

**HYDRODYNAMIC CONTROLS ON THE MOVEMENT OF  
INVERTEBRATE LARVAE AND ORGANIC MATTER IN  
SMALL STREAMS**

by

Trent Hoover

Bachelor of Science, University of Alberta, 1994

Master of Science, University of Northern British Columbia, 2001

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## ABSTRACT

The movement of organisms and resources within ecosystems are essential elements in the productivity, stability, and distribution of communities. This thesis examines how water velocity, a defining factor of lotic systems, influences the dispersion of benthic organisms and particulate organic matter in small stream ecosystems. Variation in movement-related behaviours in two rheophilous ('flow-loving') mayflies (*Epeorus* and *Baetis*) and two rheophobic ('flow-avoiding') mayflies (*Ameletus* and *Paraleptophlebia*) were compared to determine how benthic organisms disperse between and within habitat patches in hydrodynamically complex landscapes. The degree to which water velocity and particle shape influence the retention of organic matter (including deciduous leaves, conifer needles, red-cedar fronds, and branch fragments) was examined to determine how physical factors determine detrital resource availability in streams.

Although water velocity did not influence the crawling rates of *Baetis* and *Ameletus* in daylight conditions, both mayflies dispersed rapidly upstream in low-velocity flows in dark conditions. Drift rates of both mayflies were lower in daylight than dark conditions, and were generally inversely related to their habitat preferences. Escape responses in grazing *Epeorus*, *Baetis*, and *Ameletus* larvae in a range of flow conditions showed that retreat distance was more sensitive than flight initiation distance to variation in water velocity, suggesting that

hydrodynamics mediate the risks of predation and the costs of flight in stream systems. Comparisons of the transport distances of live larvae, dead larvae, and passive tracer particles in low and high water velocities showed that drift distance varied substantially among taxa, and that behavioural control over drift distance generally declined as water velocity increased.

While organic matter particles generally travelled further in high-velocity reaches, leaves were retained in riffles when they impacted on protruding clasts, while 'stiff' particles were retained when they settled into streambed interstices. Leaves placed in high-velocity microhabitats were broken down more slowly than leaves in low-flow areas, likely due to the exclusion of large-bodied detritivores.

In conclusion, this thesis supports the view that hydrodynamic forces control trophic interactions and local population dynamics in stream ecosystems by directly altering the physical – and sometimes behavioural – processes of particle entrainment, transport, and deposition.

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The research described in Chapters 2, 3, and 4 was approved by the UBC Animal Care Committee (Certificate number A00-0177).

## **DEDICATION**

For my wife Shelley, of course.

## **CO-AUTHORSHIP STATEMENT**

Chapters 2 through 6 represent manuscripts that have been (or will be) published with two or more authors. In all instances, Trent Hoover was responsible for the identification and design of the research program, performing the research, data analyses, and manuscript preparation. Other authors contributed funding to the project or made editorial contributions to the manuscripts.

# **CHAPTER 1: INTRODUCTION**

## **The Physical ‘Habitat Templet’ of Streams**

Organisms display an astonishing array of traits that allow them to acquire resources, survive environmental stresses and predators, and reproduce. One of the principal goals of ecology is to understand the relationships that exist between this biological diversity and the environmental variation present within and among habitats. Southwood (1977) wrote that “the multitude of ecological strategies that we observe in nature arise from the evolutionary ‘tradeoffs’ of costs versus benefits in the process of adaptation to habitats”. If habitat provides the templet upon which evolution forges the life history strategies of organisms (Southwood 1977, Townsend and Hildrew 1994), then the biological responses of individuals, populations, and communities will be tightly coupled to the physical factors that define habitat structure (Palmer et al. 1996, Hart and Finelli 1999, Biggs et al. 2005). In aquatic systems, fluid dynamic forces are key physical factors driving many important ecological processes, including dispersal (Elliott 2002), resource acquisition (Hughes and Dill 1990), predation (Lancaster et al. 1990, Hart and Merz 1998), resource movement and distribution (Kobayashi and Kagaya 2004), respiration (Finelli et al. 1999), and competition for resources (Hart and Finelli 1999).

In many streams, shallow depths, relatively steep gradients, and irregular bed topographies ensure that flows within the channel are fully turbulent and

highly three-dimensional, and that depth-averaged and near-bed water velocities are spatially and temporally variable (Carling 1992, Hart et al. 1996, Buffin-Bélanger and Roy 1998, Hoover and Ackerman 2004). Hydrodynamic factors are recognised as the most important factors shaping the benthic ecosystems of lotic systems, and the generally unidirectional flows of streams and rivers have shaped the morphology, (Weissenberger et al. 1991, Pommen and Craig 1995), behaviour (Soluk and Craig 1988, Olden et al. 2004), diversity (Quinn and Hickey 1994), and community structure and dynamics (Hershey et al. 1993, Lancaster and Hildrew 1993) of the invertebrate fauna that inhabit these temporally variable and spatially heterogeneous benthic landscapes. This dissertation will examine how habitat unit- and microhabitat-scale variation in water velocity controls the movement of benthic invertebrates and one of their principal resource types – organic matter – in stream systems. Both invertebrate distribution and organic matter abundance are critical determinants of ecosystem function in many stream systems (Scarsbrook and Townsend 1993, Wallace et al. 1997, Lepori et al. 2005), and thus a quantitative description of how water velocity influences these processes will also describe an ecologically important way that the physical habitat template constrains the evolution of stream invertebrate life histories.

## **Invertebrate Dispersal**

Invertebrate drift, the downstream transport of entrained benthic invertebrates in the turbulent and generally unidirectional flows that exist in open channels, plays an important role in the population dynamics and community ecology of many lotic systems (Palmer 1995, Palmer et al. 1996, Fonseca and

Hart 2001, Koehl et al. 2007). In streams, downstream drift allows benthic invertebrate larvae to rapidly emigrate from areas of unfavourable habitat (Holomuzki and Van Loan 2002), escape predators (Forrester 1994, Wooster and Sih 1995, Peckarsky 1996), exploit patchily distributed resources that are variable in space and time (Rowe and Richardson 2001), and colonise unexploited areas downstream (Palmer et al. 1996). However, the movement of invertebrates between habitat patches is constrained both by environmental heterogeneity and the dispersal strategies adopted by dispersing organisms. Drifting larvae risk being transported into and settling within areas of the streambed landscape with unfavourable flow regimes (Otto and Sjöström 1986, Lancaster et al. 1996). With and King (1999) note that “what ultimately influences the success of individuals in locating suitable habitat, or some other patchily distributed resource, is the scale of movement relative to the scale of patchiness.” The dispersal success of organisms will decline if individuals are unable either to find new habitat patches or to traverse areas of unsuitable (matrix) habitat (With and King 1999).

Unlike organisms that disperse by crawling and are thus able to continually assess the quality of patches they encounter, drifting stream insects must settle to accurately assess patch value. As such, they may rely on a combination of behavioural adaptations (such as swimming, Otto and Sjöström 1986) and physical processes (such as greater settlement rates in areas of low velocity and turbulence intensity; Lancaster et al. 1996) to ensure dispersal success. While the influence of behaviours such as swimming and posture

modification on drift distance have been examined (e.g. Ciborowski and Corkum 1980, Allan and Feifarek 1989), little is known about how these behavioural adaptations function in turbulent and heterogeneous stream environments. This dissertation will, in part, examine how the dispersal strategies of benthic stream invertebrates are related to their habitat preferences, and act to maximise the probability of successfully dispersing between patches of suitable habitat.

Small-scale crawling movements over the bed are also important in the ecology of benthic invertebrates, especially with respect to predator-prey interactions (Peckarsky 1996, Winterbottom et al. 1997), competition for resources (Voelz and Ward 1996), and habitat selection processes (Lancaster 1996). For example, by 'looping' across the substrate (Reidelbach and Kiel 1990), filter-feeding black fly larvae can move short distances to find flow microhabitats that maximize filtration rates (Chance and Craig 1986). Upstream-downstream movements are also common in stream invertebrates. While Jackson et al. (1999) found that the relatively sedentary case-building caddisfly *Gumaga nigricula* moved only a few metres over periods of several weeks, more mobile groups such as mayflies may be able to crawl several metres daily (Elliott 1971, Bergey and Ward 1989). However, little is known about the importance of crawling movements in determining rates of movement within and between patches (but see Townsend and Hildrew 1976, Fonseca and Hart 2001, Olden et al. 2004).

In taxa that are able to use multiple movement modes, crawling movements may be the local-scale component of a complex dispersal strategy



where large-scale movements are made by drifting. To explain observed faunal distributions in the Pembina River, Ciborowski (1987) suggested that drifting mayflies might crawl towards the centre of the channel after settling from the drift. This behaviour would compensate for the lateral displacement drifting invertebrates may experience during drift in large channels. Ciborowski suggested that the observed patterns of faunal distribution might also be explained if invertebrates readily re-enter the drift when they settle in unsuitable habitat (i.e. river margins). Understanding how invertebrates use different modes of movement to disperse between habitat patches would help stream ecologists determine if colonisation processes are more important than internal processes such as predation and competition in regulating local population structure (see Palmer et al. 1996). Furthermore, estimates of the residence times of individuals in habitats of variable quality would allow stream restoration technicians to determine which invertebrate taxa are most likely to colonise reconstructed channels with different substrate types and flow regimes.

## **Dispersal Strategies**

Dispersal strategies are comprised of the behaviours that organisms express to maximise the likelihood of successfully moving from one patch of suitable habitat to another. Dispersal strategies should evolve regardless of whether the organisms disperse actively (by walking, swimming, or crawling), passively (carried in air or water currents), or employ a combination of the two. Several instances of well-adapted dispersal strategies have been documented in marine and terrestrial systems. For example, Cody and Overton (1996) showed

that the seeds of coastal populations of wind-dispersed weedy plants had shorter dispersal distances (i.e. faster fall times) than plants from non-coastal populations. Also, a recent model by Armsworth et al. (2001), suggested that larval reef fish may be able to influence the distances they advect away from their home reef by controlling their vertical position in the water column and exploiting the distribution of velocity within the boundary layer, allowing them to locate and settle in high-quality habitat patches. In both examples, propagules were at risk of dispersing into sink habitats with zero probability of subsequent reproduction or long-term survival (Morris 1991, Delibes et al. 2001), and the dispersal strategies employed increased the likelihood of successful movement among habitat patches.

If dispersing stream invertebrate larvae possess morphological and behavioural adaptations that maximise rates of habitat encounter and successful settlement, they will minimise the costs associated with lost feeding opportunities (Palmer 1995), reduce drift-associated predation (Rader 1997), and prevent dispersal into sink (matrix) habitats (Palmer et al. 1996, Delibes et al. 2001). Armsworth (2001) stated that “the frequency of suitable habitat encounters during advection determines the probability of success when relying on dispersal based strategies”. Due to the highly heterogeneous nature of streams, however, the frequency of habitat encounters and the probability of successful settlement will depend greatly on the physical characteristics of the preferred habitat type. If they behave like passive particles, drifting larvae that prefer high-shear, erosional habitats will be unlikely to encounter and settle in these types of habitat. Highly

specialised adaptations and behaviours that enhance rates of habitat encounter and settlement have been described, such as the release of sticky silk threads (Fingerut et al. 2006) and posture modification and swimming (Otto and Sjöström 1986). However, the functional relationships between drift behaviours of these types and the distribution of benthic invertebrates in streams have not yet been completely described (see Ciborowski 1987). Empirical description of settlement probabilities and the risks and costs associated with drifting are required before the adaptive significance of dispersal strategies can be understood.

Stream invertebrates that rely on drift as a means of dispersal may exhibit behaviours that allow them to preferentially settle in areas of suitable habitat. Regularly drifting taxa such as the mayfly *Baetis* and the amphipod *Gammarus* appear to exhibit greater control over the drift process than rarely drifting taxa (Elliott 2002), and Ciborowski and Corkum (1980) showed that behavioural control over drift distance is positively correlated with the tendency of stream organisms to exhibit diel drift periodicity. However, the efficacy of settlement-oriented drift behaviours may decline as current velocities increase. In Ciborowski and Corkum's (1980) study, behavioural control over drift distance decreased as water velocity increased, and was minimal when velocities reached 26 cm/s, especially for larger individuals of the mayfly *Ephemerella subvaria*. Ciborowski and Corkum (1980) predicted that *E. subvaria* should then accumulate in slower river reaches, but noted that pattern was not observed in field studies; *E. subvaria* nymphs were consistently found in faster reaches year round (Kovalak 1978). This suggests that the dispersal strategy of rheophilous

taxa such as *E. subvaria* may involve post-settlement migration to preferred habitat patches. A greater understanding of how drifting invertebrates modify their drift behaviours as they encounter different regimes of velocity or turbulence intensity would help ecologists evaluate how hydrodynamics influence patterns of faunal distribution in streams and rivers.

The dispersal movements of drifting stream invertebrates will ultimately be disadvantageous if they are transported into sink habitats, which may have inadequate food resources, contain unfamiliar predators, or be characterised by energetically-costly hydrodynamic regimes and physical environments. However, there may be a number of strategies that drifting invertebrates can adopt to avoid settling in undesirable habitats. (1) Individuals can drift repeatedly, re-entering the drift if, upon settlement, they find that the habitat they encounter is unsuitable. This strategy ('*drift-dominated*') may require individuals to drift several times to locate a suitable habitat patch, and may not be efficient for those taxa that prefer high-shear habitats due to the low probability of settling where shear stresses are high. (2) Individuals can drift, settle, and then crawl across the bed to locate adequate habitat conditions. This strategy ('*crawling-dominated*') may be effective for taxa that prefer habitats that are typically patchily distributed at small scales (e.g. patches of periphyton on the upper surface of stones), or are difficult to access by drifting alone (e.g. patches of high-shear habitat). If the risk of drift-associated mortality is too great, or the likelihood of encountering a patch while drifting is too low, stream invertebrates using this type of strategy may not enter the drift at all, and may instead disperse

by crawling alone. (3) Individuals can settle directly into patches of suitable habitat. This strategy (*'passive settlement-dominated'*) will be effective for only two groups of organisms; those that possess highly effective settlement behaviours or morphologies (e.g. swimming, silk thread release), and those whose habitat requirements match the physical characteristics of passive settlement locations. The efficacy of this strategy will be greatest if drifting individuals are able to indirectly assess the quality of habitat patches before settling, perhaps by using secondary cues such as turbulence intensity or water velocity. (4) Individuals settle, but do not readily re-enter the drift or crawl extensively in search of more suitable habitat (i.e. larvae become essentially sessile once settled). This type of strategy (*'lottery'*) is common in dispersing marine larvae (see Palmer et al. 1996, Armsworth et al. 2001), and may be effective where the scale of patchiness is very large relative to the scale of movement (see With and King 1999). In stream environments, a 'lottery' strategy may be efficient for those taxa with broad habitat requirements or for groups for which movement carries a significant risk of mortality. It is important to note that physical (e.g. transport and deposition) and ecological (e.g. predation) constraints on movement differ between day- and night-time periods and among ontogenetic stages of the same organism (Allan and Feifarek 1989, Buffagni et al. 1995, McIntosh and Peckarsky 1999), potentially producing light condition- and size-dependent movement behaviours.

The various movement modes – and combination of modes – that can be used to disperse among patches in linearly-arranged landscapes such as

streams can be illustrated by a simple conceptual model of between-patch movement (Fig. 1-1). An individual attempting to disperse from an 'initial' patch to a 'new' patch downstream must necessarily cross the matrix environment between patches (e.g. With and King 1999). To do so, stream invertebrates can either enter the drift (e), or cross the patch boundary by crawling (p) in either an upstream or downstream direction (Bergey and Ward 1989). If the likelihood of successful between-patch movement depends upon movement mode, then individuals that adopt the less efficient movement mode will be selected against, producing species-specific rates of drift entry or crawling dispersal (Fig. 1-1). Once suspended, and depending on the hydrodynamic characteristics of the channel (Ciborowski 1987) and the behaviours adopted by the drifting larvae (Ciborowski and Corkum 1980, Fingerut et al. 2006), the larvae will either settle (s) in the patch it left, in the matrix environment, or in a new patch downstream. Likewise, the crawling behaviours of larvae may be dependent on local flow conditions, leading to habitat-specific dispersal rates (Olden et al. 2004) that may also be biased in either an upstream or downstream direction (Bergey and Ward 1989). In this fashion, the relative degree to which various benthic invertebrates rely on each movement mode can be contrasted, and compared to their habitat preferences in order to examine how dispersal behaviours function in physically heterogeneous stream landscapes.

## **Organic Matter Movement**

The food webs of many small streams are based largely upon terrestrially derived leaf litter, which provides both food and habitat for decomposers and

detritivorous organisms (e.g. Cummins et al. 1989, Richardson 1992, Wallace et al. 1997). While the primary sources of allochthonous organic matter are riparian deciduous trees in many systems, coniferous trees can also contribute substantial amounts of material to streams where riparian forests are dominated by trees of this type (Richardson et al. 2005). Leaf litter is generally carried downstream until it is retained, where it is then broken down by a combination of physical, chemical, and biological processes (Webster and Benfield 1986, Webster et al. 1999). Where channels effectively retain inputs of terrestrial materials and downstream transport is limited, allochthonous inputs to streams will serve as a basal food resource for local food webs. In contrast, if streams act as highly efficient conduits for the transport of materials downstream, organic matter will be exported, and will enter the food webs of more retentive reaches downstream.

Numerous studies have shown that channel features such as streambed sediments, debris dams, and channel banks influence the retention of deciduous leaf litter and woody debris (Ehrman and Lamberti 1992, Entekin et al. 2008). However, we know little about how stream channels retain coarse, suspended organic materials of different types such as coniferous needles or small wood fragments. The spatial distribution of retained detrital material in streams also influences its availability to detritivorous invertebrates. For example, Kobayashi and Kagaya (2005) found that leaf litter breakdown by invertebrate shredders was greater in mid-pool patches than in riffle or near-edge patches. If the geomorphological features of stream channels act as crucial elements in the

retention of terrestrial inputs, the strength of the trophic linkages between riparian forests and adjacent streams will depend on the physical characteristics of the channel itself.

## Chapter Summary

In the research reported in this dissertation, manipulative field and lab experiments were used to examine how water velocity influences the movement of benthic organisms and particulate organic matter in small streams, and thus controls the continual redistribution of organisms and resources in these systems (see Townsend 1989).

Chapters 2, 3, and 4 explore the role of water velocity in the movement of benthic invertebrates. In these three chapters, a comparative, experimental approach was used to determine if invertebrates that share similar hydraulic habitat preferences (i.e. hydraulic 'guilds') have evolved common strategies that reflect the risks and benefits associated with movement within and among patches of erosional (high-velocity) or depositional (low velocity) habitat. Taxa that inhabit hydraulically similar habitats may have a variety of adaptations, including benthic and drift behaviours (e.g. escape responses, crawling rates, swimming abilities) that minimise the probability of displacement into unsuitable habitats. Three of the four mayflies examined forage during the day on exposed streambed surfaces for periphyton, but vary in their habitat preferences; *Ameletus* (Ameletidae) is generally found in relatively low-velocity (pool/run) habitats, *Baetis* (Baetidae) is found in intermediate-velocity habitats (riffles), whereas *Epeorus* (Heptageniidae) inhabits high-velocity microhabitats (steps and



boulder cascades) (Palmer 1995, Reece and Richardson 2001). The fourth mayfly, *Paraleptophlebia* (Leptophlebiidae) is detritivorous, and is found in accumulations of organic matter in low-shear depositional zones such as pools and stream margins (Mattingly 1987). All four taxa were not included in each experiment, as all four mayflies could not be readily collected at all times of the year or in all streams sampled.

Chapters 5 and 6 examine the transport, retention, and breakdown of terrestrially-derived organic matter. The physical processes involved in the transport and retention of organic matter particles are similar to those that control the downstream drift and settlement of benthic organisms. However, coarse organic matter particles such as red alder (*Alnus rubra* Bong.) leaves, Douglas-fir (*Pseudotsuga menziesii* Franco) branch pieces, newly senesced and fallen Douglas-fir needles, and red cedar (*Thuja plicata* Don) fronds are generally much larger than benthic invertebrates. As a result, depth-mediated interactions between particles, flow, and protruding sediment grains likely play a more important role in transport and retention.

The progression of chapters – and the specific questions asked in each chapter – is as follows:

In Chapter 2, I examine if the dispersal rate and dispersal mode of stream invertebrates are influenced by local water velocity and light level. Quantifying the upstream and downstream movements of mayfly larvae (*Baetis* and *Ameletus*), I ask three specific questions: (1) Are the dispersal rates of these mobile invertebrates correlated with habitat preference, and are drift and benthic

crawling movements greatest in the water velocities that least match the habitat preferences of each mayfly? (2) Are rates of drift greater in the dark than in daylight conditions for all water velocities? (3) Are the distances that mayflies disperse upstream by crawling during the day less than distances dispersed upstream in the dark?

In Chapter 3, I examine the role that water velocity plays in the escape behaviours (flight initiation distance, retreat distance, and escape mode) of three herbivorous stream mayflies, *Ameletus*, *Baetis*, and *Epeorus*, as a means of examining relative rates of entry into the drift. Given the potential for water velocity-mediated tradeoffs between the risk of predation and costs of escaping, I ask two specific questions: (1) Do the flight initiation distances and retreat distances of stream invertebrates larvae increase with velocity in accordance with the predictions of optimal escape theory (Ydenberg and Dill 1986, Cooper and Frederick 2007)? (2) As mayflies that enter the drift risk displacement into low-velocity areas of the stream (Lancaster et al. 1996), are mayfly taxa that are generally found in low-velocity habitats more likely to use drifting or swimming escape modes than would taxa that prefer high-velocity habitats?

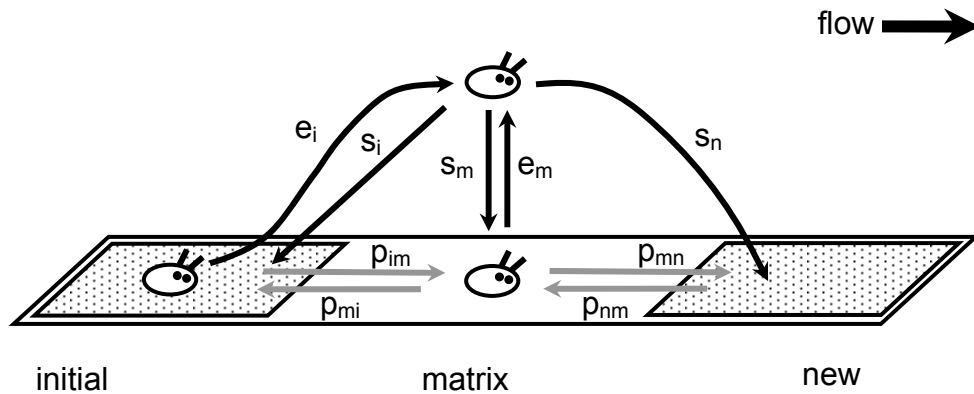
In Chapter 4, I quantify the roles that behaviour, morphology, and water velocity play in determining the distances that stream invertebrates (*Epeorus*, *Baetis*, *Ameletus*, and *Paraleptophlebia*) drift in shallow, turbulent streams. By comparing the hitting distances of live mayfly larvae, dead conspecific larvae, and passive tracer particles in slow and fast currents, I evaluate the degree to which behavioural control varied with flow conditions and among taxa. I ask

three specific questions: (1) Do live larvae and dead larvae drift the same distance, and does the degree of behavioural control over drift (i.e. the difference between live and dead larvae) vary with velocity? (2) Do dead larvae and passive tracer particles drift similar distances, and does the degree of morphological control (i.e. the difference between dead larvae and tracer particles) vary with velocity? (3) Do the transport and settlement characteristics of drifting invertebrate larvae vary among taxa, their habitat type, and with water velocity?

In Chapter 5, I examine how streambed morphology and microhabitat influence the retention and breakdown of conditioned leaf litter in small streams. I address three specific questions: (1) what physical factors play the greatest roles in leaf retention processes, and do these processes differ between riffles and pools? (2) Are rates of leaf litter breakdown related to the small-scale topographical features of the streambed locations in which they settle? (3) How does streambed stone geometry influence leaf litter retention?

In Chapter 6, I describe the transport and retention characteristics of four different types of conditioned OM particles – alder leaves, branch pieces, conifer needles, and red cedar fronds. By describing variability in the transport and retention characteristics of these organic matter types in two geomorphologically and hydraulically distinct reach types (pools and riffles), I address two specific questions: (1) How rapidly do the physical properties (settling velocity) of different types of organic matter change with immersion time? (2) Do transport and retention patterns of these four types of organic matter vary between riffles and

pools? (3) Can the settlement patterns of conditioned organic matter particles be predicted using simple indices such as Rouse numbers?



**Figure 1-1**

Diagram of a simple heuristic model of the suite of potential movement pathways and movement modes available to a stream organism dispersing downstream from one patch of suitable habitat to another in a spatially heterogeneous stream landscape. The initial (upstream) and new (downstream) patches of suitable habitat are stippled, while the matrix (unsuitable habitat) separating the two habitat patches is white. Individuals can employ drifting or crawling (pedestrian) modes (or a combination of the two) to move among patches. For instance, for any given individual about to disperse downstream, there will be some likelihood that it will enter the drift; once entrained, it can settle back in the initial patch, settle in the matrix between habitat patches, or can settle in a new habitat patch. Individuals may also use swimming as a means of short, within-patch movements (not shown here). Potential movement pathways include the following: entrainment in the initial patch and the matrix =  $e_i$  and  $e_m$ , respectively; settlement in the initial patch, the new patch, and the matrix =  $s_i$ ,  $s_n$ , and  $s_m$ , respectively; crawling (pedestrian) movements from the initial patch into the matrix, from the matrix upstream to the initial patch, from the matrix downstream to the new patch, and from the new patch upstream to the matrix =  $p_{im}$ ,  $p_{mi}$ ,  $p_{mn}$ , and  $p_{nm}$ , respectively. Entrainment and settlement movements are indicated by solid black arrows. Flow is left to right.

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## **CHAPTER 2: UPSTREAM AND DOWNSTREAM MOVEMENTS IN STREAM INVERTEBRATES: DOES DISPERSAL MODE CHANGE WITH LIGHT LEVEL AND WATER VELOCITY?<sup>1</sup>**

### **Introduction**

The movements of animals within patches of suitable habitat often differ substantially from their movements in non-habitat 'matrix' environments between patches (Baars 1979, Kohler 1984, Schooley and Wiens 2003, Olden et al. 2004). These habitat-dependent movement rates are often interpreted as evidence of behavioural strategies that maximise the foraging opportunities of organisms moving within suitable patches, and minimise the time spent travelling between patches (Krebs 1978, Kohler 1984). Habitat-dependent movement rates can directly influence a wide range of ecological processes, such as rates of immigration into and emigration from local habitat patches (Townsend 1989), predator-prey dynamics (Cooper et al. 1990, Wooster and Sih 1995), and herbivore-host interactions (Jonsen et al. 2001). The majority of theoretical (e.g. Hiebeler 2000) and empirical (e.g. Schooley and Wiens 2003) studies of animal movements have been conducted on terrestrial systems where landscape-scale directional gradients, if present, are weak. In contrast, less is known about how the movements of invertebrates in lotic ecosystems are influenced by the

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<sup>1</sup> A version of this chapter will be submitted for publication. Hoover T., Yonemitsu N. and Richardson J.S. Upstream and downstream movements in stream invertebrates: Does dispersal mode change with light level and water velocity?

directionality superimposed on the streambed landscape by the downstream movement of water.

While the dispersal movements of many organisms are restricted to a single movement mode (e.g. crawling alone, Schooley and Wiens 2003), many stream insects can move between habitat patches using three distinct movement modes – crawling, swimming, and drifting (Lancaster 1999, Englund and Hambäck 2004). Both drifting and crawling allow stream invertebrates to respond to local variation in biotic and abiotic factors. Stream invertebrates have been shown to enter the drift in response to numerous factors, including water velocity, light, invertebrate predators, benthic-feeding and drift-feeding fish, benthic density, food resource availability, refuge availability, and substrate type (McIntosh and Townsend 1998, Corkum et al. 1977, Rader and McArthur 1995, Kohler 1985, Culp et al. 1991, Peckarsky 1996, Winterbottom et al. 1997). Where suitable habitat patches are isolated within large expanses of inhospitable matrix environments, drift may be the only movement mode that permits individuals to readily move between patches (Rader and McArthur 1995). Crawling is also an important mode of movement, allowing benthic invertebrates to locate food resources, access refuges, and escape from predators (Kohler 1984, Wooster and Sih 1995, Peckarsky 1996, Lancaster 1999). While some studies have shown that the crawling movements of stream insects are generally biased in an upstream direction (Elliott 1971b, Elliott 2003), others have suggested that they are biased in the downstream direction (Bergey and Ward 1989). If movement mode or movement direction vary with local environmental

factors such as water velocity, then the spatial distribution of these factors across the streambed will influence local population dynamics.

In stream ecosystems, water velocity is a critical determinant of habitat type and quality for benthic organisms (Statzner and Higler 1986). Water velocities are highly spatially variable, especially immediately adjacent to the bed in the zone inhabited by benthic invertebrates. Water velocity varies substantially and systematically at several spatial scales across the streambed landscape, such as from the front to back of individual stones (Hoover and Ackerman 2004), and from riffles to pools (Jowett 1993). As such, stream invertebrates will encounter areas of the streambed whose flow regimes are unsuitable when dispersing between patches of suitable habitat in either upstream or downstream directions. If, like their terrestrial counterparts, stream invertebrates have evolved dispersal strategies that allow them to move efficiently between patches of habitat by adopting different movement patterns in habitat types of differing suitability (Schooley and Weins 2003), the movement patterns of benthic taxa should vary with water velocity. However, studies that have examined the degree to which stream invertebrate movement modes and rates are dependent on local water velocity have primarily focussed on taxa with limited mobility such as blackfly (Simuliidae) larvae (e.g. Fonseca and Hart 2001) and cased caddisfly (Trichoptera) larvae (e.g. Olden et al. 2004). If local water velocity influences either the drift entry or benthic crawling rates of highly mobile stream insects such as mayflies, then the spatial distribution of velocities across the streambed

may control the movement, and thus the landscape-scale distribution, of these organisms (see Elliott 1971b, Ciborowski 1987).

Light level, another proximal environmental cue that directly influences stream invertebrate activity, also has the potential to influence rates of dispersal between patches. Light level mediates the activity levels of many benthic invertebrates. Where drift-feeding fishes are present invertebrate drift is primarily nocturnal (McIntosh et al. 2002), a behavioural pattern that reduces the risk of predation for drifting insects (Flecker 1992). However, surprisingly little is known about how light level influences the crawling movements of stream invertebrates. Less clear is the effect of diel changes in light intensity on macroinvertebrate activity; studies have shown both that the foraging activities of mayflies are primarily diurnal (Allan et al. 1986) and primarily nocturnal (Culp et al. 1991, Peckarsky 1996). Likewise, we know little of diurnal variation in rates and direction of crawling movement, or of distances that benthic invertebrates can disperse in short periods of time.

The purpose of this study was to determine if the dispersal rate and dispersal mode of stream invertebrates are influenced by local water velocity and light level. Using a series of experimental channels, we examined the upstream and downstream movements of two mayflies whose grazing herbivorous larvae are common in streams of coastal British Columbia. Larval *Baetis* are typically found in fast-flowing riffle habitats whereas *Ameletus* larvae are found in slower pool and run habitats. We hypothesised that (i) the dispersal rates of these mobile invertebrates would be correlated with habitat preference, and both drift

and benthic crawling movements would be greatest in water velocities that least match the habitat preferences of each mayfly (i.e. for *Baetis*, movement in slow flows > movement in fast flows, while for *Ameletus*, movement in slow flows < movement in fast flows). Assuming that drift is a riskier mode of dispersal during the day than during the night when drift-feeding fish are present (Flecker 1992), we further hypothesised that (ii) rates of drift would be greater in the dark than in daylight conditions for all water velocities. While potentially less risky than drifting, actively crawling over the substratum during the day still entails considerable risk from benthic-feeding fishes, and the activity patterns of many invertebrates from streams where fish are present are strongly nocturnal (Culp et al. 1991). As such, we also hypothesised that (iii) the distances that mayflies dispersed upstream by crawling during the day would be less than distances dispersed upstream in the dark. Downstream crawling dispersal was not examined explicitly in this study, as it is difficult to separate the relative contributions of downstream crawling and short drift movements to creating downstream movement distributions. In order to assess potential heterogeneity in individual-level movement behaviours (see Skalski and Gilliam 2000), we also examined the degree to which measured dispersal distributions exhibited leptokurtosis (higher central peak and larger tails than a normal distribution).

## Methods

The effects of light level and water velocity on the benthic movements and downstream drift of the mayflies *Baetis* and *Ameletus* were examined in a series of artificial flow-through stream channels using a 2 × 4 (light level × water



velocity) experimental design. The stream channels used were located adjacent to Mayfly Creek, a third order, high-gradient mountain stream in the Malcolm Knapp Research Forest near Maple Ridge, British Columbia. Based on preserved subsamples of the larvae used, *Ameletus* larvae used were primarily *A. validus* McDunnough, while the *Baetis* larvae were primarily *B. tricaudatus* Dodds.

The channels were constructed from white plastic rain gutters (approximately 10 cm wide and 8 cm deep), and were 3.0 meters long. Four channels were used, and the channel bottoms were lined with coarse gravel (average grain diameter = 3.7 cm, SD = 0.9 cm). Water supplied to the channels was diverted from Mayfly Creek through an intake structure, settling tank, head tank, and manifold (see Kiffney and Richardson 2001 for a description of the Mayfly Creek diversion structure and experimental channels). Trials were conducted in autumn 2004 (September 25 to October 30) and autumn 2005 (October 16 to October 30).

### **Collection and release of mayfly larvae**

Mayfly larvae were collected from Mayfly Creek by carefully hand-disturbing the streambed substratum upstream of a dipnet. All material collected in the net was placed in a white tray, and individual *Ameletus* and *Baetis* larvae were transferred into holding jars using a large pipette. The collected mayflies were released into a series of experimental channels, each with one of four velocity ranges; 5 – 15, 15 – 25, 25 – 35, and 35 – 60 cm/s. In order to minimise disturbance, mayflies were transferred into the channels within 30 minutes of

collection. In each velocity range, mayfly release trials were replicated four times in two light conditions; 'light', where light conditions were daytime ambient (generally sunny to partially overcast), and 'dark', where the channels were covered with a large black tarpaulin (light levels underneath were reduced to virtually zero). The dark treatment simulated nighttime light conditions, and allowed us to examine how the movements of stream insects are modified by light level without the influence of confounding factors such as diurnal changes in water temperature.

In each trial, 30 mayflies (15 larvae of each of the two taxa) were transferred into a 20 cm long centrally-located section of a 3.0 m-long channel (i.e. 1.4 – 1.6 m downstream from the channel inlet). Larvae were prevented from immediately dispersing beyond this central section of the channel by mesh barriers (500  $\mu$ m nylon mesh). After an acclimatization period of approximately 45 minutes, the barriers were removed allowing mayflies to disperse both upstream (into the section of channel 0 – 1.4 m downstream from the inlet) and downstream (into the section of channel 1.6 – 3.0 m downstream from the inlet). Attempts were made to remove all larvae clinging to the mesh of downstream barriers as they were removed; however, complete removal was difficult as some larvae tended to release into the drift as the barrier was lifted from the channel. After the barriers were removed, larvae were allowed to disperse for three hours. A net placed at the end of each channel caught all larvae drifting out of the channels during the three hour dispersal period. At the end of this time, 500  $\mu$ m mesh barriers were placed in the channel at 20 cm intervals. The gravel from

each 20 cm section was removed piece-by-piece and cleaned with a jet of water, allowing the invertebrates contained in that section to be collected, identified to genus, and enumerated.

All mayflies used were 3 – 7 mm in length (total body length, excluding cerci). *Ameletus* and *Baetis* were selected as the study organisms for two reasons. First, larvae of these two taxa have markedly different habitat preferences; *Ameletus* is a grazer generally found in low velocity stream habitats such as pools and runs, while *Baetis* is a grazer with a noted preference for high velocity riffle habitats (see Rader 1997, Rosenfeld 2000). Second, both taxa have distinct morphological and behavioural attributes that allow them to be quickly and accurately identified in the field while alive, a necessary feature for field observations of behaviour. Live *Ameletus* larvae have distinct light/dark banding on the abdomen (a feature lost in preserved specimens), and swim in a linear fashion with very rapid vertical oscillations of their abdomen. *Baetis* larvae have uniformly-coloured abdomens with two terminal cerci and, after swimming, sink holding the end of their abdomen flexed forward over the anterior portion of their abdomen and thorax.

### **Data analysis**

The numbers of invertebrate larvae recovered from each channel section and channel-end drift nets were used in two types of analyses to provide information on different aspects of invertebrate movement in the experimental channels. In the first set of analyses, distributions of larvae upstream of (and including) the release point were used to calculate upstream dispersal curves

and dispersal coefficients; this type of analysis provides information on upstream dispersal distances and the rates of upstream movement. This analysis does not, however, provide any insight into downstream movement by crawling or drifting. In the second set of analyses, statistical comparisons of the mean dispersal parameters of each treatment (i.e. proportion of larvae moving upstream, proportion of larvae not dispersing away from the point of release, proportion of larvae drifting from the channel, mean benthic dispersal distance, and mean upstream dispersal distance) provide information on differences in upstream, downstream, and drifting dispersal among the experimental treatments for the two mayfly taxa.

To calculate the dispersal curves and coefficients, the numbers of larvae collected in and upstream of the central 'release' section (i.e. 0 – 1.6 m) were fit to the exponential decay model

$$D = ae^{-bL}$$

where  $D$  is the proportion of larvae dispersing distance  $L$  (where  $L$  is the midpoint of each 20 cm section of the channel),  $a$  is the y-intercept (i.e. the proportion of larvae not dispersing), and  $b$  is the dispersal coefficient. Large values of  $b$  indicate a rapid decline in the number of dispersing individuals with distance, and hence a low rate of net movement. To increase the precision of the estimate of  $b$  for each treatment, mean values of  $D$  (an average of the larvae travelling distance  $L$  in the four replicates) were used. Paired t-tests were subsequently used to determine if the dispersal coefficients, and hence upstream dispersal,

differed between light and dark treatments for *Ameletus* and *Baetis* across all velocity ranges.

For each trial, the numbers of larvae collected at each distance were also used to calculate five mean dispersal parameters. These dispersal parameters included the proportion of larvae moving upstream (total larvae collected from channel sections 0 – 1.4 m / all larvae in the channel at the beginning of the dispersal period), and the proportion of larvae not dispersing away from the point of release (total larvae collected from channel section 1.4 – 1.6 m / all larvae in the channel at the beginning of the dispersal period). The numbers of larvae collected from drift nets during the three-hour dispersal period were used to determine the proportion of insects drifting from the channel (= total insects in the drift net at the end of the dispersal period / total insects in the channel at the beginning of the dispersal period). The mean net distance travelled by all larvae recovered from the channel as well as the mean net distance travelled by larvae not dispersing downstream (i.e. the mean net distance travelled by the larvae recovered upstream of and from the release section) were also calculated. A 2 × 4 analysis of variance (ANOVA) was performed on each dispersal parameter. Predictor variables consisted of two light levels (ambient daytime and dark) and the four water velocity ranges. Interactions were tested, but were not significant in all cases, and so were not reported. All data were examined for non-normality, and analyses were conducted on transformed data where appropriate. All proportions (e.g. proportion of animals drifting) were arcsine-square root transformed. Analyses were performed in Systat v.10 (Systat 2000).

## Results

The percentage of larvae recovered ranged from 85% to 100%, with all animals being recovered in the majority of the trials.

### Upstream dispersal movements

The relationship between distance upstream and the proportion of insects travelling that distance was generally well described by the exponential decay model  $D = ae^{-bL}$  ( $r^2$  values ranging from 0.741 to 0.999). Values of the dispersal coefficient  $b$  varied substantially between species and light conditions, and among velocities (Table 2-1), indicating that patterns of upstream dispersal varied among treatments.

Comparisons of the dispersal coefficient  $b$  indicate that while *Ameletus* larvae consistently moved upstream more in dark than light conditions, *Baetis* larvae did not show a consistent response related to light level. For *Ameletus* larvae,  $b$  was significantly greater in light than dark conditions across all velocity treatments (paired t-test,  $t = 4.31$ ,  $df = 3$ ,  $p = 0.023$ ). However,  $b$  did not differ between light and dark conditions for *Baetis* larvae (paired t-test,  $t = -1.04$ ,  $p = 0.38$ ). The dispersal curves (Fig. 2-1) show that the upstream movement patterns of *Ameletus* and *Baetis* were similar in full-light conditions across all velocities. However, in dark conditions *Ameletus* larvae showed greater upstream movement in high velocities than did *Baetis* larvae.

In full-light conditions, the dispersal curves show there was a slight increase in the upstream movement of *Ameletus* larvae as water velocity increased (Fig. 2-1). This general pattern is also seen in the dispersal coefficient

$b$  (Table 2-1);  $b$  decreased from 10.24 (5 – 15 cm/s) to 7.12 (35 – 60 cm/s), indicating an increase in upstream movement. In dark conditions, *Ameletus* larvae demonstrated a broad upstream movement at the lowest velocity (5 – 15 cm/s) (Fig. 2-1). The relatively poor fits of the upstream movements of *Ameletus* larvae at higher velocities to the exponential decay model (see Table 2-1) are due to upstream peaks in the proportion of larvae dispersing. These upstream peaks are located at 0.2 m in the highest velocity (35 – 60 cm/s), 0.4 m in the second-highest velocity (25 – 35 cm/s), and 0.6 m in the second-lowest velocity (15 – 25 cm/s). This indicates that while a substantial proportion of the *Ameletus* larvae released travelled upstream at all velocities in the dark, the distance they travelled decreased as water velocity increased.

In full-light conditions, the patterns of upstream movement of *Baetis* larvae were similar in all velocities (Fig. 2-1). This lack of a relationship between upstream movement and velocity can also be seen in the dispersal coefficients (Table 2-1). The dispersal coefficients did not vary systematically with velocity, and ranged from 5.19 (25 – 35 cm/s) to 8.14 (5 – 15 cm/s). In dark conditions at the lowest velocity (5 – 15 cm/s), the upstream dispersal of *Baetis* larvae was likely greater than indicated by the dispersal coefficient  $b$  for that treatment ( $b = 7.93$ ). The relatively poor fit ( $r^2 = 0.85$ ) of the upstream movement data to the exponential decay model was due to the accumulation of larvae at the upstream end of the channel (see Fig. 2-1; *Baetis* / dark / 5 – 15 cm/s). In three hours, substantial numbers of *Baetis* larvae dispersed 1.5 m from the centre to the upstream end of the channel, indicating that the movement rates of some larvae

exceeded 0.5 m/h. However, the presence of both upstream and channel-centre (i.e. release point) peaks in the distribution indicates that only a limited subset of the larvae dispersed rapidly upstream, while a substantial proportion of the released larvae did not disperse. The patterns of upstream dispersal in the remaining three velocity treatments (15 – 25, 25 – 35, and 35 – 60 cm/s) suggest that upstream movements decrease with velocity, although this trend is not clear (see Table 2-1).

### **Differences in movement modes between light conditions**

While comparisons of the dispersal curves and dispersal coefficients provide information on the patterns of upstream movement, statistical comparison of specific indices of movement (e.g. mean distance travelled, proportion drifting) indicated that light conditions strongly modified not only the upstream movement of both *Ameletus* and *Baetis* larvae, but also influenced the downstream drift of these taxa as well.

*Ameletus* larvae were more mobile in dark than full-light conditions (Table 2-2). Significantly more larvae drifted out of the channels during the experiment in dark than light conditions ( $p = 0.005$ ) (Fig. 2-2). The benthic movements of *Ameletus* larvae were also more pronounced in the dark. In the dark, larvae that dispersed in the upstream direction travelled significantly further ( $p = 0.019$ ) (Fig. 2-3), and more larvae dispersed away from the point of release ( $p = 0.005$ ) compared to the light conditions. A greater proportion of the larvae moved upstream in the dark than in the light, although the difference was not significant ( $p = 0.069$ ).



