HYDRAULIC HABITAT PREFERENCES OF THE TORRENTIAL MAYFLY

Epeorus longimanus (Ephemeroptera: Heptageniidae): THE ECOLOGICAL

IMPORTANCE OF NEAR-BED FLOWS

by

Trent Hoover

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Abstract

The larval stage of the mayfly *Epeorus longimanus* (Ephemeroptera: Heptageniidae) is an inhabitant of torrential stream habitats. It possesses several adaptations to high velocity environments, including a flattened body shape, a tilted head shield, and a "sucker-like" arrangement of abdominal gills. In order to relate the behavioural and morphological adaptations of *E. longimanus* to its habitat requirements, the distribution of this mayfly and a suite of environmental parameters were measured at a range of spatial scales (*i.e.* watershed, within-stream, and within-stone scales).

Benthic macroinvertebrates were collected at 39 stream sampling sites throughout the lower portion of the Torpy River watershed in eastern British Columbia, in order to (1) identify the particular habitat preferences of larval *Epeorus*, and (2) examine the community structure of benthic macroinvertebrates in a northern watershed. Several environmental variables (*e.g.* discharge, stream surface slope, substrate size, pH, conductivity, riparian vegetation, etc.) were measured and related to patterns of faunal abundance using canonical correspondence analysis (CCA); this ordination technique divided the collected invertebrate taxa into four functional assemblages, each with well-defined habitat requirements and trophic relationships. The results of the CCA showed that *Epeorus* larvae prefer high discharge streams with coarse substrata. To further examine the habitat requirements of this genus, benthic samples and several descriptors of the flow environment of the stream environment (*e.g.* mean velocity, near-bed velocity, depth, substrate size, Froude number, etc.) were obtained at 50 regularly located sampling sites in two adjacent, high-discharge streams with coarse bed material. Observed patterns of abundance of *Epeorus* were significantly and negatively related to velocity, depth, channel Reynolds number, and relative roughness.

The near-bed hydraulic environment of shallow torrential streams was characterised by measuring velocity profiles, near-bed ($U_{0.002m}$) and mean ($U_{0.5D}$) velocities, and shear stresses (τ_w) over the surface of five experimentally deployed and three naturally occurring stones in a high-discharge stream in the Torpy River watershed. The velocity profiles measured above the stones regularly deviated from the "classic" log-normal shape. The profiles were often "wedge-shaped"; velocities were greatest a few millimetres above the bed, and decreased logarithmically below and above this height. Wall shear stresses and near-bed velocities generally increased from the front to the rear of each stone.

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The daytime and night-time distributions of *E. longimanus* were recorded and related to shear stress, periphyton biomass, and substrate characteristics (*e.g.* stone roughness, topography). During the daytime, larvae preferred areas of the stone surface with high shear stress; during the night-time, larvae preferred areas of the stone surface with higher elevation and attached boundary layer flows. Periphyton density was significantly related to stone surface roughness and stone surface topography. A stone reversal experiment suggested that hydrodynamic factors, rather than food (periphyton) availability, proximally influence the microdistribution of *E. longimanus* larvae; however, the precise nature of the forces to which they respond remains unknown. *E. longimanus* larvae were also found to exhibit a strong diurnal migration, generally migrating to the upper surface of streambed stones at night, and retreating to the underside of the stones during the day.

This study represents one of the first detailed examination of the relationship between the distribution of microscale hydrodynamic parameters, (e.g. shear stress, near-bed velocity) and benthic organisms at organism-defined spatial scales. The results demonstrate that fluid dynamics are the proximate factor that determines the microdistribution of benthic organisms in torrential stream environments. Additional research is required to investigate the ecological importance of these small-scale hydrodynamic parameters. In order to understand the behaviour and ecology of benthic stream organisms, models of flow in natural stream channels must be expanded to include patterns of flow at small, organism-defined scales immediately adjacent to the bed.

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Chapter 1

The influence of fluid dynamics on freshwater invertebrates: morphological, behavioural, and ecological adaptations

Summary

- Hydrodynamic forces are potentially the most important factors influencing the distribution, biology, and trophic interactions of benthic invertebrates in lotic environments.
- 2. Mean flows can be characterised by a series of directly measured hydrodynamic variables (*i.e.* mean velocity, depth, discharge) and parameters (Reynolds number, Froude number). Reynolds number and Froude number are of value in comparing flows between sites, as they are non-dimensionalised indices describing flow regime and surface flow conditions, respectively.
- 3. Measurements of flows immediately adjacent to the bed are relatively difficult to obtain, and as such, are rarely encountered in the literature. However, because they more closely represent the flows that benthic invertebrates experience, characterisation of fine-scale flows immediately above a substrate provides greater insight into the microhabitat preferences of stream invertebrates than do descriptors of mean flows. Fine-scale flow descriptors include shear velocity, shear stress, roughness Reynolds number, boundary layer thickness, and the thickness of the viscous sublayer. The importance of quantifying stream flow at several spatial scales is discussed.
- 4. The microhabitat preferences of benthic stream invertebrates are closely related to the hydrodynamic characteristics of the environments they inhabit. Flow microenvironments influence the predator-prey interactions, movement, and feeding efficiency of benthic organisms. Generally, primary consumers possess specialised morphological and behavioural adaptations to specific hydraulic habitats, while predators tend to be 'hydraulic generalists'.
- 5. Many invertebrates utilise the current to migrate downstream ('drift'). The numbers of individuals drifting generally peaks at night, suggesting that this behaviour may be an adaptation to search for more favourable microhabitats while avoiding visually oriented fish predation. However, size-related increases in drift suggest that entry into the drift is not always active, and may, in some cases, be the result of the erosion of invertebrates from the bed during times of increased activity.

- 6. Stream invertebrates, especially those inhabiting high-velocity habitats, often demonstrate a shift in microhabitat preferences as they grow. This type of ontogenetic shift may be largely due to the changes in hydrodynamic forces (*i.e.* lift, drag, and shear stress) that larvae experience as they increase in size.
- 7. In order to maintain contact with the substrate, benthic invertebrates that inhabit areas of the streambed exposed to high velocities often exhibit marked morphological adaptations that manipulate local flow fields to reduce the erosional effects of lift and drag. Adaptations include flattened bodies that concentrate lift over the legs and body shapes that delay boundary layer separation.
- 8. Suspension-feeding invertebrates (generally Trichoptera and simuliid Diptera) depend on suitable near-bed flow velocities to ensure an adequate supply of seston. Due to the intimate relationship between flow velocity and suspension-feeder ecology, suspension-feeding taxa often exhibit marked morphological adaptations for specific flow regimes. The behavioural adaptations of mayfly species that manipulate flow fields to excavate prey or suspension-feed are also discussed.

Introduction

The physical forces created by moving water are recognised as the most important factors shaping the benthic community in rivers and streams. The ever-present, generally unidirectional flow of streams has shaped the morphology (Weissenberger et al. 1991; Collier 1994; Pommen and Craig 1995), behaviour (Osborne and Herricks 1987; Soluk and Craig 1990; Wetmore et al. 1990; Holomuzki and Messier 1993), diversity (Growns and Davis 1994; Quinn and Hickey 1994) and community structure (Lancaster and Hildrew 1993) of the invertebrate fauna which inhabit this complex environment.

The distributions of benthic stream fauna are spatially and temporally variable. Many macroinvertebrate species migrate to the underside of streambed stones during the daylight hours, and return to the exposed, upper surfaces of the stones during the night (Allan et al. 1986; Peckarsky 1996). Examination of the daytime and night-time distributions of benthic fauna reveals species-specific patterns of abundance, which are in turn related to a variety of physical and biological factors. While many taxa demonstrate marked preferences for sheltered, depositional habitats (Bouckaert and

Davis 1999), others prefer exposed conditions (*e.g.* the upper surfaces of stones), where they are subjected to high velocities, high shear stress, and relatively thin boundary layers (Nowell and Jumars 1984). While it is more expensive energetically to move about and forage in such conditions, invertebrates that inhabit this type of extreme microhabitat may benefit from more abundant algal food resources (Quinn et al. 1996), greater oxygen availability (Wiley and Kohler 1980; Golubkhov et al. 1992), and decreased predation risk (Peckarsky et al. 1990; Hansen et al. 1991; Hart and Merz 1998). As such, the benthic macroinvertebrates that inhabit lotic systems are subject to an ecological dilemma. Benthic organisms benefit from hydraulic conditions that maintain interstitial microhabitats, elevate oxygen levels, reduce predation, and provide an energetically inexpensive method of downstream movement. These same hydrodynamic forces, however, are those acting to dislodge grazers from feeding sites, erode the streambed, and limit feeding opportunities of both predators and herbivores. The morphological and behavioural adaptations that have evolved in benthic fauna ensure that the ecological benefits of inhabiting these extreme habitats do not outweigh the costs.

Thesis overview

In this study, manipulative field experiments and surveys of naturally occurring benthic communities in a montane watershed in east-central British Columbia were used to examine the relationship between the distribution of stream invertebrates and physical factors across a range of spatial scales. Specifically, the ecological preferences of a single stream invertebrate, the torrential mayfly *Epeorus longimanus* (Ephemeroptera: Heptageniidae), were examined in detail. Mayflies of the genus *Epeorus* are grazers, and feed largely on growths of periphyton that encrust the upper surface of stones in high-velocity, mountainous streams (Resh and Rosenberg 1984). Three separate studies were used to examine the habitat requirements of this mayfly. (1) The large-scale (*i.e.* watershed- to stream-scale) habitat preferences and community associations of *Epeorus* spp. were examined in the tributaries of the lower portion of the Torpy River watershed using canonical correspondence analysis, a multivariate ordination technique. (2) The reach-scale habitat preferences of *Epeorus* spp. were measured by comparing local densities of this mayfly with a range of variables that describe channel and flow conditions (*e.g.* depth, mean velocity, and bed roughness). (3) The within-stone microhabitat preferences of *E. longimanus* were further characterised by comparing the microdistributions of mayfly larvae, near-bed water velocity, bed shear stress, periphyton, and several

stone surface variables (e.g. stone roughness) over the surface of five experimentally deployed and three naturally occurring streambed stones. These measurements allowed for an assessment of the factors that determine the distribution of torrential mayflies in high-gradient, mountainous streams.

Stream hydrodynamics

When describing flow in open channels, physical scientists commonly employ a large number of hydrodynamic parameters and ratios. As such, the task of the stream ecologist interested in the interactions between moving water and the community structure, behaviour, or functional morphology of benthic invertebrates can be challenging, as much of the existing literature provides little insight into which measurements are biologically or ecologically relevant. In addition, the technology for measuring flows at small spatial scales in the field is often expensive and/or difficult to employ. Not surprisingly, these difficulties have resulted in some misinterpretation of hydrodynamic phenomena (see Gore 1978; Buffagni et al. 1995). Fortunately, there has been an increased interest in these issues (*e.g.* Collier 1994; Hart et al. 1996; Bouckaert and Davis 1999), and several excellent reviews on the flow microenvironment of streams and rivers have been published (Nowell and Jumars 1984; Davis 1986; Davis and Barmuta 1989; Carling 1992; Hart and Finelli 1999).

Mean flows in channels

The movement of water is the most dominant physical feature in rivers and streams (Statzner and Higler 1986; Davis and Barmuta 1989), yet only relatively recently have ecologists begun to examine the biology and community ecology of benthic fauna in the context of relevant hydrodynamic theory (but see Ambuhl 1959). However, before one can characterise the flows experienced by macroinvertebrates at organism-defined spatial scales, an understanding of the basic principles of the mean motion of water in channels is essential. Even in straight, flat-bottomed channels, flow is complex and highly three-dimensional (White 1999). As streams are rarely, if ever, straight, and generally have rough, irregular beds, flows are spatially and temporally variable, and difficult to model (Young 1992; 1993; Hart et al. 1996). As a result, characterisation of flows in natural channels is usually achieved through extensive measurement. The most basic description of the stream environment necessarily includes mean velocity (U), channel depth (D), discharge (Q), and the wetted perimeter (P). An indication of turbulence intensity can be obtained by recording high-frequency

variations in velocity (u'); however, the response times of most instruments currently used to measure velocity in streams (*e.g.* propeller velocimeters) are too low to make such measurements meaningful (see Bouckaert and Davis 1998).

Reynolds number

The mean motion of flow in streams can be characterised by the Reynolds number (see Davis and Barmuta 1989). Analytic solutions (*e.g.* Navier-Stokes) that describe boundary layer flows do not exist for the conditions that are found within naturally occurring lotic systems, especially rivers and streams with irregular bed geometry and water surface topography. Solutions of the Navier-Stokes equation exist only for steady, uniform flows, where depths of flow do not vary over time, and shape, size, roughness, and slope of the channel are constant in the *y* direction. Such conditions are rarely, if ever, found in natural systems. Yet, the Navier-Stokes equation allows for a description of the flow in any given circumstance when inertial effects predominate over viscous effects, or vice versa. The resultant ratio of inertial to viscous forces is known as the Reynolds number (Re), and is an indicator of the turbulent properties of flow. Reynolds number is determined as

$$Re = UI/v$$
(1-1)

where U is velocity, I is the length scale, and o is the kinematic viscosity of water. When characterising flow in open channels, U is the mean channel velocity (generally measured at 60% of the total depth; see White 1999), and the length scale I is the total channel depth or the hydraulic diameter. Where calculated Reynolds numbers are less than unity (see figure 1-1), viscous forces dictate flow behaviour, and the influence of inertia can be neglected; such flow is said to be *laminar*. Streamlines are smooth and linear, and the water apparently 'slides' in layers (Carling 1992). However, when Reynolds numbers exceed unity, inertial effects predominate, and the immediate effects of viscosity can be neglected (Vogel 1994). Flow in this case is said to be *turbulent*, and is characterised by irregular, secondary motions. However, the critical value at which flow becomes turbulent varies depending on the frame of reference and the conditions of the boundary. In open channel flows, Reynolds numbers less than 500 suggest laminar flow, and the transition to fully turbulent flow occurs between Re = 10,000 and Re = 100,000. With the exception of extremely

shallow streams of water (*i.e.* a sheet of water sluicing over bedrock) or unusually slow streams (*i.e.* shallow, nearly stagnant channels), mean flow in natural systems is nearly always turbulent. Flows where the Reynolds number falls between 500 and 10000 are said to be *transitional*, and may oscillate between turbulent and laminar flow. However, the range of Reynolds numbers at which flows become turbulent is dependent on the conditions of the boundary. Streams whose beds are composed of coarse substrata make the transition to turbulence at lower Reynolds numbers than streams and rivers whose bottoms are made up of sand or fine gravels (Vogel 1994). In flow past the different regions around a submersed object, both laminar and turbulent flow may be present (Silvester and Sleigh 1985; Vogel 1994).

Froude number

The mean motion of flow in streams can also be described using the Froude number. The Froude number (Fr) is a dimensionless ratio of inertial to gravitational forces, and is calculated as

$$Fr = U/(gD)^{0.5}$$
 (1-2)

where U is mean velocity, g is acceleration due to gravity, and D is channel depth. Froude number is used to distinguish between the two predominant flow regimes in moving water. Froude numbers less than unity (Fr < 1) are seen in flows which are characterised by deep, smooth flowing water. This is termed subcritical, or *tranquil*, flow. Flow disturbances such as surface waves are propagated both up and downstream in subcritical conditions. Froude numbers greater than unity (Fr > 1) exist in flows that are characterised by broken, white water. This is alternately termed supercritical, or *shooting*, flow. In these circumstances flow disturbances are propagated only downstream. The transition from supercritical flow to subcritical flow is often accompanied by an abrupt elevation of the water surface known as a *hydraulic jump* (a form of shock that occurs when downstream depths are too great to maintain supercritical flow; see White 1999). Where flows accelerate from subcritical to supercritical flow, an abrupt decrease in surface elevation known as a *hydraulic drop* can also be seen.

Reynolds number and Froude number are widely used to describe flow in open channels (Vogel 1994). Although their use has been criticised by some workers as inappropriate (in that they describe mean rather than near-bed flows; *e.g.* Hart et al. 1996), Reynolds number and Froude

number often correlate highly with distributions of benthic macroinvertebrates (Gore 1978; Wetmore et al. 1990; Buffagni et al. 1995). Reynolds number and Froude number are also of crucial importance in laboratory-based research, where flumes are employed to simulate the stream environment. An accurate reproduction of field conditions relies heavily on the measurements and design of experimental flumes (Lacoursière and Craig 1990); well-designed flumes provide simplification of flow conditions so that flows can be "summarized from their constituent parts" (Craig 1993).

Near-bed flows

Flows moving over, through, and around the substratum of streams are very complex. Patterns of bulk flow, such as the plunging jet upstream of a hydraulic jump (where Fr > 1) or the fully turbulent flows of a bouldery, torrential stream (where Re > 100,000) are readily observed, measured, and understood. More difficult to observe are the complex, fine-scale patterns of flow that occur at the interface between streambed and moving water. Stream organisms exist almost exclusively in a zone that extends only a few millimetres above the surface of the substrate, and it is in this zone that the majority of the biotic processes in streams take place.

The boundary layer

As the water moves over the surface of the streambed, friction is created between the solid substrate and the moving water immediately adjacent to the surface. As a result, water immediately adjacent to the boundary has a velocity of zero. This 'no-slip' condition (referring to the fact that when a fluid moves over a solid, the fluid tends to shear above the boundary rather than 'slip' over the surface) results in a characteristically logarithmic velocity gradient above the bed. Although the velocity gradient is generally steepest immediately adjacent to the surface of the substrate, the velocity-retarding influence of the boundary may extend to the surface of the water in shallow flows, while in deeper channels the flow structure far from the bed may be entirely unaffected. This boundary-influenced layer of water is termed the *boundary layer* (see Figure 1-2). The thickness of the boundary layer (δ) has been variously defined as the distance from the boundary at which water velocity reaches 90% (Silvester and Sleigh 1984; Vogel 1994) or 99% (Prandtl 1952; Jumars and Nowell 1984; White 1999) of the mean velocity. There is no sharply defined delineation to the outer limit of the boundary layer, as the transition from viscid to inviscid flow is continuous (Silvester and

Sleigh 1984). The thickness and flow conditions of the boundary layer (see Figure 1-2) are influenced by a number of physical factors, including water depth and velocity, channel slope, substrate roughness, and the dynamic viscosity of the fluid.

Flow conditions within the boundary layer can be described by the local Reynolds number,

$$Re_{x} = U_{x}x/v \tag{1-3}$$

where U_x represents velocity at the distance downstream (x) over which the boundary layer has developed (usually the distance from the leading edge of a flat plate), and v is kinematic viscosity. Relatively large local Reynolds numbers indicate correspondingly thin boundary layer thicknesses. However, while the rate and nature of boundary layer growth over flat plates with well-defined leading edges are well understood (White 1999), the growth of boundary layers over rough bottoms in natural systems is not (see Bathurst 1994; Buffin-Belanger and Roy 1999). Over the topographically rough bottoms of natural streams, boundary layers repeatedly grow, detach, reattach, and grow again as water flows downstream. As a result of the regular interruption of boundary layer growth, boundary layers in gravel/cobble streams rarely, if ever, reach an equilibrium thickness (Nowell and Jumars 1984; White 1999). Unfortunately, measurement of boundary layer conditions in naturally occurring systems remains relatively rare. With the exception of the fine-scale measurements obtained by Hart et al. (1996), the majority of studies on near-bed flow environments have failed to measure water velocities close enough to the bed to describe the hydraulic habitats experienced by stream benthic fauna.

Shear velocity and shear stress

Due to the exaggerated deformation of the velocity profile near the bottom, the boundary layer can also be regarded as a zone of shearing flow (see Figure 1-3). Shear velocity (U*), identified as an ecologically important factor by several workers (*e.g.* Carling 1992), is related to the shear stress acting on the bed. Shear stress (or, wall shear stress τ_w), is defined as

 $\tau_{\rm w} = \rho U^{*2} \tag{1-4}$

where the square of shear velocity (U*) is multiplied by the density of the fluid (ρ). The relationship between velocity (u) and shear velocity (U*) within the boundary layer is described by the von Karman – Prandtl law of velocity distribution, or the law of the wall (see Bergeron and Abrahams (1992) for a complete discussion),

$$u_z = U^*/\kappa \ln[(z-d)/z_0]$$
 (1-5)

where u_z is velocity at height above the substrate z, κ is von Karman's constant (empirically determined to be 0.4), d is the "zero-plane displacement", and z_0 is the bed roughness length (see Appendix 2). However, while the ecological significance of shear velocity and shear stress are recognised, they are rarely determined in field studies. The relatively rare appearance of U* in the literature is due, in part, to its method of determination. Estimates of shear velocity are typically derived from the slope obtained by regressing velocity (u) on the logarithm of height above the bed (ln z),

$$U^* = \kappa \left[(u_1 - u_2) / (\ln z_1 - \ln z_2) \right]$$
(1-6)

where κ is von Karman's constant, u_1 and u_2 are velocities at distances from the boundary z_1 and z_2 . This relationship can alternatively, be expressed as

$$U^* = \kappa m \tag{1-7}$$

where m is the slope of the regression of velocity (u) on the log of the distance from the boundary (z). Several measurements of velocity in the log-layer adjacent to the boundary are required to obtain an accurate velocity profile and statistically accurate estimate of U*. Moreover, equations 1-5 and 1-6 can only be applied in the log-layer where the plot of U on In z is linear. Obtaining a sufficient number of velocity measurements can be difficult; the few instruments capable of measuring flows at the fine spatial resolution required are extremely difficult to deploy close to the streambed in shallow, naturally-occurring channels (see Hart et al. 1996).

Davis and Barmuta (1989) reported that a reasonable estimate of the shear velocity U* could be obtained from measurements of the relative bed roughness (a ratio of channel depth D to the height of the roughness elements k) and mean velocity U.

$$U/U^* = 5.75 \log(12 D/k)$$
 (1-8)

Unfortunately, this method of estimating shear velocity is limited to applications where only reachaveraged values of U* are desired, and is probably of little value in determining U* at the small spatial scales necessary to characterise the hydraulic habitats of benthic invertebrates. The principal variables in Equation 1-8 (*i.e.* U, D, and k) are descriptors of average, rather than near-bed, channel characteristics. Hart et al. (1996) found that the velocity 10 cm above the surface of stream cobbles was a poor predictor of velocities near the surface, making any estimation of near-bed flow characteristics from mean channel velocities suspect. In addition, Carling (1992) states that for natural channels, estimates of roughness factors are related both to the size and packing characteristics of gravel or cobble streambeds. Consequently, determinations of shear velocity (U*) are best made from velocity profile data (using Equation 1-6), rather than estimation methods (as in Equation 1-8). Higher values of U* will indirectly influence the growth of both algal and invertebrate taxa by increasing the fluxes of dissolved materials in near-bed flows. Higher shear velocities result in more rapid diffusion of nutrient supplies to periphytic diatoms (see Vogel 1994), and higher oxygen supply to mayflies such as *Epeorus* (Palmer 1995) and *Ecdyonurus* (Buffagni et al. 1995); many benthic organisms thrive in high velocity, exposed microhabitats (Vogel 1994).

The near-bed flows to which benthic invertebrates are exposed can also be described using the Reynolds roughness number (Re*), an index of turbulence at the fluid-boundary interface. The Reynolds roughness number is given as

$$Re^* = U^* k_s / v \tag{1-9}$$

where U* is shear velocity, k_s is Nikuradse's roughness factor, and v is kinematic velocity. The viscous sublayer remains intact when Re* < 3.5; such flows are said to be *smooth-turbulent* (Carling 1992; see also Davis and Barmuta 1989). When the values of Re* fall between 3.5 and 68 (3.5 and

100 in Vogel 1994), near-bed flows are in a transitional state, and the viscous sublayer develops intermittent turbulent disruptions. When the bed roughness exceeds the theoretical height of the viscous sublayer (see equation 1-10 below) or shear velocities (U*) become too great, the viscous sublayer disappears, and hydraulically *rough-turbulent* flow occurs (Re* > 68) (Carling 1992). The thickness of the viscous (or laminar) sublayer (δ) can be estimated using the following formula,

$$\delta' = 11.6 v / U^*$$
 (1-10)

where v is kinematic viscosity, and U* is shear velocity (Carling 1993). Ambuhl, in his seminal work on the microhabitats of stream insects (1959), suggested that species living in high velocity environments were, in fact, living in the viscous sublayer, experiencing only minimal turbulence and relatively low velocities. While this represented a major advancement in behavioural hydrodynamic theory, his findings were not as widely applicable as he believed. In most naturally occurring flows, the viscous sublayer is absent (Carling 1992), and near-bed flows are fully turbulent. In addition, Statzner and Holm (1982) found that boundary layers were much thinner, relative to the body height of the mayfly *Ecdyonurus*, than Ambuhl had reported (see below). Statzner and Holm suggested that the conflicting results were due, in part, to the relatively large size of the tracer particles used by Ambuhl (larger particles may be unsuitable for detecting the fine-scale details of velocity gradients in the boundary layer). Staztner and Holm (1982; 1989) demonstrated that the patterns of flow around the bodies of benthic insects are more complex than previously thought; rather than being protected from the forces of the current by a viscous sublayer or thick boundary layer, velocity gradients are actually steeper over the bodies of the insects where they protrude into the flow.

Organisms that inhabit streambed surfaces that are exposed to moving water must be able to maintain contact with the substrate. However, the velocity gradients in the microhabitats preferred by many benthic stream organisms are often quite steep (see figure 1-3). As a result, the forces of lift and drag acting to dislodge individual invertebrates can be quite substantial. The force due to drag (F_d) is defined as

 $F_d = \frac{1}{2} C_d \rho S U^2$ (1-11)

where C_d is the drag coefficient (a function of shape, orientation, and Reynolds number), ρ is the density of the fluid, S is surface area (alternatively defined as the frontal area of an organism; Weissenberger et al. 1991), and U is velocity (Vogel 1994). The biological validity of this relationship was demonstrated by Weissenberger et al. (1991), who found that drag acting on three benthic macroinvertebrate species was proportional to the square of near-bed velocity. However, as noted by Vogel (1994), application of Equation 1-11 to estimate the drag experienced by benthic organisms must be approached with care; the drag coefficient (C_d) is not a constant but rather a dimensionless form of drag (drag per unit area divided by the dynamic pressure) and varies with velocity. At the relatively high Reynolds numbers (Re \approx 1000, where the characteristic length is body length) experienced by macroinvertebrates inhabiting high velocity habitats, flow separation generally occurs somewhere along the body of the invertebrate. As a result, dynamic pressure differences between front and rear are substantial (the energy of decelerating fluid in the turbulent wake at the rear is lost through viscous damping and dissipated as heat) and the total drag is almost entirely due to pressure drag rather than skin friction (Vogel 1994).

The strong velocity gradients inhabited by many benthic invertebrates also generate lift forces acting to dislodge organisms from the substrate. The force due to lift (F₁) can be calculated as

$$F_{1} = \frac{1}{2} C_{1} \rho S U^{2}$$
(1-12)

where the variables ρ and U represent the density of water and velocity, C₁ is the coefficient of lift (again, a function of shape, orientation, and Reynolds number), and S represents area (Vogel 1994). Statzner and Holm (1982; 1989) found that as flow crossed the bodies of various organisms it was compressed, creating even stronger velocity gradients over the organism. Statzner and Holm (1982) noted that maximum compression occurred over the thorax of *Ecdyonurus venosus*, and interpreted this as an adaptation to concentrate the forces of lift over the legs of the organism. Weissenberger et al. (1991) noted that the generally 'airfoil'-like form of many aquatic invertebrate taxa (*e.g.* the mayfly *Epeorus*) generate substantial lift forces, and also found that the mayfly *Ecdyonurus* was able to actively reduce lift by altering its body orientation.

Invertebrates inhabiting high velocity, torrential habitats should possess morphological and/or behavioural adaptations that identify them as having adopted one of two strategies to maintain contact with the substrate. Organisms should either be notably streamlined (a shape that delays boundary layer separation, reducing pressure drag but experiencing higher lift as a trade-off), or should more closely approximate a bluff body (reducing lift by increasing pressure drag due to early flow separation). *Rhithrogena* and *Epeorus* (Heptageniidae: Ephemeroptera) appear to belong to the first class; lift produced by their streamlined bodies is countered by a sucker-shaped arrangement of abdominal gills which acts as a 'sucker' to help keep them in contact with the substrate (see Vogel 1994; Collier 1994). Pupal blepharicerid (Diptera) belong to the second class; the low pressure zone associated with vortices produced by separating flow at the rear of the body enhance respiration.

The influence of bed geometry on stream flows

The presence of large-scale flow structures, such as horseshoe (solenoidal) vortices, wake separation zones, and eddies are often accounted for in contemporary stream research (Nowell and Jumars 1984; Bouckaert and Davis 1998; Buffin-Belanger and Roy 1998). For example, Young (1992; 1993) proposed a system to classify near-bed flow regimes based on the height and spacing of bed roughness elements, which serves primarily as a descriptor of bed/flow interactions rather than a method of classifying flows immediately adjacent to the bed. For example, when the mean roughness height exceeds mean depth, the flow is categorised as chaotic. This characterisation, which includes the majority of torrential flows, suggests that the near-bed flows of shallow channels with substrates composed primarily of boulders are unpredictable. An earlier classification by Davis and Barmuta (1989) was based on additional hydraulic parameters, such as Reynolds number, Froude number, shear velocity, and the thickness of the viscous sublayer. While these parameters are essential for the description of the near-bed flow environment, they cannot be measured easily in all instances. Davis and Barmuta (1989), therefore, proposed that the distribution of near-bed flow regimes can be estimated from vertical velocity profiles or even single measurements of mean velocities. However, while several studies have measured near-bed velocity gradients in order to establish the link between mean and near-bed flows in natural stream channels (e.g. Hart et al. 1996; Buffin-Belanger and Roy 1998), the ecological validity of the proposed classification of Davis and Barmuta (1989) remains uncertain.

Bed or wall shear stress is one of the most important factors limiting the distribution of benthic invertebrates (Davis and Barmuta 1989; Dittrich and Schmedtje 1995; Robertson et al. 1997).

Statzner and Muller (1989) developed a set of standardised hemispheres of different densities (FST hemispheres) which, when deployed on the stream channel bottom, indicate the total shear stress at the site. FST hemisphere results are, however, influenced by local bed topography (Dittrich and Schmedtje 1995) and provide a spatially integrated measurement of shear stress (Statzner and Muller 1989). The latter attribute has lead to their widespread use in the determination of the hydraulic conditions in streams at the reach and patch scale (Peckarsky et al. 1990; Lancaster and Hildrew 1993; Waringer 1993; Robertson et al. 1997). However, this technique provides little insight into small-scale distributions of bed shear stress on the surface of the substrate or the responses of individual insects to local shear stress production.

Bed shear stress has also been quantified using estimates of shear velocity obtained from the slope of the semi-logarithmic plot of the velocity profile (e.g. Wiberg and Smith 1991; Li 1994; Rempel et al. 1999). In cases where the channel bed is topographically simple and boundary layer profiles can be accurately predicted from existing theory (see Schlichting 1979), this method provides wall shear estimates at the spatial resolution required to describe small-scale flow environments near the bed. However, although widely applied, the validity of this method of estimating wall shear stress is limited for several reasons. The model applies to topographically simple channels where the boundary layer has a characteristically logarithmic vertical distribution of velocity (Bergeron and Abrahams 1992). This velocity distribution is often assumed to be universal in open channels (e.g. Davis and Barmuta 1989), but bed irregularities (bedforms), including sand ripples and dunes (Li 1994), pebble clusters (Buffin-Belanger and Roy 1998), cobbles (Bergeron 1994; Bathurst 1994), and streambed boulders (Hart et al. 1996), create pressure gradients which distort the boundary layer velocity distribution. In addition, boundary layer development can be inhibited in instances where the flow depth is limited, such as shallow tidal flows and shallow rivers (Nowell and Church 1979). As a result, estimates of shear stress obtained from either mean velocity measurements or relatively coarse velocity profile measurements in natural channels are potentially in error. Substantial errors in this method were confirmed by Hart et al. (1996), who demonstrated that boundary layer profiles in natural channels are likely to be too heterogeneous and complex to be easily explained by existing boundary layer theory. The relationship between bed geometry, mean flows, and wall parameters can only be examined by detailed mapping of velocities above the substrate (Davis and Barmuta 1989; Wetmore et al. 1990).

The distribution of velocity above a topographically complex streambed is a product of the relationship between bed geometry and various flow variables. Bathurst (1994) showed that in streams where the ratio of depth (D) to bed material diameter (d_k) was greater than 10, velocity profiles adopted a semi-logarithmic distribution. Nowell and Church (1979), experimentally manipulating roughness spacing in a flume using a slightly lower relative submergences (D/d_k = 8), found that the velocity profile above the bed roughness elements (Lego[®] blocks, in their case) noticeably deviated from the normally accepted semi-logarithmic shape. Nowell and Church (1979) further speculated that in natural channels with relative submergences lower than D/d_k= 8, velocity profiles would not follow a simple logarithmic distribution, and methods that estimate mean velocity based on a few measurements and the assumption of a log-normal profile would have significant errors. Young (1992) stated that in cases where D/d_k ≤ 3, flow is chaotic, the structure of the flow is very complex, and the distribution and magnitude of near-bed velocities will be dependent on the shape of the local bed geometry.

The flow in high gradient, mountain channels with coarse bed material is known to be substantially different from that in topographically simple channels. Jarrett (1990) demonstrated that the velocity profiles of mountain rivers (D/d_k > 3) are non-logarithmic. Velocity profiles recorded by Jarrett are distinctively "S-shaped"; near-bed velocities are lower and near-surface velocities are higher than a logarithmically distributed velocity profile. He suggested that near-bed velocities are reduced as a result of form drag induced by the cobble and boulder bed material. Bathurst (1994) also investigated the velocity distribution of mountain rivers, and found similarly S-shaped velocity profiles in mountain river sites. However, Bergeron (1994) examined the flow structure in gravel-bed streams whose relative submergences ranged from $1.63 > D/d_k > 8.58$, and found that the majority of velocity profiles were neither semi-logarithmic in shape nor s-shaped. Velocity profiles over the topographically simple portions of the bed conformed closely to a "typical" semi-logarithmic shape, but then, as flow passed over obstacles on the bed (bedforms), the rising bed elevation created local flow acceleration and an associated pressure gradient. Bergeron (1994) concluded that the resulting nonlogarithmic velocity profiles consisted of two or more semi-log linear segments joined at inflection points ("knots"). Flow profiles some distance downstream of the bedforms continued to be nonlogarithmic due to boundary layer separation and associated regions of recirculating flow.

Although the degree of relative submergence (D/d_k) may seem like a simple and easily employed rule of thumb by which the degree of near-bed velocity profile distortion may be estimated, it is important to note that almost all of the above studies were conducted at relatively coarse spatial scales. Li (1994), investigating near-bed flows over sand ripples at high spatial resolutions, found substantial near-bed velocity profile distortion even though relative submergences were relatively high $(D/d_k > 10)$. Similarly, Way et al. (1995), studying the relationship between macroinvertebrate habitat requirements and bedform / flow interactions over preformed, grooved concrete substrates with high relative submergences $(D/d_k >>10)$, also found velocity profiles that deviated from the expected lognormal distribution. This suggests that velocity profile distortion may develop near the bed in any case where water flows over a geometrically irregular surface, creating heterogeneous pressure gradient distributions.

Although there is a solid empirical foundation for the examination of near-bed flows in natural stream channels, their general applicability, especially in torrential streams, is limited for three reasons. First, the vast majority of studies are conducted in streams and rivers where $D/d_k > 1$. Torrential streams often have relative submergences less than 1 due to relatively shallow flows and extremely coarse bed material. As relative submergences decrease, flows should become increasingly complex and three-dimensional. Second, due to the types of instrumentation used, previous measurements of velocity profiles in natural streams have often failed to determine the shape of the velocity profile immediately adjacent to the bed (but see Li 1994; Hart et al. 1996). Third, the bed compositions of stream channels investigated in most studies are generally composed of finer materials than that regularly found in torrential stream channels. Flows over large bedforms are likely to be substantially different than flows over finer, more evenly distributed bed materials.

A number of techniques exist to quantify flows within a few millimetres of the bed. Of these instruments, only a few, such as the constant-temperature anemometer (CTA) and the laser-Doppler anemometer (LDA), are capable of measuring velocities at the spatial resolutions required to quantify near-bed flow variables. Unfortunately, these types of instruments are notoriously difficult to deploy in the field (Hart et al. 1996). Other more routinely deployed devices, such as propeller flow meters (Wetmore et al. 1990), bucket-wheel current meters (Rempel et al. 1999), electromagnetic current meters (EMCMs) (Bergeron 1994; Buffin-Belanger and Roy 1998), and acoustic doppler velocimeters (ADVs) (Bouckaert and Davis 1998) are robust but are incapable of measuring flows within millimetres

of the bed. The measurement of pressure difference by a Preston tube resting on a solid surface has been used to directly measure shear stress (Preston 1954), providing an alternative to estimating shear stress using the semi-logarithmic regression method. The addition of a static tube to a Preston tube deployed in this fashion results in a Preston-static tube (PST), a device capable of measuring wall shear stresses in flows characterised by curved streamlines (Ackerman et al. 1994). In addition to measuring shear stresses, a Preston-static tube can also be used to measure water velocities above the substrate (*i.e.* deployed as a Pitot-static tube) at spatial scales approximating the diameter of the dynamic tube (Ackerman and Hoover 2001).

Meso-scale patterns: the link between macro- and micro-hydraulics

Natural systems are patchy in space and time. Stream ecosystems are heterogeneous, both in terms of physical (hydrodynamic parameters, substrate size, light, oxygen) and biological (algal and faunal densities) characteristics (*e.g.* Palmer 1995). Ecologists have long sought to understand how small-scale heterogeneity in the stream environment affects the population dynamics, community ecology, and individual behaviour of benthic taxa (see Nowell and Jumars 1984; Davis and Barmuta 1989; Carling 1992 for reviews). As hydrodynamic parameters are the most important environmental factors influencing patterns of invertebrate diversity and abundance (Statzner and Higler 1986), the ecological, behavioural, and morphological adaptations of benthic organisms to hydraulic environments are predictably diverse.

Perhaps the single greatest topic of discussion among workers investigating the biology of invertebrates in lotic systems is the relevance of routinely measured parameters. For example, variables that describe channel morphology may be correlated with the abundance or distribution of certain species. Buffagni et al. (1995) found that the distribution of the mayfly *Rhithrogena semicolorata* is related to bed roughness. However, given the complex relationships that exist between bed geometry and hydrodynamic factors, *R. semicolorata* may, in fact, be responding to a suite of hydraulic variables (*i.e.* mean and near-bed velocity, depth, turbulence, or substrate roughness) that are functionally related to channel morphology (see Newbury 1984; Robert et al. 1996; White 1999). Stream macroinvertebrates are taxonomically and morphologically diverse (Resh and Rosenberg 1984), but generally range in size from one to several millimetres. Thus, relating patterns of invertebrate abundance to hydraulic or hydrologic factors quantified at relatively large

scales (one to several orders of magnitude larger than the body size of benthic taxa) may provide little useful information on the proximal factors that influence the behaviour of individual organisms. These methodologies may, however, help understand the population biology of benthic taxa. While many benthic invertebrates are recognised as having well-defined preferences and adaptations for particular velocity ranges and substrate sizes, the mechanisms that link large-scale physical factors to small-scale patterns of invertebrate behaviour are not well understood.

Benthic-lotic coupling in the stream environment

The interaction between flow and streambed geometry creates localised variations in nutrient supply, food exchange, and erosive shear (Davis 1986). In turn, these factors have considerable indirect influences on the biotic processes of the stream environment, such as predator-prey and grazer-producer interactions (e.g. Osborne and Herricks 1987; Peckarsky and Wilcox 1989). The patterns of invertebrate abundance and diversity that are a product of these abiotic and biotic interactions have been recognised by a number of workers (Jowett et al. 1991; Holomuzki and Messier 1993; Quinn and Hickey 1994; Collier et al. 1995). The association of patterns of abundance with hydrodynamic parameters has led to the development of habitat suitability models for several species (e.g. Deleatidium spp.; Jowett et al. 1991). Increasing numbers of studies of this type have led to the development of methodology and techniques appropriate for the description of the characteristics and distribution of 'patches' of hydraulically similar microhabitats across the streambed. Several comprehensive reviews (Nowell and Jumars 1984; Davis 1986; Davis and Barmuta 1989; Carling 1992) have stressed the importance of appropriately describing the small-scale hydrodynamic variation inherent in the stream environment, and suggest a suite of variables to do so. Indeed, significant relationships have been found between the abundances of invertebrate taxa and both simple (e.g. discharge, depth, and velocity) and complex (e.g. Reynolds number, Froude number) hydrodynamic parameters.

Several studies have examined the microdistributions of sedentary and semi-sessile species (*i.e.* suspension-feeding caddisfly and simuliid (black fly) larvae; see Table 1-1). Suspension-feeding caddisflies (Trichoptera) are a trophically important group as they trap and process suspended particulate organic matter (POM) in a stream segment, increasing the efficiency of the local recycling of available resources (Wallace and Merritt 1980; Voelz and Ward 1996). Similarly, suspension

feeding black fly larvae (Diptera: Simuliidae) constitute an important pathway for energy flow in stream ecosystems (Merritt et al. 1996), transforming collected ultrafine POM (0.45 - 50 µm) into fine POM (50 µm - 1mm), a form more readily utilised by stream organisms (Merritt 1987). Voelz and Ward (1996) found that the distributions of the suspension-feeding caddisflies Arctopsyche grandis and Brachycentrus occidentalis were largely restricted to the lower sides and bottoms of stones, where they were exposed to velocities less than 20 cm s⁻¹. Individuals of both species aggregate underneath the leading edge of cobbles and boulders. While the flow patterns beneath stones would be complex (Statzner et al. 1988), flow entering the underside of stones from the front might be relatively unidirectional compared to the water exiting the side and rear of the stones. Voelz and Ward (1996) suggest that the distributions of these net-spinning caddisflies reflect the best local filtering velocities. and may also reflect areas with desirable levels of turbulence. Several studies (e.g. Wetmore et al. 1990) have reported that suspension-feeding caddisflies prefer the exposed tops and sides of stones where the flow is typically rapid, has higher Froude numbers (average Fr = 0.6), and higher stream surface slopes. These microhabitats represent areas of converging streamlines, and the locally highest rates of seston delivery. However, Voelz and Ward (1996) suggest that the observed microhabitat preferences may, in fact, be seasonally variable. B. occidentalis and A. grandis exhibit seasonal shifts in positioning behaviour, moving into more exposed locations only during the late summer months when many of the previous studies had been conducted. Given that the underside of stones and interstitial spaces represent an important niche in streams (Voelz and Ward 1996; Robertson et al. 1997; also see Resh and Rosenberg 1989), future research on the nature of flows beneath substrate elements is needed. For example, the presence of a solenoidal (horseshoe) vortex around the front of the stone (Nowell and Jumars 1984; Craig 1996; Bouckaert and Davis 1998) would presumably alter the velocity and turbulence of the water entering the underside of stones, further influencing the microhabitat preferences of these suspension-feeding caddisflies.

The net spinning hydropsychid caddisfly *Hydropsyche* also relies on local current to deliver an adequate supply of seston; as such, current velocity acts as an important selective pressure in determining net mesh aperture and food particle size (Fuller and Mackay 1980). Using hydrodynamically calibrated artificial substrates deployed in a natural stream, Osborne and Herricks (1987) found distributions of *Hydropsyche* to be related to flow patterns and turbulence intensity rather than average velocity. High degrees of hydraulic niche overlap were noted among the four species of

Hydropsyche studied (H. betteni, H. sparna, H. cheilonis, and H. bronta); larvae of all four species were found in regions of rapidly spiralling vortices. These vortices may serve to increase the rates of seston capture by increasing capture rates without substantially increasing drag on the body of the insect (see Lacoursière 1992). The findings of Osborne and Herricks (1987) agree with earlier hypotheses (e.g. Fuller and Mackay 1980) which suggest that variations in turbulence could be an important factor determining interspecific differences in microhabitat preferences among hydropsychid caddisflies. Similarly, Quinn and Hickey (1994) found that the suspension-feeding caddisfly taxa of New Zealand rivers were primarily associated with patches of high velocity and high turbulence intensity, and suggested that these two variables increase the particle capture rates of net-spinning suspension-feeders. Turbulence is thought to be important to suspension-feeding caddisflies with respect to their energy budget; while an organism will probably expend more energy maintaining a position in areas of higher velocity, the construction of nets in an area of rapid spiralling flows might act to increase rates of seston delivery (Osborne and Herricks 1987). This conclusion is supported in part by the findings of Peckarsky et al. (1990), who found that densities of Hydropsyche instabilis increase with FST hemisphere number, an indicator of surface velocities and shear stresses (see Statzner and Müller 1989). Peckarsky et al. (1990) also note, however, that H. instabilis spins a net of relatively coarse mesh, which may be regarded as an adaptation for high velocities. Similarly, the predatory caddisfly Plectrocnemia conspersa, which spins a silk net to ensnare invertebrate prey, modifies the design and aperture size of its net as flow rates increase (Townsend and Hildrew 1979).

The heterogeneous distribution of near-bed velocity in streams plays an ecologically important role in determining the distribution of stream microcrustacea, a group comprised of smail-bodied cladocerans, copepods, and ostracods. Stream microcrustacea maintain an important trophic link in lotic ecosystems by feeding on detritus and detritus-associated organisms. While the patterns of microdistribution and abundance of other benthic invertebrate taxa have been associated with specific hydraulic habitats defined by a variety of hydrodynamic factors, Robertson et al. (1997) found that the distributions of microcrustacea are influenced by the fluctuations in flow associated with flood events ('spates'). Epibenthic microcrustacea, taxa which inhabit the surface of the substratum, are particularly susceptible to erosion; ostracods can be displaced at velocities as low as 2 cm s⁻¹, and the cyclopoid copepod *Eucyclops* becomes numerous in the drift at 7.5 cm s⁻¹ (Richardson 1992). The average near-bed velocities of streams in which benthic microcrustacea abound frequently exceed

these values. During and after flood events, microcrustacea persist in flow refugia, areas of the streambed that retain low hydraulic stresses, even at high flows. Following the periods of high discharge that accompany rainfall or seasonal runoff, these flow refugia provide a source of microcrustacea from which denuded or disturbed areas of the bed can be repopulated. Epibenthic microcrustacea tend to be relatively broad-bodied, and dominate the species assemblage in streams that have large dispersive fractions (essentially, areas of the stream bed which maintain low shear stresses, even during disturbance events; Robertson et al. 1997). Similarly, Shiozawa (1991) found that epibenthic microcrustacea were associated with low-velocity patches of the streambed containing deposits of fine organic material and silts. Interstitial species, which are often slender and vermiform, comprise the majority of microcrustacean species in high velocity streams that have low dispersive fractions. Unlike epibenthic species, interstitial taxa, such as harpacticoid copepods, benefit from periods of high erosive forces. High bed shear stresses minimise the deposition of fine particles which, over time, tend to clog the pore space in bed gravels, reducing both flow-through rates and levels of oxygen experienced by subsurface taxa (Robertson et al. 1997).

A test of the intermediate disturbance hypothesis by Townsend et al. (1997) provides an interesting perspective on the ecological role of flow refugia in determining the community composition of stream benthos. The intermediate disturbance hypothesis, whose early uses include an examination of patterns of diversity in coral reefs and tropical rain forests by Connell (1978), proposes that in patchy and dynamic environments, intermediate levels of physical disturbance should produce the highest species diversity. Intermediate levels of disturbance establish a ecological compromise between highly unstable systems where frequent disturbances produce a community composed primarily of a limited number of highly tolerant taxa able to rapidly colonise impacted patches, and stable systems where rare disturbances result in communities dominated by a few, competitively superior, species. Daily disturbances in flow (a result of hydropower regulation of the channel discharge) resulted in a loss of heptageniid mayflies in Swedish rapids (Malmovist and Englund 1996), a trend attributed to increases in the sedimentation of transported fine particles associated with lower current velocities (generally, particles < 1 mm in diameter). In an undisturbed catchment, Townsend et al. (1997) found that macroinvertebrate diversity was greatest at sites that experienced intermediate levels of flood-related disturbance. Variations in taxonomic richness were related to indices of bed disturbance, and Townsend et al. (1997) suggest that the primary location of flow refugia were low-

velocity 'dead spaces' between large substrate elements. Invertebrate diversity decreased as the proportion of the bed material composed of fine sediments increased. Periods of high flow are thought to reduce the amount of fine sediment stored within streambeds, increasing oxygen availability (Robertson et al. 1997) and the percentage of available interstitial space. However, Townsend et al. (1997) acknowledge that the small-scale hydrodynamic factors that invertebrates detect and in turn respond to remain largely unexplored.

The microdistribution of benthic grazers is also a function of the distribution of algal food resources. However, the growth of epiphytic algae (especially diatoms, the preferred food of many grazing invertebrate taxa) is, in turn, also a function of small-scale patterns of flow and variations in velocity (Quinn et al. 1996; see also Resh and Rosenberg 1984). As a result, the environmental factors that determine the microhabitats of grazers and algae can be difficult to separate. Jowett et al. (1991) found that while the abundance of the mayfly Deleatidium was correlated with a combination of Froude number and substrate size, it was most highly correlated with periphyton biomass. Similarly, Palmer (1995) found that the mayflies Epeorus and Baetis grew to larger sizes in high velocity environments with homogeneously distributed food resources, while Poff et al. (1990) demonstrated that current has a significant influence on algal abundance and invertebrate species composition in high velocity streams. The thinner boundary layers and higher shear velocities associated with microhabitats exposed to high velocities would reduce the diffusional distance to the boundary, increasing rates of nutrient and oxygen delivery to organisms on the stream bed (Carling 1992; Davis 1986). This would benefit the growth of both periphyton and invertebrate grazers, many of which have relatively inefficient gills (Wiley and Kohler 1980; Golubkhov et al. 1992). An accurate separation of the flow requirements of primary producers and consumers awaits an experimental manipulation of algal communities across a range of microhabitat velocities.

Invertebrate drift: migration using bulk flow

Flowing water is used widely by stream macroinvertebrates for movement. While upstream movements of benthic invertebrates by crawling (Winterbottom et al. 1997) and swimming against the current (Abelson 1997; Rader and McArthur 1995) have been recorded, the vast majority of migratory movements in lotic environments are downstream, in the direction of least resistance. Either accidentally or intentionally, stream benthic invertebrates often enter the moving water column above
the substrate, and are carried downstream. Stream invertebrates actively enter the drift in order to escape fish and invertebrate predators, avoid competitors, or migrate to areas of higher food availability (Hildrew and Townsend 1982; Wooster and Sih 1995; Forrester 1994). Other factors influencing invertebrate drift include sunlight, discharge, turbidity, oxygen, and substrate (see Wiley and Kohler (1984) for a review). Although diurnal patterns vary between species, the numbers of stream invertebrates drifting during the day is generally low and constant, followed by dramatic increases at night (Sagar and Glova 1992). Rates of invertebrate drift are highest at dawn and dusk in many species. Several authors (*e.g.* Forrester 1994) have hypothesised that diel periodicity in drift addresses a significant source of selective pressure. Drifting invertebrates are an important source of food for many stream fishes, which feed almost entirely during the day as they rely on visual acuity to locate and attack prey (Walsh et al. 1988). As such, there should be strong selection pressure against behaviours (including drift) that expose individuals to visually oriented predation by fish.

