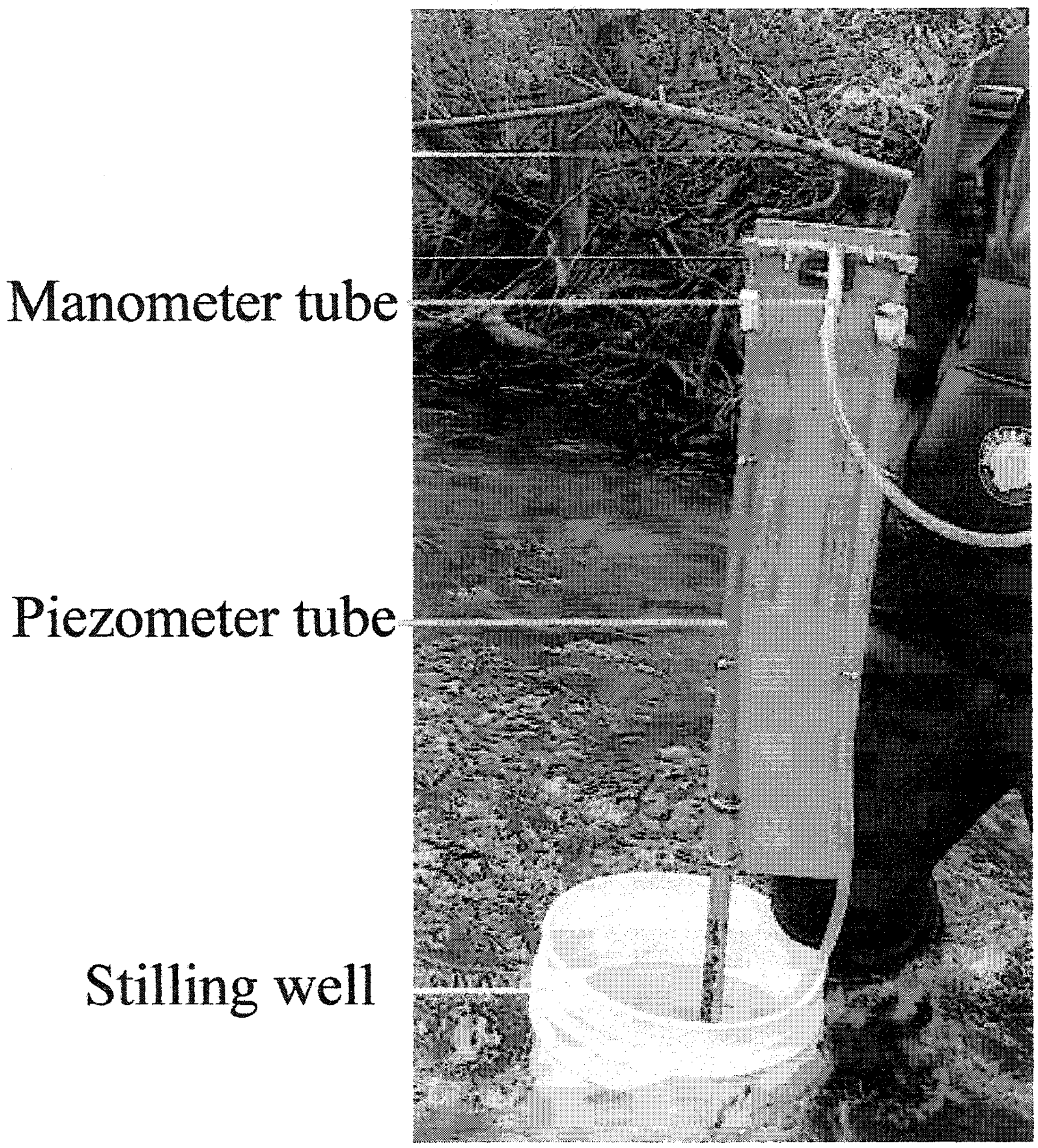


Fig. 3.6. Measurement of vertical hydraulic gradient (VHG) with a mini-piezometer attached to a manometer which facilitates accurate reading of water levels for measurement of VHG. The mini-piezometer tube was driven into the substrate (inside a pipe) and the manometer tube was positioned so that it opened to the stream water. Vertical hydraulic gradient was determined as the difference between the water levels in the two tubes. The stilling well was a plastic bucket with the bottom removed and holes in the sides that allowed water to circulate through the pipe.

Vertical hydraulic gradient was calculated using the following formula (Lee and Cherry, 1978):

$$VHG = \Delta h / \Delta d \tag{3.4}$$

where VHG = vertical hydraulic gradient (unitless), Δh = the difference in hydraulic head (m), Δd = depth of piezometer screen below the surface of the streambed (m). Differences in values of VHG among patches were not related to the day of sampling for each season/area. Calculated VHG values were assigned to 5 different ranks to reflect the approximate nature of these measurements, with each rank corresponding to an interval of 0.1 or more in VHG as follows (strong downwelling <-0.15, weak downwelling -0.15 to -0.05, weak to undetectable vertical flow -0.05 to 0.05, weak upwelling 0.05 to 0.15, strong upwelling >0.15).

3.2.3 Statistical analysis

Data collected from each season/area were analyzed separately. Macroinvertebrate data from concurrent samples in the riffle and run sites were examined using cluster analysis to determine if data from different sites would be combined in the subsequent analysis. For the cluster analysis, macroinvertebrate density was expressed as the percent of total individuals in a given patch to standardize for differences in total macroinvertebrate density among patches. Cluster analysis was performed using Sorensen distance and the group average linkage method with the statistical software package PC-ORD® (version 4).

Relationships among macroinvertebrate densities, environmental variables and patch location

Relationships between environmental variables or patch location and macroinvertebrate density were examined for all community taxa simultaneously ("combined community taxa densities") using Redundancy Analysis (RDA) and for selected groups of macroinvertebrates individually using multiple regression (MR), correlation and scatterplots. Redundancy analysis is a method of direct gradient analysis that evaluates the strength of associations among multiple species and environmental variables (ter Braak, 1994). Spatial variables were calculated from the x-y co-ordinates of each patch using the terms of a cubic equation as demonstrated in Borcard *et al.*, (1992) to analyze the spatial structure of the data. Correlations between pairs of variables were examined using the calculation of correlation coefficients for data sets with a relatively small number of variables and using RDA correlation biplots for data sets with a larger number of variables (see Appendix III for details). The significance of selected correlations between individual taxa and environmental variables in RDA correlation biplots was tested using t-value biplots (diagrams showing approximate t-values of the regression coefficients in RDA solutions; ter Braak and Šmilauer, 2002). The appropriate assumptions were checked for each statistical test, including assumptions of linearity, independence of error terms, error normality and equal variance for MR and the assumption of linearity for correlation. Spearman correlation was used for all simple correlation analyses because of the large number of variables with a non-normal distribution. Results from Spearman correlation are given as coefficients of determination (r_s^2 values) in the results (section 3.3, p.128) for consistency with chapter 2 (see section 2.2.6, p. 83 for explanation) and the use of coefficients of determination in regression model results in this chapter. In MR analyses, the small number of values that were missing for some variables were replaced with the variable mean (see section 3.3, Results, p.128 for values of n). All statistical analyses were done using the software packages Statistica® (version 6.0) and SPSS® (version 10), except for cluster analysis which was done using PC-ORD® (version 4) and redundancy analysis which was done using CANOCO® (version 4.5).

General procedure for redundancy analysis

For redundancy analysis, the same basic procedure and scaling options were used for all data sets. Prior to RDA, the assumption of linear species response to environmental variables was verified using detrended correspondence analysis (DCA) of each set of macroinvertebrate data (ter Braak and Šmilauer, 2002). The values of all environmental variables were transformed by normalization since some variables were measured in different units (Jongman, 2002). Taxa densities (which had skewed distributions) were log transformed to increase the robustness of the analysis and to reduce the dominance of the solution by more abundant taxa (ter Braak and Šmilauer, 2002). Redundancy analysis was performed using the options of "focus on inter-species correlations" with species data centred but not standardized (CANOCO, version 4.5; ter Braak, 1994). Species scores were divided by the standard deviation post-analysis to construct RDA correlation biplots (ter Braak, 1994).

Relative importance of different types of variables to macroinvertebrate distribution

The relative importance of different types of variables (e.g. substrate/detritus *versus* hydraulic variables) to macroinvertebrate densities was determined for the combined community taxa data using redundancy analysis (RDA) and for individual taxa using multiple regression (MR). For both RDA and MR, statistical selection was used to select the variables that were most closely related to macroinvertebrate densities. Then, partitioning of the variation in macroinvertebrate density was carried out to determine the amount of variation that could be explained entirely ("uniquely explained") by one type of environmental variable, by shared variation in both types of environmental variables ("explained by shared variation"), and the amount that could not be explained by either type of variable ("unexplained variation"). Roughness values of near-bed flow were excluded from these analyses because of concerns about the accuracy of the width-based method of measuring roughness (see p. 30 of section 1.1.3 and p. 97 of section 2.4.2 for details). Also, since roughness values were calculated from measures of substrate size (p. 73 of section 2.2.2), they may have reflected substrate structure more accurately than the actual roughness (i.e. the resistance of the streambed to flow).

Statistical selection was performed using backwards stepwise selection for MR models and forwards selection for RDA models. If several variables had similar strengths of correlation to the macroinvertebrate data (i.e. r-values differed by less than 0.03), the variable that represented the most general measure of a given characteristic (e.g. total POM rather than a specific size fraction of POM) was included in the final model. Two variables of each type (e.g. substrate/detritus and hydraulic) were included in RDA models to give an equal number of variables of each type so that the macroinvertebrate variation explained by each type was strictly comparable (Borcard *et al.*, 1992). (Exploratory data analysis had shown that two was typically the maximum number of significant variables for this data set).

Partitioning of variation in macroinvertebrate densities between different types of environmental variables was determined for RDA and MR as follows. For redundancy analysis, RDA and partial RDA were used as described by Borcard *et al.*, (1992). Then the significance of the relationship between the macroinvertebrate and the environmental data, after accounting for the influence of covariables, was tested using Monte Carlo permutations under the reduced model recommended for small data sets (ter Braak and Šmilauer, 2002). For MR models of individual taxa, variation partitioning was calculated from both the regression model and semipartial correlation coefficients according to Hair *et al.* (1998). Based on the results of these analyses, multiple regression was also used to evaluate the relationship of detritus to surface flow to explore the possibility of flow affecting macroinvertebrate distribution indirectly through detritus.

The potential importance of vertical hydraulic gradient (VHG) to macroinvertebrate density and the distribution of detritus was analyzed separately from that of other hydraulic variables due to the large number of missing VHG values (see section 3.3.3, p. 137). The relationship between VHG and macroinvertebrate taxa densities in those patches where VHG was measured was examined using a RDA correlation biplot. To determine whether the amount of detritus varied with VHG, Mann-Whitney-U tests were used to compare detritus in patches with different levels of VHG in each season/area.

3.3 Results

3.3.1 Comparison of macroinvertebrate communities and environmental conditions between the riffle and run

The riffle and run sites had distinct macroinvertebrate taxonomic composition and different environmental conditions, but not all differences were consistent between seasons/areas (i.e. the downstream area sampled in the summer and the upstream area sampled in the fall). The percent taxonomic composition in all 5 riffle site patches was distinct from patches at the run site for the fall upstream samples indicating that the two sites had distinct communities (Fig. 3.7). In contrast, the taxonomic composition in

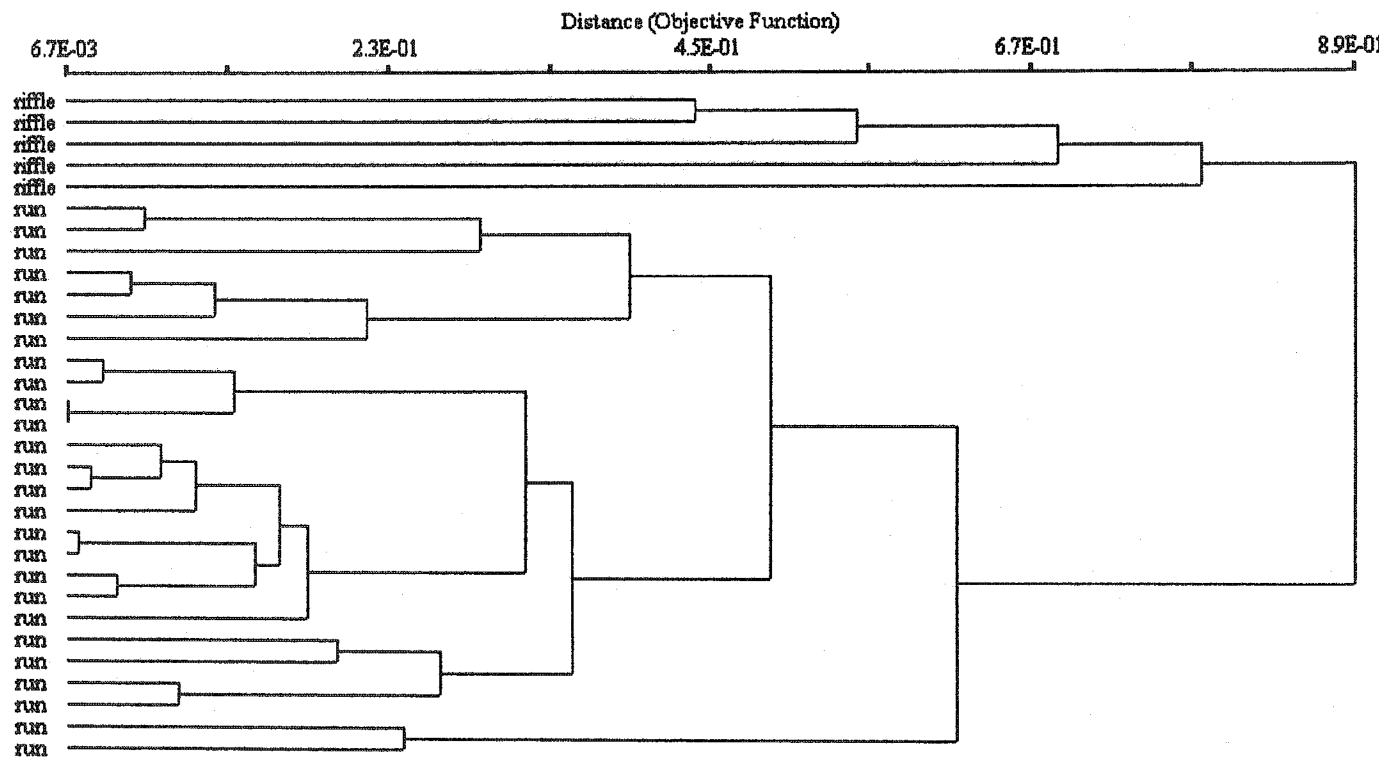


Fig. 3.7. Comparison of percent taxonomic composition of macroinvertebrates in fall upstream samples collected from patches of the riffle or run site on the West River. Sample grouping was determined from cluster analysis. The distance scale indicates similarity of sample groups where samples with branches that join at shorter distances are more similar.

summer downstream samples did not vary predictably between riffle and run sites (Fig. 3.8). In both seasons/areas, patches at the riffle site had much more deposited detritus, more heterogeneous (i.e. higher coefficient of uniformity) substrate size, smaller substrate size composition and less algal cover than patches at the run site (Table 3.4). Flow conditions also varied between sites, but did not vary consistently between seasons. For example, in summer downstream patches, roughness was lower and depth was higher at the riffle site than at the run site, whereas in fall upstream patches, shear velocity, Froude number and mean velocity were higher at the riffle site than the run site. Vertical hydraulic gradient also varied between sites (Table 3.4). Overall, riffle site patches had environmental conditions that were distinct from run patches in both seasons/areas and distinct taxonomic composition in fall upstream samples. Therefore, riffle samples were excluded from the subsequent analyses relating macroinvertebrates to environmental conditions, except for taxon-specific relationships which were examined separately for each site.

3.3.2 Comparison of environmental conditions and macroinvertebrate communities between seasons/areas of the run site

At the run site, hydraulic conditions were different in summer downstream and fall upstream patches (Table 3.4) largely because discharge was much higher during the summer survey than the fall survey (Fig. 3.3, p. 112). Patches in the summer downstream area had higher mean velocity, Froude number, and shear velocity than fall upstream patches while depth and roughness were similar between patches in both seasons/areas (Table 3.4). Vertical hydraulic gradient could only be measured in about half of the sampled patches in each season/area, typically those with smaller substrate size, because of

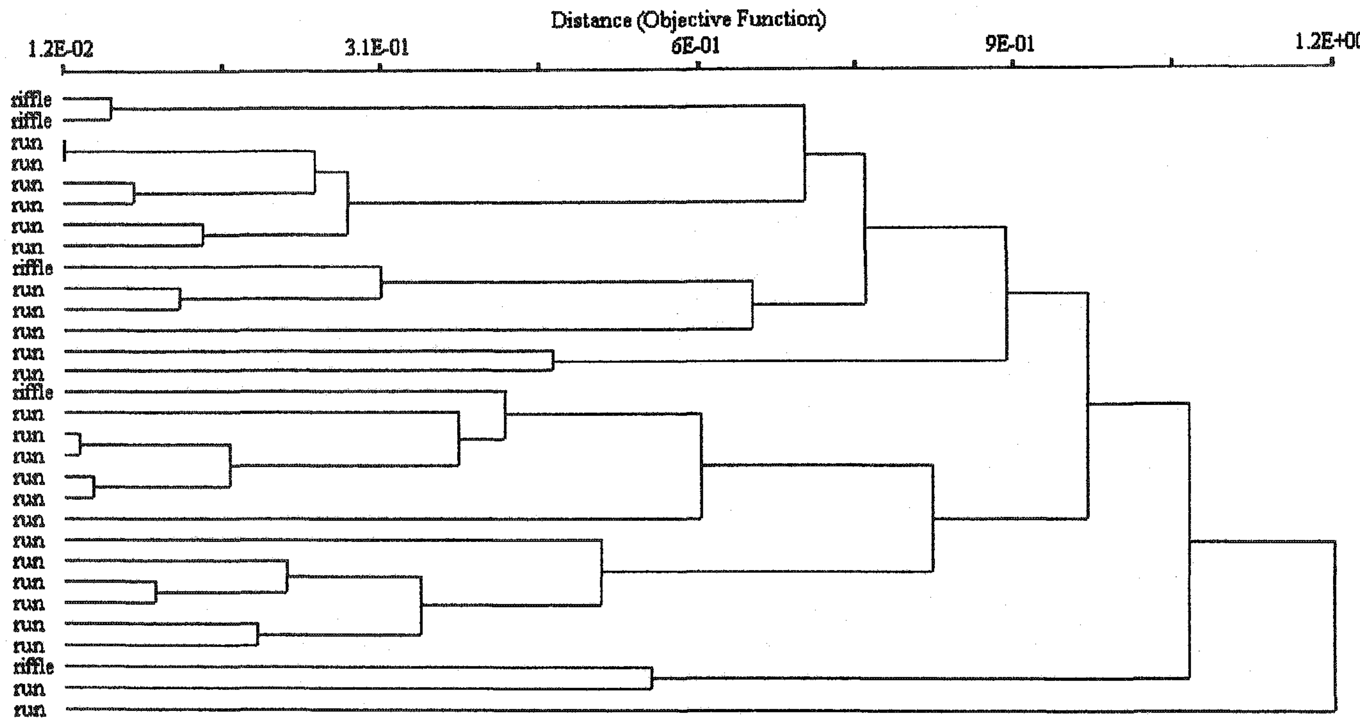


Fig. 3.8. Comparison of percent taxonomic composition of macroinvertebrates in summer downstream samples collected from patches of the riffle or run site on the West River. Sample grouping was determined from cluster analysis. The distance scale indicates similarity of sample groups where samples with branches that join at shorter distances are more similar.