Average larval displacement did not differ between light and dark conditions ( $p = 0.71$ ) (Fig. 2-4), indicating that dispersal increased equally in both upstream and downstream directions. This suggests that *Ameletus* did not shift from crawling dispersal to downstream drifting as conditions changed from light to dark.

Significantly more *Baetis* larvae drifted in the dark than in full light conditions ( $p = 0.004$ ) (Fig. 2-2), similar to the pattern observed for *Ameletus* larvae. Differences in the benthic movements of *Baetis* larvae between light and dark conditions were not as pronounced as *Ameletus*, however. There was no difference in the proportion of larvae moving upstream in the two light conditions ( $p = 0.37$ ), and while there was a trend that larvae that dispersed upstream moved further in the dark than the light (Fig. 2-3), the difference was not significant ( $p = 0.11$ ). However, average larval displacement was significantly further downstream in dark than light conditions ( $p = 0.023$ ) (Fig. 2-4). This suggests that *Baetis* may shift from crawling dispersal to drifting dispersal as light conditions change from light to dark. In addition, significantly more larvae dispersed away from the point of release in dark conditions than in the light ( $p = 0.002$ ).

Excluding those animals that drifted from the channels, the net displacement of released *Ameletus* larvae was generally in the downstream direction, whereas the net displacement of *Baetis* larvae was generally upstream in daylight conditions and downstream in dark conditions (Table 2-3).

## The role of water velocity in movement

Water velocity also influenced the movement of *Ameletus* and *Baetis* larvae, although neither mayfly taxon responded as strongly to changes in flow as they did to variation in light level.

Significantly more *Ameletus* larvae drifted out the channels as velocity increased ( $p = 0.023$ ). However, the response was not linear but rather exhibited a u-shaped relationship (Fig. 2-2), with the lowest proportion drifting at 15-25 cm/s, and the greatest number drifting at high velocities (35-60 cm/s). At the highest velocity (35 – 60 cm/s) similar proportions of larvae drifted out of the channels in light and dark conditions. As water velocity increased, the average displacement of *Ameletus* larvae increased in the downstream direction ( $p = 0.011$ ) (Fig. 2-4). Although similar, the relationship was not identical for light and dark conditions. At low velocities *Ameletus* larvae appeared to move upstream to a greater extent, but moved further downstream at the highest velocity. This is likely due to velocity-related differences in the pattern of upstream movement between light and dark conditions (see Fig. 2-1, Fig. 2-3). However, movements related only to benthic movement were not strongly related to velocity alone, including the proportion of larvae moving upstream ( $p = 0.49$ ), the mean distance larvae dispersed upstream ( $p = 0.51$ ; Fig. 2-3), and the proportion of larvae not dispersing ( $p = 0.58$ ).

The movements of *Baetis* larvae were only weakly related to water velocity. The proportion of *Baetis* larvae that drifted out the channels did not increase with velocity alone ( $p = 0.67$ ). However, more *Baetis* larvae drifted from

the channels at the lowest velocity (5 – 15 cm/s) than at intermediate velocities (Fig. 2-2). As water velocity increased, the average displacement of *Baetis* larvae increased in the downstream direction ( $p = 0.037$ ) (Fig. 2-4). Unlike *Ameletus*, however, the pattern differed substantially between light and dark conditions, with the downstream movement of *Baetis* increasing more rapidly with velocity in dark conditions. All measurements of benthic movements were not strongly related to velocity alone, including the proportion of larvae moving upstream ( $p = 0.49$ ), the mean distance larvae dispersed upstream ( $p = 0.51$ ) (Fig. 2-3), and the proportion of larvae not dispersing ( $p = 0.58$ ).

### **Kurtosis of movement distributions**

All cases had sample sizes  $> 20$ , allowing for significance testing (kurtosis different than zero). For both *Ameletus* and *Baetis*, movement distributions were generally significantly leptokurtotic in light conditions (Table 2-4). The only exception was the *Baetis* / Light / 25-35 cm/s treatment. In contrast, the movement distributions of *Ameletus* and *Baetis* in dark conditions were much less peaked, and were significantly leptokurtotic only in the high velocity treatment (35 – 50 cm/s, both taxa), and the *Ameletus* / Dark / 15-25 cm/s treatment (Table 2-4). Leptokurtosis in these distributions suggests a substantial degree of population-level heterogeneity in movement-related behaviours.

### **Discussion**

Determining how organisms move and are continually redistributed across a landscape requires a mechanistic understanding of how temporal and spatial

variation in key environmental factors can modify movement-related behaviours. Our study shows that for the stream mayflies *Ameletus* and *Baetis*, the patterns of upstream and downstream movement produced by crawling and drifting are not only taxon-specific, but are also sensitive to both light level and water velocity, factors known to mediate the costs and risks associated with the occupancy of streambed habitat patches (e.g. Kohler and McPeck 1989, Hart and Merz 1998). As expected, movements of the riffle-dwelling mayfly *Baetis* and the pool/run mayfly *Ameletus* were generally greater in dark conditions than in full-light conditions. However, the responses of both mayflies to variation in water velocity, a physical factor of broad ecological importance, were unexpectedly complex and not entirely consistent with the hypothesis that dispersal rates are inversely correlated with habitat preferences.

### **Upstream dispersal**

Accurate measurements of upstream dispersal rates are crucial to understanding within-stream population processes of benthic invertebrates. However, while several studies have examined the downstream dispersal rates of drifting invertebrates (e.g. Elliott 1971a, Townsend and Hildrew 1976), relatively few have measured rates of upstream movement. In this study, both *Ameletus* and *Baetis* demonstrated the capacity for rapid upstream dispersal by crawling. Especially in dark conditions in low flows, individuals of both taxa moved upstream at rates as high as 0.50 m/h (median upstream movement rates were approximately 0.13 and 0.33 m/h for *Ameletus* and *Baetis*, respectively). In a small stony English stream, Elliott (2003) found that the maximum upstream

dispersal rates of three mayflies, *Baetis rhodani*, *Ecdyonurus venosus*, and *Rhithrogena semicolorata*, were very similar, ranging from 0.23 m/h (median 0.043 m/h) for *B. rhodani* to 0.33 m/h (median 0.054 m/h) for *R. semicolorata*. The movement rates of the mayflies in this study are notably higher. This may have been due to low food availability, or other indicator of low habitat quality, in the experimental channels. When periphyton density, and thus food availability, was low, Kohler (1984) showed that the movement of *Baetis tricaudatus* was approximately five times faster between food patches than within food patches. Other factors, such as ontogenetic stage, may have also contributed to the relatively rapid upstream crawling rate. For example, immediately prior to emerging as an adult, the mayfly *Leptophlebia cupida* moved upstream at a rate of up to 10 m/h (Hayden and Clifford 1974).

In this study, the upstream crawling dispersal rates of larvae were dependent on both light level and water velocity; however, the responses of the two mayfly taxa were complex. At the lowest velocity, the upstream movements of both mayflies were notably higher in dark than in light conditions; at higher velocities, differences in upstream movement rates between light and dark conditions were not as pronounced. While this would appear to suggest that light and water velocity influenced the crawling movements of *Ameletus* and *Baetis* in a similar fashion, examination of the dispersal curves showed that the two taxa were responding differently to these two factors. At the lowest velocity, both taxa showed little upstream dispersal in full-light conditions. In the dark, however, the upstream dispersal distribution of *Ameletus* larvae was unimodal with a broad,

central peak, suggesting that released larvae exhibited rapid, diffusive movements. At higher velocities, upstream modal peaks were apparent in the movement distributions of *Ameletus*. The position of the modal peak approached the origin as velocity increased, suggesting that the movement rate of an upstream-dispersing subpopulation may have been constrained in some manner by hydrodynamic forces (see Olden et al. 2004). In contrast, the upstream dispersal distribution of *Baetis* was bimodal in the lowest flow conditions, with both central and far-upstream peaks, indicating the existence of two subpopulations, one exhibiting little or no movement and another dispersing rapidly upstream by crawling. At the lowest flow, upstream crawling movements of both mayflies were more extensive in the dark than in the light. Nocturnal crawling movements may minimise the risk of predation by benthic-feeding fishes (Cowan and Peckarsky 1994) or may reduce exposure of surface-crawling larvae to harmful ultra-violet radiation (Donahue and Schindler 1998).

### **Drift dispersal**

Generally, more larvae drifted from the channels in dark than in light conditions, especially at low velocities. Many stream invertebrates demonstrate nocturnal peaks in rates of drift entry (e.g. Corkum et al. 1977, Flecker 1992). Several factors have been associated with these peaks in invertebrate drift rate, including escape behaviours to avoid predation by benthic-feeding fishes (Culp et al. 1991), behavioural responses that act to minimise the risk of daytime predation by visually-oriented drift-feeding fishes (e.g. Miyasaka and Nakano 2001, McIntosh et al. 2002), and avoidance of predation by benthic invertebrate

predators (Wooster and Sih 1995). Neither invertebrate nor vertebrate predators were present in the channels, and thus direct interactions with predators could not have produced different drift rates between light and dark conditions. However, the water used in the experimental channels was drawn from a stream reach that supported a resident population of cutthroat trout (*Oncorhynchus clarki*), and chemical cues released by drift-feeding fish predators can induce nocturnal drift in mayfly larvae (McIntosh et al. 2002).

The drift movements of both *Ameletus* and *Baetis* larvae were sensitive to water velocity in the channels. In the dark, when movement rates were greatest, the drift rates of both mayflies exhibited a distinctly 'u-shaped' relationship with water velocity. The 'u-shaped' relationship between drift rate and velocity observed here for both mayflies differs from the relatively linear pattern observed in other studies. For example, Corkum et al. (1977) found that in dark conditions drift of *Baetis vagans* declined with velocity over the range of current speeds examined in this study. Corkum et al. (1977) reported that at 10 cm/s approximately 90% of the larvae drifted in 5 hours, while at 50 cm/s less than 20% drifted over the same period, indicating a high rate of emigration from low-flow habitat patches. Rapid emigration of *Baetis* larvae from streambed patches has been noted in other studies. Richards and Minshall (1988) found that most of the *Baetis bicaudatus* larvae arriving to high-food patches in streams arrived via the drift, and speculated that rates of emigration must be very high to maintain observed densities. In dark conditions, we found that nearly 40% of the *Baetis* larvae emigrated by drifting in three hours from channels with low current

velocities. As low water velocities reduce the distances drifted by stream invertebrates (Elliott 2002), the elevated drift rate of both *Ameletus* and *Baetis* at the lowest water velocity suggests that larvae may have entered the drift repeatedly before emigrating from the channels.

It is also interesting to note that the daytime drift rates of both mayflies were greatest at the highest water velocity used in this study. Although it is difficult to infer from this study why daytime drift rates increased with velocity, there are several possible explanations. For instance, drifting in high-velocity habitats may be less risky than drifting in low-velocity habitats, as the proportion of detected prey that are captured by drift-feeding fish declines with velocity (see Hughes and Dill 1990). High water velocities may also increase the probability of accidental dislodgement from the substrate during crawling or foraging movements, although accidental entrainment of *Baetis* larvae in high-velocity microhabitats is presumably limited. Kohler (1985) demonstrated that in current speed of 30 cm/s, the entry of *Baetis* larvae into the drift was primarily under behavioural control. Several studies have reported that the dramatic increases in current velocity during spates are accompanied by increased drift rates (e.g. Anderson and Lehmkuhl 1968), but it is unclear if this is the result of increased drift distance, increased entry into the drift as a result of behavioural shifts that occur, or increased accidental entry as a result of scouring from the bed (Brittain and Eikeland 1988, Lancaster et al. 1996).



## Upstream-downstream biases in movement

The potential for landscape-scale shifts in the distribution of benthic invertebrate populations in streams can be inferred from directional biases in the drift and crawling movements of larvae. When larvae that drifted from the channels were excluded, our analyses showed that the movements of mayfly larvae in this study were not consistently biased in either upstream or downstream directions. Whereas the benthic movements of *Ameletus* appeared to be generally biased in the downstream direction, the movements of *Baetis* were condition-dependent and were biased downstream in the dark and upstream in the light, with the exception of the highest velocity where more individuals moved downstream than upstream. Bergey and Ward (1989) showed that both drift and substrate-associated movements strongly biased the displacement of several mayflies, including *Baetis tricaudatus*, in the downstream direction in both daylight and dark conditions. These trends contradict the results of Elliott (1971b), who found that the crawling movements of stream insects were biased in the upstream direction, and were greater near banks where water velocities were slower. While movement patterns of this type suggest that rates of upstream movement may be velocity-dependent, Elliott (2003) found that not only were crawling movements of several mayfly taxa strongly biased in the upstream direction, but water velocity did not influence the rate of movement of benthic invertebrate taxa.

Other studies, however, have established a relationship between water velocity and crawling movements. For example, Poff and Ward (1992) found that

the benthic foraging movements of the caddisfly *Agapetus boulderensis* were slower, more linear, and more upstream-directed in areas of higher water velocity. However, even if crawling movements are biased in the upstream direction, relatively short, within-patch, drift movements have the potential to produce a net downstream displacement of stream invertebrate populations, especially where drift entry rates or water velocities are high. For instance, *Baetis* larvae in the channels were displaced further downstream in dark conditions than in the light, indicating that the nocturnal drift behaviours of this mayfly act to continually redistribute larvae to habitat patches downstream. In contrast, while it increased with water velocity, the net downstream displacement of *Ameletus* larvae was similar in light and dark conditions. Compared to *Baetis*, *Ameletus* is not as drift-prone, and nocturnal increases in drift appear to be balanced by nocturnal increases in upstream crawling movements.

The higher drift rates and downstream biases in benthic movement in dark conditions indicate that connectivity between upstream and downstream patches is asymmetrical. Asymmetrical connectivity is a property of patch networks where a directionality is superimposed on movements by physical forces such as wind (Schooley and Wiens 2003) or water currents (Hoffman et al. 2006). In this study, the degree of asymmetry is dependent on the behavioural responses of organisms to environmental factors. During daylight hours when the movement of *Baetis* is not strongly biased downstream, the connectivity between upstream and downstream patches may be relatively symmetrical. However, during the night, when drift movements contribute more substantially to the movement of

mayfly larvae, upstream-downstream asymmetry will become more pronounced. However, streambed landscapes are a mosaic of high- and low-velocity patches at nested hierarchical spatial scales (Wiens 2002), and our results indicate that directional biases in movement are also dependent on local flow conditions. Before a landscape-scale approach can be used to model population processes, a mechanistic understanding of the behavioural bases of animal movement is required to understand how spatial heterogeneity in abiotic factors can structure between-patch migration rates and patterns of patch occupancy (Fonseca and Hart 2001, Englund and Hambäck 2004).

### **Did movement match habitat preferences?**

The drift rates of larval *Ameletus* and *Baetis* generally supported a hypothesis of habitat-specific movement, indicating that rates of movement are greatest in those patches whose physical characteristics least well match an organism's habitat preferences. In dark conditions, where mayfly larvae were generally most mobile, the proportion of larvae that emigrated from the channels by drifting was lowest in flows that matched the preferred velocity range of each mayfly. Larval *Ameletus* inhabit slow riffle and pool habitats; Rosenfeld (2000) reported high densities of *Ameletus* larvae in Mayfly Creek both in pools and in slow riffles (mean velocities of 4.9 and 16.4 cm/s, respectively). Drifting from patches with high water velocities will allow *Ameletus* larvae to rapidly disperse downstream into more suitable patches with lower water velocity, where low shear stresses might enhance settlement (Lancaster et al. 1996). In dark conditions, *Baetis* emigrated at the highest rate from channels with the lowest

water velocity. *Baetis* larvae show distinct preferences for high-velocity riffle habitats (Negishi and Richardson 2003). Emigrating from low-flow patches by drifting will allow for the rapid movement of *Baetis* larvae to high-flow reaches downstream. However, successful settlement in high-velocity streambed patches also requires specialised swimming or settlement behaviours that allow individuals to reach the bed in high-flow microhabitats (see Otto and Sjöström 1986, Lancaster 1999, Fingerut et al. 2006).

It is important to note that *Ameletus* drift rates were elevated at the lowest velocity range tested, especially if emigration rate is a sensitive indicator of habitat value (Fonseca and Hart 2001). It is possible that, although mean flow rates were in accord with the observed habitat preferences of this mayfly, other aspects of the hydraulic microhabitat may have been unsuitable. For example, flows within the coarse gravel substrate used may have been much slower than the mean velocities recorded above the surface of the gravels (Nowell and Jumars 1984), creating flow conditions slower than those preferred by *Ameletus*.

Habitat-dependent emigration rates have also been recorded in other stream invertebrates. Corkum et al. (1977) found that the drift rates of mayfly larvae were related to their habitat preferences in both light and dark conditions; drift of the rheophilic mayfly *Baetis vagans* decreased with velocity, whereas drift rates of the pool mayfly *Paraleptophlebia mollis* increased with velocity. Similarly, blackfly (*Simulium vittatum*) larvae, filter-feeders whose preference for high-velocity microhabitats allow them to maximise food intake and minimise the threat of predation (e.g. Hart and Merz 1998), have been shown to readily

emigrate from slow flow areas by drifting (Fonseca and Hart 1996). However, rapid movement rates are not always associated with emigration from unsuitable habitat patches. Hoffman et al. (2006) showed that the movement rate of the grazing caddisfly *Agapetus boulderensis* was greater in low-flow habitats than in higher flows, although low-velocity habitats supported higher densities of larvae. However, *A. boulderensis* constructs a case, and the movement of this caddisfly may be impeded in higher flows. For the two mayflies examined in this study, rates of crawling dispersal did not seem as strongly linked to their habitat preferences as were drift rates, although rates of upstream dispersal were elevated in low-flow conditions in the dark for both mayfly taxa. This suggests that for mobile stream invertebrates, drift movements are used for rapid movement between patches, while crawling may be more important as a within-patch search mode.

Although considerably variable, the upstream and downstream movement rates of larvae in different current velocities indicates that despite the inherent physical heterogeneity of these systems, streambed landscapes are permeable to the movement of stream insects. While substantial proportions of the released larvae moved very little, many larvae were able to disperse either upstream or downstream at all flow velocities. The potential for rapid dispersal across the streambed in all velocities by two movement modes (crawling and drifting) suggests that the distribution of mobile organisms such as mayfly larvae is not likely to be as constrained by colonisation history as are less mobile stream invertebrates such as blackfly larvae (see Fonseca and Hart 2001). Empirical

(Lancaster et al. 1996) and modelling (Bond et al. 2000) studies have suggested that the distribution of water velocity is an important control of patch immigration processes in stream landscapes, especially where drifting invertebrates are dependent on low-flow areas to settle. Our results show that by influencing rates of behavioural entry into the drift, water velocity can also affect rates of emigration from patches. Many studies suggest that drift supplies more colonists to habitat patches than does crawling (e.g. Townsend and Hildrew 1976), but where rates of emigration by drift are low, crawling may play a disproportionately important role in determining the flux of individuals between habitat patches. For example, crawling may be a key mode of immigration to microhabitat patches where very high current velocities hinder settlement from the drift.

The post-dispersal distributions of upstream-dispersing mayfly larvae in the channels were generally leptokurtotic, especially in full-light conditions. Leptokurtotic movement distributions have been recorded in several studies of mobile organisms such as stream fish (e.g. Fraser et al. 2001) and terrestrial invertebrates (e.g. Morales 2002). Leptokurtotic distributions can be generated by population heterogeneity in behavioural traits that influence movement. For instance, Fraser et al. (2001) showed that distances moved by a Trinidad killifish *Rivulus hartii* were significantly related to boldness, and that heterogeneity in this trait was a primary cause of the leptokurtotic movement distributions recorded for this species in the field. Skalski and Gilliam (2000) hypothesized that a population heterogeneity model, where individuals within a population can exist in either 'fast' or 'slow' movement states, can produce the leptokurtotic

distributions that characterize the movement patterns of many animal populations. Although it is possible that the leptokurtosis evident in the upstream movements of *Ameletus* and *Baetis* is due to heterogeneity in movement mode (crawling vs. swimming), it is unlikely as swimming is used primarily as a means of escape by many lotic invertebrates (e.g. McIntosh and Townsend 1998). Leptokurtosis in upstream movement distributions of stream invertebrates more likely indicates heterogeneity in crawling rate or crawling behaviours. Several other studies have noted substantial variation in crawling rate. For instance, Kohler (1984) found that when it encountered patches of abundant food resources, the movement rate of *Baetis* larvae decreased dramatically, and the turning angle between moves increased. Both of these behavioural shifts would produce lower net displacement in food patches than in the matrix between patches. Similarly, Hart (1981) showed that the caddisfly *Dicosmoecus gilvipes* tended to move in straight lines between patches and moved more slowly when in high-quality patches. If larval movement rates are sensitive to hunger level (see Kohler and McPeck 1989), then variation in a factor such as gut fullness could have acted to create population-level heterogeneity in movement rates.

While several studies have examined the movement patterns of less mobile groups such as caddisfly (e.g. Olden et al. 2004) and blackfly (e.g. Fonseca and Hart 2001) larvae, relatively little is known about the movement of more mobile groups such as mayflies and stoneflies, which are key members of the benthic community in many systems. In order to understand how spatial heterogeneity in streams influences community- and population-level processes,

we need to know more about the landscape-scale constraints on the movement behaviours of stream invertebrates. Although difficult to obtain, organismal-scale records of the paths made by dispersing stream invertebrates would provide a mechanistic understanding of movement; such data could then be used to parameterise random walk or cellular automata models (see Bond et al. 2000). Such advances would allow for the creation of a general theoretical framework that will allow us to assess the role of different movement modes in creating and maintaining patterns of organismal distribution in streams.



**Table 2-1**

Estimates of intercept (a) and dispersal coefficient (b) of upstream dispersal of mayfly larvae based on fits to a negative exponential model ( $D = ae^{-bL}$ , where D is the proportion of larvae released that moved distance L upstream) for two mayfly taxa. Larvae were released in four different current velocities under either light or dark conditions; n = 8 in all cases. Values are means (with 1 SE in parentheses)

	a	b	$r^2_{adj}$	p
<i>Ameletus</i> , Light				
5 – 15 cm/s	0.800 (0.023)	10.24 (1.10)	0.993	<0.0001
15 – 25 cm/s	0.850 (0.015)	10.79 (0.76)	0.997	<0.0001
25 – 35 cm/s	0.702 (0.038)	7.23 (1.07)	0.974	<0.0001
35 – 50 cm/s	0.741 (0.018)	7.12 (0.45)	0.995	<0.0001
<i>Ameletus</i> , Dark				
5 – 15 cm/s	0.345 (0.029)	2.07 (0.31)	0.922	<0.0001
15 – 25 cm/s	0.596 (0.061)	5.72 (1.37)	0.910	0.0001
25 – 35 cm/s	0.588 (0.096)	4.83 (1.07)	0.803	0.0016
35 – 50 cm/s	0.419 (0.081)	2.38 (0.81)	0.741	0.0038
<i>Baetis</i> , Light				
5 – 15 cm/s	0.728 (0.028)	8.14 (0.91)	0.987	<0.0001
15 – 25 cm/s	0.719 (0.018)	7.21 (0.48)	0.994	<0.0001
25 – 35 cm/s	0.659 (0.021)	5.19 (0.36)	0.992	<0.0001
35 – 50 cm/s	0.770 (0.008)	7.30 (0.21)	0.999	<0.0001
<i>Baetis</i> , Dark				
5 – 15 cm/s	0.572 (0.072)	7.93 (2.85)	0.853	0.0007
15 – 25 cm/s	0.618 (0.019)	5.04 (0.35)	0.992	<0.0001
25 – 35 cm/s	0.792 (0.045)	36.32 (165.82)	0.972	<0.0001
35 – 50 cm/s	0.833 (0.015)	11.36 (0.89)	0.997	<0.0001

**Table 2-2**

Results of ANOVA on the effects of lighting condition (light vs. dark) and current velocity on various movement parameters (degrees of freedom are 1,34 for lighting condition, 3,34 for velocity)

	<i>Ameletus</i>				<i>Baetis</i>			
	Light/Dark		Velocity		Light/Dark		Velocity	
	F	p	F	p	F	p	F	p
Mean distance (all)	0.14	0.71	<b>4.59</b>	<b>0.011</b>	<b>5.93</b>	<b>0.023</b>	<b>3.30</b>	<b>0.037</b>
Mean distance upstream	<b>6.35</b>	<b>0.019</b>	0.79	0.51	2.81	0.11	1.75	0.19
Proportion drifting <sup>a</sup>	<b>9.62</b>	<b>0.005</b>	<b>3.83</b>	<b>0.023</b>	<b>10.24</b>	<b>0.004</b>	0.53	0.67
Proportion moving upstream <sup>a</sup>	3.63	0.069	0.83	0.49	0.84	0.37	1.60	0.22
Proportion not dispersing <sup>a</sup>	<b>9.63</b>	<b>0.005</b>	0.66	0.58	<b>12.21</b>	<b>0.002</b>	0.38	0.77

<sup>a</sup> data arcsine(square root) transformed

**Table 2-3**

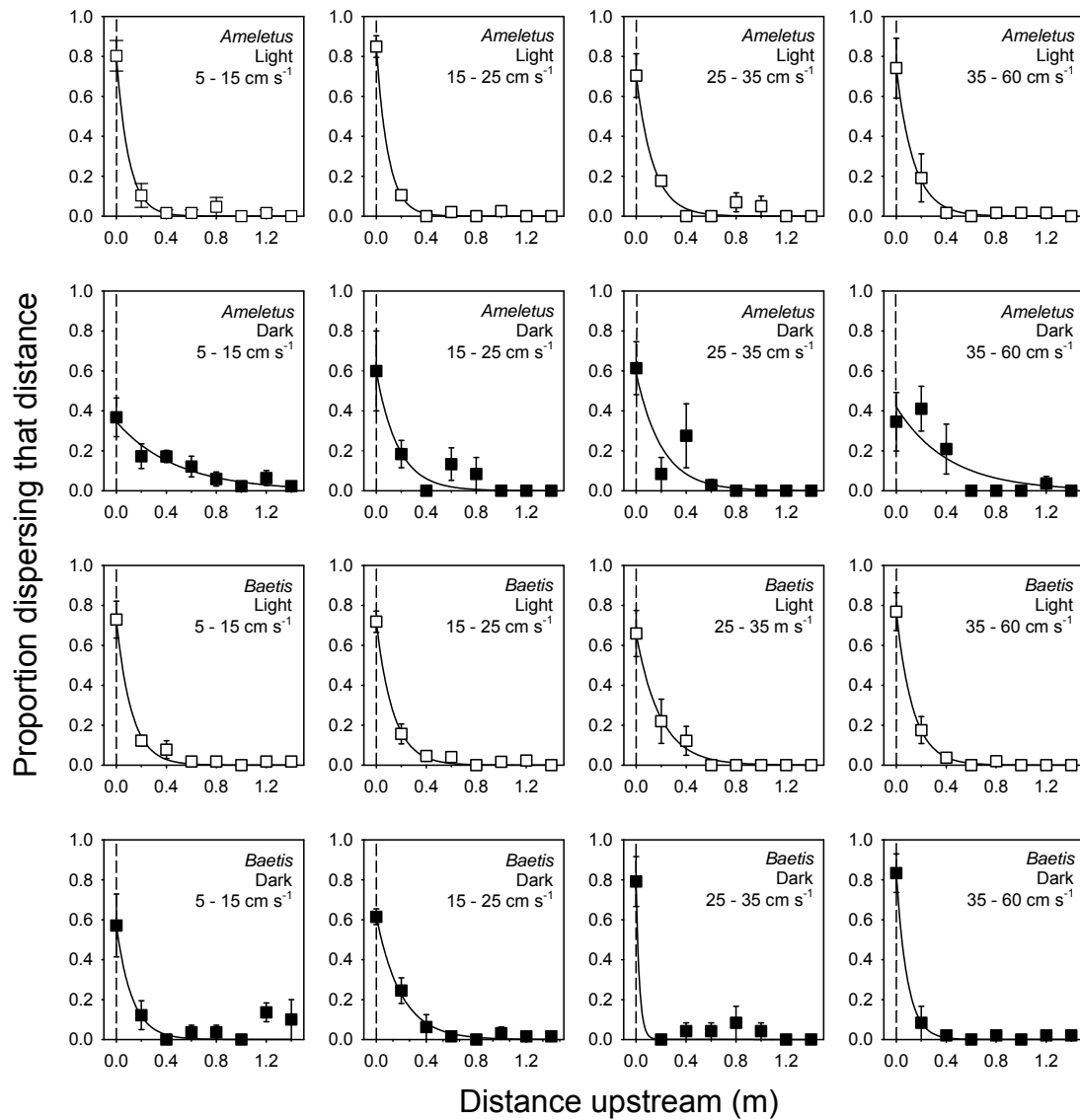
Median distances moved by upstream- and downstream-dispersing mayfly larvae, and the net displacement ( $D_{\text{down-up}}$ ) of mayfly larvae recovered from the channels, where  $D_{\text{down-up}} = (n_{\text{down}} - n_{\text{up}}) / (n_{\text{down}} + n_{\text{up}})$ ; values  $> 0$  indicate net downstream displacement, and values  $< 0$  indicate net upstream displacement (all values exclude animals that drifted from the channels)

	Median up (m)	Median down (m)	$D_{\text{down-up}}$
<i>Ameletus</i> , Light			
5 – 15 cm/s	0.5	0.2	0.17
15 – 25 cm/s	0.2	0.4	0.57
25 – 35 cm/s	0.2	0.6	0.31
35 – 50 cm/s	0.2	0.4	-0.053
<i>Ameletus</i> , Dark			
5 – 15 cm/s	0.4	0.4	-0.14
15 – 25 cm/s	0.2	0.3	0.46
25 – 35 cm/s	0.4	0.4	0.36
35 – 50 cm/s	0.2	0.8	0.45
<i>Baetis</i> , Light			
5 – 15 cm/s	0.4	0.2	-0.043
15 – 25 cm/s	0.2	0.4	-0.037
25 – 35 cm/s	0.2	0.4	-0.053
35 – 50 cm/s	0.2	0.4	0.43
<i>Baetis</i> , Dark			
5 – 15 cm/s	1.0	1.2	0.048
15 – 25 cm/s	0.5	0.6	0.29
25 – 35 cm/s	0.7	0.7	0.71
35 – 50 cm/s	0.8	0.8	0.48

**Table 2-4**

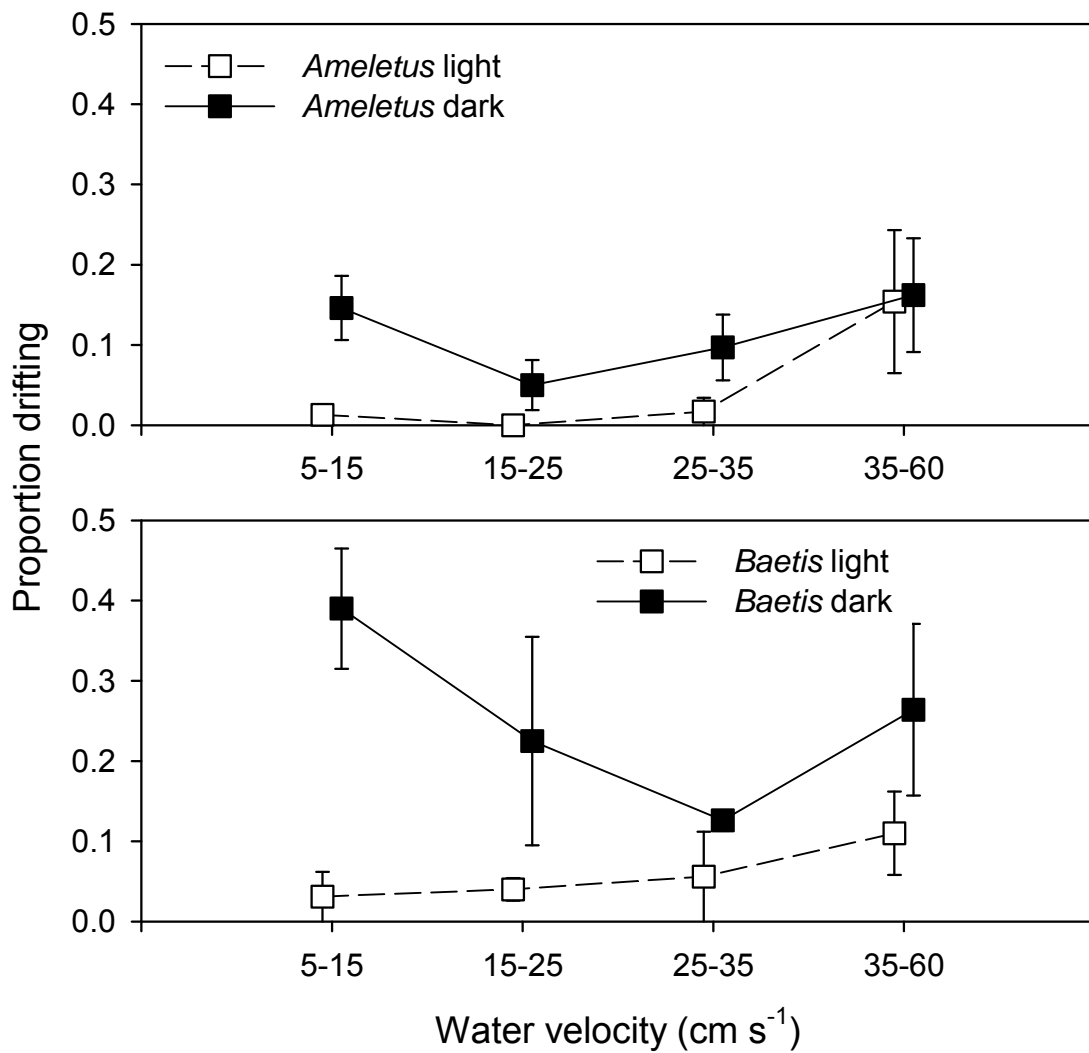
Kurtosis of the upstream movement distributions for each category of lighting condition and water velocity, for both mayfly taxa examined, where  $G2 > 2$  is significantly leptokurtotic.

	N	Kurtosis (G2)	SE	p
<i>Ameletus</i> , Light				
5 – 15 cm/s	55	<b>3.23</b>	0.63	<b>&lt; 0.002</b>
15 – 25 cm/s	50	<b>2.34</b>	0.66	<b>&lt; 0.01</b>
25 – 35 cm/s	50	<b>4.54</b>	0.66	<b>&lt; 0.001</b>
35 – 50 cm/s	33	<b>2.31</b>	0.80	<b>&lt; 0.02</b>
<i>Ameletus</i> , Dark				
5 – 15 cm/s	51	0.22	0.66	> 0.05
15 – 25 cm/s	42	<b>3.06</b>	0.72	<b>&lt; 0.005</b>
25 – 35 cm/s	32	0.24	0.81	> 0.05
35 – 50 cm/s	23	<b>4.57</b>	0.94	<b>&lt; 0.005</b>
<i>Baetis</i> , Light				
5 – 15 cm/s	62	<b>5.37</b>	0.60	<b>&lt; 0.001</b>
15 – 25 cm/s	65	<b>5.12</b>	0.59	<b>&lt; 0.001</b>
25 – 35 cm/s	41	0.30	0.72	> 0.05
35 – 50 cm/s	48	<b>5.00</b>	0.67	<b>&lt; 0.001</b>
<i>Baetis</i> , Dark				
5 – 15 cm/s	30	-0.40	0.83	> 0.05
15 – 25 cm/s	36	1.26	0.77	> 0.05
25 – 35 cm/s	21	1.02	0.97	> 0.05
35 – 50 cm/s	28	<b>2.59</b>	0.86	<b>&lt; 0.02</b>



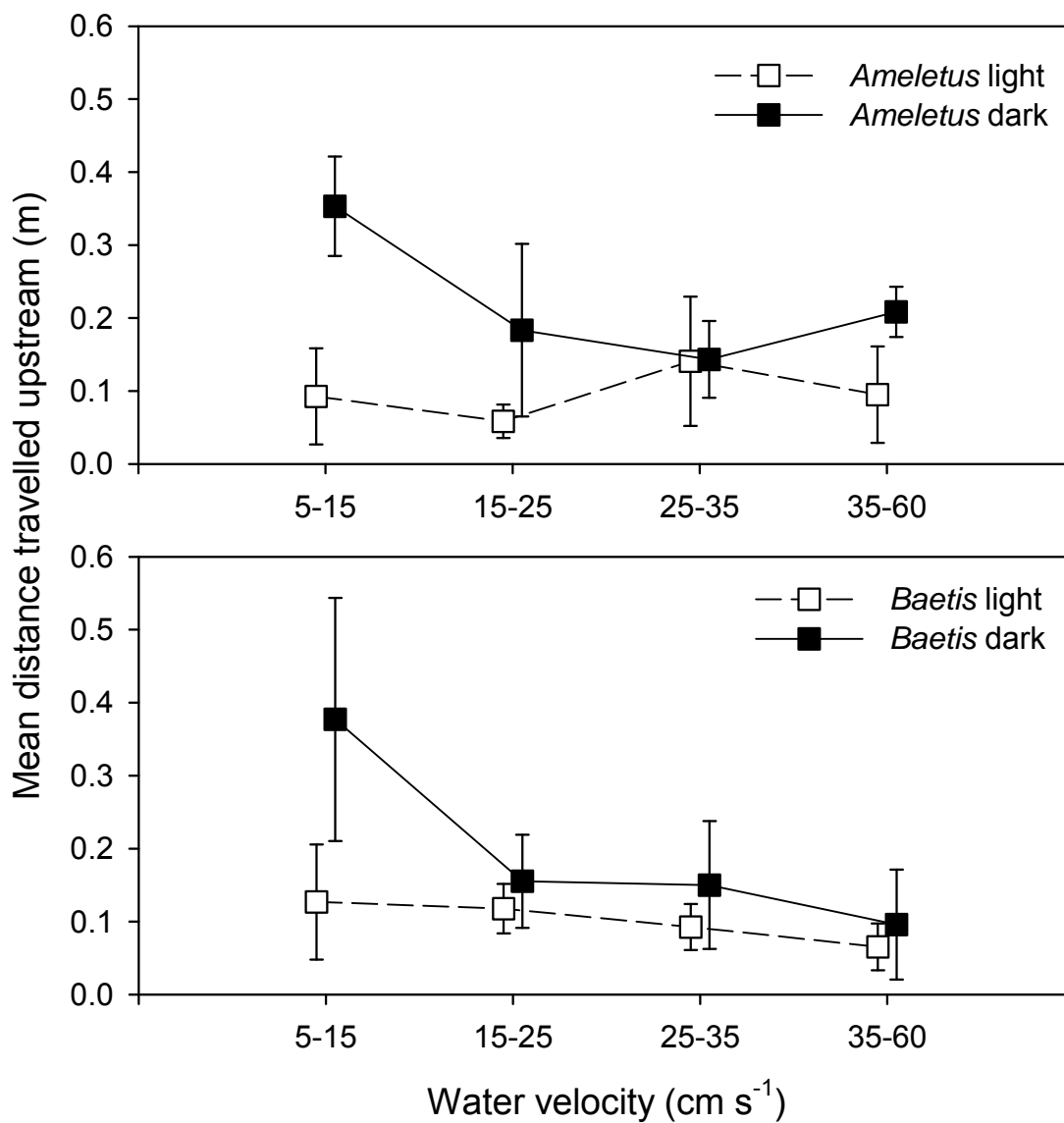
**Figure 2-1**

Upstream dispersal curves for two mayflies, *Ameletus* (upper two rows) and *Baetis* (lower two rows), in daylight (open symbols) and dark (solid symbols) conditions in four different current velocities; velocities increase left to right. Dashed vertical lines indicate the point of release. Error bars = 1 SE.



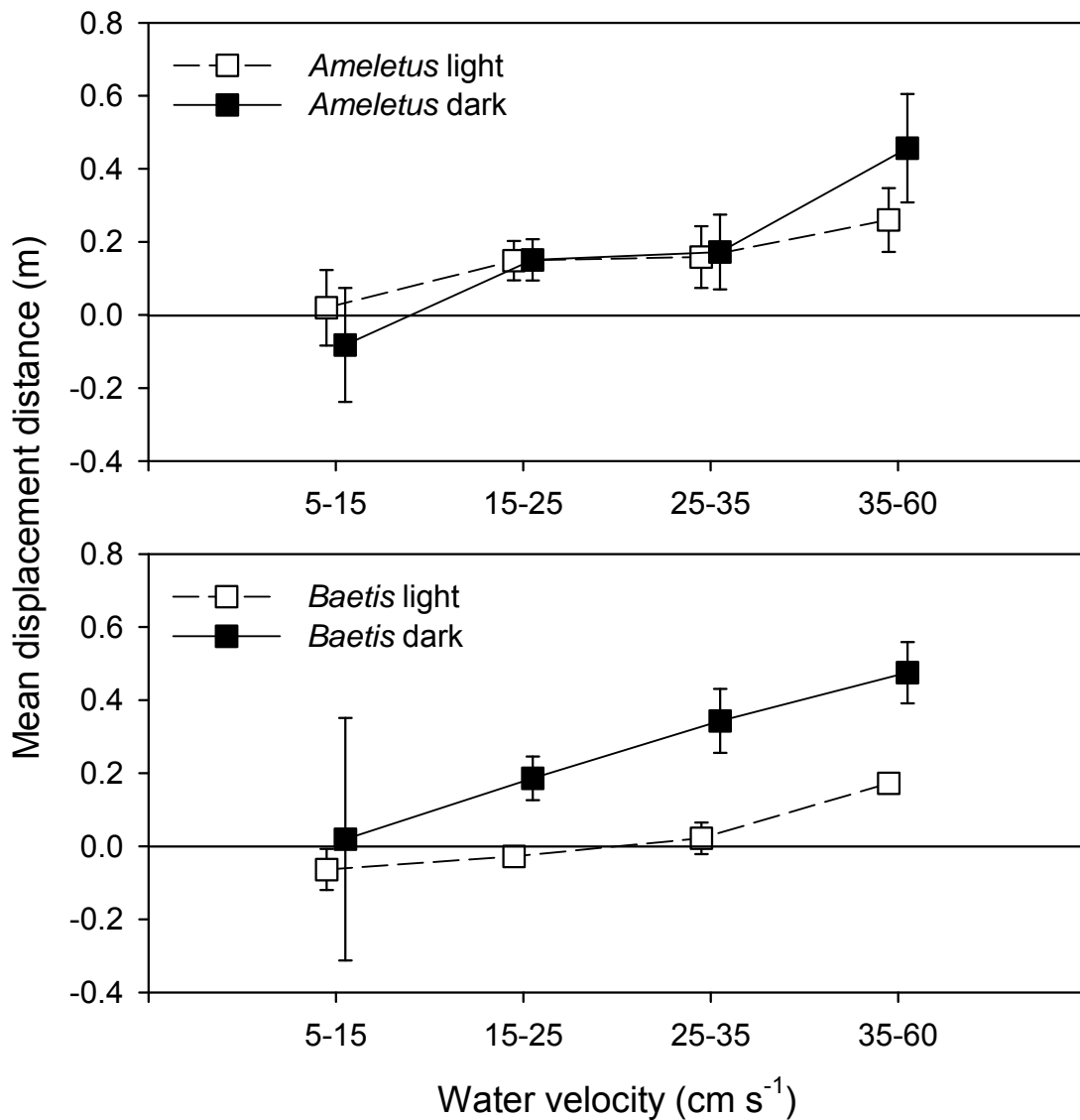
**Figure 2-2**

Drift rates of released *Ameletus* and *Baetis* larvae in daylight (open symbols) and dark (solid symbols) conditions in four current velocities. Drift rates of larvae of both taxa show a 'u-shaped' relationship with velocity in dark conditions. Error bars = 1 SE.



**Figure 2-3**

Mean distances travelled upstream by released *Ameletus* and *Baetis* larvae in daylight (open symbols) and dark (solid symbols) conditions in four current velocities. Error bars = 1 SE.



**Figure 2-4**

Mean distance dispersed by released *Ameletus* and *Baetis* larvae in daylight (open symbols) and dark (solid symbols) conditions in four current velocities. The horizontal line (0.0 m) indicates the point of release, positive values indicate downstream displacement, negative values indicate an upstream displacement. Means do not include those larvae that drifted from the channels. Error bars = 1 SE.