Invertebrate drift is generally thought to be an active process, where invertebrates detach from the substrate in order to migrate downstream (Wooster and Sih 1995). However, the precise mechanisms by which invertebrates detach from the streambed to initiate downstream movement have not yet been investigated. Whether stream insects simply detach from the surface of the streambed, swim briefly upward, or initiate a change in body position that creates sufficient lift to impel them upward into the water column is as yet unknown. However, several authors have noted that there are disproportionately high densities of large size classes of many species in the drift (e.g. Lancaster et al. 1996; Sagar and Glova 1992). Similarly, it has been noted that large invertebrates are more susceptible to erosion than smaller members of the same species; this variation in risk of detachment from the substrate is presumably due to the greater pressure drag and lift experienced by larger individuals (Davis 1986; also see Weissenberger et al. 1991, and equations 1.11 and 1.12). Winterbottom et al. (1997) found that larger stoneflies of the predatory species Leuctra nigra were more likely to become detached from the substrate during changes in discharge than small individuals. Both Winterbottom et al. (1997) and Lancaster and Hildrew (1993) note that small L. nigra were able to move more easily in high velocities. Peckarsky and Cowan (1995) found that the activity levels of several predator (Megarcys signata and Kogotus modestus) and prey (Cinygmula sp., Epeorus deceptivus, Baetis bicaudatus, and Ephemerella infrequens) species increased at night, as did their use of the exposed upper surfaces of stones. Given that stone surfaces exposed to the flow

generally have higher local velocities, higher shear stresses, and thinner boundary layers than interstitial surfaces (Nowell and Jumars 1984; Davis 1986), it is possible that the diel periodicity of drift is due, at least in part, to the accidental dislodgement of diurnally active individuals moving over highrisk hydraulic patches rather than intentional detachment for the purpose of migration. This is supported by the conclusions of Poff and Ward (1991), who interpreted the increases in drift associated with periods of increased discharge to an increases in the accidental detachment ("scour") of invertebrates from the streambed. Periodic drift due to accidental detachment should be more pronounced in species that lack specific adaptations to high flow environments, yet are present in a wide range of hydraulic microhabitats (*i.e. hydraulic generalists*).

Once entrained in the drift, the responses of stream invertebrates vary. The length of time that an invertebrate spends in the drift before returning to the stream bottom (the return rate) is a result of the interaction between the hydraulic transport properties of the stream channel and the behavioural responses of the individual (Lancaster et al. 1996). Hydraulic 'dead zones' (areas of the stream bed where water is held in transient storage - stream margins, turbulent eddies, vortices attached to boulders or logs, and backflows associated with pools or bends) provide opportunities for invertebrates to regain the substrate. Lancaster et al. (1996) found that channels with the highest mean velocities had the lowest return rates, but also report that streams whose beds had high proportions of dead zones had relatively high rates of return, regardless of velocity. They also suggest that turbulence and channel-specific depth may increase the length of time invertebrates are entrained.

By altering their behaviour, some invertebrates can alter the length of time spent in the drift. At very low velocities, some invertebrate taxa can actively increase time spent drifting (Poff and Ward 1991). Winterbottom et al. (1997) found that the length of time spent in the drift by the leuctrid stonefly *Leuctra nigra* was entirely dependent on flow and the hydraulic characteristics of the channel. The inability of *L. nigra* to behaviourally modify its return rate is consistent with the findings of Lancaster et al. (1990) which show that *L. nigra* is a poor colonizer and disperses slowly. However, the length of time that the nemourid stonefly *Nemoura pictetii* spends in the drift is independent of flow factors. Behavioural control of return rate allows nemourids to colonise new substrates rapidly (Winterbottom et al. 1997; Lancaster et al. 1996), an attribute which allows individuals to minimise the length of time they are exposed to predation by fish. The capacity to efficiently utilise downstream transport in

moving waters is also important to the feeding ecology of stream herbivores. The mayflies *Baetis bicaudatis* and *Epeorus deceptivus* grew to larger body sizes when high velocities allowed them to drift successfully between high resource patches (Palmer 1995). Interestingly, the growth of these two grazing species was maximised when they entered the drift less frequently. Increases in time invested to 'search' (in the drift) for higher resource patches may be beneficial; however, time spent searching results in lost feeding opportunities in a patch of known resource availability.

Ontogenetic shifts in hydraulic habitat and microdistribution

The influence of moving water on a stationary body is dependent on spatial scale, as indicated by the Reynolds number. As benthic invertebrates generally increase in size and mass during their growth and development, one might expect to find size-related shifts in behaviour and microhabitat preference (see Table 1-1).

The spatial niches of organisms change as they increase in size. Osborne and Herricks (1987) found ontogeny-related differences in microhabitat velocities among four ecologically similar species of the caddisfly Hydropsyche. H. cheilonis, H. sparna, and H. bronta occupied areas of the substratum where maximum velocities reached 25 cm s⁻¹, while the larvae of *H. betteni* were found in velocities as high as 35 cm s⁻¹. Although the degree of hydraulic niche overlap between the four species is high, H. betteni is roughly 10 - 15% larger at each instar than the other three hydropsychid species, which are virtually identical in size. Osborne and Herricks (1987) noted a similar intraspecific trend; larger, higher instar larvae of the four Hydropsyche species were capable of inhabiting regions of higher microhabitat velocities. The results of Osborne and Herricks suggest that sizerelated differences in hydrodynamic tolerances are a function of body size, rather than functional changes in capture net mesh dimensions. Collier et al. (1995) found that larger larvae of the hydrobiosid caddisflies Hydrobiosis parumbripennnis and Costachorema callistum tended to be more common in higher velocities than smaller larvae. Collier et al. (1995) concur that this difference is a function of the larger physical sizes of higher instars, and suggest that the large anal prolegs used by caddisflies to move over the substrate in fast currents may be more effective in maintaining position as they increase in size.

Intraspecific variations in distribution of the leptophlebiid mayfly *Deleatidium* is size related as well (Collier 1994). While the velocity preferences of this species are relatively broad, it is generally

found in areas of higher flow (Jowett et al. 1991). Collier (1994) found that the abundance of smaller nymph size classes was greatest in relatively low-velocity patches (<40 cm s⁻¹), while larger nymphs reached their highest densities in higher velocity habitats (>90 cm s⁻¹). Collier (1994) suggests that size-related differences in distribution might be a reflection of changes in oxygen requirements as individuals grow. Increases in size result in lower surface-to-volume ratios, which may, in turn, restrict respiratory gas exchange rates. Higher flow rates thin the boundary layers associated with invertebrate gills, resulting in increased diffusion of respiratory gases (Nowell and Jumars 1984). However, while oxygen and food supplies may be more readily available at high velocities, the proportion of total drag attributable to pressure drag is greatest for larger, late instar larvae (see Vogel 1994). For stream insects, especially grazers foraging in high velocity microhabitats, this is a necessary tradeoff. Individuals can either avoid areas where high velocities and erosional forces (lift and drag) threaten to detach them from the substrate, or possess morphological and/or behavioural adaptations to counter the effects of lift and drag (Weissenberger et al. 1991; Collier 1994). For example, Buffagni et al. (1995) found that the velocity preferences of the mayflies Rhithrogena semicolorata and Ecdyonurus venosus, both obligate inhabitants of high flow environments, did not change with increasing size. Rather, larger individuals of both species tended to prefer substrates of greater roughness. Buffagni et al. (1995) suggest that bed roughness may provide a better descriptor of complex hydraulic characteristics near the stream bottom, citing turbulence and 'force of flow' as possible factors. These species may be taking advantage of flow microrefugia, small-scale surface irregularities that produce localised areas of relatively thick boundary layers (Davis and Barmuta 1986). Larger mayflies may find maintenance of position in these areas to be less expensive energetically. A similar use of flow microrefugia was noted in the caddisfly Hydropsyche (Osborne and Herricks 1987); larvae are often found associated with small depressions and imperfections in the substrate surface. This may allow these suspension-feeding caddisflies to hold their nets in the higher velocities of the upper boundary layer, while restricting the exposure of the bulk of their bodies to the low shear stress, lift, and drag of a locally-thickened boundary layer.

Benthic predators, which are not directly dependent on the epiphytic food resources available in high velocity patches, would not be expected to show the same specific adaptations to high velocity microhabitats. Winterbottom et al. (1997) found that large stoneflies of the species *Leuctra nigra* were more susceptible to changes in discharge than were smaller individuals, and suggested that while

larger individuals were more likely to be eroded, smaller *L. nigra* were able to move more easily over exposed areas of the stream bed at high velocities. Similarly, Lancaster and Hildrew (1993) reported that the distribution of small, early instar *L. nigra* did not change with increases in flow, and were generally associated with high velocities and coarse substrates. Thus, the distributions of stream predators (which rarely demonstrate specific adaptations to counter the erosional effects of high velocities; see below) may not be the result of a preference for low-velocity habitats. Rather, high near-bed velocities may act to prevent stream invertebrate predators may from foraging in high velocity habitats, where prey is often abundant.

Hydrodynamics, prey, and predation: eating in the fast lane

Given the ecological importance of morphological and behavioural adaptations to both stream hydrodynamics (*e.g.* Quinn et al. 1996) and predator-prey interactions (*e.g.* Tikkanen et al. 1997), it is of little surprise that research on the relationship between hydrodynamics and predator-prey interactions is growing. Basic ecological tenets state that harsh environments and physical disturbances weaken interactions between species (see Menge 1976). In freshwater lotic environments, where hydrodynamics play a pivotal role across physical scales ranging from river-wide zonations (Statzner and Higler 1986) to fine-scale respiratory currents over invertebrate gills (Wiley and Kohler 1980), one would expect to find a wide range of ecological and behavioural responses linking predator and prey (see Table 1-1).

Peckarsky et al. (1990) provided the first formal test of the harsh-benign hypothesis in the stream environment, gauging the influence of hydraulic-habitat preferences on predator-prey interactions. The harsh-benign hypothesis, originally developed to explain the relative roles of predation and competition in structuring marine rocky intertidal communities (Menge 1976), can be used to assess the impact of predatory invertebrates on prey populations along a gradient of hydraulic regimes. Peckarsky et al. (1990) found that densities of the predatory stonefly *Dinocras cephalotes* peaked at FST hemisphere 11 (see Statzner and Müller (1989) for a description of the FST apparatus), indicating a preference for medium-range flows and shear stresses. However, the prey species of *D. cephalotes* (including *Hydropsyche* (Trichoptera), *Baetis* (Ephemeroptera), assorted Chironomid species, and the amphipod *Gammarus* (Crustacea)) showed preferences for higher flow conditions (average of FST hemisphere 18). When prey were distributed across a range of habitats,

predation impacts on the prey were significant only in those patches with hydraulic regimes favourable to the predators. The flatworm predator *Dugesia dorotocephala* is similarly limited in its predation on larval blackflies (*Simulium vittatum*). Hart and Merz (1998) found that while *D. dorotocephala* will readily attack black fly larvae when it encounters them, the flatworm is poorly adapted to high velocities. As a result, high velocity sites not only acted as flow-mediated refuges from predation, but also coincided with areas where the feeding rates of the food-limited, suspension-feeding black fly larvae are maximised. Peckarsky et al. (1990) suggest that reductions in prey populations are not entirely due to predation; predator avoidance behaviours, including drift (Wooster and Sih 1995) and migration (Peckarsky and Cowan 1995) account for the majority of the observed community change. However, the criteria by which predators and prey perceive hydrodynamic conditions as being either 'harsh' or 'benign' remain unknown for most species.

Microhabitat overlap between prey and predator species may determine encounter rates, but this does not necessarily translate into prey preferences. Prey preferences are not only a function of availability, but also species-specific handling times and attack success rates (Sih and Wooster 1994). The periodid stonefly Diura bicaudata demonstrates a strong preference for black fly larvae prey, even though microhabitat overlap with black fly species is minimal. D. bicaudata has the highest degree of microhabitat overlap with several species of mayfly, including Baetis, Ephemerella, and Heptagenia, yet rarely utilised them as prey (Tikkanen et al. 1997). Tikkanen et al. (1997) also found that baetid mayflies were able to risk interactions with predators due to highly effective escape manoeuvres. Interestingly, however, Palmer (1995) reported that rates of predation by the stonefly predator Megarcys signata on Baetis bicaudatis were higher at 10 cm s⁻¹ than 30 cm⁻¹, as the swimming escape response of Baetis is less effective at lower velocities. It is possible that the higher shear stress, greater turbulence intensity, or thinner boundary layers at higher velocities interferes with the ability of M. signata to recognise the 'hydrodynamic signature' of the swimming baetids (see Peckarsky et al. 1990). Alternatively, once the escape response is initiated, higher velocities may reduce the rate of predation success by transporting prey out of the attack range of predators more quickly.

Invertebrate predators also use hydrodynamic cues to detect prey and discriminate between preferred and non-preferred prey species. Peckarsky and Wilcox (1989) found that the periodid stonefly *Kogotus modestus* never attacked motionless mayfly prey, but was able to use the pressure

wave patterns associated with swimming escape behaviour of the mayfly *Baetis bicaudatus* to recognise and attack this preferred prey species. Based upon the pressure wave patterns, *K. modestus* was also able to distinguish *B. bicaudatus* from *Ephemerella infrequens*, a non-preferred mayfly prey species.

Black fly (simuliid) larvae increase the chance of surviving an attack by an invertebrate predator by detaching into the drift or vigorously biting the head region of the predator (Tikkanen et al. 1997). These tactics are, unfortunately, relatively ineffective; black fly larvae are the preferred prey of predators such as the stonefly Megarcys signata, which attack blackflies with a relatively high capture probability when they are encountered. Yet rates of predation of black fly larvae are relatively low, due to a separation of the hydraulic niches of predator and prey. Suspension-feeding simuliid larvae aggregate in exposed microhabitats, preferably attaching in areas of low shear stress but relatively high velocity (Lacoursière 1992), while M. signata prefers low velocity microhabitats along the periphery of streams. The microsite preferences of Simulium also moderate the predatory impacts of freshwater triclad flatworms on aggregations of larval black flies (Hansen et al. 1991; Hart and Merz 1998). Due to the incomplete microhabitat overlap between triclads and their simuliid prey, the flatworms are unable to forage in areas of the bed that contain the highest densities of simuliids. Muotka and Penttinen (1994) found that the stonefly predator Isoperla grammatica is similarly excluded from the microhabitat preferred by the larval black fly Simulium sublacustre. They suggest that I. grammatica either simply avoids the areas of high current velocity preferred by the black fly larvae, or is competitively excluded from foraging in exposed areas by a species that moves more efficiently over the surface of stones at high velocities. High velocity patches do not provide a refuge from all stream predators, however. The microhabitat preferences of S. sublacustre and the predatory caddisfly Rhyacophila obliterata overlap highly when local water velocities reach 40 - 60 cm s⁻¹; this results in high rates of consumption of the sedentary black flies by this large, active rhyacophilid predator (Muotka and Penttinen 1994).

The importance of invertebrate predators to stream communities is also reduced during the hydraulic restructuring that occurs during floods and spates. Increases and redistributions of velocity and shear stress accompany increases in stream discharge. These often rapid changes can cause losses and changes in community structure (Lancaster 1996). Animals may be lost from microhabitats subject to high erosional forces, while individuals in low-flow refugia may remain

essentially unaffected (Lancaster and Hildrew 1993; Winterbottom et al. 1997). The individuals in these refugia, coupled with those that migrate into them during the disturbance event, will be available to recolonise denuded areas of the streambed when the distributions and levels of velocity and shear stress return to average. Lancaster (1996) found that the alderfly Sialis fuliginosa did not significantly shift its microdistribution with changes in discharge. As a result, the total impacts of this predator decreased during periods of hydraulic disturbance. Consumption of prey remained at pre-disturbance levels for those individuals found in refugia, but was reduced throughout the remainder of the streambed where prey populations had been reduced. Lancaster suggests that because S. fuliginosa is an active forager, it may simply be unable to feed efficiently in fast currents. However, flow disturbance events have very different effects on the feeding ecology of the caddisfly Plectrocnemia conspersa, a primarily lie-and-wait predator which spins silken nets in which prey become entangled. Lancaster (1996) found that, unlike S. fuliginosa, rates of prey consumption by P. conspersa increased during spate events. The microdistribution of P. conspersa remains similar to that of the invertebrate species it preys upon; it is uniformly distributed across hydraulic habitats at low flows, and becomes abundant in flow refugia during periods of high discharge. Increased rates of predation by P. conspersa may be a function of the increased movements of migrating prey in the process of searching for and moving into areas of lower velocity and shear stresses. However, Winterbottom et al. (1997) noted that the mobility of P. conspersa was related to increases in discharge; this suggests that changes in distribution of this caddisfly may be, in part, a result of dislodgement of individuals caught in exposed areas of high shear stress during flood-associated increases in discharge. This suggests that while the harsh-benign hypothesis may provide insight into the impacts a predator may have on prey populations across a wide range of hydraulic conditions, its application may be limited to those species that show well-defined hydraulic preferences. The predatory impacts of those species that are able to modify their predatory behaviour to accommodate the microhabitats occupied by a range of prey species may be less dependent on predator/prey microhabitat overlap.

Fine-scale flows: behavioural and morphological hydrodynamics

Fine-scale manipulations of flow

The benthic invertebrate taxa of lotic systems have evolved a range of adaptations to cope with hydrodynamic forces. They have, in many cases, coupled complex behaviours with specialised morphologies to utilise the energy of their environment (see Table 1-1). For example, the bodies of the larvae of the aquatic beetle genus Sclerocyphon (Coleoptera: Psephenidae) locally modify the thickness of the boundary layer to produce a suite of ecological and energetic benefits. Using dye injection, Smith and Dartnall (1980) found that these unique larvae live in turbulent environments, where turbulent boundary layers develop in high velocity flows. The streamlined, flattened bodies of Sclerocyphon (figure 1-4) modify the developing boundary layer, increasing the thickness of the local viscous sublayer. A thickened viscous sublayer reduces the risk of dislodgement as Sclerocyphon grazes the epiphytic diatoms and other algae found on the upper surfaces of boulders and cobbles (Quinn et al. 1996). However, life within the viscous sublayer has disadvantages; the diffusion of respiratory gases within the viscous sublayer relies upon the relatively slow rates of molecular diffusion. In situations where the viscous sublayer is sufficiently thick to impair respiration, Sclerocyphon creates its own respiratory current using the anal tracheal gills located beneath the last abdominal tergite. The larvae extrude, then actively pump these gills, creating an area of localised turbulence at the rear of the body. This results in increased rates of respiration and waste removal while minimising increases in overall drag on the body. However, as Reynolds numbers increase, the viscous sublayer thins (Carling 1992), exposing the bodies of larval Sclerocyphon to a turbulent boundary layer. In these circumstances, Smith and Dartnall (1980) suggest that continued vortex production at the rear of the body is possibly no longer of use in ventilation, but rather may be acting to minimise pressure drag. In these high velocities, a secondary current that forces small amounts of water between the lateral laminae produces a phenomenon known as boundary layer suction. Boundary layers over the insect are further thinned, while boundary layer separation is delayed. As a result, pressure drag produced by the body of Sclerocyphon is reduced.

As mentioned above, the bodies of the stream invertebrates that inhabit the exposed surfaces of the streambed have long been regarded as being adapted to the hydraulic forces of their environment. Ambuhl (1959) felt that dorso-ventral flattening could be regarded as an adaptation to maximise the proportion of the body in the boundary layer, avoiding, to the greatest extent possible,

mean water velocities. This idea was generally accepted until Statzner and Holm (1982) re-examined the fine-scale flow patterns around the body of the mayfly Ecdyonurus venosus, the same species that Ambuhl had studied 23 years earlier. They found that Ecdyonurus, and presumably similar mayfly species, are not simply "living a sheltered life in the boundary layer". Moreover, the water moving over the body of E. venosus is far less smooth than Ambuhl had originally reported. Statzner and Holm (1982) found that water approaching the front of the mayfly slowed down substantially near the substrate at the front of the animal. Though Statzner and Holm (1982) do not discuss this trend, this pattern possibly indicates the presence of a horseshoe (solenoidal) vortex immediately in front of the head of the insect. The isovels ('layers' of equal water velocity) are then compressed as water flows up over the length of the thorax, then re-expand over the abdomen, suggesting that the lift and friction forces are concentrated over the thorax, where the legs of *E. venosus* are in contact with the bottom. Statzner and Holm (1982) regard this as an adaptation to maintain contact with the substrate in high velocities. Weissenberger et al. (1991) found that the morphology of Ecdyonurus counters much of the lift created by the steep velocity gradients over the thorax. The large head shield of this species can be angled to create negative angles of tilt, which reduces lift forces. The broad legs of Ecdyonurus, which are shaped like aerodynamic 'spoilers', can be angled to press the body down against the substrate. These morphological and behavioural adaptations can produce negative lift forces, minimising the energy Ecdyonurus must expend to maintain contact with the substrate. Alternatively, Weissenberger et al. found that Epeorus, another heptageniid mayfly, does not possess similar lift-reducing adaptations. The airfoil-shaped body of *Epeorus* produced much higher lift forces, which it apparently counters by anchoring itself to the substrate. Epeorus did, however, have the lowest drag coefficient of the species examined (Weissenberger et al. 1991).

Of special interest is the relationship between lift, drag, and the morphology of the perlid stonefly *Perla bipunctata* (Weissenberger et al. 1991). The lift forces experienced by this stonefly, which does not exhibit any specialised adaptations for life or movement in high flow environments, remain at very low levels until water velocities reach approximately 50 cm s⁻¹. Above this velocity, the lift forces experienced by an individual stonefly increase rapidly. This supports the results of Muotka and Penttinen (1994), which suggest that a threshhold velocity exists, beyond which stonefly predators (generally 'hydrodynamic generalists') are prevented from seeking prey due to

hydrodynamic constraints. As lift forces increase, hydraulic generalists such as stonefly predators may experience difficulties maintaining contact with the substrate.

Many benthic insect taxa (*e.g.* Diptera, Trichoptera) must enter a pupal stage before they can become reproductively mature adults (Resh and Rosenberg 1984). During the pupal stage, aquatic insects are generally immobile, and must therefore rely on the position adopted in the final larval instar to provide a continuous source of oxygen. Voelz and Ward (1996) found that the pupal cases of the caddisfly *Brachycentrus occidentalis* were clumped on the underside of the downstream side of boulders, a highly turbulent site which should provide high levels of dissolved oxygen while minimising shear stresses that might dislodge the pupating insects. A different approach is adopted by pupating blepharicerid larvae. Pommen and Craig (1995) found that morphological features of blepharicerid pupae produce respiratory vortices that interact with the pupal gills to create a unique, and efficient, method of plastronic gas exchange (see Vogel 1994).

The "scorpion posture", adopted by the mayfly *Ephemerella* when confronted by predators, is characterised by a vertical flexion and extension of the terminal abdominal segments and terminal filaments. Although recognised as a defensive behaviour by Peckarsky and Penton (1988), they ascribe it a largely mechanical function. Rather, this distinctive behaviour may play one of several hydrodynamic roles. The mayfly *Cloeon dipterum* positions its abdomen in a similar manner in order to initiate sufficient thrust during escape manoeuvres, during which accelerations can reach as high as 6.5 m s⁻² (Craig 1990). This suggests that the scorpion posture may reflect a 'pre-swimming' readiness on the part of *Ephemerella*. Alternatively, the extension of the abdomen and anal cerci into the upper levels of the benthic boundary layer may distort the flow fields around the animal's body, confusing predators as to the precise location and identity of the prey.

The fluid mechanics of suspension feeding and 'erosional hunting'

Several species of stream macroinvertebrate manipulate the hydrodynamics of their immediate surroundings in order to enhance feeding efficiency. Benthic taxa variously create vortices that enhance the efficiency of specialised suspension-feeding structures, erode soft sediments to expose buried prey, and re-suspend deposited organic food particles from the stream bed (see Table 1-1). The creation and manipulation of vortices requires specialised morphological features and

behavioural adaptations. Consequently, taxa that employ hydraulic manipulation to acquire food are generally among the most unique denizens of the benthic community.

The predatory larvae of the mayfly species *Pseudiron centralis* employ an unusual method of hunting for and feeding on their preferred prey, larval chironomids that live concealed in the benthic sands of large northern rivers. *Pseudiron* larvae adopt a peculiar posture, positioning themselves on the upstream slopes of sand dunes, arching their thorax upward while holding their head and mouthparts close to the substratum (figure 1-5). Soluk and Craig (1990) found that this directs flow downward, resulting in the generation of a solenoidal vortex in front of the animal. The increased velocity of this 'horseshoe' vortex erodes sand in front of the animal, exposing their chironomid prey. As prey becomes exposed, it is seized and ingested by the mayflies. The mayfly slowly moves backward, excavating prey in a continuous trench.

The predatory activities of the mobile stonefly *Dinocras cephalotes* also result in the erosion of fine sediments (Statzner et al. 1996). The ecological importance of this stonefly approaches that of a keystone species (Jones et al. 1994), due to the large influence this species has on erosional processes in stream riffle habitats. The night-time activity levels of *D. cephalotes* larvae increase when prey are scarce; it is this patrolling for prey that leads to increased bioturbation of sediments. Increases in sediment transport in turn lead to increases in the depth of interstitial spaces. However, increased foraging activities were noted only in hydraulic habitats preferred by the stonefly (optimal shear stresses of 0.39 - 1.58 N m⁻² for *Dinocras*; see Peckarsky et al. 1990). The authors suggest that increases in sediment entrainment by this stonefly are merely incidental, a behavioural 'by-product' of increased activity. If local shear stresses are already close to incipient motion thresholds for sand, then the hydrodynamic disturbance provided by the presence of a stonefly will likely result in local increases in entrainment (Statzner et al. 1996). However, it is possible that increases in interstitial space could directly benefit these predators if localised erosion exposed larval chironomids, a known prey item of other stoneflies of the same family (Perlidae, see Stewart and Harper 1996).

Soluk and Craig (1988) also investigated a unique method of suspension feeding utilized by the lotic mayfly *Ametropus neavei*. This mayfly also inhabits marginal regions of shifting sands in rivers throughout the holarctic region, and are found most commonly in velocities ranging from 18 - 30 cm s⁻¹. In relatively slow flows, these mayflies simply bury themselves, leaving only their head and caudal filaments exposed (Clifford and Barton 1979). However, when the flows of their environment

exceed approximately 8 cm s⁻¹, the behaviour of Ametropus changes. They orient themselves facing into the flow, and clear a shallow pit immediately in front of their head, and extend their prothoracic legs above them into the flow (Figure 1-6). They sweep their prothoracic legs towards their mouthparts every few seconds, with the rate of 'sweeping' increasing with velocity. Soluk and Craig (1988) found that modified microtrichia found on the forelegs were capturing food particles from the water column. The microtrichia function as an aerosol (or "hydrosol") filter (Braimah 1987), rather than a sieve (LaBarbera 1984), in that particles impact or collide with filter elements due to fluid dynamic forces. Aerosol filters capture particles much smaller than the spacing between filter elements (LaBarbera 1984). The minimal surface area required for aerosol capture presumably confers on Ametropus the same benefits it provides for other suspension-feeding aquatic fauna such as black fly (Diptera: Simuliidae) larvae (Chance and Craig 1986) - relatively low pressure drag. This reduction in drag is especially important for Ametropus, as the sand dune-like habitats inhabited by this species do not provide a source of firm attachment. In addition, Soluk and Craig (1988) found that the forelegs, which are presumably held in the upper levels of the boundary layer, direct relatively rapidly moving water downward in to the pit. In conjunction with the head and antennae, this creates a stable, horizontally rotating solenoidal vortex. The increased velocities of the redirected flow entrain food particles, while the vortex serves to keep the particles suspended and passes them over the collecting apparatus (hairy coxal plates, labrum, and mouthparts) multiple times. The authors suggest that the pit may also act as depositional trap, because shear stresses in pits are typically lower than those of surrounding sediments (Nowell and Jumars 1984).

Another group of suspension feeders that manipulate vortices to enhance feeding efficiency are the larvae of the dipteran family Simuliidae (the blackflies). The various species of the genus *Simulium* enjoy a nearly cosmopolitan distribution, and are found in the running waters of streams from the arctic to the tropics (Craig 1977; Merritt et al. 1996). Due to the medical importance and pestiferous nature of simuliid adults, the feeding and positioning behaviour of the larvae have been studied extensively (Craig and Chance 1982; Chance and Craig 1986; Hart et al. 1991; Lacoursière 1992; Merritt et al. 1996), leading to some success in controlling populations using particulate, ingestible insecticides. As suspension feeders, simuliid larvae are elegantly adapted to moving water, manipulating local flow to create specialised patterns of vortices that gather food and bring it to the mouth, remove wastes, and facilitate respiration.

Chance and Craig (1986) present one of the most detailed studies on the interaction between the behaviour and hydrodynamics of black fly larvae. Larvae orient themselves with their posterolateral surface upstream, and twist their bodies 90 - 180°. This longitudinal twisting of the body results in one labral fan being closer to the substratum, while the other is held up into the upper boundary layer (Chance and Craig 1986). The rotation also results in the adoral (concave) surface of the labral fans being exposed to the flow. With few exceptions (Craig 1977), simuliid larvae capture food from water using these modified labral fans, whose microtrichial structure is modified to present a nearly hydrodynamically ideal structure to the flow, resulting in minimal drag. The body is deflected from vertical by the flow, with angle of deflection increasing with velocity. The angle of deflection was once thought to be passive, regulated by drag acting on the body of the insect (Maitland and Penny 1967; Chance and Craig 1986). Lacoursière (1992), however, found that posture is in part behaviourally determined. The feeding stance is an outcome of feedback between flow forces and behaviour that acts to maintain the labral fans in an optimal feeding position. When disturbed, black fly larvae exhibit a characteristic "avoidance reaction"; they cease feeding and pull down closer to the substrate into the decreased velocities of the lower boundary layer.

The adaptive significance of the positioning of the labral fans is only fully realised when it is placed in context of the flow patterns generated by the unique morphology of this insect (Figure 1-7). In addition to the longitudinal twisting of the body, black fly larvae 'yaw' their bodies across the mean flow up to 20°. This posture has a peculiar influence on the vortices generated by the modified cylindrical form of these larvae. Flow approaching near the substratum slows as it reaches the stagnation point at the front of the body, then accelerates (by a factor of 1.6 to 1.7) as the flow separates and passes on either side of the body just outside the 'horseshoe' vortex (Chance and Craig 1986). If the body approximated a symmetrical, but tilted, cylinder, the paired vortices generated would rise up the downstream side of the body, and detach at the top in a classic von Karman trail (Vogel 1994). However, due to the fact that the body is positioned across the flow as well as being twisted, only one of the paired vortices rises up the body while the other simply slips to the side and is carried, rotating, downstream. The upper vortex, which has greater angular velocity than the lower vortex due to the greater distance it must travel around the larval body, resuspends fine particulate organic matter that has been deposited on the substrate. This vortex then rises up the downstream side of the larval form, passing through the lower labral fan. As mean current velocities

increase, the angle of deflection of the larval body increases, resulting in the larvae lying closer and more parallel to the substrate. Although the cross-sectional area of the vortex discharging into the lower labral fan decreases, overall discharge changes very little due to increased velocities and a thinner boundary layer (Vogel 1994).

While the lower labral fan filters water only from the attached, rising vortex, the upper labral fan captures food particles from an entirely different volume of water. The upper labral fan is held up into the upper levels of the boundary layer, where it is exposed to velocities higher than that of the body and lower labral fan. As velocities increase and angle of bodily deflection increases, the labral fan is exposed to higher velocities, but is maintained at approximately the same position in the boundary layer (Lacoursière 1992). The filtering efficiency of the labral fans is reduced as velocity decreases. Larval blackflies decrease the aperture opening between the rays of the labral fan as velocities decrease. At low velocities, Reynolds numbers are sufficiently low that a 'viscous zone' (viscous effects predominating at low Reynolds numbers at the scale of individual filter elements; see Braimah 1987) occupies most of the apertural space surrounding the rays and microtrichia. Lacoursière and Craig (1993) estimated that 97% of the apertural space was occupied by this 'viscous zone' at velocities of 3.6 cm s⁻¹. However, as Reynolds numbers increase, less of the apertural space is occupied by these viscous effects (28% at 40 cm s⁻¹; Lacoursière and Craig 1993).

Directions for future research

The behavioural and morphological adaptations of benthic invertebrates to the unidirectional flow of stream environments are diverse. Yet, due to the cosmopolitan nature of stream hydrodynamics in lotic systems worldwide, stream ecologists can enjoy an unparalleled discourse on the complex interactions between physics and biology in rivers and streams. The challenge that lies before behavioural and physical ecologists is twofold. First, data relating the biology of stream taxa to hydraulics must be collected and analysed in a manner appropriate to the question asked. Too often, authors seem content with a level of discussion that approximates 'this species seems to prefer *medium* velocities'. If a more complete understanding of the role that moving water plays in stream ecosystems is ever to be achieved, stream ecologists must become more comfortable with the concepts of shear, eddy production, and boundary layers (among others). Second, the nature of the flow that is actually experienced by animals on the substrate must be more thoroughly examined. The

validity of studies of large-scale processes and patterns will continue to be limited unless we understand the nature of flow in natural systems at organism-defined scales.

-4

Table 1-1. Selected examples of behavioural and morphological

adaptations of stream invertebrates to hydrodynamics

Category	Taxon / Adaptation (reference)	Inferred functional advantage
Morphology / flow interactions	1. Larvae of the caddisfly Sericostoma selysi from high velocity areas had heavier, narrower cases than those larvae from lower velocities (Delgado and Carbonell 1997).	 Larvae in high velocities are more easily able to resist drag, reducing the risk of becoming detached from the bed.
	2. Water penny larvae (<i>Sclerocyphon</i> ; Coleoptera: Psephenidae) were highly streamlined, and controlled the boundary layer over their bodies by suction through the lateral laminae (Smith and Dartnall 1980).	2. Streamlining and boundary layer suction allow larvae to maintain their position and move over the substrate in high velocity, highly turbulent flows.
	3. Flow lines were compressed over the front of the <i>Ecdyonurus cf. venosus</i> , and boundary layer separation occurred over the bodies of <i>E. venosus</i> and <i>Ancylus fluviatilus</i> (Gastropoda) (Statzner and Holm 1982).	3. Lift is concentrated over the thorax of <i>E.</i> venosus (where the legs are in contact with the substrate), and boundary layer separation over both taxa suggests that the boundary layer may not be thick enough to provide substantial protection from high near-bed velocities.
	4. Steepest velocity gradients were found close to the bodies of several benthic taxa (Gastropods Ancylus, Acroloxus, and Potamopyrgus, the amphipod Gammarus, the larval caddisflies Anabolia, Micrasema, and Silo), where parts of their bodies protruded furthest into the flow (Statzner and Holm 1989).	4. Simultaneous morphological adaptations to the forces of lift, pressure and friction drag, erosion, diffusion are impossible; adaptations will be a reflection of the organisms size and Reynolds number, and will change as the organism grows.
	5. The mayfly <i>Ecdyonurus</i> tilted its head shield, and had femurs shaped like 'spoilers', while the mayfly <i>Epeorus</i> resisted lift by anchoring itself to the substrate. The drag forces experienced by the invertebrates were proportional to the square of the velocity (Weissenberger et al. 1991).	5. The morphological adaptations of <i>Ecdyonurus</i> produce 'negative' lift, and press its body against the substrate in high-velocity flows. <i>Epeorus</i> experiences high lift due to its 'airfoil' shape, but counters this by attaching itself firmly to the substrate.
Micropositioning	1. Abundances of suspension-feeding black fly (<i>Simulium vittatum</i>) larvae were significantly related to velocity measured 2 mm above the bed. Maximum near-bed acclerations exceeded 1 x 10 ⁴ cm s ⁻² (Hart et al. 1996).	1. Particle interception rates are a function of near-bed velocities and turbulence intensities; <i>S. vittatum</i> larvae position themselves in locales that maximise rates of particle delivery. Forces due to acceleration reaction may be greater than the forces imposed by pressure drag on these suspension-feeding larvae.
	2. Simulium vittatum larvae gathered in boundary layer separation zones, and avoided areas of maximal shear stress (Lacoursière 1992).	2. Larvae can detect (and migrate to) areas of the bed with velocity profiles that will maximise particle flux through their labral fans while minimising drag on the bulbous posterior portion of their abdomen.
	3. The suspension-feeding caddisflies <i>Arctopsyche grandis</i> and <i>Brachycentrus</i> <i>occidentalis</i> preferred the bottoms and lower lateral sides of rocks rather than the upper, current-exposed, surfaces (Voelz and Ward 1996).	3. The microdistributions of <i>A. grandis</i> and <i>B. occidentalis</i> may minimise predation and the risk of accidental detachment while allowing for 'acceptable' rates of particle capture and respiration.
	4. The suspension-feeding caddisfly <i>Brachycentrus occidentalis</i> preferred microhabitats with higher velocities, shallower depths, higher water surface slopes, and higher Froude numbers (Wetmore et al. 1990).	4. Larvae may choose sites with accelerating flow to maximise particle- capture rates; however, as <i>B. occidentalis</i> larvae must extend their legs into the flow to suspension-feed, velocities must not be so high that food particles are washed away before they can be transferred to the mouth.

Habitat selection	1. The macroinvertebrate communities associated with the front (solenoidal vortex) and downstream (wake) regions of stream boulders were distinctly different (Bouckaert and Davis 1998).	1. Benthic fauna associated with different microflow regions around stream boulders may not be responding to water velocity, but rather to other hydrodynamic factors (<i>i.e.</i> turbulence intensity) and/or factors related to hydrodynamics that are directly linked to the ecology of benthic organisms (<i>i.e.</i> denosition of particulate organic
	2. Invertebrate abundance was positively correlated with roughness and negatively correlated with slope. Associations of taxa with similar adaptations to flow to specific velocities, Reynolds numbers, roughness Reynolds number, and shear velocity were noted (Growns and Davis 1994).	 (i.e. deposition of particulate organic matter, exchange of dissolved gases). 2. Invertebrate taxa with similar morphological or behavioural adaptations to flow can be classified as belonging to one of three 'flow exposure groups': obligates (found in turbulent, high shear habitats), <i>facultatives</i> (found in habitats with greater bed roughness), and <i>avoiders</i> (found in high velocity habitats where fluxes of dissolved oxygen and organic matter may be maximised).
	3. Densities of the mayflies <i>Rhithrogena</i> and <i>Baetis</i> were greatest at depths of 1.5 m before flooding, but shifted to depths of 0.5 m and 0.2 m during periods of high discharge. Densities of the suspension-feeding caddisfly <i>Hydropsyche</i> were greatest at 1.5 m during all months; however, the location of the 1.5 m depth shifted laterally during floods (Rempel et al. 1999).	3. Many invertebrate taxa move from deeper water to shallower water during floods, possibly using the shore zone as a flow refugium during flood events.
	4. Distinct microcrustacean assemblages were associated with areas of the streambed that retained low shear stress during periods of high discharge (Robertson et al. 1997).	 Areas of low shear stress ('refugia') may enable the survival of epbenthic microcrustacea during periods of high discharge.
	5. A relationship was found between the microdistribution of several stream taxa and various descriptors of the near-bed flow environment (including the estimated thickness of the laminar sublayer) (Statzner 1981).	5. The distribution of various taxa reflects their degree of rheophily and dependence on high-velocity microhabitats. Many macroinvertebrates (<i>e.g.</i> suspension- feeders) prefer habitats with specific hydraulic charactenistics (<i>e.g.</i> certain ranges of turbulence, viscous sublayer thicknesses, etc.)
Ontogenetic shifts in habitat selection	1. Larger nymphs of the rheophilous mayflies <i>Rhithrogena semicolorata</i> and <i>Ecdyonurus gr.</i> <i>venosus</i> preferred rougher substrata (Buffagni et al. 1995).	1. As nymphs increase in size, their hydraulic preferences (<i>i.e.</i> for specific velocities or turbulence intensities) change; larger nymphs may be able to move and graze successfully in high-velocity habitats where smaller nymphs would be swept from the bed.
	2. Larger net-spinning hydropsychid caddisfly larvae were found at higher velocities than smaller, less mature larvae. However, net mesh size did not increase with velocity among species (Osborne and Herricks 1987).	2. Body size, rather than net mesh size, limits the distribution of net-spinning caddisflies.

Suspension feeding	1. The body of <i>Simulium vittatum</i> produced downstream, paired vortices; one of the vortices rose up the downstream side of the body, and passed through the lower of the two labral fans. The second, higher labral fan filtered water from the upper boundary layer. Larvae positioned side-by-side mutually enhanced flow between them (Chance and Crain 1986)	1. The downstream vortex created by the body of <i>S. vittatum</i> enhances feeding (by entraining particles from the substrate). The upper labral fan captures entrained particles convected from upstream. The morphology of these larvae also minimise drag while maximising particle-capture rates
	 The feeding stance of Simulium vittatum was found to be the result of feedback between the behaviour of the larvae and drag forces. The aperture size of the labral fans (filtering elements) increased with increases in velocity (Lacoursière and Craig 1993). 	 The interaction between behaviour and morphology maximises the particle-capture efficiency of the larvae (4 – 26 times more efficient than previously thought).
	3. The mayfly Ametropus neavi suspension-fed using modified foreleg trichia, and by inducing a horizontally-rotating solenoidal vortex within a specially constructed pit (Soluk and Craig 1988).	3. The vortex enhances the delivery of seston to the particle-capture elements, and allows larvae to inhabit the noncohesive beds of sand-bottom rivers.
	4. The larvae of four species of net-spinning hydropsychid caddisflies (<i>Hydropsyche betteni</i> , <i>H. sparna</i> , <i>H. cheilonis</i> , and <i>H. bronta</i>) were found primarily in areas with rapidly spiralling vortices (Osborne and Herricks 1987).	4. Particle-capture rates of net-spinning caddisflies are dependent on flow patterns, not just velocity. Larvae preferred faster, turbulent flows to slower, more laminar flows. Turbulence (especially spiralling flows) may entrain particles or increase the flux of particles through the net of hydropsychid caddisflies.
Predator avoidance	1. Black fly larvae abundance (Simulium vittatum) was negatively related to flatworm abundance (Dugesia dorotocephala, a predator) and positively related to velocity (Hart and Merz 1998).	1. S. vittatum larvae prefer faster velocities not only to maximise rates of suspension feeding, but also to minimise the risk of predation by predators that are not adapted to high velocity habitats.
	2. Densities of prey (<i>Baetis rhodani</i> and Chironomidae) were reduced by the stonefly predator <i>Dinocras cephalotes</i> only in hydraulic regimes favourable to the predator (Peckarsky et al. 1990).	2. Stream prey species can minimise the threat of predation by moving into areas of the streambed with abiotic regimes unfavourable to predators (hydraulic refugia).
Predation	1. Predation by the caddisfly predator Rhyacophila obliterata on larval blackflies (Simulium sublacustre) was greatest in areas of greatest microhabitat overlap (where velocities ranged from 40 – 60 cm s ⁻¹) (Muotka and Penttinen 1994).	1. Prey acquisition rates will be greatest if predators are able to successfully access the hydraulic habitats inhabited by prey species.
	2. The stonefly predator <i>Kogotus modestus</i> used the pressure wave patterns produced by escaping mayfly prey to distinguish between non-preferred (<i>Ephemerella infrequens</i>) and preferred (<i>Baetis bicaudatus</i>) prey species (Peckarsky and Wilcox 1989).	 Use of hydrodynamic cues allows K. modestus to selectively predate on preferred prey.
	3. Larvae of the mayfly <i>Pseudiron centralis</i> arched their bodies and lowered their heads to create a solenoidal vortex, which eroded a pit in front of their bodies (Soluk and Craig 1990).	3. The solenoidal vortex erodes chironomid prey from the sandy sediments that <i>P. centralis</i> larvae inhabit; the mayfly larvae seize any prey exposed in the eroded pit.
Movement (swimming)	1. The mayfly <i>Cloeon dipterum</i> was found to have a highly streamlined shape, and small, but projecting, gills (Craig 1990).	1. The streamlined shaped of <i>C. dipterum</i> confers no advantage during swimming (due to relatively low Re), but becomes important during 'acclerative escape motions', as a streamlined shape gives a low coefficient of added mass.

1. Flow variation did not influence the respiration rates of the mayfly *Cinygmula grandifola*, but at lower velocities the respiration rates of the stoneflies *Stenopsyche marmorata* and *Skwala pusilla* were compromised (Golubkhov et al. 1992).

2. The pupa and gills of Blepharicerid larvae acted as 'bluff bodies', and paired vortices (and associated regions of low pressure) formed downstream of the gills (Pommen and Craig 1995).

 At low dissolved oxygen levels, mayflies moved into positions on the substrate that were more exposed to the current (Wiley and Kohler 1980). 1. The stonefly taxa generally inhabit highvelocity microhabitats, and as such, are unable to respire efficiently unless gas exchange is enhanced by water flowing over their gills. *C. grandifola*, generally found in interstitial spaces or low-flow areas of the streambed, is not dependent on flowing water to maintain respiration rates.

2. By generating vortices, the pupal gills of Blepharicerid larvae enhance gas exchange rates (due to the reduced solubility of air in low-pressure areas).

3. Stream mayflies are able to behaviourally compensate for low oxygen levels by moving into high velocity microhabitats; presumably, respiration in these locations is enhanced by thinning boundary layers over their gills, and subsequently increasing rates of diffusion of dissolved gases.

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References

- Abelson, A. 1997. Settlement in flow: upstream exploration of substrata by weakly swimming larvae. Ecology 78: 160-166.
- Ackerman, J.D., L. Wong, C. R. Ethier, D.G. Allen, and J.K. Spelt. 1994. Preston-static tubes for the measurement of wall shear stress. J. Fluids Eng. 116: 645-649.
- Ackerman, J.D., and T.M. Hoover. 2001. Measurement of local bed shear stress in streams using a Preston-static tube. Limnol. Oceanogr. 46: 2080-2087.
- Allan, J.D., A.S. Flecker, and N.L. McClintock. 1986. Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioural drift. Limnol. Oceanogr. 31: 1057-1065.
- Ambuhl, H. 1959. Die Bedeutung der stromung als okologischer faktor. Schweizerische Zeitschrift fur Hydrologie 21: 133-264.
- Bergeron, N.E., and A.D. Abrahams. 1992. Estimating shear velocity and roughness length from velocity profiles. Water Resour. Res. 28: 2155-2158.
- Bouckaert, F.W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biol. 40: 77-86.
- Braimah, S.A. 1987. The influence of water velocity on particle capture by the labral fans of larvae of Simulium vittatum (Diptera: Simuliidae). Can. J. Zool. 65: 2359-2399.
- Buffagni, A., G. Crosa, and R. Marchetti. 1995. Size related shifts in the physical habitat of two mayfly species (Ephemeroptera). Freshwater Biol. 34: 297-302.
- Carling, P. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biol. 28: 273-284.
- Chance, M.M., and D.A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64:1295-1309.
- Clifford, H. F., and D. R. Barton. 1979. Observations on the biology of *Ametropus neavei* (Ephemeroptera: Ametropododae) from a large river in northern Alberta, Canada. Can. Entomol. 111: 855-858.
- Collier, K. 1994. Influence of nymphal size, sex and morphotype on microdistribution of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in a New Zealand river. Freshwater Biol. 31: 35-42.
- Collier, K.J., G.F. Croker, C.W. Hickey, J.M. Quinn, and B.S. Smith. 1995. Effects of hydraulic conditions and larval size on the microdistribution of Hydrobiosidae (Trichoptera) in two New Zealand rivers. New Zea. J. Mar. Fresh. Res. 29(4): 439-451.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.
- Craig, D.A. 1977. Mouthparts and feeding behaviour of Tahitian larval Simuliidae (Diptera: Nematocera). Quaest. Entomol. 13: 195-281.
- Craig, D.A. 1990. Behavioural hydrodynamics of *Cloeon dipterum* larvae (Ephemeroptera: Baetidae). J. N. Am. Benthol. Soc. 9: 346-357.
- Craig, D.A. 1993. Hydrodynamic considerations in artificial stream research. J. N. Am. Benthol. Soc. 12: 324-328.

- Craig, D.A. 1996. Some of what you should know about water, or K.I.S.S. for hydrodynamics ('Keeping It Stupidly Simple). http://www.inhs.uiuc.edu./nabs/resrc/kiss.htm (reprinted from Bull. N. Am. Benth. Soc. 35: 178-182).
- Craig, D.A., and M.M. Chance. 1982. Filter feeding in larvae of Simuliidae (Diptera: Culicomorpha): aspects of functional morphology and hydrodynamics. Can. J. Zool. 60: 712-724.
- Davis, J.A. 1986. Boundary layers, flow microenvironments, and stream benthos. *in* Limnology in Australia, eds. P. De Deckker and W.D. Williams, Dr W. Junk Publishers, East Melbourne, Australia.
- Davis, J.A., and L.A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biol. 21: 271-282.
- Delgado, J.A., and R. Carbonell. 1997. Case features of caddisfly larvae (Sericostoma selysi) as related to water velocity and potential to drift. J. Freshwater Ecol. 12: 193-197.
- Forrester, G.E. 1994. Diel patterns of drift by five species of mayfly at different levels of fish predation. Can. J. Fish. and Aquat. Sci. 51: 2549-2557.
- Fuller, R.L., and R.J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can J. Zool. 58: 2239-2251.
- Golubkhov, S.M., T.M. Tiunova, and S.L. Kocharina. 1992. Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. Aquatic Insects 14: 137-144.
- Gore, J.A. 1978. A technique for predicting in-stream flow requirements of benthic macroinvertebrates. Freshwater Biol. 8: 141-151.
- Growns, I.O., and J.A. Davis. 1994. Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. J. N. Am. Benthol. Soc. 13: 417-438.
- Hansen, R.A., D.D. Hart, and R.A. Merz. 1991. Flow mediates predator-prey interactions between triclad flatworms and larval black flies. Oikos 60: 187-196.
- Hart, D.D., and C.M. Finelli. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Ann. Rev. Ecol. Syst. 30: 363-395.
- Hart, D.D., and R.A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow mediated refuges. Oecologia 114: 263-273.
- Hart, D.D., R.A. Merz, S.J. Genovese, and B.D. Clarke. 1991. Feeding posture of suspensionfeeding larval black flies: the conflicting demands of drag and food acquisition. Oecologia (Berlin) 85: 457-463.
- Hart, D.D., B.D. Clark, and A. Jasentuliyana. 1996. Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.
- Hildrew, A.G., and C.R. Townsend. 1982. Predators and prey in a patchy environment: a freshwater study. J. Anim. Ecol. 51: 797-815.
- Holomuzki, J.R., and S.H. Messier. 1993. Habitat selection by the stream mayfly *Paraleptophlebia guttata*. J. N. Am. Benthol. Soc. 12: 126-135.
- Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.
- Jowett, I.G., J. Richardson, B.J.F. Biggs, C.W. Hickey, and J.M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalized *Deleatidium* spp.

habitat suitability curves, applied to four New Zealand Rivers. New Zea. J. Mar. Fresh. Res. 25: 187-200.

