Patch-Specific Disturbance in Steep Streams: A Geomorphic Framework

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Contents

Declaration

I hereby declare that I composed this thesis and that the work described therein is my own and has not been submitted for any other degree or professional qualification except as specified.

David Oldmeadow

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Abstract

Floods are an obvious source of disturbance for benthic invertebrates. A rise in discharge can result in a reduction in invertebrate populations, change in physical habitat and loss of resources. The persistence of invertebrate populations in streams that experience frequent flooding may be dependent on the size and spacing of refugia, and the flux of individuals between refugium and non-refugium patches. In this thesis I propose a framework to characterise the size and spacing of refugia in steep streams, based on a geomorphological classification of the streambed. Focusing primarily on four aspects, the physical attributes, particle movement and invertebrate assemblage associated with each morphological patch, and the hydraulic influence on invertebrate drift and settlement, I test the response of invertebrates to floods of different magnitudes on each patch type, Loose, Degraded and Structured. Patch type differed in sedimentological character. This was reflected in entrainment thresholds. Loose patches were mobilised by low magnitude flood events, contributing to phase I sediment transport. Degraded patches were mobilised by larger events, contributing to phase II sediment transport, and Structured patches remained stable. Bedload data in combination with mapping of the patch types provides a surrogate measure of size and spacing of area mobilised. Bedload equations predict particle size mobilised, but only during phase I transport. A strong association of invertebrate assemblage with patch type was detected. Distribution of some species was restricted to Structured patches. Contribution of Structured patches to invertebrate abundance is much greater than their areal extent suggests. I hypothesised that the hydraulic environment of a Structured patch, step, promotes drift settlement. *Baetis rhodani* and *Simulium* sp show no change in drift and settlement over a step, despite a large increase in velocity and turbulence. *Hydropsyche pellicudula* and *Ecdyonurus torrentis* drift further. The hydraulic environment of the step constrained the settlement and distribution of *E. torrentis*. The difference in drift response between the mayfly species is due to a complex interaction between behaviour and hydraulic environment. I contend this is driven by body morphology. A net loss occurred on all patch types during after flooding, although the assemblage on Structured patches was more resistant. Species-specific response was complex, and not related to particle movement. Loose patches, despite complete mobilisation, accumulated individuals, but this varied between flood events. Particle movement was only weakly linked with the processes responsible for the post-flood pattern of invertebrates. The patch classification does not discriminate on the basis of these processes, and may not provide a useable framework to characterise size and spacing of refugia in steep streams.

Chapter one Introduction

How do populations and communities persist in an environment that is subject to physical disturbances that can result in loss of individuals? This is an important question facing basic and applied ecologists, and relevant to all ecosystems. There are two general 'solutions' to this question: A population may exploit temporal synchronicity between the disturbance and life phase or habitude. Alternatively, a population may occupy a large enough space so that the disturbance of any particular habitat within that space becomes inconsequential to the population as a whole. Thus, the proportion of the population lost during a disturbance is sufficiently small that the impact on population persistence is trivial. (DeAngelis & Waterhouse, 1987, Lancaster & Belyea, 1997). If a population goes extinct in one habitat or at one time, recruitment can be derived from another. This second 'solution' is considered by most ecologists to be the most likely explanation, a view that has been incorporated into mathematical models (e.g. DeAngelis & Waterhouse, 1987, Petratis *et al.*, 1989, Lancaster & Belyea, 1997) and stimulated many ecological studies. Central to this explanation are the concepts of heterogeneity in the physical environment and disturbance refugia, where the negative effects of disturbance are lower than the surrounding area (spatial) or lower at another time (temporal), and thus loss of individuals is reduced.

In streams, fluctuations in flow are an obvious source of disturbance for benthic invertebrates. Droughts can bring about a variety of patterns in longitudinal patchiness as streams dry up, resulting in habitat loss, altered hydraulic regimes, deterioration of water quality and high temperatures (Cowx *et al.*, 1984, Chessman &

Robinson, 1987). Lake (2000) described droughts as a press disturbance that may arise sharply and is then maintained at a constant level. Flooding, however, is considered a pulse disturbance (Lake, 2000), a comparatively short-term and sharply delineated event. A rise in discharge can result in an increase in depth and velocity and an associated increase in shear stress exerted on the bed and the movement of particles, resulting in a change in the immediate physical habitat (e.g. Kondolf *et al.*, 1991). Both types of disturbances can result in population loss of benthic invertebrates, changes in physical habitat and loss of resources (Lake, 2000).

In this thesis I focus on flood disturbance and the use of refugia by benthic invertebrates. In streams that experience frequent flooding, the persistence of benthic invertebrate populations is reliant on the existence of refugia (Lake, 2000). The spatial attributes of refugia (e.g. size and spacing) and the mechanism of refugia use (e.g. whether organisms accumulate in refugia during flooding and re-distribute after) can influence final population sizes and persistence (Lancaster & Belyea, 1997). My main interest here lies in trying to characterise, simultaneously, the spatial attributes of refugia in streams (i.e. size, spacing and number), the drift and settlement potential of invertebrates into refugia during flooding (i.e. accumulation) and the loss of individuals from non-refugium areas. To do this, I propose a framework based in a better understanding of the relationships between stream channel morphology and fluvial processes, and fluvial process and invertebrate dislodgement, drift and settlement. I use steep headwater streams as a case system to develop the framework and investigate these relationships.

1.1 Persistence in Streams

For populations to persist in flowing waters, the ability of an organism to adhere or cling to the surface of the substrate is clearly important (Allan, 1995). Many benthic invertebrates in streams exhibit a variety of anatomical adaptations that directly enhance attachment to the substrate and permit them to withstand the physical forces of flowing water (Statzner & Holm, 1989, Allan, 1995). *Simulium*, for example, uses specialised prolegs to attach to a silk mat spun onto the substrate surface, and some species, e.g. *Simulium vittatum*, can resist flows up to 3.3 m/s (Eymann, 1998). Blepharoceridae possess a row of six ventral suckers that reduce the risk of dislodgement and allow for free movement under high flows (~ 2 m/s) (Frutiger, 1998). All Ephemeroptera, Plecoptera and Trichoptera posses tarsal claws of varying sizes and shapes that aid attachment, the efficiency of which may depend also on the texture of the substrate (Lancaster, 1999a). Such adaptations are often referred to as resistance traits, and reduce the probability of dislodgement (and potential loss of individuals) during periods of high hydraulic stress, such as floods.

An organism's potential for dislodgement, however, depends on the hydraulic stress it experiences relative to the force required to dislodge it from the substrate. For most benthic organisms living in streams, the critical shear stress for dislodgement is below that required for the entrainment of the surface particles they inhabit (e.g. Hart, 1992, Borchardt, 1993, Imbert & Perry, 2000). During flooding, however, hydraulic forces can increase to the point at which particles are mobilised. To persist in streams subject to frequent flooding, invertebrates must therefore exploit a variety of spatial and temporal refugia, areas where hydraulic forces are below the threshold for dislodgement or particle movement.

Scales and Mechanisms of Refugia Use

Benthic invertebrates may lessen the impact of flooding by exploiting refugium at a variety of spatial and temporal scales. The mechanisms of refugia use are diverse, however, and depend on both spatial and temporal attributes of the physical environment, plus physiology, morphology and mobility of the organism.