Table 3.4. Comparison of median or mean values of environmental variables in summer downstream versus fall upstream samples of the West River run site. For definition of substrate/detritus abbreviations see Table 3.2, p.115 and Table 3.3, p.120.

Variables	Summer downstream:				Fall upstream:			
	run site		riffle site		run site		riffle site	
	n	median/mean	n	median/mean	n	median/mean	n	median/mean
Hydraulic variables:								
depth (m)*	25	0.18	5	0.24	26	0.19	5	0.19
mean velocity* (m/s)	25	0.60	5	0.67	26	0.33	5	0.68
Froude number	25	0.43	5	0.52	26	0.24	5	0.46
shear velocity (m/s)	22	0.085	5	0.087	22	0.068	5	0.082
roughness	25	2.12	5	1.56	26	2.44	5	1.78
vertical hydraulic gradient[a]	11	weak upwelling	2	weak downwelling and weak to undetectable vertical flow	13	weak to undetectable vertical flow	4	strong downwelling
Substrate/detritus								
total POM (g)	23	3.49	5	7.25	26	3.20	5	6.55
CPOM (g)	25	0.20	5	0.57	26	0.46	5	0.66
surf LL (g)	25	0	5	0	26	0.0857	5	0
FPOM (g)	23	2.97	5	6.75	26	2.62	5	5.03
silt (g)	25	4.43	5	10.12	26	6.50	5	4.85
sand (g)	25	273.22	5	519.90	26	134.68	5	497.29
median substrate size (phi)*	25	-6 .5 (cobble)	5	-5 (pebble)	26	-7.4 (cobble to boulder)	5	-5 (pebble)
coefficient of uniformity	25	16	5	32	26	4	5	8
algal cover (%) *	25	33	5	3	26	26	5	0

*mean values given for variables with approximately symmetrical distributions
[a] ranked data see section 3.2.2., p. 124 for corresponding values of VHG

problems inserting the mini-piezometer. In the summer downstream survey, most measured patches had upwelling, whereas in the fall upstream survey, most measured patches had very weak vertical flow or downwelling.

Substrate size and detritus also varied between season/areas (Table 3.4). Total POM and algal cover were similar in summer downstream and fall upstream samples of the run site (Table 3.4). However, there was more CPOM and the substrate size was larger and less heterogeneous in fall upstream samples than in summer downstream samples (Table 3.4). The size composition of detritus (total POM) also varied between seasons/areas; for example, a greater portion of the detritus in the fall upstream samples was composed of CPOM and UFPOM than in the summer downstream samples (Fig. 3.9).

The macroinvertebrate community had different densities, but similar richness and some similarities in taxonomic composition in the two seasons/areas (Tables 3.5, 3.6). The median density of macroinvertebrates in fall upstream samples was approximately twice as high as in summer downstream samples (Table 3.5). In the summer downstream samples 50 taxa were recorded, 30 of which were rare (<1% total individuals), and in the fall upstream samples, 55 taxa were recorded, 28 of which were rare (Table 3.5). In both seasons/areas, macroinvertebrate communities were dominated by chironomids, the mayflies *Baetis* and Ephemerellidae and the riffle beetle larvae *Optioservus* (Table 3.6). Certain taxa were more abundant in one season/area than the other. For example, the black fly larvae *Simulium*, Tubificidae worms, and "other subfamilies" of chironomids (mostly Orthocladiinae) were more abundant in summer downstream samples than the fall upstream ones and Tanypodinae, Chironominae, and *Ephemerella* were more abundant in fall upstream samples than summer downstream ones.

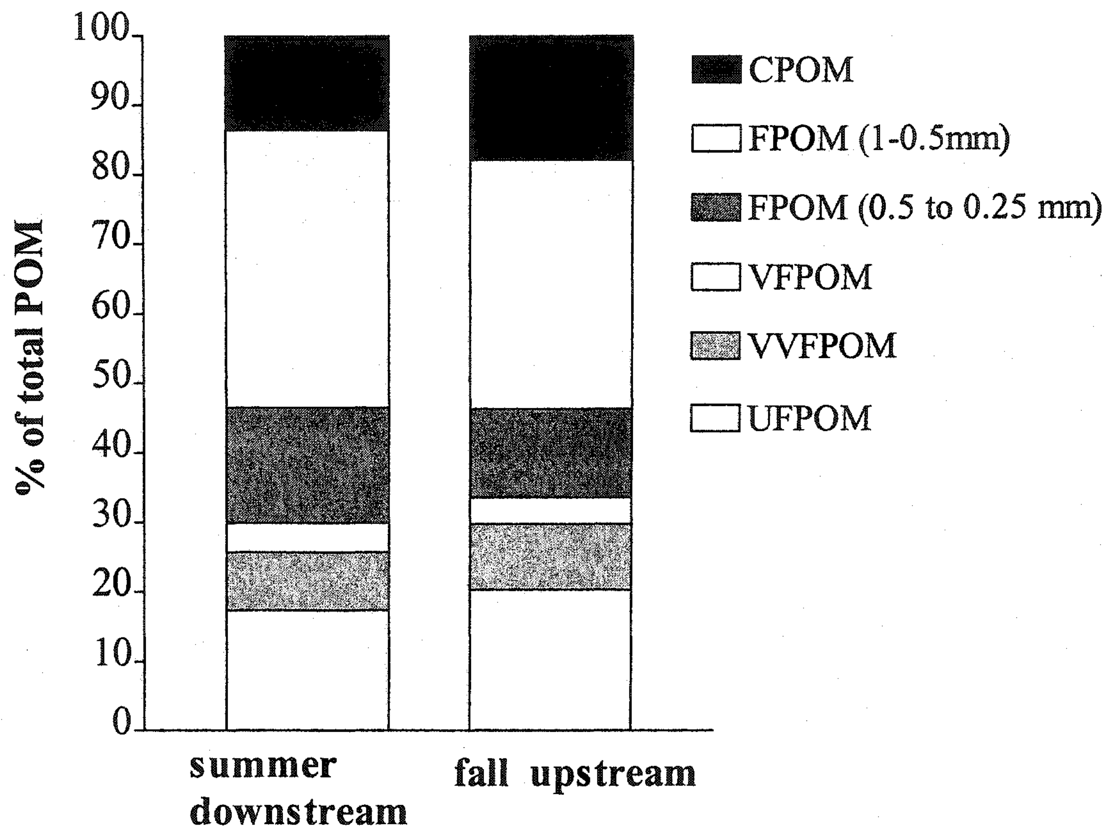


Fig. 3.9. Detritus size composition for combined samples. Samples were collected from the West River run site in each season/area. Size classes of detritus are graphed from largest to smallest from top to bottom (see Table 3.2, p. 107 for definition and particle sizes of detritus variables).

Table 3.5. Comparison of density (no./m^2) , richness and number of rare taxa in macroinvertebrate communities in summer downstream and fall upstream samples of the run site on the West River.

Measure	**Summer downstream**	**Fall upstream**
median density (no./m^2)	13741	29344
richness (total number of taxa)	50	55
number of rare taxa[a]	30	28

[a]<1% of total individuals

Table 3.6. Percent taxonomic composition of macroinvertebrates in samples collected from the West River run site in each season/area. Only those taxa that are dominant (>1% of total individuals) in at least one season/area of samples are listed.

	Percent of total individuals (all samples in each season/area):	
Taxon	**Summer downstream**	**Fall upstream**
Diptera (flies):		
Chironomidae (individuals too small or young to identify beyond farmily)	1	<1
Chironominae	11	29
Tanypodinae	<1	5
other subfamilies of chironomids (mostly Orthocladiinae)	22	8
Antocha	1	1
Dicranota	1	<1
Empididae	<1	1
Simulium larvae	5	<1
Simulidae pupae	1	<1
Ephemeroptera (mayflies):		
Baetis	14	13
Ephemerellidae (individuals too small or young to identify beyond family)	10	8
Drunella	1	<1
Ephemerella	<1	9
Paraleptophlebia	2	2
Heptagenia	1	<1
Plecoptera (stoneflies):		
Plecoptera (individuals too small or young to identify beyond order)	1	<1
Perlodidae	<1	1
Chloroperlidae	<1	1
Leuctridae or Capniidae	1	2
Trichoptera (caddisflies):		
Micrasema	<1	2
Rhyacophila	4	2
Coleoptera (beetles):		
Optioservus larvae	11	9
Non-insect taxa:		
Nematoda	1	1
Tubificidae	8	2
Ostracoda	1	<1
Copepoda	1	<1

3.3.3 Relationships between macroinvertebrate community taxa densities and environmental variables at the run site

Similar correlations were often seen between the density of a given macroinvertebrate taxon and several different environmental variables because many environmental variables were inter-correlated in each season/area (RDA, Fig. 3.10, 3.11, Table 3.7, 3.8). In the summer downstream samples, the density of many dominant taxa (>1% of total individuals) increased with FPOM (except for the VFPOM and VVFPOM size fractions), decreasing substrate size (i.e. decreasing median substrate size, increasing sand and increasing silt), decreasing algal cover, and the presence of strong upwelling (Fig. 3.10, Table 3.8). The densities of many dominant taxa were also weakly related to depth and roughness, since shallow areas with lower roughness generally had more detritus and smaller substrate size (Fig. 3.10, Table 3.8, see Fig. 3.12 for photos of typical patches). In the fall upstream samples, the densities of many dominant taxa increased with higher POM >0.25 mm (combination of CPOM and FPOM >0.25 mm), decreasing substrate size and decreasing algal cover, and were also weakly related to a gradient of increasing "hydraulic stress" (increasing shear velocity, mean velocity, Froude number and roughness) and increasing depth (Fig. 3.11, Table 3.8, see Fig. 3.12 for photos of typical patches).

The densities of most, but not all, dominant taxa had similar relationships to environmental variables in a given season/area with a general pattern of increased density with increased detritus. In the summer downstream samples, the densities of most dominant taxa were more closely related to FPOM than CPOM. The densities of several taxa including the caddisfly *Rhyacophila*, the black fly larvae *Simulium* and Simulidae pupae were not significantly related to FPOM or CPOM (t-value biplots, t-value 2 to -2, also see Fig. 3.10). Unlike other dominant taxa in the summer downstream samples, *Simulium* larvae and Simulidae pupae increased significantly with Froude number (t-value

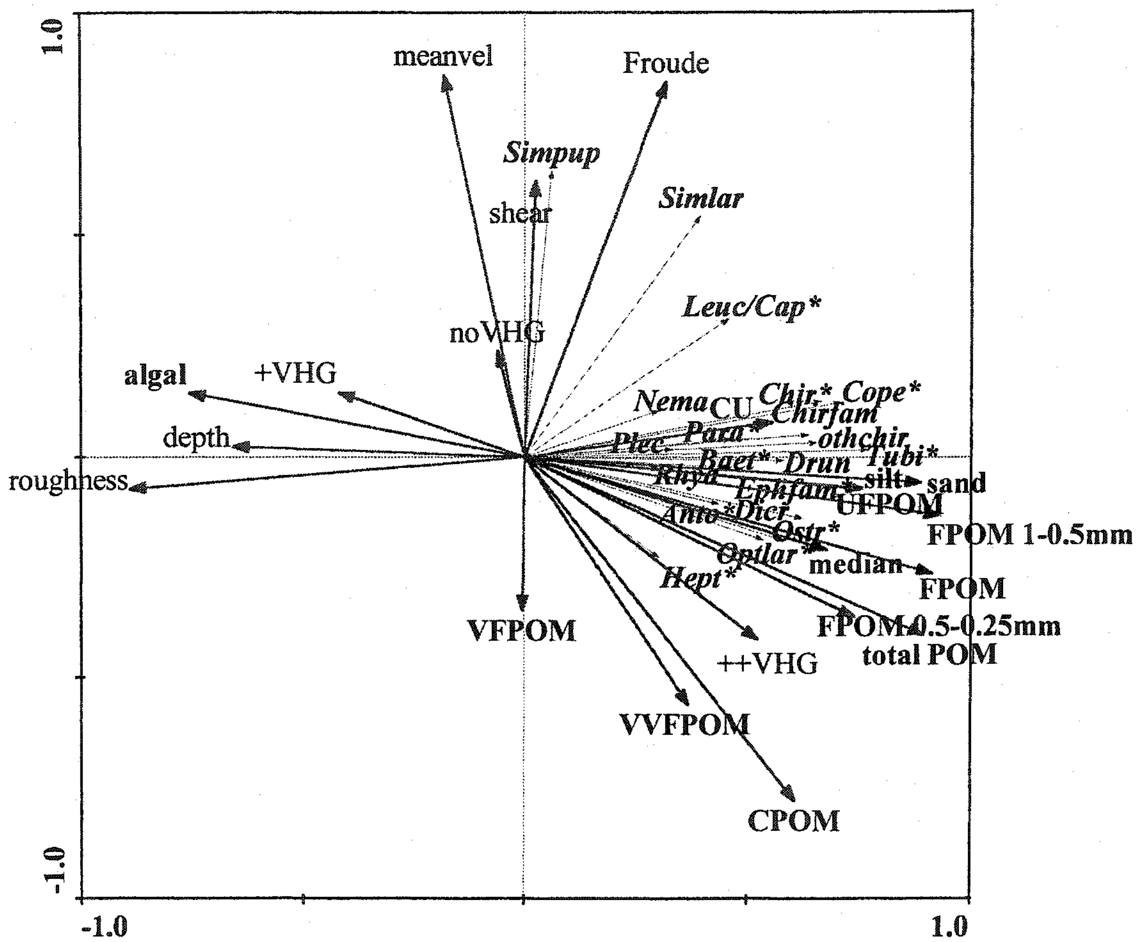


Fig 3.10. Relationships among macroinvertebrate community taxa densities and environmental variables in summer downstream samples as determined by redundancy analysis (RDA). Samples were collected from patches at the West River run site. The RDA biplot shows approximate correlations among variables (rare taxa not shown; see Appendix III for biplot interpretation guidelines). For definition of variable abbreviations, see Table 3.2, p.115 for detritus; Table 3.3, p.120 for substrate, and Table 3.7 for hydraulic variables and macroinvertebrate taxa. * indicates deposit-feeding detritivores.

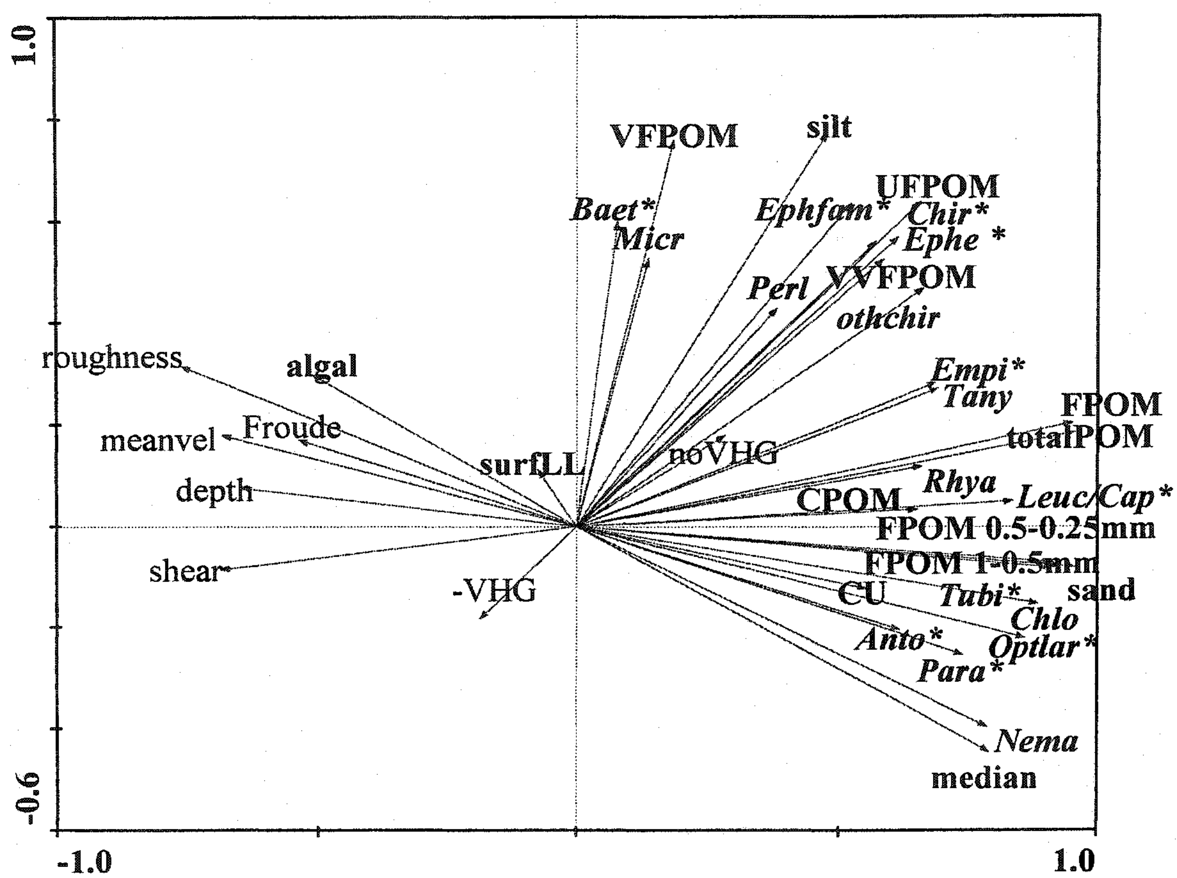


Fig. 3.11. Relationships among macroinvertebrate community taxa densities and environmental variables in fall upstream samples as determined by redundancy analysis (RDA). Samples were collected from patches at the West River run site. The RDA biplot shows approximate correlations among variables (rare taxa not shown; see Appendix III for biplot interpretation guidelines). For definition of variable abbreviations, see Table 3.2, p.115 for detritus; Table 3.3, p.120 for substrate, and Table 3.7, for hydraulic variables and macroinvertebrate taxa. * indicates deposit-feeding detritivores..