- LaBarbera, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. Am. Zool. 24: 71-84.
- Lacoursière, J.O. 1992. A laboratory study of fluid flow and microhabitat selection by larvae of Simulium vittatum (Diptera: Simuliidae). Can. J. Zool. 70: 582-596.
- Lacoursière, J.O., and D.A. Craig. 1990. A small flume for studying the influence of hydrodynamic factors on benthic invertebrate behaviour. J. N. Am. Benthol. Soc. 9: 358-367.
- Lacoursière, J.O., and D.A. Craig. 1993. Fluid transmission and filtration efficiency of the labral fans of black fly larvae (Diptera: Simuliidae): hydrodynamic, morphological, and behavioural aspects. Can. J. Zool. 71: 148-162.
- Lancaster, J. 1996. Scaling the effects of predation and disturbance in a patchy environment. Oecologia 107(3): 321-331.
- Lancaster, J., A.G. Hildrew, and C.R. Townsend. 1990. Stream flow and predation effects on the spatial dynamics of benthic invertebrates. Hydrobiologia 31: 337-349.
- Lancaster, J., and A.G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. J. N. Am. Benth. Soc. 12: 385-393.
- Lancaster, J., A.G. Hildrew, and C. Gjerlov. 1996. Invertebrate drift and longitudinal transport processes in streams. Can. J. Fish. Aquat. Sci. 53: 572-582.
- Lancaster, J., and A. L. Robertson. 1995. Microcrustacean prey and macroinvertebrate predators in a stream food web. Freshwater Biol. 34: 123-134.
- Maitland, P. S., and Penny, M. M. 1967. The ecology of the Simuliidae in a Scottish River. J. Anim. Ecol. 36: 179-206.
- Malmqvist, B., and G. Englund. 1996. Effects of hydropower-induced flow perturbations on mayfly (Ephemeroptera) richness and abundance in north Swedish river rapids. Hydrobiologia 341: 145-158.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecol. Monogr. 46: 355-369.
- Merritt, R. W. 1987. Do different instars of *Aedes triseriatus* feed on particles of the same size? J. Am. Mosq. Control Assoc. 3: 94-96.
- Merritt, R.W., D.A. Craig, R.S. Wotton, and E.D. Walker. 1996. Feeding behaviour of aquatic insects: case studies on black fly and mosquito larvae. Invert. Biol. 115: 206-217.
- Muotka, T., and A. Penttinen. 1994. Detecting small-scale spatial patterns in lotic predator-prey relationships: statistical methods and a case study. Can. J. Fish. Aquat. Sci. 51: 2210-2218.
- Nowell, A.R.M., and M. Church. 1979. Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. 84: 4816-4824.
- Nowell, A.R.M., and P.A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303-328.
- Osborne, I.L., and E.E. Herricks. 1987. Microhabitat characteristics of *Hydropsyche* (Trichoptera: Hydropsychidae) and the importance of body size. J. N. Am. Benthol. Soc. 6: 115-124.

- Palmer T.M. 1995. The influence of spatial heterogeneity on the behaviour and growth of two herbiverous stream insects. Oecologia 104: 476-486.
- Peckarsky, B.L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology 77: 1888-1905.
- Peckarsky, B.L., and M.A. Penton. 1988. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology 70: 1203-1218.
- Peckarsky, B.L., and R.S. Wilcox. 1989. Stonefly nymphs use hydrodynamic cues to discriminate between prey. Oecologia 79: 265-270.
- Peckarsky, B.L., S.C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. Freshwater Biol. 24: 181-191.
- Peckarsky, B.L., and C.A. Cowan. 1995. Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos 74(3): 513-521.
- Poff, N.L., and J.V. Ward. 1991. Drift responses of benthic macroinvertebrates to experimental streamflow variation in a hydrologically stable stream. Can. J. Fish. Aquat. Sci. 48: 1926-1936.
- Poff, N.L., N.J. Voelz, J.V. Ward, and R.E. Lee. 1990. Algal colonization under four experimentallycontrolled current regimes in a high mountain stream. J. N. Am. Benthol. Soc. 9: 303-318.
- Pommen, G.D.W., and D.A. Craig. 1995. Flow patterns around gills of pupal net-winged midges (Diptera: Blephariceridae): possible implications for respiration. Can. J. Zool. 73: 373-382.
- Prantl, L. 1952. Essentials of Fluid Dynamics. Hafner, New York, NY.
- Preston, J.H. 1954. The determination of turbulent skin friction by means of Pitot tubes. J. Royal Aeronaut. Soc. 58: 109-121.
- Quinn, J.M., and C.W. Hickey. 1994. Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. Freshwater Biol. 32: 489-500.
- Quinn, J.M., C.W. Hickey, and W. Linklater. 1996. Hydraulic influences on periphyton and benthic macroinvertebrates: simulating the effects of upstream bed roughness. Freshwater Biol. 35: 301-309.
- Rader, R.B., and J. V. McArthur. 1995. The relative importance of refugia in determining the drift and habitat selection of predaceous stoneflies in a sandy bottomed stream. Oecologia, 103: 1-9.
- Rempel, L.L., J.S. Richardson, and M.C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. J. N. Am. Benthol. Soc. 18: 34-48.
- Resh, V. H., and D. M. Rosenberg. 1984. The Ecology of Aquatic Insects. New York: Praeger Publishers.
- Resh, V. H., and D. M. Rosenberg. 1989. Spatial-temporal variability and the study of aquatic insects. Can. Ent. 121: 941-963.
- Richardson, W. B. 1992. Microcrustacea in flowing water: experimental analysis of washout times and a field test. Freshwater Biol. 28: 217-230.
- Robert, A., A.G. Roy, and B. De Serres. 1996. Turbulence at a roughness transition in a depth limited flow over a gravel bed. Geomorphology 16: 175-187.

- Robertson, A.L., J. Lancaster, L.R. Belyea, and A.G. Hildrew. 1997. Hydraulic habitat and the assemblage structure of stream benthic microcrustacea. J. N. Am. Benthol. Soc. 16: 562-575.
- Sagar, P.M., and G.J. Glova. 1992. Diel changes in the abundance and size composition of invertebrate drift in five rivers in South Island, New Zealand. N. Zea. J. Mar. Freshwater Res. 26:103-114.
- Shiozawa, D.K. 1991. Microcrustacea from the benthos of nine Minnesota streams. J. N. Am. Benthol. Soc. 10: 286-299.
- Sih, A., and D.E. Wooster. 1994. Prey behaviour, prey dispersal, and predator impacts on stream prey. Ecology 75:1199-1207.
- Smith, J.A., and A.J. Dartnall. 1980. Boundary layer control by water pennies (Coleoptera: Psephenidae). Aquat. Insects 2: 65-72.
- Soluk, D.A., and D.A. Craig. 1988. Vortex feeding from pits in the sand: a unique method of suspension feeding used by a stream invertebrate. Limnol. Oceanogr. 33: 638-645.
- Soluk, D.A., and D.A. Craig. 1990. Digging with a vortex: flow manipulation facilitates prey capture by a predatory stream mayfly. Limnol. Oceanogr. 35: 1201-1206.
- Statzner, B. 1981. The relationship between "hydraulic stress" and microdistribution of benthic macroinvertebrates in a lowland running water system, the Schierenseebrooks (North Germany). Arch. Hydrobiol. 91: 192-218.
- Statzner, B., U. Fuchs, and L.W. Higler. 1996. Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology. Water Resour. Res. 32: 2279-2287.
- Statzner, B., J.A. Gore, and V.H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. J. N. Am. Benthol. Soc. 7: 307-360.
- Statzner, B., and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16: 127-139.
- Statzner, B., and T.F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow: an old question studied by means of a new technique (Laser Doppler Anemometry). Oecologia 53: 290-292.
- Statzner, B., and T.F. Holm. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. Oecologia 78: 145-157.
- Statzner, B., and R. Muller. 1989. Standard hemispheres as indicators of flow characteristics in lotic benthos research. Freshwater Biol. 21: 445-459.
- Stewart, K.W., and P.P Harper. 1996. Plecoptera. *in* An Introduction to the Aquatic Insects of North America. *Eds.* R.W. Merritt and K.W. Cummins. Kendal/Hunt Publishing Co., Dubuque, IA.
- Tikkanen, P., T. Muotka, A. Huhta, and A. Juntunen. 1997. The roles of active predator choice and prey vulnerability in determining the diet of predatory stonefly (Plecoptera) nymphs. J. Anim. Ecol. 66: 36-48.
- Townsend, C. R., and A. G. Hildrew. 1979. Form and function of the prey catching net of *Plectrocnemia conspersa* larvae (Trichoptera). Oikos 33:412-418.
- Townsend, C.R., M.R. Scarsbrook and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnol. Oceanogr. 42: 938-949.

Voelz, N.J., and J.V. Ward. 1996. Microdistributions of filter-feeding caddisflies (Insecta: Trichoptera) in a regulated Rocky Mountain river. Can. J. Zool. 74: 654-666.

Vogel, S. 1994. Life in moving fluids. Princeton, NJ.: Princeton University Press.

- Wallace, J.B., and R.W. Merritt. 1980. Filter feeding ecology of aquatic insects. Ann. Rev. Entomol. 25: 103-132.
- Walsh, G., R. Morins, and R.R. Naimans. 1988. Daily rations, diel feeding activity and distribution of age-0 brook trout, *Salvelinus fontinalis*, in two subarctic streams. Environ. Biol. Fishes 21: 195-205.
- Weissenberger, J., H.-Ch. Spatz, A. Emanns, and J. Schwoerbel. 1991. Measurement of lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m·s⁻¹. Freshwater Biol. 25: 21-31.
- Wetmore, S.H., R.J. Mackay, and R.W. Newbury. 1990. Characterization of the hydraulic habitat of Brachycentrus occidentalis, a filter-feeding caddisfly. J. N. Am. Benth. Soc. 9: 157-169.
- White, F.M. 1999. Fluid Mechanics 4th Edition. WCB McGraw-Hill, Boston.
- Wiley, M.J., and S.L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Can. J. Zool. 58: 618-622.
- Wiley, M., and S.L. Kohler. 1984. Behavioural adaptations of aquatic insects. *in* The Ecology of Aquatic Insects. *Eds.* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York.
- Winterbottom, J.H., S.E. Orton, and A.G. Hildrew. 1997. Field experiments on the mobility of benthic invertebrates in a southern English stream. Freshwater Biol. 38: 37-47.
- Wooster, D., and A. Sih. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos 73: 3-8.
- Young, W.J. 1992. Clarification of the criteria to identify near-bed flow regimes. Freshwater Biol. 28: 383-391.
- Young, W.J. 1993. Field techniques for the classification of near-bed flow regimes. Freshwater Biol. 29: 377-383.



Figure 1-1. Reynolds number conditions for the occurrence of turbulent flows in open channels (see text for description of flow conditions in each case).



Α.



Β.

Figure 1-2. (A) Representation of the boundary layer in shallow water. The flow conditions of the bed layer may be turbulent or laminar, depending on hydraulic conditions. (B) The logarithmic boundary layer plotted on log-normal axes. The shear velocity (U*) is inversely proportional to the slope of the profile. The characteristic roughness length (z_0) can be estimated as the x-intercept of the regression line. U* and z_0 can be estimated from the profile only if the profile is log-normal (modified from Carling 1992).



Figure 1-3. Diagram of the forces acting on a particle within a velocity gradient (velocity gradient shown as vectors on the left side of the diagram). The force due to lift (F_1) acts to 'pull' the particle upwards, the force due to drag (F_d ; integrated pressure drag and skin friction) acts to 'pull' the particle downstream, while shear stress (τ_w) acts to 'roll' the particle in the downstream direction. The thickness of the boundary layer (the height above the substrate at which velocities reach 90% of mainstream velocities) is denoted as δ . Flow is from left to right.



Figure 1-4. (a) Dorsal and (b) ventral views of a *Sclerocyphon* (Coleoptera: Psephenidae) larvae, showing the streamlined body form and lateral laminae. 1. Operculum covering gills; 2. Slot between lateral laminae. (reproduced from Smith and Dartnall 1980).



Figure 1-5. Diagram of the patterns of flow used by *Pseudiron centralis* (Ephemeroptera: Pseudironidae) to excavate prey from sand beds. This mayfly positions its body to create the necessary conditions for the formation of a solenoidal ("horseshoe") vortex, which it then uses to excavate prey from the sediment (reproduced from Vogel 1994; redrawn from Soluk and Craig 1990).



Figure 1-6. Diagram of feeding posture adopted by larvae of the river mayfly *Ametropus neavi* (Ephemeroptera: Ametropodidae). Arrows indicate the direction of flow (reproduced from Soluk and Craig 1988).



Figure 1-7. Diagram of the flow patterns around the body of the black fly larva (*Simulium vittatum*, Diptera: Simuliidae). The flow in the diagram is from left to right, and the larva is yawing toward the viewer. Length of larva = 6.0 mm (reproduced from Merritt et al. 1996).

Chapter 2

Environmental influences on macroinvertebrate distribution at reach and watershed scales

Summary

- The relationship between within-watershed and within-stream distributions of benthic invertebrates was investigated in the tributaries of the lower Torpy River watershed in east-central British Columbia.
- 2. The relationship between invertebrate community structure and several environmental variables was analysed using canonical correspondence analysis (CCA), a direct ordination technique. Aquatic macroinvertebrates were primarily distributed along a physical gradient (related to streambed substrate composition and discharge) and secondarily along a hydrochemical gradient (related to conductivity and dissolved oxygen).
- The CCA ordination divided the sampled invertebrates into four functional assemblages. Each assemblage had well-defined habitat requirements (erosional vs. depositional) and trophic relationships (e.g. scraper, collector-gatherer, etc.).
- 4. Based on the results of the CCA, the habitat preferences of the heptageniid mayfly *Epeorus*, a representative torrential invertebrate, were further determined in two high discharge streams in the Torpy watershed.
- 5. Densities of late instar *Epeorus* larvae were significantly and negatively correlated to velocity (U), depth (D), channel Reynolds number (Re), and relative roughness (D/k_{ave}). Habitat requirements of this mayfly may be related to food resource (periphyton) availability, predation, ontogenetic shifts (*e.g.* pre-emergence behaviour), and/or physiological requirements.

Introduction

One of the primary objectives of ecology is to understand the ways in which environmental factors influence the distribution of organisms. In streams, the structure of the benthic community and the distribution of organisms are influenced by water temperature (Hawkins et al. 1997), water

chemistry (Plenet et al. 1996; Williams et al. 1997), food resource availability (Hearnden and Pearson 1991; Shannon et al. 1994), bed roughness (Growns and Davis 1994), substrate composition (De March 1976) and an array of biotic interactions (*e.g.* Hart and Merz 1998). Stream hydraulics, however, are generally thought to be the single most important physical factor influencing the structure of benthic invertebrate communities. The forces generated by moving water have substantial effects on the feeding, habitat selection, and inter-specific interactions of benthic fauna (Peckarsky and Wilcox 1989; Wetmore et al. 1990; Quinn et al. 1996). Hydraulic variables related to community structure include discharge and discharge stability (Malmqvist and Englund 1996), mean (Hearnden and Pearson 1991) and near-bed (Growns and Davis 1994) velocity, water surface slope (Danehy et al. 1999), thickness of the viscous sublayer (Statzner and Higler 1986), and turbulence intensity (Bouckaert and Davis 1998).

Several authors have noted that changes in faunal assemblages occur from the headwaters to the mouth of a stream. The river continuum concept (Vannote et al. 1980) attributes such longitudinal gradients in macroinvertebrate diversity to system-wide shifts in metabolic, nutrient, and energetic factors. Subsequently, Statzner and Higler (1986) demonstrated that flow characteristics (i.e. 'stream hydraulics') are the most important factor controlling the zonation of stream invertebrate taxa. Growns and Davis (1994) suggested that the apparently contradictory conclusions of Vannote et al. (1980) and Statzner and Higler (1986) might, in fact, be complementary, as hydrodynamic factors strongly influence numerous components of the stream environment, and, as a result, have pervasive effects on ecological processes in streams. Several studies (e.g. Growns and Davis 1994) have demonstrated that the headwater-to-valley gradient along which macroinvertebrate taxa are distributed is defined by a number of hydraulic and channel factors, including stream width, water surface slope, Froude number, Reynolds number, bed roughness, and shear velocity. Hydrodynamic variables are also related to the distribution of macroinvertebrates between streams and within Danehy et al. (1999) found that macroinvertebrates were distributed along an watersheds. environmental gradient related to stream width and water surface slope, while Robertson et al. (1997) demonstrated that, in addition to hydrochemical variables, near-bed flow characteristics influenced the community structure of benthic microcrustacea in several streams.

Clear patterns in the microhabitat preferences of individual macroinvertebrate taxa have been demonstrated by numerous studies. Stream invertebrates respond to small-scale variations in light

and UV intensity (Donahue and Schindler 1998), predation (Muotka and Pentinnen 1994), substrate roughness (Way et al. 1995), and food availability (Vaughn 1986). Near-bed hydraulic conditions also influence habitat preferences by determining the levels of lift, drag, and shear stress experienced by organisms on the streambed (Statzner and Holm 1989; Weissenberger et al. 1991). Hydraulic forces may also influence benthic organisms indirectly, by mediating levels of predation (Hart and Merz, 1998) and the availability of food resources (*e.g.* periphyton, see Vaughn 1986; Quinn et al. 1996), as well as ecologically important physical factors such as substrate particle size composition and oxygen availability (Golubkov et al. 1992; Carling et al. 1998).

Several studies have demonstrated that simple hydraulic parameters (*e.g.* mean velocity, depth) are correlated with the distribution of individual taxa (*e.g.* Collier 1993). Generally, however, the habitat preferences of stream invertebrates are closely correlated with various combinations of hydrodynamic parameters (*i.e.* Froude number, Reynolds number, etc.) that better define the near-bed flow environment. For example, Collier et al. (1995) found that the distribution of larvae of the hydrobiosid caddisflies *Costachorema* and *Hydrobiosis* were positively related to water velocity, Froude number, boundary layer Reynolds number, and inferred shear velocity. Similarly, Quinn and Hickey (1994) found that of all hydraulic parameters estimated, boundary Reynolds number was most strongly correlated with the distributions of several benthic invertebrate taxa in two New Zealand rivers.

Many stream invertebrates that live in high velocity microhabitats exhibit adaptations to hydraulic stress. Black fly larvae reduce drag by modifying body posture (Lacoursiere 1992), while the mayfly *Ecdyonurus* alters femoral angle in order to counter the typically high lift forces of high-velocity habitats (Weissenberger et al. 1991). Invertebrates that live on the upper surfaces of streambed stones exposed to high water velocities often exhibit morphological adaptations to maintain contact with the substrate. Blepharicerid larvae possess a row of ventral suckers (Vogel 1994), while the abdominal gills of several mayfly species (*e.g. Deleatidium* var. *myzobranchia* (Collier 1994), *Rhithrogena*, and *Epeorus* (Vogel 1994)) are also arranged to form a ventral "sucker-like" disk. Delgado and Carbonell (1997) found that the cases of the caddisfly *Sericostoma selysi* collected in high velocity habitats were heavier and more narrow than those from individuals collected in slower habitats, and interpreted this as an adaptation to counter lift and minimise drag, thus decreasing the probability of accidental entrainment. Studies by Robertson et al. (1995; 1997) and

Rempel et al. (1999) suggest that invertebrates lacking morphological adaptations to high velocities may instead rely on behavioural adaptations, and move into microhabitats characterised by low hydraulic stresses (*i.e.* low shear stress areas of the bed (including interstitial spaces), low velocity reaches, and shore zones).

Many studies have also shown that the habitat preferences of stream invertebrates are related to large-scale environmental gradients such as substrate characteristics, discharge, mean velocity, hydrochemistry, and groundwater inputs (*e.g.* De March 1976, Growns and Davis 1994; Malmqvist and Englund 1996; Williams et al. 1997). As many of these factors are related to geographical or geomorphological features of the watershed, changes to the catchment of a stream are inevitably reflected in the stream itself. For example, forestry activities adjacent to streams are known to increase turbidity, increase inputs of coarse particulate organic matter, change temperature regimes, and alter primary production (Gurtz et al. 1980; Noel et al. 1986; Growns and Davis 1991). The structure of the benthic community changes rapidly in response to logging-induced alterations of the stream environment (Newbold et al. 1980; Wallace and Gurtz 1986), and changes in the benthic invertebrate community structure may persist nearly two decades later (Carlson et al. 1990; Stone and Wallace 1998).

Given these observations, it is surprising that the majority of studies of stream invertebrate habitat preferences have examined the distribution of organisms at a single spatial scale. Distributions of biota and related environmental factors are often quantified at watershed, reach, or even smaller (patch or stone) scales; but rarely is more than one spatial scale considered in the same study. Remarkably, few studies have attempted to examine how the factors that directly influence the microdistributions of stream invertebrates at small scales are linked to the distribution of the same organisms within the stream system or watershed. For example, water velocity has been identified as a factor that influences the distribution of stream invertebrates within watersheds, stream systems, reaches, and on the surface of individual stones (Quinn and Hickey 1994; Hart et al. 1996; Danehy et al. 1999). However, only a few authors have attempted to determine if large-scale, community-level responses to variation in velocity are closely related to the microhabitat preferences of the constituent taxa with respect to velocity (but see various works by B. Statzner and others, including Statzner and Higler (1986) and Statzner and Holm (1989), see also Muotka and Pentinnen (1994)).

The goal of the present study is to examine the community-level and taxa-specific responses of stream macroinvertebrates to hydrochemical, physical, and riparian factors. A two-part experimental design was employed to accomplish this. First, canonical correspondence analysis (CCA) was used to examine community-level responses to a suite of commonly measured environmental factors (*e.g.* dissolved oxygen, temperature, bed composition, etc.) in gravel-, cobble-, and boulder-bed tributaries of a mountain watershed in north-central British Columbia. Second, the fine-scale habitat preferences of torrential mayfly larvae (*Epeorus* spp.) (Ephemeroptera: Heptageniidae) were measured in two high-discharge streams in the study area (the preferred habitat type of *Epeorus* larvae, based on the results of the CCA). *Epeorus* was chosen as a model organism as it shows watershed-wide preferences that can also be examined at within-stream spatial scales. The measurement of the habitat characteristics of this torrential mayfly genus at the two spatial scales (within-watershed and within-stream) allowed for an assessment of the linkages between the environmental factors that produce distributions of torrential fauna at large and small scales.

Methods and Materials

Watershed study area

The Torpy River watershed is located approximately 90 km east of Prince George, in the MacGregor Range of east-central British Columbia. The study area consisted of the southern portion of the watershed, and encompassed the 116 tributaries that flow into the lower section of the Torpy River. This portion of the watershed is bounded on the west by the confluence of the Torpy and West Torpy Rivers (54° 02' 12" N, 121° 25' 51" W), and on the east by the furthest extent of forestry roads which provide access to the region (53° 49' 58", 120° 57' 49" W), near the confluence of the Torpy River with the Fraser River. This portion of the Torpy River valley has been logged continuously since 1963, and rates of disturbance due to forestry activities have increased in the last decade due to salvage harvests of conifer stands killed by western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst) (Lepidoptera: Geometridae).
Watershed-scale sampling

During the late summer and fall of 1996, a biological, geomorphic, and hydrochemical survey was conducted on all permanent (non-ephemeral) tributaries of the Torpy River within the study area. At each stream sampling site, several geomorphic, hydrochemical, and riparian factors were measured, including conductivity, pH, temperature, dissolved oxygen, substrate composition, catchment size, riparian vegetation composition, stream surface slope, discharge, and the presence of logging activity within the catchment. Conductivity and dissolved oxygen (DO) were measured using a multimeter (Corning Checkmate 90; Corning, Acton, Maine), and pH was measured using a Canlab pH meter (model 607; VWR Canlab, Mississauga, Ontario). Temperature was measured using an alcohol thermometer (+/- 0.2°C), and stream surface slope (%) was measured using an inclinometer.

Substrate composition was assessed at each sampling site by visually estimating the areal coverage of various sizes of substrate particles (using methodology modified from Allan (1995)). Substrate size was defined by the diameter of the substrate elements (streambed stones): boulders > 300 mm, cobbles 75 - 300 mm, gravels 4 - 75 mm, fines < 4 mm. The bed of each stream sampling site was categorised as belonging to one of five classes, based on the areal coverage of the predominant particle size class: (1) boulder/cobble substrate (areal coverage by boulders > 30%), (2) cobble/gravel substrate (areal coverage by cobbles > 30%), (3) gravel/fines substrate (areal coverage by gravels > 30%), (4) inorganic/organic fines (areal coverage by fine sediments > 40%), or (5) organic fines/organic debris (areal coverage by organic debris > 40%).

The riparian vegetation adjacent to each stream was classified as being dominated by one of the following plant species assemblages and/or functional plant types; (1) closed coniferous canopy, dominated by white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), and western hemlock (*Tsuga heterophylla*), (2) closed mixed canopy, dominated by conifers in combination with several deciduous species including *Populus* spp., paper birch (*Betula papyrifera*), and alder (*Alnus* spp.), and having shade tolerant species such as devil's club (*Oplopanax horridus*) beneath the canopy, (3) closed deciduous canopy, (4) open canopy, where riparian vegetation was dominated not by tree species but rather by various herbaceous plants including thimbleberry (*Rubus parviflorus*), goat's

beard (*Aruncus diocius*), and various fern species, and (5) wetland areas dominated by grasses and wetland species such as skunk cabbage (*Lysichiton americanum*).

The discharge (Q) of each stream was determined using one of two methods. In larger streams (Q < 0.01 m³ s⁻¹, approximately), velocity was measured at 60% of depth across a relatively uniform stream section at regular intervals. The product of the velocity and area (section width x depth) of each section were summed to estimate discharge (*as per* Danehy et al. 1999). In smaller streams, which flowed under the access road via a culvert rather than a bridge, discharge was estimated by multiplying the cross-sectional area of the flow through the culvert (calculated from culvert diameter and maximum water depth) by the average water velocity (measured at 60% of maximum culvert water depth).

An index of the catchment area size of each stream was obtained by averaging the distances from each stream to the two nearest streams. Between-stream distances were measured perpendicular to the stream, along the forestry access road in the lower Torpy River valley, using the vehicular odometer (the road paralleled the Torpy River). This variable was included in the ordination analyses as the factor AVEDIST (AVErage DISTance) as it is an index of the relative width of the catchment basin of a stream at the sampling point, rather than a true measure of the area of a stream's catchment.

All sampling sites were located upstream of access roads or other disturbances (a minimum of 3 m) in order to minimise the influence of local anthropogenic activities on the biotic and abiotic components of the stream environment.

Watershed-scale macroinvertebrate sampling

Of the 116 streams in the lower Torpy River watershed, 28 streams had beds composed of gravels, cobbles, and/or boulders, and 88 streams had beds composed of fine organic material and/or inorganic silt and clay. Invertebrate samples were collected in streams whose beds were composed of coarse bed material. Of these 28 streams, the substrates of 15 were comprised of gravel or gravel/cobble riffles (riffle habitat), and the substrates of 2 were comprised primarily of boulders (boulder cascade habitat). Three invertebrate samples were obtained in each of these streams (*i.e.* 3 replicate samples in representative riffle or boulder reaches). The remaining 11 streams had reaches of both riffle and boulder cascade habitats. In each of these 11 streams, 6 invertebrate samples were

obtained (*i.e.* 3 replicate samples in riffle habitat, 3 replicate samples in boulder cascade habitat). In total, invertebrates were sampled at 39 benthic sampling sites (*i.e.* 15 riffle streams (one sampling site each) + 2 boulder cascade streams (one sampling site each) + 11 streams with diverse substrates (two sampling sites per stream) = 39 sampling sites). As three invertebrate samples were collected at each site, a total of 117 invertebrate samples were obtained.

A modified Surber sampler (sampling area = 0.090 m^2 , modified by the addition of a removable sample 'trap') was used to obtain invertebrate samples at all sampling sites. At sampling sites whose beds were composed primarily of gravel or gravel/cobble riffles, the area within the sampler frame was disturbed to a uniform depth of 5 cm, and any larger stones (diameter > 10 cm) were cleaned by hand to remove any attached invertebrates. At sites where the streambed was composed almost entirely of boulders and large cobbles, the Surber sampler was placed over a representative boulder, and the boulder was scrubbed by hand to dislodge attached invertebrates. The boulder was then removed, and the remaining gravels were disturbed to a uniform depth in order to collect the remaining invertebrates. Samples were preserved and fixed in the field using 70% ethanol, sorted under a dissection microscope (2 - 6X), and identified to the lowest practical taxonomic level, usually family or genus.

Within-stream macroinvertebrate sampling

Over a two-week period in 1997 (July 23 - August 5) 50 benthic samples were obtained from two adjacent tributaries of the Torpy River using a modified Surber sampler (sampling area = 0.090 m²). The two streams (streams 48 and 56) were hydrochemically similar, but differed with respect to physical parameters (Table 2-1). As such, the two streams represent a range of physical microenvironments available to stream macroinvertebrates. In order to prevent bias in the selection of sampling sites and to ensure that a representative range of benthic microenvironments were sampled in each stream, Surber samples were taken in the centre of the channel (rather than the thalweg), regularly (rather than randomly) every 10 m. Macroinvertebrates were preserved, fixed, and separated from debris using the methods detailed above. Abundance of the heptageniid mayfly *Epeorus* was determined for each sample. The microhabitat preferences of *Epeorus* were examined in further detail as this mayfly genus was thought, based on the results of the canonical correspondence analysis, to represent a typical member of the "torrential fauna" (Vogel 1994).

Before each sample was collected, several environmental variables were measured at each sampling site, including mean velocity, near-bed velocity, stream depth, and stream width. Mean velocity (U) was measured at 60% of total depth using a propeller velocimeter (propeller diameter = 3.0 cm; Swoffer current velocity meter model 2100; Swoffer Instruments Inc. Seattle, Washington). An integrated measurement of near-bed velocity was obtained by deploying the propeller velocimeter 2 cm above the bed, the minimum distance from the bed the velocimeter can be deployed without the propeller striking the surface (nominally, this velocity was measured 2 cm above the bed, hence $U_{0.02m}$). After benthic samples had been obtained, the lengths of the four largest stones contained within the sampling area were measured.

Table 2-1. Comparison of environmental factors between streams sampled in

	Stream 48 ^a	Stream 56 ^a	
Hydrochemical Factors			
Conductivity (µS)	218.0	247.0	
PH	8.30	7.75	
Physical Factors			
Discharge (m ³ s ⁻¹)	0.191	0.332	
Average Surface Slope (%)	4.1	3.3	
Average Distance (km) b	0.50	0.95	

microhabitat preference analysis

^a stream 48 (km 22.0 Lower Torpy Road), stream 56 (km 25.8 Lower Torpy Road)

^b average of distance to the two adjacent streams (an indicator of catchment size)

For each sampling site, several substrate and hydraulic parameters were calculated, including Froude number (Fr), channel Reynolds number (Re), average stone length (L_{ave} ; calculated as the mean of the longest-axis diameters of the four largest stones), standard deviation of stone length (L_{SD}), and relative roughness (D/k_{ave}). Channel Reynolds number and Froude number are determined as

$$Re = UI/v$$

(2-1)

and

$$Fr = U/(aD)^{0.5}$$

(2-2)

respectively, where U is velocity, I is the characteristic length scale (in this case, channel depth), υ is the kinematic viscosity of water, g is gravitational acceleration (9.81 m s⁻²), and D is channel depth. See appendix 1 for notation and formulae.

Data Analysis

Macroinvertebrate community structure was related to the measured environmental variables using canonical correspondence analysis (CCA). CCA is a gradient analysis technique that directly relates species abundances to environmental gradients (ter Braak 1986); such forms of ordination are appropriate to summarise the relationship of taxa to environmental variables when species show unimodal response curves to environmental gradients (see Palmer 1993; ter Braak 1986). CCA ordination analysis of the 117 benthic samples was conducted using CANOCO version 3.2 (ter Braak 1991).

In CCA, the weighted average indicates the 'centre' of the species distribution along a given environmental variable (ter Braak 1986). The difference in the weighted average of several species indicates the differences in the distribution of those species along the environmental variable. Species that place highest along an environmental variable ('vector') will have the highest weighted average with respect to that environmental variable. The significance of the extracted CCA axes was tested by an unrestricted Monte Carlo simulation (999 permutations).

In order to minimise the influence of 'rare' taxa on the ordination, several taxa were excluded from the analyses (Gauch 1982). 'Rare' taxa were identified as those taxa whose 95% confidence interval of the pooled abundances included zero. This method removes taxa with relatively few occurrences; it is, however, biased towards removing those taxa that are relatively abundant at the few sites where they occur. The 24 remaining taxa were included in the analysis, and were given equal weighting. Throughout the analysis outliers were not removed; all samples were examined, and thought to represent biologically valid observations.

Two transformations of the taxa abundance and environmental data were undertaken. (1) As the distribution of individuals of a species are often highly contagious and have highly variable absolute abundances (see Williams et al. 1997), taxa abundances were ln(x+1) transformed, and

related to environmental variables using canonical correspondence analysis (CCA), as described by ter Braak (1986). (2) Since all environmental variables were measured on different scales, they were normalised prior to analysis to a mean of zero and a variance of one (ter Braak 1986; ter Braak 1995).

A preliminary principal components analysis (PCA; using Statistica 5.1, Statsoft, Oklahoma) was undertaken to assess whether there was collinearity between environmental variables. The PCA showed that there was a high degree of collinearity between the geographic variable KM (distance along the long axis of the watershed) and the logging (LOGPROX) and defoliation (DEFOL) variables. In order to account for the variation in invertebrate community structure due to either naturally occurring or anthropogenically induced geographical variation, and to account for seasonal variation in macroinvertebrate community structure (order of stream sampling along the watershed axis was sequential rather than random), KM was included as a covariate in the CCA ordination.

To ensure that analysis of the macroinvertebrate community incorporates the distinct species assemblages that exist at small spatial scales, macroinvertebrate abundances at each sampling site (rather than stream averages) were included in the CCA ordination. Univariate analyses were conducted on 'reach-averaged' rather than 'stream-averaged' data (*i.e.* analyses conducted on stream sampling site data). This approach was adopted to ensure that habitat-specific responses in community and taxa-specific variables were not lost when riffle and boulder-cascade were combined to produce an average value.

Coefficients of determination (R²) of regression analyses are reported as percentages (R² x 100).

Results

Distribution within the watershed

In total, ten environmental variables were measured and included in the CCA ordination analysis. A summary of the major variables is presented in Table 2-2.

Macroinvertebrates were present in all 117 benthic samples collected at the 39 stream sampling sites. A total of 55 macroinvertebrate taxa were collected, with the taxonomic richness of the sampling sites ranging from 1 to 16 taxa. No single macroinvertebrate taxon was collected at

every sampling site. Several genera were, however, relatively widespread, including the stonefly *Zapada* and the predatory caddisfly *Rhyacophila*, which were found at 94.9% and 92.3% of the sites sampled, respectively. Several mayfly genera, including *Drunella*, *Rhithrogena*, and *Baetis*, were also relatively common in the study area. Taxonomic richness tended to decrease with increasing discharge (ANOVA, F(1,115) = 11.67, p < 0.001) (Figure 2-1). However, total invertebrate abundance was not related to discharge. This suggests that the benthic invertebrate community in larger (*i.e.* higher discharge) streams was dominated by fewer species. Stream hydrochemistry was also related to discharge. While the conductivity of low discharge streams was variable, the conductivity of higher order streams was relatively uniform at about 250 μ S (Figure 2-2).

Table 2-2. Major environmental characteristics of the tributaries of the lower

Torpy River watershed

	All Streams in the lower Torpy River watershed (n=116)		Benthic Sample Sites ^a (n=39)	
Environmental variables	Mean (SD)	Range	Mean (SD)	Range
Substrate composition ^b	-	-	1.51 (0.75)	1-3
Discharge (m ³ s ⁻¹)	0.070 (0.15)	0 ^e – 0.63	0.20 (0.20)	0.01 - 0.63
Average distance ^c (km)	0.41 (0.15)	0 ^e - 1.20	0.59 (0.31)	0.10 - 1.20
pH	7.76 (0.42)	6.30 - 8.40	8.13 (0.24)	7.35 - 8.40
Dissolved Oxygen (%)	86.34 (9.19)	50 - 100	93.23 (5.35)	69 - 100
Riparian Vegetation ^b	-	-	2.23 (0.53)	2-4
Stream Surface Slope (%)	5.46 (5.38)	0 ^e - 46.50	6.02 (3.86)	1.2 - 19.0
Conductivity (µS)	241.8 (82.1)	30.6 - 404	258.0 (39.5)	195 - 400
Riparian Defoliation ^d	-	-	0.28 (0.45)	0-1
Logging ^d	-		0.28 (0.45)	0-1

^a benthic macroinvertebrates samples were obtained at all stream sites which had gravel, gravelcobble, or boulder substrates.

^b an index (see text for description)

^c average distance to the two adjacent streams, measured perpendicular to the stream channel

^d dichotomous variables

^e approximately zero – unable to measure accurately using methods employed

- not calculated for sites where invertebrate samples not obtained

Taxonomic richness was related to degree of stream catchment disturbance (ANOVA, F(2,114) = 11.24, p = 0.023) (see also Table 2-3). Streams with relatively recent logging activity (within the decade preceding the study; mean richness per sample = 6.79 taxa, SE = 0.51) had significantly fewer taxa than streams with unlogged catchments (mean richness = 8.92 taxa, SE = 0.53) (Tukey's HSD, p = 0.020). The taxonomic richness of streams with less recent logging activities

(10 - 36 years before the study was conducted; mean richness = 8.79 taxa, SE = 0.48) was not significantly different than streams with either recently logged (Tukey's HSD, p = 0.68) or unlogged (Tukey's HSD, p = 0.37) areas.

CCA ordination

Canonical correspondence analysis ordination of the 117 benthic samples distinguished the influence of chemical (pH, conductivity, dissolved oxygen), physical, (stream surface slope, discharge, substrate size, and average distance to adjacent tributaries), and riparian (riparian vegetation and defoliation indices, and logging activities within catchment) factors on macroinvertebrate community composition. CCA ordination separated the stream sampling sites first by physical variables related to stream size and then by hydrochemical factors (Table 2-3). Axes I and II explained 59.5% of the total variance in the 'species-environmental variables' relationship (see Table 2-4 for a summary). The Monte Carlo test showed that axis I was significantly related to the species data (p = 0.01). CCA axis I was most strongly correlated with substrate composition ($r_{I} = 0.8696$) and discharge ($r_{I} = -0.7515$), while CCA axis II was most strongly correlated to conductivity ($r_{II} = -0.4783$) and dissolved oxygen ($r_{II} = 0.4257$); in addition, pH had a high intraset correlation with axis II ($r_{II} = 0.3898$). The weighted averages of each macroinvertebrate taxa on the measured environmental variables are displayed in a biplot (Figure 2-3), split for clarity into taxonomic and environmental variable components.

The CCA biplot (Figure 2-3) and axis loadings (Table 2-3) indicate the existence of four functional assemblages of stream invertebrates (Table 2-5). The first assemblage (AS1) includes the taxa in the upper left quadrant of the biplot, and includes the trichopterans *Agapteus*, *Lepidostoma*, and *Arctopsyche*, as well as the stoneflies *Kogotus* and *Zapada*. AS1 taxa were generally erosional zone clingers, and include several shredder-detritivores (see Table 2-5). The preferred habitats of these genera include high discharge streams with high surface slopes, coarse substrates, and low conductivity. The riparian areas of streams whose benthic communities were dominated by AS1 species were typically closed coniferous and deciduous canopies. The second assemblage (AS2) includes taxa located in the upper right quadrant of the biplot, and includes the stonefly *Visoka*, the caddisfly *Rhyacophila*, the mayfly *Yoraperla*, larval coleoptera of the family Elmidae, and dipteran larvae of the families Psychodidae, Empididae, and Chironomidae. Genera included in the AS2

assemblage were trophically diverse with leaf/litter associations (collector-gatherers and shredders). The AS2 assemblage included both erosional and depositional zone taxa that are categorised as clingers and burrowers (see Table 2-5). AS2 taxa were found at sites with low pH and fine substrates, but were poorly associated with discharge and riparian variables. Taxa of the third functional assemblage (AS3) are found in the lower right quadrant of the biplot, and are separated from AS2 taxa primarily on the basis of stream surface slope and conductivity. The AS3 assemblage includes the mayfly Cinygmula, larvae of the dipteran families Tabanidae, and Tipulidae, the Uenoid trichopteran Neothremma, and Oligochaeta. AS3 taxa were generally depositional zone burrowers, and were largely collector-gatherers (see Table 2-5). Benthic habitats dominated by the AS3 assemblage included small, closely spaced streams with high conductivity, low slopes, and fine substrates. Riparian vegetation at AS3 sites tended to consist of open canopies, grasses, and wetland plant species. The fourth functional assemblage (AS4) includes the mayfly genera Epeorus, Rhithrogena, Drunella, and Baetis, as well as the caddisfly Glossosoma and the stoneflies Megarcys and Chloroperlidae. AS4 taxa were generally clingers and scrapers associated with erosional habitats (see Table 2-5). Sites preferred by these taxa had typically high discharge, large substrates, and high pH.

The Baetid mayfly *Baetis* had high, negative loading on both axes I and II. This demonstrates a strong association with sites characterised by large substrates (cobbles and boulders). *Baetis* also has a high weighted average with respect to pH, and a low weighted average with respect to slope. *Baetis* abundance was only weakly associated with discharge, suggesting that stream size is not a strong habitat determinant for this genus. The weighted averages of Tipulidae and the caddisfly *Neothremma* (Uenoidae) demonstrate a strong preference of these two taxa for very small streams with low slope, high conductivity, and open, wetland-type riparian vegetation.

Abundance of the heptageniid mayfly *Epeorus* in tributaries of the Torpy River was more closely related to the physical stream gradient (axis I) than the hydrochemical gradient (axis II) (Table 2-6). This indicates that the habitat preferences of *Epeorus* include high discharge streams with coarse substrates.

Table 2-3. Intraset correlation coefficients of environmental variables with the

		Intraset corre	lation coefficients ^b
Environmental variables c	Label	Axis I	Axis II
Substrate composition	SUBSTR	86.96	7.45
Discharge	Q	-75.15	33.53
Averaged distance	AVEDIST	-70.77	39.36
pH	pH	-62.28	-38.98
Dissolved Oxygen	DO	-49.15	-42.57
Riparian Vegetation	RIPARIAN	-38.48	-27.55
Stream Surface Slope	SLOPE	22.20	31.09
Conductivity	COND	9.81	-47.83
Riparian Defoliation	DEFOL	-5.94	27.52
Logging	LOGPROX	3.33	-13.11

first two axes of the Canonical Correspondence Analysis (CCA)^a

^a environmental variables standardised to unit mean and variance (species data ln(x+1) transformed).

^b intraset correlation coefficients = $100 \times r$

^c variables ordered with respect to loadings on axis I.

Table 2-4. Summary of Canonical Correlation Analysis (CCA) of lower Torpy

River watershed data^a

CCA axis	1	10	and a second sec	Σ of Eigenvalues
Eigenvalues	0.258	0.099	0.076	2.221*
Species-environment correlation	0.878	0.729	0.685	
Cumulative % variation explained				
 Species data 	12.1	16.8	20.4	
- Species – env. relationship	43.0	59.5	72.2	

^a geographical variable KM entered as covariate in CCA

* Monte Carlo test of significance of extracted axes: overall test F = 4.13, p = 0.01, Trace Statistic = 0.60

Distribution within the stream

The ordination analysis (CCA) demonstrated that hydraulic and substrate factors appeared to be relatively important in determining the habitat preferences of the torrential mayfly *Epeorus*. Subsequently, the densities of *Epeorus* (ln(x+1) transformed densities) at 50 sites in two adjacent high-discharge streams (stream 48, n = 25; stream 56, n = 25) were measured and related to a series of hydraulic and substrate variables using single and multiple regression analyses (see Table 2-7). In independent regression analyses, channel depth (D) and mean water velocity (U) each accounted for a significant amount of the variation in *Epeorus* abundance ($R^2 = 16.73\%$ and $R^2 = 25.36\%$, respectively; see Figures 2-4 and 2-5). Depth and velocity accounted for 33.20% of the variation in *Epeorus* abundance in multiple regression analysis, while channel Reynolds number (Re) accounted

for 16.83% (see Figure 2-6). Relative roughness (D/kave) was also significantly related to Epeorus abundance (Figure 2-7). Near-bed velocity (U_{0.02m}), average stone length (L_{ave}), maximum stone length (L_{max}), stone length variation (L_{SD}), and Froude number (Fr) did not explain significant amounts of the variation in mayfly abundance.

Table 2-5. Summary of ecological data ^a for common macroinvertebrate taxa collected in tributaries of the lower Torpy River^b

Assemblage Taxa	Habitat	Habit	Trophic Relationship
AS1			
Agapteus	Erosional	Clingers	Sc, C – G
Arctopsyche	Erosional	Clingers	C-F
Kogotus	Erosional	Clingers	Pr
Zapada	Erosional	Sprawlers / clingers	Sh – D
Lepidostoma	Erosional – Depositional	Climbers – Sprawlers – Clingers	Sh – D
AS2			
Visoka	NA	NA	NA
Yoraperla	NA	NA	Sh – D, Sc
Rhyacophila	Erosional	Clingers	Pr, C – G, Sh – H
Elmidae	Erosional	Clingers	C, G, Sc
Psychodidae	Depositional	Burrowers	C-G
Chironomidae	Erosional - Depositional	Burrowers	C – G, F, Pr
AS3			
Tabanidae	Depositional	Sprawlers / burrowers	Pr
Cinygmula	Erosional	Clingers	Sc, C – G
Oligochaeta ^c	Depositional	Burrowers	NA
Empididae	Erosional – Depositional	Sprawlers / burrowers	Pr (some C – G)
Tipulidae	Erosional – Depositional	Burrowers	Sh – D, C – G
Neothremma	Erosional	Clingers	Sc, C – G
AS4			
Baetis	Erosional - Depositional	Climbers / clingers	C – G, Sc
Chloroperlidae	Erosional	Clingers	Pr, Sc, C – G
Megarcys	Erosional	Clingers	Pr
Drunella	NA	Clingers / sprawlers	Sc, Pr
Glossosoma	Erosional	Clingers	Sc
Rhithrogena	Erosional	Clingers	C – G, Sc
Epeorus	Erosional	Clingers	C – G, Sc

^a ecological information from Merritt and Cummins (1996), except where otherwise noted ^b see Figure 2-3 for ordination diagram

^c ecological information from Thorp and Covich (1991)

C = collector, D = detritivore, F = filterer / suspension-feeder, G = gatherer, H = herbivore, Pr = predator, Sc = scraper, Sh = shredder, NA = information not available

In streams 48 and 56, densities of Epeorus were generally highest in shallow flows (D < 0.20

m), at low velocities (U < 30 cm s⁻¹), and at relatively low channel Reynolds numbers (Re < 100,000).

Epeorus densities appeared to decrease with increases in all three hydraulic factors (Figures 2-4, 2-5,

and 2-6). There was, however, a weakly significant relationship between channel depth and velocity

(R^2 =7.73%) (Figure 2-8). Regression analysis revealed a strong relationship between mean velocity (U) and near-bed velocity ($U_{0.02m}$) (R^2 = 45.47%) (Figure 2-9). In addition, densities of *Epeorus* were significantly higher in stream 48 than stream 56 (t = -5.47, p < 0.001).

Table 2-6. Cumulative fit of Epeorus (Heptageniidae) abundance data against

environmental axes (canonical correspondence analysis ^a)

	Axis I	Axis II	Total variance explained
Cumulative fit	19.13%	21.80%	31.38%
(as percent of total variance)			
⁸ for summany and Table 2.4			

for summary see Table 2-4

Table 2-7. Simple linear and standard multiple regressions of *Epeorus* microdistribution ^a and various hydraulic and substrate characteristics

			1 10 TO DOL TO DO.	
Parameter (simple regress.)	R ²	ANOVA(df) = F	β (slope)	p-value
Depth (D)	16.73%	(1,48) = 9.64	-8.29	0.0032
Mean velocity (U)	25.36%	(1,48) = 16.31	-4.42	< 0.001
Near-bed velocity (U _{0.02m})	4.74%	(1,48) = 2.39	-2.63	0.13
Maximum stone length (Lmax)	2.34%	(1,48) = 1.15	4.85	0.29
Average stone length (Lave)	5.31%	(1,48) = 2.69	13.70	0.11
Stone length SD (L _{SD})	0.080%	(1,48) = 0.040	2.30	0.84
Relative roughness (D/kave)	23.17%	(1,48) = 14.47	-0.56	< 0.001
Froude number (Fr)	3.63%	(1,48) = 1.81	-2.21	0.19
Reynolds number (Re)	31.19%	(1,48) = 21.80	-0.000013	< 0.001
Parameter (mult. regress.)				
Depth + Mean U	33.20%	(2,47) = 11.68	-5.91, -3.71	0.023, 0.0014
2				

^a Epeorus densities In(x+1) transformed

Discussion

The measured environmental factors were important in determining the benthic macroinvertebrate community structure in the 39 streams examined in the lower Torpy River watershed. Once geographical variation was accounted for, hydraulic and substrate variables appeared to be of primary importance in determining the macroinvertebrate species assemblages, while hydrochemical factors were of secondary importance. CCA ordination separated macroinvertebrate assemblages first by substrate composition, discharge, and catchment size, and second by conductivity and dissolved oxygen (see Tables 2-3 and 2-4). While several of these parameters (e.g. discharge, catchment size) may not be exactly those experienced by benthic

invertebrates, they do reflect the overall habitat structure and environmental gradients to which the benthic community responds. This conclusion is supported by similar findings elsewhere (*e.g.* Malmqvist and Englund 1996; Danehy et al. 1999).

Rather than measuring macroinvertebrate diversity and abundance at the stream scale (*i.e.* sampling large areas of the stream bed or obtaining mean values of species richness and abundance by averaging several replicated samples), ordination analyses were conducted at the 'patch' scale (*i.e.* the area encompassed within the frame of the Surber sampler). Although several studies have shown that even relatively small areas may encompass several substantially different flow microhabitats (*e.g.* Hart et al. 1996; Robert et al. 1996), the size of the 'patch' (Surber sampler area) utilised in the present study was small enough (approximately 0.09 m²) that the benthic community enclosed therein would be exposed to a similar range of environmental factors. This 'patch-scale' analysis was used because the structure of the benthic community, rather than invertebrate abundance or richness, was the objective of the ordination analysis. This patch size is large enough to include taxa commonly found within the reach, yet small enough that invertebrates collected within a single sample should belong to a characteristic assemblage that is influenced by a common set of environmental and biotic factors.

Taxonomic richness

The results indicate that taxonomic richness generally decreases with increasing discharge within the range measured. This result conflicts with the observations of Growns and Davis (1994) and Statzner and Higler (1986) who reported that taxonomic richness increased with increasing discharge. However, Figure 2-1 demonstrates that the relationship between benthic community composition and discharge is complex, and may, in part, be dependent on spatial scale (*i.e.* small-scale habitat characteristics). Among small streams (Q < 0.1 m³ s⁻¹), taxonomic richness is highly variable. As discharge increases (Q > 0.1 m³ s⁻¹), the variation in taxonomic richness between streams decreases substantially, and fewer invertebrate taxa are present. This suggests that discharge and discharge-related parameters (including substrate composition, hydraulic variables, channel morphology, etc.) may have the strongest influence on community composition in large, high-order streams. The substantial variation in taxonomic richness among low discharge, low-order streams suggests that as stream size decreases, factors other than discharge are more important in

structuring the benthic invertebrate community. Although an inverse relationship between discharge and taxonomic richness was unexpected, there are several possible explanations to account for these results.