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## **CHAPTER 3: DOES WATER VELOCITY INFLUENCE OPTIMAL ESCAPE BEHAVIOURS IN STREAM INSECTS?<sup>2</sup>**

### **Introduction**

Natural selection has produced a wide array of efficient predator-avoidance and escape behaviours in prey animals. These behaviours often represent tradeoffs between the need to survive interactions with predators and the energetic constraints of acquiring food resources (Dill 1987, Lima 1998, Cooper and Vitt 2002, Cooper and Frederick 2007). Optimal escape theory (Ydenberg and Dill 1986, Cooper and Frederick 2007) predicts that prey should begin to flee from an approaching predator when the predator reaches a point at which the risk of predation equals the costs of escape. The complex relationships among predation risk, flight cost, and the distance at which prey flee from predators have been examined in several taxa, including lizards (Vitt et al. 2002, Cooper et al. 2003), marmots (Blumstein and Pelletier 2005), and cichlid fishes (Dill 1990). However, a primary difficulty in assessing optimal escape theory is that the risk of predation and the cost of escape are typically measured in different 'ecological currencies'. For example, various prey species estimate the risk of predation by assessing the speed of approach (Cooper et al. 2003), directness or angle of approach (Cooper 1997, Cooper et al. 2003), or distance

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<sup>2</sup> A version of this chapter will be submitted for publication. Hoover T. and Richardson J.S. Does water velocity influence optimal escape behaviours in stream insects?

to refuge (Dill 1990). In contrast, the costs associated with escaping from predators have been measured in lost feeding opportunity (Dixon and Baker 1988, Peckarsky 1996, Blumstein and Pelletier 2005), or time spent in refuge after escape (Martín and López 1999, Rhoades and Blumstein 2007).

In streams a single factor – water velocity – may mediate both the risks of predation and the costs of flight for benthic invertebrate prey. Several studies suggest that in streams predation risk declines as current velocity increases. In low-velocity habitats, benthic invertebrates are susceptible to predation by a diverse assemblage of predators, while in high-velocity microhabitats the risk of both invertebrate and fish predation is reduced. For example, the rates of predation on blackfly (*Simulium* spp.) larvae by highly mobile stonefly predators (Malmqvist and Sackmann 1996) and flatworms (Hansen et al. 1991, Hart and Merz 1998) are substantially lower in high-velocity microhabitats than in low-flow areas (see also Peckarsky et al. 1990). Drift- and benthic-feeding fish predators also forage primarily in low-velocity habitats (generally less than 20 cm/s) as a result of energetic tradeoffs (Hughes and Dill 1990, Facey and Grossman 1992, Rosenfeld and Boss 2001).

The cost of flight of benthic prey may also be mediated by water velocity, where flight costs are maximised when water velocity closely matches the flow preferences of the prey. Fleeing from optimal habitat patches results not only in lost feeding opportunities (McIntosh and Townsend 1996), but may also result in greater physiological and energetic costs than flight from sub-optimal habitats. For instance, the respiratory efficiency of stream invertebrates that ordinarily

inhabit microhabitats with fast currents is compromised in regions of the streambed with slow flows (Golubkov et al. 1992, Bäumer et al. 2000). Likewise, invertebrates that are typically found in slow currents lack the morphological adaptations required to efficiently occupy or move in high-velocity habitats (e.g. Weissenberger et al. 1991). Even the costs of flight associated with lost feeding opportunities may be related to water velocity, as several studies indicate that herbivorous stream invertebrates are morphologically and behaviourally adapted to feed on the algal types associated with their preferred current velocities (e.g. McShaffrey and McCafferty 1988, also see Poff et al. 2003). As a result, the net costs of fleeing from predators while occupying an optimal habitat patch are greater than while occupying patches with flows that are either faster or slower. Although several studies have speculated about the tradeoffs between the cost of escape and the risks associated with the presence of predators in lotic habitats (e.g. Peckarsky 1980, Kohler and McPeck 1989, Culp et al. 1991), no study to date has explicitly tested how the predator avoidance and escape strategies of stream organisms incorporate assessments of cost and risk.

If the risk of predation is greater in slow-current than fast-current habitats while the cost of escape varies with the habitat preferences of each prey species (e.g. for a slow-current prey, the costs of escape in slow flows > fast flows), then the relationship between optimal escape distance and water velocity will be a function of the habitat preference of the prey. In Figure 3-1, two curvilinear risk curves represent the relative risk of predation faced by invertebrate prey in low- and high-velocity microhabitats, where the risk of predation is independent of the



habitat preferences of the prey (i.e. risk is always greater in low- than high-velocity habitats), but increases exponentially as the distance to the predator decreases (see Ydenberg and Dill 1986, Cooper and Vitt 2002). Two linear cost curves represent the costs associated with flight from predators, where costs are greater in the habitat that most closely matches the flow preferences of the prey. Vertical dotted lines at the intersections of the curves represent the optimal flight initiation distance (FID) of prey that prefer either slow or fast currents. If food resources are equally abundant across all habitats, the optimal FID of stream invertebrates that prefer fast currents should be short at high velocities, but much greater at low velocities. In contrast, the optimal FID of invertebrate prey that prefer slow currents should be similar in both low and high current velocities, due to the relatively high costs of escape in low-velocity habitats. If retreat distance (RD; the distance a fleeing prey retreats before stopping) is also a function of the tradeoffs between assessments of predation risk and the cost of flight made by prey, then it should exhibit a taxa-specific relationship with water velocity similar to that of FID.

The goal of this study was to examine the determining role that water velocity plays in the escape behaviours of three herbivorous stream mayflies, *Ameletus*, *Baetis*, and *Epeorus*. All three mayflies forage during the day on exposed streambed surfaces for periphyton, but vary in their habitat preferences; *Ameletus* is generally found in relatively low-velocity (pool/run) habitats, *Baetis* is found in intermediate-velocity habitats (riffles), whereas *Epeorus* inhabits high-velocity microhabitats (steps and boulder cascades). Perlid and perlodid

stoneflies are known to prey on all three taxa (Peckarsky and Penton 1989a, 1989b, Peckarsky 1996, T. Hoover personal observation). Using a simulated predator, we initiated flight responses in individual mayfly larvae across a range of current velocities in order to determine if these benthic invertebrates use flow as an indicator of the risk of predation or the costs associated with flight. Three measures of escape behaviour – FID, RD, and escape mode (crawling, swimming, or drifting) – were measured for each encounter in order to assess if local current velocity influences optimal escape behaviours, and to determine the potential role of escape mode and escape distance in emigration from habitat patches.

Given the potential for velocity-mediated tradeoffs between the risk of predation and costs of escaping, we hypothesized that (1) the FID and RD of *Epeorus* larvae would decrease with current velocity, while escape behaviours of *Ameletus* would vary little with current velocity. The responses of *Baetis* would be expected to be intermediate between those of *Epeorus* and *Ameletus*. As mayflies that enter the drift risk displacement into low-velocity areas of the stream (Lancaster et al. 1996), we also hypothesized that (2) mayfly taxa that are generally found in low-velocity habitats would be more likely to use drifting or swimming escape modes than would taxa that prefer high-velocity habitats (i.e. drift and swim escape rates of *Ameletus* > *Baetis* > *Epeorus*). We also examined the trajectories of mayfly larvae that swam to escape the simulated predator in order to assess the effectiveness of swimming as a means of escape from benthic and drift-feeding predators.

## Methods

The behavioural responses of mayfly larvae to a simulated predator were examined in an experimental field-based channel located adjacent to Blaney Creek, a bouldery, third-order mountain stream located in the Malcolm Knapp Research Forest (49.272°N, 122.586°W) near Maple Ridge, British Columbia. Mayfly larvae used in the study were collected from Blaney Creek; *Epeorus* spp. larvae were collected from high-shear habitats (upper surfaces and sides of boulders in riffles and cascades), *Baetis* sp. larvae from riffles, and *Ameletus* spp. larvae from exposed surfaces of streambed stones in pools and runs. All mayflies used were early- to mid-instar larvae (without darkened wingpads); larval body length (excluding terminal cerci) ranged between 1.7 and 6.9 mm (*Ameletus* (2.9 – 6.9 mm), *Baetis* (1.7 – 4.9 mm), and *Epeorus* (3.0 – 6.8 mm)). *Baetis* (primarily *B. tricaudatus* Dodds), *Ameletus* (primarily *A. validus* McDunnough), and *Epeorus* (primarily *E. longimanus* Eaton, with the possible inclusion of a few *E. albertae* McDunnough) are abundant members of the periphyton-grazing community in high-gradient coastal streams of British Columbia. All three mayflies are regularly observed feeding on the upper surface of streambed stones in coastal streams during the day (T. Hoover, personal observation). Many of the coastal streams in which these mayflies are found, including Blaney Creek, sustain populations of cutthroat trout (*Oncorhynchus clarki*), a benthic- and drift-feeding salmonid predator (see Zhang and Richardson 2007).

The experimental channel used was 4.9 m long, 0.40 m wide, with 0.40 m high sidewalls, and during the study had a fixed bed slope of 1.0%. One entire sidewall was constructed of transparent acrylic panels, allowing for an unobstructed side view of the channel floor and the behaviour of benthic invertebrates in the channel. Water supplied to the channel was diverted from Blaney Creek; valves on the supply pipes, coupled with a variable-height weir at the downstream end of the channel, provided precise control of flow depth and velocity. For this study, the bed of the channel was covered with a single layer of unglazed terra cotta tiles (11 × 11 cm). The tiles used were suspended on trays above the bed of Blaney Creek for ten days prior to the experiment, allowing for the growth of periphyton on the upper surface of the tiles. The tiles were then placed tightly edge-to-edge in the channel, creating a continuous surface with abundant food resources for herbivorous mayflies.

Mayfly larvae were collected from Blaney Creek by carefully hand-brushing streambed stones upstream of a dipnet. Larvae collected in the net were separated from detritus and transferred into holding jars using a wide-mouthed pipette. Within 15 minutes of collection, the larvae were transferred into the channel by gently swirling each jar and slowly decanting the water and larvae while holding the jar at the water's surface. The water velocity in the channel was lowered (generally < 5 cm/s) prior to the introduction of the mayflies, in order to minimise the numbers of mayflies transported out of the channel. Approximately 60 mayflies were introduced along the length of the channel at a time. After the mayflies had settled to the bed, the water velocity was then slowly

raised to one of three test velocities (5, 15, and 40 cm/s, measured at mid-depth). The mayflies were then allowed to acclimatise and disperse throughout the channel for 30 minutes.

A simulated predator (SP) was used to initiate escape responses in the larvae. The SP consisted of a small black plastic disk (diameter = 8.0 mm, thickness = 4.0 mm; see Fig. 3-2) similar in cross-section to a stonefly. The black disk was fastened to the end of a long (length = 80 mm), thin (diameter = 0.5 mm) metal shaft, which permitted the SP to be moved smoothly across the channel floor by a researcher holding the end of the shaft (see Fig. 3-2). In each trial, the SP approached an individual larva from the upstream direction. This allowed the larva to detect the SP using both visual and hydrodynamic cues (see Peckarsky 1980). Starting from a position several centimetres directly upstream, the SP was slowly moved towards the larva, and stopped when the larva began its escape response.

Mayfly responses to the simulated predator were recorded from the side using a digital video camcorder (Panasonic PV-GS65) mounted on a tripod. To minimise the disturbance that observers may have on mayfly behaviour, the video camera operator and SP manipulator worked in low-light conditions in a darkened tent-like 'blind' enclosure that extended the entire length of the channel and was fixed to the upper edge of the channel sidewall. The observers could thus view and film mayfly behaviours inside the channel through a small opening (approximately 15 cm high and 30 cm long) while remaining virtually invisible to

the mayfly larvae. All trials were conducted in late June 2005 in the daytime, between 10:00 and 16:00.

For each trial, frame-by-frame analysis of the video was used to record escape mode (crawling, swimming, or drifting), FID, RD (measured for crawling and swimming escapes only), larval body length (excluding cerci), and the duration (in milliseconds) of the escape response (Fig. 3-2). RD and time spent in retreat were used to calculate the net escape velocity. Movement distances and larval body lengths were made using the SP diameter (8.0 mm; included in the video frame) for scale. For *Ameletus* larvae with swimming retreats, swimming trajectories were quantified by tracing the outline of the swimming larva in each video frame (1/30 second intervals). As the video camera was positioned slightly higher than the bed of the channel (the angle of the camera was approximately 10° above the horizontal plane), measurements in the vertical plane (i.e. the height that swimming larva travelled above the bed) may have been slightly underestimated; measurements made in the horizontal plane (FID and RD) were not as strongly affected. As retreat distances were generally short (often < 10 mm) and perpendicular to the camera's line-of-sight, distance perspective errors were minor. A consistent flow depth was maintained throughout the experiment (mean = 9.4 cm, SE = 0.13 cm). Only those mayflies in the central part of the channel (1.0 – 3.0 m downstream from the inlet) were included in behavioural trials.

Flight initiation distance was measured as the distance between the SP and the mayfly larva at the instant when the mayfly began to retreat from the SP.

RD was measured as the distance between the position of the mayfly immediately prior to initiating an escape and the position of the mayfly when it stopped retreating. The RD of drift escapes could not be measured as drifting larvae were quickly carried out of the frame of the video. Rapid escape movements (crawling, swimming, or drifting) were easily distinguished from foraging movements, as the latter were much slower and in the upstream direction.

After all trials were concluded, flow visualisation using rhodamine dye was used to determine the spatial extent of the recirculating region of the turbulent wake extending downstream of the SP in all three velocities.

### **Data analysis**

Linear regression analyses were used to examine the relationship between larval body length and escape behaviours (i.e. FID, RD, and retreat velocity). A Bonferroni correction of alpha was made when testing the significance of regression analyses (nine regression analyses of body length against escape parameters per taxon, corrected alpha = 0.0056). Differences in the proportions of *Ameletus* larvae that adopted various escape modes (crawling, swimming, or drifting) in each of the three velocities were examined using a chi-squared test.

Within-taxa differences in escape behaviours (FID, RD, and retreat velocity) among velocities were tested using one-way analysis of variance (ANOVA) for taxa (*Baetis* and *Epeorus*) that exhibited only one escape mode (crawling). *Ameletus* larvae exhibited two escape modes (crawling and

swimming) in all three velocities, and as such, among-velocity and between-mode differences in escape behaviours were tested using a two-way ANOVA (two modes  $\times$  three velocities). In all tests, when main effects were significant, specific comparisons were made using Tukey's HSD.

Between-taxa comparisons of escape behaviours were made using two-way ANOVA. Due to the fundamental differences in escape behaviours demonstrated by crawling and swimming *Ameletus* larvae, these two groups were treated as separate 'taxa' in between-taxa comparisons (i.e. four taxa  $\times$  three velocities).

All analyses, with the exception of the chi-squared test, were conducted using Systat v.10 (Systat 2000).

## Results

All mayfly larvae approached by the simulated predator (SP) responded by initiating escape movements. While all *Baetis* and *Epeorus* larvae retreated from the SP by crawling downstream, *Ameletus* larvae used three different escape modes. Most *Ameletus* larvae (71.2%) retreated by crawling backwards, downstream, away from the SP. A smaller number (27.2%) fled from the predator by swimming, and a small minority (1.6%) escaped by drifting. The proportion of *Ameletus* larvae that escaped by crawling decreased with velocity, but the difference was not significant ( $X^2 = 6.05$ ,  $p = 0.20$ ).



## Intraspecific comparisons

Larval body length was not significantly related to FID, RD, or retreat velocity for *Ameletus* (either swimming or crawling), *Baetis*, or *Epeorus* (ANOVA, all  $p > 0.015$  at a corrected alpha of 0.0056).

Flight initiation distance did not differ significantly among velocities for *Ameletus* (ANOVA,  $F(2,117) = 0.63$ ,  $p = 0.54$ ), *Baetis* (ANOVA,  $F(2,107) = 1.48$ ,  $p = 0.23$ ), or *Epeorus* ( $F(2,42) = 1.75$ ,  $p = 0.19$ ), although in the latter case, FID appeared to decrease with velocity (Fig. 3-3). FID was significantly shorter for those *Ameletus* larvae that retreated by swimming than those that escaped by crawling (ANOVA,  $F(1,117) = 14.88$ ,  $p < 0.001$ ).

Water velocity played an important role in determining how far larvae retreated from the SP (Fig. 3-4). RD of *Baetis* larvae differed significantly among velocities (ANOVA,  $F(2,107) = 3.12$ ,  $p = 0.048$ ); larvae retreated further (about twice as far) in the highest velocity (40 cm/s) than in the lowest velocity (5 cm/s) (Tukey's HSD,  $p = 0.045$ ). While the crawling RD of *Ameletus* did not vary with velocity (ANOVA,  $F(2,86) = 1.77$ ,  $p = 0.18$ ), the RD of *Ameletus* larvae that swam in escape did increase with velocity (ANOVA,  $F(2,31) = 7.90$ ,  $p = 0.002$ ). The distances travelled by the two *Ameletus* larvae that escaped by drifting were much greater than the distances travelled by crawling or swimming larvae, and exceeded the range of field of the video camera (i.e. drift distances  $> 100$  mm). The RD of *Epeorus* larvae also varied among velocities (ANOVA,  $F(2,42) = 3.38$ ,  $p = 0.044$ ). However, in contrast to *Baetis* and *Ameletus*, the RD of *Epeorus* larvae decreased with velocity, and was much greater at the lowest velocity than

either the mid-velocity (Tukey's HSD,  $p = 0.063$ ) or the highest velocity (Tukey's HSD,  $p = 0.044$ ).

The retreat velocity of *Ameletus* larvae with swimming escapes significantly increased with current velocity (ANOVA,  $F(2,31) = 5.90$ ,  $p = 0.007$ ), although because swimming escapes were generally in the downstream direction, an increase in downstream retreat velocity may be due to the increasing water velocity rather than an increase in swimming speed. In contrast, retreat velocity did not differ significantly among velocities for *Ameletus* with crawling escapes (ANOVA,  $F(2,86) = 1.06$ ,  $p = 0.35$ ), crawling *Epeorus* (ANOVA,  $F(2,42) = 0.26$ ,  $p = 0.78$ ), or crawling *Baetis* (ANOVA,  $F(2,107) = 2.63$ ,  $p = 0.077$ ), although the retreat velocity of *Baetis* larvae tended to decrease with velocity (not significant).

### **Interspecific comparisons**

Escape behaviours varied substantially among the three taxa. FID varied significantly between the mayflies (ANOVA,  $F(3,266) = 12.39$ ,  $p < 0.001$ ) (Fig. 3-3). The FID of *Ameletus* that escaped by swimming was significantly less than crawl-retreating *Ameletus*, *Baetis*, and *Epeorus* larvae (Tukey's HSD, all  $p < 0.001$ ). The FID of *Epeorus* larvae was significantly greater than both *Ameletus* and *Baetis* (Tukey's HSD, all  $p < 0.015$ ), while the FID of *Baetis* and *Ameletus* that crawled to escape were not different (Tukey's HSD,  $p = 0.98$ ).

Retreat distances also varied among taxa (ANOVA,  $F(3,266) = 17.01$ ,  $p < 0.001$ ) and among velocities (ANOVA,  $F(2,266) = 3.32$ ,  $p = 0.038$ ). A significant interaction term between taxa and velocity (ANOVA,  $F(6,266) = 6.39$ ,  $p < 0.001$ ),

however, demonstrates that the RD of the three mayflies varied differently as velocity increased (Fig. 3-4). The RD of *Epeorus* was substantially greater at the lowest velocity than the other mayflies, but decreased as velocity increased. In contrast, the RD of *Baetis* and 'swimming' *Ameletus* increased with velocity, while the mean RD of 'crawling' *Ameletus* did not vary with velocity.

The velocity at which larvae escaped from the SP varied significantly among taxa (ANOVA,  $F(3,266) = 422.05$ ,  $p < 0.001$ ) and between velocities (ANOVA,  $F(2,266) = 15.85$ ,  $p < 0.001$ ). However, the interaction term between taxa and velocity was also significant (ANOVA,  $F(6,266) = 11.54$ ,  $p < 0.001$ ), indicating that the relationship between escape velocity and water velocity varied among taxa. Generally, the escape velocity of swimming *Ameletus* exceeded the crawling rate of crawling *Ameletus*, *Baetis*, and *Epeorus*, while the crawling escape rate of *Epeorus* was greater than that of *Ameletus* and *Baetis* (i.e. swimming *Ameletus* > crawling *Epeorus* > crawling *Ameletus* = crawling *Baetis*) (Table 3-1).

Flow visualisation using dye injection showed that the recirculating region of the turbulent wake extending downstream of the simulated predator was relatively extensive. At 5 and 15 cm/s, the recirculating region extended 10.9 – 12.6 mm and 10.8 – 12.9 mm downstream, respectively. At 40 cm/s, the region was somewhat shorter, and extended 8.5 – 9.5 mm downstream of the SP.

### **Biomechanics of swimming escape behaviours**

*Ameletus* larvae resting on the bottom often used a swimming escape manoeuvre in response to the approach of a simulated predator. Swimming

escapes (“rapid start” or “rapid turn about” manoeuvres, Brackenbury 2004) began with a dorsal flexion, where the body of the larva was arched backwards to the extent that the dorsal surface of the head and thorax of a larva approached the dorsal surface of the abdomen (e.g. position 2 in each panel of Fig. 3-5). Although the quality of the video precluded any detailed examination of swimming biomechanics, escaping larvae also presumably laterally rotated simultaneously, as by 0.07 seconds into the escape (position 3) larvae had re-oriented with their dorsal surfaces upward. After this rapid reversal of direction, larvae swam briefly downstream (generally for 0.07 to 0.10 seconds) before swimming toward the bed. While some larvae returned to the bed in a ‘head-downstream’ orientation (Fig. 3-5, middle panel), the majority of larvae rotated as they approached the bed, coming to rest in a ‘head-upstream’ orientation (e.g. Fig. 3-5, top and bottom panels). During swimming escapes in all velocities, *Ameletus* larvae generally reached a maximum height of 2 – 4 mm above the bed (average maximum height reached = 2.9 mm, range = 0.8 – 5.7 mm) (Fig. 3-6). As swimming larvae were moving through a fluid boundary layer (T. Hoover, unpublished data) in a current, it was difficult to estimate the exact swimming speeds of escaping *Ameletus* larvae. However, examination of swimming trajectories (Fig. 3-5 and 6) suggests escaping larvae may swim at speeds as high as 20 cm/s.

## Discussion

The behavioural responses of mayfly prey to a predatory threat not only determines the rate at which predators capture prey and thus directly impact prey

populations, but, depending on the type of prey response, may also influence the emigration rates of prey from local habitat patches (Wooster and Sih 1995, Lima 1998). Flight initiation distance, retreat distance, and escape mode are potential indicators of the tradeoffs that benthic prey make when assessing the risk of predation and the costs of fleeing from predators. While the escape behaviours of *Ameletus*, a slow-current mayfly, did not vary with water velocity, the RD of *Epeorus*, a fast-current mayfly, did dramatically decrease with water velocity. Provided that water velocity influences the costs and risks of predation in streams, the escape strategies of these two mayflies follow the predictions of optimal escape theory, indicating that these invertebrates balance the shifting tradeoffs between risk of predation and the costs of flight in different flow conditions. However, the escape behaviours of *Baetis* did not appear to correspond with the predictions of optimal escape theory, possibly due to the broad habitat preferences of this genus. Generally, RD appeared to be more sensitive to variation in water velocity than FID, indicating that RD may be a better indicator of the tradeoffs that benthic invertebrate prey make between minimising predation risk and managing the costs of escape.

### **Water velocity influences retreat distance but not flight initiation distance**

Flight initiation distance did not vary with water velocity for any of the three mayflies. Optimal escape theory predicts that escape behaviours will be initiated when the risk of predation equals the costs associated with fleeing from the approaching predator. As FID did not vary among flow conditions as expected, the functions that relate cost of flight and risk of predation with the initiation of

escape behaviours may have different forms than those assumed in our conceptual model. For instance, the FIDs of *Ameletus* and *Baetis* (and *Epeorus* at the highest water velocity) that used crawling escapes were remarkably uniform (approximately 7 - 10 mm), and correspond closely with those reported for *Baetis* larvae fleeing from a stonefly predator (*Kogotus*) (Peckarsky and Penton 1989a), and for *Baetis tricaudatus* retreating from fish (*Rhinichthys cataractae*) or stonefly (*Claasenia sabulosa*) predators while in a patch with abundant food resources (Scrimgeour and Culp 1994). In all cases, the range of flight initiation distances is similar to the body length of the larvae used, and may represent a predator-to-prey distance at which the risk of capture increases dramatically. If this is true, an increase in FID may not necessarily translate into a substantial reduction in the probability of capture by a predator. The FID of *Ameletus* larvae that retreated by swimming was significantly shorter than those that escaped by crawling. If swimming escapes are more effective – though possibly more energetically costly – than crawling escapes, then this pattern demonstrates that the escape behaviours of this mayfly are variable, and sensitive to variation in predation threat.

Alternatively, FID may be constrained by the perceptual abilities of the prey or other physiological or ecological factors. The FID recorded for the three mayflies corresponds closely with the extent of the region of recirculating flow associated with the turbulent wake extending downstream of the simulated predator. It is possible that mayfly prey use this as a hydrodynamic cue to accurately determine the proximity of a predator approaching from the upstream

direction. However, this is undoubtedly not the only physical cue used by mayfly prey, as Peckarsky and Penton (1989a) showed that *Baetis* larvae also responded to stonefly predators approaching from the downstream direction. Understanding the hydrodynamic and visual cues used by mayfly prey to detect predators is a critical goal in understanding predator-prey dynamics in topographically and hydrodynamically complex streambed landscapes.

The RD of larval *Epeorus* decreased sharply with water velocity, whereas the RD of *Ameletus* was uniform in all flow conditions. This supports our conclusion that for benthic invertebrates, RD is a more sensitive indicator of a prey's perception of the costs and risks associated with an approaching predator than are flight initiation behaviours, which may be tightly constrained by the perceptual abilities of the prey. To our knowledge, this study is the first to explicitly interpret RD as being subject to the same risk/cost tradeoffs as FID. Empirical studies of optimal flight behaviours have almost exclusively focused on the FID of refuge-seeking animals (Dill 1990, Vitt et al. 2002, Cooper et al. 2003, Blumstein and Pelletier 2005) as a measure of how prey assess risk level. However, for prey that do not flee to a refuge, RD may more accurately reflect the level of risk perceived by prey, as prey remain exposed to the predator after flight. While many terrestrial vertebrate prey species rely heavily on sight to continually assess the immediate risk posed by predators (e.g. Vitt et al. 2002), stream insects have limited visual acuity and instead rely upon a combination of hydrodynamic, chemical, and visual cues (Peckarsky and Penton 1989a, Tikkanen et al. 1994). Retreat distance may especially reflect costs of escape in

instances where movement is energetically costly, prey remain vigilant for some time after escape, or prey cross habitat patch boundaries during escape retreat movements and thus suffer substantially reduced foraging opportunities. The RD of *Ameletus* and *Baetis* generally did not exceed 15 mm, suggesting that larvae were likely to remain in the same patch after flight. In contrast, the mean RD of *Epeorus* larvae in low-velocity flow conditions was much longer (> 60 mm), increasing the likelihood of crossing patch boundaries. When *Epeorus* larvae were threatened by the simulated predator in high-velocity flow conditions that were similar to its preferred habitat, their RD, and potential costs of flight, were substantially reduced. Unexpectedly, the RD of *Baetis* increased with velocity, contradicting our predictions of a moderate decrease in RD as flow increased.

### **Escape mode varies with risk of predation and risk of displacement**

Crawling, rather than swimming or drifting, dominated the escape behaviours of all three mayflies. However, as predicted, the two mayflies associated with high-velocity habitats (*Baetis* and *Epeorus*) exclusively used crawling escapes, while *Ameletus* (generally found in low-velocity habitats) regularly used both crawling and swimming escape modes. Invertebrates associated with high-flow habitats may rely primarily on crawling escapes to minimise the likelihood of being accidentally displaced downstream from a habitat patch, especially during daylight hours when the risk of predation from drift-feeding fishes is elevated. Although very little is known about how benthic invertebrates perceive and respond to heterogeneity in habitat structure at organismal scales (but see Olden et al. 2004), crawling movements may allow



benthic larvae to detect habitat patch boundaries and, if necessary, adjust their movement to remain in the patch (see Kohler 1984, Rice et al. 2008). Where patches are small relative to the movement of individuals, even short escape movements may increase the likelihood of displacement from habitat patches (Englund and Hambäck 2004). Although surprisingly little is known about the distances that invertebrate prey retreat from predators by crawling (but see Peckarsky 1980, McIntosh and Townsend 1998), crawling may provide prey with a degree of control over escape distance and direction not possible with swimming or drifting.

The exclusive use of crawling escapes by *Baetis* and *Epeorus* larvae are in marked contrast to the multiple escape modes – including drifting and swimming – used by *Ameletus*. This suggests that the costs or risks associated with leaving the substrate to escape benthic predators are greater for mayfly taxa that inhabit high-velocity microhabitats. Drifting may be more costly in high-velocity habitats due to the increased likelihood of displacement from an area of suitable habitat. The downstream displacement of drifting stream invertebrates increases with current velocity (Elliott 2002), and larvae that drift from high-velocity microhabitats are likely to be deposited in low-flow areas of the stream (Lancaster et al. 1996, Bond et al. 2000). Furthermore, dorso-ventrally flattened heptageniid mayflies such as *Epeorus* have limited swimming abilities compared to mayflies like *Ameletus* and *Baetis* with streamlined cylindrical bodies (Chapter 4, also see Craig 1990). As such, *Epeorus* may have little ability to actively exit the drift, and once entrained may be more susceptible to fish predation than

other taxa. Several studies have also noted that heptageniid mayflies are less likely than other taxa to enter the drift as a result of interactions with predators (e.g. Walton 1980, Peckarsky 1980). Stream invertebrates that inhabit slow-flow areas of the bed would not risk being swept downstream, and may more readily swim to escape than their rheophilous counterparts.

The crawling escapes used by *Baetis* larvae in this study contrast strongly with the results of several other studies that found that *Baetis* larvae primarily enter the drift to escape benthic predators (e.g. Peckarsky 1980, Peckarsky and Penton 1989a, Scrimgeour and Culp 1994, Peckarsky 1996). Crawling escapes may have dominated in our study because local food resources were abundant (Scrimgeour and Culp 1994), and the apparent risk of entering the drift was elevated due to the odour of drift-feeding fish (McIntosh et al. 2002). While the *Baetis bicaudatus* larvae studied by Peckarsky and Penton (1989a) in a Colorado stream used all three escape modes, swimming and drifting escapes were almost exclusively used only if larvae came directly into contact with a stonefly predator, either real or modelled. Peckarsky and Penton (1989a) found that when approaching predators were avoided prior to contact, crawling escapes or 'freezing' (no movement) were the primary behavioural responses. All larvae in our study initiated escape movements before the 'predator' approached close enough to contact them. The simulated predator used in this study may either have created a stronger hydrodynamic signal, been more visible, or may have approached prey at a slower rate than the stonefly predator it was created to simulate. Although prey appear to rely primarily on hydrodynamic cues to warn

them of the approach of both benthic (Peckarsky and Penton 1989a) and fish (Tikkanen et al. 1994) predators, the specific nature of the signal remains unknown.

While no fish were present in the channel during the experiment, the water used was drawn from a stream containing cutthroat trout (*O. clarki*), and several studies have shown that *Baetis* larvae drift aperiodically when fish are absent, but drift almost exclusively at night when chemical cues indicating drift-feeding fish are present (Tikkanen et al. 1994, McIntosh et al. 2002). This undoubtedly is a critical factor in the almost complete absence of drift escapes by *Baetis* larvae in this study.

#### **Retreat distances are related to rates of emigration from habitat patches**

Predator impacts on local prey densities often reflect changes in prey movement rather than consumption by predators (Sih and Wooster 1994, Peckarsky et al. 1990), although a shift from movement control to consumption control may be expected as spatial scale increases (Englund 1997). At the very small spatial scales (~ 10 cm) examined in this study, movement initiated by the presence of a predator influenced not only the local distribution of prey, but likely would have increased emigration rates from habitat patches in naturally-heterogeneous streambed landscapes. Predator-induced redistribution of individuals within and between patches may be especially important for invertebrates like *Epeorus* that prefer exposed, high-velocity habitats, which are often highly heterogeneous at small spatial scales (Hoover and Ackerman 2004). In this study, the RD of larval *Epeorus* were short (< 20 mm) in high-velocity

conditions. However, RD can vary substantially among different escape modes (e.g. for *Ameletus*, crawling < swimming < drifting), indicating that the strength of predator-induced movements will depend not only on microhabitat type, but will also vary between species with different escape behaviours.

The predation risks associated with each of the three escape modes used by benthic invertebrate prey are likely very different. While the swimming escapes of *Ameletus* produced rapid movements away from the predatory threat, Peckarsky et al. (1994) showed that the stonefly predator *Megarcys* preferentially attacked swimming mayfly prey, while ignoring non-swimming (crawling) prey. Larval *Ameletus* in this study appeared to switch from crawling to swimming escapes when the 'predator' approached very close (< 7mm, approximately); this distance may represent a threshold below which the risk of predation during a swimming escape is less than that of attempting a crawling escape. Craig (1990) examined escape swimming in the morphologically similar mayfly *Cloeon dipterum* (Baetidae) and concluded that the streamlined shapes of swimming mayflies are adapted to minimise the added-mass coefficient during rapid acceleration in swimming manoeuvres, maximising escape velocity. The escape velocities and acceleration of *Ameletus* larvae are very similar to those recorded for *C. dipterum*. During the initial phase of swimming escapes, the abdomen of *Ameletus* appears to remain in contact with the substrate. This interaction between the body of the mayfly and the substrate may act to further increase escape velocity (Craig 1990). These adaptations likely reduce the probability of capture by stonefly predators, while the short duration of the escape manoeuvres

and the limited height above the substrate attained by swimming *Ameletus* may minimize the risk of predation by drift-feeding fishes during escapes (see Scrimgeour and Culp 1994, McIntosh et al. 2002).

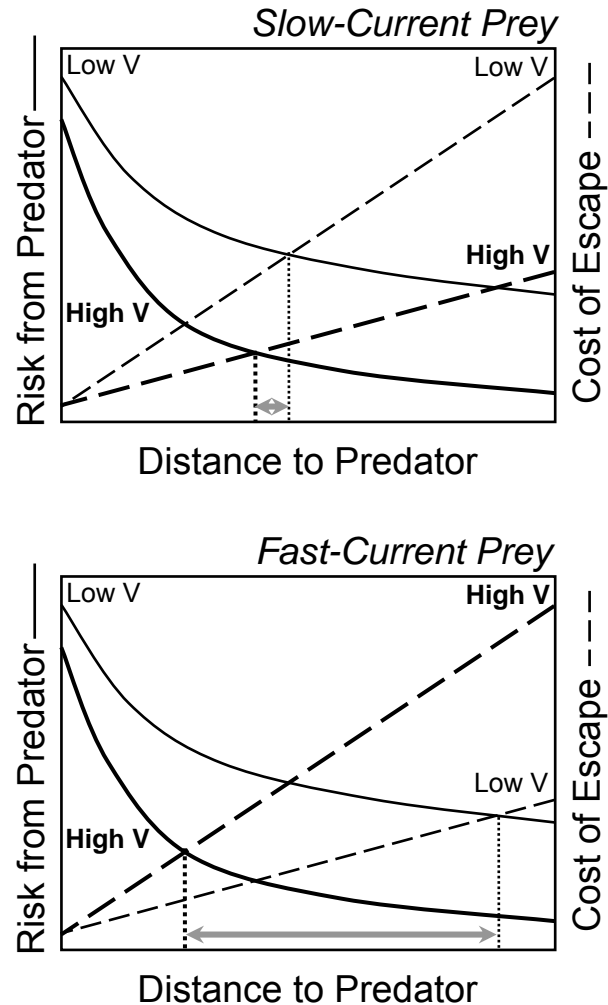
## **Conclusions**

While many studies have acknowledged that local prey abundances can be controlled by predator-driven emigration, our results indicate that in benthic ecosystems these processes are also a function of velocity-mediated changes in escape behaviours. While optimal escape theory may be used to clarify the influence that environmental factors may have on escape behaviours, this study demonstrates that it is difficult to rigorously apply theoretical models of this type without knowing the form of the functions that relate predation risk and flight costs with distance to an approaching predator. Stream communities, however, may represent tractable systems in which these functions might be empirically developed, especially since much is already known about the fitness costs of flight from predators (e.g. Scrimgeour and Culp 1994). As both capture by predators and unnecessary displacement from a patch of abundant resources act to reduce prey fitness, prey should use any available information that allows them to increase the accuracy with which they assess the risk of mortality or the costs of escape. This study indicates that these invertebrates can also incorporate risk- and cost-mediating environmental factors into their escape strategies.

**Table 3-1**

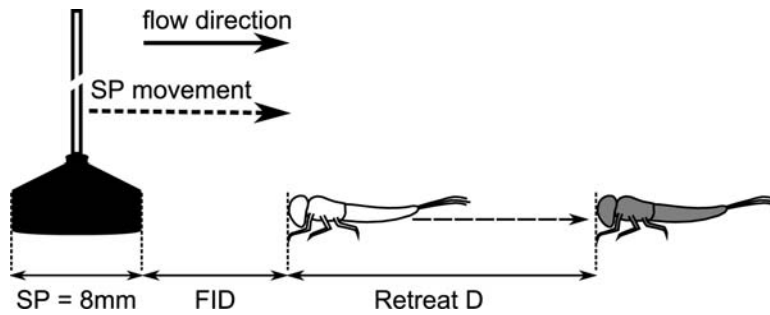
Mean escape velocities of three stream mayflies in response to a simulated predator in three current velocities (5, 15, and 40 cm/s)

	Escape velocity (mm/s) (SE)		
	5 cm/s	15 cm/s	40 cm/s
<i>Ameletus</i> (crawling)	13.8 (0.8)	14.4 (0.9)	12.5 (1.1)
<i>Ameletus</i> (swimming)	85.6 (10.5)	104.0 (10.7)	140.1 (9.3)
<i>Baetis</i> (crawling)	10.7 (0.5)	10.0 (0.7)	8.9 (0.6)
<i>Epeorus</i> (crawling)	26.6 (5.9)	28.2 (4.2)	31.3 (2.9)



**Figure 3-1**

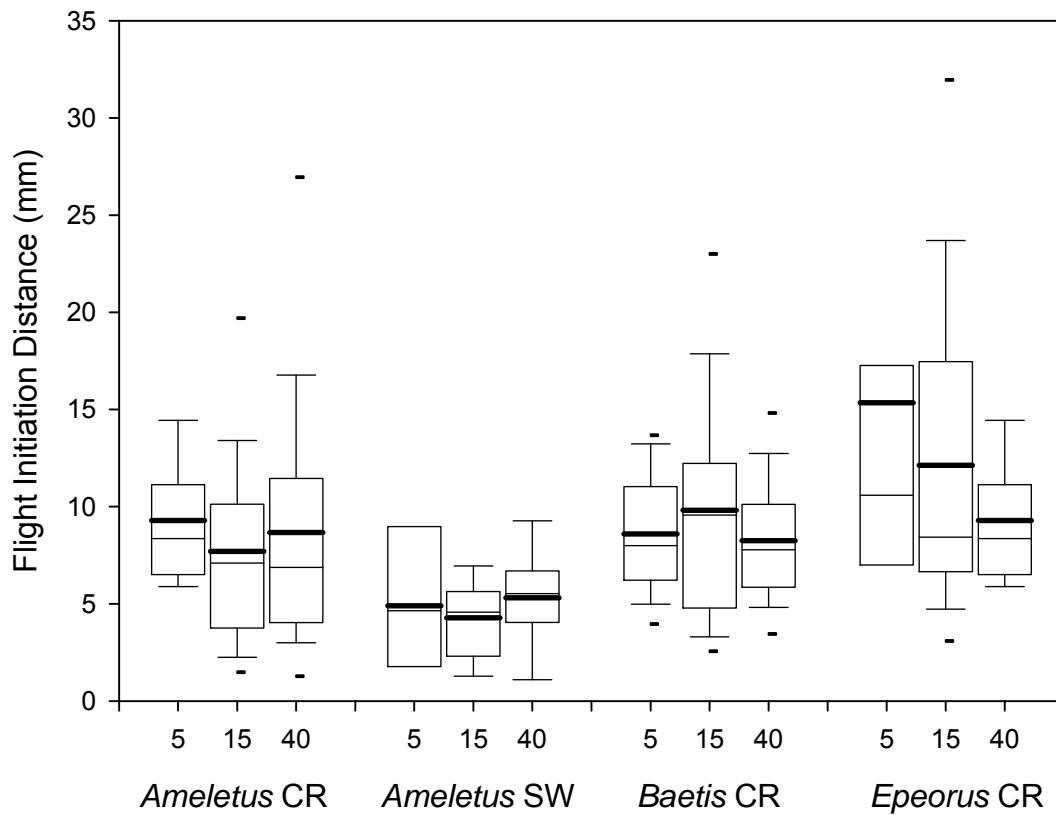
Optimal flight initiation distances (dotted lines) are the points on the distance axis below the intersections of the risk (solid lines) and cost (dashed lines) curves. Optimal flight theory predicts that if the slope of the risk curve is altered by water velocity, and the slope of the linear cost curve is influenced by both water velocity and the habitat preferences of the prey, the optimal flight initiation distance will vary little with current velocity for slow-current prey (grey arrow, top panel), but will decline with current velocity for fast-current prey (grey arrow, bottom panel). Low-velocity current curves = fine lines, high-velocity current curves = bold lines. Adapted from Ydenberg and Dill (1986) and Cooper et al. (2003).



**Figure 3-2**

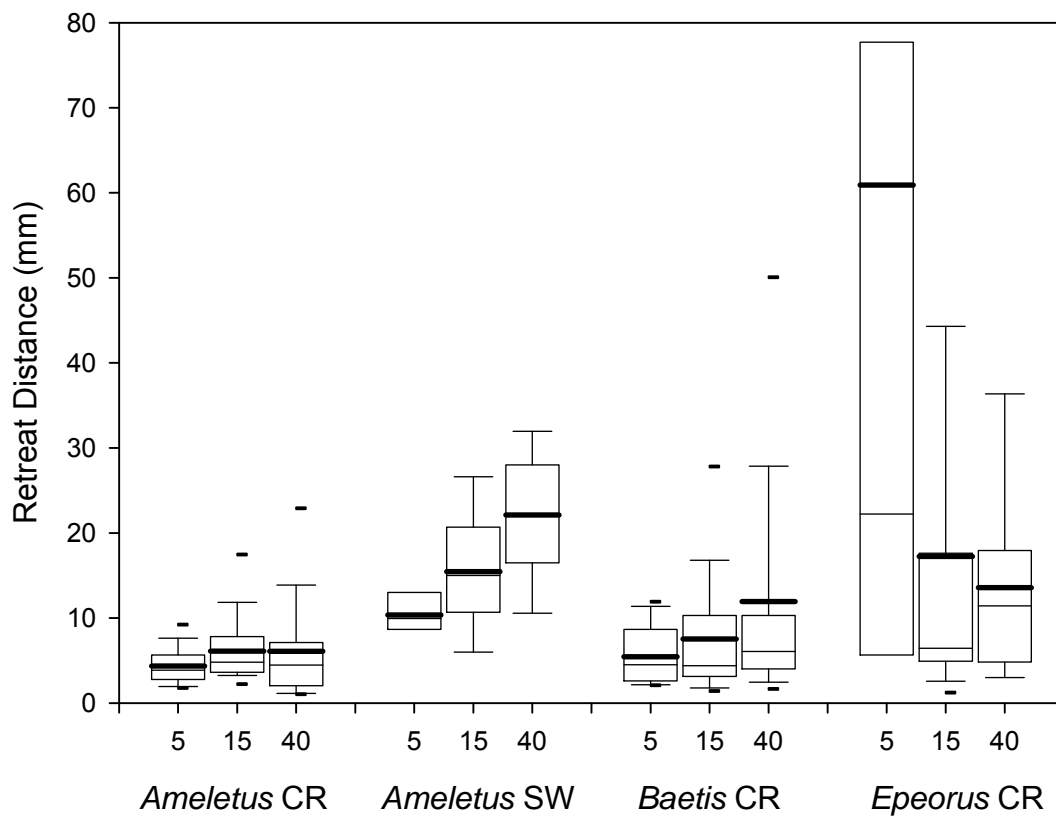
Diagram of experimental setup used to measure escape responses in stream mayfly prey. The simulated predator (SP), a black disk 8mm in diameter, approached mayfly prey (white outline = initial position) from the upstream direction until escape movements were initiated. When the escape retreat of each mayfly was complete (grey outline = final position), the flight initiation distance (FID) and retreat distance (RD) were recorded.