Table 3.7. Legend for variable abbreviations in graphs in this chapter.

Variable abbreviation	Variable name
hydraulic variables:	
shear	shear velocity
Froude	Froude number
meanvel	mean velocity
depth	depth
roughness	roughness
-VHG	weak downwelling (VHG = -0.05 to -0.15)
noVHG	weak to undetectable vertical flow (VHG = -0.05 to 0.05)
+VHG	weak upwelling (VHG = 0.05 to 0.15)
++VHG	strong upwelling (VHG = >0.15)
macroinvertebrate taxa: (**=deposit-feeding detritivore*[a])	
Diptera (flies):	
Chirfam	Chironomidae (individuals that were too small to identify beyond family)
*Chir**[1]	Chironominae
Tany	Tanypodinae
othchir	other subfamilies of chironomids (mostly Orthocladiinae)
*Anto**[2]	*Antocha*
Dicr	*Dicranota*
*Empi**[2]	Empididae
Simlar	*Simulium* larvae
Simpup	Simulidae pupae

continued..

Table 3.7. cont.

Variable abbreviation	Variable name
Ephemeroptera (mayflies):	
*Baet**[3]	*Baetis*
*Ephfam**[3]	Ephemerellidae (individuals that were too small to identify to beyond family)
Drun	*Drunella*
*Ephe**[3]	*Ephemerella*
*Para**[3]	*Paraleptophlebia*
*Hept**[3]	*Heptagenia*
Plecoptera (stoneflies):	
Plec	Plecoptera (individuals that were too small to identify to beyond order)
Perl	Perlodidae
Chlo	Chloroperlidae
*Leuc/Cap**[4]	Leuctridae or Capniidae
Trichoptera (caddisflies):	
Micr	***Micrasema***
Rhya	*Rhyacophila*
Coleoptera (beetles):	
*Optlar**[5]	*Optioservus* larvae [1]
Non-insect taxa:	
Nema	Nematoda
*Tubi**[6]	Tubificidae
*Ostr**[7]	Ostracoda
*Cope**[7]	Copepoda

[a] Most species in taxon feed predominately on deposited detritus

REFERENCES

[1]Coffman and Femington, 1996; [2]Courtney *et al.*, 1996; [3]Edmunds and Waltz, 1996; [4]Stewart and Harper, 1996; [5]White and Brigham, 1996; [6]Wetzel *et al.*, 2000; [7]Clifford, 1991

Table 3.8. Interpretation of inter-correlations among environmental variables in samples in each season/area of the West River run site, as shown in redundancy analysis correlation biplots (Fig. 3.10, p. 138, 3.11, p.139). Groups of hydraulic variables or substrate/detritus variables are listed that are moderately to strongly correlated to each other and thus have similar strengths of correlations to macroinvertebrate taxa densities. Groups with > 2 variables have been assigned names. Groups of substrate/detritus variables that are correlated with groups of hydraulic variables are also listed. See Table 3.2, p.115 for definition of detritus variable abbreviations.

Inter-correlated hydraulic variables (variables/(group name))	Inter-correlated substrate/detritus variables (variables/(group name))	Substrate/detritus groups correlated with hydraulic variable groups
	Summer downstream	
depth, roughness	totalPOM, FPOM, FPOM 1-0.5mm, FPOM 0.5 to 0.25mm, UFPOM, decreasing median substrate size, sand, silt, decreasing algal cover ("increasing FPOM (except VFPOM and VVFPOM)/ decreasing substrate size and algal cover")	"increasing FPOM (except VFPOM and VVFPOM)/ decreasing substrate size and algal cover" negatively correlated with depth/roughness
mean velocity, Froude number	CPOM, VVFPOM	CPOM/VVFPOM weakly negatively correlated with mean velocity (very weak correlation with Froude)
		strong upwelling correlated with "increasing FPOM (except VFPOM and VVFPOM)"/decreasing substrate size and algal cover and with CPOM/VVFPOM
	Fall upstream	
mean velocity, Froude number, roughness, depth, shear velocity ("gradient of increasing hydraulic stress and depth")	totalPOM, FPOM, FPOM 1-0.5mm, FPOM 1-0.25 mm, CPOM, decreasing median substrate size, sand, decreasing algal cover ("increasing POM > 0.25mm/ decreasing substrate size and algal cover")	"gradient of increasing hydraulic stress and depth" negatively correlated to "increasing POM > 0.25mm/ decreasing substrate size and algal cover"
	VFPOM, VVFPOM, UFPOM, silt ("increasing fine POM and silt")	

A. Summer
downstream

B. Fall
upstream

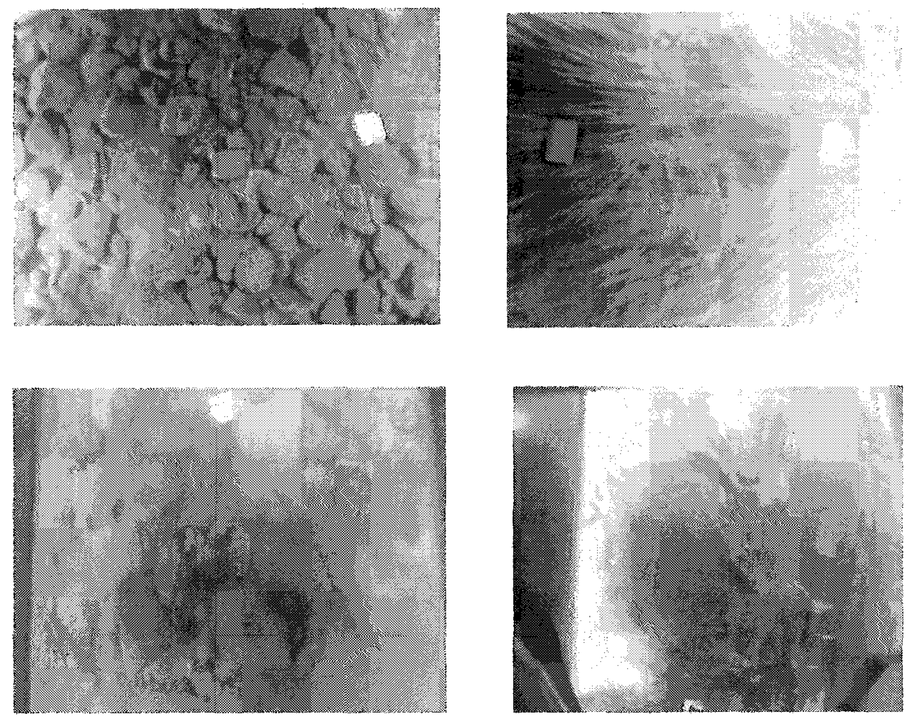


Fig. 3.12. Photos of typical patches at the run site of the West River with commonly observed combinations of environmental characteristics. Summer downstream patches (A): left: small substrate size, low algal cover, shallow depth, low roughness and high FPOM (not visible); right: patch with opposite characteristics to that to the left. Fall upstream patches (B): left: small substrate size, low algal cover, low hydraulic stress, shallow depth and high POM > 0.25 mm (not visible); right: patch with opposite characteristics to that to the left.

biplot, t-value >2 or <-2, also see Fig. 3.10). (However, the distribution of Simulidae pupae could not be compared with environmental variables with great certainty since over 58% of individuals collected in the summer downstream area occurred in one patch.) In the fall upstream samples, the density of all dominant taxa increased with increasing total POM and decreasing median substrate size, except *Baetis* and *Micrasema* which were not closely related to either variable (RDA, Fig. 3.11). Interestingly, the pattern of increasing density of most taxa with increasing detritus was observed for both the deposit-feeding detritivores and the taxa classified as other functional feeding groups in both seasons/areas (Fig. 3.10, 3.11).

In contrast to the relationship with detritus, most taxa densities were only weakly related to the variation in hydraulic variables that was not shared by variation in substrate/detritus. This trend was shown by partial RDA and RDA using those environmental variables that were the best predictors of the combined taxa densities (i.e. all taxa densities analyzed simultaneously) for the entire community (Fig. 3.13). In the summer downstream samples, 20% of the variation in densities of all macroinvertebrate taxa among patches could be explained uniquely by the best predictors of the substrate/detritus variables (FPOM and CPOM; partial RDA, RDA, Fig. 3.13). A smaller proportion of the variation in combined community taxa densities (10%) could be explained by shared variation of FPOM and CPOM with the best predictors of the hydraulic variables (depth and Froude number; partial RDA, RDA). In the fall upstream samples, a similar amount of variation in the combined community taxa densities among patches could be explained uniquely by the best predictors of the substrate/detritus variables (total POM and median substrate size) as in the summer downstream samples. In addition, for fall upstream samples, 22% of variation in taxa densities could be explained by shared variation of these substrate/detritus variables with the best predictors of the

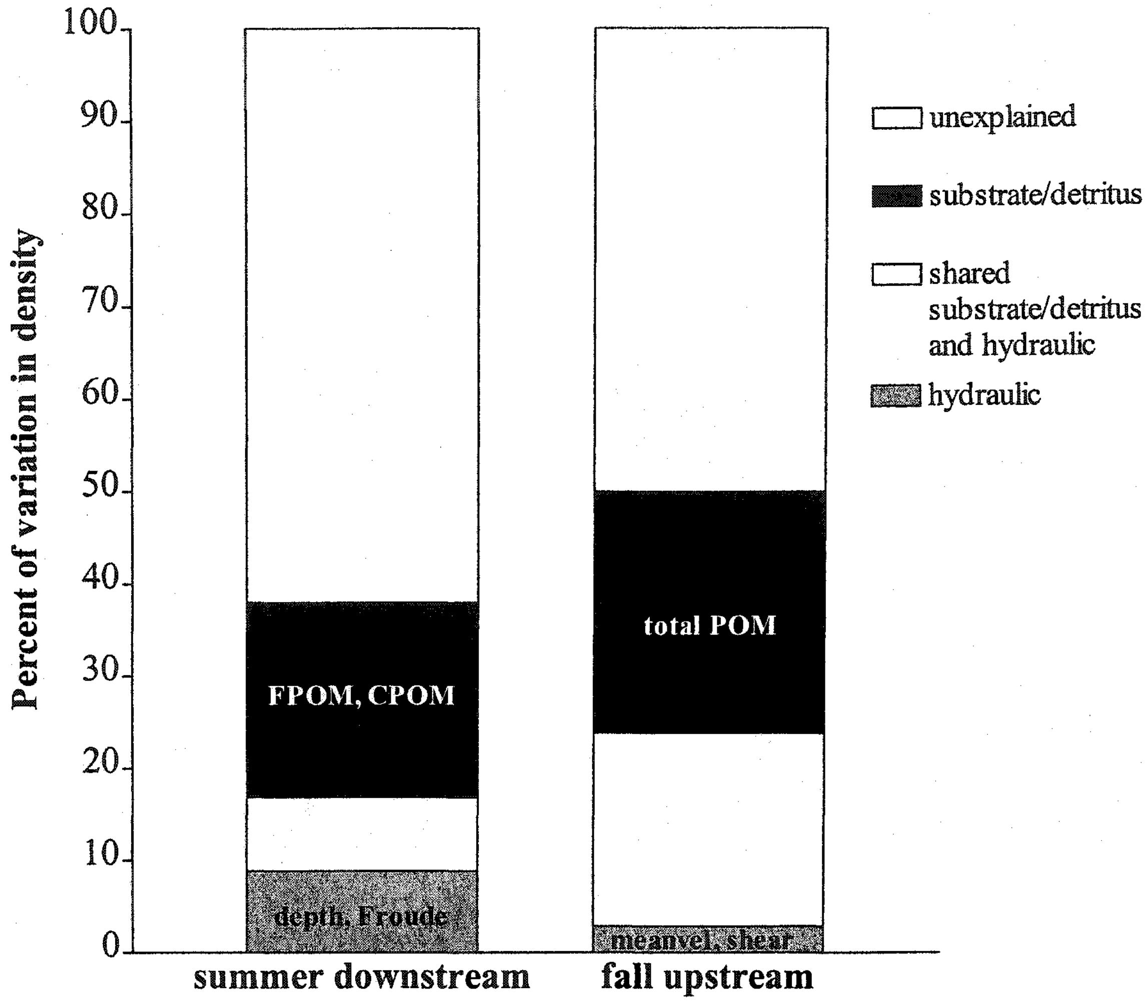


Fig. 3.13. Proportion of variation in macroinvertebrate community taxa densities that can be explained by hydraulic and substrate/detritus variables. Data were collected from patches of the West River run site in each season/area. The hydraulic and substrate/detritus variables that explained the most variation in taxa densities were used in the analysis (variables listed on graph bars; see Tables 3.2, p.115 and 3.7, p. 140 for definition of variable abbreviations). Redundancy analysis was used to determine the proportion of variation that could be explained uniquely by the hydraulic and substrate/detritus variables and by variation that was shared by both types of variables. The variation explained uniquely by hydraulic variables was not significant ($P>0.05$) in either season/area.

hydraulic variables (mean velocity and shear velocity; partial RDA, RDA, Fig. 3.13). In both seasons/areas, very little of the variation in combined community taxa densities could be explained uniquely by hydraulic variables, and a large amount of the variation in taxa densities was not explained by any of the measured environmental variables (RDA, Fig. 3.13).

Vertical hydraulic gradient

The combined densities of taxa in the entire macroinvertebrate community were not significantly related to vertical hydraulic gradient in patches where VHG could be measured for either season/area ($P>0.05$ for RDA solutions). However, the correlation of macroinvertebrate density with VHG was significant for certain dominant taxa in the summer downstream samples (Fig. 3.14). The "tiny Plecoptera group", which consisted of small individuals in early stages of development that could not be identified beyond order, had higher density in patches with some upwelling than patches with weak to undetectable vertical flow. Three other dominant taxa (the mayfly *Drunella*, the cranefly larvae *Dicranota* and tubificid worms) were significantly more abundant in patches with strong upwelling than patches with weaker upwelling or weak to undetectable vertical flow (Fig. 3.14). However, these patches were also characterized by small substrate size and high detritus, so the density of these taxa was also related to several substrate/detritus variables as well as VHG (RDA, see Fig. 3.10, p.138).

Spatial variation of macroinvertebrate densities

The distribution of the total density of macroinvertebrates (i.e. the total number of macroinvertebrates per area) among patches was not random. The total density of macroinvertebrates had an aggregated or clumped distribution in both seasons/areas of the

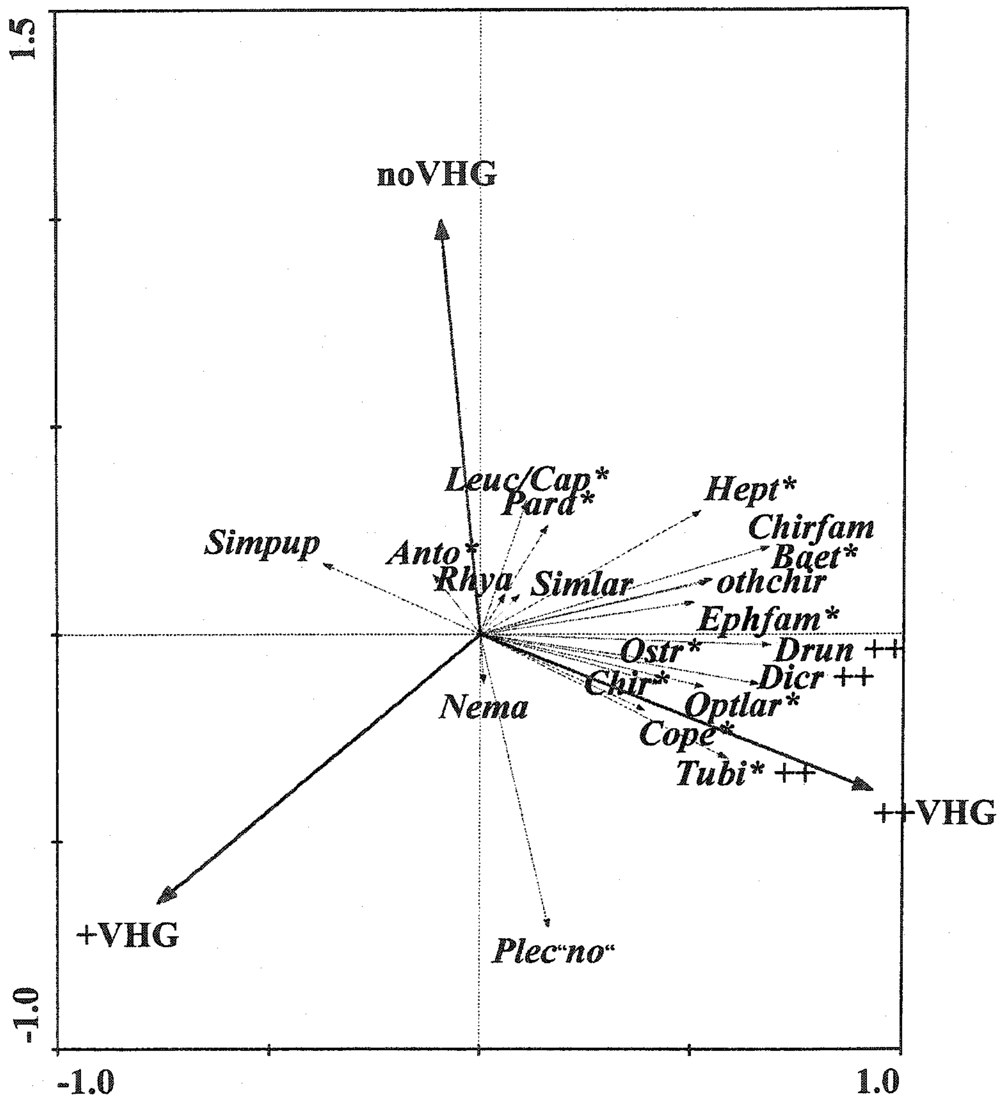


Fig 3.14. Relationships between macroinvertebrate taxa densities and vertical hydraulic gradient (VHG) in summer downstream samples as determined by redundancy analysis (RDA). The variation in taxa densities explained by the RDA solution is 28% (both axes not significant, P>0.05, n =11). Significant correlations between macroinvertebrate densities and VHG (t-value biplots, t-value >2 or <-2) are indicated by "++" for ++VHG and "no" for noVHG . Samples were collected from patches at the West River run site. The RDA correlation biplot shows approximate correlations among variables (rare taxa not shown; see Appendix III for biplot interpretation guidelines). For definitions of variable abbreviations, see Table 3.7, p. 140 indicates deposit-feeding detritivores.