First, small-scale habitat complexity or chemical factors may be more important in influencing the structure of the benthic community in small streams than in large streams. For example, conductivity, which is relatively consistent ($\sim 250 \ \mu$ S) at discharges greater than 0.1 m³ s⁻¹, is highly variable in streams with low discharge. Similarly, Growns and Davis (1994) found that while conductivity is variable in small streams, it is more consistent (about 250 μ S) in streams of greater discharge. As such, if invertebrate diversity were strongly influenced by hydrochemical factors, taxonomic richness would be expected to be highly variable in low discharge streams, and more uniform in larger streams. This explanation agrees with the observed pattern. The relative importance of conductivity is supported by the results of the ordination analysis; intraset correlation coefficients of the CCA (see Table 4-3) reveal that conductivity is the most important hydrochemical factor influencing community composition. Similarly, Williams et al. (1997) found that the invertebrate community structure in eastern Canadian springs was dependent on water chemistry, especially on ionic composition and concentration. However, while both groundwater and surface water inputs may play an important role in determining invertebrate community structure, their individual effects are difficult to discern (Jones and Holmes 1996).

There may also be a shift in the importance and nature of small-scale hydraulic factors such as boundary layer thickness and substrate-flow interactions (Carling 1992; Young 1992; Hart et al. 1996) as streams increase in size (see Newbury 1984). However, the present study measured only a single, large-scale hydraulic factor (discharge) in each stream within the watershed-scale study area. The influence of small-scale hydraulic factors on the community structure in first-order streams is poorly understood, and requires further study.

In addition, inter-stream variation in streambed disturbance regime could, in part, account for the observed pattern of decreased taxonomic richness with increased discharge. Surface runoff-fed streams tend to be 'flashy' and subject to frequent bed disturbance, while spring-fed streams are more stable and, as a result, subject only to infrequent bed disturbance. Input sources of small streams in the Torpy watershed are diverse, and include snowmelt, surface runoff, and groundwater (springs) (*personal observation*). As such, disturbance intensity and frequency may be substantially

more variable between first-order streams than between higher-order streams, which have multiple inputs from diverse sources. Townsend et al. (1997), applying the intermediate disturbance hypothesis, found that species richness was low both in streams with frequent, intense bed disturbance (where relatively few, rapidly colonising species dominate the assemblage) and very infrequent bed disturbance (where relatively few, competitively superior species dominate the assemblage). As such, inter-stream variation in invertebrate diversity among small streams within the study area may be due, in part, to variable disturbance regimes, with streams with the highest taxonomic richness having intermediate frequencies of bed disturbance. Similarly, higher order streams with greater discharge could have increasingly stable beds, which leads to a community dominated by fewer, competitively superior invertebrate species.

The pattern of decreasing invertebrate taxa richness with increasing discharge may also be the result of a community-level response to an unmeasured physical factor related to discharge. For example, mean channel velocity, average substrate particle size, and channel width increase with discharge (Newbury 1984; Hubert and Kozel 1993). This corroborates the observation of Townsend et al. (1997) who noted that richness increased with the percentage of the bed made up of small particles (8 - 32 mm in diameter). While Townsend et al. (1997) attributed this trend to a decrease in bed stability, it seems likely that it was due, at least in part, to the interaction between near-bed flow and bed roughness. However, the results of the present study and those of Townsend et al. (1997) conflict with the results of several studies relating channel characteristics to community structure. While the present study found that faunal richness was greatest in smaller streams, Statzner and Higler (1986) and Growns and Davis (1994) found that richness was greatest in the mid-reaches of streams. Both studies suggest that the highest species richness should occur in the areas of the highest hydraulic variation, where several species assemblages overlap due to habitat heterogeneity. This result also contradicts, at least superficially, the river continuum concept proposed by Vannote et al. (1980), which states that species richness is highest in mid-order reaches where environmental variation in greatest. It is important to note, however, that faunal richness in the present study was measured at the patch scale. In very small streams, a single patch (0.090 m², as defined by this study) can encompass a relatively large proportion of the streambed, and as such, may contain a number of microhabitat types (e.g. near-shore and thalweg zones, or high-velocity and low-velocity zones). In larger streams, where stream width was far greater than the width of the sampler, each

patch enclosed fewer microhabitat types (*i.e.* relatively uniform benthic habitat was sampled within the quadrat represented by the Surber sampler frame). As such, it is important to limit interpretation of the results to the patch scale. It is likely that total invertebrate diversity is greater in high discharge streams due to greater habitat complexity, more spatially diverse interstitial spaces, and greater hydraulic variability (Growns and Davis 1994; Statzner and Higler 1986; Townsend et al. 1997). If this assessment (greater habitat variation per patch in smaller streams) is accurate, then the observed pattern of decreasing richness with increasing discharge may actually support the river continuum concept, even though the taxonomic richness per reach may actually be greater. More research is needed to determine if the relationship between species richness and stream order is dependent on the spatial scale at which invertebrate fauna are sampled.

Forestry activities in the watershed also appear to have an impact on the benthic invertebrate community. Streams whose catchments were disturbed by relatively recent logging activities had significantly fewer taxa than streams with undisturbed catchments. Logging activities are known to affect stream invertebrate communities; Newbold et al. (1980) found that macroinvertebrate diversity was lower in streams without riparian buffer strips than in those whose banks were protected with buffer strips. The decreased taxonomic richness in streams with adjacent logging may be the result of a shift in community structure. Stone and Wallace (1998) found that clearcutting reduced the proportion of scraper taxa in a mountain stream and increased the proportion of shredders. The proximity of the conductivity vector to the logging vector on the ordination diagram (Figure 2-3) suggests that logging activities increase water conductivity. This concurs with the findings of Growns and Davis (1991) who found that logging within the catchment of a stream significantly increased streamwater conductivity. They further suggested that increased conductivity was, in part, responsible for shifts in invertebrate community structure. In the present study, however, the weak relationship of the logging variable with either environmental axis suggests that the influence of forestry activities on invertebrate community composition in the Torpy watershed is limited.

Community structure – CCA ordination

The underlying physical gradient represented by the first CCA axis is associated with physical stream factors; large discharge streams with coarse substrates lie on the left of the ordination diagram, while small streams with beds composed of relatively fine particles lie on the right. The

eigenvalues and intraset correlation coefficients suggest that this environmental gradient has the greatest influence on the structure of the macroinvertebrate communities in tributaries of the Torpy River watershed. Ordination analyses of benthic community structure by several other authors have also found that a physical gradient dominates benthic community structure. Danehy et al. (1999) found that the first axis was most strongly correlated with water surface slope and mean channel width, and attributed this to the dominant effect of headwater-to-valley environmental gradients on the macroinvertebrate community structure. Marchant et al. (1985) and Rossaro and Pietrangelo (1993), in separate studies of large-scale variation in benthic communities, both found that the underlying environmental gradient represented by the first axis was related to substrate particle size.

CCA ordination of the benthic community divided the common invertebrate fauna into four functional assemblages, each associated with a distinct habitat type defined by physical and hydrochemical factors. Notably, the invertebrates of both the AS1 and AS4 assemblages were positively correlated with stream hydraulics (CCA axis I), and are categorised as clingers inhabiting erosional habitats (Merritt and Cummins 1996). However, the taxa included in assemblage AS1 are generally dependent on allochthonous inputs as a food resource (two shredder-detritivore genera and a collector-gatherer), while the taxa of AS4 are almost exclusively scrapers, dependent on autochthonous production (periphyton) as a food source. This suggests that AS4, which includes the heptageniid mayfly *Epeorus*, may represent a functional assemblage that inhabits (*i.e.* a boulder-torrent guild). Likewise, AS1 may represent an assemblage (*i.e.* a cobble/gravel riffle guild) that inhabits riffle habitats of high-discharge streams.

The positive relationship between discharge and the suspension-feeding hydropsychid caddisfly *Arctopsyche* (AS1) supports earlier observations that the local abundances of hydropsychid and simuliid suspension-feeding taxa are related to high water velocities (Osborne and Herricks 1987; Growns and Davis 1994). However, while *Arctopsyche* was categorised as a flow obligate by Growns and Davis, it was not grouped with the other flow obligate taxa (*e.g. Epeorus, Rhithrogena*, etc.) in the ordination diagram (Figure 2-3). This suggests that other variables, such as channel slope, may be important in the microhabitat preferences of this genus. Hubert and Kozel (1993) reported that water surface slope was significantly and positively related to environmental factors that have been found to

be related to the habitat preferences of suspension-feeding taxa, such as the proportion of the bed composed of boulders (see Wetmore et al. 1990; Voelz and Ward 1996).

Invertebrates included in the third functional assemblage (AS3) were negatively correlated with stream hydraulics. This functional assemblage is composed largely of collector-gatherer, burrower taxa. Hearnden and Pearson (1991) found that benthic macroinvertebrates with trophic relationships of this type were strongly associated with detrital deposits in pools with coarse substrates. Leaf litter deposits and current intensity are strongly related (Minshall 1984), and Growns and Davis (1994) suggest that detrital material (FPOM and CPOM), the food resource of collector-shredder taxa, is unlikely to accumulate in areas of the stream bed with high current velocities. Wiggins (1996) classified most AS3 taxa (including psychodid, tabanid, tipulid, and empidid dipterans, as well as oligochaetes) as being depositional zone taxa. Several AS3 taxa have distinct adaptations for burrowing rather than movement on the exposed surface of the streambed, suggesting that these taxa belong to the flow avoiders are generally shredders. Taxa lying on the right side of the ordination diagram could be expected to be associated with depositional rather than erosional habitats, where low currents enhance the deposition of both CPOM and FPOM (Hearnden and Pearson 1991).

Interestingly, the clinger mayfly *Cinygmula* was included in assemblage AS3, even though it is generally classified as an erosional zone genus (see Edmunds and Waltz 1996). This suggests that *Cinygmula* may not be as dependent on high velocity microhabitats as other erosional zone species. This result supports the findings of Golubkhov et al. (1992), who observed that *Cinygmula grandifola* was not as sensitive to the decreases in oxygen uptake associated with low flow velocities as other rheophilous species.

Four of the six taxa included in the fourth functional assemblage group (AS4) have distinct adaptations that allow them to live in high velocity habitats and minimise the probability of being detached from the substrate. The heptageniid mayflies *Epeorus* and *Rhithrogena* have an abdominal gill arrangement that forms a sucker-shaped ventral disk, which is thought to function as a "suction cup" which prevents accidental detachment (Vogel 1994). The hairy ventral disk of *Drunella* is thought to function in similar fashion. The grazing caddisfly *Glossosoma* cements its case to large streambed stones, preventing it from being eroded from the bed. All four taxa would be categorised

as flow obligates, based on the criteria of Growns and Davis (1994) who placed stream invertebrates into three flow exposure groups (obligates, facultatives, and avoiders) based on behavioural and morphological adaptations to flow. These four taxa are only weakly associated with axis II, suggesting that the habitat preferences of flow obligates are determined almost entirely by physical (flow and substrate characteristics) rather than hydrochemical (*e.g.* conductivity) factors. AS4 taxa predictably show strong associations with coarse substrates. Erosional habitat grazers should be strongly associated with boulder and cobble substrates, as larger stones provide a relatively stable substrate for the growth of periphyton; smaller bed particles tend to be eroded and entrained at lower velocities (Minshall 1984).

Comparing the positions of the macroinvertebrate taxa within the ordination diagram to the known trophic relationships of the taxa demonstrates the ecological validity of CCA ordination. Organisms with similar habitat requirements and ecological roles have strong associations in Figure 2-3. There are invertebrate predators associated with each of the four functional assemblages, suggesting some degree of resource partitioning among common predatory taxa. The predatory caddisfly *Rhyacophila*, one of the most ubiquitous invertebrate taxa in the Torpy River watershed, had a very weak weighted average with respect to axis II, demonstrating that it may be relatively insensitive to variations in water chemistry. The mayfly *Rhithrogena*, another commonly occurring benthic insect, was also very weakly associated with axis II. This suggests that while common invertebrate taxa may demonstrate preferences to certain ranges of physical habitat types, they may be relatively tolerant of a wide range of hydrochemical conditions. Additionally, the ordination sheds light on the ecological status of several taxa whose habitat preferences are poorly understood. For instance, the mayfly *Drunella*, included in AS4 and shown to be strongly associated with axis I, is likely a erosional zone species (along with several other AS4 taxa including *Epeorus* and *Rhithrogena*).

The microdistribution of *Epeorus*

Large-scale environmental factors (*e.g.* discharge, substrate composition, disturbance regime) determine the availability of niches within stream systems, and thus determine if certain taxa will be present. However, small-scale factors are of greater importance in determining the distribution of invertebrates within each reach or riffle. Increasingly, stream hydraulics are thought to be the

single most important factor determining the distribution of benthic organisms (see Davis and Barmuta 1986; Carling 1992; Hart et al. 1996). So, while CCA ordination demonstrates that the mayfly *Epeorus* was associated with physical variables related to stream hydraulics (discharge, substrate composition), the spatial scale was too coarse to clearly define the microhabitat preferences of this genus. However, correlation of several physical stream factors with the distribution of *Epeorus* within two adjacent streams sheds light on the relationship between watershed-scale and small-scale patterns of distribution of benthic invertebrates. Neither simple parameters (U, U_{0.02m}, D, various substrate factors) nor ratios of parameters (Re, Fr, D/k_{ave}) provided the strongest correlations with *Epeorus* abundance (Table 2-7). Moreover, while a multiple regression model incorporating both velocity and depth explained 33.2% of the variation in *Epeorus* density, interpretation may be difficult. Larval *Epeorus* preferred a distinct range of depth and velocity conditions, namely depths less than 20 cm, mean velocities less than 30 cm s⁻¹, channel Reynolds number less than 100,000, and relative roughness (D/k_{ave}) less than 3. In other words, larvae preferred shallow, slow flows over rough beds.

Local densities of *Epeorus* were significantly and negatively related to mean velocity and channel depth. This result was unexpected, as the distinct morphological adaptations of *Epeorus*, a known rheophilous, torrential macroinvertebrate, suggest that larvae should display a marked preference for high velocity flows. Collier (1994) found that *Deleatidium* var. *myzobranchia*, which has large overlapping gills in a sucker-like arrangement similar to that of *Epeorus*, was restricted to velocities greater than 0.90 m s⁻¹. Collier speculated that the morphological adaptations of *Deleatidium* allowed it to withstand high velocities and thus access areas of higher quality food resources. Weissenberger et al. (1991) note that *Epeorus*, though subject to substantial lift forces at high velocities (due to its 'airfoil' shape), is able to attach itself firmly to the surface of the bed, preventing accidental dislodgement from the substrate.

It is difficult to separate the effects of velocity, depth, and bed morphology (see Minshall 1984; Newbury 1984; Carling 1992), and as such, there are several possible explanations for this apparent discrepancy. Stream insects exist almost exclusively in a zone that extends only a few millimetres above the surface of the substrate. *Epeorus* is no exception; the microhabitat preferences of this genus are undoubtedly determined by near-bed rather than mean flows. The results, however, show that velocities near the bed ($U_{0.02m}$) are correlated to mean velocities. If velocities measured at

2 cm above the bed ($U_{0.02m}$) are, in turn, correlated to velocities immediately adjacent to the bed (e.g. $U_{0.002m}$), then it would appear that local densities of *Epeorus* are related to low velocities. However, the relationship between mean velocity and velocity immediately adjacent to the bed at the scale of the larvae (~ 2 mm) may be not be consistent across the range of relative roughnesses (see Hart et al. 1996). As depth decreases and substrate roughness increases (primarily due to increased substrate particle size), velocities adjacent to the bed approach (or, in some cases, exceed) mean velocity due to flow constriction and the development of pressure gradients (see chapter 3). Thus, in shallow channels with low relative roughness, near-bed velocities may be higher than predicted by conventional boundary layer theory (see White 1999), and the distribution of *Epeorus* may be in response to some as yet unmeasured variable (*e.g.* near-bed turbulence intensity $u'_{0.002m}$). Substantial research into the distribution and nature of near-bed hydraulic parameters is needed before results of this kind can be interpreted with certainty.

A more probable explanation is that *Epeorus* larvae are not, in fact, responding to velocity, but rather to other factors related to velocity. Depth, relative roughness, and substrate composition are significantly related to mean velocity (Nowell and Jumars 1984; Minshall 1984; Newbury 1984). As such, the preferences of *Epeorus* may be for shallow sites with low relative roughness, rather than low velocity. Larval Epeorus graze periphyton (mainly diatoms) from the exposed upper surfaces of streambed stones. Food resource availability may be higher in shallower areas; growth rates of periphyton are higher in shallow flows, as photosynthetically active radiation (PAR) is attenuated to a lesser degree. This interpretation is supported by Wellnitz et al. (1996), who concluded that light is the most important abiotic factor regulating algal abundance in streams. In addition, streambeds composed of larger particles are more stable (Minshall 1984), providing a site for long-term accumulation of algae. As such, beds with low values of D/kave should provide a more suitable site for periphyton growth, and have, as a result, greater resources available to grazing invertebrates. A positive relationship between grazer abundance and periphyton abundance was demonstrated by Vaughn (1986), who found that densities of the trichopteran grazer Helicopsyche borealis were highest in areas of high algal chlorophyll a; larvae drifted from food-depleted areas of the substrate. Similarly, Kerans (1996) found that the hydropsychid grazer Hydropsyche slossonae used periphyton availability to assess microhabitat quality.

Oxygen availability may also be a factor in microhabitat selection. *Epeorus* larvae are intolerant of low oxygen concentrations, and are dependent on flow over their abdominal gills to obtain sufficient dissolved oxygen to survive (*personal observation*). When the height of the substrate roughness is less than three times the total depth ($D/k_{ave} < 3$), flow is considered "chaotic" (Davis and Barmuta 1989; Young 1992; 1993). Flow conditions immediately adjacent to the bed in chaotic flows are poorly understood (see Hart et al. 1996; chapter 3), but may provide microflow conditions that enhance gas exchange. However, this is not likely the sole factor determining the microhabitat preferences of the genus, as *Epeorus* larvae often migrate to the underside of stones during the day (see chapter 4) where current velocities are substantially lower than the upper surface of streambed stones.

Chaotic flows may also act to reduce the threat of predation. Bull trout (*Salvelinus confluentus*), common in tributaries of the Torpy River (G. Cho, UNBC grad student, unpublished data) may be unwilling to move into shallow, chaotic flows to feed. Similarly, American Dippers (*Cinclus americanus*) may be unable to forage efficiently in chaotic flows. However, while several studies (*e.g.* Hart and Merz 1998; Peckarsky et al. 1990) have demonstrated that high velocities can reduce invertebrate predation on stream insects, few studies have examined the effect of chaotic flows on predation intensity. More research on the ecological importance of flow regime is needed.

An alternative explanation for the observed pattern of decreasing *Epeorus* density with increasing velocity is a possible ontogenetic shift in microhabitat preferences. Knopp and Cormier (1997) report that prior to emergence (which generally occurs in July and August), larval *Epeorus* in western Canada move from high velocity habitats into slower areas of the streambed. As samples were collected in late July / early August, pre-emergence behaviours may be a factor. Collier (1994) found that last instar males of the rheophilous mayfly *Deleatidium* var. *myzobranchia* preferred lower velocity habitats than females, possibly reflecting pre-emergence movement into suitable emergence sites. Increases in larval size may also, in part, explain the apparent preferences of larval *Epeorus* for relatively low-velocity habitats. Larger, later instar larvae of the caddisflies *Arctopsyche grandis* and *Brachycentrus occidentalis* are found in less current-exposed locations, possibly due to the greater "current forces" to which larger individuals are subjected (Voelz and Ward 1996). Preferences of larval *Epeorus* for areas of greater relative roughness may also be related to larval development. Buffagni et al. (1995) found that nymphs of the torrential mayfly species *Rhithrogena*

semicolorata and Ecdyonurus venosus moved into rougher areas in their last instar, possibly to find suitable sites for emergence. However, in the present study, larval abundance was correlated with relative bed roughness but not with substrate particle size. Although seemingly contradictory, this result can be explained if relative roughness is an important predictor of the flow conditions immediately adjacent to the surface of the substrate (*i.e.* turbulence intensity and structure, etc.) to which larval mayflies are exposed. Substrate roughness influences several relevant flow parameters including turbulence intensity and boundary layer conditions (Davis and Barmuta 1989; Young 1992; Robert et al. 1996).

Mean velocity (measured at 60% of the total depth) proved to be more closely related to the distribution of *Epeorus* than measurements of near-bed velocity (recorded 2.0 cm above the bed). This suggests that mean velocity may be a better predictor of the habitat preferences of *Epeorus*. Similarly, mean velocity may be a better indicator of flow conditions at the "patch" scale (*i.e.* in this case, 0.090 m²) than a single measurement of near-bed velocity obtained in the centre of the patch. This is undoubtedly due to the heterogeneous nature of near-bed flows. Hart et al. (1996) found that near-bed velocities differed as much as fourfold over distances as small as a few centimetres. Interactions between streambed geometry and the current can produce variable local flows, and measurements of near-bed velocity are likely to be dependent on bed geometry and variation in microflow regime at the measurement point. This result supports the findings of Quinn and Hickey (1994) who found that in cobble-bedded channels, mean velocity was approximately as good a predictor of invertebrate variables as complex hydraulic parameters, while in more variable environments (especially over gravel beds), complex variables were more closely associated with invertebrate distributions.

Contrary to expectations, Froude number (Fr) was not a good predictor of *Epeorus* distribution. Orth and Maughan (1983) found significant relationships between several macroinvertebrate taxa and Froude number. Similarly, Wetmore et al (1990) found that Froude number was the best predictor of feeding sites of the caddisfly *Brachycentrus occidentalis* and black fly larvae (*Simulium vittatum*). However, positioning with respect to Froude number may be important only in suspension-feeding taxa. *B. occidentalis* and *S. vittatum* are both suspension-feeding taxa, and Wetmore et al. (1990) suggest that the microhabitat preferences of these larvae (Fr = ~ 0.6 and ~ 0.7, respectively) are the result of larvae positioning themselves in zones of converging flow lines in

order to maximise seston delivery (often, larger Froude numbers are associated with accelerating flows where distances between adjacent, parallel streamlines are decreasing, which in turn increases the discharge per unit of cross-sectional area). If the primary ecological significance of Froude number is as an indicator of particle capture efficiency, it may be relatively unimportant to grazing macroinvertebrate taxa. Jowett et al. (1991) found that Froude number was not a good predictor of abundances of Deleatidium, a grazing mayfly. Rather, they found that mean velocity, depth, and substrate characteristics acted as better predictors of local larval abundance. In addition, Wetmore et al. (1990) found that the distribution of the grazing caddisfly Glossosoma intermedium, though poorly related to Froude number, was significantly and negatively related to depth. The results of the present study similarly demonstrate that Froude number was not significantly related to Epeorus distribution, while mean velocity, depth, Reynolds number, and relative roughness (a substrate characteristic) were. This suggests that the physical factors to which grazing and suspension-feeding invertebrates respond may be different. Suspension-feeding organisms may position themselves in microflow regimes that maximise particle capture rates, while herbivorous macroinvertebrate taxa may prefer flow regimes that maximise algal growth and gas exchange while minimising predation and the probability of accidental detachment from the substrate.

It is important to note, however, that the environmental factors measured in this study may not be those to which stream invertebrates are responding proximally. Several authors, including Wetmore et al. (1990) and Davis and Barmuta (1989), note that conventional samplers and field techniques often sample across several microhabitats. As such, using these techniques (*i.e.* propeller velocimeter, Surber sampler), it is difficult to discern the nature of the factors that *Epeorus* larvae respond to. Even a relatively small patch of cobble streambed may contain diverse flow types that vary substantially with respect to important flow descriptors. While many studies have found significant relationships between invertebrate ecology and a variety of flow characteristics, the nature of the hydrodynamic parameters to which benthic invertebrates actually respond remains largely unknown. These proximal hydrodynamic parameters may be related to micro-scale factors. For example, Hart et al. (1996), using a hot-film anemometer to measure near-bed flows in a natural stream channel, found that black fly larvae (*Simulium vittatum*) abundance was related to current velocity measured 2 mm above the bed (approximately the height of the labral fans). However,

studies of this kind are rare, and research on the relationship between macroinvertebrate behaviour and flows immediately adjacent to the bed (at the scale of the organisms of study) is needed.

Conclusions

The results of the present study support the hypothesis that hydrodynamic forces are the underlying ecological gradient that determines the distribution of benthic stream invertebrates at both the community and taxa-specific levels. Ordination divided the benthic fauna into distinct assemblages based primarily on physical factors (substrate, substrate composition, etc.) and secondarily on hydrochemical factors (pH, conductivity, etc.). However, while this result provides insight into the relative ecological importance of the various parameters, it does little to elucidate the proximal mechanisms that produce these functional assemblages.

Further research is required to identify the parameters to which benthic organisms respond. However, this may prove difficult as many flow variables are intimately related (*e.g.* near-bed velocity and shear stress). For example, the results of the present study reveal that the abundance of the mayfly *Epeorus* was negatively related to channel Reynolds number. However, channel Reynolds number is a ratio that incorporates both channel depth and mean velocity. While it is possible that *Epeorus*, and other benthic invertebrate taxa, may respond to flow characteristics associated with low Reynolds number (*e.g.* specific regimes of eddy generation), or may have direct preferences for low velocities or shallow depths, it is possible that they are also responding to additional, unmeasured environmental parameters that are associated with either depth or mean velocity (*e.g.* near-bed velocity, bed roughness, UV radiation, etc.). To adequately describe the habitat preferences of any species of stream invertebrate, a combination of substrate and hydraulic parameters should be measured throughout the range of habitat types inhabited by the species.

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References

- Allan, J.D. 1995. Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, London, UK.
- Bouckaert, F.W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biol. 40: 77-86.
- Buffagni, A., G. Crosa, and R. Marchetti. 1995. Size-related shifts in the physical habitat of two mayfly species (Ephemeroptera). Freshwater Biol. 34: 297-302.
- Carling, P.A.. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biol. 28: 273-284.
- Carling, P.A., J.J. Williams, A. Kelsey, M.S. Glaister, and H.G. Orr. 1998. Coarse bedload transport in a mountain river. Earth Surf. Proc. Landforms 23: 141-157.
- Carlson, J.Y., C.W. Andrus, and H.A. Froehlich. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A. Can. J. Fish. Aquat. Sci. 47: 1103-1111.
- Collier, K.J. 1993. Flow preferences of larval Chironomidae (Diptera) in Tongariro River, New Zealand. N. Zea. J. Mar. Freshwater Res. 27: 219-226.
- Collier, K. 1994. Influence of nymphal size, sex, and morphotype on microdistribution of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in a New Zealand River. Freshwater Biol. 31: 35-42.
- Collier, K.J., G.F. Croker, C.W. Hickey, J.M. Quinn, and B.S. Smith. 1995. Effects of hydraulic conditions and larval size on the microdistribution of Hydrobiosidae (Trichoptera) in two New Zealand rivers. N. Zea. J. Mar. Freshwater Res. 29: 439-451.
- Danehy. R.J., N.H. Ringler, and R.J. Ruby. 1999. Hydraulic and geomorphic influences on macroinvertebrate distribution in the headwaters of a small watershed. J. Freshwater Ecol. 14: 79-91.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biol. 21: 271-282.
- Delgado, J.A., and R. Carbonell. 1997. Case features of caddisfly larvae (*Sericostoma selysi*) as related to water velocity and potential to drift. J. Freshwater Ecol. 12: 193-197.
- De March, B.G.E. 1976. Spatial and temporal patterns in macrobenthic stream diversity. J. Fish. Res. Board Can. 33: 1261-1270.
- Donahue, W.F., and D.W. Schindler. 1998. Diel emigration and colonization responses of blackfly larvae (Diptera: Simuliidae) to ultraviolet radiation. Freshwater Biol. 40:357-365.
- Edmunds, G.F. Jr., and R.D. Waltz. 1996. Ephemeroptera. *in* An Introduction to the Aquatic Insects of North America Third Edition. *Eds.* R.W. Merritt and K.W. Cummins. Kendall/Hunt Publishing Company, IA.
- Gauch, H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge.
- Golubkhov, S.M., T.M. Tiunova, and S.L. Kocharina. 1992. Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. Aquatic Insects 14: 137-144.

- Growns, I.O., and J.A. Davis. 1991. Comparison of the macroinvertebrate communities in streams in logged and unlogged catchments 8 years after harvesting. Aust. J. Mar. Freshwater Res. 42: 689-706.
- Growns, I.O., and J.A. Davis. 1994. Longitudinal changes in near-bed flows and macroinvertebrate communities in a Western Australian stream. J. N. Am. Benthol. Soc. 13: 417-438.
- Gurtz, M.E., J.R. Webster, and J.B. Wallace. 1980. Seston dynamics in southern Appalachian streams: effects of clearfelling. Can. J. Fish. Aquat. Sci. 37: 624-631.
- Hart, D.D., B.D. Clark, and A. Jaentuliyana. 1996. Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.
- Hart, D.D., and R.A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow-mediated refuges. Oecologia 114: 263-273.
- Hawkins, C.P., J.N. Hogue, L.M. Decker, and J.W. Feminella. 1997. Channel morphology, water temperature, and assemblage structure of stream insects. J. N. Am. Benthol. Soc. 16: 728-749.
- Hearnden, M.N., and R.G. Pearson. 1991. Habitat partitioning among the mayfly species (Ephemeroptera) of Yuccabine Creek, a tropical Australian stream. Oecologia 87: 91-101.
- Hubert, W.A., and S.J. Kozel. 1993. Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. J. Freshwater Ecol. 8: 177-183.
- Jones, J.B., and R.M. Holmes. 1996. Surface-subsurface interactions in stream ecosystems. Trends Ecol. Evol. 11: 239-242.
- Jowett, I.G., J. Richardson, B.J.F. Biggs, C.W. Hickey, and J.M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. N. Zea. J. Mar. Freshwater Res. 25: 187-199.
- Kerans, B.L. 1996. The influence of periphyton and rock texture on the diel drift periodicity of a Hydropsychid caddisfly. J. Freshwater Ecol. 11: 163-169.
- Knopp, M., and R. Cormier. 1997. Mayflies: An Anglers Study of the Trout Water Ephemeroptera. Greycliff Publishing, Helena, MT.
- Lacoursiere, J.O. 1992. A laboratory study of fluid flow and microhabitat selection by larvae of Simuliium vittatum (Diptera: Simuliidae). Can. J. Zool. 70: 582-596.
- Malmqvist, B., and G. Englund. 1996. Effects of hydropower-induced flow perturbations on mayfly (Ephemeroptera) richness and abundance in north Swedish river rapids. Hydrobiol. 341: 145-158.
- Marchant, R., L. Metzeling, A. Graesser, and P. Suter. 1985. The organization of macroinvertebrate communities in the major tributaries on the LaTrobe River, Victoria, Australia. Freshwater Biol. 15: 315-331.
- Merritt, R.W., and K.W. Cummins. 1996. An Introduction to the Aquatic Insects of North America Third Edition. Kendall/Hunt Publishing Company, IA.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. *in* The Ecology of Aquatic Insects. *Eds.* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York, NY.
- Muotka, T., and A. Pentinnen. 1994. Detecting small-scale spatial patterns in lotic predator-prey relationships: statistical methods and a case study. Can. J. Fish. Aquat. Sci. 51: 2210-2218.

- Newbold, J.D., D.C. Erman, and K.B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37: 1076-1085.
- Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. *in* The Ecology of Aquatic Insects. *Eds.* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York, NY.
- Noel, D.S., C.W. Martin, and C.A. Federer. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. Env. Manag. 10: 661-670.
- Nowell, A.R.M., and P.A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303-328.
- Orth, D.J., and M.E. Maughn. 1983. Microhabitat preferences of benthic fauna in a woodland stream. Hydrobiol. 106: 157-168.
- Osborne, L.L., and E.E. Herricks. 1987. Microhabitat characteristics of *Hydropsyche* (Tricoptera: Hydropsychidae) and the importance of body size. J. N. Am. Benthol. Soc. 6: 115-124.
- Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230.
- Peckarsky, B.L., and R.S. Wilcox. 1989. Stonefly nymphs use hydrodynamic cues to discriminate between prey. Oecologia 79: 265-270.
- Peckarsky, B.L., S.C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a test of the harsh-benign hypothesis. Freshwater Biol. 24: 181-191.
- Plenet, S. H. Hugueny, and J. Gilbert. 1996. Invertebrate community responses to physical and chemical factors at the river/aquifer interaction zone II. Downstream from the city of Lyon. Arch. Hydrobiol. 136: 65-88.
- Quinn, J.M., and C.W. Hickey. 1994. Hydraulic parameters and benthic invertbrate distributions in two gravel-bed New Zealand rivers. Freshwater Biol. 32: 489-500.
- Quinn, J.M., C.W. Hickey, and W. Linklater. 1996. Hydraulic influences on periphyton and benthic invertebrates: simulating the effects of upstream bed roughness. Freshwater Biol. 35: 301-309.
- Rempel, L.L., J.S. Richardson, and M.C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. J. N. Am. Benthol. Soc. 18: 34-48.
- Resh, V.H., and D.M. Rosenberg (*Eds*). 1984. The Ecology of Aquatic Insects. Praeger Publishers, New York, NY.
- Robert, A., A.G. Roy, and B. De Serres. 1996. Turbulence at a roughness transition in a depth limited flow over a gravel bed. Geomorphology 16: 175-187.
- Robertson, A.L., J. Lancaster, and A.G. Hildrew. 1995. Stream hydraulics and the distribution of microcrustacea: a role for refugia? Freshwater Biol. 33: 469-484.
- Robertson, A.L., J. Lancaster, L.R. Belyea, and A.G. Hildrew. 1997. Hydraulic Habitat and the assemblage structure of stream benthic microcrustacea. J. N. Am. Benthol. Soc. 16: 562-575.
- Rossaro, B., and A. Pietrangelo. 1993. Macroinvertebrate distribution in streams: a comparison of CA ordination with biotic indices. Hydrobiol. 263: 109-118.
- Shannon, J.P., D.W. Blinn, and L.E. Stevens. 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A. Freshwater Biol. 31: 213-220.

- Statzner, B., and T.F. Holm. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. Oecologia 78: 145-157.
- Statzner, B., and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16: 127-139.
- Stone, M.K., and J.B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biol. 39: 151-169.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.
- ter Braak, C.J.F. 1991. CANOCO A FORTRAN program for Canonical Community Ordination. Version 3.12. Microcomputer Power, Ithaca, New York.
- ter Braak, C.J.F. 1995. Ordination. *in* Data Analysis in Community and Landscape Ecology. *Eds.* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. Tongeren. Cambridge University Press.
- Thorp, J.H., and A.P. Covich. 1991. Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego, CA.
- Townsend, C.R., M.R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnol. Oceanogr. 42: 938-949.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.
- Vaughn, C.C. 1986. The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). Freshwater Biol. 16: 485-493.
- Vogel, S. 1994. Life in Moving Fluids, 2nd Edition. Princeton University Press, Princeton, NJ.
- Voelz, N.J., and J.V. Ward. 1996. Microdistributions of filter-feeding caddisflies (Insecta: Trichoptera) in a regulated Rocky Mountain river. Can. J. Zool. 74: 654-666.
- Wallace, J.B., and M.E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. Am. Midland Nat. 115: 25-41.
- Way, C.R., A.J. Burky, C.R. Bingham, and A.C. Miller. 1995. Substrate roughness, velocity refuges, and macroinvertebrate abundance on artificial substrates in the lower Mississippi River. J. N. Am. Benthol. Soc. 14: 510-518.
- Weissenberger, J., H.-Ch. Spatz, A. Emanns, and J. Schwoerbel. 1991. Measurement of the lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m s⁻¹. Freshwater Biol. 25: 21-31.
- Wellnitz, T.A., R.B. Rader, and J.V. Ward. 1996. Importance of light and nutrients in structuring an algal community in a Rocky Mountain stream. J. Freshwater Ecol. 11: 399-413.
- Wetmore, S.H., R.J. Mackay, and R.W. Newbury. 1990. Characterization of the hydraulic habitat of Brachycentrus occidentalis, a filter-feeding caddisfly. J. N. Am. Benthol. Soc. 9: 157-169.

White, F.M. 1999. Fluid Mechanics - 4th Edition. WCB McGraw-Hill, Boston.

- Wiggins, G.B. 1996. Trichoptera Families. *in* An Introduction to the Aquatic Insects of North America – Third Edition. *Eds.* R.W. Merritt and K.W. Cummins. Kendall/Hunt Publishing Company, IA.
- Williams, D.D., N.E. Williams, and Y. Cao. 1997. Spatial differences in macroinvertebrate community structure in springs in southeastern Ontario in relation to their chemical and physical environments. Can. J. Zool. 75: 1404-1414.
- Young, W.J. 1992. Clarification of the criteria to identify near-bed flow regimes. Freshwater Biol. 28: 383-391.
- Young, W.J. 1993. Field techniques for the classification of near-bed flow regimes. Freshwater Biol. 29: 377-383.

Chapter 2 - Figures



Α.



Β.

Figure 2-1. Taxonomic richness of macroinvertebrate taxa in relation to stream discharge. A. Taxonomic richness measured per 'patch' (per Surber sample, ~ 0.090 m²). B. Taxonomic richness measured per stream (total taxa collected in all three benthic sample replicates per stream). Macroinvertebrates identified to lowest convenient taxonomic level, usually genus.





Figure 2-3. (next page) Canonical correspondence analysis (CCA) biplot for the 24 benthic macroinvertebrate taxa and the 11 environmental variables of the lower Torpy River, British Columbia. For clarity, the biplot has been divided into constituent taxonomic (top) and environmental (bottom) variable components. Taxa scores labelled with open circles, environmental variables (vectors) labelled with arrows. A ln(x+1) transformation was performed on the taxa data. The following environmental variables are indices: DEFOL (riparian vegetation defoliation index; 0 = intact riparian vegetation, 1 = defoliated riparian vegetation), SUBSTR (substrate composition; higher values indicate increasingly fine bed material), LOGPROX (logging activities in proximity of stream catchment; 0 = no logging activity in catchment, 1 = logging in catchment), and RIPARIAN (riparian vegetation index; higher values indicate increasingly open streamside vegetation). See Methods and Materials and Tables 2-4 and 2-5 for further clarification of abbreviations used.





Figure 2-4. Relationship between abundance of *Epeorus* larvae and channel depth (D) in streams 48 and 56 in the lower Torpy River watershed, British Columbia.



Figure 2-5. Relationship between abundance of *Epeorus* larvae and mean velocity (U, measured at 0.6D – see text for details) in streams 48 and 56 in the lower Torpy River watershed, British Columbia.



Figure 2-6. Relationship between abundance of *Epeorus* larvae and channel Reynolds number (Re) in streams 48 and 56 in the lower Torpy River watershed, British Columbia.



Figure 2-7. Relationship between abundance of *Epeorus* larvae and relative roughness (D/k_{ave}) in streams 48 and 56 in the lower Torpy River watershed, British Columbia.


Figure 2-8. Relationship between mean velocity (U) and depth (D) measured in streams 48 and 56, located in the lower Torpy River watershed, British Columbia.



Figure 2-9. Relationship between near-bed velocity ($U_{0.02m}$ – velocity measured 2 cm above the bed) and mean velocity (U – measured at 0.6D). See text for details.

Chapter 3

Near-bed hydrodynamics above boulders in shallow torrential streams

Summary

- The near-bed hydraulic environment inhabited by torrential stream fauna was characterised by recording velocity profiles, near-bed velocities, and shear stress distributions over the upper surface of eight streambed boulders in a mountain stream located in east-central British Columbia. Flow at the study site was rough-turbulent.
- 2. Velocity profiles above the boulders regularly deviated from a semi-logarithmic shape. Velocity profiles were often found to be 'wedge-shaped', with velocities increasing from the free surface downward, reaching a maximum a few millimetres above the stream bed; velocities below this point decreased rapidly and logarithmically towards the bed surface. Near-bed acceleration resulting from flow constriction by the curved leading edge of the boulder protruding upward is proposed as the mechanism producing this distinctive velocity distribution.
- 3. Wall shear stress (τ_w), measured using a Preston-static tube (PST) was generally lowest over the leading edge of the boulders, and increased over the upper surface, reaching a maximum near the rear of the stone (upstream of the point of flow separation, where the shear stress dropped off abruptly). High shear stresses were also recorded on the sides of the boulders.
- 4. Wall shear stress measurements made using the PST were similar to shear stress estimates made using the law of the wall (*i.e.* the velocity gradient method; estimating τ_w based on the slope of the regression of U on In z) only at locations where velocity profiles were log-normally distributed. Where velocity profiles were wedge-shaped, the velocity gradient method underestimated τ_w compared to the direct measurements made using the PST.
- Bed geometry was found to be an important influence on near-bed flows in shallow streams with low relative submergences. Possible mechanisms by which bed geometry may influence nearbed flow parameters are discussed.

Introduction

The hydrodynamic forces created by moving water are perhaps the most important factors governing the behaviour, distribution, and ecology of benthic invertebrates in stream environments (Carling 1992; Hart et al. 1996; Hart and Finelli 1999). Benthic organisms living on the exposed surfaces of boulders and gravels are subjected to a suite of hydraulic forces that are variable in both time and space (Hart et al. 1996; Buffin-Belanger and Roy 1998). While at first glance this environment may seem hostile, there are benefits to living in habitats of this type. For example, high near-bed velocities decrease the risk of predation (Peckarsky et al. 1990; Hart and Merz 1998), increase the respiratory efficiency of the gills of stream benthic insects (Wiley and Kohler 1980; Pommen and Craig 1995), and increase the rate of seston delivery to suspension-feeding benthic invertebrates (Wetmore et al. 1990; Lacoursière 1992). However, high velocities also increase the lift, drag, and shear stress acting to dislodge invertebrates from the substrate (Weissenberger et al. 1991; Vogel 1994; also see Denny 1994; Delgado and Carbonell 1997).

In addition to their role in regulating the biology of streams, hydrodynamics influence a number of physical processes, including dissolved oxygen levels (Moog and Jirka 1999), near-bed flow patterns (Jarrett 1990; Bergeron 1994), the level and structure of turbulence (Robert et al. 1996; Buffin-Belanger and Roy 1998; Sukhodlov et al. 1998), bed roughness (Nikora et al. 1998) and bedload movement (Blizard and Wohl 1998). Yet, despite the numerous studies that have been conducted within streams, few descriptions of stream flow have been made at spatial scales important to stream organisms (*i.e.* within millimetres of the surface of the becl; see Hart et al. 1996). Moreover, the generation of eddies, wall shear stress, and other boundary layer phenomena, which take place at these spatial scales, are likely to have direct effects on stream organisms.

A number of recent studies have stressed the need to study the biology and environment of benthic invertebrates at the small spatial scales at which they experience flow (Carling 1992; Hart et al. 1996). However, due to the difficulty of characterising flow at organism-defined scales, most research efforts continue to examine the biology of stream macroinvertebrates at reach, or even watershed scales. It is reasonable to suggest that an understanding of the proximate and ultimate forces that shape the behaviour, ecology, and morphology of stream macroinvertebrates will be gained by examining the hydraulic processes of streams at biologically relevant spatial scales. This

is especially true of torrential streams where benthic organisms depend on high velocity habitats for nutrient delivery, protection from predation, and gas exchange (Vogel 1994).

Given the importance of small scale fluid phenomena to stream organisms, and the relative rarity of studies at these scales, it seems timely to describe the near-bed hydraulic environment experienced by larval insects in torrential streams with steep slopes and coarse substrates. To achieve this end, this study has three specific goals: (1), to examine the distribution of velocities over the upper surfaces of torrential stream boulders; (2), to measure the range and distribution of shear stress on stream boulders; and (3), to characterise the local channel hydraulics of torrential stream environments. This will be achieved through description of the flow environment of a shallow stream at high spatial resolution, as well as measurements of wall shear stress in a natural channel.

Methods and materials

Study Area and Experimental Approach

The study site was located on a tributary of the Torpy River, located approximately 90 km east of Prince George, British Columbia, Canada (Figure 3-1). The 20 m study reach was a single thread, generally straight channel, with an average stream surface slope of 3.2%, although local water surface slopes regularly exceeded 70%. The bed was composed primarily of boulders and cobbles with patches of coarse gravel in the interstices (pockets) between the larger substrate elements (see chapter 2 for a definition of stone size classes). Streambed gravels were poorly cemented, due to the high gradient and seasonally variable discharge of the study stream. The maximum discharge of the stream recorded at the site during the study period (Aug.15 to Oct.15, 1998) was 0.43 m³ s⁻¹ on October 2, 1998.

In order to examine the relationship between bed geometry, bulk flow, near-bed flow, and the benthic biota, a series of stones (also referred to as boulders depending on size; see below) were deployed in the stream channel at the site. Thirty stones (ranging in size from 22 – 36 cm in diameter; *i.e.* small boulders, referred to below as stones or boulders, depending on size) were collected from the banks of streams within the Torpy River watershed, with care taken to obtain stones from above the high-water line. Obtaining stones in this fashion ensured that they would not have prior accumulations of dried biofilm from previous immersions, a factor that might influence

subsequent growth of periphyton. Light coloured (off-white to tan), naturally rounded stones were chosen in order to facilitate the observation of insect and algal distributions, as well as minimise the influence of substrate colour on insect behaviour. The stones were subsequently removed to the Aquatic Sciences Laboratory at UNBC, where they were cleaned with a stiff nylon brush and marked with an identification number and a 5 x 5 cm grid of points (Figure 3-2). The reference grid provided an accurate and reliable system to facilitate the recording of the distribution of hydraulic and biotic parameters over the surface of each stone. The reference points were distributed in a modified Cartesian grid, the centre of which was a datum located at the intersection of the longest and second longest orthogonal axes (*i.e.* the centre of the upper surface of the stone). Both the grid and the identification number were applied to the stone using an indelible black felt marker (Sharpie[®] Permanent Marker; Sanford, USA).

The stones were deployed in the active channel at the study site on August 20, 1998. In order to ensure that the stones were placed in 'natural' orientations, where possible, naturally occurring boulders were removed from the stream bed and replaced with stones of similar shape and volume. In addition, to minimise hydraulic interactions between substrates (see Davis and Barmuta 1989; Young 1993), the stones were placed in the channel at approximately 1 m intervals in an offset pattern, such that no stone was immediately upstream of another. After deployment, the stones were left undisturbed for 10 days in order to accumulate the biofilm, periphyton, and benthic invertebrates characteristic of the stones of the surrounding stream bed. During this time the densities of larval Epeorus longimanus (a representative high velocity, torrential habitat species) were monitored on each of the deployed stones. After the acclimatisation period had ended, a series of measurements were made on the five stones that had the highest densities of *E. longimanus*. The measurements, which were used to estimate the preferred microhabitat of this torrential mayfly, included stream bed / water surface profiles, wall shear stress distributions, midline and midpoint velocity profiles, and identification of basic flow patterns through flow visualisation using fluorescein dye (see below). For comparison and verification, the flow fields of three additional naturally occurring boulders with similarly high densities of E. longimanus were also examined in the same manner.

Some of the techniques were tested under field and laboratory conditions prior to their use in the field. Specifically, to compare the hydraulic conditions measured at the torrential stream site (stream 48) with the hydraulic conditions of relatively simple channels, a velocity profile, shear stress

estimate, and stream bed / water surface profile were obtained over a gravel bed riffle in an adjacent stream of lower average slope (1.5%) but similar discharge. Three velocity profiles were also collected in a laboratory flume at UNBC (20 cm x 20 cm x 200 cm long) at different velocities (0.242, 0.382, and 0.465 m s⁻¹).

Apparatus

The water surface and stream bed topography were measured in transects above each of the deployed and natural stones using a stream hydraulics profiling device, similar to the Wilson Creek flow profiler used by Wetmore et al. (1990). Whereas the Wilson Creek profiler consisted of a point gauge mounted on a triangular tripod table, the apparatus used in this study consisted of a rectangular, field deployable stage (table) with an adjustable leg at each corner. A cylindrical PVC socket (3" diameter) was mounted vertically in the centre of the field stage, permitting the quick and easy interchange of the two types of apparatus used to quantify the stream environment; (1) a point gauge to measure water surface / stream bed topography, and (2) a Preston-static tube (see below, and Appendix 4) to measure water velocity and shear stress. The field stage, while minimising disturbance to local flows, also allowed the Preston-static tube and point gauge to be fixed at any height with a minimum of flow-induced vibration. The stage consists of a rectangular aluminium frame (40 x 152 cm) which could be levelled above the stream using the adjustable aluminium legs and a circular liquid bubble level. Positioning of the Preston-static tube in the streamwise (x) direction was made possible by a smaller (40 x 40 cm) aluminium stage which could be adjusted on the rails formed by the long axis of the larger frame. The second, smaller frame in turn supports an acrylic sheet (36 x 40 x 1 cm), in the centre of which the point gauge was fixed. The acrylic sheet, capable of sliding over the second aluminium frame on polyethylene runners, provided positioning in the cross-stream (y) direction, while a rack and pinion gauge fitted with a vernier scale provided positioning in the vertical (z) plane. Using this method, the Preston-static tube or point gauge could be positioned accurately at any point above the surface of the stream bed.

Measurements of near-bed velocity profiles were made using a small-scale Preston-static tube (PST), essentially a Pitot-static constructed of a 90° bevelled tip syringe needle fixed to a sidebored syringe needle (tube diameter = 0.88 mm; see Ackerman et al. (1994) for a detailed

description). The Preston-static tube differs from a standard Preston tube in that the dynamic pressure port (which faces into the flow) is coupled with a static pressure port (on the sidewall). As a result, the difference between static pressure p_s and dynamic (or stagnation) pressure p_0 can be measured, and velocity or shear stress can be determined, depending on deployment (see below). A Validyne model CD379-1-2 membrane-type differential pressure transducer (Validyne Engineering; Northridge, CA), connected to the Preston-static tube via 2.0 m of flexible pressure lines (inside diameter = 3 mm), was used to measure differential pressure. Before each set of measurements was taken, the pressure lines connecting the Preston-static tube and pressure transducer were visually inspected for the presence of any introduced air bubbles that would potentially alter pressure transmission. Both the pressure transducer and the pressure lines were periodically flushed in order to minimise the possibility of the presence of trapped air, which would bias the differential pressure measurements. The pressure difference (which is related to velocity; see equation 3-2 below) was expressed as a voltage by a Validyne portable indicator (model CD379). Fifteen voltages were recorded over the course of approximately 30 seconds, due to the relatively slow response time of the Preston-static tube / pressure lines / pressure transducer system. These voltages were converted to differential pressure, then averaged.