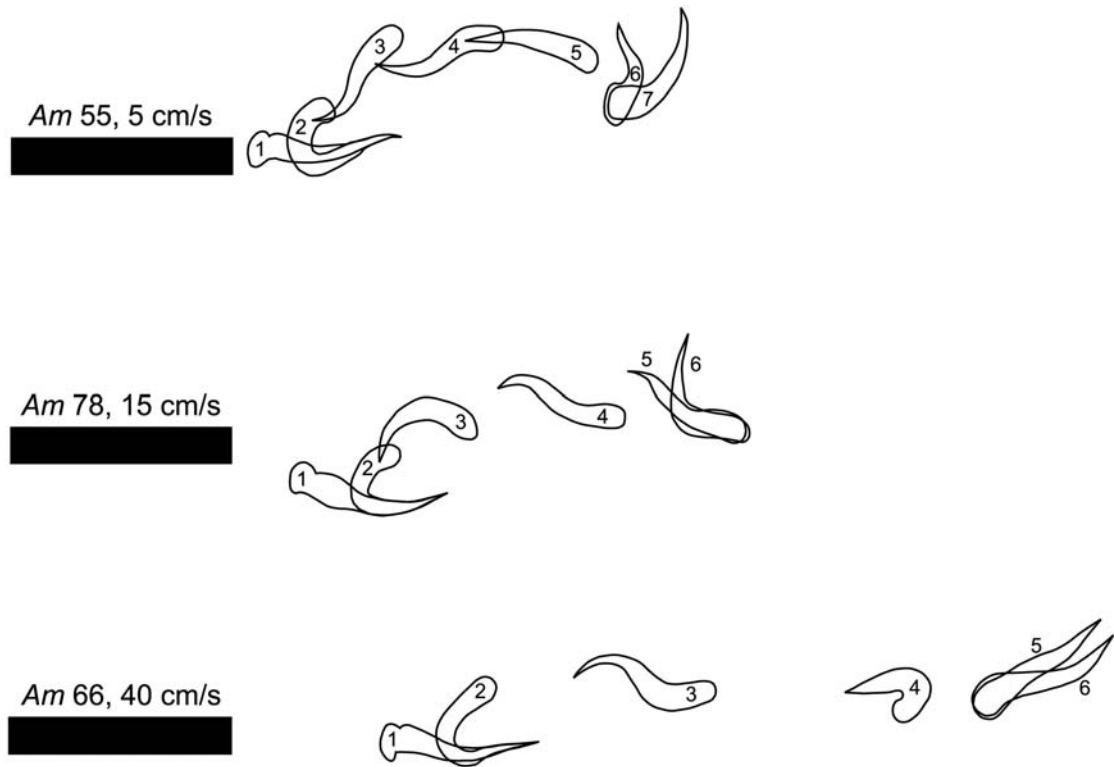
**Figure 3-3**

Boxplots showing variation in flight initiation distance (FID) in three mayflies in three water velocities (5, 15, and 40 cm/s). The FID of crawling and swimming larvae are shown; CR = crawling escapes, SW = swimming escapes. Thick black line = mean, thin black line = median, boxes represent 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers represent 5<sup>th</sup> and 95<sup>th</sup> percentiles; outliers are shown.



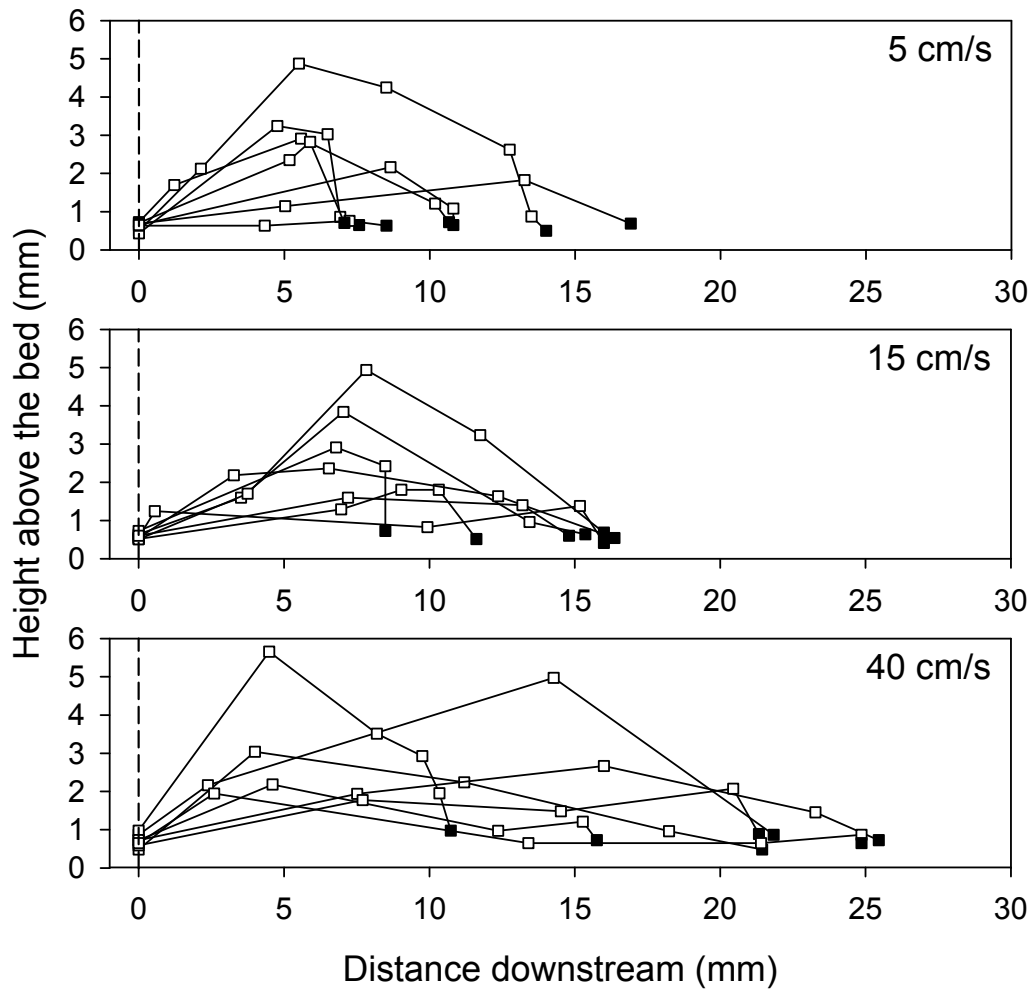
**Figure 3-4**

Boxplots showing variation in retreat distance (RD) in three mayflies in three water velocities (5, 15, and 40 cm/s). The RD of crawling and swimming larvae are shown; CR = crawling escapes, SW = swimming escapes. Thick black line = mean, thin black line = median, boxes represent 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers represent 5<sup>th</sup> and 95<sup>th</sup> percentiles; outliers are shown.



**Figure 3-5**

Representative examples of swimming escape trajectories of escaping *Ameletus* larvae in three water velocities (top = 5 cm/s, middle = 15 cm/s, bottom = 40 cm/s). The black bar represents both the position of the simulated predator (SP) at the time of escape initiation and the spatial scale (SP diameter = 8 mm). Each numbered outline represents the larval position in successive video frames (1/30 second intervals). The extreme dorsally-oriented flexion characteristic of swimming escapes is evident in position 2 in all sequences.



**Figure 3-6**

Examples of the vertical and horizontal extent of representative swimming escape trajectories ( $n = 7$ ) of escaping *Ameletus* larvae in three water velocities (top = 5 cm/s, middle = 15 cm/s, bottom = 40 cm/s). All larvae initiated escapes at 0 mm; subsequent points in each trajectory represent the position of each larva in successive video frames (1/30 second intervals).

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## **CHAPTER 4: SINK OR SWIM? THE RELATIVE IMPORTANCE OF HYDRODYNAMIC, BEHAVIOURAL, AND MORPHOLOGICAL FACTORS IN DETERMINING THE DISTANCES DRIFTED BY STREAM INVERTEBRATES<sup>3</sup>**

### **Introduction**

The suspension and transport of larval organisms in fluid currents plays a critical role in the population dynamics and community ecology of many freshwater and marine systems (Palmer 1995, Palmer et al. 1996, Abelson and Denny 1997, Fonseca and Hart 2001, Koehl et al. 2007, Lancaster 2008). In streams, downstream drift allows benthic invertebrate larvae to rapidly emigrate from areas of unfavourable habitat (Holomuzki and Van Loan 2002), escape predators (Peckarsky 1996), exploit patchily distributed resources that are variable in space and time (Rowe and Richardson 2001), and colonise unexploited areas downstream (Fonseca and Hart 2001). However, drifting larvae risk being transported into and settling within areas of the streambed landscape with unfavourable flow regimes (Otto and Sjöström 1986, Lancaster et al. 1996). This can be especially problematic for those organisms with well-

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<sup>3</sup> A version of this chapter will be submitted for publication. Hoover T., Yonemitsu N. and Richardson J.S. Sink or swim? The relative importance of hydrodynamic, behavioural, and morphological factors in determining the distances drifted by stream invertebrates.

defined preferences for specific hydraulic habitat types (e.g. Collier 1994, Wellnitz and Poff 2006).

The distances drifted by stream invertebrate larvae are highly variable, and have been shown to be a function of current velocity (Elliott 2002), turbulence (McNair et al. 1997), the size, shape, density of the larvae (Fonseca 1999), and the behaviour of the larvae (Otto and Sjöström 1986, Allan and Feifarek 1989, Fingerut et al. 2006). Larval behaviours such as swimming or posture modification may either increase (Otto and Sjöström 1986) or decrease (Ciborowski and Corkum 1980) transport distance. Turbulence may also increase the transport distances by reducing the settling rate of larvae, but the importance of this factor in invertebrate drift has yet to be empirically examined in lotic systems (but see Fingerut et al. 2006). Furthermore, while it is recognised that quasi-periodic, coherent turbulent structures such as detaching eddies and 'bursting' phenomena play an important role in the suspension and transport of sediment (Sumer and Oguz 1978, Cellino and Lemmin 2004), it is not known if they influence the drift of invertebrate larvae.

As an ecological extension of sediment transport theory, McNair et al. (1997) identified four basic problems that must be addressed in order to develop a framework to understand the downstream transport of invertebrate larvae or detrital particles in turbulent flows: 1) How does a particle become entrained in the water column? (2) Once entrained, how long does it take for a particle to reach the bottom? (3) How far does an entrained particle travel before it hits the bottom? (4) When it reaches the bottom, what determines whether a particle

attaches (ceases downstream movement) or reflects (immediately re-enters the water column)? In this paper, to gain insight into the third and fourth problems, we address how water velocity and species-specific movement-related behaviours influence downstream transport distances and rates of attachment/reflection. While several studies have developed advection-diffusion models to examine the transport properties of neutrally- or nearly neutrally-buoyant particles such as invertebrate larvae (Denny and Shibata 1989, McNair et al. 1997, McNair 2006), empirical examinations of the roles of flow and settling velocity on larval transport remain rare in lotic systems (also see Ciborowski 1987, Allan and Feifarek 1989, Fonseca 1999, Elliott 2002, Fingerut et al. 2006).

Here we examine the effects of water velocity and behaviour on the transport and settlement of four stream mayflies, *Epeorus* (Heptageniidae), *Baetis* (Baetidae), *Ameletus* (Ameletidae), and *Paraleptophlebia* (Leptophlebiidae). *Epeorus*, *Baetis*, and *Ameletus* are abundant members of the periphyton-grazing community in high-gradient streams of south-western British Columbia (Reece and Richardson 2001), while *Paraleptophlebia* is detritivorous, feeding on both coarse and fine particulate organic matter (Mattingly 1987). All four mayflies are regularly preyed upon by both fish and invertebrate predators, are known to actively drift, and exhibit distinct habitat preferences especially with respect to water velocity (Poff and Ward 1991, Palmer 1995, Rader 1997). *Epeorus* larvae are found in very high velocity microhabitats in cascades and steps, and *Baetis* larvae inhabit riffles (Wellnitz and Poff 2006). In contrast, *Ameletus* larvae are found on the exposed surfaces of streambed stones in pools

and runs, whereas *Paraleptophlebia* spp. larvae are found in low-velocity depositional microhabitats in pools and channel margins (Kobayashi and Kagaya 2004). Comparing the transport properties of these four mayflies to their habitat preferences will expose the constraints that larvae face when attempting to directly settle in a patch of suitable habitat.

The goal of this study was to quantify the functional roles that behaviour, morphology, and water velocity play in the distances that drifting invertebrate larvae are transported downstream in shallow, turbulent streams. We conducted experiments in a field-based experimental channel to determine if the hitting distances ( $x'_s$ ) and total transport distances ( $x_s$ ) of live mayfly larvae were similar to those of dead conspecific larvae and a single type of passive particle of similar size and transport properties. The transport and settlement rates of four mayflies and passive particles were examined in slow and fast currents in order to evaluate the degree to which behavioural control varied with flow conditions or among taxa. To address these issues, we asked three specific questions, i) Do live larvae and dead larvae drift the same distance, and does the degree of behavioural control (i.e. the difference between live and dead larvae, see Ciborowski and Corkum 1980) vary with velocity? ii) Do dead larvae and passive tracer particles drift similar distances, and does the degree of morphological control (i.e. the difference between dead larvae and tracer particles) vary with velocity? iii) Do the transport and settlement characteristics of drifting invertebrate larvae vary among taxa, their habitat type, and with water velocity?

## Methods

All experiments were conducted in an experimental channel located adjacent to Blaney Creek, a steep, bouldery, third-order mountain stream in the Malcolm Knapp Research Forest (49.272°N, 122.586°W) near Maple Ridge, British Columbia, Canada. The experimental channel was 495 cm long, 40 cm wide, and 40 cm deep, and had a fixed bed slope of 1.0%. One entire sidewall was constructed of transparent acrylic panels, allowing for an unobstructed view of the channel floor and the behaviour of benthic insects released inside the channel. Water passed through the channel only once before being discharged back into Blaney Creek. For further details on the use of the channel see Harrison et al. (2006). For this study, a rough bed was created in the channel by placing gravel, cobbles, and coarse sand from Blaney Creek into the channel, and then exposing this material to high-flow conditions ( $> 70$  cm/s) for two hours. This created a bed (mean grain diameter = 8.2 cm, standard deviation (SD) = 5.1; mean grain protrusion = 1.5 cm, SD = 1.1; range = 0 – 3.8 cm) with naturally-evolved microtopography that appeared similar to gravel/cobble riffle habitats in Blaney Creek.

We used a factorial experimental design to compare the transport processes of live mayfly larvae, dead mayfly larvae, and passive tracer particles (uniformly-shaped particles with transport properties similar to those of dead larvae) in shallow turbulent flows over a rough bed. Live larvae, dead larvae, and passive particles were released in two flow conditions; low-velocity conditions ( $U = 9.2$  cm/s, SD = 0.6) were approximately one-third that of the high-velocity

conditions ( $U = 30.7$  cm/s,  $SD = 1.1$ ). Water depth was similar in both flow conditions (low-velocity depth =  $7.0$  cm,  $SD = 0.6$ , high-velocity depth =  $7.7$  cm,  $SD = 0.3$ )

Mayfly larvae used in the study were collected from various microhabitats in Blaney Creek. *Epeorus* larvae were collected from high-shear habitats (upper surfaces and sides of boulders in riffles and cascades), *Baetis* larvae from riffles, *Ameletus* larvae from exposed surfaces of streambed stones and bedrock surfaces in pools and runs, and *Paraleptophlebia* larvae from accumulations of organic matter in low-velocity depositional areas. Generally, early- to mid-instar larvae without darkened wingpads were used (see Table 4-1 for body lengths of larvae used).

Mayfly larvae were collected from Blaney Creek by slowly hand-disturbing the streambed upstream of a dipnet. All material thus collected in the net was transferred into a white tray, and *Epeorus*, *Baetis*, *Ameletus*, and *Paraleptophlebia* larvae were transferred individually into holding jars using a large pipette. In this way, mayfly larvae were continually submersed during handling, and were moved without grasping them with forceps. In order to minimise disturbance, mayflies were released in the channels within 20 minutes of collection. Live and dead larvae of each mayfly taxa were released in both flow conditions. To ensure that the dead larvae released had natural body positions and specific gravity, live larvae were heat-killed by briefly immersing individuals in hot water ( $90 - 95^{\circ}\text{C}$  for 2-5 seconds), and used soon thereafter.

The settling velocities of dead larvae were measured empirically by releasing heat-killed larvae of each taxon in a 30 cm high settling tower (*Epeorus* n = 43, *Baetis* n = 65, *Ameletus* n = 34, *Paraleptophlebia* n = 48). The time it took for each larva to settle the final 5 cm was recorded and used to calculate the terminal still-water settling velocity ( $w_s$ ). The total body length (excluding terminal cerci) of each larva was measured with callipers.

Although live larvae released in the channel could not be identified to species, a subsample of the larvae collected were preserved and later identified, revealing that *Epeorus* larvae used were primarily *E. longimanus* Eaton, with the possible inclusion of a few individuals of *E. albertae* McDunnough, *Baetis* larvae were primarily *B. tricaudatus* Dodds, *Ameletus* larvae were primarily *A. validus* McDunnough, and *Paraleptophlebia* were primarily *P. temporalis* McDunnough with the possible inclusion of some *P. gregalis* Eaton. Larvae of all four mayflies are active during the day; the three herbivorous mayflies were regularly observed feeding on the upper surface of streambed stones in Blaney Creek during the day, while *Paraleptophlebia* was seen actively moving within detrital accumulations during daylight hours (T.M. Hoover, personal observations).

Passive particles with transport properties similar to stream invertebrates were created by incrementally adding small amounts of titanium dioxide pigment (density = 4.23 g/cm<sup>3</sup>) to melted beeswax (density = 0.97 g/cm<sup>3</sup>). When the desired density (1.005 g/cm<sup>3</sup>; prior tests showed that slightly negatively-buoyant particles have transport properties similar to mayfly larvae) was reached – tested by dropping small droplets of the molten material into a salt solution – the

beeswax / titanium dioxide mixture was poured into a plate and cooled. A corer was then used to punch small cylinders from the sheet of cooled wax mixture. This produced small pellets of the desired size (diameter = 4.0 mm, length = 2.5 mm).

Forty live and forty dead larvae of each taxon and forty passive particles were released individually 10 mm above the bed in each of the two velocity treatments (9 and 31 cm/s). Larvae were released from a pipette with a broad (approximately 5 mm wide) opening, with their long axis parallel to the direction of water flow, and their heads pointing in the downstream direction (Fig. 4-1). Care was taken not to force live larvae from the pipette during release. Larvae were not collected after settlement due to the difficulties of locating cryptically-coloured larvae amongst the coarse bed material. Passive particles were released using a pair of thin-tipped forceps as they could not be easily released using the pipette.

The trajectory of each larva released was tracked visually, and the hitting distance ( $x'_s$ ) and total transport distance ( $x_s$ ) were recorded (Fig. 4-1). Where possible, the distance moved in bedload ( $x_{BL}$ ) was calculated as the difference between the two distances (i.e.  $x_{BL} = x_s - x'_s$ ). The observed dominant swimming direction (upstream, downstream, upward (towards the surface), downward (towards the bed), or passive (little or no swimming behaviour)) of each larva was also recorded. Finally, we use the terms transport (where larvae are carried downstream in suspension until they contact the bed), contact (where larvae hit the bed), and attachment (where larvae grab hold of the substrate using their



legs or mouthparts, and stop moving downstream) to distinguish between the sequential and physically distinct components of the drift process (see Fig. 4-1).

### **Data analysis**

Linear regression was used to examine the relationship between the body lengths of dead larvae and still-water settling velocity for each of the four mayfly taxa. Regression was also used to relate larval body length and the hitting distances of dead larvae released in the experimental channel.

Non-linear regression was used to fit the hitting distance data to the exponential decay model

$$P_x = P_0 e^{-kx}$$

where  $P_x$  is the proportion of larvae (or particles) yet to contact the bed at distance  $x$ , and  $P_0$  is the total proportion of particles initially released. The exponent  $k$  is the instantaneous particle contact rate (the proportion of particles contacting the bed  $\text{particle}^{-1} \text{ m}^{-1}$ ), and is referred to here as the settlement coefficient. The reciprocal of the coefficient (i.e.  $1/k$ ) provides an estimate of the distance at which 63.2% of the larvae have contacted the bed. However, the cumulative settlement curves did not conform uniformly to the exponential decay model, although  $r^2$  values generally indicated a good fit. Generally, there was an evident reduction in the slope of each settlement curve, necessitating the fitting of separate equations to the two portions of the curve. The first portion of the settlement curve (described by  $k_1$ ) was characterised by the rapid settlement of

larvae immediately after release, and the second portion of the curve (described by  $k_2$ ) was characterised by a decreased rate of particle settling.

We tested for among-taxa differences in the hitting distances of live mayfly larvae among using one-way ANOVA; separate ANOVAs were conducted for the low- and high-velocity treatments. We tested for within-taxa (state-dependent) differences in hitting distance among live larvae, dead larvae, and passive particles in low and high water velocities using a  $2 \times 3$  factorial ANOVA (slow / fast  $\times$  live / dead / passive particle). The  $2 \times 3$  ANOVA was repeated for each of the four mayfly taxa. Tukey's HSD was used to test the significance of all post-hoc pairwise comparisons. Hitting-distance data were  $\log_{10}$ -transformed prior to analyses, which satisfied the assumptions of analysis of variance. Generally, median rather than mean hitting distances are presented due to the highly skewed distribution of the data.

To quantify the role of behaviour in settlement, the transport data of live and dead larvae were combined to create two behavioural indices (BI),

$$BI_k = (k_{1-LIVE} - k_{1-DEAD}) / k_{1-MAX}$$

where values for  $k_1$  are derived from the first segment of the settlement curves of live and dead larvae, and

$$BI_{x's} = (x'_{s-DEAD} - x'_{s-LIVE}) / x'_{s-MAX}$$

where values of  $x'_s$  are the median hitting distances of dead and live larvae released in the channel. Values of these indices approach a value of 1 if settlement is due entirely to behaviour, 0 if there is no behavioural component,

and -1 if animals are actively avoiding settlement (Otto and Sjöström 1986). A similar morphological index (MI) was calculated to quantify the role of morphology in downstream transport. The morphological index

$$MI = (x'_{s-Pp} - x'_{s-DEAD}) / x'_{s-MAX}$$

was calculated using the median hitting distances of passive particles ( $x'_{s-Pp}$ ) and dead larvae ( $x'_{s-DEAD}$ ). Positive values of MI approaching 1 indicate that the morphology of the larvae enhances settlement, (i.e. decreases the hitting distance), values around 0 indicate that morphology plays no role, and negative values approaching -1 indicate that morphology reduces settlement of larvae compared to simply-shaped passive particles.

All statistical tests were conducted in Systat v.10 (Systat 2000).

## Results

### General observations

The four mayflies displayed distinctly different drift behaviours. In general, the behaviours exhibited by each taxa (passive drifting, swimming towards the surface, towards the bed, upstream, or downstream) varied little between the two velocities (Fig. 4-2). *Epeorus* larvae either passively drifted or swam downward, although *Epeorus* larvae were notably weak swimmers, often swimming weakly with their legs rather than the rapid dorso-ventral undulations of the other three mayflies. *Baetis* larvae generally swam towards the bed, although the proportion of passively drifting larvae decreased (from 0.29 to 0.04) as velocity increased. *Ameletus* larvae were notably faster swimmers than the other mayflies; after

release, *Ameletus* larvae often swam briefly downstream then very rapidly towards the bed. When released, *Paraleptophlebia* larvae generally remained passive for a few seconds, and then swam weakly towards the bed; *Paraleptophlebia* larvae often tended to intermittently drift passively or swam in directions other than toward the bed (downstream or upward).

Whereas live larvae tended to 'attach' to the bed using their tarsal claws to grasp the surface of the substrate as they contacted it, dead larvae often settled in low-flow interstices between or behind stones, or were trapped in interstitial spaces underneath stones.

### **Length-settling velocity relationships**

There was a strong positive and linear relationship between body length and the still-water settling velocity ( $w_s$ ) of dead larvae for all four mayflies (Fig. 4-3). Although the relationships between body length and  $w_s$  (Table 4-1) were similar for *Epeorus* (slope = 0.21,  $r^2 = 0.86$ ), *Baetis* (slope = 0.18,  $r^2 = 0.67$ ), and *Paraleptophlebia* (slope = 0.20,  $r^2 = 0.52$ ), the  $w_s$  of *Ameletus* larvae increased at a much higher rate with body length (slope = 0.36,  $r^2 = 0.87$ ).

The strong relationship between body length and  $w_s$  did not translate into an equally strong relation between body length and hitting distance ( $x'_s$ ) when larvae were released in the experimental channel. The relationships between body length and the  $x'_s$  of dead larvae were negative as predicted, but generally very weak. In low velocity conditions, the relationship between body length and  $x'_s$  was not significant for *Epeorus* ( $r^2 = 0.059$ ,  $p = 0.13$ ) or *Baetis* ( $r^2 = 0.026$ ,  $p = 0.32$ ), but was moderately significant for *Ameletus* (slope = -0.087,  $r^2 = 0.12$ ,  $p =$

0.026) and *Paraleptophlebia* (slope = -0.12,  $r^2 = 0.13$ ,  $p = 0.021$ ). In high velocity conditions, the relationship was not significant for *Epeorus* ( $r^2 = 0.006$ ,  $p = 0.65$ ), *Ameletus* ( $r^2 = 0.010$ ,  $p = 0.54$ ) and *Paraleptophlebia* ( $r^2 = 0.000$ ,  $p = 0.94$ ), and was significant only for *Baetis* (slope = -0.062,  $r^2 = 0.19$ ,  $p = 0.005$ ).

### **Downstream transport**

Although the slopes of the cumulative settlement curves differed among taxa and between velocities, all settlement curves shared a notable change (reduction) in slope that occurred where 60 – 90% of the larvae had contacted the bottom (for live larvae in the low-velocity current, this was generally 0.08 – 0.20 m downstream of the release point, in the high-velocity current it was 0.35 – 1.0 m downstream) (Fig. 4-4). The settlement coefficients ( $k_1$ ) of live *Epeorus*, *Baetis*, and *Paraleptophlebia* larvae were similar in low-velocity conditions (Table 4-2), while the substantially higher coefficient of *Ameletus* ( $k_1 = 28.64$ ) indicated a much more rapid settlement rate, due to the tendency of these larvae to immediately swim towards the bed when released. In high-velocity conditions, *Ameletus* larvae had higher settlement coefficients than the other three mayflies, although the difference was not as pronounced as in the low-velocity conditions (Fig. 4-4).

The settlement coefficients ( $k_1$ ) and the associated standard errors of the settlement curves indicate that live larvae generally settled at a slightly faster rate than dead larvae (Fig. 4-4). There were two exceptions to this general pattern; first, live *Ameletus* larvae settled much faster than dead larvae in the slow

velocity treatment, and second, that there was little difference in the settlement rate of live and dead *Paraleptophlebia* larvae in either velocity (Fig. 4-4).

### **Hitting distances**

The hitting distances of live larvae varied significantly among the four mayflies in both slow (ANOVA,  $F(3,156) = 10.50$ ,  $p < 0.0001$ ) and fast currents (ANOVA,  $F(3,156) = 2.88$ ,  $p = 0.038$ ) (Fig. 4-5). In both velocities, differences were due entirely to the shorter hitting distances of *Ameletus* larvae (median  $x'_s$ , slow = 0.030 m, fast = 0.185 m). In the slow current, the hitting-distance of *Ameletus* larvae was substantially shorter than the other three taxa (Tukey's HSD, all comparisons between *Ameletus* and the three other taxa  $p < 0.001$ ) (Fig. 4-5), whereas in the fast current, *Ameletus* had a slightly shorter hitting distance than *Baetis* and *Paraleptophlebia* (Tukey's HSD,  $p = 0.064$  and  $0.050$ , respectively) but not *Epeorus* (Tukey's HSD,  $p = 0.19$ ) (Table 4-2). The hitting distances of *Epeorus*, *Baetis*, and *Paraleptophlebia* did not differ significantly in either the slow (Tukey's HSD, all  $p > 0.85$ ) or fast current (Tukey's HSD, all  $p > 0.94$ ) (see Table 4-2).

### **Comparisons among live larvae, dead larvae, and passive particles**

Comparisons of  $x'_s$  among live larvae, dead larvae, and passive particles showed that while both behaviour and morphology influenced transport distance, the degree of behavioural or morphological control varied with water velocity. For *Epeorus* and *Paraleptophlebia* larvae, only water velocity had a significant effect on hitting distance ( $F(1,234) = 24.4$ ,  $p < 0.0001$  and  $F(1,234) = 35.3$ ,  $p < 0.0001$ , respectively), whereas for *Baetis* larvae both velocity ( $F(1,234) = 32.5$ ,  $p$

< 0.0001) and state ( $F(2,234) = 6.3$ ,  $p < 0.002$ ) had significant effects. Velocity ( $F(1,234) = 54.6$ ,  $p < 0.0001$ ), state ( $F(2,234) = 17.5$ ,  $p < 0.0001$ ), and the interaction between state and velocity ( $F(2,234) = 7.6$ ,  $p = 0.001$ ) all had significant effects on the hitting distance of *Ameletus* larvae (see Fig. 4-5). Live and dead larvae of all four mayflies had significantly longer hitting distances in high-velocity than in low-velocity conditions (Tukey's HSD, all  $p \leq 0.05$ ). Interestingly, passive particles released in high-velocity conditions did not travel significantly further before hitting the bed than those released in low-velocity conditions (Tukey's HSD,  $p = 0.40$ ) (Table 4-3).

The hitting distances of live larvae of all four mayflies were generally less than those of dead larvae and passive particles in low-velocity conditions; the differences, however, were not significant (Tukey's HSD, all  $p > 0.19$ ) except for *Ameletus* (Tukey's HSD,  $p < 0.0001$ ). *Ameletus* larvae travelled a very short distance (median  $x'_s = 0.030$  m) in low-velocity conditions, due to their rapid, bed-directed swimming. In high-velocity conditions, there were no significant differences between the hitting distances of live and dead larvae of any taxa, including *Ameletus* (Tukey's HSD, all  $p > 0.49$ ), indicating that behavioural control over drift distance declined for *Ameletus* larvae as water velocity increased.

Generally, the hitting distances of dead larvae and passive particles were very similar when released in low-velocity conditions (Tukey's HSD, all  $p > 0.79$ ) (Fig. 4-5). The difference between the hitting distances of dead larvae and particles increased in high-velocity conditions, although not enough to be

significantly different in most cases. In the high velocity flows, the differences between dead larvae and particles were not significant for *Epeorus* (Tukey's HSD,  $p = 0.48$ ), *Ameletus* (Tukey's HSD,  $p = 0.93$ ) or *Paraleptophlebia* (Tukey's HSD,  $p = 0.31$ ); however, the  $x'_s$  of dead *Baetis* larvae was significantly greater than that of passive particles (Tukey's HSD,  $p = 0.015$ ).

As water velocity increased, the hitting distance of passive particles increased much less than that of all four mayflies.

### **Behavioural control over hitting distance**

The behavioural indices  $BI_k$  and  $BI_{x's}$  were positive for all taxa in both flow conditions, indicating that expressed behaviours enhanced settlement to some extent in all taxa. In all instances, BI values were lowest for *Paraleptophlebia* (Table 4-4); this mayfly had little control over the distance it traveled, despite its active swimming during transport. *Ameletus* larvae had high BI values in low-velocity conditions ( $BI_k = 0.81$  and  $BI_{x's} = 0.74$ ), but relatively low BI values in high-velocity conditions ( $BI_k = 0.39$  and  $BI_{x's} = 0.23$ ), indicating that the behavioural control that *Ameletus* larvae had over hitting distance was substantially reduced as water velocity increased. In contrast, the BI of *Epeorus* and *Baetis*, the two rheophilous taxa, were relatively unchanged (Table 4-4).

### **Morphological control over hitting distance**

In low-velocity flow conditions, passive particles and dead larvae (especially larvae of *Ameletus* and *Paraleptophlebia*) had very similar transport properties (Table 4-4). Slightly negative MI values for *Epeorus* and *Baetis* ( $-0.17$



and -0.29, respectively) in low-velocity conditions show that the morphology of these two mayflies resulted in moderately longer hitting distances than the similarly-sized particles, although the differences were not significant (Tukey's HSD, all  $p > 0.05$ ). However, the MI of all four mayflies became strongly negative in high-velocity flow conditions (Table 4-4), indicating that the dead larvae generally travelled substantially further than passive particles. However, only *Baetis* larvae travelled significantly further (Tukey's HSD,  $p = 0.015$ ; all other taxa  $p > 0.05$ ).

### **Travel in bedload**

The proportion of live larvae that attached to the bed immediately (i.e. did not reflect and move downstream in bedload before settling) was high for all taxa (Fig. 4-6), although the proportion reflecting off the bed at least once prior to settlement (i.e. moved in bedload) increased with water velocity (Table 4-2). All live larvae of all four taxa settled within the channel in both flow conditions. Dead larvae, in contrast, generally only settled within the channel at low velocities, and were generally exported from the channel at high velocities (Fig. 4-6), demonstrating that attachment behaviours provide mayfly larvae with substantial control over the distance they are transported downstream and the microhabitat types in which they settle.

Comparison of the transport and settlement of dead larvae and passive particles shows that larval morphology also acted to reduce the likelihood of being exported from the channel in both velocities. Virtually all passive particles moved in bedload in the low-velocity treatment, and although all passive particles

contacted the bed during transport in the high-velocity treatment, all were ultimately exported from the channel (Fig. 4-6). This contrasts with the lower probability of export of dead larvae; for instance, in high-velocity conditions a small but consistent proportion of dead larvae released were retained in the channel (*Epeorus* = 0.13, *Baetis* = 0.08, *Ameletus* = 0.10, *Paraleptophlebia* = 0.25).

### **Sweep-ejection processes**

It was noted in several instances – especially in high-velocity (31 cm/s) flow conditions – that particles and larvae would tumble erratically (sometimes contacting the bed) in the near-bed layer for a short distance, but would then be ejected into the outer flow region ( $0.5D < z < D$ ) where they would be transported rapidly and smoothly downstream in the outer layer, during which time they would slowly settle toward the bed. Eventually these particles would re-enter the well-mixed near-bed layer, where they would again begin to tumble erratically in the turbulent flow near the bed, eventually being re-ejected. These periodic ejections of particles resulted in clear modal peaks in the hitting-distance distributions of passive particles. In 31 cm/s flow, the modal peaks were approximately 80 – 90 cm apart (Fig. 4-7), while in 9 cm/s flow the modal peaks occurred at approximately 40 – 50 cm intervals. Although present, these modal peaks were not as clearly defined in the hitting distance distributions of larvae.

## Discussion

This study shows that water velocity not only directly increases the distance that stream invertebrates drift, but can also influence the degree of behavioural control that invertebrate larvae have over the drift process. While *Paraleptophlebia* larvae appeared to have little control over drift distance, *Epeorus* and *Baetis* larvae had a moderate degree of control at both water velocities, and *Ameletus* larvae had a substantial control at a low water velocity which notably declined as flow velocity increased. The role that flow played was complex and varied substantially among species; recognising that downstream transport (quantified here as the hitting distance) and attachment to the bed (settlement sensu stricto) are separate components of the downstream drift process provides important insight into the adaptive significance of drift and how hydrodynamic factors control drift distance (see also Walton 1978, Fonseca 1999, Koehl et al. 2007).

### How do drift processes vary among taxa?

Fast, bed-directed swimming behaviours allowed *Ameletus* larvae to rapidly return to the stream bottom at low water velocities, resulting in very short hitting distances. However, behavioural control over transport declined as water velocity increased, suggesting that the swimming behaviours of this mayfly became less effective as water velocity, and hence turbulence intensity, increased. *Ameletus* larvae also demonstrated an ability to effectively attach to the bed in both low and high water velocities. Ciborowski (1983) speculated that mayflies that are strong swimmers may be able to better control their orientation

during transport, especially at high velocities, enhancing settlement when larvae contact the substrate. Our results support that conclusion, especially in light of the fact that *Ameletus* larvae actively escape from predators by swimming, and are able to effectively control their orientation when doing so (T.M. Hoover unpubl. data). The effective swimming behaviours of *Ameletus* may permit it to settle on exposed stone surfaces with moderate water velocities and abundant periphyton. The drift behaviours of *Ameletus* starkly contrasted with those of the detritivore *Paraleptophlebia*. The transport properties of live and dead *Paraleptophlebia* larvae were similar, showing little behavioural control over hitting distance in either water velocity, despite the fact that this mayfly swims actively when drifting. An ability to rapidly exit the drift may not be necessary for *Paraleptophlebia*, however, as a lack of behavioural control may increase the likelihood that this mayfly will settle in low-flow depositional microhabitats with abundant organic detritus (Kobayashi and Kagaya 2002, 2004).

The downstream drift of the two rheophilous mayflies *Epeorus* and *Baetis* were very similar, despite the fact that these two mayflies are very morphologically and behaviourally different (Palmer 1995, Wellnitz and Poff 2006). *Epeorus* is dorso-ventrally flattened and a weak swimmer, whereas *Baetis* is a streamlined mayfly that is generally recognised as being a fast swimmer capable of actively exiting the drift (Elliott 1971, Ciborowski 1983, Palmer 1995). However, while both mayflies had only limited control over hitting distance, they attached to the bed readily when they contacted it, suggesting that they may reduce total drift distances in high-velocity habitats by maximising

attachment rates rather than reducing transport distance. Interestingly, behavioural control over transport did not decline with velocity for *Epeorus* and *Baetis*. While this difference may be attributed to swimming behaviours in *Baetis*, posture modification or morphological adaptations of *Epeorus* were likely responsible for increasing sinking rates as velocity increased. Palmer (1995) compared the downstream drift of *Baetis* and *Epeorus*, and showed that *Baetis* more efficiently drifted between patches, a trend that may be attributed to the bed-directed swimming behaviours observed in this study.

Several studies have demonstrated that there is substantial interspecific variation in drift distance and settlement distributions, and have attributed this variation to differences in drift behaviours, concluding that the ability to reach the bed varies among taxa (e.g. Ciborowski and Corkum 1980, Elliott 2002, Elliott 2003, but also see Ciborowski 1983). Rather, our results indicate that the ability of drifting invertebrates to attach to the substrate when they contact it may be an equally important determinant of total drift distance. In fast flows, a strong thigmotactic response allowed > 90% of *Ameletus* larvae to attach to the bed the first time they encountered it, whereas > 50% of *Paraleptophlebia* larvae reflected when they first contacted the bed and drifted further downstream before settling. Because larvae that do not readily attach will have greater total drift distances, the ability of drifting larvae to attach may be a critical factor controlling local population abundance, particularly for organisms that inhabit exposed, erosional microhabitats. The patterns of abundance of many drift-prone stream invertebrates are a function not only of resource abundance on the bed, but also

of the flux of individuals from and into the drift (Williams and Hynes 1976, Richards and Minshall 1988, Fonseca and Hart 2001). Interestingly, morphological factors also played a role in the attachment phase of the drift process; while live larvae attached to the bed much more rapidly than dead larvae, dead larvae also attached more rapidly than passive particles.

The hitting distances of the four mayflies were not strongly related to their habitat preferences. We initially predicted that the settlement of rheophilous mayflies would possess behavioural adaptations that would clearly enhance settlement by reducing hitting distance in fast currents, while those organisms that prefer slow flows would actively exit the drift in slow currents. However, rather than depending on drift movements to deliver them directly to a new habitat patch, stream insects may utilise the drift as a component of an iterative dispersal strategy, where individuals enter the drift and settle after a relatively short distance. Settled larvae can then assess the quality of the patch; if local resource availability is too low, physical habitat characteristics are unsuitable, or if predator-free areas are insufficient, larvae can either re-enter the drift (Peckarsky 1996, Rader 1997) or disperse by crawling upstream or downstream (Elliott 2003, T.M. Hoover unpublished data). For example, although there is generally a positive correlation between black fly (*Simulium vittatum*) larvae densities and water velocities, drifting black fly larvae do not settle as readily in fast currents as they do in slow flows (Fonseca 1999, but see Fingerut et al. 2006). However, black fly larvae will drift more readily from areas of slow flow (Fonseca and Hart 1996), and Fonseca (1999) speculated that the larvae will

continue to re-enter the drift until they settle in a habitat with sufficiently high flow rates. However, it is important to recognise that the drift strategies of relatively immobile taxa such as black flies are likely fundamentally different from highly mobile invertebrate groups such as mayflies, stoneflies (Plecoptera), and caddisflies (Trichoptera). These groups can actively and rapidly disperse across the streambed by crawling, whereas the movement rates of black fly larvae are restricted by their essentially leg-less morphology (see Reidelbach and Kiel 1990). Mayfly larvae may then move rapidly among habitat patches using a combination of drifting and crawling, and rapidly assess the relative value of a number of habitat patches (Rowe and Richardson 2001, Hoffman et al. 2006). As such, many stream invertebrates may rely on drift for relatively large-scale movement within the streambed landscape, while relying on crawling to access habitat patches.

In this study, comparisons between the hitting distances of live and dead mayflies indicate that *Ameletus* larvae were able to significantly reduce their hitting distances by rapidly and actively swimming towards the bed when water velocities were low. However, the efficacy of swimming as a means of reaching the bed diminished as water velocity increased. This result contrasts with the findings of Elliott (2002), who suggested that behavioural control does not vary with water velocity. Elliott estimated the mean time spent in the drift by dividing the mean distance travelled (estimated as  $1/k$ ) by the modal water velocity to show that the time that the larvae of several stream invertebrates spent in the water column while drifting was constant, regardless of velocity. If the same

approach (using the  $k_1$  coefficient of the cumulative settlement curves) is used to estimate the time the larvae in this study spent in the drift, a similar conclusion can only be drawn for *Epeorus* and *Baetis*, the two rheophilous mayflies. As velocity increased from 9 to 31 cm/s, the estimated time in the drift increased only marginally (for *Epeorus*, from 2.1 to 2.2 seconds, for *Baetis* from 1.9 to 2.2 seconds), suggesting that behavioural control over settlement did not decline notably with velocity. However, the time that *Ameletus* and *Paraleptophlebia* spent in the drift increased notably (from 0.4 to 0.9 and from 2.1 to 3.3 seconds for the two mayflies, respectively).. These results indicate that the settling behaviours of mayflies that prefer high-velocity habitats, whether they reflected in swimming or modified body posture, are not as affected by turbulence as the behaviours of taxa that prefer low-velocity habitats. Ciborowski and Corkum (1980) noted that the settlement curves for live and dead *Paraleptophlebia mollis* were similar at all velocities tested (10 – 26 cm/s), whereas as the settlement rates of live and dead *Baetis vagans* became more similar as velocity increased, live larvae still settled considerably faster than dead larvae at 26 cm/s. This not only corroborates our conclusion that there is substantial interspecific variation in the degree of control over settlement, but that the settlement behaviours of actively swimming larvae become less effective as water velocity increases.

### **Do coherent turbulent structures play a role in drift?**

In addition to reducing the effectiveness of swimming behaviours, turbulence may control the suspension and downstream advection of drifting larvae. Turbulence is an important feature of the physical environment of



streams and rivers (Carling 1992a, b), and many studies examining the role of flow in larval or particulate transport describe turbulence as a locally isotropic process. However, in most turbulent shear flows, intermittent anisotropic structures dominate momentum transport, and include intermittent fluid motions in the near-bed region termed 'fluid bursting' (Kline et al. 1967). Accelerated fluid motions towards the bed generating high bed shear stresses are termed 'sweeps', while fluid motions away from the bed are known as 'ejections' (Carling 1992a). These bursting events lead to grain dislodgement and advection (Williams et al. 1989), and may play a similarly important role in the entrainment and transport of invertebrate larvae. Sediment grains, due to their relatively high density, are most likely to be dislodged and entrained during the sweep phase of bursting events. Stream invertebrates, because of their low specific gravity, may not only be entrained during sweeps but may also be carried into the outer regions of flow away from the bed in the characteristic upwelling of fluid associated with ejection phases, leading to suspension and rapid downstream advection.