run site (as indicated by the finding that the variance of density values was much higher than the mean). Specifically, macroinvertebrate densities tended to be higher towards one bank. This pattern was observed for both the combined community taxa densities (the densities of all taxa analyzed simultaneously) and the total density of macroinvertebrates (the sum of the densities of all taxa). Variation in the densities of the macroinvertebrate community taxa was significantly related to the perpendicular distance of samples from a given bank (transverse location) in both seasons/areas ($P<0.05$, RDA, Fig. 3.15). A similar pattern of distribution can also be seen visually by plotting the total density of macroinvertebrates in each patch at the run site (Fig. 3.16, 3.17). In both seasons/areas, total macroinvertebrate density and combined community taxa densities were higher on the shallow, gradually sloping sandy bank of the stream than in other areas of the stream, although this pattern was most pronounced in the summer downstream samples. Around a third of the variation in macroinvertebrate community densities could be explained just by transverse position in each season/area. However, most of this third of the variation could also be related to transverse variation in either the substrate/detritus or hydraulic variables (Fig. 3.15) that were the best predictors of combined community densities for a given season/area (as determined by RDA, see Fig. 3.13). Again, this pattern can be seen visually by examining the total macroinvertebrate density plots along with plots of the selected environmental variables in the patches in both seasons/areas (Fig. 3.16, 3.17).

3.3.4 Relationship of detritus to hydraulic variables

Considerable variation in macroinvertebrate density was shown to be related to shared variation in hydraulic and detritus variables, suggesting that flow might have an indirect effect on macroinvertebrates by affecting detritus. Detritus quantities were more closely related to hydraulic variables in the fall upstream samples than the summer downstream

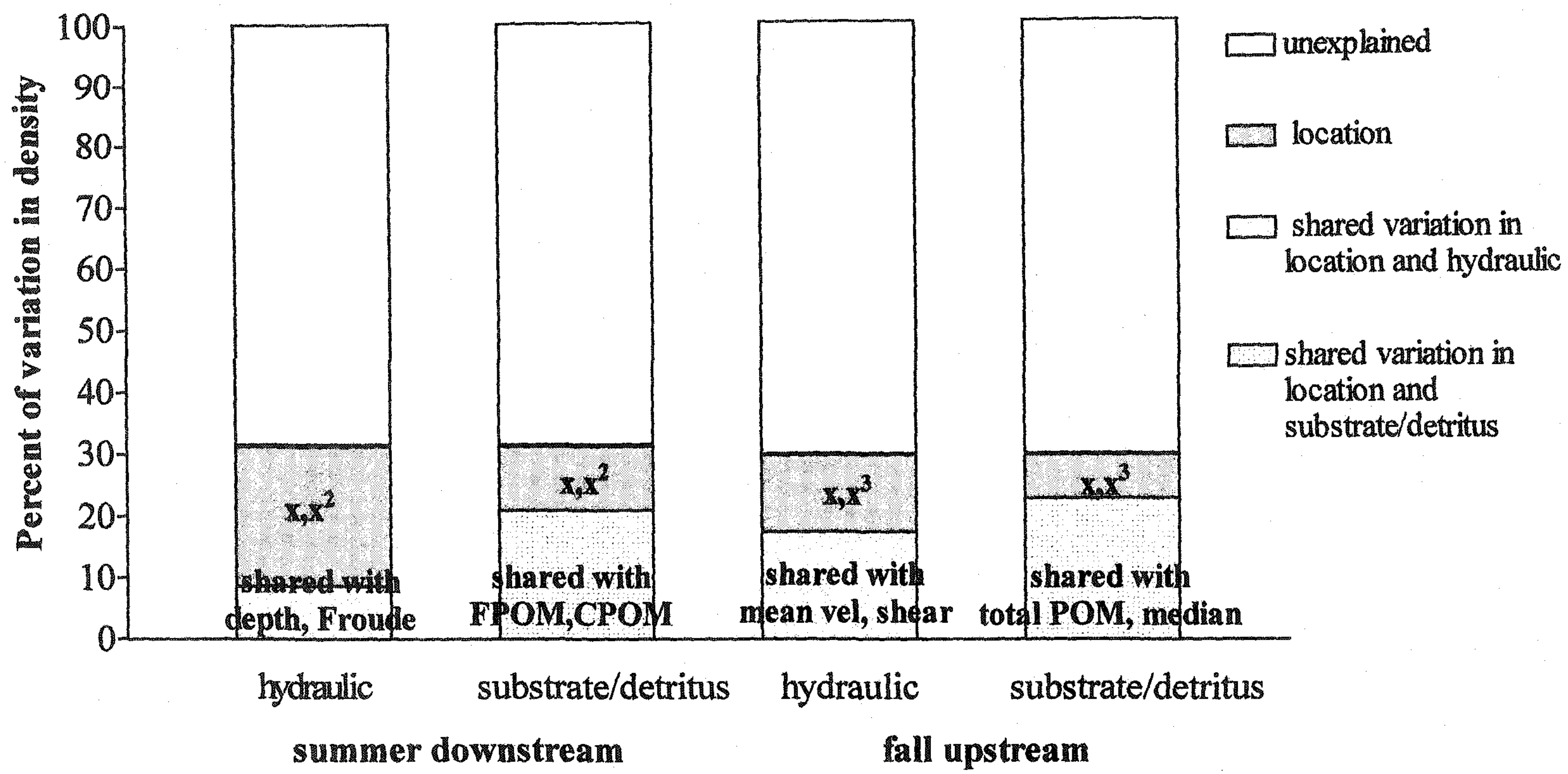


Fig. 3.15. Proportion of variation in macroinvertebrate community taxa densities that can by explained by patch location alone and by shared variation between patch location and hydraulic or substrate/detritus variables. Data were collected from patches of the West River run site in each season/area. Redundancy analysis was used to determine the partitioning of variation shown in each bar of the graph. The hydraulic and substrate/detritus variables that explained the most variation in taxa densities were used in the analysis (variables listed on graph bars; see Table 3.2 p.115 and 3.7., p.140 for definition of variable abbreviations, x=distance of patch location from a given bank).

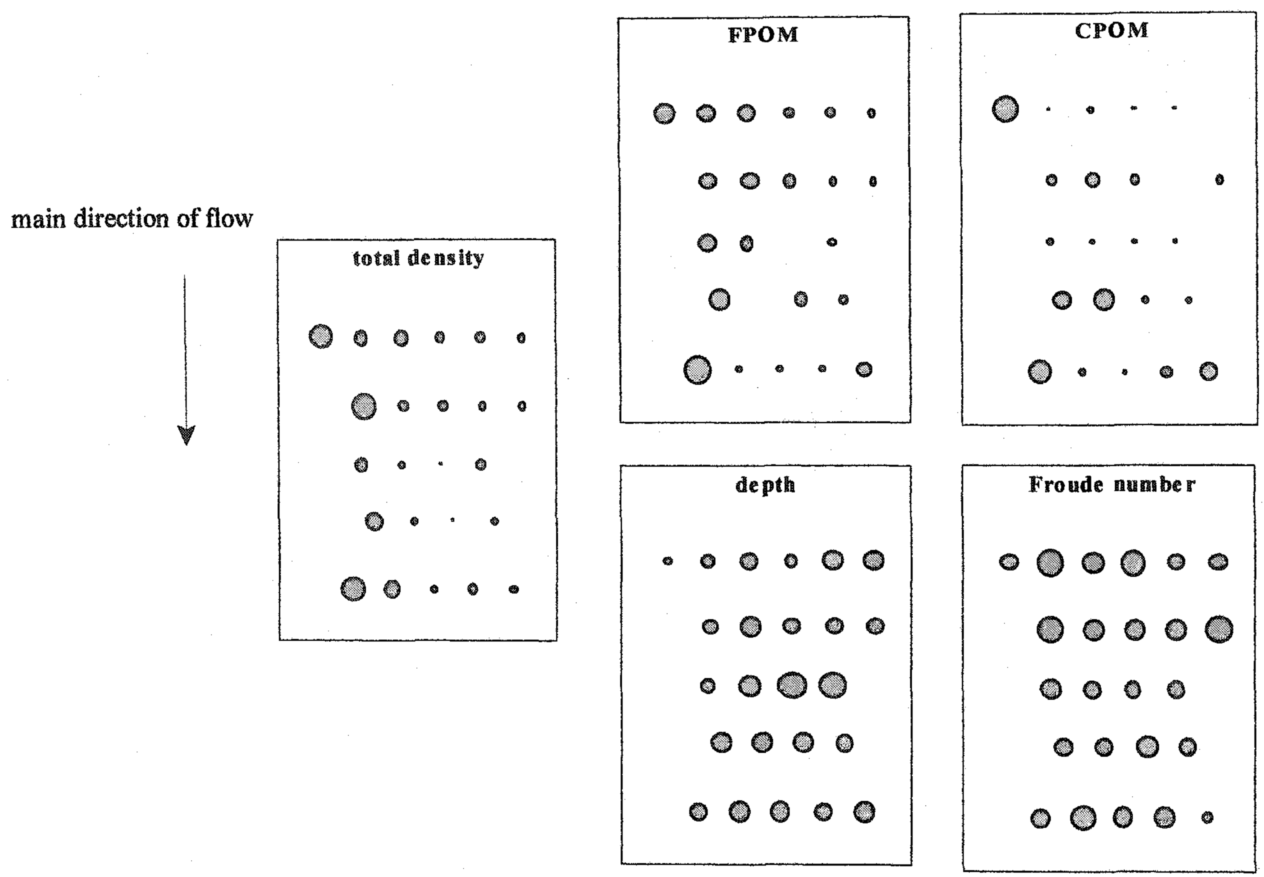


Fig 3.16. Plots showing the spatial variation in the total density of macroinvertebrates and environmental variables in summer downstream samples of the West River run site. The environmental variables shown are the substrate/detritus and hydraulic variables that were the two best predictors of the densities of all community taxa (see Fig 3.13., p.145). The "bubbles" on the plots increase in size with the value of each variable.

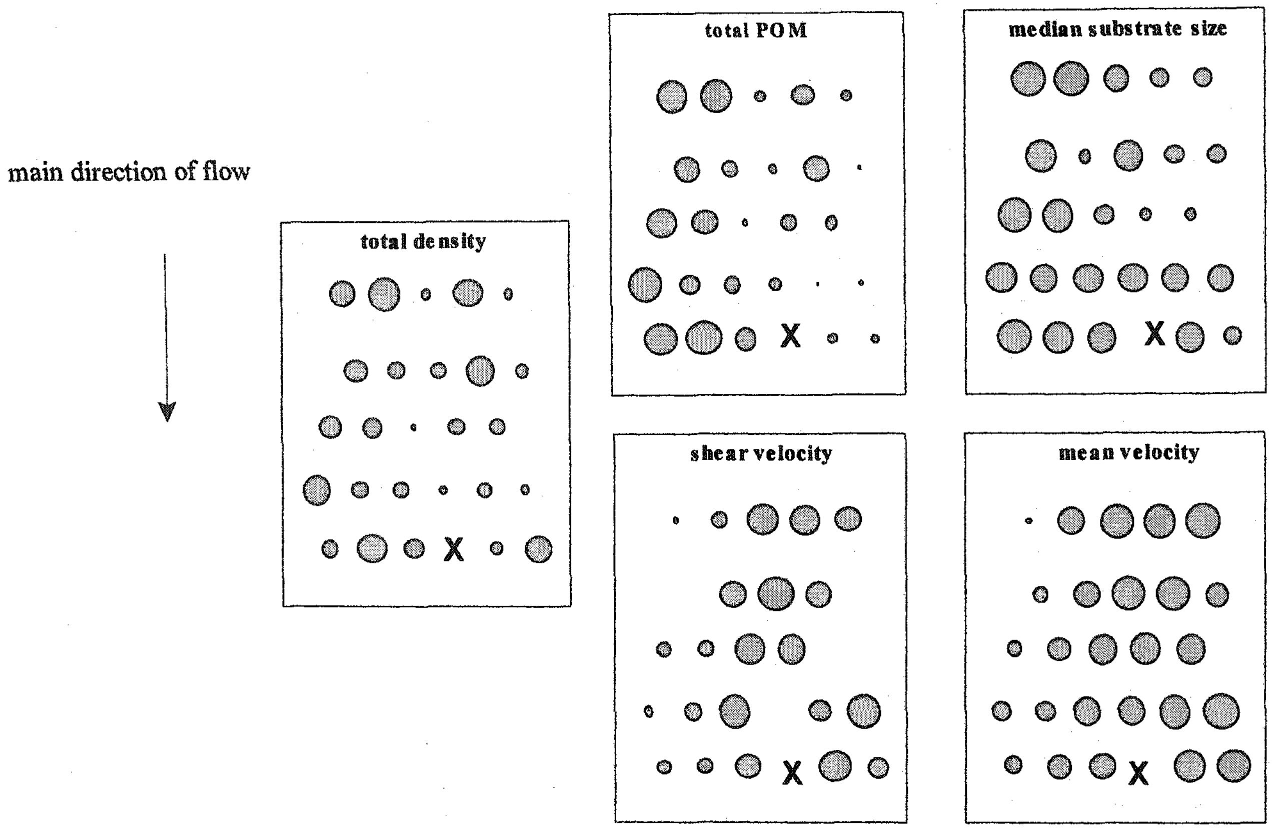


Fig 3.17. Plots showing the spatial variation in the total density of macroinvertebrates and environmental variables in fall upstream samples of the West River run site. The environmental variables shown are the substrate/detritus and hydraulic variables that were the two best predictors of the densities of all community taxa (see Fig 3.13, p.145). The "bubbles" on the plots increase in size with the value of each variable. Note that median substrate size is plotted in phi units, so larger bubbles represent smaller median substrate size.

X = location where sample was not obtained due to accidental loss of streambed material.

samples as shown by regression analysis. In the summer downstream samples, there was no significant regression model for predicting CPOM ($P>0.05$, $n = 25$) from hydraulic variables and only 21% of the variation in FPOM could be predicted using depth, the hydraulic variable that was the best predictor (for log FPOM *versus* square root of depth $r^2 = 0.21$, $P<0.05$, $n = 25$). In the fall upstream area, FPOM and CPOM were both negatively related to shear velocity. Approximately half of the variation in FPOM could be predicted from shear velocity (shear velocity log transformed, $r^2 = 0.54$, $P<0.001$, $n = 26$) and approximately a third of the variation in CPOM could be predicted from shear velocity (both variables square root transformed, $r^2 = 0.32$, $P<0.01$, $n = 26$) However, the portion of CPOM composed of surface leaf litter >32mm was not related to any of the measured hydraulic variables (multiple regression, $P>0.05$, $n = 26$). Neither FPOM nor UFPOM (both of which should be more easily transported by vertical flow than coarser detritus) were significantly related to vertical hydraulic gradient in either season/area ($P>0.10$ for Mann-Whitney U test, $n = 11$ for summer downstream and $n = 13$ for fall upstream).

3.3.5 Relationships of selected deposit-feeding detritivores to environmental variables

Several taxa showed size-related differences in how strongly they were associated with detritus. Density patterns of small individuals (those < 1mm) were usually more strongly correlated to FPOM than those of large individuals for the deposit-feeding detritivore taxa that had enough small and large individuals to analyze size patterns (5 of 5 taxa in summer downstream, 5 of 7 taxa in fall upstream; Table 3.9). However, the size-related variation in density within taxa was low compared to the variation among different taxa, and not all correlations between density of individual taxa and FPOM were significant (Table 3.9).

In contrast, there were no consistent size-related patterns with hydraulic variables. For summer downstream samples, there were no significant size-related patterns between the

Table 3.9. Strength of relationships (Spearman correlation) between densities of deposit-feeding detritivore taxa and FPOM and selected hydraulic variables for individuals with different body sizes in samples of each season/area of the West River run site[a].