One of the primary disadvantages of both Preston tubes and Pitot tubes is that they must be aligned parallel to the flow; there are substantial errors in both p_s and p_0 associated with yaw angles greater than 10 degrees (White 1999). Preliminary diagnostic tests in both the lab flume and the natural stream channels confirmed that the inaccuracies associated with positioning errors less than 10 degrees are negligible (Ackerman and Hoover 2001). When deployed in the field, flow visualisation using sodium fluorescein injected upstream of the Preston tube was used to ensure that the Preston tube was oriented parallel to the flow. To record velocity at a given height above the substrate, the Preston tube was deployed at the correct depth using the rack and pinion gauge. Then, using a long, thin needle (length = 200 mm, diameter = 1 mm), a filament of dye was injected approximately 10 mm upstream of the tube. The orientation of the tube with respect to the dye filament was then checked with a magnifying, subsurface periscope, which was oriented in the water perpendicular or downstream of the Preston-static tube. If the tube and dye trail were not parallel (*i.e.* the Preston tube was incorrectly oriented), the tube was readjusted in order to ensure that it was oriented directly into the flow.

The Preston-static tube used in this study is configured such that it can be used to directly measure wall shear stress when deployed on a surface (Ackerman et al. 1994). The Preston-static tube (PST) was developed for measuring wall shear in situations where the incorporation of a wall-mounted static pressure tap is impractical (*i.e.* around small-scale objects where flow lines may be curved), but has been recently tested for use in a variety of field and lab conditions (Ackerman and Hoover 2001).

The relationship between the voltage output of the pressure transducer and pressure head was determined by calibrating the pressure transducer by varying the pressure, produced by a column of water of known height, across the transducer membrane. A regression of head (height) against the voltage output provided the following relationship:

Head =
$$-0.00164 + (0.0508 \times voltage)$$
 (3-1)

(n = 15, R^2 = 1.00; ANOVA F(1,13) = 5.29 x 10²⁷, p < 0.001). Bernoulli's equation, which relates pressure, velocity, and height of the fluid (head), is

$$P + 1/2\rho U^2 + \rho gh = constant, \qquad (3-2)$$

where P is the pressure in the moving fluid, ρ is the density of the fluid, g is gravitational acceleration (9.81 m s⁻²), and h is the height of the fluid. Given equation 3-2, the relationship between pressure (head) and velocity is

$$U = (2g\Delta h)^{0.5},$$
 (3-3)

where the variables are as defined above. Preston (1954) demonstrated that the nondimensionalised pressure difference, x*, can be expressed as

$$x^* = \log_{10} \left[(\Delta P \times d^2) / (4\rho v^2) \right], \tag{3-4}$$

where ΔP is the pressure difference, d is the diameter, and v is the kinematic viscosity of water. Similarly, the non-dimensionalised shear stress, y^{*}, can be expressed as

$$y^* = \log_{10} \left[(\tau_w \times d^2) / (4\rho v^2) \right], \tag{3-5}$$

where τ_w is wall shear stress. Preston (1954) (also see Ackerman et al. 1994) showed that the relationship between x^{*} and y^{*} in the wall layer is

$$y^* = -1.394 + 7/8 x^*,$$
 (3-6)

which can be represented as

$$\tau_w = A \times \Delta P^{7/8}, \tag{3-7}$$

where the constant A is given as

$$A = 1 / [10^{1.394} \times (d^2/4\rho \upsilon)^{1/8}], \qquad (3-8)$$

and the pressure difference ΔP is given by

$$\Delta P = \rho g \Delta h \tag{3-9}$$

The constant A is fixed at a given water temperature and density (density ρ and kinematic viscosity υ are dependent on temperature; see appendix A in White (1999)), while the pressure difference ΔP is a function of the density of the medium (ρ), acceleration due to gravity (g; 9.81 m s⁻²), and head Δh .

Channel conditions were characterised using Froude number (Fr). Froude number, an important descriptor of flow conditions in open channels, is the ratio of mean channel velocity to the propagational velocity of a surface wave (Fr = U / $(gD)^{0.5}$). Where Froude numbers are less than unity (Fr < 1; subcritical flow), flows which are characterised by deep, smooth flowing water. Where

Froude numbers exceed unity (Fr > 1; supercritical flow), flows are characterised by broken, white water (see White 1999 and chapter 1 for further discussion).

Sampling

The shape of the water surface and stream bed were measured along downstream transects crossing the centre of the stones studied using the point gauge and vernier scale. Generally, water surface and bed elevations were obtained at 10 mm intervals over the boulders and at 20 mm intervals over the stream bed in front and rear of the boulder. The total length of each transect varied with the centreline diameter of the boulder.

Velocity profiles were recorded above the centre (datum) of each of the five deployed and two of the naturally located boulders. In addition, velocity profiles were recorded above the surface of a smaller stone (N03), and above a gravel riffle (GR). Each profile consisted of velocities taken at incrementally increasing distances from the surface of the stone (0, 1, 2, 3, 5, 7, 9, 12, 15, 18, 23, 28, and 33 mm). In instances where the water surface was greater than 33 mm from the surface of the stone, additional velocity measurements were taken at 10 mm intervals. These heights were chosen in order to provide the resolution necessary to describe both the near-bed and bulk flow fields. In all cases, velocity measurements could not be obtained in a zone extending approximately 3 – 10 mm down from the water surface, due to the periodic exposure of the PST tip to air during frequent fluctuations in depth of the highly turbulent flow. Velocity profiles were obtained at 50 mm intervals along the centre line of the upper surface of three of the deployed boulders (stones 7, 31, and 25) in order to assess the changes in flow that occur as water crosses the upper surface of stream boulders.

Distributions of wall shear stress over the surface of the five deployed boulders (stones 7, 31, 25, 23, and 10) and two of the three naturally occurring boulders (N01 and N02) were measured using the PST. In each case, the spatial distribution of shear stress was measured by recording shear stress in perpendicular transects. A streamwise transect of shear stress measurements was taken along the centreline of each boulder in the direction of flow at 25 mm intervals, while the second, cross-stream transect was taken perpendicular to the first at 50 mm intervals, crossing the streamwise transect at the centre of each boulder. The location of each shear measurement corresponded to points of the reference grid. In addition, single measurements of shear stress were

made on the upper surface of the third naturally occurring stone (N03), the gravel bed riffle (GR), and in the UNBC lab flume at the three different velocity settings.

Data Analysis

The stream bed / water surface data were plotted as profiles showing the upper and lower boundaries of the flow measured over each of the boulders. These profiles are hereafter referred to as "surface/bed contours" in order to distinguish them from the vertical velocity profiles obtained above the bed, which are termed "velocity profiles".

Conventionally, mean velocity is determined as the velocity at 60% of the total depth ($U_{0.6D}$). However, Jarrett (1990) recommends that, in the case of mountain rivers, mean velocities are more accurately approximated by mid-depth velocities ($U_{0.5D}$) than velocities at 60% of the total depth ($U_{0.6D}$). As such, for the purposes of this study, 'mean' or mid-depth velocities were estimated using Jarrett's (1990) 0.5D guideline. Near-bed ($U_{0.002m}$) and mid-depth ($U_{0.5D}$) velocities were estimated from the velocity profiles by interpolation using the velocities at the two depths of the profile that bracket the depth for which a velocity is required. The error associated with this method was thought to be minimal due to the high spatial resolution of the velocity profiles obtained (as noted above).

Velocity profiles were categorised as belonging to one of three categories; (1) *log-normal* (displaying a typical semi-logarithmic shape); (2) *wedge-shaped* (displaying a distinctive shape in which velocities increase in logarithmic fashion downwards from the water surface, reaching a maximum value at a point near the bottom, and then decreasing); or (3) *transitional* (velocity profiles showing some near-bed distortion, and appear to be intermediate between log-normal and wedge-shaped profiles). Tests of linearity (*e.g.* XLOF (Minitab 1985; Minitab Inc., State College, PA); see Bergeron 1994) were not used to determine if velocity profiles were log-linear. Rather, a vertical velocity variation index (Ü) of the relative magnitude of the difference between mid-depth and near-bed velocities (equation 3-10) was used to categorise the velocity profiles, because the vertical distribution of near-bed velocities is a primary focus of the study. The index Ü is given as

$$\ddot{U} = (U_{0.5D} - U_{0.002m}) / U_{0.5D}$$
(3-10)

where the subscripts 0.5D and 0.002m refer to 50% of the total channel depth and 2 mm from the bottom, respectively. In cases where $\ddot{U} > 0.15$, velocity profiles were categorised as being relatively log-normal (*i.e.* mid-depth velocities were substantially lower than near-bed velocities; category 1). In cases where $\ddot{U} < -0.15$ in magnitude (*i.e.* near-bed velocities substantially exceeded mid-depth velocities), velocity profiles were categorised as wedge-shaped (*i.e.* category 2). When the distribution of velocities was such that $-0.05 < \ddot{U} < 0.05$ (*i.e.* near-bed and mid-depth velocities were approximately equal), velocity profiles were categorised as transitional (*i.e.* category 3). When the magnitude of the difference between mid-depth and near-bed velocities was intermediate between categories ($-0.15 < \ddot{U} < -0.05$ and $0.05 < \ddot{U} < 0.15$), the functional type of the profile was determined by visually inspecting the plot of depth *z* against velocity *u*.

All statistical analyses (regressions, ANOVA, ANCOVA) were conducted using Statistica 5.0 (Statsoft, Tulsa, Oklahoma). Where the number of data points available for regression analyses were limited, R^2_{adi} (R^2 adjusted for a small sample size) was used as an indicator of the goodness of fit.

Results

Stream bed and water surface topography

The stream bed and water surface topographies along the centre line of each of five deployed boulders (Figures 3-3 to 3-7), three naturally occurring boulders (Figures 3-8 to 3-10), and a gravel-bed riffle (Figure 3-11) are shown below. While the surface/bed contours collected over the boulders were quite variable in shape, they shared several common features. The elevation in water surface associated with deceleration of flow (*i.e.* hydraulic drop) at a stagnation point was seen at the upstream margin (*i.e.* front) of each of the stones, although the magnitude of the hydraulic drop was limited in several cases, and influenced by phenomena upstream. Subsequent decreases in water depth associated with accelerating and partially deflected flow were seen downstream along the upper surface of the boulders (Figures 3-6, 3-7, 3-8). Increases in water surface elevation associated with a hydraulic jump were also visible downstream of the boulders (Figures 3-3, 3-4). In addition to the downstream patterns noted in the centreline transects, as the height of streambed boulders approached the depth of the water (*i.e.* relative submergences decreased), water was forced to flow around the bed elements rather than over them (*i.e.* flow became increasingly three-dimensional).

The flow around stone 7 provides a representative example of these flow features, as the stream bed was composed of gravels and cobbles of substantially smaller diameter than the deployed boulder (see Figure 3-3). The changes in water surface elevation associated with the hydraulic drop, acceleration, and re-expansion in the hydraulic jump were seen over the front, upper surface, and rear of the stone, respectively. Similarly, stone 31 was located in a relatively smooth section of the study reach, and flow features similar to those noted above were also visible (Figure 3-4). The same flow features were associated with stone 23 (Figure 3-6), although the surrounding substrate was composed of coarser bed material. Unlike the other deployed substrates, stone 25 was located below an 80 mm cascade produced by water flowing over an upstream obstruction composed of boulders and cobbles (Figure 3-5). As a result, a substantial portion of the flow plunged onto the front edge of the stone. The angle of the approaching flow and the proximity of the stone immediately upstream interacted to create a zone of recirculating, interactive flow between the two stones. Of the three naturally positioned boulders, N01 was located in a high velocity location (Figure 3-8), and provided little resistance to the flow due to bed material piled up against its leading edge. Boulder N02 was more similar to stone 7 in that it protruded into the flow, and the slope of the approaching flow was relatively flat (Figure 3-9). N03 was located in an exposed location on the stream bed, and had a substantial change in water surface slope over its surface (Figure 3-10).

Compared to flow above the boulders, relatively little variation in water surface or bed elevation was recorded above the gravel riffle (GR; Figure 3-11).

Velocity profiles

The vertical distribution of velocity and the near-bed flow regimes over the upper surface of the torrential stream boulders were characterised through the measurement of 14 velocity profiles over the five deployed boulders and three profiles over the upper surface of three naturally occurring boulders. These profiles were compared to a profile measured over a gravel riffle and three profiles obtained at various velocity settings in a laboratory flume.

Four vertical velocity profiles, separated by a distance of 50 mm, were measured above the upper surface of stone 7 (Figure 3-12). None of the profiles conformed to a logarithmic velocity profile model (see Table 3-1), although the profile obtained over the rear of the stone was distorted to a lesser extent than the profiles measured over the front of the stone. For purposes of comparison,

two additional velocity profiles were obtained over the centre of stone 7 during periods of elevated stream discharge (Aug. 7 and Sept. 30). The three velocity profiles obtained above stone 31 are shown in Figure 3-13, the four velocity profiles measured over the upper surface of stone 25 are shown in Figure 3-14, and the single velocity profiles were collected over the centres of stone 23 and stone 10 are shown in Figure 3-15. The upper surface of stone 10 extended nearly to the water surface. As a result, much of the flow was diverted around the sides of stone 10 rather than over its upper surface. One velocity profile was collected over the centre of the upper surface of stones N01, N02, and N03 (Figure 3-16). A single velocity profile was also obtained above a small stone in the gravel bed riffle site GR (Figure 3-16), located in an adjacent stream. As mentioned above, the bed of the gravel riffle site was composed of well-sorted, relatively fine gravels (see Figure 3-11).

Flow immediately above the upper surfaces of the stones exhibited a variety of patterns. In many cases, velocity profiles deviated from a semi-logarithmic velocity distribution (where velocity increases with the logarithm of distance from the bed) in that they showed substantial near-bed distortion, often in the form of high velocity 'wedges' (e.g. Figure 3-12). This was especially pronounced where the leading edge of the stone was exposed to the flow and the geometry of the stone was curved or inclined (rather than square-edged) (Table 3-1). In these instances (stones 7, 31, 23, N03), flow was constricted, and near-bed velocities (U_{0.002m}) substantially exceeded midstream (U_{0.5D}; see Table 3-2) or near-surface velocities. Although measured at various points over the upper surface of different boulders, the distorted velocity profiles shared several common features. In each case, maximum velocities decreased in a logarithmic manner towards the free surface. In each case, velocities increased logarithmically from the bed to the depth at which the maximum velocity was recorded.

Figure 3-12 shows that the velocity profile over the front (10 cm upstream of centre) of stone 7 was 'wedge' shaped (see Table 3-3 for a summary of velocity profile shapes at all stone locations). Velocity profiles obtained 5 cm upstream of the stone's centre and stone's centre were transitional (intermediate between distorted, wedge-shaped profiles and logarithmically distributed profiles), while the velocity profile 5 cm downstream of the stone's centre was approaching log-normal. While the inclined, curved leading edge of stone 7 created near bed acceleration over the front of the stone, the upper surface of the stone was generally flat. Surface flow conditions, as indicated by the Froude

number, also changed as flow crossed stone 7 (Table 3-2). Local Froude number, determined at the position of the velocity measurement, increased (10 cm upstream of centre Fr = 0.98, 5 cm downstream of centre Fr = 1.82) and became supercritical (*i.e.* Fr > 1) as flow crossed the boulder. The mean velocity also increased along the downstream transect, from $U_{0.5D} = 0.713 \text{ m s}^{-1}$ to $U_{0.5D} = 0.950 \text{ m s}^{-1}$. The height above the substrate at which maximum velocities were found increased in the downstream direction above stone 7 as well (see Figure 3-12). The boundary layer thickness δ (estimated as the height above the substrate at which velocities attain 90% of maximum) was approximately 3.5 mm at the front of the stone, and approximately 5 mm at the most downstream point measured (5 cm downstream of centre). However, assigning a precise value of δ to these locations above the boundary is difficult, due to the non-logarithmic nature of the velocity distribution.

Table 3-1. Stone surface geometry and velocity profile shape categories for all

sampled stone surface locations

Stone	Stone curvature	Profile location ^a / Profile shape ⁵						
		+100 mm	+50 mm	0 (centre)	-50 mm			
7	Leading edge ^c	Wedge	Transitional	Transitional	Log-normal			
31	Entire		Transitional	Wedge	Wedge			
25	Little ^d	-	Wedge	Wedge	Wedge			
23	Entire	-	-	Wedge	-			
10	Leading edge	-	-	Log-normal	-			
N01	Little	-	-	Transitional	-			
N02	Little		-	Log-normal	-			
N03	Entire ^e		-	Wedge	-			
GR (riffle)	Little			Log-normal	-			

^a locations at which velocity profiles were obtained are recorded with respect to the centre of the stone (*e.g.* +100 mm denotes that the profile was obtained 100 mm upstream of the stone's centre, 0 denotes the centre of the stone)

^b see text for definition

^c curvature restricted to the leading edge of the stone; the centre of the stone was relatively flat

^d the upper surface of stone 25 was relatively flat; however, the stone was inclined slightly in the upstream direction (see Figure 3-5)

^e the upper surface of stone N03 was relatively flat; however, the stone was inclined steeply in the upstream direction (see Figure 3-10)

The leading edge of stone 31 (Figure 3-4) was continuously curved, unlike stone 7. As the approaching flow crossed the front of stone 31, the rising bed elevation forced the flow near the bed to accelerate (Figure 3-14). As flow crossed the stone it became supercritical (Fr = 0.78, and Fr = 1.67, 5 cm upstream and 5 cm downstream of the centre of the stone, respectively), mean velocities increased ($U_{0.5D} = 0.575 \text{ m s}^{-1}$ to $U_{0.5D} = 0.925 \text{ m s}^{-1}$), and near-bed velocities showed a marked

increase as well (Table 3-2). The near-bed high-velocity wedge was still present above the rear of the stone, suggesting that the velocity distortion may have projected off the rear of the stone.

Stone	Date	Location on stone*	U _{0.50} (m s ⁻¹)	U0.002m (m s ⁻¹)	Rex ^b	Fr	Tw-PST
7	Aug. 31	+100 mm	0.713	0.808	47,500	0.98	2.82
7	Aug. 31	+50 mm	0.825	0.803	72,800	1.35	2.06
7	Aug. 31	0 (centre)	0.922	0.827	101,000	1.66	2.65
7	Aug. 31	-50 mm	0.950	0.720	110,000	1.82	2.17
7	Sept. 30	0 (centre)	0.870	0.738	90,000	0.96	2.24
7	Oct. 7	0 (centre)	1.260	0.783	95,400	0.77	2.51
31	Sept. 2	+50 mm	0.575	0.580	23,200	0.78	1.61
31	Sept. 2	0 (centre)	0.747	0.796	56,700	1.13	2.82
31	Sept. 2	-50 mm	0.925	1.010	103,000	1.67	3.88
25	Sept. 8	+50 mm	0.646	0.938	49,800	0.87	5.77
25	Sept. 8	0 (centre)	0.418	0.982	81,000	0.60	3.52
25	Sept. 8	-50 mm	0.550	0.770	89,500	0.91	2.83
23	Sept. 30	0 (centre)	0.527	0.598	46,000	0.97	1.50
10	Sept. 23	0 (centre)	0.610	0.519	51,300	1.28	0.761
N01	Sept. 26	0 (centre)	1.360	1.230	127,000	1.50	6.27
N02	Sept. 27	0 (centre)	0.700	0.420	36,800	0.95	0.782
N03	Aug. 7	Rear edge	0.958	1.183	88,700	1.45	6.34
Gravel riffle	Aug. 18	Centre	0.429	0.228	2130	0.41	0.217
Flume 1	July 14	1.3 m downst. ^c	0.465	0.350	284,000	0.60	0.536
Flume 2	July 14	1.3 m downst. ^c	0.382	0.290	236,000	0.41	0.339
Flume 3	July 14	1.3 m downst. ^c	0.242	0.191	155,000	0.32	0.127

Table 3-2. Summary of flow conditions for all sampled stone surface locations

^a locations at which velocity profiles were obtained are recorded with respect to the centre of the stone (*e.g.* +100 mm denotes that the profile was obtained 100 mm upstream of the stone's centre, 0 denotes the centre of the stone)

^b the distance from the leading edge (at the stagnation point) of the stone was used as the length scale to calculate local Reynolds number (Re_x); in the case of the lab flume, the distance from the mouth of the flume (1.3 m) was used

^c measurements taken 1.3 m downstream of the mouth of the flume

The upper surface of stone 25 was inclined upwards in the downstream direction (see Figure 3-5). The three velocity profiles obtained over stone 25 were distinctly wedge-shaped, and revealed high near-bed velocities (Figure 3-14). However, there was no consistent increase or decrease in either near-bed ($U_{0.002m}$) or mean ($U_{0.5D}$) velocities as flow crossed the upper surface of the stone (Table 3-2), possibly due to the highly three dimensional, complex flow patterns generated by the plunging flow. The inclined upper surface of stone 25 likely influenced both rates of acceleration and distributions of velocity.

Stone 23 (Figure 3-6) had a relatively curved upper surface, and continuous flow constriction over the front half of the stone produced a wedge-shaped velocity profile over the centre of the stone

(Figure 3-15). The shape of this profile was similar to the profiles obtained over stone 31 and the front of stone 7. Maximum velocity was recorded 2.5 mm above the substrate, and velocities decreased logarithmically above this point. The current velocity 2 mm above the bed was greater ($U_{0.002m} = 0.60$ m s⁻¹) than the mean velocity ($U_{0.5D} = 0.53$ m s⁻¹). Flow over the centre of the stone was approximately critical (Fr = 0.97).

Table 3-3. Velocity profile shapes and regression parameters used in the estimation of U* and τ_w (velocity gradient method)

Stone	date	Location on	Velocity	Regression coefficients			Tw-dLi/dinz	ANOVA	
		stone*	profile shape ^b	n	R ² adj	slope(B)°		F	p-value
7	Aug. 31	+100 mm	Wedge	4	90.90	0.0607	0.589	30.95	0.031
7	Aug. 31	+50 mm	Transit.	4	98.00	0.131	2.72	147.32	0.0067
7	Aug. 31	0 (centre)	Transit.	4	98.03	0.0915	1.34	150.60	0.0066
7	Aug. 31	-50 mm	Log-norm.	5	97.53	0.139	3.10	159.00	0.0011
7	Sept. 30	0 (centre)	Transit.	4	99.61	0.0835	1.11	776.62	0.0013
7	Oct. 7	0 (centre)	Log-norm.	7	97.65	0.111	1.96	250.82	< 0.001
31	Sept. 2	+50 mm	Transit.	5	94.53	0.0450	0.323	70.14	0.0036
31	Sept. 2	0 (centre)	Wedge	3	52.07	0.0596	0.568	3.17	0.33
31	Sept. 2	-50 mm	Wedge	3	96.98	0.110	1.94	65.38	0.078
25	Sept. 8	+50 mm	Wedge	6	98.05	0.0956	1.46	251.87	< 0.001
25	Sept. 8	0 (centre)	Wedge	4	93.13	0.104	2.33	41.66	0.023
25	Sept. 8	-50 mm	Wedge	3	97.37	0.0413	0.273	75.30	0.073
23	Sept. 30	0 (centre)	Wedge	3	94.42	0.0657	0.691	34.86	0.11
10	Sept. 23	0 (centre)	Log-norm.	3	99.09	0.130	2.62	218.90	0.043
N01	Sept. 26	0 (centre)	Transit.	3	99.84	0.0770	0.948	1259.10	0.018
N02	Sept. 27	0 (centre)	Log-norm.	6	92.64	0.0978	1.53	64.00	0.0013
N03	Aug. 7	Rear edge	Wedge	3	86.82	0.0362	0.210	14.18	0.17
Gravel riffle	Aug. 18	Centre	Log-norm.	5	96.47	0.0416	0.277	110.26	0.0018
Flume 1	July 14	1.3 m downst. ^d	Log-norm.	7	98.73	0.0591	0.559	468.14	< 0.001
Flume 2	July 14	1.3 m downst. ^d	Log-norm.	7	96.53	0.0453	0.328	168.14	< 0.001
Flume 3	July 14	1.3 m downst. ^d	Log-norm.	7	97.54	0.0418	0.280	198.46	< 0.001

^a locations at which velocity profiles were obtained are recorded with respect to the centre of the stone (e.g. +100 mm denotes that the profile was obtained 100 mm upstream of the stone's centre, 0 denotes the centre of the stone)

^b see text for definition

^c U* is calculated as the product of the slope (β) and von Karman's constant (κ = 0.4) (see Appendix 2 for a complete discussion)

^d measurements taken 1.3 m downstream of the mouth of the flume

In contrast, the velocity profile obtained over the centre of stone 10 (Figures 3-10 and 3-15) was approximately logarithmically shaped when compared to the profiles obtained above stones 7, 31, 23, and 25. However, the water depth above this boulder was the lowest of the substrates included in the study (D = 23 mm). Flow over the centre of the stone was supercritical (Fr = 1.28),

and mean velocity was $U_{0.5D} = 0.61 \text{ m s}^{-1}$. Current speed at 2 mm above the centre of stone 10 was 0.519 m s⁻¹, and $\delta \approx 1.5$ mm (Table 3-2).

There was little flow constriction over the upper surface of stone N01 (Figure 3-16); bed material deposited against the front of the stone limited the curvature at the leading edge. As expected, the velocity profile over the centre of the stone showed little evidence of near-bed velocity distortion. Near-bed velocities were high ($U_{0.002m} = 1.23 \text{ m s}^{-1}$), and the boundary layer was correspondingly thin ($\delta \approx 1.5 \text{ mm}$). The flow over the centre of stone N01 was supercritical (Fr = 1.50), and mean velocity was 1.36 m s⁻¹ (Table 3-2).

Stone N02 (Figure 3-9), although similar in exposure to flow and size to stone 7, had different geometry. The front of stone had an angular leading edge, where the front of stone 7 was rounded. Consequently, unlike the profile obtained over the centre of stone 7, the profile obtained over the centre of N02 was more logarithmically distributed, and showed no evidence of a near-bed high velocity wedge. The flow over N02 was nearly critical (Fr = 0.95), and the mean velocity was $U_{0.5D} = 0.70 \text{ m s}^{-1}$. The boundary layer thickness over the centre of N02 was 15 mm, and $U_{0.002m} = 0.42 \text{ m s}^{-1}$ (Table 3-2).

The upper surface of stone N03 was inclined in the downstream direction. The inclined surface of the stone continually constricted the flow as it crossed the upper surface of the stone. The single velocity profile collected over the apex of N03 (the rear of the stone) showed that the velocity distribution was highly wedge-shaped. The boundary layer thickness at this point was very thin ($\delta < 1$ mm), current speed at 2 mm height was 1.18 m s⁻¹, and flow over the rear of stone N03 was supercritical (Fr = 1.45) (Table 3-2).

Bed and water surface slope

The slope of the water's surface (S_s) changed dramatically as it passed over each stone (see Figures 3-3 to 3-10). High magnitude, positive rates of changes of water surface gradient in the downstream direction ($dS_s / dx > 4.0 \% \text{ cm}^{-1}$) indicated that the water surface had a strongly convex shape, while low magnitude, positive rates of change of water surface gradient ($0 < dS_s / dx < 4.0 \% \text{ cm}^{-1}$) indicated a weakly convex free surface shape. Negative rates of change of the gradient of the water surface indicate a concave water surface topography. Although the magnitude of the rate of

slope change was variable, water surfaces were generally convex over the boulders (Table 3-4). The water surface over stones 23, 25, and 31 was typically convex as it accelerated over the stone, while the free surface over stone 7 was concave.

Table 3-4. Water surface gradient (S_s) parameters for the five deployed and two natural stones

Stone	$dS_s/dx \ (\% \ cm^{-1})$	R ² _{adj} (%)	Number of measurement points (n)	p-value
7	-2.50	64.4	13	< 0.001
31	4.64	86.8	16	< 0.001
25	4.97	69.2	18	< 0.001
23	4.07	92.3	8	< 0.001
10	2.35	93.9	11	< 0.001
N01	0.83	47.7	12	0.0053
NO2 (front) ^a	-0.87	15.9	7	0.18
NO2 (rear) ^a	7.50	98.1	4	< 0.001

^a the water surface shape appeared to be segmented over stone N02 (*i.e.* the front and rear of the stone had different water surface shapes; see Figure 3-9)

Shear stress measurements from velocity gradients

Shear stress estimates were made using the velocity profile data (from determinations of U* based on the slope of dU / dlnz; see Table 3-3) for the deployed and naturally occurring boulders, gravel riffle site, and laboratory flume. In several cases, regression analyses were conducted using a limited number of points, as the logarithmic portion of the velocity profile was generally very thin (ranging from 2 - 7 mm for the boulders). Generally, the logarithmic portion of the velocity profile was thinner for wedge-shaped velocity profiles; as such, fewer data points were available for these regression analyses. Estimates of shear velocity (U*) made using velocity profile data were greater in locations where velocity profiles were log-normal (n = 5, mean = 0.044, SD = 0.017) than in locations where velocity profiles were transitional (n = 5, mean = 0.034, SD = 0.012) or wedge-shaped (n = 8, mean = 0.030, SD = 0.013).

Shear stress measurements from the Preston-static tube (PST)

The Preston-static tube (PST) was used to directly measure the distribution of shear stress on the upper surface of each of the five deployed stones (Figures 3-17 to 3-21) and two of the naturally occurring stones (N01 and N02; Figures 3-22 and 3-23). Similar shear stress distributions were observed in all five cases where the front face of the stone was exposed to the flow, providing substantial flow resistance (stones 7, 31, 23, 10, and N02). Generally, shear stress was relatively low over the front half of stones, but gradually increased, often to a maximum value, over the downstream half of each stone (Figures 3-17, 3-18, 3-20, 3-21, and 3-23, respectively). Shear stress was generally highest towards the rear of the stones, as water accelerated over the downstream edge. In two cases (stones 7 and 31), a sharp decrease in shear stress was recorded over the rear edge of the stone (see Figures 3-17 and 3-18, respectively). In both cases, flow visualisation confirmed that the shear stress measurements were obtained in or near the zone of flow separation. Flow visualisation also indicated that flow separation occurred at the rear of all stones examined in the study; however, the curvature at the periphery of the remainder of the stones prevented deployment of the PST near the zone of boundary layer separation. Some stones showed substantial lateral variation in wall shear stress (*e.g.* stones 31, 25, 10, N01). In several cases, the shear stress was lowest over the centre of the stone, and increased laterally to one or both sides.

To varying degrees, the shear stress distributions recorded on stones 25 and N01 deviated from the patterns described above. Although low over the front of the stone, recorded values of τ_w were uniformly high over the entire upper surface of stone 25 (Figure 3-19). Stone 25 was located beneath the 80 mm cascade; a jet of water that impinged on the left side (facing upstream) of the upper surface of the stone may have contributed to the high shear in that area. In addition, flow visualisation revealed that the complex pattern of flow produced by the plunging flow upstream of the stone created a zone of separated, recirculating flow at the front of the stone.

There was only a limited increase in shear stress from the front to the back of stone N01 (Figure 3-22). The shear stresses and velocities measured over stone N01 were the highest measured in the study. Very little of the front edge of the stone protruded into the flow due to gravels piled up against the leading edge.

Stone 7 exhibited unexpectedly high shear stress at the leading edge of the stone (Figure 3-17), possibly due to flow impingement in the region at the front of the stone where acceleration of the near-bed flow due to constriction is initiated. The highest shear stresses measured on stones 31 and 10 were located at the lateral peripheries, rather than the midlines, of each boulder. Flow

visualisation indicated that the flow separated at the front of the boulder and accelerated around the periphery of the stone rather than flowing over the top.

Comparison of shear stress measurements made using regression (dU / dlnz) and Preston-static tube (PST) methods

Measurements of τ_{w-PST} (i.e. based on the Preston-static tube) were plotted against simultaneously determined values of $\tau_{w-dU/dinz}$ (*i.e.* based on velocity gradient method using the slope of dU / dlnz) for comparison (Figure 3-24). The paired determinations of shear stress (τ_w) included in the analysis were obtained over the upper surface of the stream boulders (n = 17), over a gravel riffle (n = 1), and in a laboratory flume (n = 3). When all τ_{w-PST} and $\tau_{w-dU/dinz}$ measurements were pooled, there was no significant relationship between measurements of shear stress obtained using the two methods (ANOVA, F(1,19) = 0.064, p = 0.80) (Figure 3-24). If the two methods were completely equivalent, direct measurements of shear stress using the PST would not only be related to estimates of shear stress using the slope of dU / dlnz, but would be numerically similar as well. However, the relationship was significant only when the data were segregated by the shape of the velocity profile (log-normal, transitional, and wedge-shaped). Where velocity profiles were log-normal, the relationship between τ_{w-PST} and $\tau_{w-dU/dlnz}$ was significant (ANOVA, F(1,6) = 7.94, p = 0.030) (Figure 3-Moreover, the velocity gradient (U*) and direct (PST) methods of measuring τ_{w} were 25c). comparable in cases where the velocity profiles were log-normal (*i.e.* the 1:1 line of equality lies within the confidence intervals of the regression of τ_{w-PST} on $\tau_{w-dU/dlnz}$). However, there was no significant relationship between direct measurement using the PST and estimates using U* (extracted from the slope of dU / dlnz) for either wedge-shaped profiles (ANOVA, F(1,6) = 0.23, p = 0.85) or transitional profiles (ANOVA, F(1,3) = 0.070, p = 0.81) (Figures 3-25a and 3-25b). When velocity profiles displayed near-bed distortion (wedge-shaped profile cases), estimates of shear stress using the slope of dU / dlnz tended to underestimate shear stress when compared to direct measurements of wall shear using the PST.

Comparison of shear velocities (U*_{PST}) mean velocities (U_{0.5D})

Shear velocity (U*_{PST}) ranged between 3.43 and 14.19% of mean velocity (U_{0.5D}) at all points at which profiles were taken (see Table 3-2). At points where the measured velocity profile was log-normal, U* was 3.43 - 4.98% of U_{0.5D}. U* ranged between 5.44 - 6.97% of U_{0.5D} where the velocity distribution was transitional, and from 6.73 - 14.19% of U_{0.5D} where velocity profiles were wedge-shaped. U* was 4.65 - 4.98% of U_{0.5D} when velocity profiles were measured in the lab flume, and U* was 3.42% of U_{0.5D} at the gravel riffle site.

Comparison of velocity profiles

In order to compare the data from different stones, the velocity profiles were normalised by the shear velocity U_{PST}^* and the total water depth D (*i.e.* U/U^{*}, z/D; Figure 3-26). With the exception of the three atypical (impinging flow) profiles obtained above stone 25, the wedge shaped profiles are generally characterised by lower values of U_x/U_{PST}^* , while log-normal profiles are characterised by higher values.

Velocity profiles were also normalised using the velocity at mid-depth ($U_{0.5D}$) (Figure 3-27). In this case, logarithmically distributed velocity profiles were located at the lower end of the range of $U_x/U_{0.5D}$, while wedge-shaped profiles were located at the upper end of the range, demonstrating that, in many cases, velocities near the bed substantially exceeded velocities at mid-depth. Where profiles were wedge-shaped, maximum velocities were found near the bed (in all cases $z_{maxU} < 0.2D$).

Local Reynolds number, Froude number, and near-bed velocity

The distance from the stagnation point at the front of the stone (located using dye visualisation) to the point of velocity measurement (x) was used as the length scale in determining the local Reynolds number Re_x (an indicator of boundary flow conditions) for each velocity profile sampling location (Table 3-2). Calculations of Re_x were made using near-bed velocity (U_{0.002m}) rather than mean velocity (U_{0.5D}) in order to describe the boundary flow conditions more accurately, given the occurrence of wedge-shaped velocity profiles (described above). Using these criteria, local Reynolds number (Re_x) was found to be significantly related to Froude number (Fr), (R² = 41.07%; ANOVA, F(1,16) = 12.85, p = 0.0025) (Figure 3-28). However, an examination of the bed/surface contours indicates that three of the cases included in this model may have had atypical boundary

layer growth. In the first case, the plunge upstream of stone 25 created cascading flow that impinged directly upon the upper surface of the stone. In the second case, gravels piled up at the leading edge of the stone N01 may have prevented a stagnation point from developing at the leading edge of the stone. In the third case, skimming flow may have developed over stone 7 when the velocity profile was recorded on October 7, due to the increased depth resulting from rain and melting snow. When the profiles obtained in these three circumstances are excluded from the analysis, the relationship becomes more significant and meaningful ($R^2 = 81.19\%$; ANOVA, F(1,11) = 47.49, p < 0.001). Interestingly, this relationship is stronger than the relationship between near-bed velocity U_{0.002m} and mean velocity U_{0.50} (not shown).

The relationship between Froude number and shear velocity determined using the PST (U_{PST}) is shown in Figure 3-29. The positive linear association between the two measurements is significant (ANOVA, F(1,19) = 6.27, p = 0.022). The relationship between $U_{dU/dinz}^*$ (shear velocity determined the velocity gradient method) and Froude number was relatively stronger (ANOVA, F(1,19) = 9.57, p = 0.0060). Shear velocity (U_{PST}^*) was also significantly related to mean ($U_{0.5D}$) and near-bed ($U_{0.002m}$) velocity (Figure 3-30), although the relationship was stronger for $U_{0.002m}$ (ANOVA, F(1,19) = 390.37, p < 0.001) than for $U_{0.5D}$ (ANOVA, F(1,19) = 14.18, p = 0.0013).

Velocity profile shape and near-bed velocity

Sampling locations on the stream bed with characteristically logarithmic velocity profiles had significantly lower near-bed velocities ($U_{0.002m}$) (ANOVA, F(2,18) = 10.36, p = 0.0010) than locations with either transitional (Tukey's HSD, p = 0.010) or wedge-shaped (Tukey's HSD, p = 0.0014) profiles (see Tables 3-2 and 3-3). There was no significant difference in near-bed velocities between points with transitional or wedge-shaped profiles (Tukey's HSD, p = 0.91). Although there was no significant difference in mean velocity between sites characterised by the three profile types (ANOVA, F(2,18) = 1.69, p = 0.21), there was a significant interaction between the near-bed and mean velocity (Rao's R(4,34) = 10.74, p < 0.001). This indicates that unlike bed locations that were characterised by lognormal and transitional velocity profiles, mean velocities were lower than near-bed velocities in locations that had wedge-shaped velocity profiles.

A one-way analysis of covariance (mean velocity as the covariate) showed that near-bed velocity varied significantly with profile type (ANCOVA, F(2,17) = 28.17, p < 0.001). Near-bed

velocities were higher in locations with transitional and wedge-shaped velocity profiles than in locations with log-normal profiles (Tukey's HSD, p < 0.001 for both tests). There was no significant difference in near-bed velocity between locations with transitional and wedge-shaped velocity profiles (Tukey's HSD, p = 0.71). Even the relatively small distortion in boundary flows found in locations with transitional velocity profiles may restrict the application of log-normal models of velocity distribution.

Discussion

Torrential stream beds are generally composed of boulders and cobbles, with gravel filling the interstices between the larger bed materials. The boulders, however, act as the major distributed roughness elements, and provide the majority of the flow resistance in the channel (Bergeron 1994). The hydraulic habitats associated with streambed boulders are inhabited by a distinct community of benthic organisms (Bouckaert and Davis 1998), each exhibiting adaptations that allow them to thrive in high velocity and high shear stress environments (Statzner and Holm 1982; Weissenberger et al. 1991; Vogel 1994). The objectives of this study were to characterise the fluid dynamic characteristics of flow over the upper surfaces of torrential stream boulders, and to relate them to the distribution of near-bed and boundary flow parameters (*e.g.* τ_w , U*). The results of this study reveal that distinct patterns of shear stress, shear velocity, near-bed and mid-depth velocity are present over the upper surface of stream boulders, despite the complexity of the flow. Importantly, these observations differ from predictions made using open-channel hydraulic theory (White 1999). The near-bed patterns of flow recorded in this study also differ from the results of previous studies that have investigated channels with different characteristics, using different methods (*e.g.* Jarrett 1990; Hart et al. 1996; Bouckaert and Davis 1998).

Velocity profile shape: deviations from log-normal

This study demonstrates that velocity gradients above the upper surface of torrential stream boulders are heterogeneous, and regularly deviate from a semi-logarithmic shape. In many cases, water velocities increased logarithmically downward from the water surface, reaching a maximum only a few millimetres above the stream bed (*i.e.* stone surface). Below this point, velocities decreased rapidly in a logarithmic fashion towards the boundary. In these instances, the velocity gradients immediately above the stones were extremely steep, given the "no-slip" condition, and that

the measured velocities 0.5 mm above the stone surface reached as high as 1.1 m s⁻¹ and regularly exceeded 0.60 m s⁻¹. These distinct velocity distributions are referred to as "wedge-shaped" profiles, in order to distinguish them from the "S-shaped" profiles recorded elsewhere in high gradient natural channels (Jarrett 1990; Bathurst 1994). While the majority of velocity profiles recorded here showed some evidence of this type of near-bed velocity profile distortion, several profiles were approximately log-normally distributed. Log-normal profiles generally occurred where there was sufficient downstream distance for boundary layer development, which suggests that bed geometry and flow interact to create highly diverse and spatially heterogeneous near-bed flow conditions.

The wedge-shaped profiles recorded over stream boulders can be attributed to an uneven acceleration of the water column. In many cases, the leading edge of stones presented an inclined face to the flow, and, as noted by Hart et al. (1996), flow accelerated up the face of the stone. Where flow was substantially constricted as it crossed the stone (i.e. relative submergences were low and the front of the stone was inclined or curved) the water did not accelerate uniformly. Rather, flow near the bed accelerated at a greater rate than flow near the free surface, creating a jet-like structure in the near-bed flow (Figure 3-31). Velocity profiles obtained along centreline transects on stones 7 and 31 suggest that a high velocity "wedge" (a near-bed velocity profile distortion characterised by high velocities at a point immediately above the bed, above and below which velocities decline) was created at the leading edge of the stone where the rising bed elevation constricted the flow (e.g., see Figures 3-3 and 3-4). As the upper surface of stone 31 was continuously curved, near-bed flows continued to be constricted, and as a result, the high velocity wedge increased in magnitude as flow crossed the upper surface of the stone. The curvature of stone 7 was restricted to the leading edge, and as a result, near-bed flows decelerated over the stone with boundary layer development, and the high-velocity wedge was dissipated by momentum transfer. Flow near the water surface was relatively unaffected by the constriction, and accelerated in the downstream direction due primarily to gravity.

Where velocity profiles were wedge-shaped above stones 7 and 31, the core of the jet-like velocity structure (*i.e.* the 'tip' of the wedge) was located approximately 3 to 5 mm above the surface of the stone. Dissipation of the jet (or wedge) may have occurred when boundary layer thickness exceeded this height (assuming that boundary layer growth contributes substantially to viscous damping of the near-bed high velocity wedge). Based on the local Reynolds number Re_x (using near-

bed velocity $U_{0.002m}$ as the velocity term) and an estimated critical boundary layer thickness (δ_{crit} ; in this case the height above the substrate to which the boundary layer would have to develop to completely envelop the near-bed, high-velocity wedge) of 5 mm, the distance downstream (x) of the stagnation point required dissipate the wedge was approximately 164 mm above stone 7, and 162 mm above 31. The distance downstream (x) required for the development of a boundary layer of a given thickness is given by

$$x = \delta_{crit} / (0.16 / Re_x^{1/7})$$
 (3-11)

where δ_{crit} is critical boundary layer thickness and Re_x is the local Reynolds number (White 1999). The velocity profile measured downstream of this point on stone 7 had returned to log-normal, as predicted. Conversely, the most downstream velocity profile measured above stone 31 was 163 mm downstream of the stagnation point. Contrary to what was expected, the high velocity wedge dominated the near-bed portion of the velocity profiles over the entire stone. The continuously curved upper surface of stone 31 may have contributed to continual flow constriction and, as a result, continued near-bed flow acceleration.

In contrast, logarithmically distributed velocity profiles were recorded at relatively few locations above boulders at the site. At each of these points, substantial flow constriction above the stones may not have occurred, due to (1) the development of skimming flow (e.g. stone 7 during high discharge); (2) very low relative submergences (stone 10); or (3) square leading edges (stone N02). It is important to note that although velocity distributions were log-normal in each of these cases, velocities were recorded only at the centre of each stone. Near-bed flow constriction, a factor that leads to the development of wedge-shaped velocity profiles, may have occurred to a limited extent above the leading edge of each stone. However, there was no evidence of near-bed flow distortion by the time flow crossed the centre of the stone. The development of an approximately logarithmic velocity profile could then result, in part, from the low depth and long distance from the leading edge over which boundary layer growth may act to dissipate any near-bed velocity distortion. In addition, due to the limited depth, water was forced to flow round, rather than over, stone 10. This type of three-dimensional flow is poorly understood and difficult to model (see Bathurst 1994; Vogel 1994).

distinctive near-bed velocity profile distortion (wedge) that developed over the front of the boulder was subsequently lost as flow crossed the stone and boundary layer thickness increased.

Several authors investigating shallow flows in natural channels have also reported velocity distributions that do not conform to a semi-logarithmic form. The deviations from the typical logarithmically distributed velocity profile have been variously attributed to flow separation (Bergeron 1994; Hart et al. 1996), skimming flow and high flow resistance near the bed (Bathurst 1994), and the development of an internal boundary layer downstream of flow reattachment (Bergeron 1994). However, the velocity distributions reported in these studies conform to neither a log-normal distribution nor a wedge-shaped velocity profile. In these studies, maximum velocities were generally recorded near the free surface, rather than near the bed. Rather than conflict with our results, the results of Bathurst (1994), Bergeron (1994), and Hart et al. (1996) illustrate the highly heterogeneous nature of flow fields present in the boundary layer flows of shallow streams with complex bed geometry (*i.e.* rough-turbulent flows). Flow constriction over and between boulders, flow deflection by obstacles, and boundary layer separation and reattachment will all contribute to velocity profiles that vary substantially over short distance. In part, the highly heterogeneous near-bed flow environment creates the wide array of "hydraulic niches" available to stream benthic organisms (see chapters 1,2, and 4).

The S-shaped velocity profile recorded elsewhere in high gradient mountain rivers (Jarrett 1990; also see Bathurst 1994) are characterised by velocities which are lower nearer the stream bed and greater near the water surface than a logarithmically distributed velocity distribution. In these flow conditions, the logarithmic profile fails to develop due to drag induced by the coarse bed material. Although both the present study and the work of Jarrett (1984; 1990; 1993) were conducted in mountain channels with cobble and boulder bed material, vertical velocity profiles were not found to be S-shaped here. In fact, the wedge-shaped profiles recorded in the present study are approximately the inverse of S-shaped profiles. Whereas logarithmically distributed profiles overestimate near-bed velocities and underestimate near-surface velocities in S-shaped profile flow conditions (Jarrett 1990), they underestimate near-bed velocities and overestimate near-surface velocities in cases where wedge-shaped profiles characterise the flow. The different findings (S-shaped vs. wedge-shaped profiles) can likely be attributed to two factors. (1) The relative submergence of the bed material was greater in the channels studied by Jarrett (1990); as relative

depths increased, skimming flow developed, and the flow constriction required to accelerate near-bed flows did not occur. Boundary layer development is inhibited by limited flow depth in shallow channels (Nowell and Church 1979). (2) Previous studies, relying heavily on electromagnetic current meters and propeller velocimeters, have not measured flows immediately above the bed with the spatial resolution required to detect any distortions of the velocity profiles. Due to the complex bed topography of mountain streams, irregular pressure gradients will be common (White 1999), and velocity gradients will be correspondingly complex and difficult to predict.

Bathurst (1994) suggested that velocity gradients in mountain rivers would adopt a semilogarithmic shape only at relatively high relative submergences (D/d_k > 10), which is consistent with the depth proposed by Nowell and Church (1979) for the development of log-normal velocity distributions (D/d_k > 8). The results of this study provide evidence that the development of semilogarithmic velocity profiles may also be dependent on bed morphology. At the gravel bed site, velocities were log-normally distributed (D/d_k = 11.24), which conforms to the criteria of Bathurst (1994). Log-normal velocity profiles were also recorded above stone N01 at D/d_k = 0.60 and above stone 7 at D/d_k = 1.60 (when the stream was at near-flood discharge). However, gravels piled up against the leading edge of stone N01 increased the relative submergence of the stone to approximately D/d_k = 2.09. Also, because S-shaped velocity profiles develop as a result of form drag, velocity profiles above substrates that protrude farthest into the flow under skimming flow conditions may be relatively log-normal. Substrate size can also influence the shape of the velocity profile; lognormal profiles may develop over large boulders at relatively low values of D/d_k due to the relatively long distances available for boundary layer development. These results indicate that further study is required to examine the complexity of rough boundary layer flows.

The influence of bed geometry on near-bed and surface flow factors

The results show that the relationship between shear velocity (U*) and mid-depth velocity $(U_{0.5D})$ is dependent on the geometry of the channel bed. In shallow, "chaotic" flows (Young 1992), where the depth of the channel is relatively shallow with respect to the height of the substrate elements and flows are highly three-dimensional and difficult to predict, it may be not be possible to estimate near-bed flow parameters based on measurements of average water velocity. In flow over a gravel riffle, U* was 3.42% of velocity at mid-depth. This agrees with the findings of Ippen (1966),

who found that U* was 3% of free-stream velocity for water flow in a smooth-bottomed channel. In shallow flow over boulders, U* ranged between 3.97 and 14.12% of mid-stream velocities. This was consistent with results reported by Hart et al. (1996), who found that U* was approximately 10% of velocities measured 10 mm above stream boulders, and Denny and Shibata (1989), who reported that U* was between 5 and 15% of mean velocity in flows over rough bottoms. However, the results of the present study indicate that the relationship between shear velocity and free-stream velocity was also dependent on the shape of the velocity profile. Where near-bed acceleration distorted the velocity profile over boulders in shallow flows, U* was proportionally greater (6.74 - 14.19% of U_{0.5D}) than in instances where velocity profiles were log-normal (3.97 - 4.90%). This demonstrates that bed geometry substantially influences the local variability of near-bed hydraulic conditions in shallow streams. Where complex bed geometry creates an unpredictable relationship between mid-depth velocity and near-bed and wall flow parameters, measurement must replace estimation until a general theory is developed.

Due to the heterogeneous bed geometry and flow conditions at the site, it was not unexpected that velocity measured 2 mm above the bed would be a better predictor of shear velocity U* than mean velocity (measured at 0.5D). Given the relationship between shear velocity and wall shear stress ($\tau_w = \rho U^{*2}$), velocity 2 mm above the boundary should have a correspondingly significant relationship with wall shear, as this depth would be assumed to be in, or near, the log layer. At several of the measurement locations, velocity profiles deviated so strongly from the logarithmic shape that near-bed velocities ($U_{0.002m}$) exceeded velocities at mid-depth ($U_{0.5D}$). In circumstances where boundary layer profiles vary from the typical log-normal shape, approximations of wall shear stress based on mean velocity may fail to adequately describe the relationship between local flow and wall shear stress. Physical instances where this type of boundary layer and velocity profile distortion may occur include flows with wall jets, free jets, or strongly positive or adverse pressure gradients (White, 1999).

Models that predict average velocity and discharge based on the average slope of the free surface have been used extensively to interpret the flow environment in streams and rivers. However, these results show that the water surface slope is highly variable over very short distances. As flow crossed the upper surface of stream boulders, the water surface slope changed as much as 5% cm⁻¹. This indicates that while water surface geometry may be used to estimate reach-averaged

velocities (see White 1999), it is of little use in measuring velocities over shorter distances (e.g. 1 cm) in shallow, high gradient streams. Unfortunately, it is this spatial scale that is relevant to benthic macroinvertebrates. It is of interest, however, to note that the rate of change of the water surface gradient is remarkably consistent over the boulders. Positive rates of change of the water surface gradient suggest a convex surface slope shape, and thus imply supercritical approaching flow (White 1999). This conclusion may, unfortunately, represent an oversimplification of flows over boulders in natural channels. In shallow, "chaotic", flows over coarse substrates, the shape of the free surface is the product of the complex relationship between depth (and change in depth as flow crosses bedforms), bed geometry, and the specific energy of the flow. Further experimentation is required to clarify the relationship among these factors.