Lancaster & Belyea (1997) outlined a hierarchical framework of groups of mechanisms operating at different spatial and temporal scales that may allow benthic invertebrates to persist in streams subject to flooding. At large scales (i.e. > stream), for individuals that do not survive disturbances, population persistence depends on recruitment from external sources. Recruitment can either be derived from a different catchment that remained unaffected (i.e. spatial refugia), or the same catchment where generations overlap (i.e. temporal refugia). This mechanism of persistence is likely to be crucial for natural disturbances such as drought, where entire streambeds dry up (e.g. Smock *et al.*, 1994), and anthropogenic disturbances such as insecticide applications, where populations are removed from stream systems (e.g. Wallace *et al.*, 1991). It may also be important for systems where flash floods can devastate a population, e.g. desert streams (Fisher *et al.*, 1982), and high gradient colluvial streams where mass-wasting events mobilise the entire channel (Hogan, 1991).

In most gravel bed streams (i.e. rocky), only rarely is the entire streambed affected by hydraulic disturbance (i.e. high shear stress and particle movement) even during large flood events. At small scales (i.e. within the catchment), individuals may survive disturbances by changes in habitude (i.e. temporal), or survive *in situ* and or move between habitat patches that are differentially affected by the disturbance (i.e. spatial). While a flood may occur down the length of an entire stream, habitats are typically differentially affected (Pringle *et al.*, 1988), and organisms usually fare better in some habitats than others (e.g. Matthaeii *et al.*, 2000). The hyporheic zone for example, may protect eggs, pupae and diapausing stages of some benthic invertebrates during adverse seasonal conditions (Pugsley & Hynes, 1986), providing temporal refugia. Low flow zones behind large obstacles, e.g. debris dams, may remain unaffected by hydraulic disturbances during flooding and provide refugia for residents (e.g. Palmer *et al.*, 1996), i.e. spatial refugia.

Small-scale (i.e. < stream) spatial refugia are focus of most studies (Lake, 2000), and evidence suggests that these refugia may be important in some systems for some organisms, allowing for rapid recovery (< generation time) after flood events (e.g. Matthaei *et al.*, 1997). In a structurally heterogeneous channel, there may be many obstacles, holes, interstices, backwaters, debris, or large stable boulders that may offer protection from the hydraulic effects of flooding. There are, however, several different mechanisms by which organisms may use such spatial refugia. Organisms may survive *in situ*, with no re-colonisation of disturbed patches after the flood event, e.g. sessile mussels (Strayer, 1999) and epibenthic microcrustacea (Robertson *et al.* 1995). For such organisms, recolonisation of the stream bed, even on small scales, requires recruitment (e.g. Strayer, 1999). Few benthic invertebrates in the lotic environment however are truly sessile, and may move into and out of refugia patches during and after the disturbance. Lancaster & Belyea (1997) classified the use of small-scale spatial refugia into three types based on the flux of individuals between refugium and non-refugium patches; Model B, no movement (i.e. organisms survive *in situ*, e.g. sessile mussels); Model C, individuals already in refugia survive during flooding, and move out to recolonise denuded patches after, but do not accumulate in refugia during the flood; and Model D, individuals accumulate in refugia during the flood and disperse after the event to colonize denuded patches. These simplistic models emphasise the importance of the spatial attributes of refugia and the flux of individuals between refugium and non-refugium habitats for population persistance.

Most benthic invertebrates in streams are mobile and have the potential to move into refugia to escape the hydraulic effects of flooding (i.e. increased shear stress and particle movement). Small-scale studies in flumes have demonstrated that benthic invertebrates can respond to increased shear stress by crawling into crevices between particles (e.g. Holomuzki & Biggs, 1999), migrating down into the interstitial spaces of the hyporheic zone (e.g. Palmer *et al.*, 1992) or drifting to areas of low shear stress (Lancaster, 1999b). Providing evidence of small-scale movements in the field however, is more difficult as organisms cannot be observed. Nevertheless, field experiments, using mesh cages as artificial flow refugia have provided indirect evidence that, during flooding, invertebrates can accumulate in areas where the flow is reduced (Lancaster *et al.*, 1990, Winterbottom *et al.*, 1997, Lancaster, 2000).

Whether or not this involved active or passive movement of the individuals is impossible to tell. What is important is that accumulation occurred in low flow zones and individuals survived. Evidence for the accumulation of individuals within natural features of the stream environment, however, is scarce and circumstantial. For most benthic invertebrates the fate of individuals is intractable. Nevertheless, Brooks (1998) found evidence for the passive movement of chironomids and mayflies into pools during a large flood, and Palmer *et al.* (1995) found several species of copepod in low flow patches during a flood that had not previously been found there, along with an increase in abundance of other species. In another study in the same stream, Palmer *et al.* (1996) found that some low flow zones associated with debris dams also accumulated individuals during flooding. Marchant (1995) observed a seasonal downward migration of chironomid larvae into the hyporheic zone in response to increased discharge during the winter months, whereas Dole-Oliver *et al.* (1997) and Palmer *et al.* (1992) provided evidence for downward migration in response to specific flood events, although for the later this migration was not sufficient to stop dislodgement via scouring. The case for short-term movements of refugees into refugia, i.e. accumulation, is mounting. There is, however, little direct evidence of short-term movements out of refugia during or immediately after flooding to re-colonise denuded substrates.

Can Small-Scale Refugia Maintain Invertebrate Populations?

The utility of within habitat refugia to benthic inverterbrates appears to be species specific (Robertson *et al.*, 1995, Palmer *et al.*, 1995, 1996). Sessile invertebrates, e.g. mussels, may rely on inhabiting areas of the streambed that are rarely disturbed, and adult recruitment for population persistence (Strayer, 1999). Other more mobile species may actively accumulate in low flow refugia (Palmer *et al.*, 1995), or migrate into the hyporheic zone (Dole-Oliver *et al.*, 1997), to redistribute after the flood, or simply survive *in situ* on stable particles on the surface of the bed (e.g. Matthaeii *et al.*, 2000). Post-flood community recovery, and ultimately population persistence, may be due to a combination of mechanisms operating at small spatial scales (i.e. < stream, Models B, C and D, Lancaster & Belyea, 1997), and or mechanisms operating at larger scales, e.g. adult recruitment (e.g. Fisher *et al.*, 1982, Palmer *et al.*, 1996). So, how important are within-habitat refugia for post flood recovery and population persistence in streams?

The answer to this question is not straightforward. The relationships of the physical characteristics of small-scale refugia in streams and the movement of organisms, with post-flood recovery and persistence, are likely to be complex. Lancaster & Belyea (1997), using a simple mathematical model, demonstrated that under certain conditions small-scale refugia may be adequate to maintain populations in an environment that is frequently disturbed. Their results are instructive even though their model was unrealistically simple, i.e. their simulations were only for a 2-dimensional stream (and did not include the hyporheic zone) and they did not consider the possibility of discharge dependent refugia (Brooks, 1998), Total refugium area and proportion of population lost at each disturbance had a strong effect on the final population size. They also found that the size of refugium patch and aspect ratios such as total perimeter length also affected the population size after flooding. While the importance of spatial characteristics of refugia in streams has been emphasised before (e.g. Reice *et al.*, 1990, Sedell *et al.*, 1990), albeit qualitatively not quantitatively, Lancaster & Belyea (1997) also demonstrated that the flux of individuals into and out of refugium patches was important and, under some conditions, critical for population persistence.