Correlation with (r_s^2):	**FPOM**		**Shear velocity**		**Mean velocity**		**Depth**		**Froude number**	
individual size [b] :	**small**	**large**	**small**	**large**	**small**	**large**	**small**	**large**	**small**	**large**
Taxon										
summer downstream										
Baetis	__0.013__	0.003 -	0.00	__0.02 -__	0.00	0.00 -	0.08 -	__0.10 -__	0.01	0.00 -
Heptagenia	__0.045__	0.000	0.00 -	__0.01 -__	0.00 -	__0.10 -__	__0.05 -__	0.01	0.00 -	__0.20 -__
Leuctridae/ Capniidae	__0.130__	0.031	__0.12__	0.00	__0.04 -__	0.03	0.05 -	0.05 -	__0.13__	0.08
Optioservus	__0.428**__	0.362*	0.00	0.00 -	__0.17 -__	0.08 -	__0.13 -__	0.08 -	__0.03 -__	0.02 -
Tubificidae	__0.735**__	0.610**	0.00	__0.03__	__0.09 -__	0.01 -	0.19 -	__0.43 -__	0.00 -	__0.04__
fall upstream										
Baetis	__0.103__	0.001-	0.002 -	__0.079__	0.004 -	__0.063__	__0.017 -__	0.013	0.000 -	__0.124__
Ephemerella	0.365**	__0.419***__	__0.245* -__	0.242* -	0.118 -	__0.122 -__	__0.088 -__	0.066 -	__0.104-__	0.083 -
Paraleptophlebia	__0.403***__	0.267*	__0.335**-__	0.166 -	__0.222* -__	0.127 -	__0.324** -__	0.119 -	__0.109 -__	0.093 -
Antocha	0.144	__0.223*__	__0.366**-__	0.332** -	0.293** -	__0.466*** -__	__0.360**-__	0.171*-	0.157*-	__0.333** -__
Empididae	__0.517***__	0.497***	0.397**-	__0.463*** -__	0.179* -	__0.333** -__	0.172*-	__0.239*-__	0.095 -	__0.212* -__
Optioservus	__0.577***__	0.503***	0.434***-	__0.444*** -__	__0.390*** -__	0.338** -	__0.229* -__	0.171* -	__0.276** -__	0.233* -
Tubificidae	__0.748***__	0.650***	__0.466***-__	0.370** -	__0.476*** -__	0.269** -	0.306**-	__0.417***-__	__0.350** -__	0.136 -

[a]larger r_s^2 value for each taxon is highlighted and in bold, n = 25 for summer downstream, n = 26 for fall upstream samples except for correlations with shear velocity in both seasons/areas for which n =22, and with FPOM in summer downstream, for which n = 23, * P<0.05,** = P<0.01,*** = P<0.001,- = negative correlation (r-value)

[b]body size separation made by passing samples through 1 mm mesh sieve

density of these deposit-feeding detritivores and any of the hydraulic variables (Table 3.9) that were the best predictors of combined community density (as determined by RDA analysis for both seasons/areas see Fig. 3.13, p. 145). There were some significant size-related patterns associated with hydraulic variables in fall upstream samples (Table 3.9). For example, the density patterns of small individuals were more strongly negatively correlated to depth than densities of large individuals for 5 of the 7 taxa in this analysis. Also, small individuals also tended to have a stronger decrease in density with increasing shear velocity and Froude number than large individuals (5 of the 7 taxa in this analysis). However, the strengths of significant correlations between small or large individuals and hydraulic variables were generally weaker than the corresponding correlations with FPOM (Table 3.9).

Detailed examination of selected taxa and comparisons between the riffle and run site

The relationship of macroinvertebrate density to substrate/detritus and surface flow variables was examined in detail for three taxa of deposit-feeding detritivores: *Optioservus* larvae, *Antocha*, and Leuctridae/Capniidae (Table 3.10). These taxa were selected because earlier statistical analysis had shown that *Optioservus* larvae had similar relationships to the environmental variables as most dominant taxa (and therefore could be thought of as representative), while *Antocha* and Leuctridae/Capniidae had different relationships to some environmental variables in at least one season/area. Since these three taxa also had different habits (Table 3.10), this selection allowed the comparison of habitat associations between interstitial and surface-dwelling deposit-feeding detritivores. In addition, visual examination of the distribution patterns showed that the distributions were similar for smaller and larger individuals of the three taxa, so size classes could be combined.

Table 3.10. Description of deposit-feeding detritivore taxa selected for detailed analysis.

Taxon	Additional taxonomic information	Functional feeding group[a]	Habit[b]	Portion of small[c] individuals
Optioservus larvae	probably *O. fastiditus*[d]	collector-gatherer/scraper, *O. fastiditus* may feed mostly on detritus[1]	burrowers[2]	summer downstream: 54% small fall upstream: 71% small
Antocha	none	collector-gatherer[3]	clingers, in silk tube[3]	summer downstream: all small fall upstream: 59% small
Leuctridae/ Capniidae[e]	summer downstream: 68 of 229 individuals identified as 91% *Leuctra* (Leuctridae), 9% Capniidae fall upstream: 28 of 1014 individuals identified as 25% Leuctridae, 68% *Leuctra* (Leuctridae), 7% Capniidae	often shredders[4], but Leuctridae[5] may be collector-gatherers	generally sprawler-clingers[4], but small larvae are interstitial[6]	summer downstream: 82% small fall upstream: 93% small

[a]see Table 1.6, p.37 for definitions of functional feeding groups
[b]see Table 1.5, p.35 for definitions of habit
[c]size separations made using 1 mm mesh sieve, small individuals of these taxa were early instars
[d]all adults in both seasons were *O. fastiditus*
[e]Leuctridae/Capniidae were combined into a single group because they share similar habitats and biology and because they were not possible to distinguish in very small stages

REFERENCES
[1]Tavares and Williams, 1990; [2]Brown, 1987; [3]Courtney *et al.*, 1996; [4]Stewart and Harper, 1996; [5]Stewart and Stark, 1993; [6]McCafferty, 1998

The densities of all three taxa increased with detritus, and were better predicted from substrate/detritus variables than hydraulic variables, and from detritus than substrate size or algal cover (Table 3.11). At the run site, taxa densities could be predicted with greater certainty by the measured variables in the summer downstream samples than in the fall upstream samples (Table 3.11). However, strong relationships between macroinvertebrate density and environmental variables at the run site did not necessarily extend to samples taken at the riffle site. In 7 of the 8 strong relationships which were compared between sites, the patterns at the riffle site were different from those at the run site (Fig. 3.18 to 3.20).

The density of *Optioservus* larvae in both seasons/ areas of the run site was closely related to the amount of detritus (Table 3.11) and very little variation in larvae density was uniquely related to variation in hydraulic variables (Fig. 3.21). For *Optioservus*, 52 and 82% of the variation in density was explained by the measured environmental variables in summer downstream and fall upstream samples, respectively. The density of *Optioservus* larvae in sampled patches was low at the riffle compared to the run site in both seasons/areas and did not correlate to the environmental variables at the riffle site in the same way as at the run site (for those relationships examined at both sites; Fig. 3.18).

Variation in *Antocha* density was most closely related to shared variation in detritus and hydraulic variables in both seasons/areas of samples at the run site, but there was also a considerable amount of unexplained variation in *Antocha* density (Fig 3.22). In summer downstream samples, the density of *Antocha* was highest in patches with high amounts of the larger size fractions of detritus and shallow depth. In fall upstream samples, the density of *Antocha* was high in areas with abundant detritus and low mean velocity (Table 3.11, Fig. 3.22). In the fall upstream samples, for which *Antocha* distribution was compared between sites, density increased with the amount of POM 0.5 to 0.25 mm at both the riffle

Table 3.11. Relationships between densities of selected deposit-feeding detritivore taxa and hydraulic and substrate/detritus variables in samples collected in each season/area of the West River run site. Relationships were determined from redundancy analysis (RDA) correlation biplots (Fig 3.10, p.138, 3.11, p.139) and regression analysis.

Taxon	Season/area	Environmental variables (substrate/detritus or hydraulic)	Density increases[a] with following environmental variables or variable group [b] as determined by RDA correlation biplots:	Strongest relationship between taxon density and environmental variables as determined by multiple regression		
				density transformation	best predictors	r^2, significance[c]
***Optioservus* larvae**	summer downstream	substrate/ detritus	FPOM (except VFPOM and VVFPOM)/decreasing substrate size and algal cover CPOM, VVFPOM	square root	square root total POM	0.50***
		hydraulic	decreasing depth and roughness	square root	-log depth	0.24*
	fall upstream	substrate/ detritus	higher POM >0.25mm/decreasing substrate size and algal cover	square root	FPOM 0.5 to 0.25mm	0.82***
		hydraulic	gradient of decreasing hydraulic stress and depth	square root	-square root mean velocity	0.41***

continued...

Table 3.11. cont.

Taxon	Season/area	Environmental variables (substrate/detritus or hydraulic)	Density increases[a] with following environmental variables or variable groups as determined by RDA correlation biplots [b]:	Strongest relationship between taxon density and environmental variables as determined by multiple regression		
				density transformation	best predictors	r^2, significance[c]
Leuctridae/ Capniidae	summer downstream	substrate/detritus	FPOM (except VFPOM and VVFPOM)/decreasing sediment size and algal cover	log(x+1)	UFPOM	0.30*
		hydraulic	Froude number	log(x+1)	-1/Froude	0.22 *
	fall upstream	substrate/detritus	higher POM >0.25mm/decreasing substrate size and algal cover higher fine POM and silt	square root	total POM	0.71 ***
		hydraulic	gradient of decreasing hydraulic stress and depth	square root	- shear	0.40 ***
Antocha	summer downstream	substrate/detritus	CPOM, VVFPOM	log(x+1)	CPOM	0.20*
		hydraulic	decreasing depth, roughness	log(x+1)	-log depth	0.23 *
	fall upstream	substrate/detritus	higher POM >0.25mm/decreasing substrate size and algal cover	square root	FPOM 0.5 to 0.25mm	0.51***
		hydraulic	gradient of decreasing hydraulic stress and depth	square root	-mean velocity	0.39 ***

[a] taxa abundances were log (x+1) transformed for RDA correlation biplots
[b] see Table 3.8, p.142 for list of variables in each group, see Table 3.2, p. 115 for definition of detritus variables
[c] * P<0.05, ** = P<0.01, *** = P<0.001

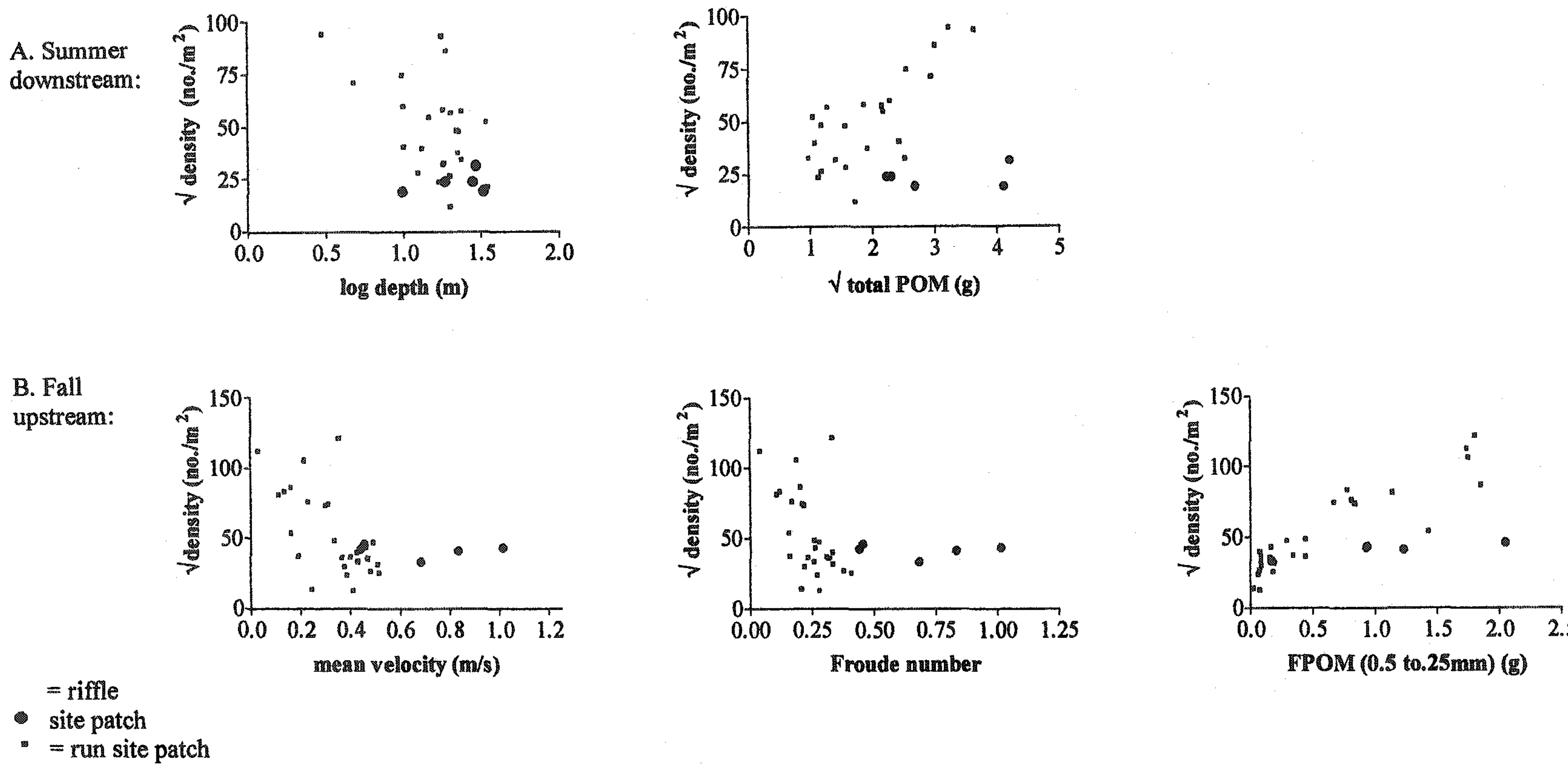


Fig 3.18. Relationship between density of *Optioservus* and selected environmental variables at run and riffle sites in A. summer downstream samples and B. fall upstream samples. The environmental variables shown were the best predictors of *Optioservus* density of the hydraulic and substrate/detritus variables (as determined by multiple regression) except for Froude number. Froude number, a dimensionless hydraulic variable calculated from mean velocity and depth, is shown since it is more reliable for comparing flow conditions between different channels than mean velocity.

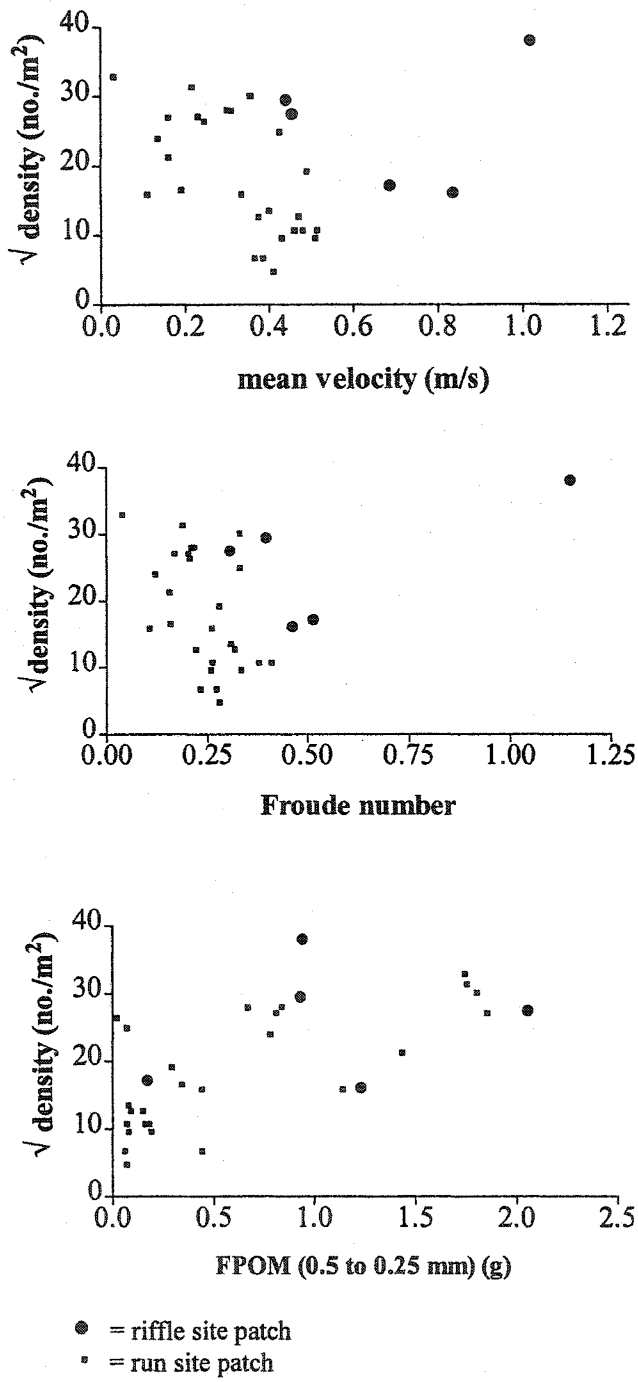


Fig 3.19. Relationship between density of *Antocha* and selected environmental variables at run and riffle sites. The environmental variables shown were the best predictors of *Antocha* density of the hydraulic and substrate/detritus variables (as determined by multiple regression) except for Froude number. Froude number, a dimensionless hydraulic variable calculated from mean velocity and depth, is shown since it is more reliable for comparing flow conditions between different channels than mean velocity.