Wall shear stress in torrential streams

Wall shear stress is commonly estimated using a determination of the shear velocity (U*) based on velocity profile data. Accurate estimates of wall shear stress are dependent on accurate determinations of U*, which are, in turn, a function of the slope of the velocity gradient. As such, errors in assessment of the thickness of the log-layer or 'overlap' layer may lead to substantial errors in estimates of U*. A visual or statistical assessment of the linearity of the near-boundary portion of the plot of dU / dlnz is usually used to determine the thickness of the log layer. However, in flow environments characterised by high velocities and high wall shear stress, the log layer can be very thin, and several measurements of velocity adjacent to the bed may be required to accurately determine the slope of the velocity gradient. Unfortunately, many instruments commonly used to measure water velocities in the field (e.g. propeller velocimeters) are incapable of measuring flows at the high spatial resolutions required. Moreover, the application of this method assumes that the shape of the near-bed velocity gradient is predictably logarithmic. The law of the wall (see White 1999) will hold for regions immediately adjacent to the wall in all flow conditions where the bed is noneroding. However, in flows where the velocity profile is substantially distorted due to the presence of either adverse or positive pressure gradients, the accuracy of the velocity gradient method of estimating shear stress is not known. Our results indicate that in instances where the velocity profiles

were non-logarithmic (*i.e.* wedge-shaped or transitional), estimates of τ_w based on the slope of dU / dlnz tended to greatly underestimate wall shear stress by an average of 60.78% (SE = 9.42%).

Where relative submergences were sufficiently high, stream flows produced a distinctive pattern of wall shear stress (τ_w) over the exposed surface of the boulders. Often, the highest shear stresses were recorded on the lateral surfaces of the boulders (see Figures 3-18, 3-19, and 3-21). Shear stress was generally low over the front of the stones, and increased towards the rear of the stone as flow accelerated. In addition, flow visualisation of basic flow patterns showed that separation occurred over the rear edge of each of the stones. This was expected, as at the range of local Reynolds numbers calculated for the deployed stones at the site (Re = 45,200 to 108,000), boundary layers should separate at the lee side of each stone, and vortices should develop and be shed in the turbulent wake of each stone (Vogel 1994). Abrupt decreases in shear stress accompany flow separation (White 1999), and this pattern was observed in two of the seven stones over which shear stress distributions were recorded. Presumably, in cases where a sudden decrease in shear stress was not recorded, measurements of shear stress were not taken sufficiently far downstream, in the zone of recirculating, detached flow. These distinctive shear stress distributions are potentially important to the ecology and behaviour of benthic invertebrates, especially those taxa that inhabit the upper surfaces of stream boulders in torrential streams (*i.e.* torrenticolous fauna; Vogel 1994). For example, grazing invertebrates that exhibit adaptations to maintain contact with the stream bed and feed in high velocity habitats may be able to utilise high-shear stress areas of the substrate as a refuge from predators that lack similar adaptations (e.g. Hart and Merz 1998).

Measurement of near-bed and wall flow conditions

There have been several methods used to measure near-bed flow conditions in streams. Among these, the FST (Fliesswasserstammtisch) hemisphere method has been used extensively to estimate flow conditions close to substrate in lotic environments (*e.g.* Statzner and Muller 1989; Dietrich and Schmedtje 1995). FST hemispheres provide estimates of near-bed "flow characteristics" or "hydraulic stress" (Statzner and Muller 1989), parameters that integrate several near-bed flow parameters including velocity, lift, drag, and shear stress. As such, FST hemispheres provide little information on the relative importance of these various flow characteristics. In practice, FST

hemispheres integrate flow conditions over relatively large horizontal and vertical distances (~50 mm and 25 mm, respectively). Consequently, the use of FST hemisphere methods may be inappropriate in investigations of small-scale phenomena, especially the fine-scale flow preferences of benthic invertebrates in shallow streams. This is especially true where velocity gradients deviate from lognormal. In these cases, the FST hemisphere method will likely misrepresent flow conditions immediately adjacent to the stream bed. Another recent development involves the use of acoustic Doppler velocimeters, which have been used to measure the Reynolds stress (*i.e.* free shear stress above the bed), rather than the wall shear stress (Bouckaert and Davis 1998). While these measurements may be of interest to issues such as mass transfer in the water column, Reynolds stress may be of limited importance in describing the immediate forces experienced by benthic insects, especially where the movement of water is highly complex and unpredictable (*i.e.* roughturbulent boundary layer conditions).

The Preston-static tube (PST) used in this study can be used to directly measure wall shear stress as well as measure current velocity immediately adjacent to the bed when deployed as a Preston-static tube (Ackerman et al. 1994; Ackerman and Hoover 2001). As such, it is capable of providing a description of the near-bed flow conditions experienced by benthic insects in high-velocity flows. The vertical distance over which the PST integrates velocity is very short (0.88 mm, the model used in this study) compared to propeller and bucket-wheel velocimeters (often > 10 mm). This high spatial resolution allows for the characterisation of flows in the region immediately above the bed (providing several measurements within 10 mm of the substrate), where other types of apparatus are limited. For example, the electromagnetic current meter used by Bergeron (1994) was unable to measure velocities closer than 19 mm from the bed. Similarly, the acoustic Doppler velocimeter, contrary to recent published reports (e.g. Bouckaert and Davis 1998), is unable to accurately measure velocities within centimetres of the bed (Finelli et al. 1999), and is thus unable to characterise the near-bed flow environment. The PST represents a simple, easily deployed device capable of measuring velocities at fine scales immediately above the bed, the region of the most relevance and interest to benthic biologists. Future PST designs could employ pressure transducers with faster response times and data logging to provide higher order moments of fluid dynamic measurements. Constant temperature (hot-film) anemometry can be used to measure near-bed velocities in streams at high spatial and temporal resolution, but is time consuming and notoriously

difficult to deploy in natural channels (Li 1994; Hart et al. 1996). Regardless, Hart et al. (1996) were able to successfully obtain near-bed velocity measurements in shallow streams using these instruments.

The results indicate that the PST provides an accurate measurement of wall shear stress when compared to the traditional velocity gradient method (*i.e.* estimating shear stress from the slope of the regression of dU / dlnz). In the rough boundary layer flow conditions present in shallow, bouldery streams, velocities are seldom logarithmically distributed, and log-layers are often quite thin and restricted to a region adjacent to the bed where most current meters are unable to measure velocity. However, where boundary layers were very thin ($\delta < 3 \text{ mm}$), assessment of the thickness of the log-layer was problematic using the PST. Where near-bed velocity distortions impinge on the upper portion of the log-layer, estimates of shear stress using the velocity gradient method will consistently underestimate τ_w . In rough boundary layer flows similar to the ones described here, it may not be possible to assess log-layer flow conditions using the coarse spatial resolution provided by other velocity measurement devices.

In ideal circumstances (uniform flow with a fully developed boundary layer over a topographically simple (flat) bed), wall shear stress measurements made using the Preston-Static tube corresponded with those obtained by estimating U* from the slope of the plot of U vs. In z (Figure 3-25; also see Ackerman and Hoover 2001). A well-developed log-layer would provide the relatively large number of velocity measurements required for an accurate estimate of the wall shear stress using the velocity gradient or shear velocity (U*) method (see Bergeron and Abrahams 1992; Biron et al. 1998). However, in flows over torrential stream boulders the log-layer is seldom thick enough to obtain an accurate estimate of U* using the velocity gradient method. The number of points used in the regression of U on In z were, in several cases, fewer than the suggested number required to accurately predict the slope of a line (Zar 1984). This is, however, a physical constraint imposed by the nature of near-bed flows over boulders in shallow streams. Near-bed velocity distortions often restricted the log-linear portion of the velocity profile to a few millimetres above the bed, limiting the number of velocity measurements that could be obtained in the log-layer. However, in instances where the velocity profile was not logarithmically distributed (i.e. wedge-shaped), estimates of shear stress were consistently lower in magnitude than measurements of shear stress made using the PST. This suggests that the log-layer may be thinner than indicated by the log-

transformed velocity profile. If this is the case, the PST will provide a more accurate shear stress value than the velocity gradient method, assuming that the log-layer is thinner than the diameter of the PST (0.88 mm). As flows are rarely logarithmically distributed in shallow torrential streams (see Hart et al. 1996; Bergeron 1994), near-bed flow parameters should be directly measured rather than estimated, if possible.

Conclusions

The unexpectedly high near-bed velocities recorded over the surface of stream boulders in this study suggest that it may be necessary to re-evaluate the ecological role played by hydrodynamic forces in shallow, high gradient, stream environments (*i.e.* rough-turbulent flows). The importance of surface and bulk flow phenomena on the distribution and behaviour of benthic taxa has been explored by several authors (*e.g.* Wetmore et al. 1990; Delgado and Carbonell 1997). However, it has generally been assumed that the velocities to which invertebrates are exposed (*i.e.* near-bed velocities; approximated in this case as U_{0.002m}) could be accurately estimated using models based upon a logarithmic distribution of velocity. However, the results of the present study show that velocities that invertebrates are exposed to may, in many cases, be greater than previously thought. Consequently, the practice of estimating near-bed flow parameters from measurements of mean velocity may lead to the underestimation of the lift and drag forces that torrential macroinvertebrates experience.

The results of the present study also demonstrate that near-bed flow conditions in shallow, torrential streams are heterogeneous. In general, near-bed velocities and wall shear stresses appear to be greatest toward the rear (upstream of the separation point) and sides of boulders exposed to the flow. Torrential stream macroinvertebrates that show a preference for these areas of the stream bed might benefit from protection from predators, enhanced feeding opportunities, or increased rates of gas exchange (*e.g.* Golubkhov et al. 1992; Hart and Merz 1998). Benthic taxa that avoid these areas of the stream bed may be unable to cope with the shear, lift, and drag forces associated with this microhabitat, or lack the adaptations necessary to maintain contact with the substrate in high velocities. The data presented here indicate that at present only

measurement can ensure an accurate characterisation of the near-bed environment experienced by torrential stream invertebrates. Until models that describe the relationship between the bed geometry, channel characteristics, and flow are developed, the relationship between near-bed hydraulics and the behaviour, morphology, and ecology of benthic taxa in high velocity habitats will remain largely unknown for most taxa.

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References

- Ackerman, J.D., and T.M. Hoover. 2001. Measurement of local bed shear stress in streams using a Preston-static tube. Limnol. Oceanogr. 46: 2080-2087.
- Ackerman, J.D., L. Wong, C. R. Ethier, D.G. Allen, and J.K. Spelt. 1994. Preston-static tubes for the measurement of wall shear stress. J. Fluids Eng. 116: 645-649.
- Bathurst, J.C. 1994. At-a-site mountain river flow resistance variation. Proc. Hydraul. Engrg. (1994), ASCE . 1: 682-686.
- Bergeron, N.E. 1994. An analysis of flow velocity profiles, stream bed roughness, and resistance to flow in natural gravel bed streams. Proc. Hydraul. Engrg. (1994), ASCE . 1: 692-696.
- Bergeron, N.E., and A.D. Abrahams. 1992. Estimating shear velocity and roughness length from velocity profiles. Water Resour. Res. 28: 2155-2158.
- Biron, P.M., S.N. Lane, A.G. Roy, K.F. Bradbook, and K.S. Richards. 1998. Sensitivity of bed shear stress estimated from vertical velocity profiles: the problem of sampling resolution. Earth Surf. Proc. Land. 23: 133-139.
- Blizard, C.R., and E.E. Wohl. 1998. Relationships between hydraulic variables and bedload transport in a subalpine channel, Colorado Rocky Mountains, U.S.A. Geomorphology 22: 359-371.
- Bouckaert, F.W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biol. 40: 77-86.
- Buffin-Belanger, T., and A.G. Roy. 1998. Effects of a pebble cluster on the turbulent structure of a depth-limited flow in a gravel-bed river. Geomorphology 25: 249-267.
- Carling, P.A.. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biol. 28: 273-284.
- Carling, P.A., J.J. Williams, A. Kelsey, M.S. Glaister, and H.G. Orr. 1998. Coarse bedload transport in a mountain river. Earth Surf. Proc. Land. 23: 141-157.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biol. 21: 271-282.
- Delgado, J.A., and R. Carbonell. 1997. Case features of caddisfly larvae (Sericostoma selysi) as related to water velocity and potential to drift. J. Freshwater Ecol. 12: 193-197.
- Denny, M.W. 1994. Extreme drag forces and the survival of wind- and water-swept organisms. J. Exp. Biol. 194: 97-115.
- Denny, M.W. and M.F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. Amer. Nat. 134: 859-889.
- Dittrich, A., and U. Schmedtje. 1995. Indicating shear stress with FST-hemispheres effects of stream-bottom topography and water depth. Freshwater Biol. 34: 107-121.
- Finelli, C.M., D.D. Hart, and D.M. Fonseca. 1999. Evaluating the spatial resolution of an acoustic Doppler velocimeter and the consequences for measuring near-bed flows. Limnol. Oceanogr. 44: 1793-1801.
- Golubkhov, S.M., T.M. Tiunova, and S.L. Kocharina. 1992. Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. Aquatic Insects 14: 137-144.

- Hart, D.D., B.D. Clark, and A. Jasentuliyana. 1996. Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.
- Hart, D.D., and C.M. Finelli. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Ann. Rev. Ecol. Syst. 30: 363-395.
- Hart, D.D., and R.A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow-mediated refuges. Oecologia 114: 263-273.
- Ippen, A.T. 1966. Sedimentation in estuaries. pp. 648-672. In Estuary and Coastline Hydrodynamics. Ed. A. T. Ippen. McGraw-Hill, New York, NY.
- Jarrett, R.D. 1984. Hydraulics of high gradient streams. J. Hydraulic Eng. 110: 1519-1539.
- Jarrett, R.D. 1990. Hydrologic and hydraulic research in mountain rivers. Water Res. Bull. 26: 419-429.
- Jarrett, R.D. 1991. Wading measurements of vertical velocity profiles. Geomorphology 4: 243-247.
- Lacoursière, J.O. 1992. A laboratory study of fluid flow and microhabitat selection by larvae of *Simuliium vittatum* (Diptera: Simuliidae). Can. J. Zool. 70: 582-596.
- Li, M.Z. 1994. Direct skin friction measurements and stress partitioning over movable sand ripples. Water Resour. Res. 30: 791-799.
- Moog, D.B., and G.H. Jirka. 1999. Stream reaeration in non-uniform flow: macroroughness enhancement. J. Hydraulic Eng. 125: 11-16.
- Nikora, V.I., D.G. Goring, and B.J.F. Biggs. 1998. On gravel-bed roughness characterization. Water Resour. Res. 34: 517-527.
- Nowell, A.R.M., and M. Church. 1979. Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. 84: 4816-4824.
- Peckarsky, B.L., S.C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a test of the harsh-benign hypothesis. Freshwater Biol. 24: 181-191.
- Pommen, G.D.W., and D.A. Craig. 1995. Flow patterns around gills of pupal net-winged midges (Diptera: Blephariceridae): possible implications for respiration. Can. J. Zool. 73: 373-382.
- Preston, J.H. 1954. The determination of turbulent skin friction by means of Pitot tubes. J. Royal Aeronaut. Soc. 58: 109-121.
- Robert, A., A.G. Roy, and B. De Serres. 1996. Turbulence at a roughness transition in a depth limited flow over a gravel bed. Geomorphology 16: 175-187.
- Silvester, N.R., and M.A. Sleigh. 1985. The forces on microorganisms at surfaces in flowing water. Freshwater Biol. 15: 433-448.
- Statzner, B., and T.F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow – an old question answered by means of a new technique (laser doppler anemometry). Oecologia 53: 290-292.
- Statzner, B., and R. Muller. 1989. Standard hemispheres as indicators of flow characteristics in lotic benthos research. Freshwater Biol. 21: 445-459.
- Sukhodolov, A., M. Thiele, and H. Bungartz. 1998. Turbulence structure in a river reach with sand bed. Water Resour. Res. 34: 1317-1334.

Vogel, S. 1994. Life in Moving Fluids, 2nd Edition. Princeton University Press, Princeton, NJ.

- Weissenberger, J., H.-Ch. Spatz, A. Emanns, and J. Schwoerbel. 1991. Measurement of the lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m s⁻¹. Freshwater Biol. 25: 21-31.
- Wetmore, S.H., R.J. Mackay, and R.W. Newbury. 1990. Characterization of the hydraulic habitat of Brachycentrus occidentalis, a filter-feeding caddisfly. J. N. Am. Benthol. Soc. 9: 157-169.

White, F.M. 1999. Fluid Mechanics - 4th Edition. WCB McGraw-Hill, Boston.

- Wiley, M.J., and S.L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Can. J. Zool. 58: 618-622.
- Young, W.J. 1992. Clarification of the criteria to identify near-bed flow regimes. Freshwater Biol. 28: 383-391.
- Young, W.J. 1993. Field techniques for the classification of near-bed flow regimes. Freshwater Biol. 29: 377-383.

Zar, J.H. 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Englewood Cliffs, NJ.



Figure 3-1. Map of British Columbia, showing the location of the Torpy River watershed.



Figure 3-2. Diagrammatic representation of the grid system and deployment of the experimentally deployed stones. A. Side view. B. Plan view. Labels are as follows: d = datum marking the centre of the stone, g = grid point, id = stone identification label.



Figure 3-3. Stream bed and water surface topography of experimentally deployed stone 7 (centreline transect) measured on Sept. 5, 1998. The white bar delineates the extent of stone 7. The four locations at which velocity profiles were obtained are shown. The location marked "3" denotes the centre point (datum) of the stone.



Figure 3-4. Stream bed and water surface topography of experimentally deployed stone 31 (centreline transect) measured on Sept. 2, 1998. The white bar delineates the extent of stone 31. The three locations at which velocity profiles were obtained are shown. The location marked "2" denotes the centre point (datum) of the stone.



Figure 3-5. Stream bed and water surface topography of experimentally deployed stone 25 (centreline transect) measured on Sept. 8, 1998. The white bar delineates the extent of stone 25. The three locations at which velocity profiles were obtained are shown. The location marked "2" denotes the centre point (datum) of the stone.



Figure 3-6. Stream bed and water surface topography of experimentally deployed stone 23 (centreline transect) measured on Sept. 30, 1998. The white bar delineates the extent of stone 23. The location at which the velocity profile was obtained is shown. The location marked "1" denotes the centre point (datum) of the stone.



Figure 3-7. Stream bed and water surface topography of experimentally deployed stone 10 (centreline transect) measured on Sept. 30, 1998. The white bar delineates the extent of stone 10. The location at which the velocity profile was obtained is shown. The location marked "1" denotes the centre point (datum) of the stone.



Figure 3-8. Stream bed and water surface topography of naturally positioned stone N01 (centreline transect) measured on Sept. 26, 1998. The white bar delineates the extent of stone N01. The location at which the velocity profile was obtained is shown. The location marked "1" denotes the approximate centre of the stone.



Figure 3-9. Stream bed and water surface topography of naturally positioned stone N02 (centreline transect) measured on Sept. 27, 1998. The white bar delineates the extent of stone N02. The location at which the velocity profile was obtained is shown. The location marked "1" denotes the approximate centre of the stone.



Figure 3-10. Stream bed and water surface topography of naturally positioned stone N03 (centreline transect) measured on Aug. 7, 1998. The white bar delineates the extent of stone N03. The location at which the velocity profile was obtained is shown.



Figure 3-11. Stream bed and water surface topography of the gravel riffle site (GR) measured on Aug. 17, 1998. The white bar delineates the diameter of the stone above which the profile was measured. The location marked "1" is the point at which the velocity profile was obtained.



Figure 3-12. Velocity profiles obtained along the centreline of stone 7. The horizontal line above each velocity profile represents the water depth at that location. Mid-depth and maximum velocities increase as flow crosses stone 7. Wedge-shaped, transitional, and log-normal velocity profiles are labelled "w-s", "tr", and "I-n", respectively. Velocity profiles measured over the centre of the stone, 5 cm upstream of centre, 10 cm upstream of centre, and 5 cm downstream of centre are labelled "0", "1", "2", and "-1", respectively. Measurement points correspond to the marked grid locations. The velocity profile at the front of the stone is wedge shaped; the near-bed flow distortion becomes less evident as flow crosses the stone.



Figure 3-13. Velocity profiles obtained along the centreline of stone 31. The horizontal line above each velocity profile represents the water depth at that location. Mid-depth and maximum velocities increase as flow crosses stone 31. Wedge-shaped and transitional velocity profiles are labelled "w-s" and "tr", respectively. Measurement points correspond to the marked grid locations. Velocity profiles measured over the centre of the stone, 5 cm upstream of centre, and 5 cm downstream of centre are labelled "0", "1", and "-1", respectively.



Figure 3-14. Velocity profiles obtained along the centreline of stone 25. The horizontal line above each velocity profile represents the water depth at that location. Velocity profiles measured over the centre of the stone, 5 cm upstream of centre, and 5 cm downstream of centre are labelled "0", "1", and "-1", respectively. Measurement points correspond to the marked grid locations. All velocity profiles above stone 25 were distinctly wedge-shaped, and labelled "w-s".



Figure 3-15. Velocity profiles obtained above the centres ("0") of stone 23 (labelled "s23") and stone 10 (labelled "s10"). The horizontal line above each profile represents the water depth at that location. Wedge-shaped and log-normal velocity profiles are labelled "w-s" and "I-n", respectively. Measurement points correspond to the marked grid locations.



Figure 3-16. Velocity profile obtained above the centres ("0") of naturally positioned stones N01, N02, and N03, and the gravel riffle site ("GR"). The horizontal line above each profile represents the water depth at that location. Wedge-shaped, transitional, and log-normal velocity profiles are labelled "w-s", "tr", and "I-n", respectively.



Figure 3-17. The distribution of wall shear stress (τ_w) over the upper surface of stone 7. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone 7. The upper right hand diagram shows a top and side view of stone 7. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-18. The distribution of wall shear stress (τ_w) over the upper surface of stone 31. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone 31. The upper right hand diagram shows a top and side view of stone 31. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-19. The distribution of wall shear stress (τ_w) over the upper surface of stone 25. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone 25. The upper right hand diagram shows a top and side view of stone 25. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-20. The distribution of wall shear stress (τ_w) over the upper surface of stone 23. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone 23. The upper right hand diagram shows a top and side view of stone 23. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-21. The distribution of wall shear stress (τ_w) over the upper surface of stone 10. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone 10. The upper right hand diagram shows a top and side view of stone 10. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-22. The distribution of wall shear stress (τ_w) over the upper surface of naturally positioned stone N01. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone N01. The upper right hand diagram shows a top and side view of stone N01. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-23. The distribution of wall shear stress (τ_w) over the upper surface of naturally positioned stone N02. Wall shear stress was measured using a Preston-static tube (PST) in two transects; a centreline transect in the direction of flow (upper left), and a second, cross-stream transect (lower right) perpendicular to the first, crossing the first transect at the centre of the stone. A composite bubble plot (lower left) shows the relative magnitude of shear stress across the surface of stone N02. The upper right hand diagram shows a top and side view of stone N02. The area superimposed on the top view of the stone corresponds to the area represented in the bubble plot. Error bars are standard error (SE).



Figure 3-24. Relationship between wall shear stress measured by the PST (τ_{w-PST}) and wall shear stress estimated from shear velocity based on the slope of of dU / dlnz ($\tau_{w-dU/dlnz}$). The 1:1 regression line ("line of equality") is shown. Locations with log-normal velocity profiles are shown as circles (solid circles = field measurements, hollow circles = lab flume measurements), transitional profiles shown as grey squares, and wedge-shaped profiles shown as solid diamonds. Error bars are standard error (SE).



Figure 3-25. Relationship between wall shear stress measured by the PST (τ_{w-PST}) and wall shear stress estimated from shear velocity based on the slope of dU / dlnz ($\tau_{w-dU/dlnz}$). Data are plotted separately, based on the velocity profile shape at the point at which shear stress was measured. Velocity profiles were wedge-shaped in (A), transitional in (B), and log-normal in (C). Locations where log-normal velocity profiles measured in the field are shown as solid circles, hollow circles indicate log-normal velocity profiles measured in the lab flume. The 1:1 regression line ("line of equality"; shown as a dotted line) is shown in each case. The linear regression line is also shown in each case (solid line). See text for significance tests of each plot. Error bars are standard error (SE).



Figure 3-26. Comparison of the velocity profiles obtained over naturally positioned boulders (n = 3), experimentally deployed boulders (n = 14), and a gravel riffle (n = 1). Velocities are normalised by shear velocity (U*) as measured by the PST. The vertical axis (distance from the boundary) is normalised by the total water depth (D). Wedge-shaped profiles are shown as a dashed line, transitional profiles shown as a solid grey line, and log-normal profiles shown as a solid black line.



Figure 3-27. Comparison of the velocity profiles obtained over naturally positioned boulders (n = 3), experimentally deployed boulders (n = 14), and a gravel riffle (n = 1). Velocities are normalised by velocities at mid-depth ($U_{0.5D}$). The vertical axis (distance from the boundary) is normalised by the total water depth (D). Wedge-shaped profiles are shown as a dashed line, transitional profiles shown as a solid grey line, and log-normal profiles shown as a solid black line.



Figure 3-28. Relationship between Froude number (Fr) and local Reynolds number (Re_x) at velocity sampling locations over the upper surface of the stones (including all experimentally deployed and naturally positioned stones). A significant relationship between the two parameters exists when all data are considered together ($R^2 = 41.07\%$; ANOVA, F(1,16) = 12.85, p = 0.0025). However, when the stones which have impeded boundary layer growth (*i.e.* flow impinging on the stone surface from above – stone 25) and situations where skimming flow has possibly developed ("non-exposed stones"; stone N01 and stone 7 during near-flood discharge) are excluded from the analysis, the relationship is more significant ($R^2 = 81.19\%$; ANOVA, F(1,11) = 47.49, p < 0.001). The regression line shown was calculated using all field data (the three lab flume points (hollow triangles) were excluded). "Exposed stones" included stones 7 (non-flood discharge), 31, 25, 23, 10, N02, and N03.



Figure 3-29. Relationship between Froude number (Fr) and shear velocity (U*). The relationship is significant ($R^2 = 25.21\%$; ANOVA, F(1,19) = 6.27, p = 0.022). The linear regression line is shown (solid line). Symbols and conventions as in figure 3-24.



Figure 3-30. Relationship between shear velocity (U*; measured using the PST) and water velocity, at mid-depth ($U_{0.5D}$) (R² = 36.62%; ANOVA, F(1,19) = 14.18, p = 0.0013) and near the bed ($U_{0.002m}$) (R² = 87.08%; ANOVA, F(1,19) = 390.37, p < 0.001).



Figure 3-31. Diagrammatic representation of the flow field above isolated boulders in shallow streams ($D/d_k < 2$). In this simplified model, the approaching flow can be characterised as having two zones. The bulk flow zone, where velocities (U_{bulk}) are relatively homogeneously distributed in the vertical direction due to momentum transfer in the turbulent flow. The second, bed influenced zone (BIZ), is characterised by reduced velocities (boundary layer effects) and turbulence generation (growing / shedding eddies, and boundary layer separation). Flow at the front of the boulder is characterised by a horseshoe vortex (HV) and stagnation point (often unstable and oscillating). As flow crosses the front of the stone, near-bed flows are constricted; the influence of the constriction is vertically limited. As a result, the flow near the bed accelerates at a greater rate than flows near the surface. However, as flow crosses the relatively smooth upper surface of the stone, boundary layer growth dissipates the near-bed, high velocity "wedge". Flows subsequently separate off the rear of the stone, giving rise to recirculating flow zone (RFZ). The depth at which maximum velocities occur (z_{maxU}) increase as flow crosses the boulder.

Chapter 4

Microdistribution of *Epeorus longimanus* and periphyton on torrential stream boulders

Summary

- Field measurements and experiments were conducted to examine the microdistribution of the torrential mayfly *Epeorus longimanus* (Heptageniidae) with respect to periphyton biomass, shear stress, and substrate characteristics (*i.e.* stone roughness, topography).
- 2. Different factors influence larval distribution during daytime and night-time periods. During the day, the few larvae that remain on the upper stone surface tend to be found in high shear stress areas on the stone surface, generally towards the rear of the upper surface of the stones. During the night-time, larvae were found on the upper surface of the stone surface, and avoided areas where boundary layer flows had detached (*i.e.* the downstream edge of the stones).
- 3. Periphyton densities were significantly related to stone surface roughness and topography (*i.e.* more algae on higher, rougher areas of the substrate). The relationship between the microdistributions of periphyton and *E. longimanus* larvae were nearly significant, suggesting that high densities of this grazing mayfly may tend to reduce local periphyton standing stock. In some cases, algal density and larval abundance appear to be inversely related.
- 4. Shear stress generally increases from the front to the rear of submerged, protuberant stones (*i.e.* stones whose upper surfaces are beneath the water surface, but protrude upward into the main flow to a greater extent than the surrounding bed material). At the rear of the stones, shear stress abruptly decreases at or near where the flow separated.
- 5. *E. longimanus* larvae migrate diurnally. Larvae generally retreat to the underside of stones during the day, and emerge during the night to graze on the upper, exposed surfaces of the stones at night. However, the rates of larval emergence and withdrawal differ, suggesting that the migration behaviour during dusk emergence may be functionally different from that of dawn withdrawal.

- 6. A stone reversal experiment suggests that the characteristic microdistribution of larval *E*. *longimanus* is a response to near-bed flow factors. However, larvae may be using this environmental cue to identify high-resource feeding areas.
- The adaptive significance of the results, especially as they relate to trophic and predator-prey interactions, are discussed.

Introduction

The examination of biotic processes at different spatial scales has become a major consideration in the study of benthic systems (*e.g.* Muotka and Pentinnen 1994; Voelz and Ward 1996). Traditionally, the importance of large-scale (*i.e.* $10 - 10^4$ m) processes has been a major focus in stream ecology, and the roles of these processes in determining macroinvertebrate diversity (Statzner and Higler 1986; Growns and Davis 1994), invertebrate drift (Lancaster et al. 1996), primary productivity (Wellnitz et al. 1996), and stream hydrology and hydraulics (Jarrett 1990) are well understood. However, microscale (*i.e.* 10^{-2} m – 1 m) phenomena, such as local variations in near-bed hydraulics, appear to be of greater ecological importance within riffle segments (Dudgeon 1982; Collier et al. 1995) and on individual stones (Muotka and Pentinnen 1994; Hart et al. 1996; Voelz and Ward 1996).

Recently, it has been suggested that the microdistribution of stream invertebrate are the result of species-specific responses to environmental factors such as substrate size (Jowett et al. 1991), substrate roughness (Casey and Clifford 1989), habitat complexity (Way et al. 1995), food resource availability (Peckarsky 1996), and hydrodynamic parameters (Statzner 1981; Collier et al. 1995). Biotic interactions, including predator-prey interactions (McIntosh and Peckarsky 1996), have also been found to play roles in determining microhabitat use by benthic invertebrates. Most studies, however, have ignored the potentially important role that interactions between environmental and biotic factors might play in determining the microdistribution of stream invertebrates (but see Muotka and Pentinnen 1995; Hart and Merz 1998).

Hydrodynamic variables are generally thought to be the most important factors affecting the ecology of benthic organisms in the stream environment (Hart et al. 1996; Carling 1992; Davis and Barmuta 1989). Near-bed velocities have been shown to influence the morphology, physiology, behaviour, and microdistribution of stream organisms (e.g. Wiley and Kohler 1980; Statzner and Holm

1982; Hart et al. 1996; Delgado and Carbonell 1997; Bouckaert and Davis 1998). However, the exact nature of the relationship between the forces generated by moving water and the biology of the benthic organisms is poorly understood, for two reasons. First, and primarily, stream ecologists have used methodologies and field techniques that are quite different in spatial scale from that of benthic invertebrates. For example, Muotka and Pentinnen (1994) found that aggregative responses of two stream invertebrate predators (Isoperla grammatica and Rhyacophila obliterata) to blackfly larvae prey in microhabitats of overlapping velocity preferences could not be detected unless they examined the distribution of the organisms at scales much smaller than those traditionally used in field experiments. Second, although it is widely recognised that benthic communities are sensitive to the forces generated by the moving water of streams, the precise nature of the hydrodynamic parameters to which stream invertebrates respond is poorly understood. The microdistribution and behaviour of benthic stream invertebrates have been variously attributed to near bed velocity (Hart et al. 1996), mean velocity (Collier 1994), turbulence intensity and Reynolds stress (Bouckaert and Davis 1998), lift and drag (Weissenberger et al. 1991), Froude number (Wetmore et al. 1990), Reynolds number (Statzner and Higler 1986), and the thickness of the viscous sublayer (Statzner 1981). This proliferation of causal factors has arisen because, in many cases, just one or two hydrodynamic parameters are measured and related to patterns of faunal abundance. Furthermore, many of the hydrodynamic parameters are closely related, and often derived from the same basic measurements of water velocity.

Several recent studies of natural flows in stream channels have examined hydrodynamic parameters (*i.e.* velocity, turbulence intensity, turbulence structure) within the benthic boundary layer (*e.g.* Hart et al. 1996; Robert et al. 1996; Buffin-Belanger and Roy 1998). Of these studies, only Hart et al. (1996) have successfully measured and related near-bed flow parameters (velocity, tubulence intensity) to the distribution of benthic invertebrates. However, the relative rarity of studies of this kind is due to the fact that the spatial resolution of conventional instruments used to measure water velocity is quite coarse. Only recently have techniques been developed that allow for the examination of water flow at the fine spatial scales (*i.e.* mm – cm) experienced by benthic invertebrates. For example, the electromagnetic current meter (EMCM) used by Robert et al. (1996) had a spatial resolution of 1.3 cm, while the hot-film anemometer used by Hart et al. (1996) had a spatial resolution of 0.7 mm. Unfortunately, the hot-film anemometer used by Hart et al. was fragile and notably difficult

to deploy and calibrate in the field. Alternatively, fine-scale velocity measurements can be made with a suitably small Pitot-static tube (White 1999). An appropriately proportioned Pitot-static tube can also be deployed as a Preston-static tube (PST), and used to directly measure wall shear stress (see Ackerman et al. 1994). This device has been tested and applied in the field (Ackerman and Hoover 2001). Wall shear stress (τ_w), which is typically measured indirectly (*e.g.* Collier et al. 1995) or ignored (*e.g.* Jowett et al. 1991), is one of the most important forces affecting benthic invertebrates exposed to flow on the stream bed (Davis and Barmuta 1989; Vogel 1994).

Stream hydrodynamics can also affect the structure of the benthic community. Peckarsky et al. (1990) demonstrated that predation effects of the stonefly predator Dinocras cephalotes on the mayfly Baetis rhodani were greatest in hydraulic habitats favourable (benign) to the stonefly. By applying the "harsh-benign" hypothesis to stream ecosystems, Peckarsky et al. (1990) illustrated that predator impacts were lower in abiotic regimes that were harsher to predators. Similarly, Tikkanen et al. (1997) reported that simuliid larvae inhabited exposed microhabitats on the upper surface of stones, where they were rarely encountered by the stonefly predator Diura bicaudata; different microhabitat preferences between predators and prey lead to lower predator/prey encounter rates, and consequently, lower rates of predation. Hart and Merz (1998) further suggested that the inability of predators to access high-velocity microhabitats might create sites which, being "harsh" to predators, act as refuges from predation. Use of flow-mediated refuges would reduce not only the direct, lethal effects of predation (Kerans et al. 1995), but also the indirect effects predators have on benthic insect prey populations, such as reduced feeding rates (Peckarsky et al. 1993; Scrimgeour et al. 1994) and increased drift (McIntosh and Peckarsky 1996). Moreover, prey species may be able to assess predation threat by associating the level of risk with some aspect of the environment (such as a characteristic range of water velocities) shared by predator and prey (Dill 1987; Peckarsky 1996).

Flow can also influence the microhabitat preferences of many benthic invertebrate taxa by mediating the availability of resources. For example, Golubkov et al. (1992) found that the rheophilous stream insects *Stenopsyche marmorata* and *Skwala pusilla* were sensitive to low levels of dissolved oxygen, and consequently were found only in high velocity microhabitats in order to maximise rates of gas exchange across their tracheal gills. This concurs with the earlier results of Wiley and Kohler (1980), who found that mayflies moved to increasingly current-exposed surfaces as dissolved oxygen concentrations decreased, presumably to increase gas transfer rates across

respiratory exchange surfaces. In addition, rates of nutrient delivery and gas exchange are higher for benthic algae in high velocity microhabitats due to thinner and increasingly turbulent boundary layers (Nowell and Jumars 1984).

The microdistribution and community structure of periphyton in streams is influenced by grazing by herbivorous invertebrate taxa (e.g. Lamberti and Resh 1985; Feminella et al. 1989; McCormick and Stevenson 1989). Karouna and Fuller (1992) found that grazing by the mayflies *Paraleptophlebia* and *Ephemerella subvaria* reduced algal densities and significantly altered the community structure. In addition, invertebrate grazers may use periphyton abundance to assess the quality of a microhabitat (Kerans 1996). However, because the microdistributions of macroinvertebrate grazers, periphyton, and near-bed flow parameters are interrelated, the relative influence of algae and flow factors on the local abundances of herbivorous stream invertebrates remains largely unknown.

Nymphs belonging to the heptageniid mayfly genus *Epeorus* are abundant in fast flowing streams across western North America (Edmunds and Allan 1964). *Epeorus* nymphs are categorised as clingers, and are found in erosional stream habitats (Edmunds and Waltz 1996). *Epeorus* is a representative torrential insect genus, displaying several adaptations to high velocity habitats including a flattened body and a ventral, "sucker-like" arrangement of gills (see Weissenberger et al. 1991; Vogel 1994). While there is some disagreement regarding the manner in which these adaptations function, it is accepted that they enable *Epeorus* to maintain contact with the substrate in high velocities. Given the association of *Epeorus* larvae with high velocity habitats, it represents an ideal model organism to examine the relationship between near-bed hydrodynamics and the benthic invertebrates that inhabit high-velocity microhabitats.

Given the linkages between hydrodynamics, predator-prey interactions, and periphyton communities, it seems reasonable to attempt to relate the microdistribution of the benthic biota of high-velocity streams to the abiotic components of the near-bed environment. While the relationships that exist between environmental parameters and the microdistribution of sessile, suspension-feeding organisms (*i.e.* caddisfly and blackfly larvae) are well documented, the microdistribution of mobile, grazing benthic macroinvertebrates such as *Epeorus longimanus* in relation to hydrodynamic forces are poorly understood. This purpose of this study is to examine the microdistributions of the mayfly *E. longimanus* and primary producers (periphyton) over the upper surface of torrential stream

boulders, and relate their distributions to a variety of environmental parameters, including near-bed hydrodynamics (*e.g.* shear stress) and stone surface characteristics (*e.g.* topography, roughness, and within-stone position). Diurnal variation in microdistribution of this grazing mayfly was also examined in order to determine if the same factors influence the distribution of *E. longimanus* larvae during day-and night-time periods.

Methods and materials

Study site and experimental design

The microdistribution of benthic invertebrates, algae, and near-bed flow parameters were examined during September and October 1998, in a 20 m reach of a third-order tributary within the Torpy River watershed (see chapter 3 for a description of the study site). Thirty small, light coloured, rounded stones, ranging in diameter from 22 – 33 cm, were marked with a 5 x 5 cm reference grid of points and deployed in the active stream channel at the study site in early August 1998 (see chapter 3 for a detailed description of the methodology used). Where possible, existing stones were removed from the stream bed and replaced with experimental stones of similar shape and volume to ensure that stream bed geometry within the reach was not altered significantly. To minimise hydraulic interactions between experimentally deployed substrates, the stones were placed in the channel at approximately 1m intervals in an offset pattern, such that no stone was immediately upstream of another (see Young 1992).

After deployment, the stones were left for 10 days to accumulate biofilm, periphyton, and benthic invertebrates characteristic of the adjacent streambed. During this time the densities of larval *E. longimanus* (a representative high velocity, torrential habitat mayfly species) were monitored on each of the experimental stones. After the acclimatisation period had ended, the distribution of periphyton, macroinvertebrates, and shear stress (*in addition to several other flow characteristics – see chapter 3*) were measured over the upper surface of the five stones that had the highest densities of *E. longimanus*.

When possible, all parameters were measured during periods of similar stream discharge in order to ensure hydrodynamic similarity between sampling dates.

Insect distribution

The number and distribution of larval E. longimanus within the 5 x 5 cm grid marked on the upper surface of each of the five stones were recorded several times over a four week period (see Table 4-1). Densities of E. longimanus larvae were determined on a per quadrat basis, and converted to areal density (i.e. E. longimanus m^2 = number of insects within a 5 x 5 cm quadrat / 0.05 m x 0.05 m). Daytime distributions were recorded on 8 dates between September 2 and October 4, 1998, while night-time distributions were recorded during the nights of September 16 and October 3, 1998. Observations of larval mayfly distributions were made using a small plexiglass sheet (20 x 10 x 0.7 cm) held against the water surface and tilted in the upstream direction such that it allowed an unimpeded view of the stream bed. Use of this device did not substantially influence the behaviour of the larvae. Prior to the experiment, other viewing devices (e.g. plexiglass observation boxes, periscope viewers, etc.) were tested, but it was observed that larger, more visible apparatus disturbed the mayflies. Night-time observations of insect distributions were made using a headlamp (Petzl Zoom (4.5 volts); Petzl Distribution Sport, Crolles, France) for illumination. As the red portion of the visible spectrum has been reported as being less visible to stream insects (McIntosh and Peckarsky 1996), a red filter over the lens of the headlamp was initially used in an attempt to minimise disturbance to the larval mayflies. However, in this case, it was observed that movement of the light source rather than colour was the source of the disturbance. Subsequently, the use of the filter was discontinued, and movement of the headlamp minimised.

Flow characterisation

Using a Preston-static tube (see below), wall shear stress (τ_w) distributions were measured across the upper surface of the experimental stones in two orthogonal transects crossing the upper surface of each stone (Figure 4-1c). Shear stress was measured every 2.5 cm (*i.e.* at every grid point, and at intermediate positions between grid points) in a streamwise transect, and at 5 cm intervals (*i.e.* at every grid point) in a cross-stream transect. The two transects intersected in the centre of the stone (position 0,0 in the marked grid). When insect and wall shear stress distributions were recorded on the same date, the insect distributions were recorded first to minimise disturbance of the larval mayflies.
Wall shear stress was measured using a Preston-Static tube (PST) (see Ackerman et al. 1994; Ackerman and Hoover 2001). The PST used consists of a 90° bevelled tip syringe needle fixed to a side-bored syringe needle (tube diameter = 0.88mm). A Validyne model CD379-1-2 membranetype differential pressure transducer (Validyne Engineering; Northridge, CA), connected to the PST via 2 m of flexible pressure lines (inside diameter = 3 mm), was used to measure differential pressure (the difference between static pressure p_s and dynamic pressure p_0), which can be converted into shear stress (see chapter 3). An average differential pressure was obtained by averaging 15 measurements obtained over approximately 30 seconds. The pressure transducer and pressure lines were periodically flushed with water in order to minimise the possibility of the presence of trapped air, which adversely affects differential pressure measurements. The accuracy of wall shear stress measurements using this method is dependent on proper orientation of the PST; the PST must be resting on the stone surface and oriented parallel to local flow such that a stagnation point forms at the dynamic tap (Ackerman and Hoover 2001). This orientation of the PST was achieved using sodium fluorescein dye and an underwater magnifying periscope viewer (Edmund Scientific, New Jersey, USA). Typically, when measuring shear stress at a point, the PST would be lowered until the tip was in contact with the surface of the stone. A filament of dye was then released immediately upstream of the PST using a hypodermic syringe fitted with a long, thin needle. Using the underwater viewer, the orientation of the dye filament was compared to the orientation of the PST. If the two were not parallel (i.e. the dynamic tap was not perpendicular to the flow), the PST was repositioned in the correct orientation using the micromanipulator and positioning elbow (see chapter 3).

The distribution of boundary layer flow conditions (attached *vs.* separated boundary layer flows) over each stone was noted using flow visualisation. Using a hypodermic syringe fitted with a long, thin needle, fluorescein dye was injected into the flow at several points immediately upstream of each of the experimental stones. The extent of areas of recirculating dye (*i.e.* backflow associated with detached boundary layer flows) above each stone were recorded.

Periphyton distribution

At the end of the field study (October 7, 1998), all five stones were removed from the stream in order to measure the microdistribution of periphyton. The stones were removed at night (to

minimise exposure to ultraviolet light) and packed in ice in an insulated cooler for transport to the aquatic sciences lab at the University of Northern British Columbia, where periphyton samples were removed in circular quadrats using a rotating brush-and-suction sampling device (diameter = 2.72 cm). The algal sampling device consisted of a PVC cylinder (closed at the upper end and encircled at the lower end with a high-density foam rubber skirt) which housed a circular, nylon-bristled brush. The brush, in turn, was connected to a rotary tool (Dremel MultiPro rotary tool model 395; Winconsin, USA) via a brass shaft. Two lines opened into the side of the cylinder. The first was a water line, which allowed a jet of cold, distilled water to be introduced when the brush was activated, creating an algal slurry. The second was a vacuum line, which drew off the slurry.

Algal samples were removed in three transects in the streamwise direction. The centre of each quadrat corresponded to a marked point (intersection) in the 5 x 5 cm reference grid (Figure 4-1b). Only the upper surface of the stone was sampled; the effectiveness of the sampling device used in this study was limited, as are other devices, when used to obtain algal samples from the curved surface at the edges of rounded stones. However, this method was shown to be as effective as direct extraction in a comparison of methods (Hoover et al. in prep.). For chlorophyll *a* analyses, each algal sample was vacuum filtered onto a glass fibre filter (GF/C; Whatman, UK), immediately frozen at -40°C, and extracted in 10 ml of 90% acetone (buffered with MgCO₃; as per Geider and Osborne 1992) for 24h at 5°C in the dark. Chlorophyll *a* concentrations were determined using a spectrophotometer (Perkin Elmer UV/Vis Lambda 2S Spectrometer; Perkin Elmer, Germany) using the methods of Geider and Osborne (1992).

Stone surface characteristics (surface roughness and topography)

A measure of stone roughness was obtained by placing a sheet of white printer/copier paper (75 g m^{-2}) over each 5 x 5 cm quadrat. The paper was held firmly against the stone surface, and a pencil (1600 HB) was rubbed firmly and evenly over the surface of the paper producing a 'graphite rubbing' of the stone surface. The texture and irregularities of the stone surface were defined on the resultant 'rubbing'. All indentations in the stone surface whose long axis exceeded 5 mm in length were then counted on each 5 x 5 cm 'rubbing', producing an estimate of the surface roughness (degree of pitting) within each quadrat.

The surface topography of each stone was determined by measuring the distance down from a level rod to each point on the grid. For example, the topographical measurement of the highest point of the stone surface was recorded as "0 cm", a grid point 1.5 cm lower was recorded as "1.5 cm", etc.

Diurnal variation in behaviour

Observations of diurnal changes in larval distribution (*i.e.* changes in numbers of larval mayflies on the upper surface of the five experimentally deployed stones) were made on two dates. The first set of observations was made from 13:00 h on Sept. 26 to 04:00 h on Sept. 27, 1998. The exact observation times varied slightly; depending on the numbers of mayflies, it took approximately five minutes to record mayfly numbers and positions and travel to the next stone. Observations were made at 2 hour intervals during the dusk hours (18:00 h – 22:00 h). In addition, a single measurement was taken at 09:00 h Sept. 27 (*i.e.* the following morning).

On the second observational date, the density and distribution of larval *E. longimanus* over the upper surface of the five experimental stones were recorded every two hours over a 22-hour period, from 14:00 h on October 3 to 12:00 h on October 4, 1998 (with the exception of the mid-night period; no record was made at 02:00 h). In all cases, all larvae visible over the upper surface of each stone were recorded. Night-time observations were made with the aid of a headlamp.

Light measurements were taken every 30 minutes using a quantum sensor and light meter (model LI-192SA and model LI-250, respectively; LI-COR Inc., Nebraska, USA), except during periods of rapid light change (dawn and dusk, approximately 08:45 h - 09:30 h and 18:00 h - 19:45h, respectively), when they were recorded every 15 min. Light measurements were made on the streambank at the study site.

Stone	Date (1998)	Depth above datum	Parameters measured			
(diameter)		(centre) (mm)	Shear	E. longimanus dist'n		
. ,		. ,. ,	stress	Day	night	
7	September 2	54	-	Yes	-	
	September 5	27	-	Yes	-	
d = 29.0 cm	September 8	28	-	Yes	-	
2010 0111	September 13	55	-	Yes	-	
	September 16	36	Yes ^a	Yes	-	
	September 26	90	-	Yes ^b	Yes	
	September 27	95	-	Yes	Yes	
	September 30	84	Yes	-		
	October 3	120	-	Yes	Yes	
	October 4	115		Yes	Yes	
31	September 2	50	Yesa	Yes	-	
01	September 5	31	-	Yesb	-	
d = 175 cm	September 8	42	_	Yes	-	
u = 11.0 om	September 13	60	-	Yes	-	
	September 16	40	-	Yes	_	
	September 17	41	Yes		-	
	September 26	96	-	Yes ^b	Yes	
	September 27	99	-	Yesb	Yes	
	October 3	118		Yes	Yes	
	October 4	114		Yesb	Yes	
25	Sentember 2	53	-	Yes	-	
20	September 5	48	Vesa	Vesb		
d = 21.0	September 8	40	Vesa	Ves		
u - 21.0	September 0	45	100	Yes	-	
	September 16	48		Vesc	-	
	September 17	48	Ves	-	-	
	September 26	55	-	Yes	Yes	
	September 27	56	_	Yes	Ves	
	October 3	88		Ves	Ves	
	October 4	82		Yes	Yes	
22	Sontombor 2	25	_	Ves	100	
23	September 2	15		Vosb		
d = 19 5 cm	September 9	10	-	Vecb		
u = 10.5 cm	September 0	22		Vec	-	
	September 15	32	-	Vos ^c	-	
	September 10	20	-	Vosb	Voc	
	September 20	66	-	Voc	Voc	
	September 27	20	- Ves	165	165	
	September 30	30	165	Voc	Voc	
	October 3	02	-	Vec	Vec	
10	October 14	00	-	VecD	103	
10	September 2	0	-	Vecb	-	
d = 27.0	September 9	10	_	Vac	_	
d = 27.0	September 0	25	_	Voc	-	
	September 16	15	_	Vecb	-	
	September 10	26	Vos	165		
	September 25	20	165	Vocb	Voc	
	September 20	63		Voc	Voc	
	October 2	80	-	Voc	Voc	
	October 3	70	-	Ves	Voc	
	LUCIODEL4	(0	-	Tes	IES	

Table 4-1. Comparison of measured parameters at all sampling dates

^a shear stress measured only at centre of stone (for purposes of comparison); entire distribution recorded on all other dates ^b stone surface examined, no *E. longimanus* present ^c *E. longimanus* distribution recorded after 18:00 h (not included in analyses)

Stone rotation experiment

The proximal relationship between hydrodynamic forces (e.g. shear stress), *E. longimanus*, and periphyton was examined by a substrate reversal experiment. The night-time microdistribution of *E. longimanus* larvae was recorded on the upper surface of three naturally occurring stones by recording the average density of larval *E. longimanus* in 5 cm bins in the downstream direction. The stones selected were comparable in both size and *E. longimanus* density to the experimental stones. After the original distribution was recorded, each of the three stones were then rotated 180° (*i.e.* the original downstream edge became the upstream edge). After 40 minutes, the microdistribution of the mayfly larvae was recorded, and the stones were rotated 180° to their original orientation. The microdistribution of the mayflies was again recorded after 40 minutes. A one-way ANOVA was used to test if the mayflies had moved to new locations (*i.e.* were proximately responding to the new distribution of near-bed flow parameters) or had remained in their original microdistribution (*i.e.* proximately responding to substrate and food resource (periphyton) factors).