The models of Lancaster & Belyea (1997) are similar to models based on the concept of a spatial 'spreading the risk' (den Boer, 1968), i.e. at any given time, a disturbance may result in a decrease in sub-populations in some patches, but an increase or no change others. Models based on this theme, and variations thereof, show that the 'spreading of risk' can be very successful in maintaining a population in the face of disturbances if there is flux, i.e. movement of individuals, between the patches (DeAngelis & Waterhouse, 1987). The spatial organization of patches however, as well as their size, also may affect net loss (Bond *et al.*, 2000a). Models such as Lancaster & Belyea (1997) and those based on the concept of 'spreading the risk' (DeAngelis & Waterhouse, 1987) highlight the importance of spatial heterogeneity and the movement of organisms between patches for population persistence.

While small-scale refugia may ameliorate the effects of flooding (e.g. Palmer *et al.*, 1996), it remains unclear as to how such refugia actually contribute to the persistence of invertebrates in streams. The models of Lancaster & Belyea (1997) and others have yet to be fully tested in the stream environment. Indeed, only Lancaster (2000) to my knowledge has examined how the spatial attributes of refugia directly affect their use by invertebrates. Using mesh cages as artificial flow refugia, Lancaster found that by increasing surface area to volume ratios (making smaller refugia), the efficiency in which the cages accumulated taxa also increased. Quantifying the relative importance of refugia for post flood recovery and population persistence is not trivial, but likely requires a good understanding of the spatial and temporal attributes of the physical environment and the life history and mobility of the organisms within that environment.

Physical Form of Refugia in Streams:

Reviews of refugia in streams have emphasised a range of morphological features of the streambed at a variety of spatial scales that may act as refugia, from individual particles to whole stream reaches and flood plains (e.g. Sedell *et al.*, 1990, Poff & Ward, 1990, Reice *et al.*, 1990). Since these reviews, the potential use of within habitat refugia by invertebrates during flooding has received a lot of attention (e.g. Dole-Oliver & Marmonier 1992, Palmer *et al.*, 1992, 1995 & 1996, Lancaster & Hildrew, 1993b, Robertson *et al.*, 1995, Dole-Oliver *et al.*, 1997, Strayer, 1999, Rempel *et al.*, 2000, Matthaei *et al.* 2000, Matthaei & Huber, 2002). Early literature however, suggested that stream benthos may migrate down into the interstitial spaces of the hyporheic zone during flooding, and be available for subsequent re-colonisation of the surface after (Williams & Hynes, 1974, Williams, 1977, 1984, Pool & Stewart, 1979, Marchant, 1995). Although large numbers of invertebrates have been found in the hyporheic zone, most are resident fauna (Boulton *et al.*, 1998). Evidence suggests that the migration of benthic fauna downwards into the sediment during flooding may be patchy (Dole-Oliver *et al.* 1997), and not be sufficient to provide refuge from the effects of flooding when deep scouring occurs (e.g. Palmer *et al.* 1992). In some systems, migration has not occurred during flooding (Gayraud *et al.* 2000), leading to the suggestion that other refugia within the channel may be more important in these systems. Indeed, empirical evidence suggests that the hyporheic zone alone is not sufficient to explain post-flood (e.g. Palmer *et al.* 1992).

During flooding some areas of the streambed may remain low flow depositional zones for much of the hydrograph (Lancaster & Hildrew, 1993a, Palmer *et al.*, 1996, Wolh & Thompson, 2000). These zones do not experience an increase in shear stress or particle mobilisation during flooding, and can act as refugia for resident fauna (Lancaster & Hildrew, 1993b, Palmer *et al.*, 1996). Robertson *et al.* (1995) provided evidence that whole stream reaches that remain low flow zones during flooding can provide refugia for meiofuana, and on a smaller scale Palmer *et al.* (1996) demonstrated that low flow associated with debris dams in a sandy bottom stream provide refugia and accumulate individuals. Generally, a reduction in flow is either associated with an obstacle, e.g. debris dam, or change in channel gradient. Stream margins however can also be areas of reduced flow, and provide refugia during flooding (Rempel *et al.* 2000).

Low flow zones may only provide refugia for benthic organisms whilst they remain zones of low flow. Many areas of the streambed however, for example behind large boulders or debris dams, become areas of high turbulence and scouring when water breaches the top, whereby particles can be mobilised and fauna and organic matter removed. During high discharge Brooks (1998) found that water rose over the top of large boulders and changed the low flow zones downstream of the boulder, areas he hypothesised to be refugia, into areas of great turbulence, removing most of the fauna. Such areas of the streambed may represent discharge-dependent refugia, sites of refuge and accumulation at one discharge (e.g. Palmer *et al.* 1996), and denudation at another (e.g. Brooks, 1998). In large rivers, however, as discharge increases and the wetted margins migrate outwards, low flow associated with the margins may still provide refugia for taxa that can move with the margins (Rempel *et al.*, 2000).

In zones of high shear stress, where particles are mobilised, invertebrates may be unable to avoid dislodgement (Reice, 1984, 1985, Rosser and Pearson, 1995, Matthaei *et al.* 1997). Such disturbances, i.e. particle mobilisation, can lead to catastrophic drift (Gayraud *et al.*, 2000), resulting in a large fraction of benthic invertebrates lost downstream (Tockner & Waringer, 1997). Large and or embedded or imbricated particles however, may remain stable in areas of high shear stress (Downes *et al.* 1998). During flooding, such particles may be a source of refugia, as other areas of the streambed are mobilised resulting in dislodgement and local denudation (Townsend, 1989). While some evidence supports this notion (e.g. Strayer, 1999, Matthaei *et al.*, 2000), it remains contentious. Even during small spates, several studies have documented decreases in benthic density but not on overturned particles (e.g. Rempel *et al.*, 1999). Indeed, loss of benthic invertebrates on stable particles during flooding can be just as great as that from mobilised particles (Bond & Downes, 2000b). For a few species, however, the top of stable particles may still provide refugia during flooding, for example *Simulium vittatum* that can resist flows up to 3.3 m/s (Eymann, 1988).

For most species, stable particles in areas of high shear stress are more than likely to provide refugia in the form of micro-low flow areas in the crevices between particles, and along the base and underneath particles. Indeed, flume studies have recorded small-scale movements in response to increased shear stress in a number of taxa, including movements to the base of and underneath particles (e.g. Holomuzki & Biggs, 1999, 2000, Lancaster, 2000). In highly turbulent flow, organisms may still risk dislodgement via small-scale turbulent eddies which can impinge into zones between particles (Roy & Buffin-Belanger, 2000). Abrasion of rock surfaces by suspended sediment loads during flooding has also been hypothesised as a mechanism resulting in damage and dislodgement from stable particles (Milner *et al.*, 1981, Downes *et al.*, 1998). Although rarely considered, abrasion has resulted in damage to diatom frustules (Blenkinsopp and Lock, 1994), fungi, moss and vascular plants (e.g. Neuman & Maxwell, 1999, 2002), and been responsible for large reductions in overall diatom density (Bergey, 1999).