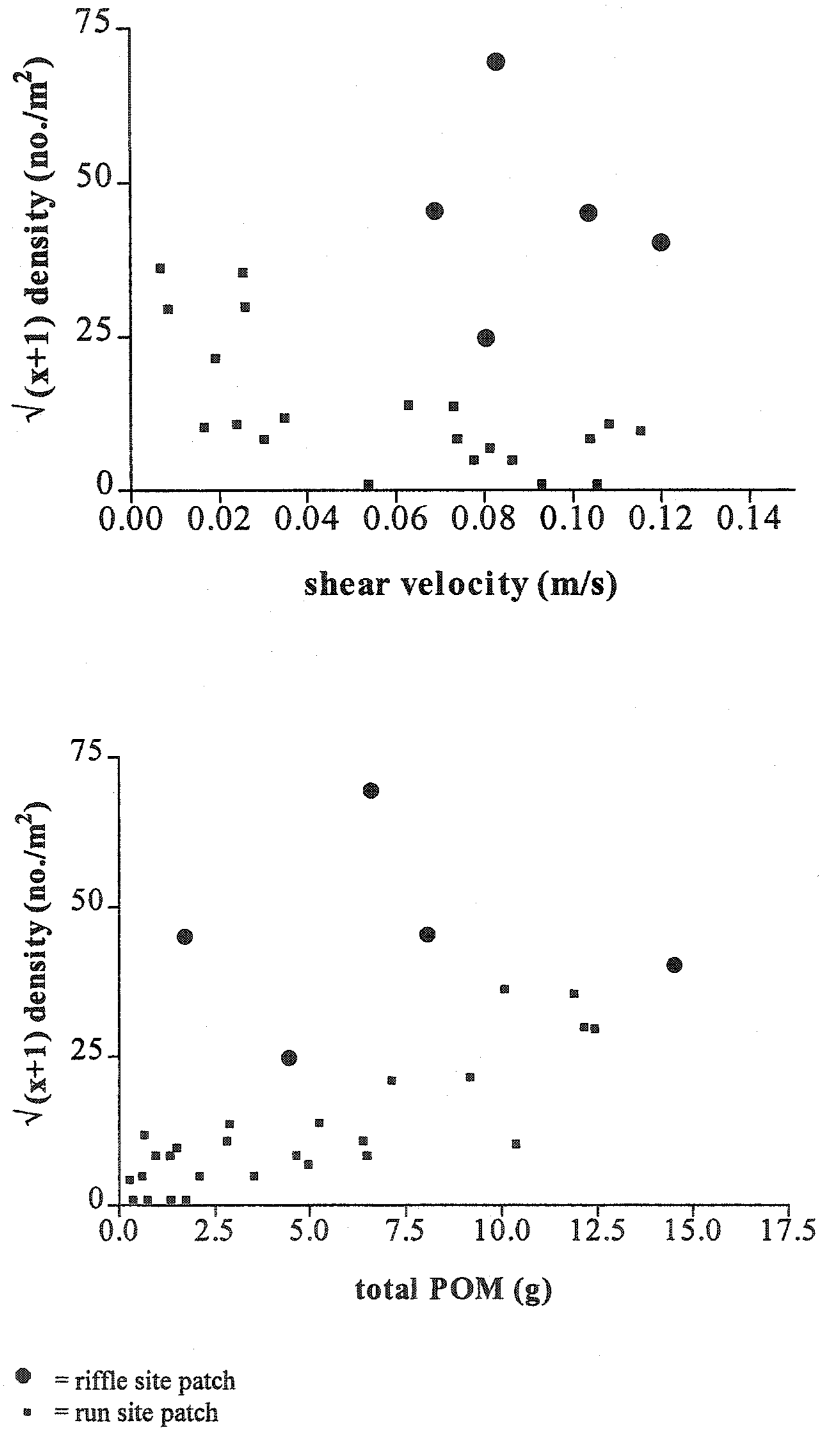


Fig 3.20. Relationship between density of Leuctridae/Capniidae and selected environmental variables at run and riffle sites. The environmental variables shown were the best predictors of Leuctridae/Capniidae density of the hydraulic and substrate/detritus variables (as determined by multiple regression).

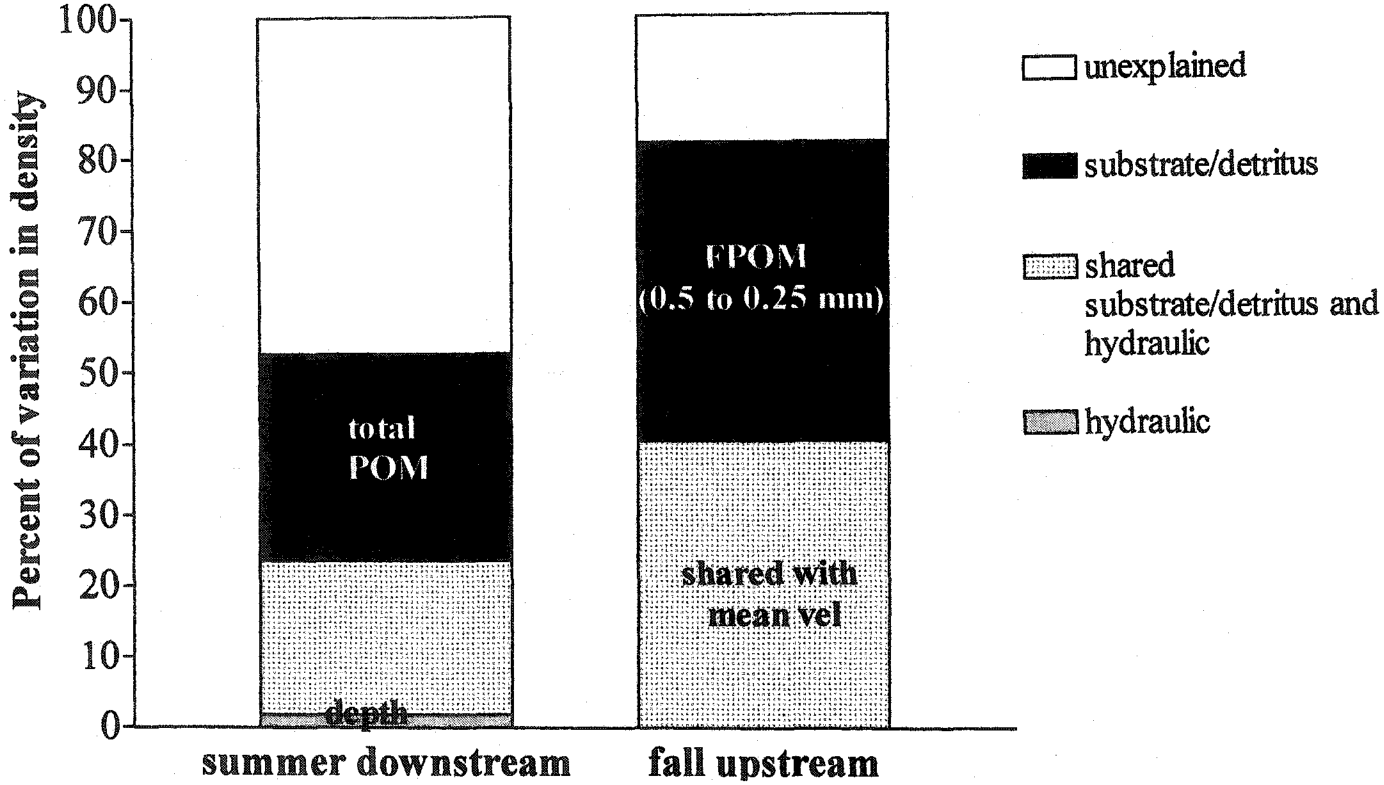


Fig. 3.21. Proportion of variation in *Optioservus* density that can be explained by hydraulic and substrate/detritus variables. Data were collected from patches of the West River run site in each season/area. The hydraulic and substrate/detritus variables that explained the most variation in *Optioservus* density were used in the analysis (variables listed on graph; see Tables 3.2, p.115 and 3.7., p.140 for definition of variable abbreviations). Multiple regression analysis was used to determine the proportion of variation that could be explained uniquely by the hydraulic and substrate/detritus variables and by variation that was shared by both types of variables.

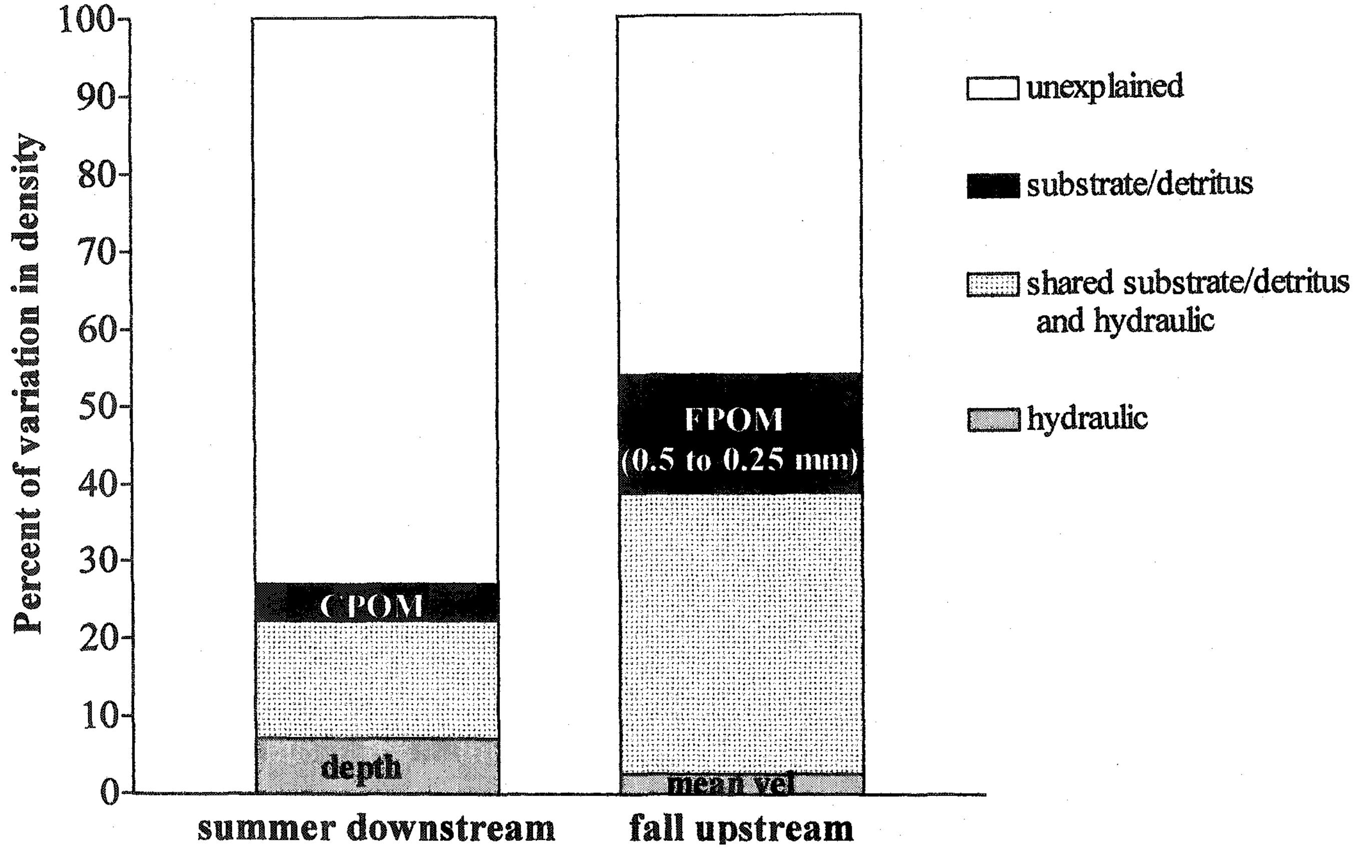


Fig. 3.22. Proportion of variation in *Antocha* density that can be explained by hydraulic and substrate/detritus variables. Data were collected from patches of the West River run site in each season/area. The hydraulic and substrate/detritus variables that explained the most variation in *Antocha* density were used in the analysis (variables listed on graph; see Tables 3.2, p.115 and 3.7., p.140 for definition of variable abbreviations). Multiple regression analysis was used to determine the proportion of variation that could be explained uniquely by the hydraulic and substrate/detritus variables and by variation that was shared by both types of variables.

and run site, but was not related to mean velocity at the riffle site (Fig. 3.19).

The Leuctridae/Capniidae group had different relationships with environmental variables in run site samples taken in different seasons/areas. Over 70% of the variation in density in fall upstream samples could be explained by the measured variables, compared to about 50% in the summer downstream samples (Fig 3.23). In summer downstream samples, the density of Leuctridae/Capniidae could be explained almost equally well by unique variation in hydraulic conditions (Froude number) and unique variation in detritus (UFPOM; Fig. 3.23). In contrast, in the fall upstream samples of the run site, Leuctridae/Capniidae density was best explained by unique variation in detritus (total POM; Fig. 2.23). Also, the density of Leuctridae/Capniidae increased with Froude number in the summer downstream samples, but decreased with Froude number in the fall upstream samples and was most closely correlated with different size fractions of detritus in each season/area. (Table 3.12). When density patterns were compared between sites (fall upstream samples), larval density was found to be higher at the riffle site than the run site and did not appear to be related those variables that were the best predictors of density at the run site (Fig. 3.20).

3.4 Discussion

3.4.1. Relative importance and inter-correlation of flow and detritus

The main conclusion of this study is that, at least in the run site on the West River, the density of macroinvertebrates in both sampling seasons was more closely related to the abundance of detritus than to hydraulic conditions. Many other studies have found that detritus abundance is closely related to macroinvertebrate densities at an intermediate spatial scale, both for actual detritus feeders and other functional feeding groups (review in Minshall, 1984; e.g. in Drake, 1984, Rempel *et al.*, 2000; Doisy and Rabeni, 2001;

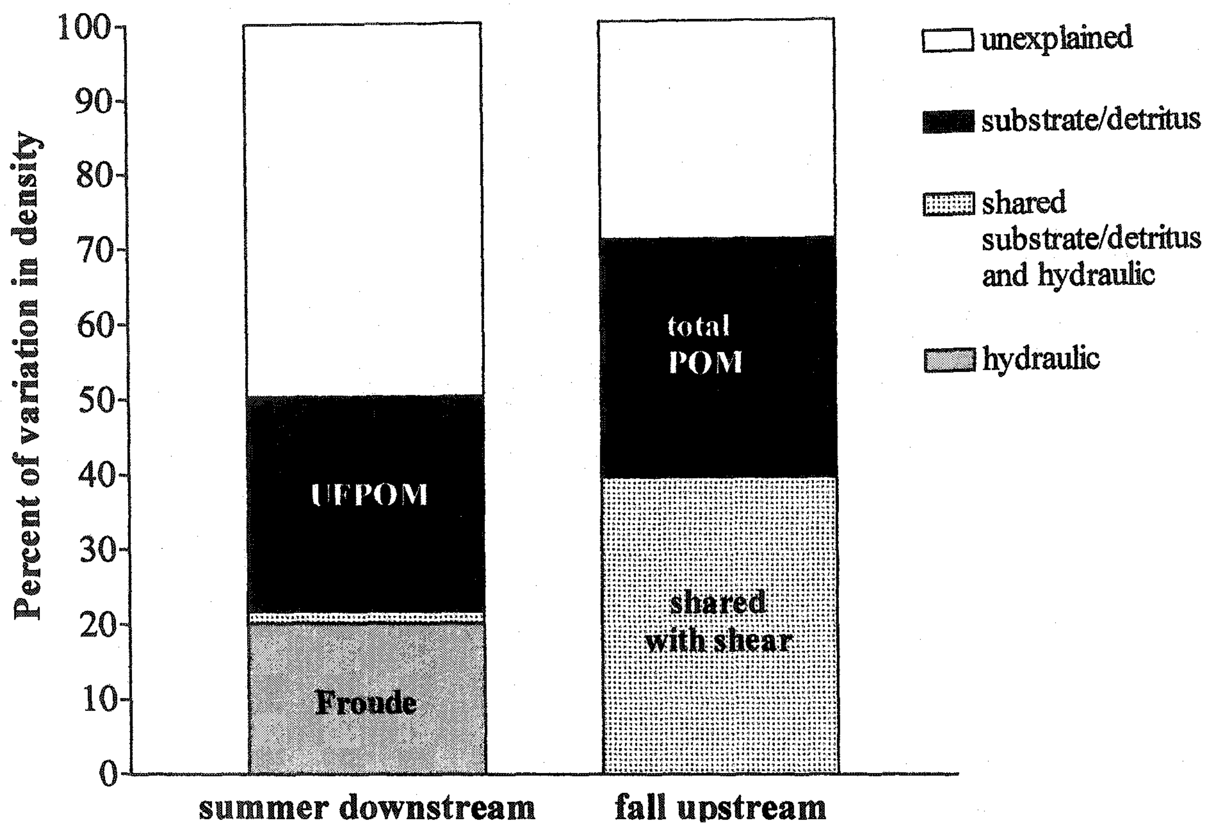


Fig. 3.23. Proportion of variation in Leuctridae/Capniidae density that can be explained by hydraulic and substrate/detritus variables. Data were collected from patches of the West River run site in each season/area. The hydraulic and substrate/detritus variables that explained the most variation in Leuctridae/Capniidae density were used in the analysis (variables listed on graph; see Tables 3.2, p.115 and 3.7., p.140 for definition of variable abbreviations). Multiple regression analysis was used to determine the proportion of variation that could be explained uniquely by the hydraulic and substrate/detritus variables and by variation that was shared by both types of variables.

Table 3.12. Comparison of strength of relationships (Spearman correlation)[a] between density of Leuctridae/Capniidae and selected environmental variables in summer downstream *versus* fall upstream samples.

Correlation between density and:	**Summer downstream**		**Fall upstream**	
	r_s^2	n	r_s^2	n
Froude number	0.196[b]*	25	0.194 -*	26
shear velocity	0.084	22	0.423 -**	22
total POM	0.162	23	0.557 ***	26
CPOM	0.048	25	0.350 **	26
FPOM	0.156	23	0.572 ***	26
UFPOM	0.269**	23	0.317 **	26

[a]Leuctridae/Capniidae log (x+1) transformed for both seasons/areas, correlations are positive unless otherwise indicated - = negative correlation (r-value), * P<0.05, ** = P<0.01, *** = P<0.001

[b]negative correlation with Froude number inverse transformed (therefore, positive correlation with Froude number)

Miyake and Nakano, 2002). There are several possible reasons for the pattern with detritus. Some macroinvertebrates at the run site, such as taxa classified as collector-gatherers and shredders, may select areas of high deposited detritus because they feed directly on this food resource (Minshall, 1984; Dobson *et al.*, 1992). Even taxa that are not classified as detritivores, for example predators, are often known to feed on detritus when they are small (Cummins and Merritt, 1996). Therefore, if these taxa are sampled when most individuals are in small stages of development, their densities may be correlated to detritus because they too are using detritus as a food resource. Large predators (such as the caddisfly *Rhyacophila* and chironomids in the subfamily Tanypodinae in the fall upstream samples in this study), could also show correlations with detritus because they are attracted to areas that have high densities of deposit-feeding detritivore prey (see discussion of predator-prey associations in Williams and Smith, 1996).

Another reason that macroinvertebrate densities show high correlations to detritus could be that fine detritus deposition was highly correlated to substrate size, which is another factor that is known to affect macroinvertebrate distribution (Barber and Kevern, 1973; Minshall, 1984). In this study, detritus was a stronger predictor than any of the substrate size variables, but at least some of the macroinvertebrate habitat selection may have been due to structural characteristics of the substrate, rather than the presence of detritus itself. Therefore, some macroinvertebrates may have been more abundant in areas with more fine detritus due to habit selection based on structural characteristics of the substrate (reviewed in Minshall, 1984).