Modal peaks were present in the hitting-distance distributions in this study, especially in those of the passive particles, indicating that bursting may play a substantial role in the suspension and advection of low-density particles such as larvae and detrital particles. Keshavarzy and Ball (1997) showed that the angle of fluid ejections varied with distance from the bed, but ranged from 20 – 40 degrees (also see Grass 1971, Robinson 1991). If the particles released in this study were quickly entrained in an ejection, and assuming a mean ejection angle

of 30 degrees, a maximum suspension of  $0.75D$  above the bed, and a corrected value of  $w_s$  (based on  $z_0 = 0.010$  m and the distance to the first modal peak) of  $0.031$  m/s, the downstream travel distance of particles suspended by ejections would be approximately  $1.1$  m. Given the uncertainty associated with these assumptions (for instance, steeper ejection angles or lower values of maximum suspension above the bed would produce shorter travel distances), the close concordance of this estimate with the measured modal interval ( $0.8 - 0.9$  m) provides compelling evidence that bursting events were an important factor in the downstream transport of particles in this study. During the study, we observed that released larvae and particles shared qualitatively similar trajectories (erratic tumbling motions in the near-bed region, followed by ejection into the outer flow region and rapid advection downstream) after release. These motions are similar to those of particles observed by Sumer and Oguz (1978) who attributed them to bursting processes. Our results show that the transport of invertebrate larvae is dominated by physical factors, and as such, bursting events will likely increase the net upward movement of entrained larvae, increasing downstream transport distances, and resulting in elongated hitting distance distributions that are not easily predicted by current models of larval transport (see McNair 2006, McNair et al. 1997). The settlement distributions of organisms with limited ability to attach to the bed upon contact, such as *Paraleptophlebia* in this study, may be especially sensitive to these phenomena. These processes that govern the near-bed movements of particles may also be critical in the transport and settlement of

larvae in marine systems (see Williams et al. 1989), though they are rarely discussed (e.g. Fuchs et al. 2007).

These results underscore the importance of incorporating an understanding of hydrodynamic processes when examining the fluid-mediated transport of larvae in turbulent flows. Many empirical (e.g. Allan and Feifarek 1989, Fonseca 1999) studies have studied the physical mechanisms of invertebrate drift using experimental channels with flat beds and logarithmic velocity distributions that are well understood (Carling 1992b). However, velocity distributions over rough beds in shallow flows are highly three-dimensional and regularly deviate from a normal logarithmic distribution, and boundary layers are rarely well developed (e.g. Hoover and Ackerman 2004). While the simplified conditions used in many studies enable researchers to relate observed patterns of drift to hydrodynamic phenomena, they can also lead to conclusions that are not representative of drift processes in natural, rough-bedded channels. For instance, the numerical simulations of Fonseca (1999) showed that the relationship between the number of larvae in transport and the distance from the point of release is linear, and suggested that the negative exponential relationship observed in field studies (e.g. Elliott 1971) is due to spatial variation in current velocity. However, the larvae and passive particles in this study were all released in relatively uniform flow conditions, yet the relationship between numbers of larvae in transport and distance (in both the hitting distance and settling distance distributions) retained the familiar exponential form reported in several studies (Elliott 1971, Larkin and McKone 1985, Allan and Feifarek 1989).

This suggests that turbulent mixing is a more likely hypothesis for this distribution (see also McNair et al. 1997, McNair and Newbold 2001), although the relative contributions of isotropic turbulence and coherent fluid motions such as eddy shedding in the lee of large sediment grains or bursting events remain to be clarified.

## **Conclusions**

It is generally recognised that in stream systems, local populations are open subunits within a network of habitat patches linked by dispersal (Palmer et al. 1996). Understanding of how environmental factors constrain the movement of stream organisms is required before spatially explicit models that describe the relative importance of internal processes and flux of individuals in local population dynamics can be developed. Studies that seek to explain the adaptive significance of drift (e.g. Elliott 2002, Holomuzki and Van Loan 2002) and the role of drift in maintaining population processes (e.g. Englund and Hambäck 2004) must acknowledge that drift, whether active or passive, is essentially composed of three distinct components – entrainment, transport and attachment – and that the degree of behavioural control over each varies among taxa and among velocities. Our results show that water velocity increases the hitting distance of larvae and reduces the efficacy of bed-directed swimming behaviours, but the degree to which it does so is dependent on the traits of the species. Furthermore, downstream transport distances, and hence rates of population spread, are influenced by the suspension of larvae in coherent turbulent structures such as sweeps and ejections.

**Table 4-1**

Summary of the physical characteristics of larvae and passive particles (Pp), including specific gravity, mean body length (excluding cerci) and still-water settling velocity ( $w_s$ )

Particle type	Specific Gravity	Mean body length <sup>1</sup> (mm) (SD)	$w_s$ (cm/s) (SD)	Mean body length <sup>2</sup> (mm) (SD)
<i>Epeorus</i>	1.05	4.6 (1.9)	1.11 (0.43)	5.6 (0.6)
<i>Baetis</i>	1.06	3.5 (1.0)	0.63 (0.23)	3.9 (0.6)
<i>Ameletus</i>	1.06	4.4 (1.2)	1.18 (0.47)	5.2 (1.3)
<i>Paraleptophlebia</i>	1.03	4.9 (1.1)	1.05 (0.30)	5.6 (0.8)
Pp	1.005	4.0 (0)	1.37 (0.15)	n/a

<sup>1</sup> measured on dead larvae used in determination of  $w_s$

<sup>2</sup> measured on dead larvae released in channel (low velocity conditions)

**Table 4-2**

Settlement coefficients calculated for initial and secondary segments of cumulative settlement curves ( $k_1$  and  $k_2$ , respectively) for the four mayflies (live and dead) and passive particles (Pp), in both slow (9 cm/s) and fast (31 cm/s) flow conditions

	$k_1$ (SE)	$k_2$ (SE)	$r^2_1$ (p)	$r^2_2$ (p)
Slow (9 cm/s)				
LIVE larvae				
<i>Epeorus</i>	6.67 (1.03)	1.36 (0.05)	0.95 (0.006)	0.97 (< 0.0001)
<i>Baetis</i>	7.08 (1.43)	0.70 (0.03)	0.97 (0.11)	0.95 (< 0.0001)
<i>Ameletus</i>	28.64 (2.96)	3.65 (0.56)	0.99 (0.005)	0.75 (< 0.0001)
<i>Paraleptophlebia</i>	6.19 (0.53)	2.88 (0.20)	0.98 (0.001)	0.94 (< 0.0001)
DEAD larvae				
<i>Epeorus</i>	4.44 (0.09)	2.70 (0.16)	1.00 (< 0.0001)	0.96 (< 0.0001)
<i>Baetis</i>	3.70 (0.10)	1.29 (0.05)	1.00 (< 0.0001)	0.96 (< 0.0001)
<i>Ameletus</i>	5.56 (0.17)	0.94 (0.10)	1.00 (< 0.0001)	0.84 (< 0.0001)
<i>Paraleptophlebia</i>	5.03 (0.18)	4.29 (0.30)	1.00 (0.0009)	0.99 (0.0004)
Passive particles				
Pp	5.47 (0.37)	2.17 (0.23)	0.99 (0.003)	0.93 (< 0.0001)
Fast (31 cm/s)				
Live larvae				
<i>Epeorus</i>	2.09 (0.06)	0.41 (0.05)	0.99 (< 0.0001)	0.78 (< 0.0001)
<i>Baetis</i>	1.89 (0.08)	1.13 (0.07)	0.99 (< 0.0001)	0.96 (< 0.0001)
<i>Ameletus</i>	3.50 (0.13)	1.82 (0.10)	0.99 (< 0.0001)	0.95 (< 0.0001)
<i>Paraleptophlebia</i>	2.43 (0.40)	1.13 (0.08)	0.94 (0.007)	0.95 (< 0.0001)
Dead larvae				
<i>Epeorus</i>	1.21 (0.11)	0.89 (0.12)	0.94 (< 0.0001)	0.89 (0.0001)
<i>Baetis</i>	0.89 (0.10)	0.20 (0.01)	0.89 (< 0.0001)	0.93 (< 0.0001)
<i>Ameletus</i>	2.15 (0.21)	0.83 (0.06)	0.96 (0.0001)	0.94 (< 0.0001)
<i>Paraleptophlebia</i>	2.13 (0.18)	0.88 (0.06)	0.98 (0.0002)	0.95 (0.0001)
Passive particles				
Pp	2.87 (0.32)	1.69 (0.18)	0.97 (0.002)	0.91 (< 0.0001)

**Table 4-3**

Summary of transport and settlement parameters of the four mayflies and passive particles (Pp), including median hitting distance ( $x'_s$ ), the proportion of larvae or particles that moved in bedload after initial contact with the bed ( $P_{BL}$ ), and the mean distance that particles moved in bedload ( $x_{BL}$ )

	Slow (9 cm/s)			Fast (31 cm/s)		
	$x'_s$ (m)	$P_{BL}$	$x_{BL}$ (se)	$x'_s$ (m)	$P_{BL}$	$x_{BL}$ (se)
LIVE larvae						
<i>Epeorus</i>	0.070	0.13	0.400 (0.093)	0.295	0.30	0.842 (0.098)
<i>Baetis</i>	0.070	0.08	0.123 (0.016)	0.390	0.15	0.870 (0.137)
<i>Ameletus</i>	0.030	0	n/a	0.185	0.08	0.417 (0.125)
<i>Paraleptophlebia</i>	0.090	0.08	0.090 (0.023)	0.260	0.53	0.772 (0.032)
DEAD larvae						
<i>Epeorus</i>	0.150	0.90	0.280 (0.016)	0.445	0.93	1.676 (0.221)
<i>Baetis</i>	0.175	0.93	1.070 (0.039)	0.575	0.68	0.310 (n/a)
<i>Ameletus</i>	0.115	0.78	0.582 (0.028)	0.240	1.00	1.505 (0.345)
<i>Paraleptophlebia</i>	0.125	0.90	0.545 (0.023)	0.315	0.95	1.046 (n/a)
Passive particles						
Pp	0.125	0.98	1.057 (0.024)	0.190	1.00	n/a

Note:  $x_{BL}$  values are necessarily calculated only from those particles and larvae that moved in bedload but subsequently settled in the channel, whereas  $P_{BL}$  values also include those particles and larvae that moved in bedload but were exported from the channel

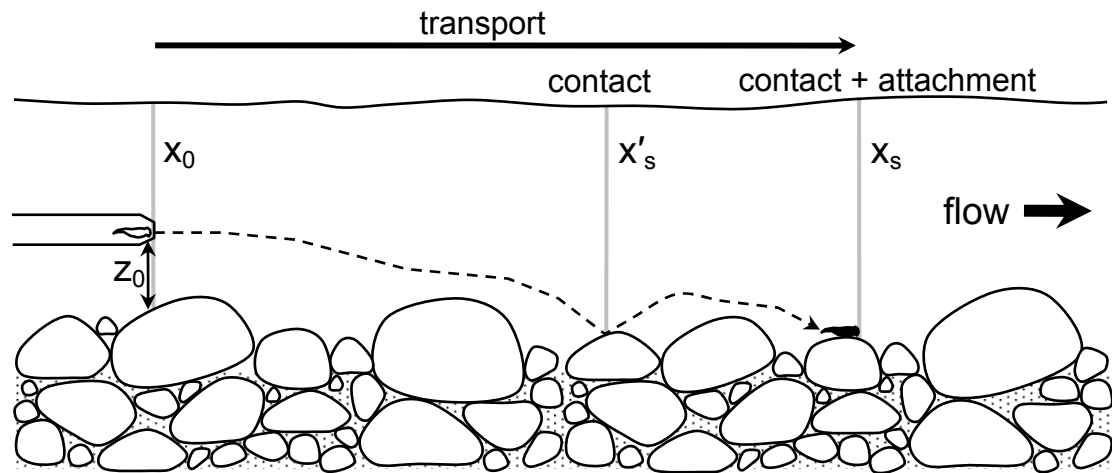
**Table 4-4**

Behavioural indices  $BI_k$  (calculated using the settlement coefficient  $k_1$ ) and  $BI_{x's}$  (calculated using the median hitting distance), and the morphological index  $MI$  (calculated using the median hitting distance)

	Slow (9 cm/s)			Fast (31 cm/s)		
	$BI_k$	$BI_{x's}$	$MI$	$BI_k$	$BI_{x's}$	$MI$
<i>Epeorus</i>	0.34	0.53	-0.17	0.42	0.34	-0.72
<i>Baetis</i>	0.48	0.60	-0.29	0.53	0.32	-0.78
<i>Ameletus</i>	0.81	0.74	0.08	0.39	0.23	-0.48
<i>Paraleptophlebia</i>	0.19	0.28	0	0.12	0.17	-0.60

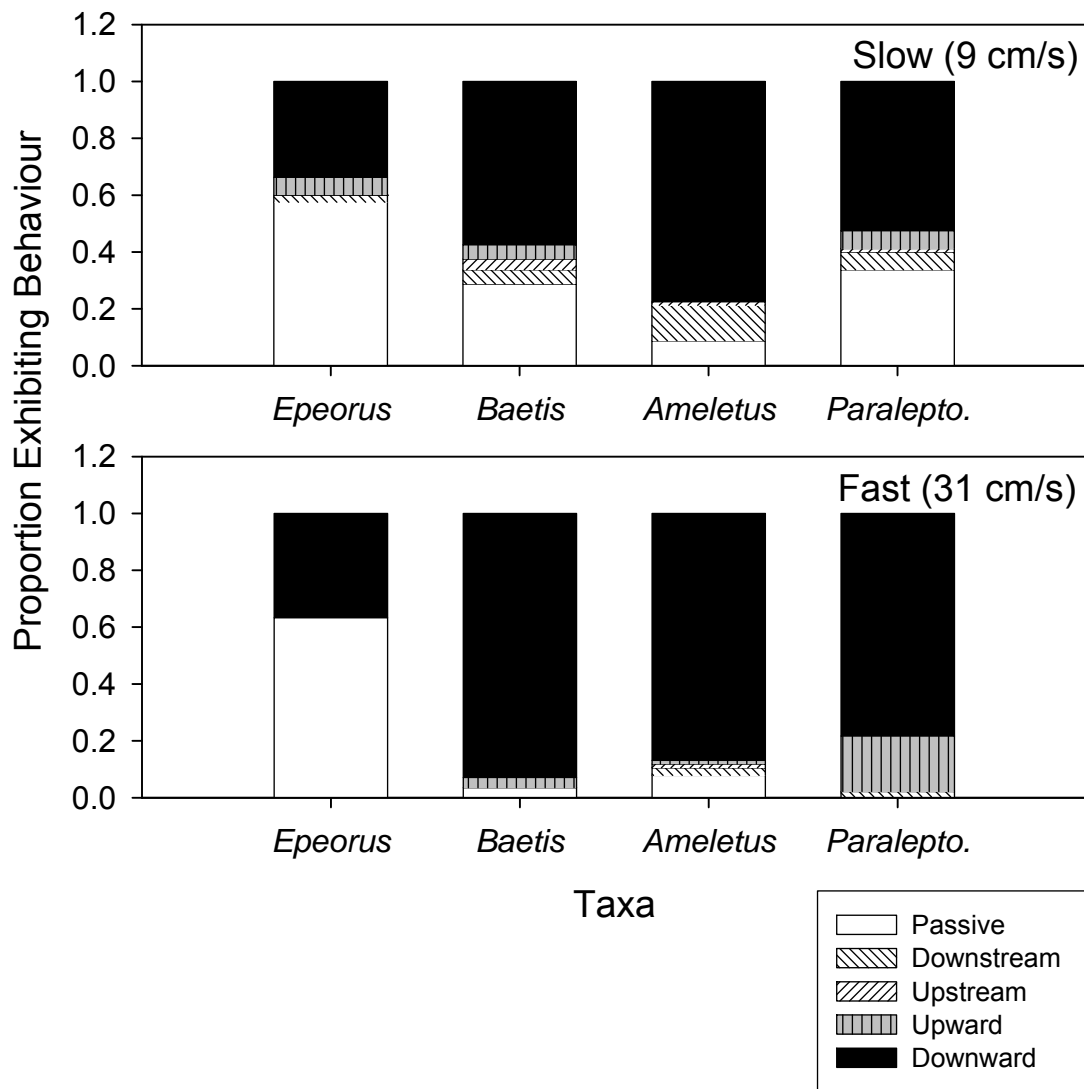
Note: positive  $BI$  or  $MI$  values indicate that behavioural activity or taxa-specific morphology enhance settlement (i.e. produce shorter hitting distances; see text for details)





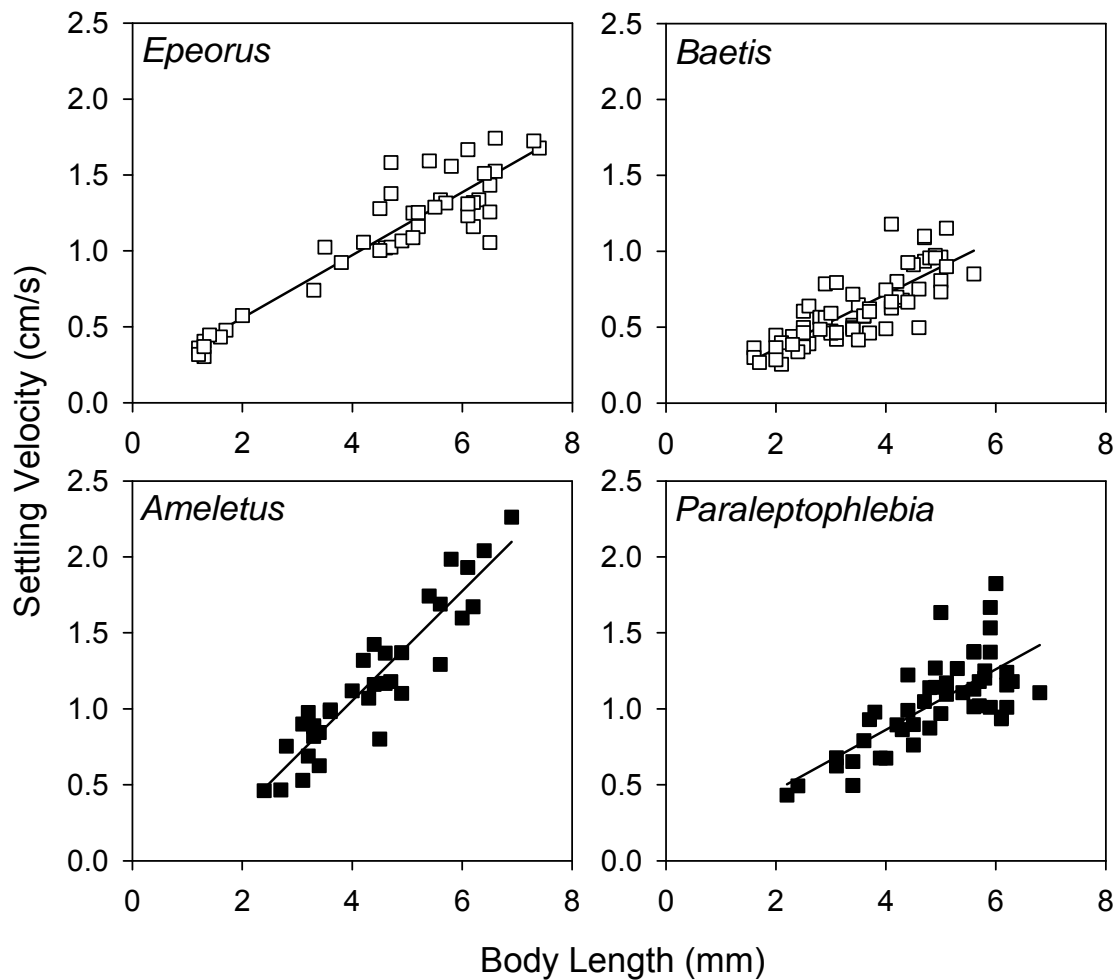
**Figure 4-1**

Diagram of setup used to release mayfly larvae in the experimental channel, showing the release point ( $x_0$ ), the hitting distance ( $x'_s$ ), and the total transport distance ( $x_s$ ).



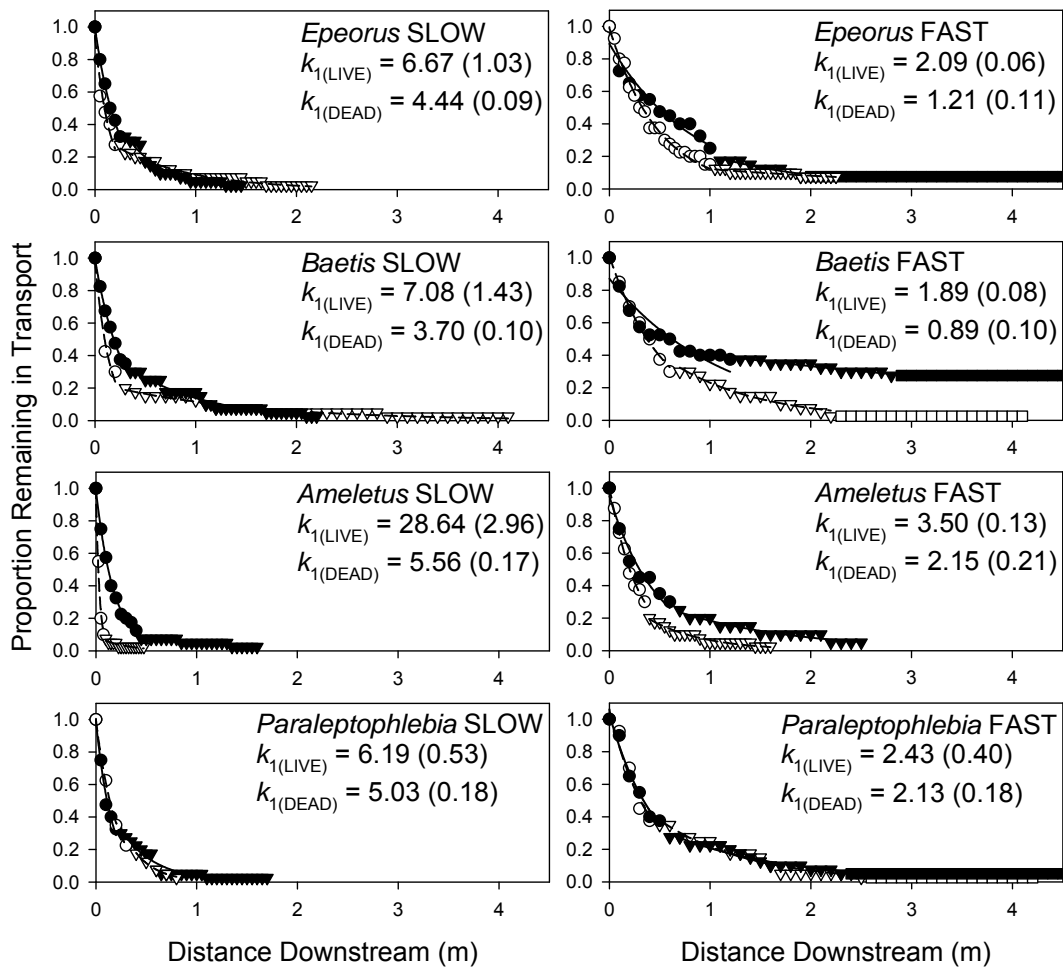
**Figure 4-2**

Dominant drift behaviours exhibited by four stream mayflies released in two water velocities (9 and 31 cm/s). Released mayflies could drift passively (little or no swimming movements) or could swim predominantly in downstream, upstream, upward (towards the water's surface), or downward (towards the streambed) directions. While swimming behaviours were generally complex and often were in more than one direction, the dominant behaviour was determined as that which occupied more of the transit time than any other behavioural type.



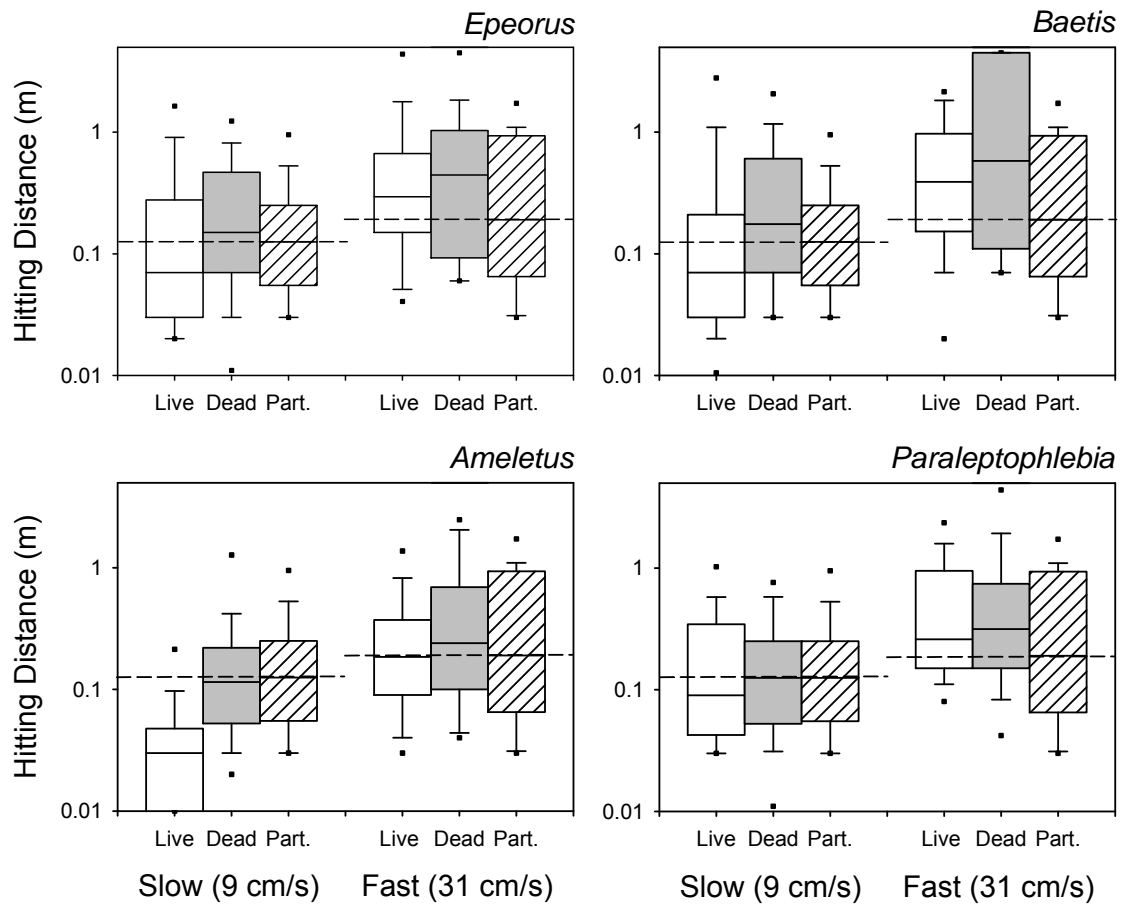
**Figure 4-3**

Relationship between larval body length (excluding cerci) and terminal still-water settling velocity ( $w_s$ ) for four mayflies (all larvae were dead). Hollow squares represent the two rheophilous taxa (*Epeorus* and *Baetis*), and solid squares represent the two low-velocity taxa (*Ameletus* and *Paraleptophlebia*). Regression lines are shown, see text for details.



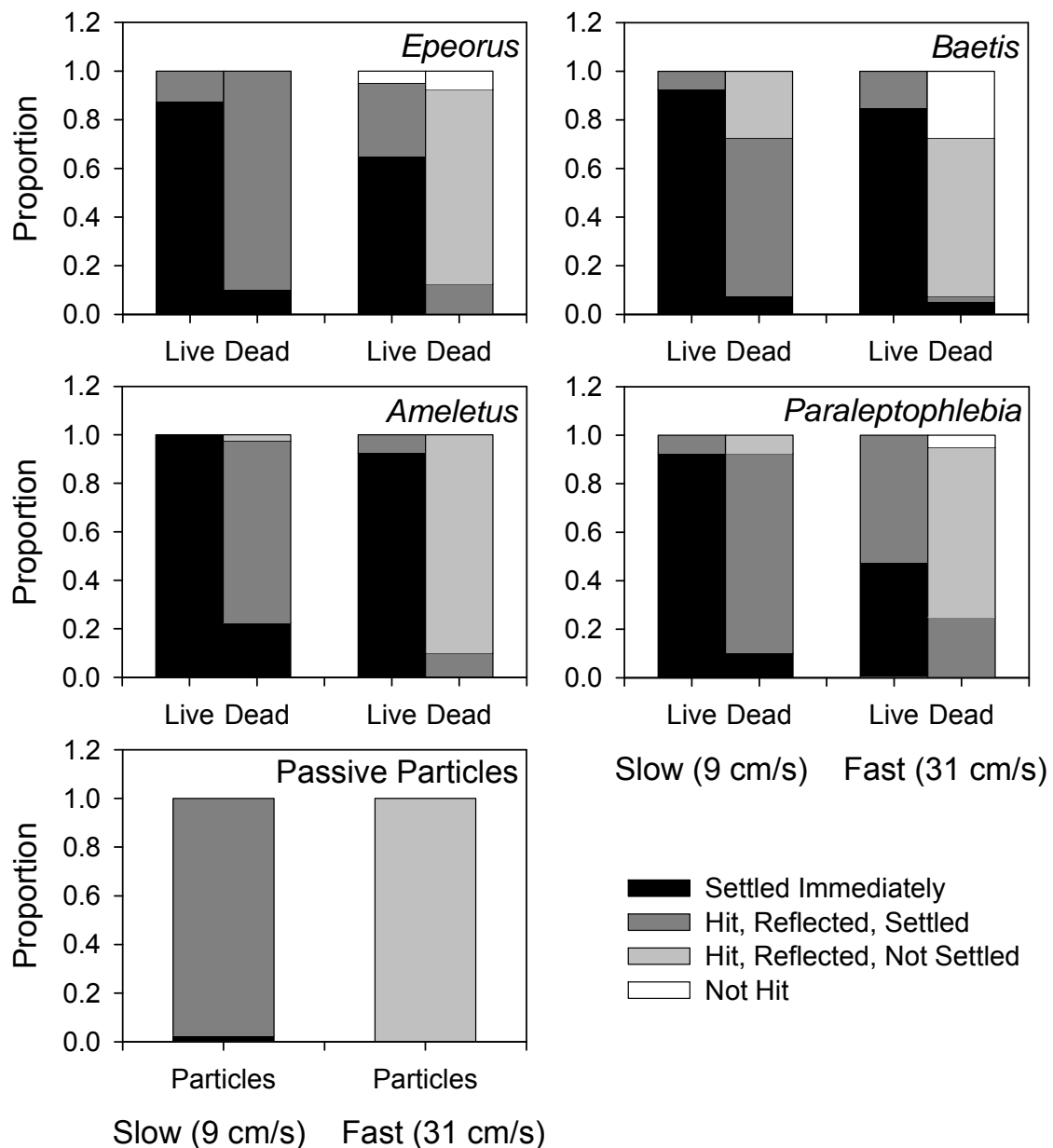
**Figure 4-4**

Cumulative settlement curves (based on hitting distance,  $x'_s$ ) for four stream mayflies released in two water velocities (9 and 31 cm/s). Points represent the proportion of larvae released that have yet to contact the substrate at the distance indicated. The settlement coefficient for the first segment of curve ( $k_1$ ) and the standard error of the coefficient (in parentheses) is shown for live and dead larvae in each plot. Hollow and solid symbols represent live and dead larvae, respectively. Separate regression lines are shown for the first and second segments of each curve (dashed lines = live larvae, solid lines = dead larvae). Circles represent the first segment of the settlement curve, triangles represent the second segment.



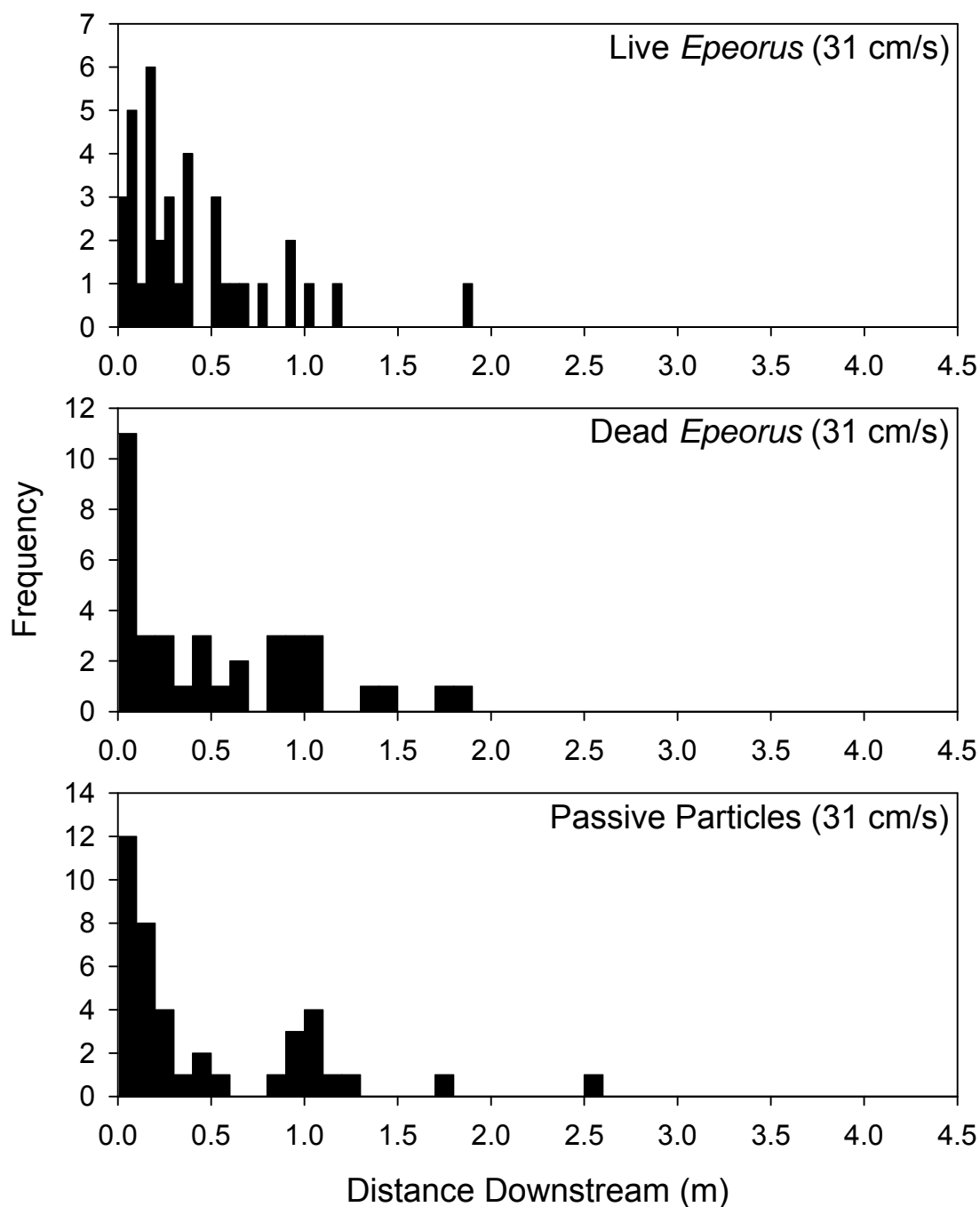
**Figure 4-5**

Boxplots showing the hitting distances of live larvae, dead larvae, and passive particles released in the experimental channel in two velocities (9 and 31 cm/s). The solid line is the median, the box represents the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers represent the 5<sup>th</sup> and 95<sup>th</sup> percentiles. The horizontal dashed line in each plot is the median hitting distance of the passive particles (included as a reference).



**Figure 4-6**

Fate of live larvae, dead larvae, and passive particles released in the experimental channel in two water velocities (9 and 31 cm/s). Larvae that “Settled Immediately” (black) and “Hit, Reflected, Settled” (dark grey) represent drift events that resulted in retention of larvae within the channel, while “Hit, Reflected, Not Settled” (light grey) and “Not Hit” (white) represent drift events that resulted in the emigration of the larvae from the channel.



**Figure 4-7**

Hitting distance distributions for live *Epeorus*, dead *Epeorus*, and passive particles released in the high-velocity flow (31 cm/s). Clear modal peaks are evident in the distribution of the passive particles, and, to a lesser extent, dead larval *Epeorus*.

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## **CHAPTER 5: FLOW-SUBSTRATE INTERACTIONS CREATE AND MEDIATE LEAF LITTER RESOURCE PATCHES IN STREAMS<sup>4</sup>**

### **Introduction**

In many small streams, terrestrially-derived leaf litter is a critical resource subsidy, providing food and habitat for decomposers and detritivorous organisms (e.g. Cummins et al. 1989, Richardson 1992a, Wallace et al. 1997). In many streams, the primary sources of allochthonous organic matter are riparian deciduous trees, whose leaves enter the stream after being shed in the autumn (McDowell and Fisher 1976). This leaf litter is generally carried downstream until it is retained, where it is then broken down by a combination of physical, chemical, and biological processes (Webster and Benfield 1986, Webster et al. 1999). These processes include abrasion by sediment particles moving in suspension or bedload (Heard et al. 1999), fungal and bacterial action (Gessner and Chauvet 1994, Sanzone et al. 2001), and fragmentation by shredders and other detritivorous invertebrates (Wallace et al. 1982, Hieber and Gessner 2002, Richardson et al. 2004).

The structure of the benthic community is influenced by the amount, type, and distribution of leaf litter that has entered the stream (Richardson 1991, Wallace et al. 1997, Rowe and Richardson 2001). However, the amount of leaf

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<sup>4</sup> A version of this chapter has been published. Hoover T.M., Richardson J.S. and Yonemitsu N. (2006) Flow-substrate interactions create and mediate leaf litter resource patches in streams. *Freshwater Biology*, **51**, 435-447.

litter available to benthic organisms is determined not only by how many leaves enter the stream, but also by how effectively the leaves are retained (Cummins et al. 1989). Due to the comparatively low specific gravity of leaf litter, leaves can only be passively deposited where water velocities and shear stresses are very low, such as in slow-moving pools and low-gradient channels (Jones and Smock 1991). However, leaf litter is also retained by fast-flowing reaches (Webster et al. 1987, 1994). Large-scale channel features such as woody debris, large boulders, encroaching riparian vegetation, and aquatic macrophytes effectively retain leaf litter (Smock et al. 1989, Webster et al. 1999, Muotka and Laasonen 2002). Leaves accumulate against the upstream face of these obstacles, creating leaf packs. Leaf packs, whether they are composed of a few or many leaves, represent discrete patches of abundant resources for detritivores (Casas 1997, Rowe and Richardson 2001, Kobayashi and Kagaya 2002).

Small-scale channel features such as streambed clasts can also retain leaf litter (Webster et al. 1987, Kobayashi and Kagaya 2002). In small streams where there is relatively little woody debris in the active channel, coarse-grained sediments can retain much of the leaf litter in transport, although fine sediments such as sand cannot (Ehrman and Lamberti 1992). Leaf packs that develop in association with individual sediment grains may be relatively small, consisting of only one or several leaves. If the degree of leaf surface area exposed to the flow is important in leaf breakdown, fragmentation of leaves in these locations may proceed more rapidly than that of the large masses of leaf litter contained in debris jams. Furthermore, leaf litter retained by sediment grains is not as stable,

and can become re-entrained when flow conditions change (Webster et al. 1999). As a result, leaves retained on individual streambed stones may represent relatively ephemeral, distributed resource patches compared to the long-term storage of large masses of leaf litter in debris jams. Knowledge of the role that substrate geometry plays in leaf litter retention will help to explicitly define the functional relationships that exist between bed material, resource patch distribution, and ecosystem processes in small streams (see Rowe and Richardson 2001, Silver et al. 2004).

Leaf transport distances are strongly correlated with increases in discharge (Webster et al. 1987, Brookshire and Dwire 2003). However, there are many variables that systematically vary with discharge that are more likely to be directly related to leaf retention. For example, channel depth, relative substrate protrusion, and velocity all change in a predictable fashion as discharge increases (see Knighton 1998). Webster et al. (1994) investigated leaf settlement processes using artificial, rectangular leaves of waterproof paper. They found that transport distances were related to depth, and concluded that the distance a leaf is transported is related to the probability that it will contact the bed. While it is clear that leaves must contact the bed before being retained, it is not known how streambed stone geometry influences the probability of leaf contact and subsequent retention.

Benthic invertebrates, including shredders, generally demonstrate strong preferences for microhabitats with characteristic ranges of bed roughness, water velocity, and degree of exposure to the flow (e.g. Bouckaert and Davis). Leaf

litter that is retained in the preferred microhabitats of detritivorous invertebrate taxa may be more readily utilised, leading to habitat-dependent variations in leaf litter breakdown rates. Knowledge of the physical processes involved in leaf retention and the formation of leaf packs will provide insight into the stability and residence times of detrital resource patches. Furthermore, as disturbance frequency and patch structure have substantial effects on invertebrate community structure (e.g. Murphy et al. 1998), the physical factors related to leaf retention and breakdown may have strong indirect effects on the benthic community.

Our study examined how physical factors related to streambed morphology influence the retention and breakdown of conditioned leaf litter in small streams. The results presented here are especially applicable to streams characterized by alternating riffle and pool subunits, flowing at baseflow discharge. The specific questions were: (1) what physical factors play the greatest roles in leaf retention processes, and do these processes differ between riffles and pools? (2) Are rates of leaf litter breakdown related to the small-scale topographical features of the streambed locations in which they settle? (3) How does streambed stone geometry influence leaf litter retention? The first two of these questions were addressed by conducting field experiments in a natural stream channel, and the third in a laboratory flume.

## **Methods**

Field experiments were conducted August to October 2002 in Spring Creek, a second-order stream located in the Malcolm Knapp Research Forest

near Maple Ridge, British Columbia. Spring Creek is located in the Coast Mountain range approximately 60 km east of Vancouver, and flows through a second-growth forest composed of Douglas-fir (*Pseudotsuga menziesii* Franco), and western red cedar (*Thuja plicata* Don). Riparian broadleaf tree species include red alder (*Alnus rubra* Bong.) and vine maple (*Acer circinatum* Pursh). These deciduous tree species contribute substantial amounts of allochthonous organic matter to coastal streams (Richardson 1992b). The substrate of Spring Creek is dominated by coarse glacial till, and the section of Spring Creek in which the study was conducted consists of well-defined, alternating riffles and pools of approximately equal length. Due to an extended period of limited rainfall, discharge during the study period was relatively stable and ranged from 0.011 m<sup>3</sup>/s (minimum; Oct. 31, 2002) to 0.014 m<sup>3</sup>/s (maximum; Sept. 6, 2002). Additional details on the physical and biological characteristics of Spring Creek can be obtained from Negishi and Richardson (2003).

### **Experimental leaves**

Fresh red alder leaves were collected in August 2002 from trees in Burnaby Mountain Park, British Columbia. After collection, the leaves were air-dried for two weeks. All alder leaves used were similar in size (mean petiole base-to-leaf tip length = 11.2 cm, SE = 0.07 cm). As the transport and settlement dynamics of conditioned leaves was the focus of the study, the leaves were soaked in dechlorinated tap water for 7 days at 5°C prior to their use. Leaves used in the leaf litter breakdown experiment (methods described below) were weighed prior to soaking ( $\pm 0.1$  mg).