There is some reason to suggest that the spatial attributes of refugia in streams can be linked to the spatial attributes of for example, low flow zones, stable particles, and down welling sites in the hyporheic zone. While this would prove very useful, it currently represents a number of challenges, least of which is quantifying the spatial pattern of these hydraulic and geomorphic features during flooding.

1.2 Defining Spatial Attributes of Refugia: Limitations and Challenges

Characterising the spatial attributes of small-scale refugia in streams is not a trivial task, and requires a good understanding of the fluvial processes involved with disturbance, such as particle movement and shear stress, as well as the species-specific responses to these mechanisms of disturbance. One of the limiting factors is an inability to easily and efficiently quantify these processes, particle movement and shear stress, at appropriate scales (Downes *et al.*, 1998, Lake, 2000).

In streams, quantification of physical disturbance has traditionally focused on measures derived from hydrologists and geomorphologists (e.g. Newbury, 1984, Townsend *et al.* 1997). They fall into two broad categories distinguished by these disciplines. Hydrological measures used to quantify aspects of disturbance include maximum discharge (e.g. Dole-Oliver *et al*, 1997), flood frequency (e.g. Poff and Ward, 1989), mean daily discharge (e.g. Sagar, 1986, Hendriks *et al.* 1995, Palmer *et al.* 1995), mean hourly discharge (Negishi *et al.*, 2002), and rainfall intensity (Flecker and Feifarek, 1994). Water velocity and depth have also been used in equations of shear stress to quantify magnitude and extent of particle movement (e.g. Cobb *et al.*, 1992, Death and Winterbourn, 1995, Muotka and Virtanen, 1995). Such measures may provide broad-brush large scale (> reach) estimates of disturbance however, provide no indication of the extent of variability in particle movement and or shear stress at scales smaller than that of the reach. Refugia such as stable particles (Matthaeii *et al.*, 2000), debris dams (Palmer et al., 1996) and patch scale (~ m^2) low flow zones (Lancaster & Hildrew, 1993b) cannot be characterised.

Criticism of hydrological methodologies (e.g. Poff, 1992, Townsend *et al.*, 1997) lead to a focus on geomorphological methods that employ direct measures of particle movement, assumed to be a more relevant measure of disturbance (Poff, 1992, Townsend *et al.*, 1997). Workers have since used techniques such as the deployment of scour chains (e.g. Matthaei *et al.*, 2003), steel plates buried to set depths (e.g. Palmer *et al.* 1992), painted particles placed directly on the bed surface (e.g. Strayer, 1999), and marking of particles *in situ* (e.g. Matthaei *et al.*, 2000), to characterise disturbance and identify potential refugia sites.

Geomorphological techniques can be used to examine the spatial pattern of particle movement and or scour and fill after flood events. Matthaei *et al.* (1999a) were able to examine the patchy movement of surface stones from sites of contrasting geomorphology by marking over 1200 stones *in situ*. Their results are instructive, supporting the notion of partial transport (Wilcock & McArdell, 1997), i.e. not all particle size fractions are mobilised at once. In a subsequent paper, Matthaei *et al.*, (2000) demonstrated that some invertebrate species used stable stones as refugia, and these stones may have accumulated individuals, although they did not attempt to use the patterns of particle movement to examine the spatial attributes of refugia, such as, size, spacing and perimeter length of patches. A similar series of papers looked at the spatial patterns of scour and fill in a gravel bed stream, and its effect on the invertebrate community two months later (Matthaei *et al.*, 1999b, Matthaei & Townsend, 2000). They found extensive variations in the pattern of scour and fill, both between sites of contrasting geomorphology and between flood events, with some species found in higher abundance on fill and scour patches than stable patches after the flood. They suggested that the observed biotic pattern in density may be an indirect result of the flood, i.e. disturbed patches represent a more 'attractive' environment for re-colonisation, rather than a direct result of dislodgement and accumulation during the flood.

In large quantities, e.g. 1000s, marking of particles *in situ* (Matthaeii *et al.*, 1999) or deployment of tracers (e.g. Haschenburger & Wilcock, 2003) can be used to characterise the spatial pattern of particle movement on scales greater than the particle itself, i.e. patch scale or larger, allowing for comparisons between sites and streams, or events. Stable particles however, do not necessarily equate directly with refugia, especially in areas of high shear stresses during flooding (e.g. Bond & Downes, 2000b). These techniques, as applied, generally provide little information of the shear stresses exerted on the bed during flooding, and thus little indication of potential low flow zones.

Estimates of shear stress during flooding are problematic, as real time measurements during peak flooding can be very hazardous. During low flows, or in easily accessible streams at higher flows (e.g. Lancaster & Hildrew, 1993a), Fliesswasserstammtisch (FST) hemispheres, a set of twenty-four hemispheres of the same size and surface properties but different densities (Statzner & Muller, 1989), have been used as a surrogate measure of shear stress (e.g. Peckarsky *et al.*, 1990, Lamouroux *et al.*, 1992, Dittrich & Schmedtje, 1995), although not without criticism (Carling, 1992, Frutiger, 1993 and Frutiger & Schib, 1993). FST hemispheres may be unreliable to provide quantitative estimates of shear stress, but they can provide a useful comparative measure of shear force exerted on the bed at patch scales (~ 1 m) or larger, providing a spatial pattern of relative shear forces across the bed and identification of low flow zones. Lancaster & Hildrew (1993a), for example, used FST hemispheres, combined with velocity measurements, to identify and characterise the relative proportion of low flow zones in several streams. They demonstrated strong differences in the supply of natural refugia in two streams, Dargall Lane and Broadstone Stream, as defined by shear force. Using experimental mesh cages as artificial flow refugia in the same two streams, Winterbottom *et al.* (1997) found that the accumulation of invertebrates in the artificial flow refugia was much greater in the stream with extensive natural low flow zones (Broadstone Stream). In contrast, invertebrates in Dargall Lane did not use the artificial refugia and they may be able to resist the flow forces more effectively, or use different refugia, such as stable particles (Winterbottom *et al.*, 1997). Robertson *et al.*, (1995), also using the data of Lancaster & Hildrew (1993a), demonstrated that whole reaches that maintained low hydraulic forces throughout a hydrograph, as well as small patches (~ 1 m^2) (Lancaster & Hildrew, 1993b), can act as a refugia for invertebrates.

The information obtained from the study of the proportion of low flow refugia in a few streams (Lancaster & Hildrew, 1993a) has been invaluable for subsequent studies that illustrate how invertebrates exploit flow refugia (Lancaster & Hildrew, 1993b, Robertson *et al.*, 1995, Winterbottom *et al.*, 1997). Clearly, many more studies are required to establish the relationships between refugium use and community composition. Using FST hemispheres, tracers or marked of particles *in* *situ* to characterise the spatial pattern of low flow zones, or particle movement, is a daunting task, even in one stream. Point measurements, which allow for some measure of spatial patterning at the patch scale, are labour intensive, especially where large areas need to be covered in high density. I refer to these methodologies (i.e. FTS hemispheres, tracers, and marking of particles *in situ*) as point measurements, because that is how they have been applied, to detail variation at the patch (~ 1 m^2) or larger scale (e.g. Lancaster & Hildrew, 1993a, Robertson *et al.*, 1995, Mattheai *et al.*, 1999). The size of the hemisphere, or the unit of the particle or tracer however, limits the scale of measurement. FST hemispheres cannot be employed to estimate shear forces at scales smaller than the hemisphere, i.e. at the scale of the invertebrate (Frutiger & Schib, 1993), and tracers cannot be used to estimate variability in particle movement at the scale of the particle.