This results of this study support the potential importance of indirect effects of flow on macroinvertebrate densities through modification of substrate/detritus. For example, the relationship of macroinvertebrate densities to substrate/detritus characteristics at the West River run site included a strong association between macroinvertebrate densities and the shared variation of substrate/detritus characteristics with hydraulic variables. Similar associations between macroinvertebrate density, detritus and hydraulic variables to those observed in this study have been found in other studies (Rempel *et al.* 2000; Doisy and Rabeni, 2001; Miyake and Nakano, 2002). These associations suggest that flow affects macroinvertebrate distribution indirectly by influencing the accumulation of detritus. For example, the decrease in detritus with increasing shear velocity in fall upstream samples at the run site in this study is consistent with known effects of shear velocity on the accumulation of detritus (Hildrew *et al.*, 1991; Peterson, 1999).

In contrast, the large amount of spatial variation in detritus at the run site that was *not* explained by the hydraulic variables suggests that other factors may have had a strong influence on the accumulation of detritus. These factors include flow conditions during previous high discharge events (Hildrew *et al.*, 1991) and the interaction of flow with substrate size. In this study, there was a negative correlation between fine detritus and substrate size, and detritus is known to accumulate efficiently in small substrate which has low rates of interstitial flow (Rabeni and Minshall, 1977; Parker, 1989). Furthermore, the abundance of detritus on the gradually sloping sandy bank of the run site is consistent with the high trapping efficiency of shallow sandy substrate in areas of slow flow observed by Wanner and Pusch (2001).

Although surface flow may have affected macroinvertebrate distribution indirectly through these different mechanisms, there was little evidence to suggest that flow had a direct (physical) effect on the densities of most dominant taxa at the run site since the variation uniquely explained by hydraulic variables was very low. In addition, the trend for small individuals of deposit-feeding detritivore taxa to decrease more in density with increasing shear velocity than large individuals, is opposite to what would be expected if the energy required to maintain position against the force of flow limited their distribution (Statzner, 1981).

The direct effects of surface hydraulics can be relatively unimportant to the distribution of many macroinvertebrates either because most individuals are living below the surface of the streambed (where they are not directly exposed to surface flow; Statzner, 1981) or because the ones that do live on the surface of the streambed are well-adapted to high forces of near-bed flow (Hoover, 2001). Dominant taxa at the run site in this study that are often abundant in subsurface habitats include the chironomids in the subfamily Chironominae, ostracods, nematodes, early instars of stoneflies (e.g. small individuals of Leuctridae/Capniidae; reviewed in Williams,1984; Boulton and Foster, 1998), the riffle beetle larvae *Optioservus* (Brown, 1987) and tubificid worms (Wetzel *et al.*, 2000). Dominant taxa at the run site that are typically found on surfaces of the streambed include the cased caddisfly *Micrasema* (Wiggins, 1996), the mayfly *Baetis*, and the free-living caddisfly *Rhyacophila* (see references in Williams, 1984 and Wiggins, 1996). *Micrasema* (Statzner and Holm, 1989) and *Baetis* (Vogel, 1994) have body shapes that minimize pressure drag (the force of flow acting against surfaces facing upstream), and *Rhyacophila* can maintain its position in current with strong claws and by attaching a silk teather-line to the substrate (Ross, 1956). Therefore the distribution of these 3 taxa may not be limited by high flow velocity or shear velocity. The only dominant taxon in this study to show a strong consistent relationship to surface flow was the black fly *Simulium,* which is a collector-filterer rather than a deposit-feeding detritivore. Black flies and many other collector-filterers use the water current for feeding and have better feeding efficiencies under certain flow conditions (reviewed in Hart and Finelli, 1999). In this study, as well as in a study by Wetmore *et al.* (1990), *Simulium* was more abundant in patches with high Froude number than those with low Froude number.

Finally, it is possible that hydraulic properties of surface flow that were not quantified in this study were more closely related to macroinvertebrate distribution than the measured hydraulic variables. For example, some of the characteristics of flow not measured in this study that have been related to macroinvertebrate distribution in other descriptive field studies include three-dimensional patterns of flow around rocks (Bouckaert and Davis, 1998) and the level of near-bed turbulence as quantified by roughness Reynolds number (Quinn and Hickey, 1994). Therefore, it is possible that this study underestimates the influence of surface flow on macroinvertebrate distribution because the description of the hydraulics of flow in patches is incomplete.

3.4.2 Pattern of spatial variation in macroinvertebrate densities and environmental characteristics

An aggregated pattern of macroinvertebrate density was observed in this study as has been found in many other studies (Ulfstrand, 1967; Cummins, 1992). In this study, the aggregated pattern of higher densities towards one bank was closely related to the spatial structure of substrate/detritus and flow variables. Therefore, there was little evidence that biotic interactions had a strong influence on this density pattern.

3.4.3 Relationship of macroinvertebrate density to vertical hydraulic gradient

The densities of some taxa (e.g. tiny stoneflies) increased significantly with upwelling in the summer downstream samples. Patches with strong upwelling also tended to have similar substrate/detritus characteristics such as small substrate size and high detritus. Thus macroinvertebrates that were abundant in these areas could have been selecting habitat based on substrate/detritus characteristics rather than characteristics related to the presence of upwelling. Pepin and Hauer (2002) found that certain benthic taxa, including several stoneflies, occurred at higher densities in upwelling zones independently of variation in substrate size. However, very few studies have examined relationships between macroinvertebrates in the surface layer of the streambed and vertical subsurface flow. The findings of this study support the need for more research to investigate such potentially important relationships (Plénet *et al.*, 1995; Pepin and Hauer, 2002).

In this study, the ability to detect relationships between vertical hydraulic gradient (VHG) and macroinvertebrate distribution was limited since VHG could only be measured in approximately half of the sampled patches. For subsequent studies, methods of characterizing vertical flow such as seepage meters (Lee and Cherry, 1978) or temperature probes (see Alexander and Caissie, 2003) could allow measurement of vertical flow in a greater proportion of streambed areas than the mini-piezometer used in this study.

3.4.4 Implications of inter-correlations among environmental variables

Many environmental variables in this study were inter-correlated, making it difficult to distinguish specific relationships between macroinvertebrate density and the different environmental variables. Inter-correlation of environmental variables also limits the conclusions about macroinvertebrate habitat preference that can be made from descriptive field studies, since it can lead to spurious correlations between macroinvertebrates and environment variables (Statzner, 1981; Minshall, 1984). For this study, partitioning of variation was a useful statistical technique to describe relationships of macroinvertebrates with moderately inter-correlated variables, such as surface flow and detritus variables, and to formulate hypotheses about the causes of these relationships. However, experimental work would be required to test these hypotheses and to differentiate relationships of macroinvertebrates with variables that were highly inter-correlated in this study such as fine detritus and substrate size (see Chapter 4 for further discussion).

3.4.5 Comparison of relationships between sites and seasons/areas

Dramatic differences were seen between the two sites in this study. In particular, the strong relationships between detritivore taxa density that were observed at the run site did not extend to the riffle site for 7 of the 8 relationships examined at both sites. It is difficult to make definite conclusions about patterns at the riffle site due to the small number of patches sampled at this site. However, community composition of macroinvertebrates can vary among sites in different sections of a stream independently of hydraulics and detritus (Doisy and Rabeni, 2001). Although variables such as detritus may be good predictors of taxa densities at intermediate spatial scales, other factors such as substrate stability may be more important at reach scales (e.g. among sites; Miyake and Nakano, 2002). The lower substrate stability of the riffle site compared to the run site in this study could account for the differences in macroinvertebrate density between sites. Also, low substrate stability at the riffle site may have had an influence on variation in macroinvertebrate densities among patches that overrode the influence of substrate/detritus.

Samples collected at the run site generally showed similar relationships between macroinvertebrate density and environmental variables in both seasons/areas. Those environmental variables that were the best predictors of macroinvertebrates densities (e.g. amounts of FPOM and total POM) were also generally similar in both seasons/areas. However, some taxa had different habitat associations in summer downstream samples than fall upstream samples. For example, Leuctridae and Capniidae stoneflies had different associations with Froude number and specific size fractions of detritus in each season/area. Such differences in habitat association may reflect seasonal changes, for example, changes in the species composition and body size of taxa that result in changes in taxa habitat preference. However, it is also possible that differences between seasons/areas of the run site reflect differences between areas rather than the seasons.

The amount of variation in macroinvertebrate density that was not explained by the environmental variables measured in this study was high for fall upstream samples, but even higher for summer downstream samples of the run site. However, the amount of variation in macroinvertebrate density that was not explained by standard hydraulic and substrate/variables was also high in other similar studies (e.g. Quinn and Hickey, 1994; Rempel *et al.*, 2000; Lloyd and Sites, 2000). The unexplained variation in macroinvertebrate density in this study could be attributed to many factors that could apply to both seasons/areas. For example, macroinvertebrate distribution among patches could be affected by environmental conditions outside the patch area (Hart and Finelli, 1999; Beisel *et al.*, 2000) such as the amount of detritus present in nearby locations. Other habitat characteristics that were not evaluated in this study include periphyton abundance and near-bed turbulence (see review in Minshall, 1984; Hart and Finelli, 1999). Another factor contributing to the unexplained variation could have been that grouping taxa or size classes to evaluate community patterns may have added "noise" to these models, since the environmental variables usually explained more variation in density for individual taxa than when all taxa were combined. Finally, error in measuring the environmental variables could have increased the variation in macroinvertebrate density that was not explained by these variables. Potential sources of measurement error include the effect of leaching during sample preservation on detritus weights (Appendix I) and the difficulty of accurately measuring near-bed flow on an intermediate spatial scale (section 2.4, p.96).

The trend for higher unexplained variation in macroinvertebrate density in summer downstream samples than fall upstream samples at the run site could also be explained by several factors. It is interesting to note that a trend of more specific macroinvertebrate associations with substrate/detritus in fall samples than in summer samples was also found in studies by Barber and Kevern (1973) and Corkum (1992). Differences in the strength of relationships between density of deposit-feeding detritivores and detritus can occur with changes in the amount of available of detritus (Corkum, 1992). However, those size portions of detritus that were the best predictors of macroinvertebrate densities in this study were present in similar amounts in both seasons/area. A more likely explanation for the trend of higher unexplained variation of macroinvertebrate density in summer downstream samples is that the influence of unmeasured environmental variables was higher in these samples than in fall upstream samples. However, the density of macroinvertebrates was higher in fall upstream samples than the summer downstream samples which may have resulted in higher statistical power to detect correlations in fall upstream than summer downstream samples (see discussion of statistical artifacts in prediction of macroinvertebrate density in Statzner and Holm, 1989). Further study would be required to determine which of these factors are important at the West River study locations.

4. Conclusions and general discussion

4.1 Summary

4.1.1 Evaluation of methods to characterize near-bed flow

1. Mean velocity was a useful indicator of shear velocity in this study because it was correlated to shear velocity values obtained using the standard method of velocity profiles, and because it was easy to measure. However, the correlation between mean velocity and shear velocity was weaker in summer downstream surveys than in fall upstream surveys of the main study sites. Since discharge was highest during the downstream summer surveys, this difference may have been due to the presence of complex flow patterns at high discharge levels.

2. Testing of different methods of evaluating near-bed flow showed that width-based roughness determined using the simple equation of Winget (1985) was a practical and reliable method of comparing roughness among patches. The roughness values obtained with this method were well correlated to those obtained with the more standard method of evaluating roughness based on the unevenness of streambed height (r^2=0.57). However, the addition of width-based or height-based roughness values did not provide a significantly better model for predicting shear velocity than mean velocity alone.

3. Although roughness values did not improve the estimation of shear velocity, roughness was related to the extent of spatial variation in shear velocity (from velocity profiles) within patches. The variation within patches increased with patch roughness and was considerable in some patches with high roughness (e.g. coefficient of variation among 3 points > 80%). Therefore, in patches with high roughness, shear velocity measured at a single point may not reflect the average shear velocity within the patch.

4. Based on the results of testing, mean velocity and velocity profiles were selected to evaluate shear velocity and width-based roughness was selected to measure roughness for the macroinvertebrate component of this study.

4.1.2 Relationship of stream macroinvertebrate distribution to detritus, substrate composition and flow conditions

1. In the West River, macroinvertebrate taxa densities in patches at the run site increased with the amount of detritus and with decreasing substrate size and algal cover. Community macroinvertebrate taxa densities were more closely related to substrate and detritus characteristics (20%, 25% of variation uniquely explained by substrate/detritus) than to hydraulic variables (4%, 8% of variation uniquely explained by hydraulic variables) for both downstream summer and upstream fall samples. This pattern was observed for most of the dominant taxa including deposit-feeding detritivores and other functional feeding groups. Macroinvertebrate densities were more closely related to detritus than to substrate characteristics in most analyses. However, many detritus and substrate variables were highly inter-correlated and the relationship of macroinvertebrate density to different highly inter-correlated variables was similar. In contrast, densities of black fly larvae (*Simulium*) and pupae (Simulidae), the only dominant collector-filterers in this study, were positively related to the hydraulic variable of Froude number. Also, the densities of four dominant taxa were significantly higher in patches with strong upwelling than in other patches in downstream summer samples.

2. Macroinvertebrate density was most closely related to fine size portions of detritus (FPOM) in downstream summer samples. In upstream fall samples, CPOM and FPOM were highly inter-correlated, and macroinvertebrate densities were closely related to both sizes of detritus and to total POM. Body size was also important to the relationship of

macroinvertebrate density to detritus. The densities of smaller individuals tended to be more closely correlated to FPOM (with about 10% more of variation in density explained for those taxa that were analyzed) than densities of larger individuals.

3. Although there was little evidence of direct effects of flow on most macroinvertebrate taxa, the distribution of macroinvertebrates at the run site may have been influenced indirectly by flow through the modification of substrate and detritus. In the downstream summer and upstream fall samples, 10% and 22%, respectively, of the variation in community taxa densities was related to shared variation in detritus and hydraulic variables. In addition, up to 54% of the variation in detritus could be explained by hydraulic variables measured at the time of sampling.

4. The relationship between macroinvertebrate density and substrate and detritus was similar for both seasons/areas of the run site. Overall, the pattern of spatial variation in macroinvertebrate densities within the run site was closely related to variation in the measured environmental variables. For example, the environmental variables explained 37-50% of the overall variation in combined community taxa densities, around 2/3 of the variation in combined community taxa densities that occurred with transverse location, and up to 82% of the variation in the density of deposit-feeding detritivores that were analyzed individually. Strong relationships between substrate/detritus variables and the densities of the deposit feeding-detritivores *Antocha*, *Optioservus* and Leuctridae/Capniidae observed at the run site were not consistent with those observed at the riffle site for 7 of the 8 relationships examined at both sites. This observation could be explained by differences between sites in environmental conditions such as substrate stability that caused differences in macroinvertebrate response.

4.2 Relevance

This study makes relevant contributions to research on methods of measuring near-bed flow appropriate for stream ecology studies and to research on relationships between macroinvertebrate distribution and environmental conditions. The results of this study also have applications to related fields of scientific study.

First, a major finding of this study is that relatively simple methods of evaluating near-bed flow (such as the use of mean velocity to indicate relative values of shear velocity) may be appropriate for comparing near-bed flow in different areas of stream sections with relatively simple flow structure. However, the observed relationship between mean velocity and shear velocity varied between the two seasons/areas of the main study sites. This pattern supports results from other studies that suggest the accuracy of certain methods may vary with flow conditions (Lancaster and Hildrew, 1993; Quinn and Hickey, 1994; Dittrich and Schmedtje, 1995). Also, although other studies (e.g. Carling, 1992a, Frutiger and Schib, 1993) have suggested that fine-scale variation in flow over areas of high roughness may limit the usefulness of velocity profiles for measuring shear velocity at intermediate spatial scales, the author is not aware of studies other than this one that have tested this.

Second, the macroinvertebrate component of this study adds to our understanding of several topics, including the inter-relationship of flow and substrate/detritus, the importance of vertical hydraulic gradient, variation in macroinvertebrate habitat associations and the spatial structure of stream ecosystems. This research project is important as a "synthetic" study that examines the importance of two different types of inter-related environmental variables to macroinvertebrate distribution. There are few other studies of macroinvertebrate distribution that examine different aspects of both flow and substrate/detritus in such detail. Using a detailed analysis of both these factors, this study was able to show the relative importance of flow *versus* substrate/detritus to the macroinvertebrate community studied as well as the potential importance of indirect effects of flow through substrate/detritus.

Vertical hydraulic gradient (VHG) is an aspect of streamflow that has not been examined in many other studies of benthic macroinvertebrates in the surface layer of streambeds (Stanford and Ward, 1993; Plenet *et al.*, 1995; Boulton *et al.*, 1998). The results of this study suggest that the densities of certain taxa may be related to VHG and provide important support for further research on this under-studied topic.

The analysis of different categories of macroinvertebrates in this study adds to our knowledge about which categories may be useful for predicting macroinvertebrate habitat associations (i.e. how macroinvertebrate density is correlated to environmental characteristics). For example, *Simulium*, which was the only collector-filterer taxon at the study site, had a habitat association that was different from those of other taxa. However, there was no clear distinction between the relationships of deposit-feeding detritivores and most other taxa with detritus, perhaps due to the feeding of many taxa not classified as detritivores on detritus in early life stages. Also, the body-size related trends in the habitat associations of several deposit-feeding detritovores in this study show that it is possible to describe habitat associations more precisely in some cases by analyzing individuals with different body sizes separately.

It is often true that "local conditions beget local results" (Muttkowski and Smith (1929) cited in Hawkins, 1985). In this study, relationships between macroinvertebrate densities and environmental conditions at the run site did not even apply completely to the riffle site, which was less than 0.3 km upstream on the same river. The variation among locations in this and other studies (e.g. Drake, 1984; Doisy and Rabeni, 2001) shows the importance of studying macroinvertebrate relationships with the environment in different locations before making any generalizations. Since very little study of stream macroinvertebrates has been done in Prince Edward Island, this study expands the geographical range covered by research in this field.