## Experiment 1: Leaf transport and retention

To examine the roles of bed geometry and channel characteristics in the transport and retention processes of leaf litter in small streams, we performed a series of experimental leaf releases in three riffles and three pools in Spring Creek at baseflow conditions (see Table 5-1). The riffles and pools selected were relatively homogeneous throughout their lengths with respect to physical characteristics (i.e. velocity, bed roughness, etc.) (see Table 5-2). Preliminary releases of alder leaves in Spring Creek at baseflow conditions showed that, in general, leaves travelled further in riffles than in pools before being retained. To accommodate for these inter-reach differences in transport distance, conditioned leaves were released in 500 cm reaches in the three riffles and in 250 cm reaches in the three pools. Prior to the experimental release of leaves, all naturally settled leaves were removed from the test reaches. Although logs, twigs, and other forms of coarse woody debris are known to effectively retain leaf litter travelling in suspension (Ehrman and Lamberti 1992, Brookshire and Dwire 2003), there was very little coarse organic matter of these types in the test reaches.

Before release, each leaf was oriented parallel to and immediately below the water surface. Leaves were released individually and tracked visually until they settled on the streambed ( $n = 51$  in each riffle,  $n = 52$  in each pool). If the settled leaf was stable and did not become re-entrained after several seconds, the total distance travelled ( $x_s$ ) was recorded. Mean velocity ( $U$ ; taken at 60% of the total depth) was measured immediately upstream of the settlement point of

each leaf using a Swoffer current velocity meter (Model 2100). The cross-stream diameter ( $\Phi_y$ ) and roughness height ( $D$ ) of the largest stone in contact with the settled leaf (in riffles, generally the stone upon which the leaf was retained) was also recorded (Fig. 5-1A). Total water depth ( $d$ ) was measured immediately upstream of the settlement point of each leaf. Spatial autocorrelation in the distribution of settled leaves may occur if leaves are released at a single point in the channel. To avoid this, we released leaves not only at the head of each reach, but also at several different distances downstream from this point. This ensured that leaves settled throughout the reach. Water velocity, depth, and bed roughness characteristics varied little over the lengths of the six reaches; this within-reach physical homogeneity allowed for statistical comparisons of conditions measured at leaf settlement locations and a similar number of locations which were measured to determine mean channel conditions (reference locations).

Channel conditions were assessed by making measurements of the same suite of substrate and channel variables at 10 cm intervals along centreline transects of the six reaches. One longitudinal transect was made down the centre of each of the three riffles (i.e. 0 to 500 cm at 10 cm intervals,  $n = 51$  reference location measurements). To ensure similar sample sizes for statistical comparison, and to maintain the same spacing of reference locations, two parallel longitudinal transects (20 cm apart) were made down the centre of each of the three pool reaches (i.e. 0 to 250 cm at 10 cm intervals,  $n = 2 \times 26 = 52$  reference location measurements). This produced slightly different sample sizes

in the number of reference location measurements for riffle and pool reaches (i.e.  $n = 51$  and  $52$ , respectively). At each reference location, depth ( $d$ ), and mean velocity ( $U$ ) were measured. To measure the characteristics of the substrate in each reach, a 5.4 cm diameter circular ring (approximately the area of an alder leaf) was placed on the substrate at every reference location point. The cross-stream diameter ( $\Phi_y$ ) and roughness height ( $D$ ) of the largest stone that was entirely or partially contained within the circular area delineated by the ring was then measured.

Two bed geometry indices were calculated from the depth and bed roughness measurements made at each reference and leaf settlement point. Relative protrusion ( $H_d$ ), a measure of the degree to which substrate elements protrude upward into the flow, is the ratio of stone roughness height ( $D$ ) to channel depth ( $d$ ) (i.e.  $H_d = D/d$ ). Stone aspect ratio ( $A_r$ ), an index of substrate shape, is the ratio of stone roughness height ( $D$ ) to cross-stream stone diameter ( $\Phi_y$ ) (i.e.  $A_r = D/\Phi_y$ ). Higher values of  $A_r$  indicate relatively tall, narrow stones, while lower values of  $A_r$  indicate flatter, wider stones.

Leaf transport data were fit to the negative exponential retention model

$$N_x = N_0 e^{-kx}$$

where  $N_0$  is the number of leaves released, and  $N_x$  is the number of leaves remaining in transport at distance  $x$  (McLay 1970, Speaker et al. 1984). The slope,  $-k$ , is the instantaneous leaf retention rate (the number of leaves  $\text{leaf}^{-1} \text{cm}^{-1}$ ), and the reciprocal of  $k$  (i.e.  $1/k$ ) is an estimate of the average distance leaves travel in the reach before retention.

## **Experiment 2: Leaf breakdown**

Using a  $2 \times 2$  factorial design, we compared the rate of alder leaf breakdown in two reach types (pools and riffles) and two types of bed location that differed in their degree of exposure ('exposed' and 'sheltered' locations). In August - September 2002 individual alder leaves were attached to streambed stones, using two 2 mm rubber bands per leaf. Where possible, existing streambed stones were used; in all other cases, stream bank stones were used, but were placed in natural orientations on the streambed. Leaves were attached in either exposed or sheltered positions on each stone. The two exposure treatments mimicked the settlement locations of leaves that were retained either on the upper surfaces of protruding streambed stones (exposed locations) or in the interstices between stones (sheltered locations). Exposed leaves were affixed to the upper edge of the upstream face of the anchoring streambed stones, while sheltered leaves were attached to the lower leading edge of stones, with approximately half of the leaf constricted in the interstitial space under the front edge of the stone. The central vein of each leaf was oriented horizontally in all cases. Twenty leaves were fixed to the bed of Spring Creek in each of the four treatments. Similarly sized stones were used as anchors in all cases (mean longest-axis diameter of the anchoring stones = 6.9 cm, SE = 0.2 cm). Water velocity was measured approximately 5 cm upstream of each anchoring stone.

After ten days in the stream, the anchoring stones were removed from the stream. Remaining leaf litter was transferred into individually marked plastic bags, sealed, and frozen at  $-10^{\circ}\text{C}$ . The samples were later thawed, and leaf litter

was separated from any non-leaf material contained in the samples using a dissection microscope. The leaf litter samples were oven-dried at 60°C for a minimum of 24 hours, then weighed to the nearest 0.1 mg. The dried samples were then put into a muffle furnace for 2 hours at 550°C and reweighed to obtain ash-free dry mass. This measurement of ash-free dry mass was used in determinations of leaf mass loss in order to account for fine inorganic sediments that may have accumulated on the surface of the leaves while in the stream.

### **Experiment 3: Substrate geometry and leaf retention**

To examine the role of substrate geometry in leaf retention, we released artificial leaves upstream of substrate models (see Fig. 5-1B) whose geometry varied with respect to aspect ratio ( $A_r$ ) and leading edge angle ( $\theta$ ), and determined the efficiency with which each substrate retained the leaves. The experiment was performed in a recirculating laboratory flume (located in the Civil Engineering Hydraulics Lab, University of British Columbia) that was 750 cm long, 15 cm wide, and 48 cm deep. To provide flow conditions similar to those recorded in the riffles of Spring Creek, the mean velocity in the flume was held constant at 30 cm/s throughout the experiment. A 200 cm section of the flume bed was covered in a single layer of 1.5 cm diameter glass marbles, creating turbulent boundary-layer flow conditions in the channel. Experimental substrates were fixed to centre of the bed of the channel 180 cm downstream from the leading edge of this rough-bedded section.

The artificial substrates were made of wood and painted with flat white enamel paint, in order to ensure consistent surface textures and similar frictional

properties in all cases. Substrates were made with leading edge angles ( $\theta$ ) of  $90^\circ$ ,  $75^\circ$ ,  $60^\circ$ ,  $45^\circ$ , and  $30^\circ$ , and with aspect ratios ( $A_r = D:\Phi_y$ ) of 1:0.5, 1:1, 1:1.5, 1:2, and 1:2.5 (i.e. 25 substrates in total). Each substrate was 3.7 cm high, and when secured to the bed of the flume the top of the substrate protruded 3.4 cm above the upper surface of the marble bed. The width of the substrates varied with aspect ratio. For example, the width of substrates with aspect ratios of  $A_r = 1:1$  were 3.7 cm, while substrates with aspect ratios of  $A_r = 1:2$  were 7.4 cm wide. The total length (lower surface) of the substrates increased as the leading edge angle decreased (total substrate length = 3.7 cm +  $[3.7 / \tan\theta]$ ). The water depth in the flume, measured from the upper surface of the marble-roughened bed to the water surface, was 6.6 cm for all trials.

Artificial leaves were regular ovals (L 6.7 × W 3.3 cm) cut from acetate transparency film (3M, USA). The periphery and centre of the artificial leaves were marked with permanent ink to increase their visibility while under water. Each artificial leaf was released immediately above the bed (with the edge of the leaf approximately 3 mm above the bed, the long axis of the leaf horizontal and the blade perpendicular to the flow direction). Each artificial leaf was released 5 cm upstream of the leading edge of a test substrate. Releasing the artificial leaves in this fashion permitted them to contact the substrates in a manner similar to that in which entrained alder leaves encounter protruding streambed stones in natural stream environments. We released 50 leaves upstream of each of the 25 substrates, and calculated the proportion of artificial leaves retained by each.

## **Data analysis**

In the leaf transport and settlement experiment, differences in the substrate geometry and channel variables measured at leaf settlement locations and reference locations were tested using a one-way ANOVA, with site included in each analysis as a blocking variable (complete block design). For graphical representation, data from replicate sites were pooled as intersite differences were minimal.

In the leaf breakdown experiment, a  $2 \times 2$  factorial ANOVA was used to test for differences in alder leaf breakdown rates between reach types (riffles and pools) and between leaf exposure treatments (exposed and sheltered positions on the streambed). Post-hoc ANOVAs were subsequently conducted to test for differences in leaf breakdown rates within reach types. Water velocity and depth were measured at each leaf deployment location three times during the experiment; when the leaves were deployed, mid-way through the experiment, and when the leaves were removed. These measurements were averaged, producing time-integrated measures of the flow conditions (water velocity and depth) to which each deployed leaf was exposed during the experiment. All data were analysed using JMPIN 4.0.3 (SAS 2000).

## **Results**

### **Experiment 1: Leaf transport and retention**

Leaf retention in the six reaches fit the exponential decay model  $N_x = N_0 e^{-kx}$ , with all coefficients of determination ( $r^2$ ) being  $\geq 0.80$  (Table 5-1).

There were distinct differences in leaf retention patterns between the two reach types. Pools had higher retention coefficients than riffles (Table 5-1), indicating that at baseflow, these reaches retained conditioned leaf litter more efficiently than riffles. Leaves travelled further in riffles (mean travel distance = 222.4 cm) than in pools (mean travel distance = 87.3 cm).

Riffles and pools shared similar substrate characteristics. Stone aspect ratio was similar in all riffles and pools (Table 5-2), while the diameter and roughness height of streambed stones was similar in all sites except Pool 2, where streambed gravels were relatively less coarse (average stone diameter = 5.9 cm) (Table 5-2). As pools were deeper than riffles, the relative protrusion of streambed stones was greater. Velocity was substantially greater in the riffles than in the pools (Table 5-2).

### **Riffles – comparisons between reference and leaf settlement locations**

In riffles, protuberant clasts were the primary retentive structures. Generally, leaves were observed to travel in suspension through riffles, occasionally contacting then reflecting off the bed, until they stopped abruptly after coming into contact with and becoming trapped upon the upstream face of a protruding stone. Streambed geometry and flow characteristics at leaf settlement locations were significantly different than those measured at reference locations (Tables 2 and 3). Leaf settlement locations were characterized by significantly greater stone roughness heights ( $F(1,302) = 46.1, p < 0.0001$ ) and stone aspect ratios ( $F(1,302) = 22.4, p < 0.0001$ ) than reference locations (Fig. 5-2). There was, however, no difference in the relative protrusion of streambed stones



between reference locations and leaf settlement locations ( $F(1,302) = 1.9$ ,  $p = 0.17$ ). There were also significant differences in flow parameters between reference locations and leaf settlement locations. Water velocity measured immediately upstream of leaf settlement locations was significantly lower than at reference locations ( $F_{1,302} = 13.2$ ,  $P < 0.001$ ), while water depth was significantly greater ( $F_{1,302} = 7.64$ ,  $P = 0.006$ ) (Fig. 5-2).

### **Pools – comparisons between reference and leaf settlement locations**

In pools, leaves were retained when they passively settled to the streambed. Settling leaves hit and reflected off large, protrusive streambed stones while settling, eventually coming to rest atop smaller stones in the deeper interstices between the largest stones. Several channel and bed geometry characteristics differed significantly between reference and leaf settlement locations (see Tables 2 and 3). Depth was significantly greater at leaf settlement locations than at reference locations ( $F(1,308) = 42.9$ ,  $p < 0.0001$ ) (Fig. 5-2). In contrast, stone height ( $F(1,308) = 28.4$ ,  $p < 0.0001$ ), relative protrusion ( $F(1,308) = 48.8$ ,  $p < 0.0001$ ), and stone aspect ratio ( $F(1,308) = 5.74$ ,  $p = 0.017$ ) were all significantly greater at reference locations than at leaf settlement locations (Fig. 5-2). There was no difference in water velocity between reference locations and leaf settlement locations ( $F(1,308) = 0.55$ ,  $p = 0.46$ ).

### **Experiment 2: Leaf breakdown rates**

Leaf breakdown rate was dependent both on reach type (riffle vs. pool) and the degree of leaf exposure on the streambed (Fig. 5-3). Leaves broke down more quickly in pools than in riffles ( $F(1,76) = 19.24$ ,  $p < 0.001$ ), with only

very small fragments of leaf remaining in many instances. However, differences in leaf breakdown rates between exposed and sheltered locations were not consistent between pools and riffles, as shown by a significant interaction term (exposure  $\times$  reach;  $F(1,76) = 7.25$ ,  $p = 0.009$ ). In riffles, breakdown was slower (i.e. there was more leaf mass remaining after the study period) for leaves exposed on the upper surface of streambed stones than those leaves in sheltered locations ( $F(1,38) = 4.39$ ,  $p = 0.043$ ). In pools, however, leaf breakdown was significantly slower in sheltered locations than in exposed locations ( $F(1,38) = 4.70$ ,  $p = 0.037$ ). Water velocity was significantly greater at the leaf deployment locations in riffles (mean riffle velocity = 32.3 cm/s) than in pools (mean pool velocity = 3.7 cm/s) ( $F(1,78) = 266.10$ ,  $p < 0.0001$ ).

The breakdown of exposed leaves in riffles was negatively related to the water velocity ( $U$ ) measured in front of each leaf (percent leaf mass remaining =  $(0.80 U) - 9.42$ ;  $r^2 = 0.36$ ;  $F(1,18) = 9.91$ ,  $p = 0.006$ ). However, water velocity was not related to the breakdown of leaves located in sheltered microhabitats in riffles ( $r^2 = 0.093$ ), exposed leaves in pools ( $r^2 = 0.010$ ) or sheltered leaves in pools ( $r^2 = 0.050$ ).

The substantial amounts of alder leaf mass lost in ten days in Spring Creek indicate that rates of mass loss were substantially greater than those reported in other studies where alder (*Alnus* spp.) leaf packs were deployed in riffle habitats. Assuming that the alder leaves deployed singly in Spring Creek lost mass according to the exponential decay model  $M_t = M_0 e^{-kt}$  (where  $M_0$  and  $M_t$  are the dry mass of the leaves at the beginning and end of the experiment,  $t$  is

time spent in the stream, and  $-k$  is the mass loss coefficient), estimates of the rates (loss rate  $\text{day}^{-1}$ ) at which leaves placed in Spring Creek riffles lost mass are 0.19 (exposed riffles) and 0.27 (sheltered riffles). Although there are undoubtedly many factors that vary between studies (e.g. water temperature, detritivorous taxa present, leaf handling and deployment, etc.), a comparison of these studies shows that alder leaf breakdown proceeds more rapidly as the size of the leaf pack decreases ( $r^2 = 0.70$ ;  $F(1,8) = 19.0$ ,  $p = 0.002$ ) (Fig. 5-4). Leaf packs composed of green-picked alder leaves (Maloney and Lamberti 1995; this study) appear to break down at a substantially greater rate than leaf packs of abscised alder leaves.

### **Experiment 3: the role of substrate geometry in leaf retention**

Substrate leading edge angle ( $\theta$ ) and substrate aspect ratio ( $A_r$ ) were important factors in artificial leaf retention. Substrates with high aspect ratios (i.e. narrow relative to height) or with leading edges that were vertical or nearly vertical retained artificial leaves at the greatest rate (Fig. 5-5). All substrates with vertical leading edges (i.e.  $\theta = 90^\circ$ ) retained 100% of leaves released. However, the relationship between leading edge angle, aspect ratio, and leaf retention demonstrated unexpected complexity, as shown by asymmetry in the response surface plotted in Fig. 5-5. Substrates that were wide relative to their height ( $A_r = 1:2, 1:2.5$ ) and that had low-angled leading edges ( $\theta \leq 60^\circ$ ) retained leaves less effectively than all other substrate shapes. Substrates whose height and width were similar ( $A_r = 1:1$ ) retained leaves most effectively.

## **Discussion**

Determining how resource subsidies are incorporated into recipient food webs requires not just an understanding of the amount of resources transferred from the donor system, but also of the physical mechanisms of resource delivery that ultimately determine the distribution of those resources. How and where terrestrially-derived leaves are retained on the streambed determines how resource patches (i.e. leaf packs) are created, and to which constituent species of the stream community these resources are available. The results of this study showed that leaf litter retention in a small stream was a function of the interaction between water flow and streambed geometry. The spatial distribution of retained leaf litter will thus vary between reaches that differ substantially with respect to mean water velocity and bed-related factors such as the relative protrusion of streambed stones. Leaves were retained in shallow, high-velocity reaches (riffles) when they encountered relatively narrow, protruding clasts, whereas leaves passively settled to the bed in slow-moving, deeper reaches (pools). This demonstrates that in terms of leaf retention, bed structure is a more important factor in riffles than in pools. Leaf litter breakdown rates varied between these two habitat types, with leaves losing mass more rapidly in pools than in riffles. However, breakdown rates also varied between microhabitats (exposed and sheltered streambed locations).

### **The role of geomorphology in leaf retention**

In Spring Creek, leaves released in riffle reaches were retained as they encountered protruding streambed stones with high aspect ratios. Leaf litter and

other types of suspended coarse organic matter may accumulate at these locations, creating spatially discrete patches of food and habitat resource (Richardson 1992a, Kobayashi and Kagaya 2002, also see Rowe and Richardson 2001). Depths measured at leaf settlement locations were significantly greater than those measured at reference locations, demonstrating that at baseflow conditions leaves in transport are not likely to be retained in the shallowest parts of riffles. The relatively large size of alder leaves may prevent them from being transported into these shallow sections, facilitating the retention of alder leaf litter in the active channel where it will continue to be accessible to detritivores if discharge declines.

Leaf settlement locations in riffles were also characterised by significantly lower water velocities. Flow stagnates at the leading edge of bluff bodies in moving water, creating a zone of lower velocity (see Nowell and Jumars 1984). The mean of water velocities measured at reference points will also tend to be greater because these measurements include relatively flat areas of the bed with little roughness; water would accelerate over these 'plane' beds where leaf litter would not be retained. Due to the complex nature of flows over rough, natural beds (e.g. Hoover and Ackerman 2004), it is difficult to assess the role of water velocity in leaf retention. Clearly, however, flow is an important factor; leaves are generally flat and flexible, which allows them to be 'wrapped' around the upstream side of in-stream obstacles such as protruding stones and woody debris in riffles by the force of flow (Cummins et al. 1980, Kobayashi and Kagaya 2002, this study). Ehrman and Lamberti (1992) suggest that retention is related

to sediment grain size, and that retention is a function of the probability of a particle encountering the bed or other retentive structure (also see Webster et al. 1994). Alder leaves released in the shallow riffles of Spring Creek often contacted several stones before being retained. This suggests that leaf retention is not entirely a function of encounter with the bed alone, but rather is also dependent on the likelihood that the leaf will encounter a retentive structure on the bed (e.g. a protruding streambed stone with a high-angle upstream face). Furthermore, it is likely that a large proportion of the area of the leaf may have to contact a retentive surface before the leaf can be retained.

Alder leaves released in pools travelled short distances before settling passively to the bed. The experiment was conducted during the late summer and early autumn when channel discharge was low, hence, mean velocities in the pools were low (4.2 – 7.0 cm/s). Compared to the riffles, there was little variation in leaf transport distance in pools, indicating that leaves settling to the bed in these conditions would accumulate in a common location rather than forming dispersed patches (see also Kobayashi and Kagaya 2002, Silver et al. 2004). The aggregations of leaves in pools have a loose, open structure, and may be much larger in size. Leaves settle passively in low-flow areas where the shear stress is insufficient to mobilise them, but will become re-entrained when discharge increases. Both the physical structure of leaf packs in pools and the hydraulic conditions in which they form may influence the fashion in which this resource subsidy is incorporated into the stream food web (see Jonsson and Malmqvist 2000, Kobayashi and Kagaya 2002).

The patterns of alder leaf retention in Spring Creek suggest that flow-substrate interactions acted to partition leaf litter inputs between riffles and pools. In Spring Creek, leaves traveled 2.6 times further in riffles than in pools, primarily due to the low velocity of the pool reaches. At these baseflow conditions, all conditioned leaves that enter pool reaches would have been retained, whereas a small percentage of leaves were transported through riffles into the pools below. If alternating riffle and pool reaches are relatively long and are approximately equal in length, then each reach will be primarily supplied with the leaf litter that enters the stream locally. However, the number of leaves transported through riffles into the pool below will increase as riffle length decreases or the retentive capacity of the riffle declines (e.g. has fewer retentive structures). At baseflow, geomorphologically distinct riffle-pool reaches may disconnect the downstream movement of leaves. This pattern applies only to whole leaves; as leaves are broken down, the rate at which remaining fragments are retained on protuberant clasts may decline (see Webster et al. 1987). It is also important to note that the retention patterns of freshly fallen leaves will also be much different. Leaves that are not yet conditioned will float on the water's surface. As such, passive retention in pools is unlikely, and retentive structures in riffles and the periphery of streams may thus play a primary role in the retention of newly delivered material. Fresh leaves conditioned in these 'retention zones' will then be re-entrained during spates, distributing conditioned leaf litter among streambed microhabitats.

## **Microhabitats and leaf litter breakdown**

In Spring Creek, leaf litter placed in exposed, high-shear stress locations in riffles broke down more slowly than leaf litter in all other microhabitat types (sheltered riffle, exposed and sheltered pool locations). In Swedish streams, Lepori et al. (in press) found that current velocity was the single best predictor of the rate of mass loss of alder leaves (but see Reice 1974). They attributed this to mechanical fragmentation during high flows. However, leaves placed in exposed locations in Spring Creek riffles lost the lowest proportion of mass. This demonstrates that while mechanical fragmentation, either by shear stress or by scouring by sediments moving in suspension or bedload (Heard et al. 1999), may be primarily responsible for leaf fragmentation at high discharges, it is not the most important factor determining rates of leaf litter breakdown in small streams at baseflow.

Several authors have shown that both shredder abundance and diversity has a strong influence on the rate of leaf litter breakdown in streams (Sedell et al. 1975, Jonsson and Malmqvist 2000, Richardson et al. 2004). However, substantial variation in leaf breakdown rates between microhabitat types in Spring Creek (exposed and sheltered positions in riffles and pools) suggests that not all retained leaf litter is equally accessible to all detritivorous taxa. Those detritivorous invertebrate taxa that show marked preferences for low-velocity microhabitats may be unable to access leaf litter retained in high-velocity habitats (see Richardson 1992a). As a result, leaf litter retained in riffles may be available



only to a limited subset of the benthic detritivore community, producing low rates of biological fragmentation.

Kobayashi and Kagaya (2002) showed that litter patches in riffles and pools had distinct macroinvertebrate assemblages. Shredder taxa in pools tended to be dominated by cased caddisfly larvae, whereas shredders in riffles were primarily stoneflies. They suggest that cased caddisflies are unable to effectively penetrate the tightly packed accumulations of leaves in riffles. Direct interactions between detritivores and geomorphological factors may also influence rates of leaf litter breakdown in pools. For example, the signal crayfish *Pacifastacus leniusculus* is a large, abundant detritivore in Spring Creek, but is found in high densities only in low-velocity pool habitats (C. Bondar, UBC, pers. comm.). Although crayfish are known to be directly responsible for a large proportion of total leaf breakdown in many stream systems (e.g. Schofield et al. 2001), the relatively large size of crayfish may prevent them from accessing leaf litter fragments in small interstitial spaces. Other large shredders (such as *Lepidostoma* sp., a cased caddisfly found in streams of the MKRF; Reece and Richardson 2000) may be similarly unable to access leaf litter stored in interstitial spaces. The differences in leaf breakdown rate between microhabitat types in Spring Creek pools (exposed > sheltered) may thus be a function of the physical limitations of detritivorous taxa.

Processes involved in leaf fragmentation in streams, such as microbial and macroinvertebrate colonisation of leaf litter, may be dependent on the size or surface area-to-volume ratio of the patch. Cummins et al. (1980) suggest that

the breakdown of leaves inside leaf packs may be limited by the development of anaerobic conditions inside the accumulation of leaves. Most studies examining leaf litter breakdown rates have used leaf packs consisting of large masses of leaves (e.g. Sedell et al. 1975), often enclosed in mesh bags or cages (Heard et al. 1999, Richardson et al. 2004). In the autumn and early winter, deciduous leaves can accumulate in large masses on the streambed, and the use of leaf packs adequately simulates these conditions. However, red alder, a common riparian species in western North America, drops leaves throughout the summer months (Richardson 1992b, Richardson et al., in press). These leaves are often retained singly, or in accumulations consisting of only a few leaves, on the streambed.

The rates of alder leaf breakdown reported in this study exceed those reported elsewhere (e.g. Jonsson and Malmqvist 2000, Maloney and Lambert 1995). This difference may be due in part to the use of single leaves, rather than leaf packs, in this study; leaf breakdown rate appears to be inversely correlated with initial leaf pack mass (Fig. 5-4). However, breakdown rates may also be strongly influenced by the developmental age of the leaves used. The lignin content and toughness of deciduous leaves increase as they develop, and the breakdown rates of leaves retained in streams are inversely related to lignin concentration (Royer and Minshall 2001). Green, less tough alder leaves with lower lignin content may be colonized more readily by microbial decomposers and consumed more quickly by shredders (Motomori et al. 2001). Furthermore, the leaves used in this study were soaked for several days prior to their

placement in the stream; this conditioning may have also resulted in faster breakdown rates (Motomori et al. 2001).

This study shows that flow-substrate interactions influence the availability and distribution of leaf litter, a crucial resource subsidy to many streams. If the restoration of the ecological function of streams is a goal of stream ecologists, it will be necessary to account for the physical pathways by which terrestrial subsidies are incorporated into stream ecosystems. Many restoration efforts have attempted to increase the retentive capacities of streams by adding large-scale retentive structures like woody debris or boulder clusters (e.g. Muotka and Laasonen 2002, Negishi and Richardson 2003, Lepori et al., in press). While this may increase the retention of leaf litter, it may create only large isolated patches that provide food and habitat for some species, but neglect the requirements of other taxa that thrive in smaller, isolated patches in high-velocity habitats. The addition of large, angular bed material to restored riffles may help to create resource patches of this type.

**Table 5-1**

Physical characteristics and leaf litter transport parameters (mean with 1 SE in parentheses) of the six study reaches used in the leaf transport and retention experiment. The term  $-k$  is the leaf retention coefficient, and is derived from the slope of the exponential decay model  $N_x = N_0 e^{-kx}$  ( $r^2$  indicates the fit of the data to the model) ( $n = 51$  leaves released in each riffle,  $n = 52$  in each pool)

Reach	Width (cm)	Total reach length (cm) <sup>a</sup>	Mean leaf transport time (s)	Mean leaf transport distance (cm)	$-k$ (cm/s)	$r^2$
Riffle 1	126 (6.0)	640	13.84 (0.64)	226.20 (16.40)	0.75	0.98
Riffle 2	162 (13.6)	560	12.25 (1.13)	276.18 (22.45)	0.55	0.80
Riffle 3	101 (7.1)	600	8.91 (0.70)	164.69 (13.36)	0.97	0.98
Pool 1	314 (7.4)	710	17.0 (0.89)	109.14 (5.14)	2.51	0.94
Pool 2	251 (4.0)	730	21.68 (0.91)	57.96 (3.75)	4.00	0.88
Pool 3	260 (18.2)	480	15.58 (0.94)	94.67 (7.11)	2.04	0.94

<sup>a</sup> experimental portions of the reaches were a fraction of total reach length

**Table 5-2**

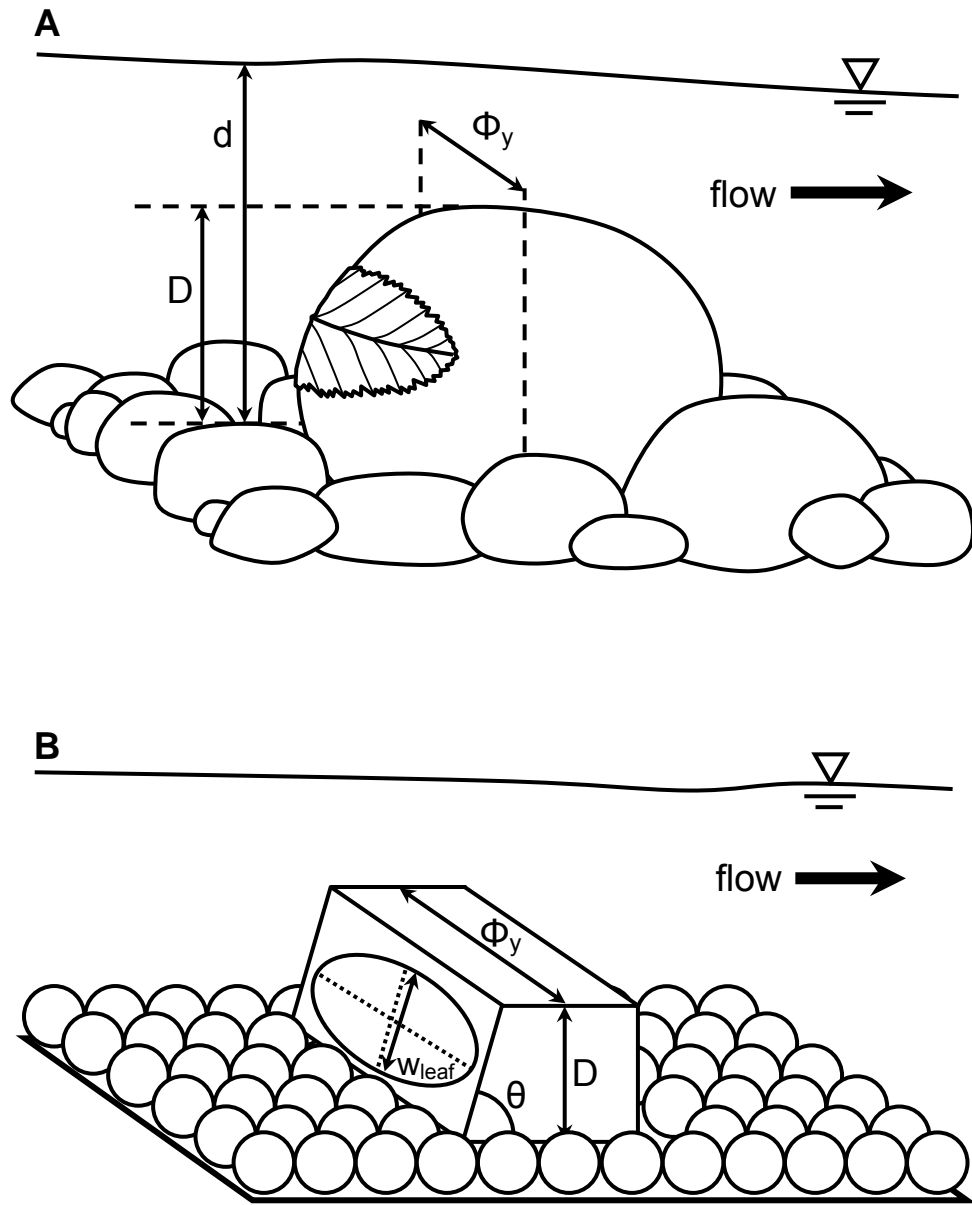
Channel and bed variables measured at reference locations in the three riffle and three pool reaches used in the leaf transport and retention experiment (n = 51 for riffles, n = 52 for pools) (means with 1 SE in parentheses)

Reach	Depth (cm)	Mean velocity (cm/s)	Stone diameter (cm)	Roughness height (cm)	Relative protrusion	Aspect ratio
Riffle 1	9.08 (0.65)	37.33 (2.95)	9.51 (0.56)	4.63 (0.39)	0.70 (0.09)	0.53 (0.07)
Riffle 2	8.89 (0.40)	29.90 (1.76)	10.68 (0.67)	4.68 (0.30)	0.56 (0.04)	0.48 (0.03)
Riffle 3	7.40 (0.49)	28.12 (1.33)	11.66 (0.71)	5.68 (0.48)	0.92 (0.11)	0.50 (0.04)
Pool 1	16.32 (0.51)	6.42 (0.24)	12.16 (0.67)	5.58 (0.36)	0.37 (0.03)	0.49 (0.03)
Pool 2	20.73 (0.76)	4.19 (0.22)	5.86 (0.35)	3.19 (0.28)	0.17 (0.02)	0.54 (0.03)
Pool 3	17.65 (0.40)	7.00 (0.23)	12.58 (0.80)	5.07 (0.38)	0.30 (0.02)	0.41 (0.03)

**Table 5-3**

Channel and bed variables measured at leaf settlement locations in the three riffle and three pool reaches used in the leaf transport and retention experiment (n = 51 for riffles, n = 52 for pools) (means with 1 SE in parentheses)

Reach	Depth (cm)	Mean velocity (cm/s)	Stone diameter (cm)	Roughness height (cm)	Relative protrusion	Aspect ratio
Riffle 1	10.50 (0.40)	25.27 (1.66)	13.84 (0.87)	7.50 (0.53)	0.72 (0.05)	0.57 (0.03)
Riffle 2	9.47 (0.40)	30.98 (1.56)	11.17 (0.67)	6.88 (0.31)	0.77 (0.04)	0.67 (0.03)
Riffle 3	8.59 (0.45)	22.39 (1.27)	10.31 (0.56)	7.42 (0.39)	0.91 (0.04)	0.78 (0.05)
Pool 1	20.31 (0.35)	7.00 (0.32)	9.43 (0.64)	4.11 (0.31)	0.21 (0.02)	0.46 (0.03)
Pool 2	22.91 (0.54)	3.77 (0.18)	5.13 (0.27)	1.86 (0.16)	0.085 (0.01)	0.37 (0.03)
Pool 3	19.66 (0.39)	6.39 (0.26)	9.11 (0.57)	3.73 (0.37)	0.19 (0.02)	0.42 (0.04)



**Figure 5-1**

Diagrams of the substrate parameters measured for each retained natural and artificial leaf. (A) Red alder leaf retained by a streambed stone;  $D$  = roughness height,  $d$  = total depth,  $\Phi_y$  = maximum substrate diameter (cross-stream direction). (B) Artificial leaf retained by an experimental substrate in the laboratory channel;  $D$  and  $\Phi_y$  are as above,  $\theta$  = angle of the upstream face of the substrate, and  $w_{leaf}$  = leaf width. The heavy arrow marked 'flow' indicates flow direction in both diagrams.

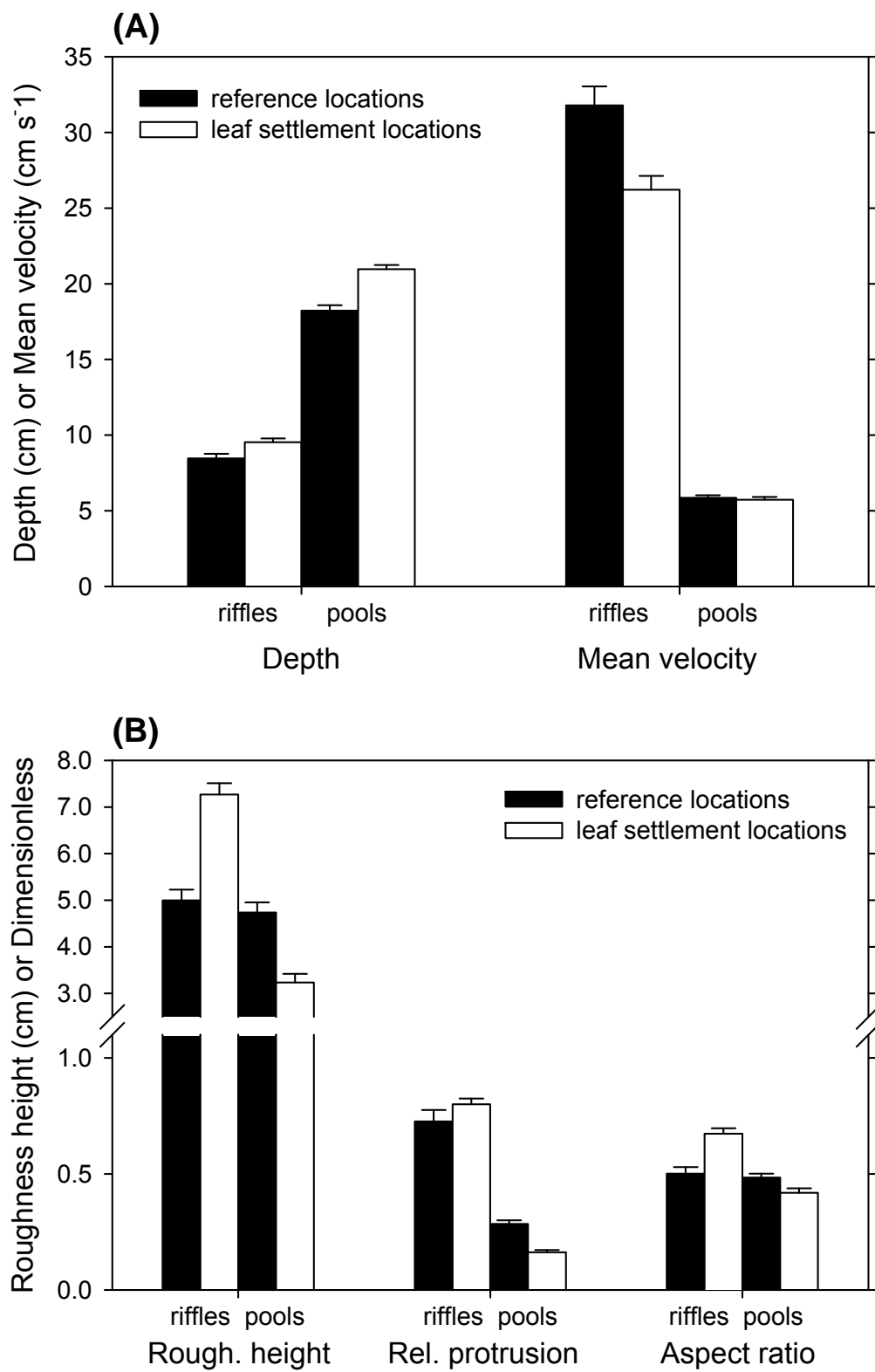
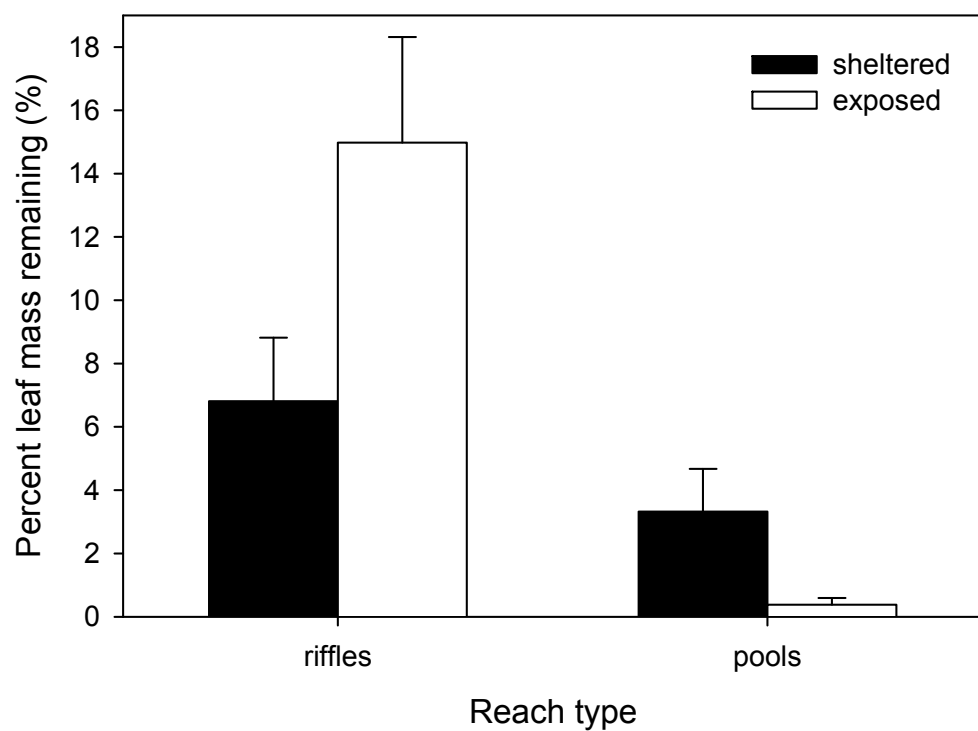


Figure 5-2

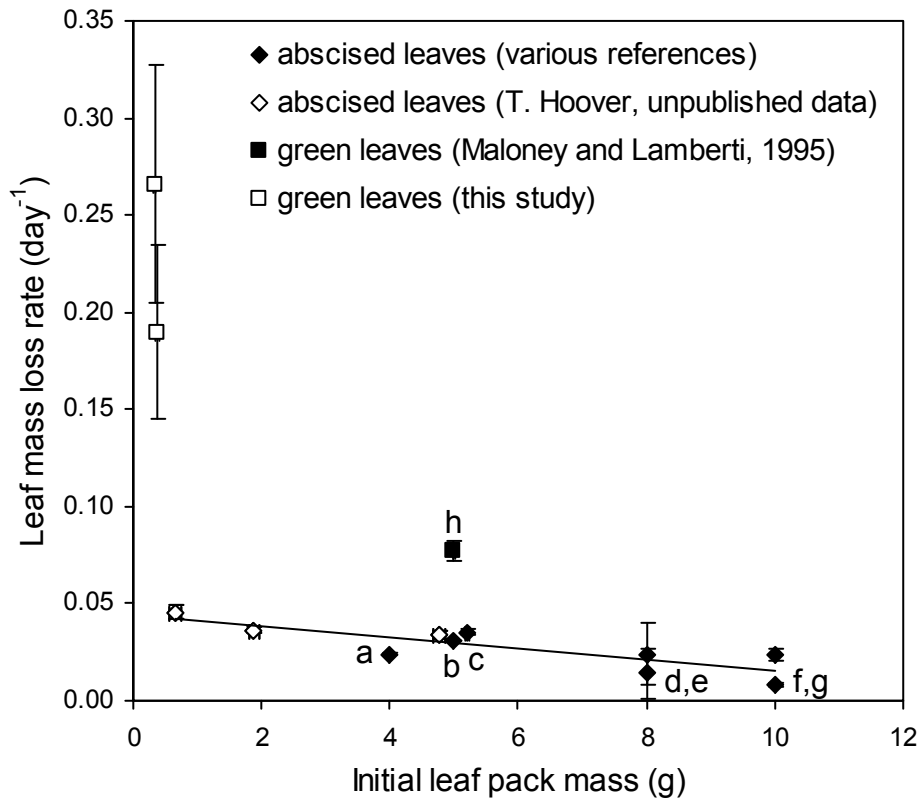


**Figure 5–2** (*previous page*) Comparison of channel characteristics measured at reference locations and leaf settlement locations. (A) Water depth and velocity. (B) Indices of streambed morphology; roughness height, relative protrusion, and aspect ratio (relative protrusion and aspect ratio are dimensionless). All variables measured in three riffle and three pool reaches (sites pooled; n = 156 for pools, n = 153 for riffles). Bars = means, error bars = 1SE.