In erosional zones, four mechanisms of disturbance can act on benthic invertebrates, resulting in dislodgement; two demonstrated mechanisms, particle movement and shear forces (e.g. Rosser & Pearson, 1995, Biggs & Holomuzuki, 2000), and two probable mechanisms, abrasion and turbulence. In some stream systems, such as high gradient streams, particle movement and shear stress can be strongly de-coupled. That is, due to the development of particle structures such as stone clusters (Brayshaw, 1984) and their inherent stability (Church *et al.*, 1998), the relationship between particle mobilisation and shear stress is non linear (e.g. Ryan *et al.*, 2002). To characterise the spatial pattern of particle movement and shear forces in such systems would require an intensive sampling programme using multiple techniques. Defining the spatial attributes of refugia is currently limited not only by the necessarily large workload, but also the inability to define and properly measure potential disturbance mechanisms such as abrasion and turbulence. I suggest an alternative approach that uses the morphology of the stream channel to classify streambed areas as potential refugia (or not) and according to the likely disturbance mechanism.

1.3 A Geomorphologic Approach

Spatial heterogeneity in streams is central to the concept of refugia (Sedell *et al.*, 1990, Poff & Ward 1990), and is largely influenced by the shape of the streambed and the particles on it, i.e. geomorphology. Previous reviews on disturbance and the role of refugia for post disturbance recovery and population persistence have emphasised the importance of geomorphology (e.g. Poff & Ward, 1990, Sedell *et al.*, 1990, Reice *et al.*, 1990, Lake, 2000), and several studies have linked fluvial features, such as bedform structures (Biggs *et al.*, 1997), pool units (Scarsbrook & Townsend, 1993), and debris dams (Palmer *et al.*, 1996) with refugia.

One of the basic tenants of geomorphology is that physical processes, such as hydraulic forces and particle movement, produce repeatable and identifiable structures within the landscape, and the stream environment is no exception (Leopold, 1964). Many geomorphological classifications, at a variety of scales, describe fluvial features that can be easily identified and mapped in the field (e.g. Bisson *et al.*, 1981, Grant *et al.*, 1990, Whiting & Bradely, 1993, Montgomery & Buffington, 1997, Halwas & Church, 2002). Classifications of geomorphic features may therefore provide a framework to which characteristic fluvial processes, such as particle entrainment, scour, deposition, and flow structures, can be attributed. These processes influence invertebrate dislodgement (Palmer *et al.*, 1992, Richardson, 1992, Rosser & Pearson, 1995), drift and settlement (Hart & Finelli, 1999), and avoidance behaviour (Lancaster, 1999a, Holomuzki & Biggs, 1999, 2000), and thus it may be possible to characterise morphological features according to their disturbance potential in ecological terms, e.g. flow refugia.

Geomorphic features may act as a surrogate measure for shear stress and particle movement potential, and mapping these features may provide an alternative approach to characterise the spatial attributes of refugia in streams. For example, Palmer *et al.*, (1995 & 1996) in a series of studies on patch-specific effects of disturbance on meiofauna, defined patch types on the basis of channel morphology and sediment characteristics. With detailed near-bed velocity measurements during flooding, injected dye observations, and critical entrainment threshold estimates (determined from an earlier study, Palmer *et al.*, 1992), they were able to characterize the flow environment (depositional or erosional) and particle entrainment potential of each patch type during flood events, and found, in general, that morphological patch type related approximately to refugium potential. Invertebrates were dislodged from coarse particle patches and sandy mid channel patches, but were largely maintained in debris dams. This series of studies highlights the importance of considering the fluvial processes involved with species specific dislodgement and flux during flooding. They found that some fine patches associated with debris dams not only retained fauna, but also accumulated individuals during flooding. However, overall dam attributes (e.g. dam size, number of branches) were not useful in predicting which dams harboured patches that accumulated individuals and which dams did not. They found that low near-bed velocity and water flux was actually the best predictor of accumulation (Palmer *et al.*, 1996). Indeed, they found a remarkable match between accumulation and underlying physical processes.

The work by Palmer *et al.* (1995 & 1996) underscores the need to understand what physical processes are responsible for the link between geomorphic feature and biotic pattern during flooding. For geomorphic features to prove useful for characterising the spatial attributes of refugia in streams, they have to be directly linked with these physical processes.

1.4 Thesis Aim

The aim of this thesis is to develop a geomorphological classification of steep streams that is linked to the physical processes responsible for invertebrate dislodgement and flux in these systems. I have chosen to undertake the study in steep streams because these systems have a very distinct morphology that changes dramatically over relatively small scales (~ 10 m) (Grant *et al.*, 1990), and so provides an excellent system within which to characterise morphological features.

The thesis is partitioned into six parts, each representing a chapter in the main body of the thesis;

1) Proposing a New Morphological Classification of Steep Streams:

With few exceptions (e.g. Grant *et al.*, 1990, Whiting & Bradley, 1993, Montgomery & Buffington, 1997) most classification schemes partition the stream into elements based on descriptive measures alone (e.g. Bisson *et al.*, 1981), rather than also considering physical processes. This limits the use of the classification for assessing the response of biota to flooding, as processes such as particle entrainment or flow dynamics are not directly associated with the physical units. In this section I will propose a new classification scheme, based on the process-based channel unit classification scheme of Grant *et al.* (1990).

2) Physical Attributes of the Units within the New Classification:

The physical attributes, e.g. sediment size, structure, location, of each of the physical units in the classification will be described and measured in two steep streams.

3) Particle movement within each Unit:

In this chapter I examine the movement of particles in each unit over a range of discharges. The theory behind the new classification proposed in (1) suggests that each unit should have very different particle entrainment thresholds. That is, the units should be closely linked with the process of particle movement.

4) Invertebrate Assemblages Associated with each Unit:

In this chapter I evaluate the relevance of the new classification for invertebrates in steep streams, and characterise the distribution pattern of invertebrates across the units at base flow. This information provides crucial background for a subsequent comparison of patch-specific assemblages before and after flooding.

5) Influence of hydraulic environment associated with a Unit on Invertebrate Drift and Settlement:

I this chapter I investigate the small-scale interactions between invertebrate behaviour and the hydraulics associated with a physical unit, a 'step'. I specifically test whether the step reduces drift distance and promotes settlement and accumulation.

6) Patch-specific response of invertebrates to flooding:

What I advocate is a pluristic approach, in which a detailed understanding of geomorphology and fluvial processes is incorporated with an understanding of the response of invertebrates to mechanisms of disturbance, such as particle movement and shear stress, as well as drift and settlement. In this chapter I examine the change in invertebrate assemblage on each of the physical units after flood events of different magnitude, relating the process of particle movement and shear stress to invertebrate response. I test whether the geomorphic classification does indeed provide a framework that will allow the characterisation of the spatial attributes of refugia in streams.