Analyses

All mayfly microdistributions recorded between 08:00 h and 18:00 h (all dates) were averaged to produce a mean daytime microdistribution, while records between 20:00 h and 06:00 h were averaged to produce a mean night-time microdistribution. Dusk and dawn observations (06:00 h - 08:00 h and 18:00 h - 20:00 h, respectively) were not used in these analyses, in order to minimise the influence of the rapidly changing light level and corresponding changes in larval behaviour on analyses. In order to relate larval microdistributions to environmental factors measured over a period of several weeks, mean daytime and night-time larval densities were determined for each 5×5 cm quadrat (see Table 4-1 for dates). To account for among-stone differences in biotic and abiotic parameters, stone diameter (a discrete, continuous variable) was included in all ANOVA models as a covariate, and in all standard multiple regression models as a covariable.

Data were examined for normality and homogeneity of variance (Kruskal-Wallace W test and data visualisation including boxplots and frequency histograms). Daytime and night-time abundances of *E. longimanus* were not normally distributed. However, ln(x+1) and $x^{0.5}$ transformations of these data did not meaningfully increase the normality of the data. As a result, in order to maximise the

interpretability of the results, all analyses were performed using the untransformed mayfly distribution/abundance data.

As shear stress was measured at fewer points on the surface of the experimental stones than all other variables, two multiple regression analyses were performed with per quadrat mayfly density (daytime and night-time densities of *E. longimanus*) as the response variable. As such, for the ANOVAs, a Bonferonni adjustment of α was used (Tabachnick and Fidell 1996), and the level of significance was reduced from $\alpha = 0.05$ to $\alpha = 0.025$.

All analyses were conducted using Statistica 5.1 (1996; Statsoft, Tulsa, Oklahoma).

Results

It was possible to observe the behaviour and position of larval insects on the upper surface of stream stones, and the generic identity of individual insects could be determined. With the exception of extremely rare observations of larval blackflies (Simuliidae), and larval mayflies of the genera *Baetis* and *Rhithrogena*, the habitat represented by the upper surface of the stones was inhabited exclusively by larval *Epeorus longimanus* (Heptageniidae).

Abiotic factors influencing the microdistribution of E. longimanus

The microdistribution of *E. longimanus* larvae was dependent on both within- and amongstone factors. When *E. longimanus* larvae were present on the upper surface of the stones in high numbers (generally at night), they were at highest densities upstream of the flow separation zone (at the downstream edge), near the stones' centre. There was no significant differences in per quacIrat mayfly densities among stones during the night-time (ANOVA, F(4,130) = 0.40, p = 0.81). There was, however, a significant difference in mayfly densities among stones during the day (ANOVA, F(4,130) = 5.08, p < 0.001) (Figure 4-2A).

An ANCOVA was performed on daytime and night-time densities of *E. longimanus*, with boundary layer flow conditions as the predictor variable and stone diameter included as a covariate. During the night, there were significantly greater densities of mayflies in areas of the stones with attached boundary layer flows compared to areas with separated flows (F(1,132) = 8.83, p = 0.0035) (Figure 4-2B). In the daytime, although not significant (F(1,132) = 3.41, p = 0.067), the trend was similar. In addition, regression analysis shows that night-time and daytime distributions of *E*. *longimanus* were significantly and positively related ($R^2 = 21.12\%$; ANOVA F(1,133) = 35.62, p < 0.001) (Figure 4-3). This trend demonstrates that although daytime densities were much lower, daytime microdistributions of *E. longimanus* were similar to those observed at night.

During the night, per quadrat densities of *E. longimanus* varied significantly with streamwise (x) distance along the upper surface of the stones (ANCOVA, F(6,127) = 4.32, p < 0.001) (Figure 4-4). When the mayfly distributions of all stones were pooled, there were more mayfly larvae in the centre of the stones than at either the upstream or downstream edges (Figure 4-4; Table 4-2). However, there was no corresponding trend in daytime distributions of *E. longimanus* larvae (ANCOVA, F(6,127) = 1.63, p = 0.15).

Table 4-2. Post-hoc comparison of means (Tukey's HSD test) following the significant ANCOVA on night-time distribution of *Epeorus longimanus* and streamwise (x) position

Position (x)	+15 cm	+10 cm	+5 cm	0 cm ^a	-5 cm	-10 cm	-15 cm
+15 cm	-						
+10 cm	ns	-					
+ 5 cm	ns	ns	-				
0 cm ^a	ns	0.039*	ns	-			
-5 cm	ns	ns	0.037*	ns	-		
-10 cm	ns	ns	ns	0.067	0.063	-	
-15 cm	ns	ns	ns	0.053	0.050	ns	-

* significant at α=0.05

ns = p > 0.075

^a centre of stone.

Two sets of standard multiple regressions were performed between larval mayfly distribution (as the response variable) and a series of environmental factors (as predictor variables). Due to unequal sample sizes in the data subsets, the multiple regressions were performed separately. In the first multiple regression analysis, mayfly distribution (daytime and night-time microdistributions, analysed as subsets) was included as the response variable and shear stress as the predictor variable. In the second multiple regression analysis, mayfly distribution (again, daytime and night-time microdistributions, analysed as subsets) was included as the response variable as the response variable. In the second multiple regression analysis, mayfly distribution (again, daytime and night-time microdistributions, analysed as subsets) was included as the response variable, and streamwise (x) position within the stone, stone surface roughness, and stone topography were included as the

predictor variables. In all analyses, stone diameter was included in both models as an ordinal, discrete variable to account for among-stone differences

There were marked differences in the factors influencing the microdistributions of *E*. *longimanus* larvae between day and night periods. During the daytime, there were significantly more larval *E. longimanus* in areas of the substrate with higher shear stress (Figure 4-5), and on stones with larger diameters (Table 4-3; see also Figures 4-6 to 4-10). During the night-time, however, there was no significant relationship between larval microdistribution and either shear stress or stone diameter.

Larval microdistribution during the day was also positively related to streamwise position and stone diameter, and negatively related to topography (*i.e.* there were more larvae higher and further back on exposed stone surfaces; Table 4-4). During the night, larval microdistribution was only related to topography (*i.e.* more larvae higher on exposed stone surfaces; Table 4-4). However, the relationship between mayfly microdistribution and stone roughness approached significance (p = 0.087), suggesting that there may be more mayflies on rough stone surfaces during the night.

Table 4-3. Multiple regression analyses of the relationship between the microdistributions of periphyton and *Epeorus longimanus* (daytime and night-time distributions) and wall shear stress (τ_w)

Model	R^2	(df) = F	shear stress (τ_w)		Stone diameter ^a		
			p-value	β	p-value	β	
a) daytime E. longimanus	36.15%	(2,36) = 10.19	0.021	16.66	< 0.001	22.96	
b) night-time E. longimanus	2.08%	(2,36) = 0.38	0.61	25.47	0.42	31.44	
c) periphyton ^b	5.11%	(2,36) = 0.67	0.53	-0.16	0.27	-0.19	

^a stone diameter entered into the model as an ordinal discrete variable to partition out variance due to among-stone differences

^b presented as mass of chlorophyll a per cm²

Biotic factors influencing microdistribution of *E. longimanus*

The relationship between benthic biota, bed characteristics, and stream hydraulics was variable among stones. On stone 7, the centreline distributions of *E. longimanus* and periphyton had an inverse relationship, as did shear stress and *E. longimanus* density (Figure 4-6). However, this trend was not consistent among all stones. While the shear stress on the surface of stone 31 increased from the front of the stone to the back, where it sharply declined, there is no clear

association with either algal or mayfly distributions (Figure 4-7). Similarly, on stone 23, there was a distinct increase in shear stress from front to back of the stone, where flow eventually separated (Figure 4-8). While this was mirrored by a front-to-back increase in mayfly densities, algal biomass tended to be greatest over the front and centre of the stone. Again, on stone 10, there was a similar front-to-back increase in shear stress (Figure 4-9). However, this was poorly related to the distribution of algae and mayflies, which tended to be inversely related (*E. longimanus* densities highest, algal biomass lowest over the centre of the stone). The shear stress over stone 25 was relatively uniform over the surface of the stone (Figure 4-10), with the exception of the leading edge (due to wake interference from upstream roughness elements). While there was little variation in algal densities over the surface of stone 25, densities of *E. longimanus* increased from the front to the back.

Table 4-4. Multiple regression analyses of the relationship between the microdistribution of *Epeorus longimanus* (daytime and night-time) and streambed characteristics

Model	R^2	(df) = F	p-value	β
A) daytime E. longimanus	22.95%	(4,130) = 9.68	< 0.001	
Explanatory variables				
Streamwise position (x)			0.014	6.40
Roughness			0.82	-0.15
Topography			< 0.001	-7.26
Diameter ^a			< 0.001	13.51
B) night-time <i>E. longimanus</i> Explanatory variables	25.75%	(4,130) = 11.28	<0.001	
Streamwise position (x)			0.38	12.72
Roughness			0.087	6.21
Topography			< 0.001	-66.57
Diameter ^a			0.50	13.86

^a stone diameter entered into the model as an ordinal discrete variable to partition out variance due to among-stone differences

Factors influencing the microdistribution of periphyton

There were significant differences in periphyton growth among the five stones (ANOVA F(4,61) = 10.49, p < 0.001) (see Figures 4-6 to 4-10). Two standard multiple regressions were performed between periphyton growth (measured as mass of chlorophyll *a* cm⁻²) as the response variable and streamwise distance, stone roughness, topography (height on stone), and local *E*.

longimanus density (the first and second regression models including daytime and night-time mayfly microdistribution densities, respectively) as predictor variables. Stone diameter was included in both models as an ordinal, discrete variable to account for among-stone differences. In both cases, only three of the variables contributed significantly to prediction of algal microdistribution density (Table 4-5); roughness, topography, and stone diameter (the latter variable reflecting significant among-stone differences). Periphyton biomass tended to be greater higher on the stone surface, and greater algal densities were found in areas of the stone surface with greater surface roughness. In addition, the relationship between algal density and daytime and night-time microdistributions of *E. longimanus* approached significance (p = 0.060 and p = 0.055, respectively), suggesting that algal densities were reduced in areas of the stone surface where densities of *E. longimanus* were higher. Algal biomass tended to be highest over the centre of the stones, and lowest on the upstream and downstream edges (Figure 4-11); this difference, however, was not significant (ANCOVA, F(4,57) = 1.05, p = 0.39). Periphyton microdistribution was not significantly related to shear stress (Table 4-3; see also Figure 4-6 to 4-10).

An ANCOVA was performed on algal densities, with boundary layer flow conditions (separated *vs.* attached boundary layer flows) as the predictor variable and stone diameter as the covariate. While there tends to be more periphyton growth in those areas of the stone surface with attached boundary layer flows (Figure 4-12), the difference is not significant (ANOVA; F(1,63) = 2.65, p = 0.11).

Diurnal variation in positioning

E. longimanus displayed a distinct diel periodicity in their positioning (Figures 4-13 & 4-14). There were significantly more larvae on the upper surface of the stones during the night-time hours than there were during the day (ANOVA, F(1,268) = 58.35, p < 0.001). It is important to note, however, that daytime withdrawal of larvae from the upper surface of the stones was not complete. Daytime densities of *E. longimanus* on the upper surface of the stones were approximately 10% of night-time densities. While there were significant differences in daytime densities among stones, the daytime distribution of *E. longimanus* was significantly correlated with both shear stress and topography (Tables 4-3 & 4-4). This suggests that mayflies that remain on the upper surface of the

stones during the day were found predominantly in high shear stress areas near the apex of the stone surface.

Table 4-5. Multiple regression analyses of the relationship between the microdistribution of periphyton to streambed characteristics and grazing mayfly densities

Model	R^2	(df) = F	p-value	β
A) Periphyton density ^a	29.76%	(5,60) = 5.08	< 0.001	
Variables Streamwise position (x) Roughness <i>E. longimanus (day)</i> Topography Diameter ^b			0.20 < 0.001 0.060 < 0.001 0.016	0.11 0.093 -0.0049 -0.30 -0.26
B) Periphyton density ^a	29.92%	(5,60) = 5.12	< 0.001	
Variables Streamwise position (x) Roughness <i>E. longimanus (night)</i> Topography Diameter ^b			0.38 < 0.001 0.055 < 0.001 < 0.001	0.072 0.10 -0.00080 -0.35 -0.36

^a mass of chlorophyll a per cm²

^b stone diameter entered into the model as an ordinal discrete variable to partition out variance due to among-stone differences

The withdrawal of the mayfly larvae from the upper surface of the stones at dawn was abrupt compared to the variable timing of the emergence at dusk (Figure 4-15). There was an abrupt change in larval density on the upper surface of the stones at dawn (~07:00 h). The withdrawal of individuals from the upper surface coincided with the onset of detectable light levels in the morning. However, larval emergence was more gradual. Larvae began to emerge during late afternoon, when light levels were still relatively high, and continued to move to the exposed upper surface of the stones until well after dusk. The asymmetry between the highly variable rates of emergence and the relatively rapid withdrawal suggests that additional factors other than light level may have influenced the migration rates of *E. longimanus* from the underside of stream boulders to the upper surface. Net migration of larvae was limited during the night; there was little change in larval density between 23:00 and 05:00 h.

The handling of the stones during the stone reversal experiment did not noticeably disturb the *E. longimanus* larvae. Larvae did not immediately or rapidly migrate from their original positions. Larval densities before and after stone handling were similar, and few, if any, larvae drifted from the stone surface.

Figure 4-16 shows the results of the stone reversal experiment. In all three cases, there were generally higher densities of *E. longimanus* on the downstream portion of the stone (Figure 4-16a). When the stones were reversed, the mayflies retreated downstream to new positions on what were originally the leading edges of the stones (Figure 4-16b). When the stones were returned to their original orientations, the mayflies reversed their movements, and returned to their original distributions (Figure 4-16c). This demonstrates that the proximal factor to which *E. longimanus* responded was local, near-bed hydrodynamic factors rather than distribution of algal food resources. There was a significant *time* x *distribution* interaction (ANOVA, F(12, 42) = 3.86, p < 0.001). The rotation of the stones resulted in a significantly different distribution of mayflies. Post-hoc linear regressions show that the initial (before initial rotation) and final (after the second rotation when stones were returned to their original orientation) distributions of *E. longimanus* on the upper surface of the three stones were significantly related ($R^2_{adj} = 33.0\%$; ANOVA, F(1,121) = 11.98, p = 0.0023). The initial and rotated (after the stone had been rotated 180°) distributions of *E. longimanus* were not related ($R^2_{adj} = 0.98\%$; ANOVA, F(1,121) = 0.21, p = 0.65).

Discussion

The objective of this study was to examine the microdistribution of a highly mobile species of grazing heptageniid mayfly (*Epeorus longimanus*) with respect to near-bed flow parameters, streambed characteristics, and the microdistribution of algal food resources across the surface of torrential stream boulders. The results of the present study suggest that the proximate relationship between primary producers, grazers, and environmental variables may be more complex than previously thought. As hypothesised, the microdistribution of *E. longimanus* was significantly related to several environmental parameters, each measured at organismal spatial scales. However, the

results revealed that the functional relationship between the microdistributions of this torrenticolous grazer, periphytic algae, and near-bed and substrate characteristics differed between day- and night-time periods, suggesting important behavioural inputs into the relationship.

The importance of scale

The densities of *E. longimanus* larvae and periphyton were significantly different among stones of similar size located adjacent to one another in the same reach. This demonstrates the importance of the spatial scale at which the behaviour of benthic biota is examined. The planar area of each of the stones used in this study was similar to the area traditionally sampled in benthic ecology studies. Surber or box-type samplers, which sample relatively large areas of the stream bed (~ 500 cm²), are often used to sample both the density and diversity of benthic taxa (e.g. Hynes 1971; Statzner 1981; Dudgeon 1982). If employed in this study, however, such methods would have sampled across several microhabitat types (e.g. sides vs. upper surfaces of streambed stones) and the microdistributions of both *E. longimanus* and the environmental parameters that influence the positioning of individual larvae would not have been detected. In order to determine which parameters influence the behaviour and ecology of stream invertebrates, the immediate environment of the invertebrates must be characterised at the spatial scales of the organisms themselves, rather than the scale of the observer.

Recent studies have measured either the microdistribution of benthic taxa or environmental factors at small spatial scales, but rarely are both sets of parameters measured at fine, organismdefined scales (*but see* Hart et al. 1996). For example, Voelz and Ward (1996) examined the microdistribution of the caddisflies *Arctopsyche grandis* and *Brachycentrus occidentalis* using 3 x 3 cm quadrats, but measured current velocity only at the front, top, and bottom (leading edge) of each stone. In order to examine the spatial relationship between biotic and abiotic parameters at the scale of a torrential stream invertebrate, the present study quantified the microdistribution of larval *E. longimanus* over the surface of stream stones using 5 x 5 cm (25 cm²) quadrats, periphyton using 5.84 cm² circular quadrats, and shear stress at even finer spatial scales (measurements either 2.5 or 5.0 cm apart).

Factors influencing microdistribution

The relationship between the microdistribution of *E. longimanus* larvae and biotic, hydrodynamic, and substrate factors differed between daytime and night-time periods. Night-time distributions of *E. longimanus* were significantly related to topography and flow separation factors. Larvae avoided areas of recirculating, separated flow, and grazed on algal growth high on the surface of streambed stones. During the night, the larvae were not strongly influenced by other measured substrate or hydrodynamic variables. However, in addition to topography, daytime distributions of *E. longimanus* on upper stone surfaces were related to shear stress and streamwise (x) distance along the stone surface. This demonstrates a diurnal shift in the functional responses of *E. longimanus* to environmental parameters. The relatively few (~10% of night-time densities) larvae that remained on the upper surface of streambed stones occupied high shear areas towards the rear of the upper stone surface.

These results are consistent with the suggestion that the factors that influence the microdistribution of benthic invertebrates are different between daytime and night-time periods. The presence of visually oriented fish predators, for instance, is generally thought to cause several stream insect species to retreat to the underside of streambed stones during the day (*e.g.* Cowan and Peckarsky 1994). This ceases to be an important determinant of insect micropositioning during the night when fish predators can no longer see their prey. Similarly, Donahue and Schindler (1998) found that simuliid larvae migrated to shaded microhabitats during periods of intense solar radiation, demonstrating that exposure to UV also influences invertebrate microposition. In this fashion, UV acts as an environmental factor that modifies behaviour only during daylight hours. The results of the present study indicate that there may be diurnal variation in the responses of benthic invertebrate taxa to environmental factors that do not vary diurnally.

Ecological hydrodynamics

During the night, there were significantly fewer larval *E. longimanus* found in areas of the stone surface where flow separation occurred (*i.e.* areas of recirculating flow at the rear and, to a lesser extent, the front of the stones). Larval *E. longimanus* tended to be found at highest densities over the centres and just downstream of the centres of the experimental stones, suggesting that they

preferred regions of stone surfaces where unidirectional, generally linear flow occurred. Peckarsky and Cowan (1995) showed that E. longimanus has distinct preferences for upper stone surfaces over upstream and downstream faces, while Rader and Ward (1990) found that mayflies in a Colorado river rarely used the front and rear sides of substrates, almost exclusively occupying the upper, lower, and lateral surfaces of substrates. Larval E. longimanus may preferentially select upper stone surface microhabitats where flow is unidirectional because they rely on several highly specialised adaptations, including a sucker-like arrangement of gills and a flattened, streamlined body shape, to maintain contact with the substrate in high velocity, high shear microhabitats. Weissenberger et al. (1991) note that in microhabitats with steep velocity gradients, organisms are at greater risk of being dislodged by lift than drag. Thus, the morphological adaptations displayed by larval E. longimanus may largely act to counter the typically high lift forces encountered by organisms on the upper surfaces of stones in torrential streams. The adaptations of this torrential mayfly enable it to effectively travel on the exposed surfaces of stones located in high velocity areas of the stream channel. E. longimanus larvae observed were able to move forward, sideways, and backward without difficulty in microhabitats where current velocities measured 2 mm above the substrate exceeded 1.0 m s⁻¹.

The efficacy of these adaptations may be reduced, or even negated, in areas of variable flow direction and high turbulence intensities. As such, the upstream and downstream faces of stones may represent areas where contact with the substrate becomes more difficult for *E. longimanus* larvae. Vortices shed from the lee side of protuberant boulders alter the structure of the flow, producing high levels of turbulence above the downstream side of boulders (Robert et al. 1996). The streambed at the study site was composed of stones that protruded upwards into the water column (*e.g.* rough-turbulent flow). Flow in channels of this type is characterised by convected eddies and flow structures whose motion is predominantly towards the bed ("sweeps"), which further acts to create unstable, turbulent flow conditions at the leading edge of exposed stream boulders. In addition, solenoidal ("horseshoe") vortices can form around the upstream side of stones protruding up into the flow (Vogel 1994; Bouckaert and Davis 1998), creating directionally variable, oscillating flows. Other torrenticolous mayfly species, including *Rhithrogena*, *Ephemerella doddsi* (see Minshall 1984) and *Deleatidium* (type *myzobranchia*) (Collier 1994), which have morphological adaptations similar to those of *E. longimanus*, would be expected to have similar microhabitat requirements.

Lacoursière (1992) also found that simuliid larvae preferred regions of artificial substrates where flow was moving in a unidirectional fashion, and generally avoided areas exposed to high turbulence and variable flow direction. However, although similar, the microdistributions of simuliid and mayfly larvae are the result of different behavioural processes. While the grazing mayfly larvae migrated to locations that minimised the probability of accidental entrainment and maximised access to algal food resources, suspension-feeding blackfly larvae chose flow microhabitats that maximised delivery rates of food particles to their labral fans while minimising drag on the posterior portion of their abdomens (Lacousière 1992; Lacoursière and Craig 1993).

Flow mediation of predator-prey interactions

Larval E. longimanus made extensive use of the microhabitat represented by the exposed, relatively high-shear upper surfaces of torrential stream stones during the night and, to a lesser extent, during the day. Although predatory invertebrates (e.g. Rhyacophila, Drunella, and Megarcys) are relatively numerous in microhabitats preferred by *Epeorus* (see Chapter 2), and were collected at the study site (T. Hoover, unpublished data), these predators were never observed on the upper surface of the experimental stones during either day- or night-time periods, during the entire two month study period. This suggests that the upper surfaces of torrential stream boulders, which are typically exposed to high velocities and high shear stress, act as flow-mediated refuges (Hart and Merz 1998) from invertebrate predation for E. longimanus larvae. This conclusion conflicts with the findings of Peckarsky and Cowan (1995), who reported that the use of upper stone surfaces by E. longimanus did not represent a refuge from stonefly predation, as they observed that stonefly predators (Kogotus) were able to access all areas of streambed stone surfaces. However, the "high flow microhabitats" in the experimental stream chambers used by Peckarsky and Cowan (1995) had average current velocities of only 15.6 cm s⁻¹, while measured mean velocities over the substrates in the present study were much higher (range = 24.2 - 136 cm s⁻¹, mean = 71.8 cm s⁻¹). The difference between the values recorded in the field in this study and the values reported by Peckarsky and Cowan (1995) suggests the existence of a threshold velocity above which some stonefly predator taxa may not be able to forage for prey.

Invertebrate predators, which generally lack the highly specialised morphological adaptations of torrenticolous grazers to maintain contact with the substrate in high velocity habitats (see

Weissenberger et al 1991; Statzner and Holm 1989; *also see* Minshall 1984; Vogel 1994), may either avoid high velocity areas (Muotka and Pentinnen 1994), or be eroded from the substrate when they attempt to access prey. Hart et al. (1996) note that while many prey species are sessile or semi-sessile and have morphological adaptations that anchor them securely to the stream bed, many predators depend on a foraging mode to search for prey, a trait which selects for high speed and manoeuvrability rather than tenacity. Additionally, predators (especially the caddisfly *Rhyacophila* and the periodid stonefly *Megarcys*) might be unable to exploit prey in high-velocity areas of the substrate due to the fact that they are generally larger that their mayfly prey, and larger organisms experience proportionally higher drag (Vogel 1994; Statzner 1981). The highly turbulent, high Reynolds number flows on exposed surfaces of torrential stream boulders may also prevent predators from recognising prey. The hydrodynamic cues (species-specific wave patterns generated by prey during escape manoeuvres) used by the predatory stonefly *Kogotus modestus* to discriminate prey species from non-prey species (Peckarsky and Wilcox 1989) might be disrupted in the highly turbulent flows above the bed of torrential stream boulders (see Hart et al. 1996).

These results support the conclusions of Hart and Merz (1998) and Peckarsky et al. (1990) who found that direct predator impacts (*i.e.* lethal encounters) to prey populations were decreased in habitats which were hydrodynamically unfavourable to the predators. During the night, when E. longimanus were grazing on the upper surface of stream boulders, the degree of microhabitat overlap between predators (which have presumably remained in interstitial spaces or on the underside of the boulders) and prey was at a minimum. As such, the rate of predator/prey encounters should also be lowest during the night. In this system, however, the flow-mediated refuge from predation coincided spatially with high resource patches (periphyton densities were also greatest on the upper surface of stones). The negative effects of flow on predators and the spatial co-occurrence of high flow and high resource microhabitats may have combined to produce a positive indirect effect on larvae, similar to that observed in simuliid larvae populations by Hart and Merz (1998). As a result, other types of indirect impacts to mayfly prey populations attributed to the presence of predators may not apply to E. longimanus larvae in torrential habitats. For instance, Peckarsky et al. (1993) found that predator avoidance behaviour by Baetis bicaudatus resulted in lower feeding rates, and, as a consequence, lower growth rates and fecundities. Similarly, Peckarsky (1996) stated that Epeorus longimanus had reduced resource acquisition rates as a cost of predator avoidance. However, due to

the spatial overlap of areas of algal resource and refuge from predation, the feeding rates of *E. longimanus* in the torrenticolous stream habitats described here were probably not reduced in this fashion. In addition, increases in predator-induced drift, such as that reported in the mayfly *Baetis* by the stonefly *Doroneuria baumanni* (Lancaster 1990), may not occur in *E. longimanus* populations due to the low probability of predator-prey encounters during night-time feeding periods. Peckarsky (1996) found the presence of the stonefly predator *Kogotus* induced very little night-time drift in *E. longimanus*. Wooster and Sih (1995), in their review of drift and activity responses of benthic invertebrates to the presence of predators, found that stream invertebrate drift increased when invertebrate predators were present; however, no studies of the responses of torrenticolous taxa were included in their analyses.

The daytime positioning of the larval *E. longimanus* that remained on the upper surface of the stones may represent a trade-off between exposure to predators and exposure to UV radiation. Several stream invertebrate taxa (*e.g.* simuliid larvae; Donahue and Schindler 1998) are known to be sensitive to UV radiation. When light levels increased to detectable levels in the morning, the majority of larval *E. longimanus* migrated to the underside of the stones. Only approximately 10% of the larvae observed on the upper surface of the stones during the night remained there during the day (Figures 4-13 and 4-14). The number of *E. longimanus* larvae that remained on the upper surface of streambed stones was related to the level of incident radiation; more larvae remained exposed on cloudy, overcast days than sunny days (personal observation). As a result, while high shear areas may act as a flow-mediated refuge from predation, levels of UV radiation may, in turn, mediate the use of these refugia.

Diel periodicity

The diel periodicity in positioning that was observed in *E. longimanus* is typical of the behaviour of mayflies seen in streams with visually oriented predators (McIntosh and Peckarsky 1996; Rader and Ward 1990). However, among-stone differences in the rates of dusk emergence and dawn withdrawal from the upper surfaces of the stones suggests that the behaviour exhibited by *E. longimanus* may be more than merely negatively phototactic. The timing of the emergence of *E. longimanus* larvae was highly variable among stones, and larvae emerged over several hours (see Figure 4-14). However, the withdrawal of larvae from the upper surface of all stones appeared to be

synchronous in that larvae withdrew to the underside of the stones within a relatively short period (< 2

h). There are two possible explanations for the apparent asymmetry in the migratory behaviour of larval *E. longimanus*. First, the response to the proximal stimulus (light level) may vary between dusk and dawn. If larval E. longimanus are cued to emerge from the underside of the stones when ambient light levels decrease below a certain threshold value, the precise timing of the emergence should vary locally due to shading by adjacent stones. In sites with narrow, deep interstices between stones, larval emergence should begin somewhat earlier. By the same rationale, the timing of larval withdrawal should appear relatively co-ordinated. The upper surfaces of the protuberant stones, being higher than the surrounding streambed, should be essentially unshaded by adjacent stones. Larvae on the upper surfaces should have been exposed to similar light levels, and thus, when ambient light exceeded the threshold value, the withdrawal behaviour should have been cued at the same time for all individuals. Second, the dusk stimulus (light dropping below the threshold value) cued E. longimanus larvae to migrate to the upper surface and begin grazing; as a result, they may have immediately begun to forage as they migrated upward, reducing their travel speed. When light levels exceeded the threshold level at dawn, larvae were cued to cease feeding and migrate to the underside of the stone, unimpeded by incidental feeding. In this manner, speed of travel during the dawn withdrawal of diurnally active invertebrate grazers inhabiting coarse substrates should exceed travel speeds during dusk emergence.

Shear stress

In all cases where the stone protruded up into the flow (*i.e.* all stones except stone 25, which was located beneath a small plunge/cascade), shear stress (τ_w) increased gradually from the front to the rear of the stone. Shear stresses recorded at the front of the boulder were generally low ($\tau_w < 1.0$ Pa), while maximum shear stress values were generally recorded near the rear of the stone, immediately upstream of the separation point. Shear stress decreased abruptly at the rear of each stone, as shear stress is zero at points of flow separation (*see* White 1999).

The relationship between the biology of benthic invertebrates and shear stress is generally poorly understood, despite several prominent reviews on the biological importance of near-bed hydrodynamics (e.g. Nowell and Jumars 1984; Davis and Barmuta 1989; Carling 1992) that

emphasised the potential importance of shear stress. Importantly, the distribution and magnitude of shear stress has yet to be measured at small (cm) scales over the rocky surface of naturally occurring stream beds. This is due primarily to the difficulty in measuring τ_w in the field. Although shear stress can be determined from the near-bed, log-linear portion of the boundary layer velocity profile, such measurements are difficult and time-consuming to obtain in high velocity, shallow flows (*see* Hart et al. 1996), and are of questionable validity in instances where boundary layer profiles are distorted by pressure gradients (*see* Chapter 3).

Statzner (1981) identified a relationship between several species of benthic invertebrates and "hydraulic stress", a factor that describes flow conditions at the surface of the substrate and is related to the theoretical boundary layer thickness. Recognising the potentially important role that bed stresses might play in benthic ecology, Statzner and Muller (1989) developed a set of standardised hemispheres (Fleisswasserstammtisch (FST) hemispheres) whose movement was correlated with boundary shear stresses and near-bed flow conditions. However, FST hemispheres were found to have several substantial limitations. Frutiger and Schib (1993) found that FST hemisphere movement was more correlated to mean velocity than near-bed velocity, and that the standardised deployment plate substantially interfered with local near-bottom microhydraulics. In addition, Dittrich and Schmedtje (1995) found that the relationship between FST hemisphere movement and wall shear stress depended on bed topography. Due to its small diameter and method of deployment, the Preston-static tube (PST) used in this study to measure the distribution of shear stress at small spatial scales does not experience these complications. Compared to other devices (i.e. hot-film anemometers; see Hart et al. 1996), the PST is relatively easy and quick to position, and is capable of directly measuring shear stress (Ackerman et al. 1994; Ackerman and Hoover 2001). As a result, the results presented here represent the only study to date that directly relates the microdistributions of benthic invertebrates and wall shear stress.

If shear stress was the primary factor influencing the microdistribution of *E. longimanus*, the mayflies should have showed either a positive (rheophilic) or negative (rheophobic) response to increasing shear stress during the night-time period when they were actively foraging on the upper surface of the stones. As this was not the case, the distribution and movement of *E. longimanus* was apparently not limited by the high shear stress recorded on the upper surface of the torrential stream stones. In fact, the results show that *E. longimanus* larvae that remained on upper stone surfaces

during the day were found in high shear areas, possibly because such areas might act to exclude visually oriented vertebrate predators such as fish (*e.g.* Bull Trout *Salvelinus confluentus*) or birds (*e.g.* the American Dipper *Cinclus americanus*). Salmonid predators, such as those found in the study reach (*Salvelinus confluentus*; G. Cho, UNBC graduate student, unpublished data), generally exhibit a lie-in-wait mode of predation (*e.g.* Hughes 1998), and generally do not actively forage in high velocity microhabitats for prey.

Stone reversal

The results of the stone reversal experiment apparently contradict the conclusion that the night-time microdistribution of *E. longimanus* is unrelated to hydrodynamic factors. In the original orientation of the stones, *E. longimanus* larvae were aggregated towards the downstream side of the upper surface of all three substrates. When the stones were rotated 180°, the larvae quickly migrated downstream on the stone surface, adopting the same relative distribution (*i.e.* with respect to local flow patterns). When the stones were again rotated 180° (returning them to their original orientation), the larvae again migrated downstream on the stone surface, returning them to their original distribution. This demonstrates that the larvae responded proximately to hydrodynamic cues, not algal densities or substrate characteristics. Although this result appears anomalous, the larval *E. longimanus* may have responded to some aspect of the near-bed flow environment (possibly shear stress τ_w , near-bed velocity U_{0.002m}, or turbulence intensity) to assess another, more directly important, ecological factor. For example, larvae may associate high-flow areas with abundant periphyton, and make use of this association to forage more efficiently. Alternatively, *E. longimanus* larvae may forage in high shear stress areas to minimise predation (Hart and Merz 1998) or maximise respiration (Wiley and Kohler 1980).

Periphyton microdistribution

Periphyton density on the upper surface of the experimental stones was significantly and positively correlated with roughness and topography (*i.e.* greater mass of chlorophyll *a* cm⁻² in higher and rougher areas of the stones). These results concur with the findings of Sanson et al. (1995) who reported a positive association between surface roughness and chlorophyll *a*. Peckarsky and Cowan

(1995) suggested that periphytic diatoms might be less prone to scouring from rough surfaces, but failed to propose a mechanism by which this might be possible. Rough surfaces provide a more suitable site for colonisation of diatoms (see Sanson et al. 1995). Furthermore, flows over rough surfaces become turbulent at lower velocities, which can, in turn, produce thicker boundary layers and viscous sublayers. Periphyton densities are known to be higher on the upper surfaces of stones (*e.g.* Vaughn 1986), a characteristic distribution produced by higher light levels (less shading and attenuation) and greater rates of nutrient delivery.

The results suggest that *E. longimanus* may have had a negative impact on periphyton density. Although marginally insignificant, periphyton density was negatively correlated with both daytime (p = 0.060) and night-time densities (p = 0.055) of *E. longimanus*. Grazing invertebrates are known to have impacts on local algal densities. For example, Quinn et al. (1996) found that periphyton density declined with increasing near-bed velocities, and attributed this result to an increase in collector-browser invertebrates. Similarly, Feminella et al. (1989) found that grazing invertebrates reduced periphyton standing crops to a constant, low level, regardless of growth conditions. Vaughn (1986) found that the trichopteran grazer *Helicopsyche borealis* aggregated on the exposed upper surfaces of stones, the microhabitat with the greatest periphyton abundance, while the results of Casey and Clifford (1989) suggest that mayfly grazers tend to aggregate on areas of the substrate with the highest periphyton densities.

No studies to date, however, have determined if *E. longimanus*, or any species of torrential grazer, locally reduce periphyton standing stock. Using the results of Cowan and Peckarsky (1994), a conservative feeding rate estimate of 6.0×10^{-7} g of pigment per animal per night can be calculated for *Baetis bicaudatus*. Assuming that *E. longimanus* and *B. bicaudatus* graze at approximately the same rate, the observed densities of *E. longimanus* should have a substantial impact on local standing crop of periphyton, grazing as much as 12% of the periphyton from the upper surface of the stones per night (based on larval densities of 400 individuals m⁻², and periphyton densities of 2.0 x 10⁻³ g pigment m⁻²). This suggests, however, that *E. longimanus* impacts on periphyton abundance and distribution should be more substantial than our results indicate. The limited impact of *E. longimanus* on periphyton density is possibly due in part to mouthpart morphology; Karouna and Fuller (1992) found that the "brusher" mouthparts of *Epeorus* have little impact on diatom densities on a variety of substrate types.

Conclusions

The near-bed flow conditions measured in this study were heterogeneous both among and within stones. The local variability in measured hydrodynamic factors (*i.e.* wall shear stress, boundary layer separation) directly influenced the behaviour and distribution of the invertebrate taxa that inhabit shallow, high-velocity streams. Spatial variation in ecologically important hydrodynamic factors such as shear stress can influence dispersal, predator / prey interactions, and feeding. However, the relationship between periphyton, invertebrate grazers, and near-bed flow conditions is complex; while *E. longimanus* larvae responded proximally to hydrodynamic factors, the larvae in turn may have, through herbivory, reduced periphyton in areas of the substrate where they aggregated. However, the growth and distribution of benthic algae is also known to be directly influenced by near-bed flows (e.g. Quinn et al. 1996). Due to the complexity of the relationship between hydrodynamics, periphyton, and benthic macroinvertebrates, studies at organism-defined spatial scales are needed before a more complete understanding of the linkages between hydrodynamics and benthic ecology can be gained.

In addition, the majority of our knowledge of the ecology of mobile benthic invertebrates is based on observation of these organisms on the upper surfaces of streambed stones. However, most stream invertebrate taxa, including those which diurnally migrate to the upper surface of stones to graze on algae, spend much of their lives in interstitial spaces within the streambed (*e.g.* Rader and Ward 1990). Few studies have attempted to examine the activity of either predator or prey species during the day in the interstitial spaces beneath stones. Clearly, we need to know more about the behaviour of benthic invertebrate taxa at a wider variety of spatial scales before we can understand the relationships that exist between flow and the distribution of benthic organisms.

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References

- Ackerman, J.D., L. Wong, C. R. Ethier, D.G. Allen, and J.K. Spelt. 1994. Preston-static tubes for the measurement of wall shear stress. J. Fluids Eng. 116: 645-649.
- Ackerman, J.D., and T.M. Hoover. In press. Measurement of local bed shear stress in streams using a Preston-static tube. Limnol. Oceanogr.
- Bouckaert, F.W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biol. 40: 77-86.
- Buffin-Belanger, T., and A.G. Roy. 1998. Effects of a pebble cluster on the turbulent structure of a depth-limited flow in a gravel-bed river. Geomorphology 25: 249-267.
- Carling, P.A.. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biol. 28: 273-284.
- Casey, R.J., and H.F Clifford. 1989. Colonization of natural substrata of different roughness and colour by Ephemeroptera nymphs using retrieval and direct observation techniques. Hydrobiol. 173:185-192.
- Collier, K. 1994. Influence of nymphal size, sex and morphotype on microdistribution of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in a New Zealand river. Freshwater Biol. 31: 35-42.
- Collier, K.J., G.F. Croker, C.W. Hickey, J.M. Quinn, and B.S. Smith. 1995. Effects of hydraulic conditions and larval size on the microdistribution of Hydrobiosidae (Trichoptera) in two New Zealand Rivers. New Zealand J. Mar. Freshwater Res. 29: 439-451.
- Cowan, C.A., and B.L. Peckarsky. 1994. Diel feeding and positioning periodicity of a grazing mayfly in a trout stream and a fishless stream. Can. J. Fish. Aquat. Sci. 51: 450-459.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biol. 21: 271-282.
- Delgado, J.A., and R. Carbonell. 1997. Case features of caddisfly larvae (Sericostoma selysi) as related to water velocity and potential to drift. J. Freshwater Ecol. 12: 193-197.
- Dill, L.M. 1987. Animal decision-making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. 65: 803-811.
- Dittrich, A., and U. Schmedtje. 1995. Indicating shear stress with FST-hemispheres effects of stream-bottom topography and water depth. Freshwater Biol. 34: 107-121.
- Donahue, W.F., and D.W. Schindler. 1998. Diel emigration and colonization responses of blackfly larvae (Diptera: Simuliidae) to ultraviolet radiation. Freshwater Biol. 40:357-365.
- Dudgeon, D. 1982. Aspects of the microdistribution of insect macrobenthos in a forest stream in Hong Kong. Arch. Hydrobiol., Suppl. 64: 221-239.
- Edmunds, G.F., and R.K. Allan. 1964. The Rocky Mountain species of *Epeorus* (*Iron*) Eaton (Ephemeroptera: Heptageniidae). J. Kansas Ent. Soc. 37: 275-288.
- Edmunds, G.F. Jr., and R.D. Waltz. 1996. Ephemeroptera. *in* An Introduction to the Aquatic Insects of North America Third Edition. *Eds.* Merritt, Richard W., and Kenneth W. Cummins. Kendall/Hunt Publishing Company, IA.

- Feminella, J.W., M.E. Power, and V.H. Resh. 1989. Periphyton resonses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biol. 22: 445-457.
- Frutiger, A., and J.-L. Schib. 1993. Limitations of FST hemispheres in lotic benthos research. Freshwater Biol. 30:463-474.
- Golubkhov, S.M., T.M. Tiunova, and S.L. Kocharina. 1992. Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. Aquatic Insects 14: 137-144.
- Geider, R.J., and B.A. Osborne. 1992. Algal Photosynthesis. Chapman and Hall, New York.
- Growns, I.O., and J. Davis. 1994. Longitudinal processes in near-bed flows and macroinvertebrate communities in a Western Australian stream. J. N. Am. Benthol. Soc. 13: 417-438.
- Hart, D.D., B.D. Clark, and A. Jasentuliyana. 1996. Fine-scale measurement of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.
- Hart, D.D., and R.A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow mediated refuges. Oecologia 114: 263-273.
- Hoover, T.M., J.L. McConnachie, and J.D. Ackerman. In prep. Measuring periphyton biomass on natural and artificial substrates of differing roughness.
- Hughes, N.F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79: 281-294.
- Hynes, H.B.N. 1971. Benthos of flowing water (methods of collection). In A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Eds. W.T. Edmonson and G.G. Winberg. IPB Handbook 17: 48-59.
- Jowett, I.G., J. Richardson, B.J.F. Biggs, C.W. Hickey, and J.M. Quinn. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. N. Zea. J. Mar. Freshwater Res. 25: 187-199.
- Karouna, N.K., and R.L. Fuller. 1992. Influence of four grazers on periphyton communities associated with clay tiles and leaves. Hydrobiol. 245: 53-64.
- Kerans, B.L. 1996. The influence of periphyton and rock texture on the diel drift of a Hydropsychid caddisfly. J. Freshwater Ecol. 11: 163-169.
- Kerans, B.L., B.L. Peckarsky, and C. Anderson. 1995. Estimates of mayfly mortality: is stonefly predation a significant source? Oikos 74: 315-323.
- Lamberti, G.A., and V.H. Resh. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae, and macroinvertebrates. Freshwater Biol. 15: 21-30.
- Lacoursière, J.O. 1992. A laboratory study of fluid flow and microhabitat selection by larvae of Simulium vittatum (Diptera: Simuliidae). Can. J. Zool. 70: 582-596.
- Lacoursière, J.O., and D.A. Craig. 1993. Fluid transmission and filtration efficiency of the labral fans of black fly larvae (Diptera: Simuliidae): hydrodynamic, morphological, and behavioural aspects. Can. J. Zool. 71: 148-162.
- Lancaster, J. 1990. Predation and drift of lotic macroinvertebrates during colonization. Oecologia 85: 48-56

- Lancaster, J., A.G. Hildrew, and C. Gjerlov. 1996. Invertebrate drift and longitudinal transport processes in streams. Can. J. Fish. Aquat. Sci. 53: 572-582.
- McCormick, P. V., and R. J. Stevenson. 1989. Effects of snail grazing on benthic algal community structure in different nutrient environments. J. N. Am. Benthol. Soc. 8: 162-172.
- McIntosh, A.R., and B.L. Peckarsky. 1996. Differential behavioural responses of mayflies from streams with and without fish to trout odour. Freshwater Biol. 35: 141-148.
- Minshall, G.W. 1984. Aquatic insect-substratum relationships. *in* The Ecology of Aquatic Insects. *Eds.* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York, NY.
- Muotka, T., and A. Penttinen. 1994. Detecting small-scale spatial patterns in lotic predator-prey relationships: statistical methods and a case study. Can. J. Fish. Aquat. Sci. 51: 2210-2218.
- Nowell, A.R.M., and P.A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303-328.
- Peckarsky, B.L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology 77: 1888-1905.
- Peckarsky, B.L., and C.A. Cowan. 1995. Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos 74(3): 513-521.
- Peckarsky, B.L., C.A. Cowan, M.A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74: 1836-1846.
- Peckarsky, B.L., S.C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. Freshwater Biol. 24: 181-191.
- Peckarsky, B.L., and R.S. Wilcox. 1989. Stonefly nymphs use hydrodynamic cues to discriminate between prey. Oecologia 79: 265-270.
- Quinn, J.M., C.W. Hickey, and W. Linklater. 1996. Hydraulic influences on periphyton and benthic invertebrates: simulating the effects of bed roughness. Freshwater Biol. 35: 301-309.
- Rader, R.B., and J.V. Ward. 1990. Diel migration of microhabitat distribution of a benthic stream assemblage. Can. J. Fish. Aquat. Sci. 47: 711-718.
- Robert, A., A.G. Roy, and B. De Serres. 1996. Turbulence at a roughness transition in a depth limited flow over a gravel bed. Geomorphology 16: 175-187.
- Sanson, G.D., R. Stolk, and B.J. Downes. 1995. A new method for characterizing surface roughness and available space in biological systems. Funct. Ecol. 5: 127-135.
- Scrimgeour. G.J., J.M. Culp, and F.J. Wrona. 1994. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. J. N. Am. Benthol. Soc. 13: 368-378.
- Statzner, B. 1981. The relationship between "hydraulic stress" and microdistribution of benthic macroinvertebrates in a lowland running water system, the Schierenseebrooks (North Germany). Arch. Hydrobiol. 91: 192-218.
- Statzner, B., and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16:127-139.
- Statzner, B., and T.F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow – an old question answered by means of a new technique (laser doppler anemometry). Oecologia 53: 290-292.

- Statzner, B., and T.F. Holm. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. Oecologia 78: 145-157.
- Statzner, B., and R. Muller. 1989. Standard hemispheres as indicators of flow characteristics in lotic benthos research. Freshwater Biol. 21: 445-459.
- Tabachnick, B.G., and L.S. Fidell. 1996. Using Multivariate Statistics, 3rd Edition. HarperCollins Publishing Co., New York.
- Tikkanen, P., T. Muotka, A. Huhta, and A. Juntunen. 1997. The roles of active predator choice and prey vulnerability in determining the diet of predatory stonefly (Plecoptera) nymphs. J. Anim. Ecol. 66: 36-48.
- Voelz, N.J., and J.V. Ward. 1996. Microdistributions of filter-feeding caddisflies (Insecta: Trichoptera) in a regulated Rocky Mountain river. Can. J. Zool. 74: 654-666.
- Vaughn, C.C. 1986. The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). Freshwater Biol. 16: 485-493.
- Vogel, S. 1994. Life in Moving Fluids, 2nd edition. Princeton University Press, Princeton.
- Way, C.R., A.J. Burky, C.R. Bingham, and A.C. Miller. 1995. Substrate roughness, velocity refuges, and macroinvertebrate abundance on artificial substrates in the lower Mississippi River. J. N. Am. Benthol. Soc. 14: 510-518.
- Weissenberger, J., H.-Ch. Spatz, A. Emanns, and J. Schwoerbel. 1991. Measurement of the lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m s⁻¹. Freshwater Biol. 25: 21-31.
- Wellnitz, T.A., R.B. Rader, and J.V. Ward. 1996. Importance of light and nutrients in structuring an algal community in a Rocky Mountain stream. J. Freshwater Ecol. 11: 399-413.
- Wetmore, S.H., R.J. MacKay, and R. Newbury. 1990. Characterization of the hydraulic habitat of Brachycentrus occidentalis, a filter-feeding caddisfly. J. N. Am. Benthol. Soc. 9: 157-169.
- White, F.M. 1999. Fluid Mechanics, 4th edition. WCB / McGraw-Hill, Boston.
- Wiley, M.J., and S.L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Can. J. Zool. 58: 618-622.
- Wooster, D., and A. Sih. 1995. A review of the drift and activity responses of stream prey to predator presence. Oikos 73: 3-8.
- Young, W.J. 1992. Clarification of the criteria to identify near-bed flow regimes. Freshwater Biol. 28: 383-391



Figure 4-1. Diagrammatic representation of the upper surface of a stone, showing the distribution of each of the types of factors sampled. A) The distribution of pre-marked points over the stone surface (delineating a 5 x 5 cm grid). The distribution of all parameters were recorded with respect to this grid; triangular marker in the middle of the stone denotes the centre of the stone ('datum'). The distribution of boundary layer flow conditions were also recorded (BF denotes the extent of the backflow region associated with boundary layer detachment at the rear of the stone). B) The distribution of algal samples (three parallel transects in the streamwise direction). The location of shear stress measurements obtained on each stone (two orthogonal transects, crossing at the centre of the stone). The location of each shear stress measurement is denoted by a solid symbol. Scale bar is shown.



Figure 4-2A. *E. longimanus* larvae density among stones, and between day- and night-time periods (error bars = SD). Data are larval densities pooled over the entire study period. While differences in per quadrat mayfly densities among stones during the night-time are not significant (ANOVA, F(4,130) = 0.40, p = 0.81), differences in mayfly densities among stones during the day are (ANOVA, F(4,130) = 5.08, p < 0.001).



Figure 4-2B. *E. longimanus* larvae density in areas of the substrate with different boundary layer flow conditions (error bars = SE). Larval densities quantified at small scales (within 5×5 cm quadrats). Data are mean larval densities, calculated from per quadrat densities measured over the entire study period and all stones.



Figure 4-3. Relationship between daytime and nighttime microdistributions of *E. longimanus* larvae. Areas of the stone surface that have relatively high densities of larvae at night tend to have high daytime densities. Data are mean larval densities, calculated from per quadrat densities measured over the entire study period and all stones. (Regression line shown; $R^2 = 21.12\%$.)