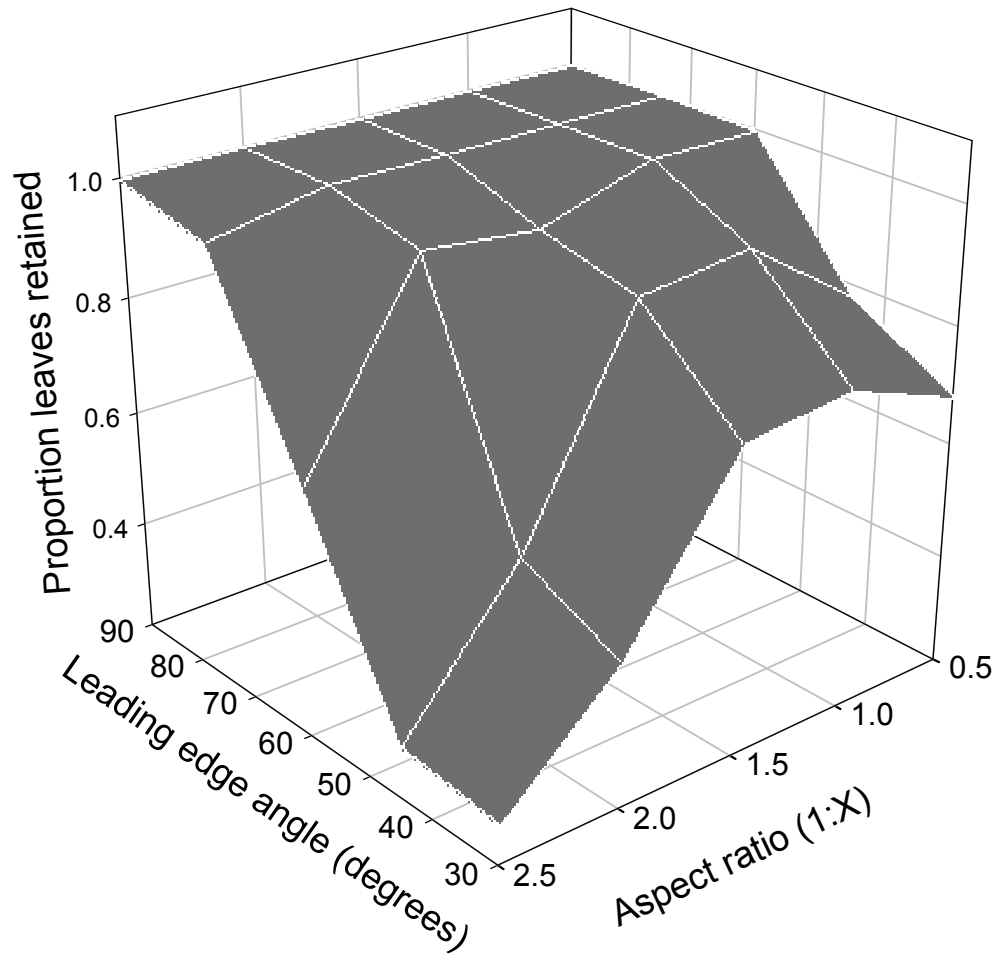
**Figure 5-3**

Degree of leaf breakdown (measured as percent leaf mass remaining after ten days) in exposed and sheltered streambed locations (see text for a description) in Spring Creek riffle and pool habitats (n = 20 in all cases). Bars = means, error bars = 1SE.



**Figure 5-4**

Comparison of leaf mass loss rate ( $-k$ ; calculated by various authors) and the initial mass of leaves contained in the leaf pack used. All studies included used similar methodology, placing alder leaves (*Alnus* spp.) in riffles in low-order streams. Values shown are from the following studies; (a) Jonsson & Malmqvist (2000); *A. incana*; *A. rugosa*; (b) Short et al. (1980), *A. tenuifolia*; (c) Hieber & Gessner (2002), *A. glutinosa*; (d,e) Pascoal et al. (2001), *A. glutinosa*; (f,g) Richardson et al. (2004), *A. rubra*; (h) Maloney & Lamberti (1995). Open squares and open diamonds are values of  $-k$  from Spring Creek riffles, this study and T. Hoover (unpublished data), respectively. Line is a linear fit ( $r^2 = 0.70$ ) to the abscised leaf data only.



**Figure 5-5**

Response surface plotted for the relationship between substrate aspect ratio, leading edge angle, and the proportion of artificial leaves retained by substrates in a laboratory channel (mean velocity = 30 cm/s, depth = 6.6 cm); 50 leaves were released upstream of each of the 25 substrates.

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## **CHAPTER 6: A COMPARISON OF THE TRANSPORT AND SETTLEMENT PROCESSES OF FOUR TYPES OF TERRESTRIALLY-DERIVED ORGANIC MATTER IN SMALL STREAMS<sup>5</sup>**

### **Introduction**

Headwater streams in forested regions receive substantial inputs of organic matter from adjacent terrestrial environments, primarily in the form of leaf litter and woody debris (Benfield 1997, Pozo et al. 1997, Webster et al. 1999). When it first enters a stream, this terrestrial organic matter (OM) is generally buoyant, and is typically retained along stream peripheries, on protruding streambed stones, or in debris jams (Muotka and Laasonen 2002, Brookshire and Dwire 2003). Material retained in such locations may be of little benefit to stream detritivores due to difficulties with access and colonization (Pretty and Dobson 2004). However, the particles become saturated with water, eventually becoming negatively buoyant. Biological breakdown mediated by microbial colonisation, fragmentation by benthic macroinvertebrates (Jonsson et al. 2001), and mechanical abrasion by shear stress and moving bedload (Heard 1999) also act to alter the size and physical properties of large OM particles. These processes produce biologically and physically conditioned OM particles that are not only more palatable and nutritious to invertebrate detritivores (Sedell et al.

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<sup>5</sup> A version of this chapter will be submitted for publication. Hoover T.M., Marczak L.B., Richardson J.S. and Yonemitsu N. A comparison of the transport and settlement processes of four types of terrestrially-derived organic matter in small streams.

1975, Bretschko and Moser 1993), but likely possess different transport characteristics than freshly-delivered allochthonous material.

Periods of elevated discharge can re-entrain this conditioned, partially decomposed organic material and redistribute it within the stream ecosystem (Wallace et al. 1995, Brookshire and Dwire 2003). The spatial distribution of retained organic matter is a key element in many important ecological processes including detrital processing, predator prey-interactions, and the assemblage of benthic invertebrate communities (e.g. Malmqvist et al. 1978, Rowe and Richardson 2001, Hoover et al. 2006). The greater food value of conditioned OM suggests that patterns of retention of this material are likely more important determinants of benthic invertebrate distributions than are the relatively short-lived patterns produced by the retention of freshly-delivered OM.

The retention of suspended OM particles is dependent on interactions between channel geomorphology, hydrodynamic parameters such as mean velocity and turbulence intensity, and the physical characteristics of the particles in transport (Cummins et al. 1989, Gorecki et al. 2006). For example, studies by Lancaster et al. (1996) and Bond et al. (2000) suggest that the settlement of drifting aquatic insect larvae is dependent on the spatial distribution of low-velocity areas of the streambed. Ehrman and Lamberti (1992), in contrast, found that the settlement of large, passive OM particles (leaves and wood) was caused primarily by 'retentive structures' such as debris dams, large woody debris, and roots, while Hoover et al. (2006) showed that the retention of leaves in a small stream was dependent on the habitat unit type; protruding stones retained leaves

in riffles, while passive deposition was the more important process in pools. However, many terrestrially-derived particles such as conifer needles and wood fragments are relatively small, dense, and inflexible compared to leaves; their transport properties, and thus distributions within a stream ecosystem, may be very different.

The majority of studies examining the transport dynamics of coarse particulate OM in streams have been conducted on the leaves of hardwood species (e.g. Webster et al. 1987, Ehrman and Lamberti 1992, Schade and Fisher 1997), artificial 'leaves' (Webster et al. 1994, Wallace et al. 1995), and sticks (e.g. yellow poplar and white pine; Webster et al. 1999). However, in many small streams of conifer forests, a large proportion of the annual input of terrestrial organic matter consists of the needles of coniferous tree species and the fronds of red cedar trees in addition to deciduous leaves (Richardson 1992). While the retention efficiency of conifer needles has generally been assumed to be lower than that of leaves (Richardson et al., in review), very few investigations of the retention dynamics of this material have been conducted (but see Pretty and Dobson 2004) despite the trophic importance of this resource subsidy (see Richardson et al. 2004). Given differences in the size, shape and quality (e.g. rate of conditioning, settling velocity) of different terrestrial material, it is reasonable to expect that coarse OM particles of different types (deciduous leaves, wood fragments, conifer needles, conifer branch pieces) will produce different settlement patterns.

Several studies of the transport and settlement characteristics of drifting insects and entrained organic matter (e.g. Webster et al. 1987, Lancaster et al. 1996, Webster et al. 1999) have shown that suspension, transport, and settlement characteristics vary substantially not only with flow conditions, but also with particle shape, size, and density. Indices that incorporate both the physical characteristics of the particles in transport and hydrodynamic conditions have the potential to accurately describe retentive processes. Rouse number ( $Ro$ ), for instance, is the ratio of a particle's settling velocity to shear velocity (which describes the turbulence acting to keep the particle entrained) (Chien and Wan 1998), and as such may be useful to predict the relationship between flow regimes and particle transport. If readily-calculated indices such as the Rouse number correlate with the transport distances of relatively large, low-density particles such as terrestrially derived organic matter, the use of this index may provide a predictive and quantitative means of describing the retention of OM in streams.

In this study we describe the transport and retention characteristics of four different types of conditioned OM particles – alder leaves, branch pieces, conifer needles, and red cedar fronds. These organic particles are ubiquitous forest-to-stream resource subsidies entering streams of southwestern British Columbia (Richardson 1992, Richardson et al. 2005). The objective of this study was to develop a concise conceptual model of the physical processes that lead to the retention of conditioned organic matter of different origin in small streams. We characterise differences in the settling velocity of these OM types and assess

variability in the transport and retention characteristics of these particles in two geomorphologically and hydraulically distinct reach types (pools and riffles) in both an artificial channel and in replicated field conditions. Three specific questions were asked: (i) How rapidly do the physical properties (settling velocity) of OM particle types change with immersion time? (ii) How do transport and retention patterns vary among conditioned OM types in different experimentally-created flow conditions and in natural settings? and, (iii) Can the settlement patterns of conditioned OM particles in small streams be predicted using simple indices such as Rouse numbers?

## **Methods**

### **Experiment 1: The influence of immersion time on buoyancy and settling velocity**

To determine how physical conditioning rates (changes in specific gravity with immersion time) vary with OM type, we recorded changes in the sinking velocity of five types of OM over 24 days. Dry, naturally senesced red alder (*Alnus rubra* Bong.) leaves, Douglas-fir (*Pseudotsuga menziesii* Franco) branch pieces, newly senesced and fallen Douglas-fir needles, and red cedar (*Thuja plicata* Don) frond fragments were collected from the forest floor adjacent to Spring Creek in the Malcolm Knapp Research Forest (MKRF, 49.272°N, 122.586°W) east of Vancouver, British Columbia. As deciduous tree leaves regularly enter coastal streams directly from the canopy throughout the growing season (see Richardson 1992), fresh green leaves of red alder obtained directly from riparian areas in the MKRF were also used. To simulate the physical

processing of conifer branches that may occur when branches fall from the canopy, the Douglas-fir branches were broken into small pieces (mean length = 5.7 cm, SD = 0.9 cm) that were comparable in size to the other OM particles used. In this study, in order to distinguish among detrital materials with different physical properties, relatively large, flat particles such as the leaves of deciduous trees are classed as 'flexible' OM particles, while relatively compact, oblong materials such as small branch pieces, red cedar frond fragments, and coniferous needles are classed as 'stiff' OM particles (hereafter referred to as branch pieces, fronds, and needles).

Thirty pieces of each of the five OM types (senesced alder leaves, green alder leaves, branch pieces, needles, and fronds) were placed in separate containers containing 2 L of 5°C tap water. The proportion of particles that remained floating and the individual settling rates of all particles no longer positively buoyant were measured at 0, 2, 4, 7, 10, 13, 16, and 24 days of immersion. Particle settling velocity ( $w_s$ ) was calculated by dividing the total settling distance by the time that each particle took to fall from the point of release until contact with the bottom. All particles were released in a horizontal orientation 5 cm above the bottom of the settling basin. This relatively short settling distance was chosen in order to minimise changes in orientation of the sinking particles. On the final date of the immersion period (24 days), settling velocities were determined by releasing particles in both horizontal and vertical orientations. As elongated particles experience lower drag (and thus higher fall

velocities) when sinking in a vertical orientation (see Vogel 1994), this additional measurement describes the maximum possible settling velocity ( $w_{\max}$ ).

## **Experiment 2: Transport and retention of conditioned OM particles in an artificial channel**

The transport and settling distances of conditioned OM were examined by releasing physically-conditioned particles (from experiment 1) in simulated 'riffle' (fast, shallow) and 'pool' (slow, deep) settings created in an experimental field-based channel located adjacent to Blaney Creek in the MKRF. The experimental channel was 4.9 m long and 0.40 m wide with 0.40 m high sidewalls, and during the study had a fixed bed slope of 1.0%. Further details of channel construction and design can be found in Harrison et al. (2006). Prior to releasing particles, we established a coarse bed in the experimental channel using cobbles, gravel, and coarse sand collected from Blaney Creek. Cobbles and gravel were placed in the channel bottom by hand (average grain diameter = 11.8 cm, SD = 3.9, mean roughness height = 5.6 cm, SD = 2.3,  $n = 40$  for all bed measurements). Coarse sand was then broadcast in the channel at high flow ( $> 1$  m/s) to create naturally-evolved streambed microtopography and grain embeddedness. Two flow settings were created simulating riffle (mean depth = 6.4 cm, SD = 2.6, mean velocity = 26.5 cm/s, SD = 7.4), and pool conditions (mean depth = 20.9 cm, SD = 2.9, mean velocity = 8.9 cm/s, SD = 1.44) typical of small streams in the region (see Hoover et al. 2006).

Using forceps, 30 particles of each of the four previously conditioned OM particle types (senesced alder leaves, branch pieces, needles, and fronds) were

released individually immediately below the water surface in the upstream portion of the channel. Green alder leaves were not included as their shape and settling velocities were virtually identical to the senesced alder leaves. All particles were released in a horizontal orientation. The total transport distance ( $x_s$ ) was recorded for each particle released. To describe the geomorphological features associated with the retention of each OM type we recorded characteristics of the streambed at the point of settlement (see Fig. 6-1), including depth at the settlement point ( $D$ ) and the cross-stream diameter of the largest clast in contact with the settled particle ( $\Phi_y$ ).

### **Null model of transport distances**

We used a simple null transport model to evaluate how particle retention processes varied among particle types and between flow conditions. The measured transport distances ( $x_s$ ) of the released OM particles were compared to expected transport distances ( $x_E$ ), which were calculated using the relationship

$$x_E = U (z_0 / w_s)$$

where  $U$  is mean channel velocity,  $z_0$  is the height above the bed at which the particle was released, and  $w_s$  is the still-water settling velocity of the particle type released (from experiment 1). The expected transport distance ( $x_E$ ) is the distance that a particle would be advected downstream in a channel with a uniform velocity distribution assuming that the settling particle is retained where it first contacts the bed. While these conditions are virtually never met in real channels,  $x_E$  nonetheless provides a rigorous model to assess the role of flow-particle and particle-streambed interactions in OM retention. Since OM particles



often rotate or tumble during transport (T. Hoover, personal observation), two values of  $x_E$  were calculated for each OM particle type;  $x_{E-min}$  (the minimum expected transport distance) calculated using the mean maximum particle settling velocity ( $w_{max}$ ), and  $x_{E-max}$  (the maximum expected travel distance) calculated using our standard estimate of settling velocity  $w_s$ .

### **Retention rates**

The retention efficiency of a stream channel (i.e. the proportion of particles retained within a given reach) can also be used to describe settlement patterns. Retention rates can be determined using the exponential decline model

$$L_x = L_i e^{-kx}$$

where  $L_x$  is the number of leaves entrained in the flow at a given distance  $x$  from the release point,  $L_i$  is the number of leaves released, and  $-k$  is the retention coefficient, which is related to the proportion of particles settling per metre (Webster et al. 1987, Schade and Fisher 1997). Larger values of  $-k$  indicate higher rates of retention. To quantify how rapidly particles were retained once they began to come into contact with the bed, retention coefficients were calculated for all OM particle types using the exponentially-declining (downstream) portion of each settlement distribution.

Within each flow condition, the transport distances of the four OM types were compared using one-way ANOVA. Measured transport distances were compared to modelled transport distances ( $x_{E-min}$  and  $x_{E-max}$ ) using one-sample  $t$ -tests. To determine if the geomorphological conditions at OM particle retention

locations differed among OM types,  $D$  and  $\Phi_y$  at the settlement locations of the four OM types were compared using one-way ANOVA; the  $D$  and  $\Phi_y$  at an equal number of streambed locations made during a streambed survey were also included in the ANOVA as an unbiased control comparison. All post-hoc comparisons were made using Tukey's Honestly Significant Differences (HSD) test.

### **Experiment 3: Transport and retention of naturally-conditioned OM in Canyon Creek**

To determine if the distinctive patterns of retention observed in our experimental channel also occur in natural streams, we experimentally released naturally-conditioned OM particles in two riffles and two pools in Canyon Creek, a second order, coastal montane stream located in southwestern British Columbia (49.331°N, 122.998°W). Naturally-conditioned OM particles were used so that we could examine the transport and retention characteristics of 'highly-conditioned', rather than 'newly-delivered', material in a natural stream.

Organic debris was hand-collected from several pools and debris jams in Canyon Creek. The collected material was gently rinsed to remove fine organic and inorganic sediment, and sorted into four categories (red alder leaves, wood fragments, needles, and frond pieces). Whereas conditioned red alder leaves and fronds could be easily identified to their species of origin, wood fragments and conifer needles could not and were likely a mixture of western hemlock (*Tsuga heterophylla* Sarg.) and Douglas-fir. Thirty particles of each type were

selected, taking care to choose pieces that were representative of the collected debris with respect to length, and degree of decomposition.

### **Site Characteristics**

Canyon Creek flows through a high-gradient, incised channel with a dense overstory (canopy closure approximately 90%) of western red cedar, western hemlock, and Douglas-fir. Riparian vegetation consists of red alder, immature western red cedar, and salmonberry (*Rubus spectabilis* Pursh). During the study (late winter 2001), average stream discharge was 0.11 m<sup>3</sup>/s. Bed material at the site was composed of cobbles and boulders of angular granodiorite and rounded alluvial material, with gravel and coarse sand between the larger bed elements.

We surveyed channel morphology over a 120 m long reach of Canyon Creek and selected two representative pools and riffles (for definitions, see Montgomery and Buffington 1997) in which to examine the transport properties of the four naturally-conditioned OM types (Table 6-1). In each of the selected habitat units, we measured depth and water velocity at 10 cm intervals in pools and at 50 cm intervals in riffles. After the completion of the OM release experiment (see below), a measure of the bed roughness of each of the four reaches was made by measuring the longest-axis diameter ( $\Phi_L$ ) of the largest stone found within a 5 cm radius at intervals of either 10 cm (pools) or 50 cm (riffles).

## **Transport and settlement of naturally-conditioned OM in Canyon Creek**

We measured transport distances in pools by releasing and visually tracking individual OM particles ( $n = 12$  for each OM type in each pool), and recording the total distance travelled using a quadrat (60 cm wide, 140 cm long) suspended over the channel. The downstream edge of the quadrat was positioned over the downstream edge of the pool. The final settlement point of particles that were not deposited within the bounds of the quadrat frame (i.e. were transported into the riffle downstream) were not recorded.

As visually tracking OM particles was not possible in highly turbulent riffle reaches, we used a block net to determine the average transport distances of OM particles in the two riffle reaches. The block net (500  $\mu\text{m}$  Nitex) was placed spanning the stream downstream of each riffle. Ten OM particles of each type were released into the channel at 0.5 m intervals upstream of the net (i.e. 0.0 m to 5.0 m, 11 upstream distances, total  $n = 110$  for each particle type), and the proportion of particles transported through the reach into the net was recorded after each set of particles were released. Only one minute per meter of channel between the release point and the net was permitted for transport time of the released OM particles; material was collected from the net after this time (e.g. material was collected 2.5 minutes after release of the material 2.5 m upstream). Material not flushed into the net within this time was assumed to have become retained within the reach. This assumption appeared valid, as virtually all particles that were transported through the test section during releases appeared in the net only a few seconds after they were released. The order of the

distances upstream of the net at which material was released was randomized. OM particles of similar sizes were used in the riffle and pool release trials and in the determination of settling velocity.

Two retention metrics were measured for each OM type in each of the four Canyon Creek reaches examined; the proportion of particles transported through ( $p_{\text{through}}$ ) the test reach (5.0 and 1.4 m long for riffles and pools, respectively), and the retention rate coefficient ( $-k$ ). In riffles, if all particles released 5.0 m upstream of the net were retained,  $p_{\text{through}}$  was taken to be 0; if particles were collected in the net,  $p_{\text{through}}$  was calculated using the regression equation used in the determination of  $-k$ .

### **Rouse number analysis of transport dynamics**

The transport and settlement of OM may be characterised using indices that describe relationships between particle characteristics and the hydrodynamic forces acting on these particles. Advection-diffusion models (e.g. McNair et al. 1997) have shown that transport distances are determined by a particle's settling velocity and the degree of turbulent mixing within the channel. Bagnold (1966) related the upward velocity of turbulent eddies to shear velocity ( $u^*$ ), and suggested that the critical condition for the suspension of sediment is related to the relationship between the sinking rate of particles ( $w_s$ ) and the upward velocities generated by turbulent eddies. This ratio of settling velocity to shear velocity is known as the Rouse number,

$$Ro = w_s / u^*$$

We determined the still-water settling velocity of each naturally conditioned particle type from Canyon Creek (using methods identical to those described in experiment 1) and calculated Rouse numbers for all OM types in all Canyon Creek pool and riffle sites. The average shear velocity ( $u^*$ ) was estimated for each of the four reaches using the following relationship (from Carling 1992),

$$U/u^* = 5.75 \log(12 D/\kappa)$$

where  $U$  is mean velocity,  $D$  is mean water depth (measured at 0.1 m intervals in both pools, and at 0.5 m intervals in both riffles), and  $\kappa$  is a roughness parameter (calculated as  $0.5\Phi_L$ ; assumes 50% particle protrusion). Rouse numbers were also calculated for all particle types in both flow conditions in the experimental channel (experiment 2). The Rouse numbers were then regressed against retention coefficients ( $-k$ ) to determine if settlement could be described by this simple index. All statistical analyses were conducted in Systat v.10 (Systat 2000).

## Results

### Experiment 1: Immersion rapidly changes buoyancy and settling velocity

The rate at which detrital particles became sufficiently saturated with water to sink varied substantially among the five OM types tested (Fig. 6-2A). All dried alder leaves became negatively buoyant after only two days of immersion, while the process was somewhat slower for fresh alder leaves (i.e. only after four days of immersion did > 50% of fresh leaves sink). The rates at which the three stiff

OM types (i.e. branch pieces, needles, and fronds) became negatively buoyant were similar (Fig. 6-2A).

Particle settling velocity ( $w_s$ ) also varied among OM types (Table 6-2). The settling velocities of alder leaves (fresh and dried), needles, and fronds had reached relatively constant values after only a few days of immersion (Fig. 6-2B), with both leaf types tending to settle more slowly than the other OM types. The mean settling velocity of immersed branch pieces slowly increased until day 13, after which it remained constant (Fig. 6-2B).

### **Experiment 2: The retention of various OM types differs between experimental riffles and pools**

Statistical comparisons of the measured transport distances ( $x_s$ ) and the modelled minimum and maximum transport distances ( $x_{E-min}$  and  $x_{E-max}$ ) of the four OM particle types in 'riffle' and 'pool' settings in the experimental channel show that there are substantial differences in the transport distances of the different OM types, and that settlement processes differed between stiff (branch pieces, needles, and fronds) and flexible (leaves) OM types.

#### **Transport distances – riffle setting**

In the 'riffle', there were significant differences in transport distance among the four OM types (ANOVA,  $F(3,196) = 31.1$ ,  $p < 0.001$ ). Branch pieces settled at a significantly shorter distance (see Table 6-3) than all other OM types (Tukey's HSD, all  $p < 0.001$ ). The transport distances of leaves, needles, and fronds were not significantly different from each other (Tukey's HSD, all  $p \geq 0.19$ ).

(Fig. 6-3A). This same pattern is evident in the retention coefficients ( $-k$ ) (Table 6-3).

A comparison of  $x_s$  with  $x_{E-min}$  and  $x_{E-max}$  shows that leaves were retained disproportionately rapidly in riffles compared to the stiff OM types (Fig. 6-3A). The measured transport distances ( $x_s$ ) of the three stiff OM types were significantly greater than both  $x_{E-min}$  and  $x_{E-max}$  (t-tests, all  $p < 0.002$ ), presumably due to the influence of turbulence, elevated in the 'riffle' conditions due to the high current velocity (see Table 6-1). In contrast, the mean measured transport distance ( $x_s$ ) of leaves was significantly greater than the modelled minimum transport distance but significantly less than the modelled maximum transport distance (i.e. for leaves  $x_{E-min} < x_s < x_{E-max}$ ; t-tests, for both comparisons  $p < 0.001$ ).

### **Transport distances – pool setting**

In the 'pool', there were also significant differences in transport distance among the OM types (ANOVA,  $F(3,196) = 83.8$ ,  $p < 0.001$ ), although the settling order differed from that seen in the 'riffle'. While branch pieces travelled the shortest distance in the 'pool', and leaves the longest, significant differences existed between all groups (branch pieces < fronds < needles < leaves (Tukey's HSD, all  $p \leq 0.001$ ) (see Fig. 6-3B). The same settling order is seen in the retention coefficients ( $-k$ ) (Table 6-3).

Comparisons of  $x_s$  with  $x_{E-min}$  and  $x_{E-max}$  show that values produced by the passive settlement model are related to the transport and settlement of OM particles in 'pool' conditions in the experimental channel. For leaves and



needles, the measured transport distance was bracketed by  $x_{E-min}$  and  $x_{E-max}$  (i.e.  $x_{E-min} < x_s < x_{E-max}$ ; t-tests, all  $p < 0.001$ ) (Fig. 6-3B). While the measured transport distances of branch pieces and fronds were significantly less than  $x_{E-max}$  (t-tests, both  $p < 0.001$ ), they were not significantly different from  $x_{E-min}$  (t-tests, branch pieces  $p = 0.12$ , fronds  $p = 0.081$ ). The branch and fronds may have rotated and sank predominantly in an 'on-end' orientation due to the low-turbulence conditions in the 'pool'.

### **Comparison of depth and bed roughness at settling locations**

Comparison of measurements of geomorphological conditions (depth, clast diameter) made at particle settlement locations with a similar number of measurements made during the channel survey indicates that the disproportionately rapid retention of leaves in the 'riffle' was due to flow-particle-streambed interactions. In the 'riffle', retained leaves were significantly associated with shallow depths and large, protruding stones, whereas particles of stiff OM types settled into deeper interstices between the larger clasts (Fig. 6-4). There were significant differences in depth (ANOVA,  $F(4,245) = 70.9$ ,  $p < 0.001$ ) and clast diameter (ANOVA,  $F(3,196) = 9.42$ ,  $p < 0.001$ ) at the settlement points of the four OM types. Leaves settled at shallower locations (Fig. 6-4) than the other types of OM (Tukey's HSD, all  $p < 0.001$ ), and leaf settlement locations were also significantly shallower than surveyed locations (Tukey's HSD,  $p < 0.001$ ); the settlement depths of the remaining OM types were similar to each other (Tukey's HSD, all  $p \geq 0.77$ ), but greater than surveyed locations (Tukey's HSD,  $p < 0.001$ ) (Fig. 6-4). Leaf settlement points were associated with

significantly larger stones than the settlement points of the other OM types (ANOVA,  $F(4,233) = 7.25$ ,  $p < 0.001$ ; Tukey's HSD, all  $p < 0.006$ ), but were not significantly different than survey data (Tukey's HSD,  $p = 0.26$ ). Only fronds were associated with smaller stones than the survey data (Tukey's HSD,  $p = 0.049$ ).

In the 'pool' setting, there were significant differences in settlement depth of the various OM types (ANOVA,  $F(4,245) = 24.7$ ,  $p < 0.001$ ) (Fig. 6-4). Leaves settled at shallower locations than all other OM types (Tukey's HSD,  $p \leq 0.02$ ), branch pieces were not significantly different than survey locations (Tukey's HSD,  $p = 0.94$ ), while fronds and needles settled in deeper areas than the other OM types (Tukey's HSD,  $p \leq 0.001$ ) and survey locations (Tukey's HSD,  $p = 0.021$ ). Clast diameter at the settlement points of the various OM types also varied significantly (ANOVA,  $F(4,245) = 22.0$ ,  $p < 0.001$ ). Notably, the three stiff OM types were associated with smaller clasts than leaves or bed survey data (Tukey's HSD, all  $p < 0.001$ ) (Fig. 6-4).

### **Experiment 3: Physical properties and transport of naturally-conditioned OM**

There were significant differences among the still-water settling velocities ( $w_s$ ) of the four types of naturally-conditioned OM particles collected from Canyon Creek (ANOVA,  $F(3,116) = 25.37$ ,  $p < 0.001$ ). Wood fragments settled at a significantly higher velocity than leaves, fronds, or needles (Tukey's HSD, all with  $p < 0.001$ ) (Table 6-2). Fronds also settled at about a 39% higher velocity than leaves (Tukey's HSD,  $p = 0.038$ ). As such, among-group differences in settling

velocity appeared to be a function of particle shape and specific gravity, rather than particle size.

### **Transport of naturally-conditioned OM particles in Canyon Creek**

In pools, all three retention metrics (i.e. the proportion of particles transported through pools ( $p_{\text{through}}$ ), the average transport distance ( $x_s$ ) of particles retained within pools, and the retention rate coefficient ( $-k$ )) indicate that wood pieces were retained most rapidly, followed by fronds (Table 6-3). Needles and leaves were retained less rapidly than wood and fronds, although the patterns of retention of needles and leaves differed slightly between the two Canyon Creek pools. In pool 1, all indices indicate that leaves were retained at the lowest rate (i.e. wood pieces > fronds > needles > leaves), whereas in pool 2, needles were retained at the lowest rate (i.e. wood pieces > fronds > leaves > needles), possibly due to the greater relative roughness of the channel bed (see Table 6-1). In both pools, few particles were deposited near the downstream edge of the quadrat, as velocities generally increased where depths decreased at the tail of the pool.

In the two riffles, the retention rate coefficient ( $-k$ ) indicates that wood fragments were retained more rapidly than the other types of OM, while leaves were retained within the riffles at a rate only slightly lower than that of wood pieces, and fronds and needles had the lowest rates of retention (i.e. wood fragments > leaves > fronds > needles) (Table 6-3).

## **Rouse number analysis of transport dynamics**

The retention of the three stiff OM particle types (wood fragments, needles, fronds) was strongly related to Rouse number. Rouse numbers calculated for stiff OM particles released in all riffle and pool reaches (includes both Canyon Creek and experimental channel reaches) were significantly and positively related to the retention rate coefficients ( $-k$ ) calculated for each reach and OM type ( $r^2 = 0.90$ , ANOVA,  $F(1,16) = 146.0$ ,  $p < 0.001$ ) (Fig. 6-5). Calculated Rouse numbers for transported leaves, in contrast, were not significantly related to  $-k$  ( $r^2 = 0.10$ , ANOVA,  $F(1,4) = 0.43$ ,  $p = 0.55$ ).

## **Discussion**

How resource subsidies are incorporated into recipient system food webs depends not only on the quantity and quality of the resources transferred (Marczak et al. 2007), but also on the physical mechanisms of resource delivery that ultimately determine the spatial distribution of those resources. In streams, variation in any one of the temporally sequential processes that contribute to detrital resource delivery – conditioning, downstream transport, and retention – may alter the instream availability and distribution of detrital resources. The OM types examined in this study varied in several key physical properties, including size, shape, conditioning rate, and settling velocity. During downstream transport, these physical properties interacted with local flow conditions and streambed morphology to create transport distances and settlement distributions that were unique to each OM particle type. Although transport distances varied among the three stiff OM types (branch pieces, needles, and fronds), the

settlement of these three particle types appeared to be strongly governed by gravitational deposition. In contrast, leaves were actively retained in riffles by protruding streambed stones in high-velocity locations. Ultimately, these differences in transport processes will likely create spatial variation in resource availability among microhabitats that differ in relative bed roughness and degree of exposure to flow, and thus may spatially partition detrital resources among channel units (e.g. riffles and pools), and between exposed and interstitial microhabitats within those channel units.

### **Processes leading to differential retention**

The physical conditioning of branch pieces, needles, fronds, and alder leaves (fresh and dried senesced) proceeded at different rates. Senesced and dried alder leaves, commonly used in detrital breakdown studies (e.g. Jonsson and Malmqvist 2004, Richardson et al. 2004, Hoover et al. 2006), rapidly became saturated, whereas other OM types were physically conditioned more slowly, especially branch pieces. The settling velocity of branch pieces slowly increased after immersion, whereas the other OM types reached a constant  $w_s$  value after only a few days. Branch pieces are relatively thick compared to other types of OM; if water penetrates the surface of various OM types at the same rate, wood pieces will require a longer period of time to become saturated than conifer needles or leaves, which are < 1 mm thick. Larger wood pieces such as large branch pieces would presumably take even longer to sink, which means that unless actively retained in debris jams, woody debris, or on boulders (Ehrman and Lamberti 1992, Webster et al. 1994), large wood pieces that are still buoyant

may be exported from stream systems during spates. The short transport distances of the wood fragments in this study can be directly attributed to their high settling velocities.

In pools, stiff OM types were retained most rapidly (wood pieces > fronds > needles) while alder leaves settled at the slowest rate and were transported the greatest distances. In riffles, the pattern of deposition was more complex, and appeared to depend on interactions between bed roughness and water velocity. Canyon Creek riffles had rougher beds and higher water velocities than the riffle created in the experimental channel, and these physical differences are reflected in the OM retention patterns. In Canyon Creek, leaves were retained more rapidly than fronds or needles (but still slower than branch pieces, which settled very quickly), whereas in the experimental channel leaf retention was similar to fronds, and only slightly less than needles. The flow-particle-streambed interactions that lead to retention appear to be fundamentally different between deciduous leaves and stiff OM particles, and between channel unit types. In riffles, broad, relatively flexible alder leaves were retained when they encountered and were wrapped around the upstream face of protruding streambed stones. This may be a key feature of leaf retention in coarse-bedded streams as 'wrapping' increases surface contact (and thus friction) between leaf and stone, which appears to act in concert with a positive pressure gradient created by the upstream flow stagnation to hold leaves in place against the obstruction. This indicates that leaves are removed from transport by inertial impaction (LaBarbera 1984), where denser-than-water particles cross

streamlines to contact a collecting element. In streams, this can result in large numbers of leaves accumulating against the upstream side of protruding streambed stones (Kobayashi and Kagaya 2002, Hoover et al. 2006). These 'leaf packs' represent relatively large, distinct, and isolated patches of detrital resources located in relatively high-velocity microhabitats. In contrast, all three stiff OM particle types were retained in riffles where they settled into deep interstices in the streambed. Although needles and fronds travelled much further than branch pieces before being retained, and there may be some degree of sieving where needles or fronds are trapped in constrictions or in narrow interstitial spaces underneath stones, it appears that gravitational deposition (LaBarbera 1984) may be largely responsible for the retention of all three OM types, as  $x_s$  similarly exceeded  $x_{E-min}$  in all instances.

In this study, all particles were retained by sediments (i.e. gravel and cobbles), as wood was scarce in the active channel (Canyon Creek) or not present (experimental channel). The importance of streambed sediments in coarse OM particle retention varies among studies. Ehrman and Lamberti (1992) found that leaves and dowels were largely retained by structures such as debris dams and large wood in a third-order Indiana stream (Juday Creek), while few particles were retained by sediments. The substrate in Juday Creek, however, was composed of relatively fine sediments (sand and gravel), which likely limited its retentive capacity. In streams where the substrate is dominated by large particle sizes (coarse gravel, cobbles, and boulder), sediments can retain most of the leaves in transport (Lamberti et al. 1988, Webster et al. 1999).

Ehrman and Lamberti (1992) suggest that the degree of leaf retention is related to the number of retentive structures per reach. This is corroborated by the results of this study, although the retentive structures examined here were protruding stones rather than wood or vegetation. Few studies (e.g. Pretty and Dobson 2004) have examined the retention of coarse material other than deciduous leaves or wood pieces. As they are relatively small, stiff, and settle rapidly, materials like needles and fronds are perhaps less likely to be retained by large wood in the channel and more likely to be retained in the streambed sediments where they are trapped in interstitial spaces between and underneath stones. In this way, it is possible that these particle types create small, widely distributed patches of detritus, among which detritivores may easily disperse (Rowe and Richardson 2001).

### **Consequences to consumers and communities**

The spatial distribution of detrital resources influences which detritivores have access to this resource, and thus how it enters benthic food webs (Kobayashi and Kagaya 2002, Kobayashi and Kagaya 2004). Macroinvertebrate communities of riffle and pools habitats are distinct, due in part to differences in organic matter abundance (e.g. Angradi 1996). In this study, particles of all three stiff types were retained in low-flow interstices in riffles. As such, this material will be available to the majority of the detritivorous organisms found in riffles, although large-bodied taxa may be prevented from accessing accumulations of smaller particles (e.g. needles) trapped in smaller crevices or beneath stones. For example, the crayfish *Pacifastacus leniusculus* (Dana) and the cased



caddisfly *Lepidostoma unicolor* (Banks) are both large, abundant detritivores in coastal forest streams of British Columbia (Rowe and Richardson 2001, Richardson 1992, Bondar et al. 2005), and have been shown to play important roles in detrital processing. The size of these detritivores may limit them to foraging on OM lying exposed on the streambed. In contrast, leaves retained in flow-exposed microhabitats may be accessible only to those shredder taxa adapted to high-flow environments (see Kobayashi and Kagaya 2002). Leaves deposited in slower velocity habitats like pools may be available to a wider range of invertebrate taxa, as gravitational deposition dominates retention in low-velocity pools, leading to accumulations of detritus, especially during periods of low flow (Kobayashi and Kagaya 2002). This type of spatial partitioning of different OM particle types among channel units within a stream may be an important factor in the establishment of different macroinvertebrate communities in these locations, and may indirectly maintain the diversity of the benthic macroinvertebrate assemblage in stream riffles (see Jonsson et al. 2001, Kobayashi and Kagaya 2004).

Spates can re-entrain and export a large proportion of the standing stock of OM in streams (Cuffney and Wallace 1989). Conditioned particles that are typically retained in exposed locations, such as leaves, may be re-entrained relatively rapidly after the onset of spates as the protruding stones that effectively retain leaves in riffles (Hoover et al. 1996) are submerged, and water velocities increase (Brookshire and Dwire 2003). Although within-channel retention of leaves might be drastically lower during spates, overbank losses or retention

within debris jams (Wallace et al. 1995, Brookshire and Dwire 2003) could become more important during large seasonal flood events. Relatively dense, compact particle types such as wood fragments that are stored in interstitial spaces between and underneath streambed stones may be entrained less readily as discharge increases. Although detrital patches consisting of wood fragments and coniferous needles may be less valuable as a food resource than accumulations of deciduous leaf material (Anderson and Sedell 1979, Richardson et al. 2004), interstitial patches of woody detritus and needles are likely more stable in space and time. Once entrained, however, the downstream transport of coarse stiff or woody OM particles would be expected to increase in a predictable fashion due to elevated water velocities and turbulence intensity. In comparison, recently fallen terrestrial plant detritus that is not yet conditioned is likely to be rapidly exported or deposited outside of the wetted channel on streambanks and in riparian vegetation during regular disturbances like seasonal floods, potentially lowering the availability of this valuable detrital resource (see Wallace et al. 1995, Brookshire and Dwire 2003).

For the three stiff OM types, Rouse number was a good predictor of particle retention rate. This suggests that for these particle types the settlement processes are largely a function of two physical factors – particle settling velocity ( $w_s$ ) and turbulence intensity (represented in this study by  $u^*$ ). As it appears to be consistent between channels and habitat unit types, this relationship could be used to increase the accuracy of current models of in-stream spatial dynamics of coarse OM (e.g. Karlsson et al. 2005, Richardson et al., in review), and predict

particle-specific relationships between OM export and discharge. When coupled with information on the relationship between water velocity and the rate of re-entrainment of settled particles, this relationship will provide a powerful mechanistic understanding of the strength of upstream-downstream trophic linkages in river networks (see Gomi et al. 2002). In contrast, the Rouse numbers of leaves in transport were not related to their retention rate. This supports our conclusion that particle-streambed-flow interactions, not gravitational deposition, control the retention of leaves in riffles.

Although Rouse number is significantly related to retention rate coefficient ( $-k$ ), it is important to note that the Rouse numbers for all types of OM in the riffles are well below 1.25, the threshold for settlement of sediment (Cheng and Chiew 1999). This suggests that little or none of the material should be deposited on the bed the riffle reaches, but should remain in suspension. However, our results show that substantial portions of all OM types were retained in the riffle reaches. This clearly shows that interactions between retentive bed structures (cobbles and coarse gravel, in this case) and the shape and size of transported particles control OM deposition in shallow, rough-bedded streams. Furthermore, water velocities are relatively low in the interstitial spaces where small stiff or woody particles are often retained, further enhancing retention of coarse OM particles. Research is needed to determine if the critical value for entrainment of organic particles differs from that of sediment grains (see Cheng and Chiew 1999).

## Conclusions

The majority of studies that examine the retention of organic material in streams have focused on inputs of deciduous material (e.g. Brookshire and Dwire 2003), despite the ubiquity of coniferous and woody material in many stream ecosystems (but see Pretty and Dobson 2004). Our study demonstrated that different types of coniferous and deciduous detritus are physically conditioned at different rates, and the resultant differences in settling velocity – when combined with the differences in shape that exist among particle types – lead directly to the spatial partitioning of OM among microhabitat types. Conditioned OM in pools is largely driven by gravitational deposition, often creating extensive accumulations of detrital material. In contrast, the retention of OM in riffles is dependent on flow-particle-streambed interactions (inertial impaction and sieving). This leads to the relatively rapid retention of deciduous leaves, a valuable detrital resource (Richardson 1991, Webster et al. 1999, Richardson et al. 2004), in exposed microhabitats, while stiff, more refractory particle types (coniferous branch pieces, needles, and fronds) passively settled into interstices between larger stones, creating smaller accumulations of this material. Conditioned organic material is more valuable as a food resource than freshly delivered OM, and as such, the processes of physical and biological conditioning interact with hydrodynamic and geomorphological factors to determine food resource quality and availability. As they play key roles in retention, the shape, size, and density of OM particles may have considerable mediating effects on the productivity and composition of the detritivore

communities that exist in hydrodynamically and geomorphologically distinct microhabitats within stream ecosystems.