Definitions:

A potential confusion exists in any discussion of lotic ecology and fluvial geomorphology as nomenclature between the two fields is often very similar. It is therefore necessary to clearly define some terms that will be used throughout this thesis. I define ***disturbance*** as any abiotic event that removes organisms and opens up space and other resources that can be used by individuals of the same or different species, e.g. a flood. I define a ***mechanism of disturbance*** as a force or process that results in the direct removal of organisms from the substrate, damage, or mortality, e.g. particle movement, shear stress or abrasion. I define ***dislodgement*** as the process of organism removal from a position on the substrate to entry into the water column. I make no distinction between passive dislodgement, resulting directly from a ***mechanism of disturbance***, and active entry resulting from a behavioral choice to let go of the substrate. In practice it is very difficult to tell if a mobile organism releases its grip to enter the drift, or is passively swept into the water column. I define ***entrainment*** as the initial process of particle transportation, whereby a particle is mobilized from a position on the streambed to entry into the water column or saltation along the streambed. ***Bedload*** is defined as the transport of particles in direct or partial contact with the bed, i.e. saltating particles. ***Suspended load*** is defined the transport of particles in suspension in the water column. I therefore make the distinction between dislodgement and entrainment as ecological and physical processes respectively. I define a ***patch*** as an area of the streambed of uniform sediment characteristics. That is, the term patch pertains to physical characteristics rather than bioic.

Chapter Two Classification of Morphological Features in Steep Streams

2.1 Introduction

Morphological classifications of the streambed exist at several scales and describe fluvial features that can be easily identified and mapped in the field (e.g. Bisson *et al.*, 1981, Grant *et al*,. 1990, Whiting & Bradley, 1993, Montgomery & Buffington, 1997, Halwas & Church, 2002). They provide a framework of bed structures and channel features to which characteristic fluvial and hydraulic processes, such as particle entrainment, deposition and turbulence generation can be attributed (e.g. Grant *et al.*, 1990, Whiting and Bradley, 1993). Collections of large boulders in steep streams for example, typically form distinct bedform features that are stable and have particularly high entrainment thresholds (Church *et al.*, 1998). These features present high form resistance (Abrahams *et al.*, 1995, Chin, 2003,) and are usually erosional environments associated with high shear stresses and turbulence (Wohl & Thompson, 2000). Patches of fine particles on the other hand typically collect in low flow depositional zones (Kondolf *et al.*, 1991), but can be easily mobilised during flood events (e.g. Barta *et al.*, 1994).

As fluvial and hydraulic processes, such as particle entrainment and deposition, and flow dynamics, largely encompass the main mechanisms of disturbance (shear stress, particle movement, turbulence and abrasion), it should be possible to characterise particular morphological features according to their disturbance potential in ecological terms, e.g. flow refugia, areas of denudation, or accumulation (e.g. Palmer *et al.*, 1995, 1996). While it may be impossible to measure all disturbance mechanisms during peak flooding, distinct streambed morphologies may represent 'predictable' suits of fluvial and hydraulic processes, and may allow us to predict where mechanisms of disturbance are likely to occur, and hence refugia.

The concept that disturbance and refugia may vary with channel morphology in a predicable way is not new (e.g. Resh *et al.*, 1988, Reice *et al.*, 1990, Sedell *et al.*, 1990, Poff & Ward, 1990, Lake 2000), but it remains largely untested (see Scarsbrook & Townsend, 1993, Palmer *et al.*, 1995 & 1996, Francoeur *et al.*, 1998, Mattheii & Huber, 2002, Negishi *et al.*, 2002). In this chapter I examine the link between streambed morphology, fluvial processes and disturbance in steep streams. I propose a morphological classification based on the process of particle movement, but also incorporating some variation in flow dynamics, that will allow testing of the following hypotheses, H_0: there is no difference in particle movement between areas of contrasting morphologies. H_0': there is no relation between invertebrate pattern after flooding (dislodgement and accumulation of individuals) and morphology. Rejection of these hypotheses suggests that the morphological classification scheme may be useful for characterising the spatial attributes of refugia in streams.

2.2 Streambed Morphology – Defining a Framework

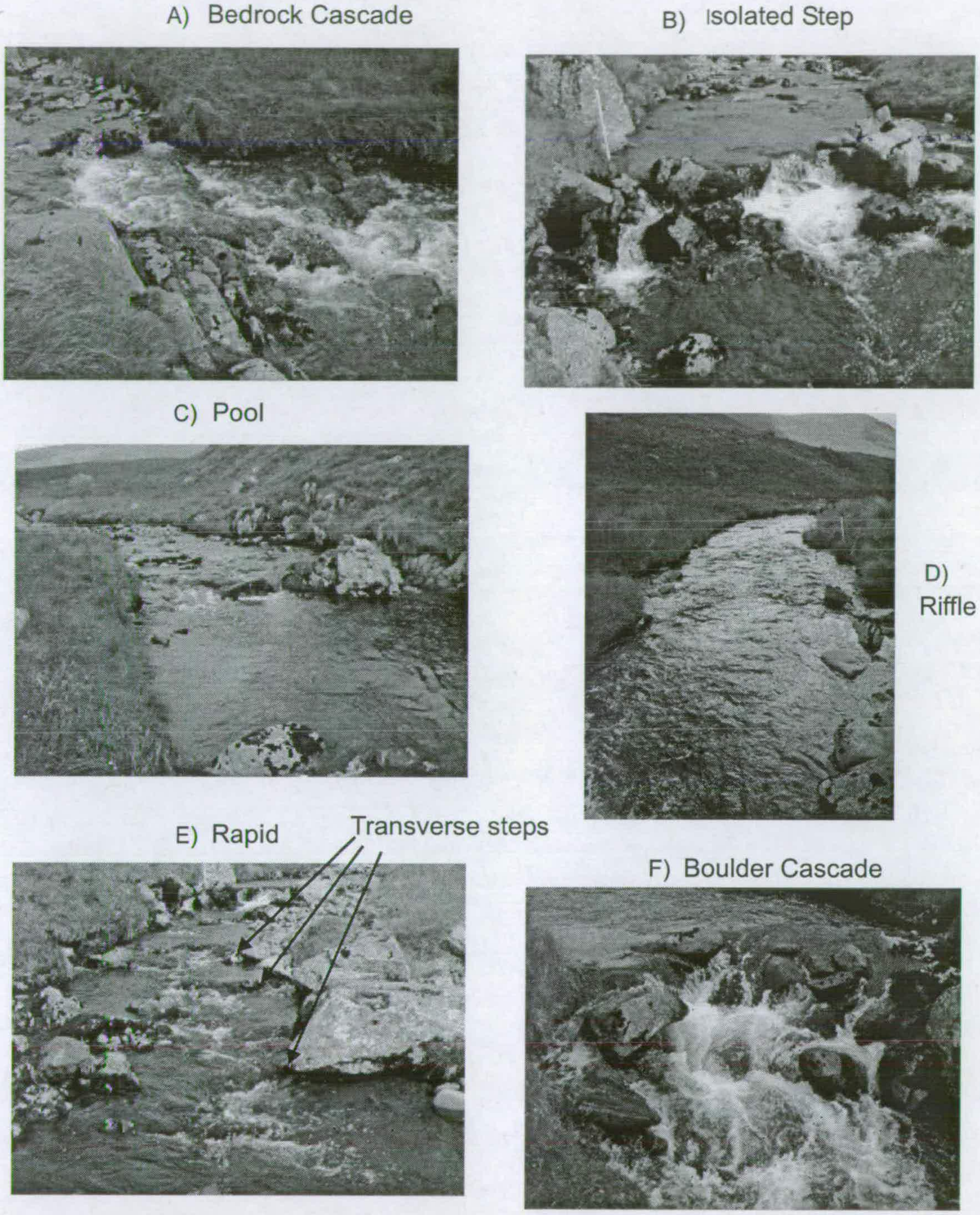
2.21 The Channel Unit Classification Scheme; a Starting Point