This study includes an analysis of spatial structure in response to research highlighting the potential importance of spatial characteristics such as proximity to macroinvertebrate distribution (Downes *et al.*, 1993; Beisel *et al.*, 2000; Palmer *et al.*, 2000). The results of this study show two interesting features of the spatial structure at the run site: the striking variation in macroinvertebrate densities with transverse location and how this pattern could be mostly explained by spatial variation in flow and substrate/detritus. Neither of these features would have been evident if, as in many studies of stream macroinvertebrates, samples had been spaced much farther apart (e.g. Doisy and Rabeni, 2001) or if sample location had not included as a variable in the analysis (e.g. Quinn and Hickey, 1994).

Finally, research relating macroinvertebrate distribution to environmental conditions at intermediate spatial scales can be applied to studies in other areas of stream ecology. For example, the stratification of benthic sampling according to differences in environmental conditions can allow researchers to maximize sampling efficiency and avoid confounding variation in macroinvertebrate abundance at smaller spatial scales with variation at larger scales (Merritt *et al.*, 1996). Easily observed environmental characteristics such as substrate size can be useful in sampling stratification because such characteristics have been shown to be related to macroinvertebrate distribution. Also, understanding the relationship between macroinvertebrate distribution and environmental conditions is important for addressing the degradation of stream ecosystems by human activity (Gore, 1994; Power *et al.*, 1995). Stream flow and streambed composition have both been heavily altered worldwide by human activities such as flow regulation (Power *et al.*, 1995) and agriculture (Waters, 1995). Research relating macroinvertebrates to environmental conditions has proven useful in mitigation efforts involving changing dam discharge releases (e.g. Morgan *et al.*, 1991) or placing structures in streams that redirect flow (e.g. Gore and Hamilton, 1996).

4.3 Future Research

Based on the findings of this study, further research is recommended on the following topics.

4.3.1 Methods of measuring near-bed flow

There is a need for further research to improve methods of measuring near-bed flow at intermediate spatial scales in streams. For example, more work is needed to develop practical methods of accurately evaluating roughness in the field. Research examining the effects of flow on macroinvertebrates would also be enhanced by the development of inexpensive and practical methods for direct measurement of near-bed flow in streams. One such potential method is the use of Preston-static tubes coupled with a three dimensional positioning device to take fine scale measurements of near-bed flow (Hoover, 2001). Also, further testing is needed to determine the appropriate number of measurements per area under different flow conditions for flow measurements taken close to the streambed.

4.3.2 Importance of substrate/detritus versus surface flow to macroinvertebrate distribution

It would be interesting to do further work to test the hypothesis that the distribution of most dominant taxa found at the West River run site is influenced more by detritus than by the direct effects of flow. This hypothesis could be tested using field experiments involving the placement of containers of substrate with similar particle sizes and varying amounts of detritus in areas with contrasting flow conditions. For example, containers with high amounts of fine detritus and containers with low amounts of fine detritus mixed with gravel substrate could be placed in areas of both high and low shear velocity. After allowing sufficient time for colonization by macroinvertebrates, the containers would be collected and analyzed to determine whether macroinvertebrate densities were more closely related to detritus or flow.

4.3.3 Comparison of macroinvertebrate habitat associations among different locations

Further work should also be done to test for differences in the relationships between macroinvertebrate densities and environmental characteristics among different locations. For example, a similar study could be done that included a greater number of samples from the riffle site to compare relationships at this site with those at the run site with greater certainty. It would also be interesting to compare macroinvertebrate habitat associations with environmental characteristics in different sections along the West River, since hydraulic conditions and detritus availability are expected to change with stream order (Statzner *et al.*, 1988; Cummins, 1992). Therefore, by including samples from different locations along the West River, it would be possible to examine macroinvertebrate response over a greater range of environmental conditions.

4.3.4 Observation of macroinvertebrate position relative to the surface of the streambed

The potential effects of near-bed flow on macroinvertebrates are much greater for individuals positioned on the surface of the streambed than for individuals in subsurface interstices (Vogel, 1994). A better understanding of this aspect of the relationship between macroinvertebrate distribution and flow could be promoted by making information on typical macroinvertebrate position relative to the surface of the streambed more easily accessible. Such information could be compiled for different macroinvertebrate taxa and developmental stages, as has been done for taxonomic functional feeding group data in Merritt and Cummins (1996).

4.3.5 Differentiating macroinvertebrate response to highly inter-correlated variables

Experimental study is recommended to differentiate macroinvertebrate response to environmental variables that were highly inter-correlated in this and other similar studies (e.g. Rempel *et al.*, 2000; Doisy and Rabeni, 2001). For example, experiments performed in flumes are useful for determining the biological importance of different hydraulic variables that are often inter-correlated in natural channels (Hart and Finelli, 1999). Flumes with spatial variation in bottom depth and surface unevenness as well as changes in flume slope and discharge can be used to obtain different combinations of hydraulic variables, including those evaluated in this study. For instance, patches at the main study sites with high shear velocity also typically had high mean velocity. In flumes, areas with higher mean velocity and lower shear velocity could be created using a steep channel slope and smooth-bottomed surface. Many experimental studies of macroinvertebrates have used flumes to evaluate the importance of different hydraulic variables in determining macroinvertebrate position on the streambed (e.g. Bournaud, 1975; LaCoursiere, 1991; Lancaster and Mole, 1999).

4.3.6 Relationship between vertical hydraulic gradient and macroinvertebrate distribution

There is a need for more field studies that compare the distribution of macroinvertebrates in the surface layer of streambed to patterns of subsurface vertical flow. Future studies should use methods of measuring vertical flow that are appropriate for a wide range of substrate size. In such studies, it would also be helpful to use sampling stratification to control for potential effects of detritus, substrate size and surface flow on macroinvertebrate distribution (see sampling stratification in Pepin and Hauer, 2002).

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Appendices

Appendix I. Experiment examining weight loss of detritus due to leaching in preservatives

Detritus can lose weight when submerged in fluids due to leaching (Bärlocher, 1992). Therefore, an experiment was performed to see if detritus weights needed to be corrected for weight loss during the storage of benthic samples in preservatives. Circular pieces of leaf litter ("leaf punches") were used to quantify detritus weight loss in this experiment. Leaf punches were produced from leaf litter that appeared similar to most deposited CPOM at the main study site for each sampling time. Leaf punches were made from *Alnus rugosa* (speckled alder) leaf litter for summer downstream samples and from *Betula alleghaniensis* (yellow birch) for fall upstream samples. Both types of leaf litter were collected from streambed locations between the riffle site and run site on the West River. Leaf litter was washed to remove attached particles, then punched using a cork borer to produce circular leaf punches 1.45 cm in diameter. Leaf punches were dried at 60°C and weighed both before and after placement in benthic samples.

After samples were collected, the parts of the samples consisting of "medium-sized" material were preserved in 5% formalin (section 3.3.2). Then one leaf punch contained in a glass vial of the preservative was placed with all but 9 of the sample buckets. Replicates of 3 leaf punches were placed with the sample material in these 9 buckets. The leaf punch preservative was changed along with that of the benthic sample when samples were transferred to 70% ethanol prior to sorting for macroinvertebrates. Then, leaf punches were dried and weighed at the same time as the sample detritus and sediment in each bucket. Weights could not be obtained for several leaf punches that broke during weighing.

Both the sample storage time and leaf punch weights were highly variable. Benthic samples were stored in ethanol for a median time of 9 days and in formalin for a median of 180 days, however storage times varied extensively among samples (Table Ia). On average, about 12% of the initial detritus weight appeared to be lost due to leaching in preservatives, with a maximum of 37% recorded (Table Ia). The variability in weight loss among replicate leaf punches was relatively high as shown by the median coefficient of variation of 25%. However, there was no clear relationship between leaf punch weight loss and storage time in ethanol, formalin, or both preservatives.

The results from this experiment indicate that weight loss of detritus due to leaching in preservatives could have been a significant source of error for detritus measurement in this study. However, these experimental results were not used to adjust sample detritus weights to compensate for leaching in preservatives for several reasons. For one, potential measurement error due to leaching in preservatives was not large enough to obscure differences in detritus weights among patches. For example, the weight of FPOM at run site patches ranged from 0.8 to 11.5 g and 0.2 to 10.8 g in summer downstream and fall upstream samples respectively. Also, weights could not be obtained for several leaf punches and the variability among replicate leaf punches was high which limited the potential accuracy of weight adjustment based on this experiment.

Table Ia. Summary of results from experiment on detritus weight loss due to leaching in preservatives. The times that benthic samples were stored in perservatives, the percent of initial leaf punch weight lost during storage, and the coefficient of variation (CV) of this weight loss for replicate leaf punches are listed.

	Median	**Range (minimum to maximum)**	**n**
sample storage time in 70% ethanol (days)	9	1 to 128	59
sample storage time in 5% formalin (days)	180	38 to 396	59
% weight loss of leaf punch	12	-2 to 37	48
CV of % weight loss among triplicate leaf punches	25	6 to 47	7

Appendix II. Estimation of rock weights

Linear regression was used to estimate weights of rocks that were too large to be easily removed from patches during benthic sampling. To construct a linear regression model, substrate particles were weighed in 5 size classes of 1 phi intervals (from -3 to -8 phi or 0.8 to 25.6 cm). All rocks were taken from benthic samples collected at the main study site. For substrate particles in the largest three size classes, average weights were determined for each sample by dividing the total weight in a given size class by the number of rocks. For particles in the smallest two size classes, substrate particles taken from a randomly selected subset of samples were weighed individually. Regression analysis was performed using the statistical software package SPSS® (version 10). Then, weights of rocks that could not be removed from patches were estimated from the length of the B-axis using the regression model in Fig IIa.

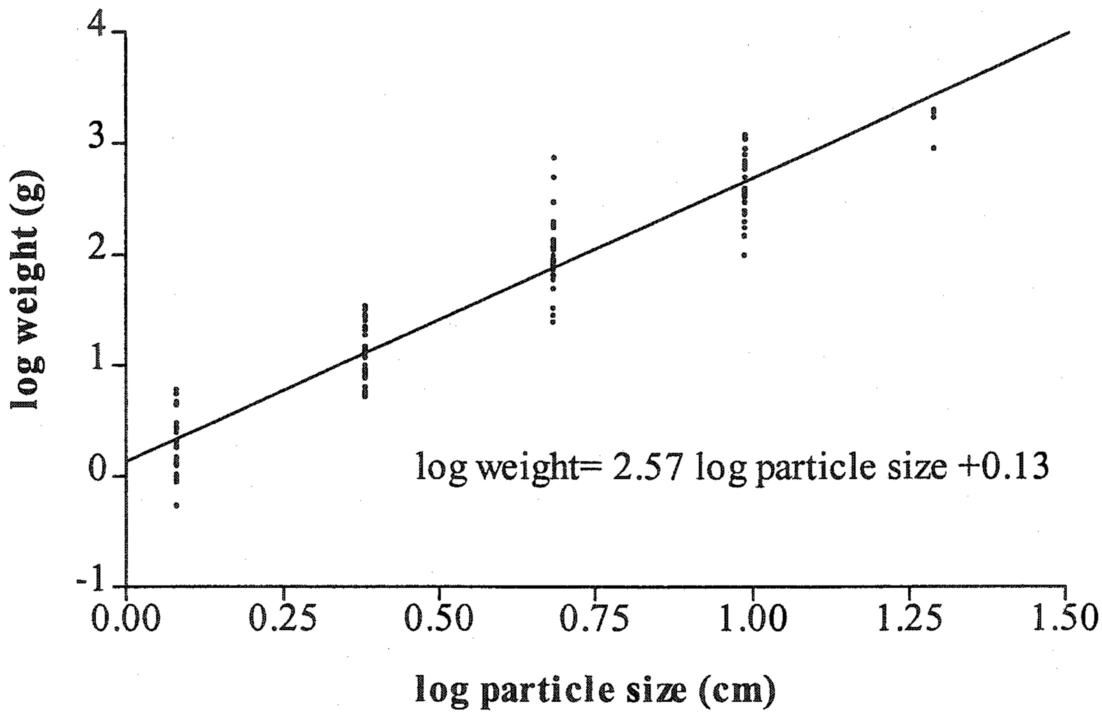

Fig. IIa. Regression model for prediction of rock weights (n=154, r^2=0.91, P<0.001). Particle size is the length of the B-axis (defined in section 3.2.2). Since weights for larger particle size classes are averages of several particle weights, the r^2 value of this regression model does not reflect the true variability of rock weight.

Appendix III. Interpretation of redundancy analysis correlation biplots

Redundancy analysis (RDA) correlation biplots are a graphical representation of a correlation matrix in which variables are represented by arrows. Redundancy analysis correlation biplots can be used to examine correlations among species variables, among environmental variables and between species and environmental variables. The correlation between two variables is read by projecting the arrowhead of the shorter variable's arrow onto the longer variable's arrow as illustrated for *Antocha* and FPOM in Figure IIIa. The intersection of the line of projection with the arrow is called the projection point. The distance of the projection point from the origin of the biplot axes indicates the strength of the correlation. Longer distances indicate stronger correlations (compare Fig IIIa and Table IIIa). The scale of r-values is indicated on the RDA correlation biplot (Fig. IIIa). If variable arrows run in opposite directions, the projection point can be determined by extending the longer arrow through the biplot origin in the direction opposite to the arrowhead as illustrated for algal cover and *Antocha* in Figure IIIa. Variables with arrows that are pointing towards different directions $>90^{\circ}$ apart are negatively correlated, whereas variables with arrows pointing in more similar directions ($<90^{\circ}$ apart) are positively correlated (ter Braak, 1994; ter Braak and Šimilauer, 2002).

The values of correlation coefficients between individual variables determined using RDA biplots are approximate (ter Braak, 1994; ter Braak and Šimilauer, 2002). Results of preliminary data analysis in this study showed that RDA correlation biplots and Spearman correlation matrices constructed from the same data set had similar r-values and showed the same general trends (see examples in Fig. IIIa and Table IIIa).

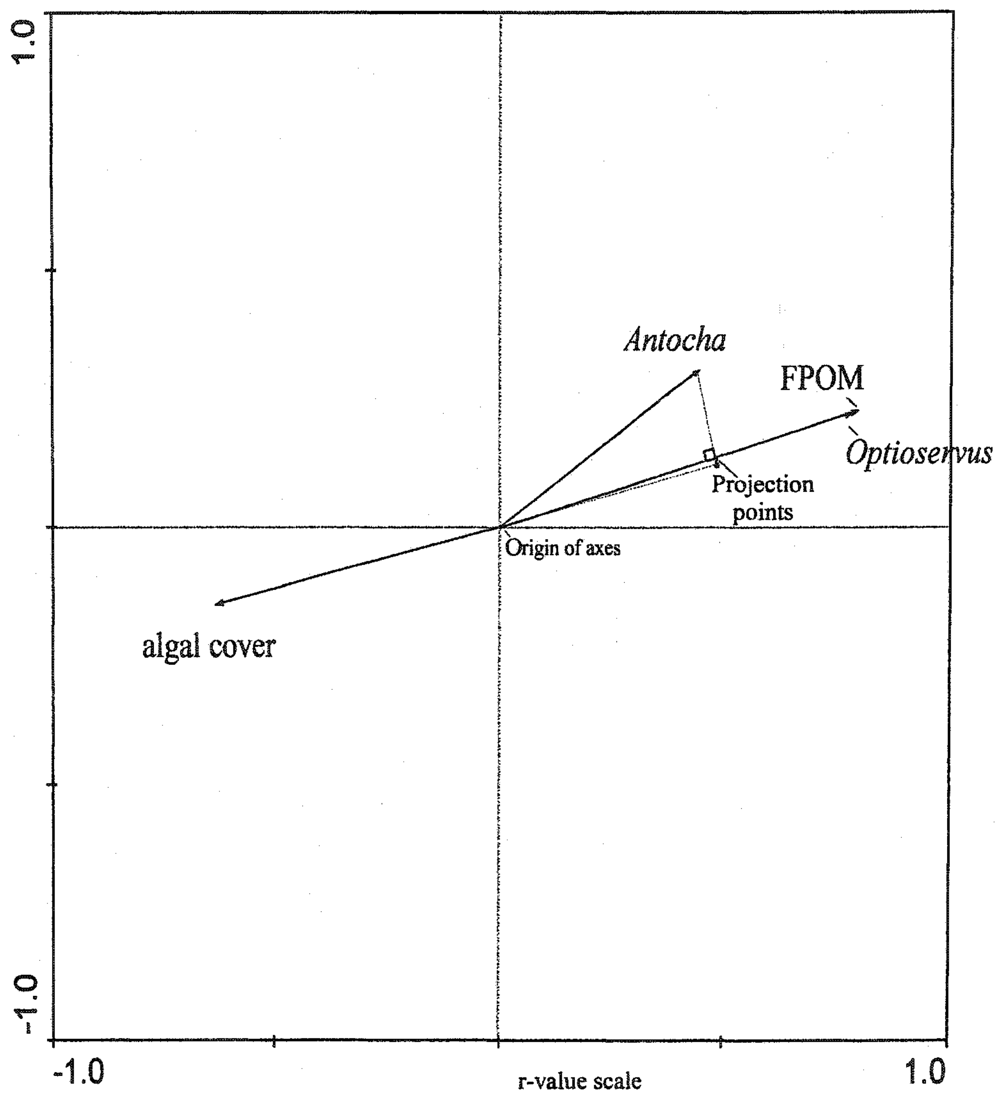

Fig. IIIa. Sample redundancy analysis correlation biplot showing the strength of relationships among the following variables: *Antocha* density, *Optioservus* larvae density, amount of fine particulate organic matter <1mm (FPOM) and percent of patch covered with algae (algal cover). The use of extrapolation to determine correlation coefficients between variables is illustrated.

Table IIIa. Sample Spearman correlation matrix for comparison of correlation coefficient values (r_s) with those shown in a RDA correlation biplot (see Fig IIIa). The data described in this Table is the same as that shown in Fig IIIa.

	FPOM	***Antocha***[a]	***Optioservus* larvae**[a]
algal cover	-0.78	-0.40	-0.5
Antocha[a]	0.45		
***Optioservus* larvae**[a]	0.65	0.42	

[a] Taxa abundances were log-transformed to improve the consistency of comparison with RDA analysis in which taxa abundances were also log-transformed.