**Table 6-1**

Channel characteristics of all experimental release reaches (Blaney Creek Experimental Channel (Exp't), and Canyon Creek (CC), British Columbia)

	Length of Test Section (m)	Total Reach Length (m)	Bed slope (%)	$\Phi$ (SD) (cm)	Depth (cm) (SD)	Velocity (m/s) (SD)	Shear velocity $u^*$ (m/s)
Exp't. 'Riffle'	4.0	4.9	1.0	11.8 (3.7)	6.4 (2.6)	0.27 (0.074)	0.054
Exp't. 'Pool'	4.0	4.9	1.0	11.8 (3.7)	20.9 (2.9)	0.089 (0.014)	0.0093
CC Riffle 1	5.0	8.2	5.4	14.4 (3.9)	11.4 (2.2)	0.60 (0.24)	0.085
CC Riffle 2	5.0	8.2	5.7	13.8 (2.7)	9.7 (2.3)	1.00 (0.20)	0.14
CC Pool 1	1.4	1.7	0.3	4.4 (1.9)	8.2 (4.9)	0.30 (0.16)	0.033
CC Pool 2	1.4	2.6	0.4	16.4 (8.7)	18.1 (7.7)	0.18 (0.17)	0.026

**Table 6-2**

Physical characteristics (lengths and still-water settling velocities) of the four types of OM particles released in the experimental channel (physically conditioned 24 days in cold tap water) and in Canyon Creek (naturally conditioned in Canyon Creek)

OM type	Length (cm)		Settling velocity (cm/s)	
	Mean	SD	Mean	SD
<i>Cold water conditioned</i>				
Red alder leaves (fresh)	13.6	2.5	0.89	0.14
Red alder leaves (senesced)	13.1	2.4	0.69	0.032
Douglas-fir branch pieces	5.7	0.9	6.03	0.22
Douglas-fir needles	2.5	0.3	1.65	0.057
Red cedar fronds	3.5	0.7	2.03	0.13
<i>Naturally conditioned</i>				
Red alder leaves	8.3	0.4	1.8	0.8
Wood pieces	1.8	1.1	3.9	1.6
Conifer needles	1.7	0.4	1.8	0.3
Red cedar fronds	2.3	1.9	2.5	1.1

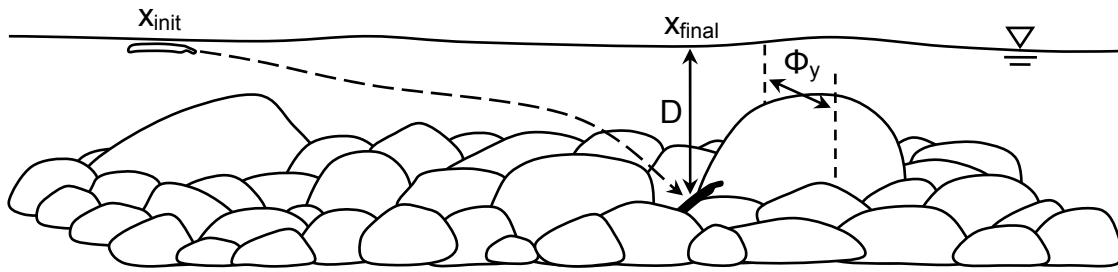
**Table 6-3**

Retention indices for four conditioned OM particle types released in 'riffle' and 'pool' conditions in the experimental channel and in natural Canyon Creek (CC) riffles and pools (see text for description of each index)

	OM type	$x_s$ (SD) (m) <sup>a</sup>	$x_{E-min}$ (m)	$x_{E-max}$ (m)	$p_{through}$	-k ( $r^2$ )	Ro
Exp't. 'Riffle'	Leaves	1.78 (0.89)	0.43	2.45	–	1.13 (0.91)	0.13
	Branches	0.43 (0.32)	0.15	0.28	–	2.56 (0.94)	1.12
	Needles	1.48 (0.83)	0.48	1.03	–	1.02 (0.98)	0.31
	Fronds	1.53 (0.86)	0.44	0.84	–	1.15 (0.97)	0.38
Exp't. 'Pool'	Leaves	1.13 (0.52)	0.47	2.67	–	2.15 (0.99)	0.75
	Branches	0.18 (0.08)	0.16	0.31	–	11.89 (0.88)	6.49
	Needles	0.75 (0.28)	0.53	1.12	–	3.70 (0.98)	1.78
	Fronds	0.52 (0.18)	0.47	0.91	–	6.28 (0.98)	2.19
CC Riffle 1	Leaves	n/a	–	–	0	0.34 (0.84)	0.26
	Wood	n/a	–	–	0	0.70 (0.88)	0.56
	Needles	n/a	–	–	0.30	0.23 (0.80)	0.26
	Fronds	n/a	–	–	0	0.28 (0.67)	0.37
CC Riffle 2	Leaves	n/a	–	–	0.31	0.24 (0.72)	0.14
	Wood	n/a	–	–	0.08	0.49 (0.72)	0.29
	Needles	n/a	–	–	0.63	0.064 (0.22)	0.14
	Fronds	n/a	–	–	0.49	0.085 (0.12)	0.19
CC Pool 1	Leaves	1.02	–	–	0.75	0.17 (0.57)	0.69
	Wood	0.38	–	–	0.17	3.35 (0.88)	1.50
	Needles	0.82	–	–	0.50	1.84 (0.94)	0.71
	Fronds	0.74	–	–	0.25	2.93 (0.98)	0.98
CC Pool 2	Leaves	0.76	–	–	0.42	1.00 (0.88)	1.30
	Wood	0.59	–	–	0	3.06 (0.93)	2.81
	Needles	0.91	–	–	0.58	1.40 (0.97)	1.33
	Fronds	0.76	–	–	0.08	3.11 (0.86)	1.84

<sup>a</sup> mean transport distances for the Canyon Creek Pools are calculated using only those particles retained within the pool; SD are not provided for CC Pools as mean values were calculated using interval data





**Figure 6-1**

Diagram of variables measured, including total transport distance ( $x_s$ ), the depth at the settlement point ( $D$ ), and the cross-stream diameter of the largest clast in contact with the settled particle ( $\Phi_y$ ).

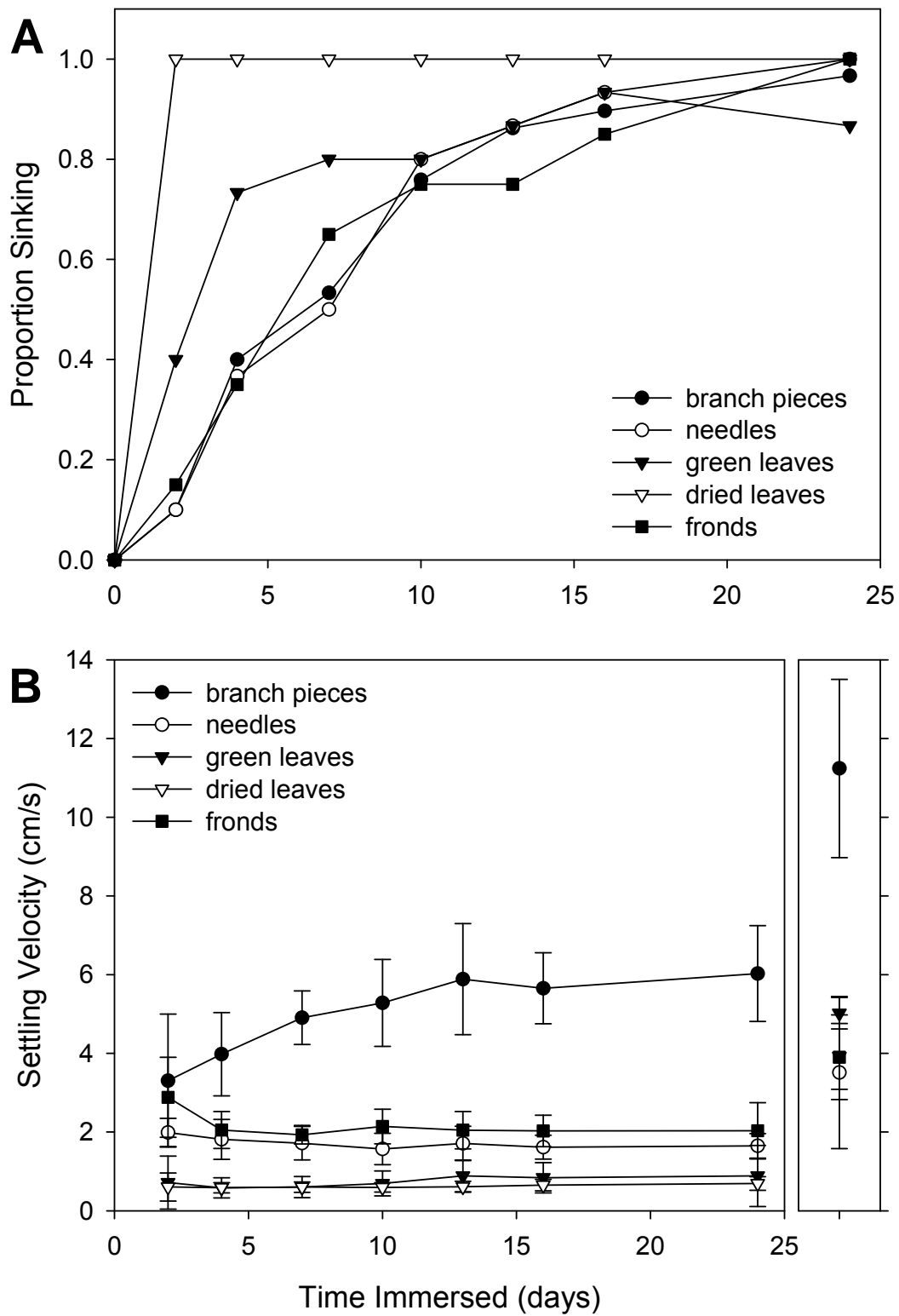
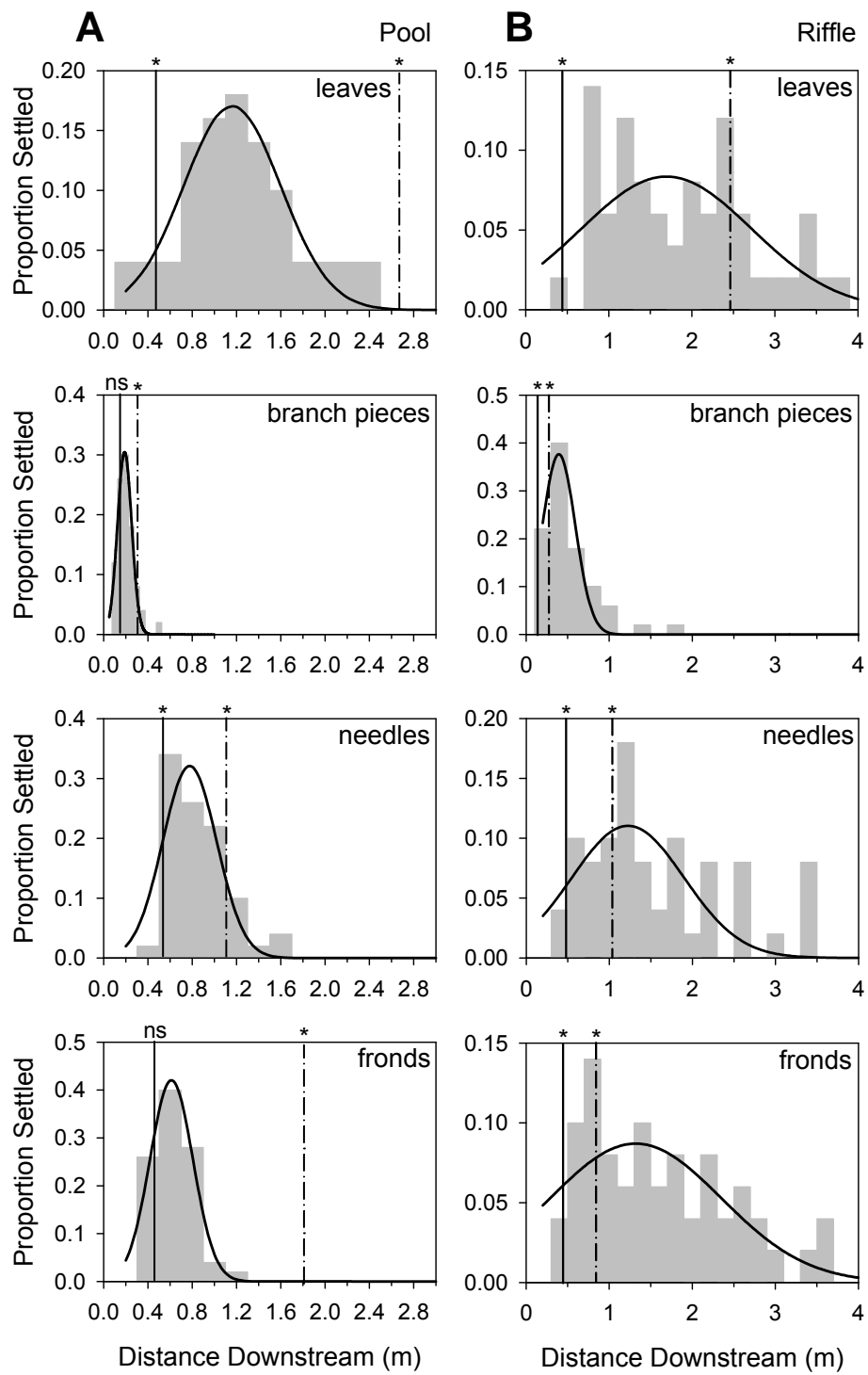


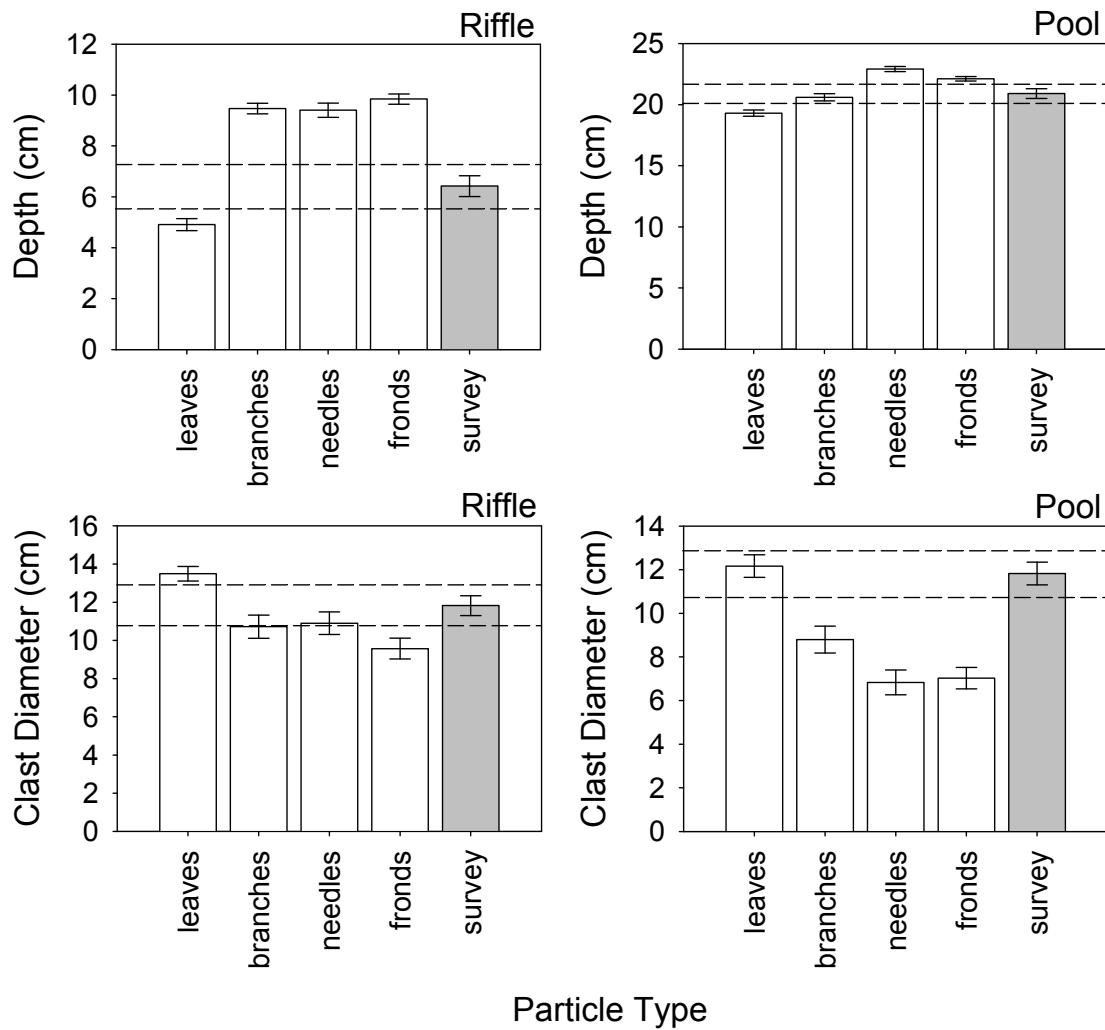
Figure 6-2

**Figure 6–2** (*previous page*) Change in (A) the buoyancy and (B) settling velocity of five types of soaked organic matter particles over 24 days of immersion. The final set of values immediately after day 24 represents the settling velocity of particles released on end. Error bars = 1 SD.



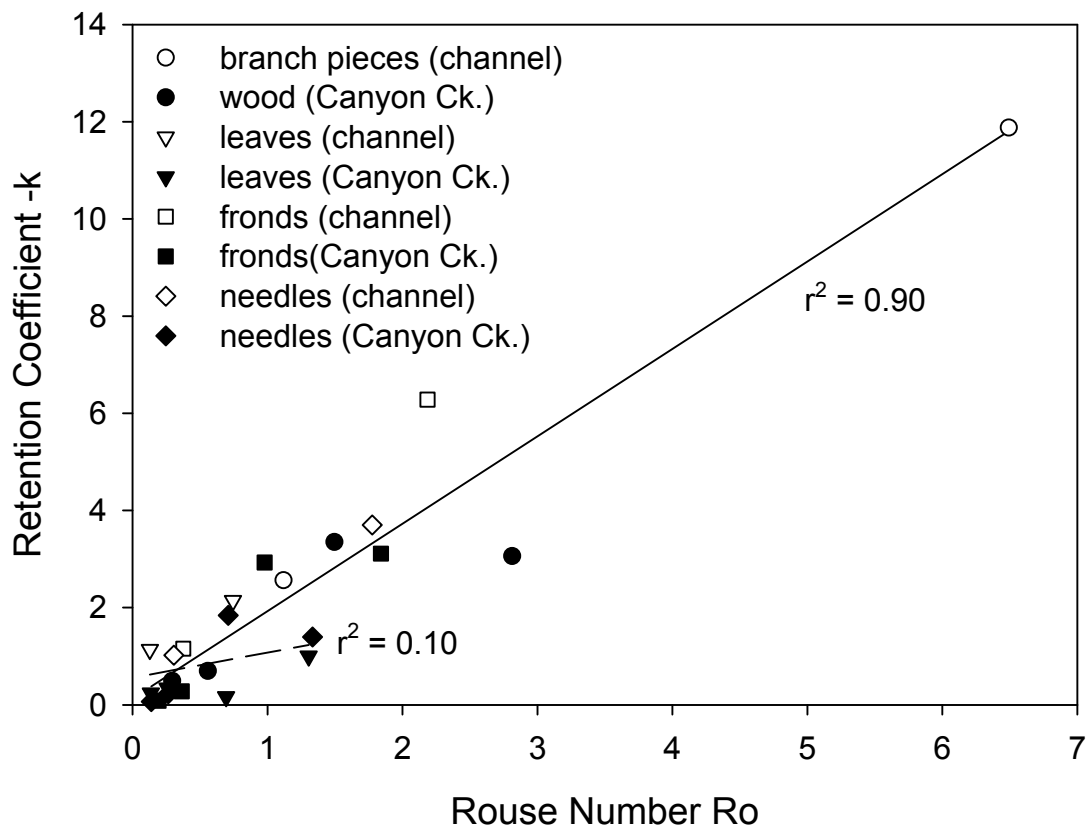
**Figure 6-3**

**Figure 6–3** (*previous page*) The proportion of organic matter particles settled at each distance (grey bars) in (A) pool and (B) riffle conditions in the Blaney Creek experimental channel. The solid vertical line represents the minimum expected transport distance ( $x_{E-min}$ ) modelled using the fastest (particles released on-end) measured settling velocity, while the dot-dash vertical line represents the maximum expected transport distance ( $x_{E-max}$ ) modelled using the slowest (particles released horizontally) settling velocity. Asterisks (\*) indicate a significant difference (one-sample t-test) between measured and modelled transport distances; 'ns' indicates no significant difference. Curves are three-parameter Gaussian curves fitted to the data. Note the finer measurement scale for the branch pieces released in the pool setting.



**Figure 6-4**

Depths and clast diameters associated with settled particles (and survey data) for riffle and pool settings in the Blaney Creek experimental channel. Grey bar is the survey data, error bars = 1 SE. The horizontal dashed lines represent  $\pm 2$  SE of the survey data.



**Figure 6-5**

Regression of retention coefficient (-k) against Rouse Number (Ro) for all OM particle types and all reaches (includes riffle and pool conditions in the Blaney Creek experimental channel, and all four Canyon Creek reaches). Solid line represents the regression of all stiff OM particle types (branch pieces, conifer needles, and red cedar fronds) ( $r^2 = 0.90$ ), and the dashed line represents the regression of flexible particles (alder leaves) ( $r^2 = 0.10$ ).

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## **CHAPTER 7: CONCLUDING REMARKS**

### **Dispersion of Invertebrates and Organic Matter in Streams**

Natural ecosystems are patchy in space and time, and streams are no exception (Pringle et al. 1988, Palmer and Poff 1997). The physical factors that define benthic habitats, including water velocity, shear stress, turbulence intensity, depth, and bed roughness vary substantially and systematically across a range of spatial scales (e.g. Hart et al. 1996, Hoover and Ackerman 2004, Chin 2002). Many studies have demonstrated that ecological processes are coupled tightly to local hydrodynamic and geomorphic conditions (see Statzner et al. 1988, Carling 1992, Palmer and Poff 1997, Hart and Finelli 1999). In this thesis, I have described the functional relationships that exist between water velocity – perhaps the single most important physical driver of lotic ecosystems – and the movement of two ecologically important ‘particle’ types, stream invertebrate larvae and coarse particulate organic matter. In doing so, I have clarified some of the mechanisms that link patterns of benthic biological diversity and environmental variation (Southwood 1977) in this dynamic ecosystem.

Relationships between stream invertebrate movement and water velocity are difficult to examine because dispersing invertebrates are not only directly influenced by hydrodynamic forces such as lift, drag, and turbulent suspension (see Weissenberger et al. 1991, Carling 1992, Fonseca 1999), but also respond behaviourally to variation in flow by modifying their foraging, feeding, crawling,

and drift entry rates (see Statzner et al. 1988, Palmer 1995, Hoffman et al. 2006). In this thesis, an experimental comparative approach was used to examine the various aspects of invertebrate dispersal (crawling, drifting, and swimming) separately, in order to clarify the roles played by behavioural processes and hydrodynamic forces. One of the predictions made by the marginal value theorem is that individuals will increase their patch residence times or will leave patches at lower resource densities as travel costs increase (Charnov 1976, Nonacs 2001). In the case of stream invertebrates, one might expect that as drift dispersal becomes less effective (i.e. drifting individuals are increasingly deposited in unsuitable habitats) and post-settlement pedestrian migration necessarily plays an increasingly large role in movement between patches, individuals will leave patches less readily. This prediction assumes that walking is more energetically costly than drifting, and that predation risk does not differ among patch types. The dispersal strategies described here provide general support for this prediction based on marginal value theory.

If patches are isolated, or among-patch movements are especially risky or costly, then larvae should be less likely to enter the drift or emigrate from suitable patches. *Epeorus* larvae, which occupy very patchily distributed high-shear habitats (the exposed surfaces of streambed stones in cascades), are likely unable to drift among habitat patches due to the difficulty of settling in habitats of this type (Chapter 4, also Lancaster et al. 1996). As such, if they enter the drift they are likely to incur the costs associated with post-settlement crawling in search of a habitat patch. As expected, *Epeorus* larvae drift less than the other

taxa examined (Fig. 7-1). Rather, crawling appears to be a dominant mode of movement for between-patch dispersal for this mayfly, as crawling (escape) movements dramatically increase as water velocity, and thus habitat suitability, decreases (Chapter 3). The very low drift rates of *Epeorus*, especially in fast currents (Palmer 1995, T.M. Hoover unpubl. data), and negative relationship between retreat distance and water velocity (Chapter 3) indicate that *Epeorus* larvae employ a 'crawling-dominated' dispersal strategy, and may rarely emigrate from patches with adequate resources.

Alternatively, repeated drifting may be means by which larvae can move among patches, as long as settlement in patches is possible. Several studies have found that *Baetis* larvae enter the drift readily, and disperse among patches primarily by drifting especially during the night or when food resources are scarce (e.g. Kohler 1985, Palmer 1995, McIntosh and Peckarsky 1999). This indicates that *Baetis* utilizes a 'drift-dominated' dispersal strategy. My results not only corroborate this, but also indicate that rates of drift entry are highly habitat-dependent (Fig. 7-1), a behavioural pattern which would increase rates of emigration from unsuitable habitat patches (see also Palmer 1995). However, the relatively limited control over settlement shown by larval *Baetis* at high velocities (Chapter 4) suggest either that this mayfly readily re-enters the drift upon settlement in a low-flow area of the streambed, or that post-settlement crawling movements play a role in among-patch benthic movements. The latter hypothesis is partially supported by results showing that the rate at which *Baetis* larvae disperse upstream also increases as velocity decreases (Chapter 2). As

many studies have quantified various aspects of the dispersal strategies of *Baetis* (e.g. Kohler 1985, Hershey et al. 1993, McIntosh and Peckarsky 1999), a substantial opportunity to further – and more completely – quantify the dispersal strategies of this widespread and ecologically important mayfly exists.

Where habitats are relatively continuous, and settlement is not physically constrained, larvae may leave the bed readily as displacement from an area of suitable habitat is unlikely. *Ameletus* larvae are found in pools and runs in high-gradient streams. Settlement of *Ameletus* is enhanced by rapid swimming, which allows them to orient to, and rapidly return to, the bed during drift (Chapter 4) or swimming escape (Chapter 3) movements. As drift distances are shortest at low water velocities and bed-oriented swimming becomes less effective as velocity increases (Chapter 4), settlement of *Ameletus* is greatest in low channel velocities (Fig. 7-1). However, results from Chapter 2 suggest that *Ameletus* drifts at a lower rate than *Baetis*, and relies on swimming rather than drift entry during escape maneuvers (Chapter 3). This, coupled with moderate crawling escape distances (Chapter 3) suggests that movement strategies of *Ameletus* may be ‘swimming-dominated’ (note that this was not one of the strategies originally proposed in Chapter 1). In baseflow conditions, pool and run habitat units may represent relatively continuous habitat types, and thus relatively short within-patch movements using swimming movements may be more important than among-patch drift-based movements for *Ameletus*.

Due to difficulties in collecting adequate numbers of *Paraleptophlebia*, all aspects of its dispersal strategy were not evaluated. However, the drift

movements of live and dead larvae were similar, suggesting that the drift strategies of this mayfly are 'passive settlement-dominated'. Drift movements of this type may be advantageous for *Paraleptophlebia* larvae, as being transported into and settling in depositional habitats (Lancaster et al. 1996) will ensure that it has access to accumulations of detrital matter (Kobayashi and Kagaya 2002, 2004), a critical food resource for this taxon (Mattingly 1987).

A similar approach can be used to assess the spatial/temporal dynamics of different organic matter types in riffles and pools (Fig. 7-2). The dramatically different shapes, settling rates, and breakdown rates of deciduous (red alder *Alnus rubra*) leaves and material of coniferous origin (e.g. Douglas-fir *Pseudotsuga menziesii* needles) appear to contribute to resource transfer rates that vary substantially among habitat unit types. Alder leaves are both retained and broken down more rapidly in pools than riffles (Chapter 5,6), suggesting that pools are an important site for the incorporation of terrestrial subsidies into benthic food webs. Although the retention and breakdown rates of leaves are slightly lower in riffles than in pools, leaf detritus retained in riffles may play a critically different role in benthic food webs as the detritivorous 'shredder' community in riffles (stonefly-dominated) is often substantially different from that in pools (caddisfly-dominated) (e.g. Kobayashi and Kagaya 2002). The retention of coniferous needles is far lower in riffles than in pools (Chapter 6), which may lead to the accumulation of fast-settling organic particles of these types in pools, a pattern noted in other studies (e.g. Kobayashi and Kagaya 2002, 2004). It is important to note that the heuristic model outlined here (Fig. 7-2) assumes that



material will be retained for only 10 days before being re-entrained and carried further downstream. Unfortunately, we know very little about how the re-entrainment of different types of deposited organic matter is influenced by either stage of decomposition or by changes in bed shear stress associated with increases in discharge. As a result, the residence times of organic matter on the bed are poorly understood, and the small-scale spatial and temporal dynamics of organic matter budgets in streams cannot easily be modeled.

## **Future Directions for Research**

In marine systems, the behaviour of dispersing planktonic larvae often plays an important role in determining transport distance and settlement success. Several studies have recorded behavioural shifts of drifting larvae in response to boundary layer characteristics (Finelli and Wetthey 2003), changes in turbulence intensity (Crimaldi et al. 2002), acoustic cues (Montgomery et al. 2001), water-borne chemical cues (Hadfield and Koehl 2004), or a combination of these factors (Koehl et al. 2007). These cues provide valuable information to dispersing larvae not only about patch proximity, but also as indicators of patch quality. It is unknown, however, how or if any of these same factors are used by drifting stream invertebrates to identify patches of habitats as they are transported downstream. Similarly, we know relatively little about the proximal cues that crawling invertebrates use to orient towards patches of suitable habitat (but see Olden et al. 2004, Hoffman et al. 2006). More research on how benthic organisms perceive the physical and biological components of their surrounding landscapes is needed before comprehensive models of stream invertebrate

dispersal and inter-patch movement can be developed. Such studies on dispersing marine larvae have provided insight into these processes in marine systems (see Abelson and Denny (1997) for a review).

While Chapters 5 and 6 in this thesis describe the physical processes of organic matter retention by streambed sediments in small streams, there are two major issues that must be resolved before the results can be generally applied. First, retentive structures other than sediments play a major role in organic matter retention in many streams. Debris dams, isolated pieces of woody debris, overhanging vegetation, and stream banks have all been shown to retain leaf litter (Smock et al. 1989, Ehrman and Lamberti 1992, Brookshire and Dwire 2003). Further research examining how structures of these types interact with local flow velocities to retain various organic matter types is needed to provide a basic understanding of organic matter transport-retention dynamics in small streams. Second, channel discharge plays an important role in organic matter transport (Jones and Smock 1991), but how particle-flow-substrate interactions are altered as discharge increases is not known. There is some indication that leaf litter may be primarily retained by sediments at baseflow discharge but increasingly retained by large, cohesive structures such as debris dams (Brookshire and Dwire 2003) as discharge increases. If this is true, then retentive processes will be tightly coupled with the spatial distribution of detrital resources; at low discharges, leaf litter may be highly distributed over the streambed in small sediment-associated patches, while high discharges during spates may mobilize leaf litter and accumulate it in large masses in debris dams. Research is needed

to quantify how discharge controls both the amount and distribution of organic detritus available to benthic detritivores in small streams.

A critical step in the process of particle and larval redistribution in streams is that of entrainment. Early debates about the relative importance of passive (physically-controlled) versus active (behaviourally-controlled) entry of larvae into the drift (Elliott 1967, Ploskey and Brown 1980) were largely resolved by subsequent studies that demonstrated that entry into the drift is largely under behavioural control (e.g. Kohler 1985). However, recent studies have indicated that passive entry of benthic invertebrates into the drift may be an important process during spates when water velocities and shear stresses are elevated (e.g. Gibbins et al. 2007). The entrainment thresholds for particulate organic particles may be similarly complex due to flow-particle-sediment interactions and trapping of particles in interstitial spaces. Fortunately, the processes that regulate the entrainment of larvae and organic matter particles are likely fundamentally similar to those involved in sediment mobilization and transport. Both sedimentologists and stream ecologists are interested in the forces acting on particles on the bed, the distance those particles are transported in bedload or suspension once mobilized, and the settlement patterns of those particles. However, sedimentologists are primarily interested in grains of sediment, while ecologists focus primarily on organic 'particles' such as invertebrates or organic matter. Sediment grains are entrained when the critical shear stress for incipient motion is exceeded (see Buffington and Montgomery (1997) for a review). Although entry into the drift for most invertebrates is thought to be under

behavioural control (Kohler 1985), a similar physical threshold for entrainment may exist for benthic invertebrates. A form of the dimensionless shear stress ( $\theta$ ) that describes entrainment conditions for sediments may be applied to describe the stresses acting on benthic organisms. Carling (1992) suggested that this might be done by replacing the relative density of the sediment particle ( $\rho_s - \rho$ ) with the relative density of the organism ( $\rho_o - \rho$ ), and having characteristic length ( $L$ ), drag coefficient ( $C_d$ ), and bed adhesion ( $\phi$ ) replace particle size, shape, and exposure parameters, respectively. A similar approach may be used to model the entrainment of organic matter particles, although complex relationships between particle shape and sediment grain geometry will have to be accounted for in the relationship (see Chapter 6), possibly by modifying values for bed adhesion. As larvae exert behavioural control over the drift entry process, these parameters may not necessarily specify entrainment conditions, but may describe conditions in which invertebrates are forced to seek less exposed flow microhabitats in order to avoid being swept from the bed.

## **Applications**

The studies presented here show clearly that the biological components of small streams are strongly coupled to physical processes. These results can inform stream management and rehabilitation projects, as both plant detritus of riparian origin and drifting insects are crucial components of stream food webs. Altering channel characteristics such as bed roughness, bed sediment geometry, or average water velocity can potentially increase – or decrease – the availability of these food resources to higher trophic levels. Organic matter of terrestrial

origin is a crucial basal food resource in many stream systems (e.g. Richardson et al. 2005), while drifting insects are a major source of food for many economically important fish species, including many salmonids (see Rader (1997) for a review). Millions of dollars are spent every year in Canada in order to restore and enhance channels and increase stream productivity in order to maximize the survivorship and production of these and other fish species. Substantial annual effort is dedicated to restoring and evaluating the ecological functioning of channels that have been impacted by forest harvest practices, hydroelectric projects, road-building, or other cultural activities (see Lepori et al. 2005, Lake et al. 2007). In many instances, maximizing the local production or immigration of benthic organisms will increase the food available to a variety of fish species. As such, understanding the linkages between organisms and their physical environment is critical in the development of predictive models that relate the structure and function of ecosystems.

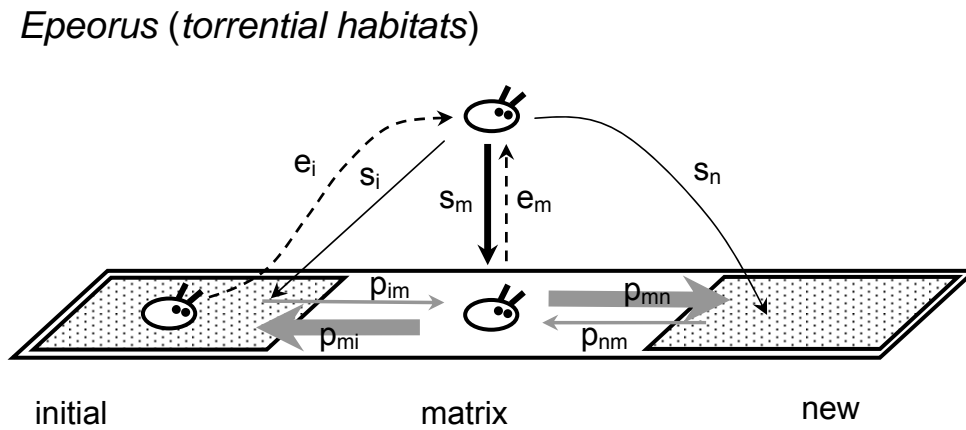
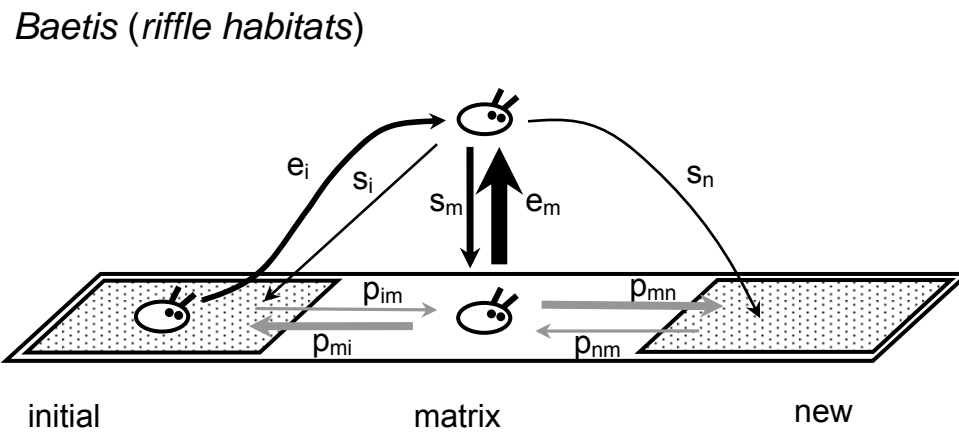
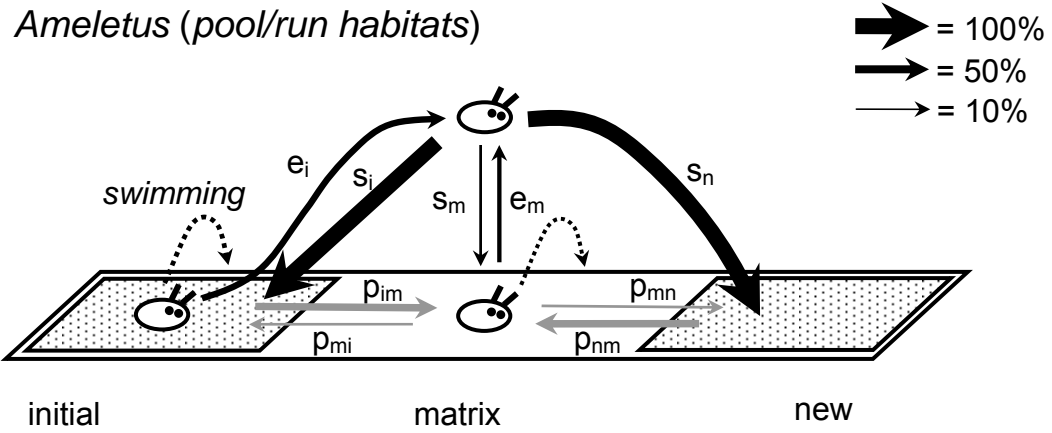
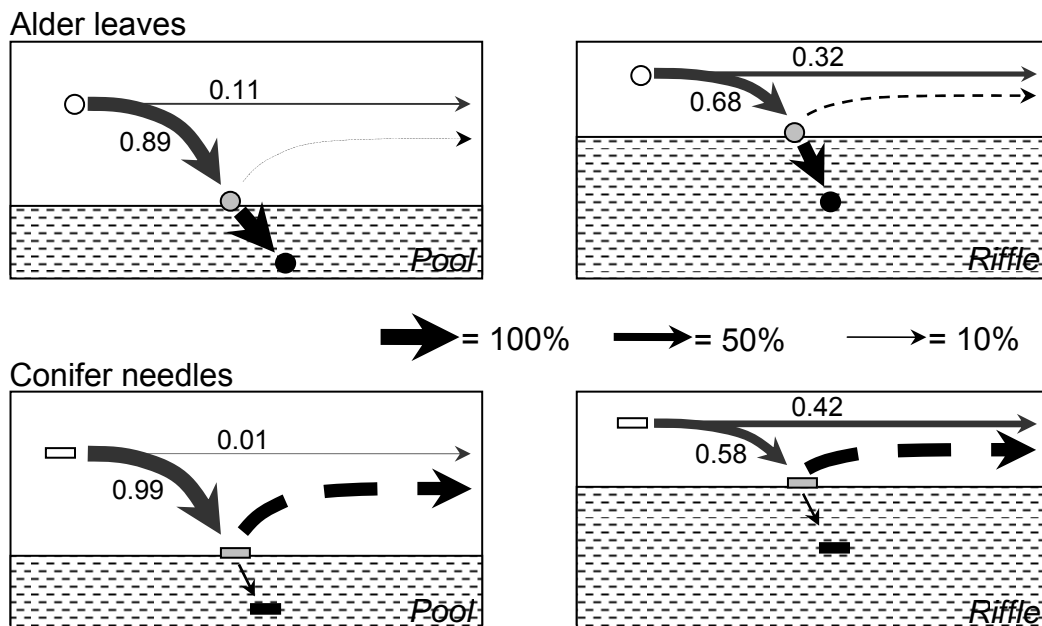


Figure 7-1

**Figure 7-1** (*previous page*) Estimates of the relative contributions of individual movement modes to between-patch movements of three mayflies (*Ameletus* (top panel), *Baetis* (middle panel), and *Epeorus* (bottom panel)) in spatially heterogeneous stream landscapes, as estimated from data in Chapters 1, 2, and 3. The initial (upstream) and new (downstream) patches of suitable habitat are stippled, the matrix (unsuitable habitat) separating the two habitat patches is white. In this heuristic model, the habitat patches of *Ameletus* larvae correspond to the low-velocity treatments in each chapter, while habitat patches of *Baetis* and *Epeorus* correspond to high-velocity treatments. Entrainment in the initial patch and the matrix =  $e_i$  and  $e_m$ , respectively; settlement in the initial patch, the new patch, and the matrix =  $s_i$ ,  $s_n$ , and  $s_m$ , respectively; crawling (pedestrian) movements from the initial patch into the matrix, from the matrix upstream to the initial patch, from the matrix downstream to the new patch, and from the new patch upstream to the matrix =  $p_{im}$ ,  $p_{mi}$ ,  $p_{mn}$ , and  $p_{nm}$ , respectively. The thickness of each vector arrow represents the importance of that movement pathway relative to the maximum value observed for that pathway in all taxa (e.g. the shortest hitting distance observed ( $x'_s = 0.03$  m) was for *Ameletus* in the low-velocity treatment, hence the arrow thickness for that movement pathway ( $s_i$ ) was 100%, and values of  $s_i$ ,  $s_n$ , and  $s_m$  for *Ameletus*, *Baetis* and *Epeorus* (and the thickness of those arrows) are scaled by that value). Dotted arrows represent swimming movements, dashed arrows represent movement pathways which were never observed but are presumed to exist (i.e. *Epeorus* larvae entering the drift). The magnitude of the crawling dispersal vectors (grey arrows) were estimated from the upstream movement rates reported (Chapter 2) for *Ameletus* and *Baetis*, and from retreat distances (Chapter 3) for *Epeorus*; upstream and downstream crawling rates were assumed to be similar, even though an upstream bias in the crawling directions of larvae was sometimes observed for *Ameletus* and *Baetis* (Chapter 2). Settlement vectors ( $s_i$ ,  $s_m$ , and  $s_n$ ) were estimated from hitting distances (Chapter 4). Swimming vectors (dotted arrows for *Ameletus* larvae) were estimated from the relative utilization of swimming escapes over other escape modes (Chapter 3). Entrainment (or drift entry) vectors were estimated from drift rates (Chapter 2) for *Ameletus* and *Baetis*, and from the relative utilization of drift escapes (zero) over other escape modes (Chapter 3) for *Epeorus*; it is important to note that drift rate data for *Epeorus* (measured in the channels used in Chapter 2; data were not included due to low sample size) also indicate that this torrential mayfly rarely enters the drift at any velocity. Flow is left to right.



**Figure 7-2**

Estimates of the relative contributions of retention and breakdown in organic matter (red alder (*Alnus rubra*) leaves (circles) and conifer needles (rectangles)) processing in riffles and pools in small streams, as estimated from data in Chapters 5 and 6. Entrained organic matter particles (white symbols) can either be exported downstream to the next channel unit, or can be retained (grey arrows). Retention is generally higher in pools (left column) than in riffles (right column). Once retained (grey symbols), organic matter particles can either be broken down (solid black arrow pointing to a black symbol) or re-entrained and transported downstream (dashed arrow). The thickness of the arrows denotes the probability of a particle in a given state (either in transport or settled) entering one of the two subsequent states (settled vs. exported downstream, or broken down vs. re-entrained and exported downstream). Habitat unit-specific retention and export values were estimated from averaged values of  $k$  (incorporating both experimental and natural channel units in Chapter 6) and the exponential decline model  $L_x = L_i e^{-kx}$ , (assumes a 2 m habitat unit length (i.e.  $x = 2$  m), see Chapter 6 for more details). Alder leaf breakdown rates were calculated from leaves placed in 'exposed' microhabitats in riffles and pools (Chapter 5), while conifer needle breakdown rates are from Richardson et al. (2004), and are assumed to be similar in riffles and pools. The proportion of particles that are re-entrained and exported downstream (dashed arrows) are estimated as the proportion of mass remaining (not yet broken down) after 10 days (i.e. a 10-day residence time). However, it is important to note that very little is known about the rates of – or shear stress thresholds for – organic particle re-entrainment.



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