The morphology of steep streams is typically dominated by morphological features such as channel spanning steps and boulder cascades (Grant *et al.* 1990, Chin, 2003). Such features occur at the scale of the channel unit (one to several stream widths in length), and have been incorporated into several classifications of the streambed (e.g. Bisson *et al.*, 1981, Grant *et al.*, 1990, Halwas & Church, 2002). Five major morphological units are commonly identified: pools, riffles, rapids, boulder cascades and bedrock cascades, and one minor unit: isolated step (e.g. Grant *et al.*, 1990) (Figure 2.1). All of these features tend to have unique channel slopes, sediment characteristics (Grant *et al.*, 1990, Halwas & Church, 2002) and associated flow dynamics (Peterson & Rabeni, 2001) (Table 2.1), and hence potentially influence particle movement and flow in unique ways (Grant *et al.*, 1990). Pools for example, typically contain fine loose material that is easily mobilized by high energy flows during flooding (Rathburn & Wohl, 2003) and may be poor refugia during floods (Scarsbrook & Townsend, 1993, Negishi, *et al.*, 2002).

Instead of strictly employing the channel unit classification scheme as a descriptor of refugium and non-refugium potential however, some modification is required to provide a scheme in which the disturbance mechanisms are more closely associated with the morphological features of interest. In particular, the scales over which the morphology is described should be the same as the spatial scales over which the mechanisms act, and should be directly related. For example, if particle movement predominantly occurs over scales of the order of 0.1 or 1 m^2, then classifying

Table 2.1 Description of channel units after Grant et al., (1990)

Channel Unit	Description	Flow Type	Gradient	Substrate
Pool	Subcritical flow without free-surface instabilities	Divergent	0.004 – 0.006	High proportion of fines. Also contains largest boulders
Riffle	Free-surface instabilities in flow, clusters maybe present but no transverse ribs.	Divergent	0.01 – 0.012	Fine fraction to boulders
Rapid	Supercritical flow, boulders organized into transverse ribs.	Straight	0.024 – 0.03	Fine fraction to boulders
Boulder Cascade	Supercritical flow, large boulders in series of short well-defined steps	Convergent Tumbling	0.05 – 0.06	Boulders
Bedrock Cascade	Water flowing directly over bedrock steps	Convergent Tumbling		Bedrock
Isolated Step	Channel spanning steps less than one width long	Plunging	0.12 +	Boulders / Logs



A) Bedrock Cascade

B) Isolated Step

C) Pool

D) Riffle

E) Rapid

F) Boulder Cascade

Figure 2.1 - Channel units within the study section of the Talla Water. Bedrock cascade (A), isolated step (B), pool (C), riffle (D), transverse step (E) and boulder cascade (F). A, B, E and F are defined as Structured patches. See text for explanation.

morphological features at scales 10 m^2 or larger (i.e. channel unit to reach scale for example) will not be useful.

I have chosen to define the classification scheme primarily on particle movement. Of the four mechanisms of disturbance (particle movement, shear stress, abrasion, turbulence) particle movement is the most tractable to measure, and where compared with other mechanisms, e.g. shear stress, it can result in a greater loss of benthic organisms dislodged from the substrate (e.g. Holomuzki & Biggs 1999, but see Bond & Downes, 2000b). Some channel units, such as boulder cascades and isolated steps, vary little in particle entrainment (Grant *et al.*, 1990). These features are composed of particles interlocked and jammed in a self-stabilising state (Church *et al.*, 1998), and represent a very stable environment that is rarely mobilised (Grant *et al.*, 1990, Lenz *et al.*, 2004). Because of the self-stabilising state, once one constituent particle is mobilised the feature is likely to be completely destroyed (Church *et al.*, 1998). These units therefore represent good predictors of the entrainment potential of the particles within them, i.e. all constituent particles are likely to be mobilsed over a very narrow band of discharge. Particle entrainment within other units however, e.g. riffle, rapid and pool, can be highly variable (e.g. Powell & Ashworth, 1995, DeVries *et al.*, 2001, Hassan & Woodsmith, 2003). Small patches of fine loose particles for example are typically present in varying quantities in these units (e.g. Kondolf *et al.*, 1991, Barta *et al.*, 1994, Larronne *et al.*, 2000, Zimmerman & Church, 2001). These units in general may therefore represent poor predictors of particle entrainment. The degree of dislodgement of benthic invertebrates from each unit may be dependent on the size and quantity of the patches of fine loose material.

By modifying the channel unit classification scheme on the basis of entrainment potential, it is hoped that major variations in particle movement will be accounted for. The unavoidable disadvantage however, is that the potential role of non-scouring mechanisms of disturbance, such as shear stress, and effect of low flow zones (i.e. areas of possible accumulation, e.g. Lancaster & Hildrew, 1993 a & b, Palmer *et al.*, 1996) are not directly addressed. That is, spatial variations in shear stress and flow may not correspond entirely with the physical units. In high gradient streams however, some morphological features are intrinsically linked with particular flow patterns, e.g. boulder cascades and steps are typically associated with highly turbulent plunging flow (Grant *et al.*, 1990). Collections of fine particles on the other hand occur in flow separation zones where flow is reduced (Kondolf *et al.*, 1991), possibly representing an area of accumulation (e.g. Palmer *et al.*, 1996). By incorporating such features into the classification, it may be possible to partly account for non-scouring mechanisms of disturbance, such as shear stress, as well as potential for accumulation.

2.22 A New Patch Classification Scheme

The proposed scheme represents a simplification of the channel unit classification scheme (e.g. Grant *et al.*, 1990), from five or six units to three morphological patch types; Structured, Loose and Degraded. The new classification however does not correspond directly to one scale, e.g. particle, sub-unit (i.e. patch), channel unit, reach (Figure 2.2). By focusing on the ecological process of interest (i.e. dislodgement via particle movement) rather than physical form to define the