Figure 4-4. The distribution of *E. longimanus* larvae (day and night) along the centre line of the upper surface of the experimental stones (error bars = SE). Data are larval distributions pooled over the entire study period. Daytime means were not significantly different. Nighttime means that were not significantly (at α = 0.05) or nearly significantly (p < 0.075) different are underlined (see Table 4-2 for exact p-values). Flow is from left to right; stone centre is denoted by streamwise distance = 0.



Figure 4-5. Relationship between *E. longimanus* density (day and night) and wall shear stress (τ_w). (Regression lines shown; upper line = daytime larval densities, $R^2 = 36.15\%$, lower line = nighttime larval densities, $R^2 = 2.08\%$.)



Figure 4-6. Distribution of larval *E. longimanus* density (error bars = SE), periphyton density (error bars = SE), and shear stress (τ_w) (error bars = SD) along the centreline transect of stone 7. Densities of *E. longimanus* larvae and periphyton appear to have an inverse relationship. Shear stress (τ_w) decreases abruptly at the rear of the stone due to flow separation. Periphyton samples were collected from the field on October 7, 1998; *E. longimanus* densities and shear stress measurements were made on various dates throughout the study period (see Tables 4-1 and 3-2, respectively).



Figure 4-7. Distribution of larval *E. longimanus* density (error bars = SE), periphyton density (error bars = SE), and shear stress (τ_w) (error bars = SD) along the centreline transect of stone 31. Shear stress (τ_w) decreases abruptly at the rear of the stone due to flow separation. Periphyton samples were collected from the field on October 7, 1998; *E. longimanus* densities and shear stress measurements were made on various dates throughout the study period (see Tables 4-1 and 3-2, respectively).


Figure 4-8. Distribution of larval *E. longimanus* density (error bars = SE), periphyton density (error bars = SE), and shear stress (τ_w) (error bars = SD) along the centreline transect of stone 23. Shear stress (τ_w) increases as flow accelerates as it crosses the stone; no measurements were obtained in the region of flow separation at the rear of the stone. Periphyton samples were collected from the field on October 7, 1998; *E. longimanus* densities and shear stress measurements were made on various dates throughout the study period (see Tables 4-1 and 3-2, respectively).



Figure 4-9. Distribution of larval *E. longimanus* density (error bars = SE), periphyton density (error bars = SE), and shear stress (τ_w) (error bars = SD) along the centreline transect of stone 10. Densities of *E. longimanus* larvae and periphyton appear to have an inverse relationship. Periphyton samples were collected from the field on October 7, 1998; *E. longimanus* densities and shear stress measurements were made on various dates throughout the study period (see Tables 4-1 and 3-2, respectively).



Figure 4-10. Distribution of larval *E. longimanus* density (error bars = SE), periphyton density (error bars = SE), and shear stress (τ_w) (error bars = SD) along the centreline transect of stone 25. Flow from upstream plunged directly on the upper surface of stone 25; as a result, shear stress is high and relatively uniform across the upper surface. Periphyton samples were collected from the field on October 7, 1998; *E. longimanus* densities and shear stress measurements were made on various dates throughout the study period (see Tables 4-1 and 3-2, respectively).



Figure 4-11. Periphyton (chlorophyll *a*) densities along the centre line of the upper surface of five experimentally deployed stones (error bars = SE). Flow is from left to right; stone centre denoted by streamwise distance = 0. Sample sizes at each streamwise distance vary due to inter-stone variation in diameter.



Figure 4-12. Periphyton density in areas of the bed (*i.e.* experimentally deployed stones) with different near-bed flow conditions (error bars = SE). Sample sizes differ due to the relatively small area of each stone over which boundary layer separation had occurred.



Figure 4-13. Densities of *E. longimanus* larvae on the upper surface of the five experimentally deployed stones (error bars = SD) during September 26 - 27, 1998. Light (photosynthetically active radiation; 400-700 nm) fluxes are also shown (heavy solid line).



Figure 4-14. Densities of *E. longimanus* larvae on the upper surface of the five experimentally deployed stones (error bars = SD) during October 3 - 4, 1998. Light (photosynthetically active radiation; 400-700 nm) fluxes are also shown (heavy solid line).



Figure 4-15. Change in *E. longimanus* density (error bars = SE) recorded on the upper surface of the experimentally deployed stones during October 3 - 4, 1998. Periods of light and dark represented by bar at bottom of figure.





Figure 4-16 (previous page). The effect of stone reversal on the positioning of *E. longimanus* larvae. (A) In their original orientations of the three stones (0°), larvae were at highest densities over the rear of the three stones. (B) After the stones were rotated 180°, the larvae moved downstream to new positions on the stone surface, although the distribution of larvae with respect to flow was similar (*i.e.* at highest densities over the rear of the stone). (C) When the stones were rotated back to their original orientations (0°), the larvae returned to their original distributions. *E. longimanus* distributions recorded approximately every 40 minutes (A: 18:58 h, B: 19:48 h, C: 20:12 h). Open arrows indicate direction of flow.

Chapter 5

Torrential stream microhabitats: flow, form, and function

Summary

- Hydrodynamics are generally thought to be the single most important factor influencing the biology of benthic organisms. However, the near-bed flow microenvironments inhabited by torrential stream fauna are poorly understood, and currently accepted models of near-bed flows may, in some cases, be misleading.
- 2. While near-bed flows in open channels with geometrically simple beds are predictable, flows in shallow streams with complex geometry and large relative roughness (*e.g.* rough-turbulent flows) are not. Pressure gradients, flow compression, and boundary layer separation ensure that the distribution of velocity in the near-bed region may rarely, if ever, conform to the standard, logarithmic model of boundary layer velocity distribution.
- 3. Where local protruding obstacles constrict flow, the near-bed portion of the boundary is distorted, creating a "wedge-shaped" velocity profile. Invertebrates inhabiting these regions of the streambed will experience greater lift, drag, and shear forces than predicted by normal boundary layer theory.
- 4. Epeorus longimanus (Heptageniidae), a torrential mayfly species, exhibits behavioural and morphological adaptations that allow it live in high velocity, high shear environments. The flattened shape and ventral, sucker-like gill arrangement of *E. longimanus* act to minimise the risk of accidental detachment from the upper surface of torrential stream boulders. The high velocity, lift, drag, and shear stress of this environment may also, in turn, act to decrease predation (by excluding both invertebrate and vertebrate predators) and increase food availability (by increasing rates of nutrient delivery to periphyton).
- The ecological implications of local heterogeneity in near-bed velocity (U_{0.002m}) and wall shear stress (τ_w) are discussed.

Physical – biological coupling in the stream environment

It is generally thought that hydrodynamic parameters are the most important environmental factors affecting the ecology of organisms in lotic habitats (*e.g.* Davis and Barmuta 1989; Carling 1992; Hart and Finelli 1999). Several studies have demonstrated that the forces of moving water influence the morphology, behaviour, distribution, trophic relationships, and intra- and interspecific interactions of benthic stream organisms (*e.g.* Chance and Craig 1986; Weissenberger et al. 1991; Collier 1994; Hart et al. 1996). However, despite the fact that the ecological importance of open channel hydraulics is widely accepted, the current understanding of stream flows at organism-defined spatial scales remains limited, especially in torrential stream environments.

Knowledge of the relationships that exist between flow microenvironments and stream biota is based largely on fine-scale measurements obtained in laboratory flumes (*e.g.* Statzner and Holm 1982; 1989; Weissenberger et al. 1991) and relatively coarse measurements of flow in naturally occurring stream channels (*e.g.* Wetmore et al. 1990; Statzner and Higler 1986; Collier et al. 1995; but see Hart et al. 1996). Laboratory-based studies use flow channels (flumes) to control basic flow variables (*i.e.* mean velocity, depth, turbulence intensity, etc.) and to minimise the influence of secondary flows and channel-specific flow patterns. As a result, flow in these channels is usually characterised by well-defined, fully developed, logarithmically distributed boundary layers with minimal turbulence, and bulk flow patterns that are approximately two-dimensional (see Statzner and Holm 1989; Weissenberger et al. 1991). Problems arise, however, when the results of these studies are used to extrapolate the near-bed flows of natural channels, and velocity distributions are assumed to approximate the standard logarithmic shape (see Carling 1992). However, this assumption is not valid in the rapidly varied, highly three-dimensional flows of torrential streams. Measurement of near-bed flows at organismal scales is needed to elucidate the relationship between benthic organisms and the hydrodynamic factors that define torrential stream environments.

The relationship between mean and near-bed flows

Vertical distributions of velocity in channels are generally thought to conform to a standard logarithmic shape (Carling 1992; White 1999). As such, the relationship between mean and near-bed velocities is reasonably predictable in geometrically simple (flat-bedded and walled) channels of

known depth. However, the flow separation, local accelerations, and pressure gradients associated with topographic irregularities and complex bed geometries lead to complex, often unpredictable, distributions of velocity in natural streams.

Mean velocities are correlated with velocities measured 2 cm above the bed (Figure 5-1A) across a variety of stream habitat types (*i.e.* riffles, pools, etc.); velocities at this height above the bed are approximately half of mean velocity. However, when mean velocity is compared to the velocity measured immediately adjacent to the bed ($U_{0.002m}$, measured 2 mm above the bed), the two determinations of velocity are approximately equal (Figure 5-1B). This suggests that where roughness elements protrude substantially into the flow of shallow channels, near-bed flows are accelerated to near-mean (or even exceeding mean) velocities. This demonstrates that the boundary layers (defined as the height above the boundary where velocities reach 90% of mean velocity) over the upper surface of protuberant stones are, in many cases, thinner than 2 mm. While benthic invertebrates in many stream habitats (*i.e.* gravel riffles) may be protected from mean velocities by thick boundary layers (Hart et al. 1996), invertebrates on the upper surface of torrential boulders may not be afforded such protection.

Near-bed flows in torrential streams

The results of the present study support the development of a model to describe the distribution of velocity within boundary layer flows above isolated roughness elements in shallow streams (where D < 3d). Flow approaching protuberant boulders in shallow torrential streams is generally turbulent due to the downstream convection of vortices detached from the lee side of upstream boulders (Hart et al. 1996). The vertical distribution of near-bed velocities approaching boulders is dependent on upstream bed geometry (for illustrative purposes will be assumed to be approximately log-normal; Figure 5-2). The vertical distribution of mean velocities higher in the water column would be expected to be relatively homogenous, as a result of efficient momentum transfer in the turbulent, high Reynolds number flow. As flow reaches the front of the boulder, a solenoidal ("horseshoe") vortex may form, provided that flow interference from upstream roughness elements is not too great (Young 1992; 1993). If the stone provides a 'bluff-body' obstacle to the flow, a stagnation point will form at the leading edge of the stone as well.

Over the upper surface of the leading edge of the boulder, patterns of water movement will be three-dimensional as the flow splits and flows over and around the stone. Flow that crosses the upper surface of the stone will be constricted by the rising, inclined leading edge of the stone. However, the flow will not accelerate uniformly in the vertical direction; acceleration is evident primarily in fluid adjacent to the bottom, producing a distinct "wedge-shaped" profile (Figure 5-2, also see chapter 3). Two factors may contribute to the development of this unusual velocity distribution. First, near-bed flows are accelerated due to flow constriction rather than gravity. This conclusion (that flow near the bottom accelerates rapidly while flow near the surface remains relatively unaffected) is supported by the jet-like properties (namely a high-velocity core region; see White 1999) of the near-bed "wedge" portion of the velocity profile (see chapter 3). Second, due to weathering of substrates in high-velocity streams, naturally occurring boulders are often characteristically rounded. The gradually curving leading edge of the front of the stones may be an essential element for the development of wedge-shaped velocity distributions. Nowell and Church (1979) did not find any evidence of a near-bed velocity profile distortion of this type when they recorded velocity profiles over equally sized, but rectangularly shaped, objects. Gradual constriction of the flow (and the development of the near-bed "wedge") may not occur when an inclined face is not presented to the flow. If wedge-shaped velocity profiles are the result of near-bed flow constriction. the distortion should be greatest at points where flow constriction is greatest. The effects of the 'noslip' condition cannot be ignored, however; boundary layer growth (and retardation of near-bed velocity) occurs downstream of the stagnation point due to the effects of viscosity.

As flow crosses the centre of protuberant stones in shallow flows, the velocity profile distortion that was created by constriction over the leading edge of the stone begins to dissipate, presumably due to momentum transfer in the free shear layer above the high-velocity wedge and frictional effects and shear stress in the boundary layer below the velocity distortion. When the thickness of the boundary layer exceeds the height above the substrate where the magnitude of the near-bed distortion is greatest (the 'tip' of the 'wedge'), the distortion disappears completely. If the streamwise diameter (length) of the stone is shorter than the distance over which the 'wedge' is dissipated, the near-bed distortion is advected off the rear of the stone

Although the development of wedge-shaped profiles in natural channels has not been discussed previously in the literature, examination of the results of earlier studies reveals that this type of near-bed velocity profile distortion has been measured previously. Given that velocity at the streambed-fluid interface must be zero, four of the five stones above which Hart et al. (1996) measured flow fields have velocity profiles that, by the criteria used in chapter 3, would be categorised as wedge-shaped. Similarly, of the 15 serial profiles measured by Bergeron (1994) along a 3.6 m shallow stream reach, one of the two profiles (his profile 4) obtained over the leading edge of protuberant stones has a near-bed high-velocity wedge. It is difficult to determine if additional profiles measured by Bergeron (1994) also have near-bed velocity distortions, as he was unable to measure velocities within 1.9 cm of the bed. In the present study, the velocity profile distortions producing the wedge were generally located within 1 cm of the bed. It is likewise difficult to assess the shapes of the velocity profiles measured by Hart et al. (1996) because they neither provide the portions of the profile more than 1 cm from the bed nor a measure of mean velocity.

Ecohydraulics of Epeorus longimanus

In shallow flows with relatively large, protuberant stones, the marked spatial heterogeneity of near-bed hydrodynamic parameters (notably near-bed velocity and wall shear stress) will have substantial impacts on the distribution and biology of benthic organisms. The highest densities of *E. longimanus* larvae were often found on the upper surface of torrential stream boulders (especially during the night), where near-bed velocities and shear stresses were generally high. Where near-bed velocity profile distortions ('wedges') increased near-bed velocity gradients, the lift and drag experienced by mayfly larvae found on the exposed upper surface of boulders in torrential streams will be substantially higher than in regions of the bed with comparable mean velocities but thicker, normally distributed, boundary layers.

Extreme hydraulic habitats do not appear to limit the movement or behaviour of this mayfly. *E. longimanus* larvae were observed to move easily about on areas of the substrate where near-bed velocities (U_{0.002m}) exceeded 1.0 m s⁻¹. Morphological and behavioural adaptations effectively counter the forces of lift, drag, and shear stress experienced by larvae in their preferred nighttime habitat. The ventral gills of larvae are arranged in a 'sucker-like' arrangement, their flattened, streamlined bodies have a relatively low drag coefficient (Weissenberger et al. 1991), and the reduction in number of anal cerci (from three to two) can also be regarded as a further adaptation to reduce drag. Furthermore, the efficacy of the morphological adaptations of this species may be augmented if coupled with behavioural modifications of body position that further reduce hydraulic stresses (as for *Simulium vittatum*; Chance and Craig 1986). Although the physical means by which these adaptations allow *E. longimanus* to maintain contact with the substrate are poorly understood, it is apparent that they allow this mayfly to thrive in high velocity, high shear environments.

Although invertebrates in high velocity habitats must incur energetic costs in order to maintain position, the results of the present study suggests that near-bed flow regimes of this type also confer substantial ecological benefits to those taxa with the requisite adaptations. A conceptual model of the relationship between hydrodynamic factors, predators, resource availability, and E. longimanus is shown in Figure 5-3. Invertebrate predators, which are generally adapted for locomotory efficiency rather than tenacity (Hart and Merz 1998), are unable to forage for prey (in this case, E. longimanus) in the high velocities to which the upper surfaces of torrential stream boulders are exposed. In this fashion, high velocity, high shear patches of the substrate may act as flow-mediated refuges from predation (Hart and Merz 1998; Peckarsky et al. 1990). Due to the direct, negative influence of flow on predators, flow may have an indirect, positive effect on local E. longimanus populations. The steep velocity gradients and high shear stresses of this environment also increase the rates of nutrient and dissolved gas delivery to the substrate surface, enhancing the growth of periphyton (especially diatomaceous species), which in turn act as a food resource of larval E. longimanus. This provides another pathway by which flow has indirect, positive effects on this mayfly. Through herbivory, larvae may have a negative impact on algal densities. However, because the near-bed flow regime also tends to exclude other grazing invertebrate taxa, interspecific competition for available algal food resources may be low, and total impacts may actually be quite limited. Finally, flow may also have a beneficial, direct influence on E. longimanus larvae. High near bed velocities and shear stresses may act to increase the respiratory efficiency of this rheophilous mayfly (see Golubkhov et al. 1992).

Stream hydraulics / invertebrate interactions

The results presented here are possibly the first report of shear stress distribution patterns across the surface of naturally occurring stream bedforms (*i.e.* generally, front-to-back asymmetry,

with shear stresses increasing from the front to the rear of the stone). As such, it may be necessary to re-evaluate the conclusions drawn by previous studies examining the microdistribution of stream insects. For example, Wetmore et al. (1990), studying the microdistribution of the suspensionfeeding caddisfly Brachycentrus occidentalis, concluded that Froude number was the best predictor of larval position. However, as shown in chapter 3, shear stress and Froude number both generally increased from the front of torrential stream boulders to the rear. Near-bed flow parameters may be a valid, untested alternative explanation for the microdistribution of suspension-feeding benthic insects. In order to estimate near-bed flows from mean velocity measurements, Wetmore et al. (1990) assumed, as have many recent studies, that the water column accelerates uniformly. The results presented here show that this assumption, if used to estimate near-bed flow conditions in shallow streams with complex bed geometries, could lead to substantial errors. Similarly, Delgado and Carbonell (1997) found that the case morphology of the caddisfly Sericostoma selysi varied with respect to water surface velocity, and subsequently attributed the differences as a response to counter the forces of drag. However, the results of this study suggest that the near-bed velocities to which benthic insects are exposed may, in fact, be only weakly related to mid-stream or near-surface velocities. As a result, the extent to and mechanisms by which shear, lift, drag, and near-bed velocities modify the behaviour and morphology of benthic insects remain largely unstudied. Moreover, the relative importance of the various hydraulic forces to which stream benthic insects are exposed remains poorly understood. The near-bed flows recorded in this study are variable over short distances, a factor that will influence the ecology of organisms inhabiting the exposed surfaces of boulders in high gradient streams. While some of the observed flow patterns conformed to commonly applied hydraulic theory (e.g. flow accelerating and becoming supercritical as it crosses boulders), some did not (e.g. wedge-shaped velocity profiles).

With a few notable exceptions, few studies have explored the near-bed flow environments of streams at the scales at which benthic invertebrates experience them. Even fewer studies have examined the range and distribution of hydraulic parameters across the streambed at these organism-defined scales. Nowell and Jumars (1984) suggested that in shallow streams with topographically complex beds (where D < 3k), the three-dimensional patterns of flow generated would be of greater importance to the ecology of benthic invertebrates than average boundary skin friction. The results of the present study show that boundary flow conditions are, indeed, heterogeneous and

highly dependent on local bed geometry. As flow accelerates over the upper surface of stream-bed stones, shear stress at the boundary increases; however, the relationship is modified substantially by the shape of the substrate over which the water is flowing. Both flow constriction (which accelerates near-bed flow at a greater rate than at mid-depth) and thin boundary layers (a result of high near-bed velocities or short distances available for boundary layer development) define the near-bed flow environment.

These findings, however, provide only a limited understanding of the relative importance of the various near-bed flow parameters to the ecology of the stream invertebrates that inhabit the upper surfaces of streambed stones. In comparison, the relative importance of the many hydraulic forces to which marine benthic invertebrates are exposed has been determined for several intertidal species. For example, Denny et al. (1985) demonstrated that acceleration reaction may perhaps be the most important force limiting the distribution of relatively large intertidal taxa, while Denny (1987) showed that lift may be the most important factor determining the distribution of intertidal mussels. However, coastal marine systems are very different from stream systems in that the flows, while of comparable velocity, are intermittent and bi-directional. In comparison, flows in stream habitats are relatively constant and unidirectional, and as such, the relative ecological importance of the various near-bed forces will be different. The forces of lift, drag, and shear will all tend to dislodge invertebrates from the substrate, but their relative importance is poorly understood.

The boundary layers measured over the upper surface of the boulders were often extremely thin (~1mm), supporting the conclusions of Statzner and Holm (1982) that benthic insects in streams are exposed to essentially free-stream velocities. In fact, at locations on the stream bed where velocity profiles were wedge-shaped rather than logarithmically distributed, benthic insects would be exposed to velocities far greater than those predicted by normal boundary layer theory. Hart et al. (1996) stated that, in shallow, high velocity stream flows the thickness of the benthic boundary layer was of sufficient thickness that benthic invertebrates (in their case, larval blackflies) would not experience free-stream current velocities. However, the velocity profiles recorded by Hart et al. (their Figure 1) would generally be classified as log-normal by the conservative Ü (vertical velocity variation) index used in this study.

Buffin-Belanger and Roy (1998) showed that the lee side of pebble clusters represents a distinct hydraulic habitat with specific flow characteristics, and further suggested that stream

invertebrates might utilise this region as a refuge. Similarly, Bouckaert and Davis (1998) demonstrated that distinct macroinvertebrate communities inhabit the horseshoe vortex region in front of and the wake region behind stream boulders. The results presented here suggest that upper surface of stream boulders may be utilised in a similar fashion by a distinct community of benthic macroinvertebrates. The locally high shear stresses, thin boundary layers, and high near-bed velocities will act to exclude macroinvertebrate predators that are poorly adapted to high flow environments (Hart and Merz 1998; Peckarsky et al. 1990), while at the same time providing abundant grazing for herbivorous insects which are adapted to the high lift and drag of torrential environments (Weissenberger et al. 1991; Vogel 1994; Delgado and Carbonell 1997). The turbulent nature of shallow, high velocity flows might also prevent fish predators from predating on insects grazing on the upper surface of torrential stream boulders (see Metcalfe et al. 1997). Salmonids, which are the primary fish predators of aquatic insects in many northern mountain streams, typically inhabit pools below riffles and feed on drifting insects (Hughes 1998) in order to minimise the energetic costs associated with swimming and maintaining position in high velocity flows. As such, shallow, high velocity habitats may provide a refuge from fish predators as well.

Directions for future research

Increasingly, ecologists are adopting the view that flow is the most important factor in the stream environment, and are incorporating measurements of near-bed hydrodynamic parameters into their experimental designs. However, before stream ecologists can decide which factors to measure and ascertain the most efficient way to measure them, they must have a comprehensive understanding of the nature of near-bed flows in naturally occurring stream channels. Before this is possible, there are two principal areas where substantial research is required. First, new models of stream function that incorporate patterns of flow at small, organism-defined scales must be developed. While currently utilised models of flow in stream channels can be used to adequately predict large-scale phenomenon such as bedload movement and mean velocity, they are less useful in cases when they are used to describe or predict the nature of the near-bed flows that define the immediate environment of both macroinvertebrate taxa and periphyton. New models of stream flow will provide not only an understanding of near-bed flow velocities, but also of turbulence, shear

stress, and the role of substrate/flow interactions. Second, stream ecologists must be prepared to investigate the behaviour and ecology of benthic organisms at the scales at which they experience flows. While there are technical difficulties associated with this type of research, the potential rewards are substantial. Lotic research at appropriate spatial scales will not only provide ecologist with a greater understanding of the nature of biological-physical coupling in these environments, but will also provide a theoretical basis that can be utilised to mitigate human impacts to rivers and streams.

References

- Bergeron, N.E. 1994. An analysis of flow velocity profiles, stream bed roughness, and resistance to flow in natural gravel bed streams. Proc. Hydraul. Eng. (1994), ASCE . 1: 692-696.
- Bouckaert, F.W., and J. Davis. 1998. Microflow regimes and the distribution of macroinvertebrates around stream boulders. Freshwater Biol. 40: 77-86.
- Buffin-Belanger, T., and A.G. Roy. 1998. Effects of a pebble cluster on the turbulent structure of a depth-limited flow in a gravel-bed river. Geomorphology 25: 249-267.
- Carling, P.A.. 1992. The nature of the fluid boundary layer and the selection of parameters for benthic ecology. Freshwater Biol. 28: 273-284.
- Chance, M.M., and D.A. Craig. 1986. Hydrodynamics and behaviour of Simuliidae larvae (Diptera). Can. J. Zool. 64:1295-1309.
- Collier, K. 1994. Influence of nymphal size, sex and morphotype on microdistribution of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in a New Zealand river. Freshwater Biol. 31: 35-42.
- Collier, K.J., G.F. Croker, C.W. Hickey, J.M. Quinn, and B.S. Smith. 1995. Effects of hydraulic conditions and larval size on the microdistribution of Hydrobiosidae (Trichoptera) in two New Zealand Rivers. New Zealand J. Mar. Freshwater Res. 29: 439-451.
- Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biol. 21: 271-282.
- Delgado, J.A., and R. Carbonell. 1997. Case features of caddisfly larvae (*Sericostoma selysi*) as related to water velocity and potential to drift. J. Freshwater Ecol. 12: 193-197.
- Denny, M. 1987. Lift as a mechanism of patch initiation in mussel beds. J. Exp. Mar. Biol. Ecol. 113: 231-245.
- Denny, M.W., T.L. Daniel, and M.A.R. Koehl. 1985. Mechanical limits to size in wave-swept organisms. Ecol. Monogr. 55: 69-102.
- Golubkhov, S.M., T.M. Tiunova, and S.L. Kocharina. 1992. Dependence of the respiration rate of aquatic insects upon the oxygen concentration in running and still water. Aquatic Insects 14: 137-144.
- Hart, D.D., and C.M. Finelli. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Ann. Rev. Ecol. Syst. 30: 363-395.
- Hart, D.D., B.D. Clark, and A. Jasentuliyana. 1996. Fine-scale measurement of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.
- Hart, D.D., and R.A. Merz. 1998. Predator-prey interactions in a benthic stream community: a field test of flow mediated refuges. Oecologia 114: 263-273.
- Hughes, N.F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79: 281-294.
- Metcalfe, N.B., S.K. Valdimarsson, and N.H.C. Fraser. 1997. Habitat profitability and choice in a sitand-wait predator: juvenile salmon prefer slower currents on darker nights. J. Anim. Ecol. 66: 866-875.
- Nowell, A.R.M., and M. Church. 1979. Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. 84: 4816-4824.

- Nowell, A.R.M., and P.A. Jumars. 1984. Flow environments of aquatic benthos. Ann. Rev. Ecol. Syst. 15: 303-328.
- Peckarsky, B.L., S.C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a test of the harsh-benign hypothesis. Freshwater Biol. 24: 181-191.
- Statzner, B., and B. Higler. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16: 127-139.
- Statzner, B., and T.F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow – an old question answered by means of a new technique (laser doppler anemometry). Oecologia 53: 290-292.
- Statzner, B., and T.F. Holm. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. Oecologia 78: 145-157.
- Vogel, S. 1994. Life in Moving Fluids, 2nd Edition. Princeton University Press, Princeton, NJ.
- Weissenberger, J., H.-Ch. Spatz, A. Emanns, and J. Schwoerbel. 1991. Measurement of the lift and drag forces in the mN range experienced by benthic arthropods at flow velocities below 1.2 m s⁻¹. Freshwater Biol. 25: 21-31.
- Wetmore, S.H., R.J. Mackay, and R.W. Newbury. 1990. Characterization of the hydraulic habitat of Brachycentrus occidentalis, a filter-feeding caddisfly. J. N. Am. Benthol. Soc. 9: 157-169.
- Young, W.J. 1992. Clarification of the criteria to identify near-bed flow regimes. Freshwater Biol. 28: 383-391.
- Young, W.J. 1993. Field techniques for the classification of near-bed flow regimes. Freshwater Biol. 29: 377-383.

White, F.M. 1999. Fluid Mechanics, 4th edition. WCB / McGraw-Hill, Boston.

Chapter 5 – Figures



В

Figure 5-1. The relationship between mean and near-bed flows. In both cases, the solid line represents the regression line fitted to the data, while the dashed line represents the 1:1 regression line (line of equality). A. Near-bed velocity ($U_{0.02m}$; velocity measured at 2 cm above the bed) versus mean velocity for 48 sites in two adjacent, high discharge streams (see Chapter 2). Predictably, near-bed velocities are correlated with, but lower than, mean velocities. B. Near-bed velocity $U_{0.002m}$; velocity measured at 2 mm above the bed) versus mean velocity (U; measured at 2 mm above the bed) versus mean velocity (U; measured at 50% of depth) for 21 sites above the upper surface of protuberant boulders (see Chapter 3). Near-bed velocities are correlated with, but similar to, the mean velocities.



Figure 5-2. Diagrammatic representation of the flow field above isolated roughness elements in shallow, torrential streams (where D < 3d; e.g., rough-turbulent flow). The approaching flow (A) has two regions; a bulk flow zone (Umean) where velocity is relatively homogenous due to high rates of momentum transfer in the high Reynolds number flow, and a bed layer (BL) zone, where velocity is retarded due to viscous and form drag effects at the bed/fluid interface. Flow in the stagnation region (B) is characterised by a solenoidal ('horseshoe') vortex (HV), and a stagnation point in the front of the stone. Over the leading edge of the stone (C), near-bed flows are influenced by the growth of a boundary layer downstream of the 'leading edge' of the stone, and acceleration of the near-bed portion of the water column due to constriction of the relatively shallow flow by the continuously curving stone surface. The two processes combine to produce a small 'kink' or 'wedge' in the nearbed portion of the velocity profile. As the distance from the leading edge of the stone grows, so does the boundary layer thickness. When flow is no longer being constricted (D), momentum transfer in the free shear layer above the 'wedge' and the continuously velocity-retarding influence of the boundary layer below the 'wedge' act to reduce the magnitude of the difference between mean and maximal (at the tip of the 'wedge') velocities. As a result, the wedge begins to dissipate. At the rear of the stone in the flow separation zone (E), the boundary layer separates, resulting in a backflow (BF), or attached vortex.



Figure 5-3. Diagram of the direct (solid arrows) and indirect (dashed arrows) relationships between flow, *Epeorus longimanus*, primary producers, and predator abundance, with the effect of each pathway indicated by a + (positive effect) or – (negative effect). The relative position of each factor signifies their relative roles; flow is always a cause and is positioned on the left, *E. longimanus* abundance is generally an effect and is positioned on the right, periphyton and predators both act as causes and exhibit effects; as such, they are positioned in the middle (adapted from Hart and Merz 1998).

Appendix 1

Notation and Formulae

Notation and formulae used throughout the thesis are listed below.

A) Notation

υ	coefficient of kinematic viscosity (m ² s ⁻¹)
δ	boundary layer thickness (m)
δ'	viscous sublayer thickness (m)
δ _{crit}	critical boundary layer thickness (m)
τ _w	wall shear stress, also denoted as τ_0 (Pa)
ρ	density of water (kg m ³)
Ψ	particle protrusion (as a proportion of diameter)
κ	von Karman's constant (empirically determined to be 0.40)
A	constant used in the determination of τ_w (see chapter 3)
Cd	drag coefficient (dimensionless)
CI	lift coefficient (dimensionless)
d	diameter of substrate elements (m)
dk	functional diameter of substrate elements (m)
D	total channel depth (m)
D/kave	relative roughness (dimensionless)
Fd	force due to drag (N)
F	force due to lift (N)
Fr	Froude number (dimensionless)
a	acceleration due to gravity (9.81 m s ⁻²)
ĥ	head (m)
k	roughness height (m)
Kave	average roughness height (m)
K.	Nikuradse's roughness length (m)
	characteristic length scale (m)
Lmax	maximum stone length (in guadrat) (m)
Lave	average stone length (of four largest stones in guadrat) (m)
Lsp	standard deviation of stone length (four largest stones in quadrat)
m	Slope of a regression (used to determine U*: see below and Appendix 2)
P	pressure term (N m ⁻²)
Q	discharge (m ³ s ⁻¹)
R	hydraulic radius (m)
Re	Revnolds number (dimensionless)
Reh	channel Revnolds number (dimensionless)
Re.	local Revnolds number (dimensionless)
Re*	Revnolds roughness number (dimensionless)
U	mean channel velocity (m s ⁻¹)
Ü	vertical velocity variation index (dimensionless)
U ₇	velocity at height above the boundary $z (m s^{-1})$
Un SD	velocity measured at 50% of depth (m s^{-1})
U0.002m	velocity measured 2 mm above the bed (m s ⁻¹)
U0.02m	velocity measured 2 cm above the bed (m s^{-1})
U*	shear velocity (m s^{-1})
X*	non-dimensionalised pressure difference (dimensionless)
V*	non-dimensionalised shear stress (dimensionless)
7	distance from the boundary (m)
70	roughness height (m)
-0	

B) Formulae

Re = UI/v	(1-1) (also equation 2-1)
$Fr = U/(gD)^{0.5}$	(1-2) (also equation 2-2)
$Re_x = U_x x/v$	(1-3)
$\tau_w = \rho U^{*2}$	(1-4)
$u_z = U^*/\kappa \ln[(z-d)/z_0]$	(1-5)
$U^* = \kappa [(u_1 - u_2)/(\ln z_1 - \ln z_2)]$	(1-6)
$U^* = \kappa m$	(1-7)
U/U* = 5.75 log(12 D/k)	(1-8)
$Re^* = U^*k_s/v$	(1-9)
$\delta' = 11.5v / U^*$	(1-10)
$F_{d} = \frac{1}{2} C_{d} \rho SU^{2}$	(1-11)
$F_1 = \frac{1}{2} C_1 \rho S U^2$	(1-12)
Head = -0.00164 + (0.0508 x voltage)	(3-1)
$P + 1/2\rho U^2 + \rho gh = constant$	(3-2)
U = (2g∆h) ^{0.5}	(3-3)
$x^* = \log_{10} [(\Delta P \times d^2)/(4\rho v^2)]$	(3-4)
$y^* = \log_{10} [(\tau_w \times d^2)/(4\rho v^2)]$	(3-5)
y* = -1.394 + 7/8 x*	(3-6)
$\tau_{\rm w} = A \times \Delta P^{7/8}$	(3-7)
$A = 1 / [10^{1.394} \times (d^2/4\rho \upsilon)^{1/8}]$	(3-8)
$\Delta P = \rho g \Delta h$	(3-9)
$\ddot{U} = (U_{0.5D} - U_{0.002m}) / U_{0.5D}$	(3-10)
$x = \delta_{crit} / (0.16 / Re_x^{1/7})$	(3-11)

 $D/k_{ave} = D/[0.5(L_{ave})]$

note: assumes Ψ =0.5

Note: the commonly determined bed roughness factor 'relative roughness' (D/k_{ave}) is more accurately designated 'relative depth' or relative submergence (see Nowell and Church 1979), as depth (D) is non-dimensionalised by the roughness factor k_{ave} . However, as is it an indicator of the degree of protrusion of the bed elements into the flow, this ratio is often referred to in this work as *relative roughness*, following the nomenclature established in Davis and Barmuta (1986).

Near-bed velocity profiles and wall shear stress (τ_w) estimation

At a given point in a channel, the shear stress acting on the wall (τ_w) can be estimated from velocity profile data using the 'law of the wall' (see Vogel 1994; Wilcock 1996; and Biron et al. 1998 for summaries). The law of the wall for the 'overlap layer' or 'log layer' is often expressed as

$$U_{z} = U^{*}/\kappa \ln(z/z_{0})$$

(1)

(2)

where U_z is the horizontal velocity at a given elevation z above the boundary, U* is the shear velocity (not a measure of velocity in the standard sense, but rather a nominal velocity related the rate at which velocity changes in the vertical direction), κ is von Karman's constant (empirically determined to be 0.40; see White 1999), and z_0 is the roughness height (a parameter whose value is dependent on the roughness of the bed). As the roughness elements associated with the surface of the boundary increase in size (*i.e.* a smooth plate becomes covered with an encrusting growth of nodulous algae, or flat slate bedrock becomes covered with gravel), the rate of transfer of momentum in the fluid, and thus shear velocity, is altered.

Shear velocity U* is defined as the square root of shear stress (τ_w) divided as the density of the fluid (ρ),

$$U^* = (\tau_w / \rho)^{0.5}$$

From this relationship, two aspects of the relationship between a moving fluid and a solid boundary are apparent. First, shear stress can be estimated from a velocity profile (by rewriting equation 2 as equation 3, and recognizing that, with care and appropriate equipment, all parameters in equation 1 can be measured in either a field or lab setting).

$$\tau_{\rm w} = \rho {\rm U}^{\star 2} \tag{3}$$

Second, wall shear stress increases directly with increases in the density and exponentially with increases in the shear velocity of the fluid. Density, however, is not likely to change much in a given channel, even if we account for fluctuations in temperature or solute load.

Despite the simple relationship between shear stress, shear velocity, and density, there can be substantial variation in the fluid dynamic parameters as fluid shears due to friction at the fluid/solid interface. If vertical transfer of momentum in the fluid is limited, the slope of the near-bed portion of the velocity profile (the plot of z on U) is relatively steep. Adjacent 'sheets' of water are moving at nearly the same velocity and 'slide' over one another only very slowly; shear stress in this case is relatively low. If the near-bed portion of the velocity profile is relatively flat, however, the velocities of adjacent 'sheets' of water are very different, and are 'sliding' over one another very quickly; shear in this instance will be relatively high.

As the slope of the velocity profile is indicative of shear stress, the law of the wall can be applied to estimate τ_w . However, the nature of the law of the wall varies depending on the relative influence of viscosity which, in turn, varies with distance from the bed. When examining flows immediately adjacent to the bed, the dominance of viscous effects (boundary layer flows are a Reynolds-scalable phenomena) must be accounted for. The law of the wall as expressed in equation 1 only applies to the portion of the water column that is strongly influenced by viscosity, generally the bottom 20% of the flow depth (see Biron et al. 1998 for a discussion). In the outer portions of the boundary layer (beyond the so-called 'overlap layer'), the log-normal nature of the profile does not apply, and the law of the wall as it appears in equation 1 no longer applies. Biron et al. (1998) demonstrated that shear stress is underestimated when the entire velocity profile, rather than the bottom 20%, is used.

As long as the log-normal portion of the boundary layer is used, equation 1 can be rewritten as

$$U^*/\kappa = dU_x / dlnz$$

(4)

$$U^*/\kappa$$
 = [slope of plot of U on Inz] = m

(5)

(6)

and further simplified as

$$U^* = m \kappa$$

where m is the slope of the plot of U on Inz. It is important to note that when making determinations of shear velocity U*, the slope of the profile must be that of the plot of U (response variable) on Inz (predictor variable); plots of Inz on U are only to be used for diagrammatic, rather than analytical, purposes. In addition, Bergeron and Abrahams (1992) note that because U is generally measured with greater error than is Inz, regressing Inz on U can lead to substantial errors in estimates of U*.

The principle of estimating shear stress using velocity profile data can be best illustrated using an example. Using a small-scale Pitot-static tube, a velocity profile was obtained over a boulder in a third class torrential stream (Figure 1; stone 7, Oct. 7, 1998; see also chapter 3). The mean velocity in this location was 1.1 m s^{-1} . The velocity profile, and especially the near-bed portion (Figure 1), appears to be log-normal. By visually inspecting the semi-log plot (z log_e transformed), it appears that the first eight points (or, within 1.28 cm of the bed) comprise the log-layer (Figure 2). A linear regression of this portion of the profile (remembering to employ the proper plot of dU / dlnz) produces the following result (Table 1).

Table 1. Linear regression of the log-layer portion of the velocity profile (Oct.7, 1998)

$U = 1.52 \pm 0.11$	5 Inz				
Predictor	Coeff.	Stand, Dev.	t-ratio	D	
Constant	1.523	0.0383	39.77	0.000	
Lnz	0.115	0.00680	16.97	0.000	
s = 0.0190	R ² = 98.0%	$R^{2}_{adj} = 97.6\%$			
Analysis of Vari	iance				·
Source	DF	SS	MS	F	p
Regression	1	0.104	0.104	287.95	0.000
Error	6	0.00217	0.00036		
Total	7	0.106			

The slope of the regression is 0.115, which, when applied in equation 6, gives a value of U* of 0.046 m s⁻¹. This value, when incorporated into equation 3, provides an estimate of shear stress of 2.12 Pa. A steeper slope, implying higher rates of shear in the log-layer (as adjacent 'sheets' of water slide over one another at a higher rate), would produce a higher value of U*, and result in a higher value of τ_w .



Figure 1. Velocity profile obtained over stone 7 on Oct. 7, 1998 using a Pitot-static tube.



Figure 2. Logarithmic plot of the velocity profile in Figure 1, showing the linearity of the first eight points (indicating the portion of the profile which corresponds to the 'log-layer' or 'overlap layer').

References

- Bergeron, N.E., and A.D. Abrahams. 1992. Estimating shear velocity and roughness length from velocity profiles. Water Resour. Res. 28: 2155-2158.
- Biron, P.M., S.N. Lane, A.G. Roy, K.F. Bradbook, and K.S. Richards. 1998. Sensitivity of bed shear stress estimated from vertical velocity profiles: the problem of sampling resolution. Earth Surf. Processes Landforms 23: 133-139.

Vogel, S. 1994. Life in Moving Fluids, 2nd Edition. Princeton University Press, Princeton, NJ.

White, F.M. 1999. Fluid Mechanics, 4th edition. WCB / McGraw-Hill, Boston

Wilcock, P.R. 1996. Estimating local bed shear stress from velocity observations. Water Resourc. Res. 32: 3361-3366.

Appendix 3

Ontogenetic changes in *Epeorus deceptivus* during the study period (Sept. – Oct. 1998)

Approximately every three weeks during the study period (September to October, 1998; specific dates shown below), 5 *Epeorus deceptivus* larvae were collected at the study site in order to determine the ontogenetic changes in morphology. During this period, head capsule width increased by 19.4% (from 1.29 mm to 1.54 mm), while total body length (not including cerci) increased by 67.3% (from 3.15 mm to 5.27 mm) (Figure 1).



Figure 1. Change in body dimensions (head capsule width and total body length excluding cerci) of *Epeorus deceptivus* during the study period (dates shown). In all cases n = 5 (bars = SD).

Appendix 4

Preston-static tube

In natural systems, accurate measurements of hydrodynamic variables such as velocity, shear velocity, and shear stress are often difficult to obtain very close to the boundary. For example, constant temperature anemometers using hot-wire or hot-film sensors are fragile and susceptible to rapid fouling (Hart et al. 1996), particle image velocimetry (PIV) techniques cannot be easily utilized where a clear side-view of the flow is not possible, and acoustic-based techniques such as acoustic Doppler velocimeters (ADVs) suffer from resolution problems due to resonance when used to measure water velocity within 30 mm of the bed (Finelli et al. 1999). However, small-scale Pitot-static tubes and Preston-static tubes do not suffer from these types of problems, and can be used to accurately measure near-bed water velocities and shear stresses.

In this study, measurements of near-bed velocity profiles and shear stress were made using a small-scale Preston-static tube (PST). The Preston-static tube used was configured to directly measure wall shear stress when deployed on a surface (Ackerman et al. 1994). The Preston-static tube was developed for measuring wall shear in situations where the incorporation of a wall-mounted static pressure tap is impractical (*i.e.* around small-scale objects where flow lines may be curved), but has been recently tested for use in a variety of field and lab conditions (Ackerman and Hoover, 2001).

The Preston-static tube (Figure 1) was constructed of a 90° bevelled tip syringe needle fixed to a side-bored syringe needle (tube diameter = 0.88 mm; see Ackerman et al. (1994) for a detailed description). The Preston-static tube differs from a standard Preston tube in that the dynamic pressure port (which faces into the flow) is coupled with a static pressure port (on the sidewall). As a result, the difference between static pressure p_s and dynamic (or stagnation) pressure p_0 can be measured, and velocity or shear stress can be determined (see chapter 3 for a description of the relationship between differential pressure, water velocity, and shear stress). A Validyne model CD379-1-2 membrane-type differential pressure transducer (Validyne Engineering; Northridge, CA), connected to the Preston-static tube via 2.0 m of flexible pressure lines (inside diameter = 3 mm), was used to measure differential pressure. Pressure differences were expressed as a voltage by a Validyne portable indicator (model CD379). In order to obtain a mean differential pressure, 15 voltages (obtained over an approximately 30 second time period) were averaged to obtain each measurement. Before measurements were taken, the pressure lines connecting the Preston-static tube to the pressure transducer were inspected for the presence of trapped air bubbles which would cause error in the differential pressure measurements. Preston-static tubes must be aligned parallel to the flow for accurate measurement. As such, before each measurement was made, the horizontal tube of the PST was oriented parallel to a fluorescein dye filament released immediately upstream from a long thin needle (length = 200 mm, diameter = 1 mm) (see chapter 3 for an additional description of Preston-static tube orientation and deployment).



Figure 1. A) The Preston-static tube measures wall shear stress using the difference between the total pressure (p_0) and static pressure (p_s). The p_{Tot} tap and ps tap are indicated (tube diameter d = 0.88 mm; the diameter of the 20G syringe needles has been exaggerated for clarity). B) Deployment device used to position the Preston-static tube. The ball-and-socket connector allows the PST to be oriented parallel to the stream flow. The deployment device is mounted on a vertical support and attached to a xyz-positioning device (not shown; see chapter 3 for a description) (see also Ackerman and Hoover 2001).

References

- Ackerman, J.D., and T.M. Hoover. 2001. Measurement of local bed shear stress in streams using a Preston-static tube. Limnol. Oceanogr. 46: 2080-2087.
- Ackerman, J.D., L. Wong, C. R. Ethier, D.G. Allen, and J.K. Spelt. 1994. Preston-static tubes for the measurement of wall shear stress. J. Fluids Eng. 116: 645-649.
- Finelli, C.M., D.D. Hart, and D.M. Fonseca. 1999. Evaluating the spatial resolution of an acoustic Doppler velocimeter and the consequences for measuring near-bed flows. Limnol. Oceanogr. 44: 1793-1801.
- Hart, D.D., B.D. Clark, and A. Jasentuliyana. 1996. Fine-scale measurement of benthic flow environments inhabited by stream invertebrates. Limnol. Oceanogr. 41: 297-308.

Appendix 5

Periphyton sampler

The measurement of the biomass or chlorophyll content of periphyton, a community that includes microbes, protists (protozoans, and algae), and fungi within a 'polysaccharide matrix' (Lock et al. 1984), is one of the most important determinations in studies of the trophic structure of stream environments (Steinman and Lamberti 1996). Analyses of periphyton have been used to infer variations in photosynthetically active radiation (Steinman 1992), ultraviolet radiation (Bothwell et al. 1994), herbivory (Lamberti et al. 1987), and water velocity (Steinman and McIntyre 1986), among others. As such, it is important that any periphyton sampling technique incorporates the following criteria: (1) that a constant proportion (preferably all) of the biomass be removed; (2) that a known area be sampled; (3) that it is possible to apply the technique under a variety of conditions; and (4) that the results are repeatable. Unfortunately, most periphyton sampling techniques (*e.g.* scraping, brushing, or direct extraction of the substrate) are lacking with respect to one, or more, of the aforementioned criteria (Cattaneo and Roberge 1991).

A device was developed to obtain algal samples from small, repeatable areas on the surface of periphyton-covered natural and artificial substrates. The device consists of a central cylinder (PVC pipe; inside diameter = 20 mm) 90 mm in length, sealed at one end and encircled by a high-density, closed-cell foam rubber skirt at the other (Figure 1). The rubber skirt extends approximately 5 mm from the end of the PVC cylinder, and is used to seal the device against the surface of the substrate from which the sample is being obtained. The cylinder contains a circular brush cut from the head of an Ultra-Stiff vegetable brush (Tupperware; Orlando, Florida) with nylon bristles (bristle length = 15 mm). This circular brush is attached to a brass shaft (diameter = 3 mm, length = 130 mm), which extends upward through the device, and emerges through a hole in the upper end of the cylindrical housing (hole diameter = 3.5 mm). The length of shaft that extends above the device was fastened in the chuck of a hand-held, rotary carving tool (Ryobi® HT20VSK; Pickens, S.Carolina). The side of the cylindrical housing was fitted with two tubing ports separated at 90°. The first port, fixed slightly higher than the other, provides an entrance for water, while the second, lower port is attached to a vacuum line, allowing for the removal, via suction, of the algae-water slurry created when the within the device.

When the device is pressed tightly against the surface to be sampled, the foam rubber skirt forms a seal against the substrate. Water is then introduced into the device via a line attached to the upper port (either a squirt bottle or distilled water tap can be used to control the flow of the water into the device), and the vacuum pump turned on. When the rotary tool is activated, the brush rotates, scrubbing algae from the substrate. The slurry produced gathers in a filter flask attached to a vacuum pump. The material can then be collected on a glass-fibre filter for determination of chlorophyll a content or organic/inorganic biomass (ash-free dry weight).



Figure 1. Diagram of the apparatus used to sample periphyton from the surface of naturally occurring and experimentally deployed substrates. The device consists of a plastic (PVC) cylinder (A), sealed at the upper end. During use, the bottom end of the cylinder is pressed to the substrate. A seal between the substrate and the cylinder is made by a high-density, foam rubber skirt (B) at the base of the cylinder. A cylindrical, nylon-bristled brush (C), is attached to a hand-held rotary carving tool (Ryobi® HT20VSK) via a brass shaft (D) (diameter = 3 mm) which extends upward through the device. Water is drawn into the device at (E). When the rotating brush is held against the substrate, the water and removed algae form a slurry that is carried off by suction (at F). The brush is shown extended from device for clarity.

References

- Bothwell, M.L., D.M.J. Sherbot, and C.M. Pollock. 1994. Ecosystem response to solar ultraviolet-B radiation: Influence of trophic level interactions. Science 256: 97-100.
- Cattneo, A., and G. Roberge. 1991. Efficiency of a brush sampler to measure periphyton in streams and lakes. Can. J. Fish. Aquat. Sci. 48: 1877 1881.
- Hoover, T.M., J.L. McConnachie, and J.D. Ackerman. In prep. Measuring periphyton biomass on natural and artificial substrates of differing roughness.
- Lamberti, G.A., L.R. Ashkenas, S.V. Gregory and A.D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. J. N. Am. Benthol. Soc. 6: 92-104.

- Lock, M.A., R.R. Wallace, J.W. Costerton, R.M. Ventullo and S.E. Charlton. 1984. River epilithon: toward a structural-functional model. Oikos 42:10-22.
- Steinman, A.D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? Oecologia 91:163-170.
- Steinman, A., and G. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295-313 in: Stream Ecology: field and laboratory exercises. Eds: Hauer, R., Lamberti, G. Academic Press.
- Steinman, A.D. and C.D. McIntire. 1986. Effects of current velocity and light energy on the structure of periphyton asemblages in laboratory streams. J. Phycol. 22: 352-361.
Stone survey form

The distributions of mayfly larvae on the upper surface of all experimentally deployed stones in the study were recorded using a form (see below) that featured a grid that reproduced the Cartesian grid marked on the surface of the stones (see chapter 3 and 4). Distributions of larvae on the surface of naturally occurring stones were recorded (using circles marked on the diagram of the stone; see below) on the same forms, by first measuring the stones (*in situ*), and then sketching the shape and extent of the stones on the form. Then, the distributions of larvae were recorded in the same manner as in the pre-marked stones.

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