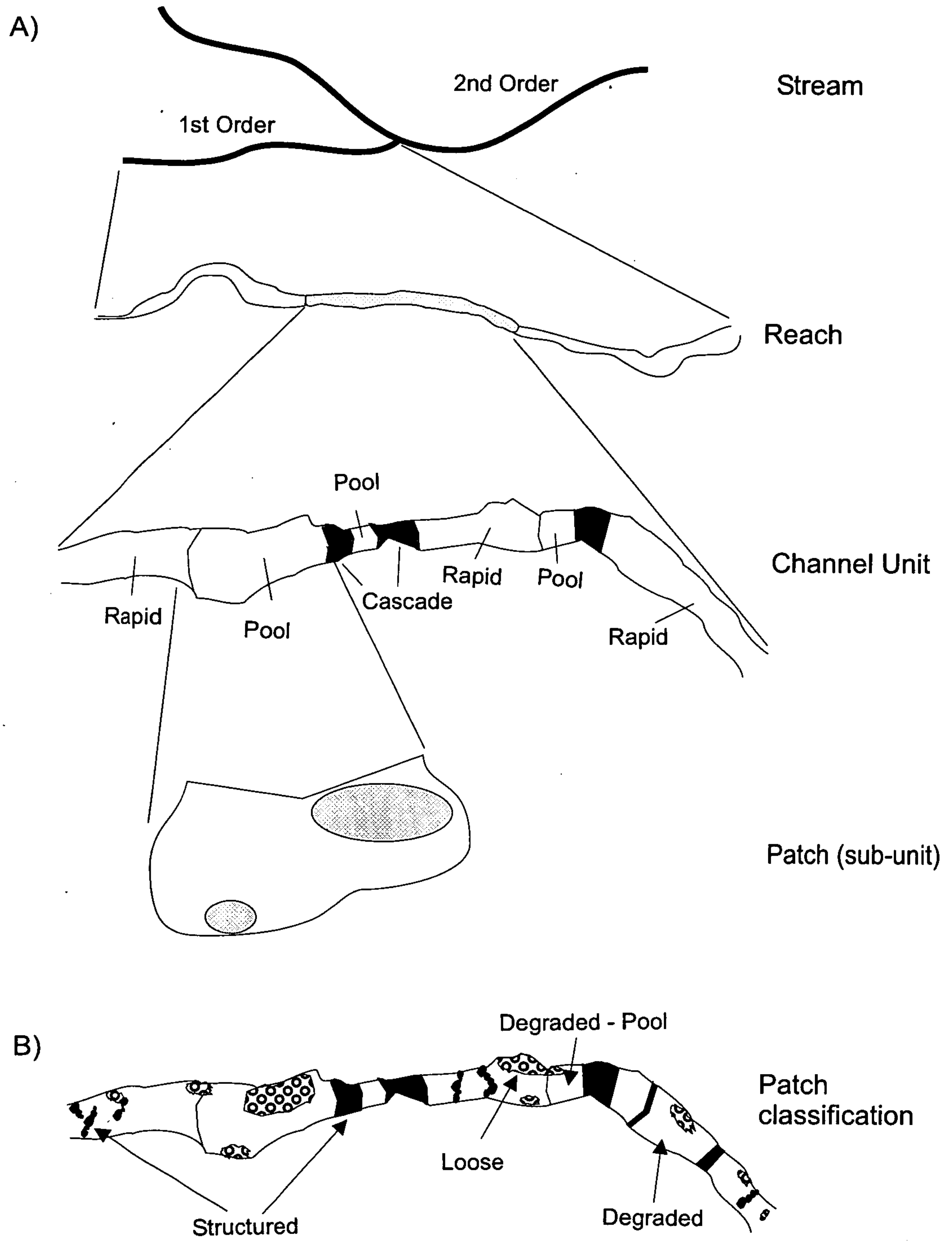


Figure 2.2 A) Schematic diagram of the hierarchical relationship of geomorphic features common in the literature (e.g. Sedell *et al.*, 1990). B) A Schematic diagram of the patch classification, incorporating features at the channel unit scale (e.g. Cascade units shown in solid black in A) and the sub-unit scale (e.g. transverse steps within Rapid units, shown in solid black in B).

classification, the classification incorporates features at both the channel unit and sub-unit (or patch) scale (Figure 2.2). It therefore does not fit neatly into the classical hierarchical framework of Sedell *et al.*, (1990) and others.

The three physical units of the patch classification nevertheless encompass the entire wetted streambed, and thus may provide a framework from which to scale up and allow comparisons of disturbance between reaches, streams and seasons. The three patch types, and their potential for disturbance are described in detail below.

A) Structured Patches:

Structured patches are morphological features of the streambed common in steep mountain streams and correspond to the channel units, boulder cascades, bedrock cascades and isolated steps, and the sub-unit, transverse step, within the rapid unit (Grant *et al*,. 1990, Halwas & Church, 2002, Figure 2.1). They are areas of the streambed composed of large boulders imbricated or jammed together, forming a stable environment where constituent particles are only mobilised during extreme flood events (return interval ≈ 10 years, Grant *et al.* 1990, 11 to 62 years estimated by Chin, 2003). Development of such structures occurs when large particles roll and bump into a more stable configuration (Church *et al.,* 1998). The arrangement of particles into an imbricated / jammed state greatly increases particle entrainment thresholds of the constituent particles, thereby stabilising the whole structure. Particle movement is therefore highly unlikely as the boulders are jammed into a self-stabilizing state.

The hydraulic environment associated with Structured patches is typically complex with, high velocity flow that tends to suppress turbulence over the top of the structures, high turbulence immediately downstream of the structure, and a cell of water near the bed flowing back upstream towards the structure (Keogh & Addison, 1996, Buffin-Belanger & Roy, 1998, Wohl & Thompson, 2000). Structured patches tend to disrupt the velocity field, accounting for a large portion of total channel resistance in steep streams and dissipating considerable amounts of energy (Lee & Ferguson, 2002, Chin, 2003). This has the effect of increasing the potential for very high shear stresses during flood events, and the generation and maintenance of high turbulence extending downstream (Wohl & Thompson, 2000), potentially reaching the surface of the bed up to10 step heights downstream (Keogh & Addison, 1996).

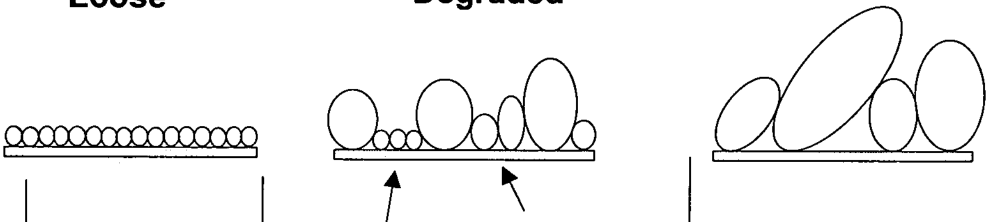
Dislodgement of some species through non-scouring disturbance mechanisms, such as shear stress near the top of the structure, and turbulence immediately downstream may be significant during flooding. On the other hand, invertebrates may avoid non-scouring disturbance mechanisms by moving to low flow zones around the base or underneath particles in Structured patches (Holomuzki & Biggs, 1999), or they may resist flow dislodgement through morphological features (e.g. suckers, Blepharoceridae, Frutiger, 1998). Structured patches may therefore provide refugia for some invertebrate taxa. Empirical evidence is scarce however, and remains inconclusive (e.g. Biggs *et al.*, 1997, Negishi, 2002, but see Matthaeii & Huber, 2002).

There is some reasoning to suggest that Structured patches, while an erosive environment, may accumulate individuals during flooding. The downward trajectory of flow over the top of the structure may force drifting individuals into the substrate, and into the re-circulation zone of flow back upstream towards the structure. As backward re-circulating flow can extend up to 10 step heights downstream, a large number of individuals may drift passively upstream towards the downstream face of the structure, staying within the low flow re-circulation zone.

B) Loose Patches:

In steep streams the occurrence of large immoveable boulders and morphological features such as transverse steps, boulder cascades and other Structured patches result in hydraulically rough boundaries and highly complex flow patterns, with localized zones of flow separation (Jarrett, 1991, Furbish, 1993). Fine sediment, rather than being routed through these systems quickly, is typically stored in zones of flow separation as small deposits (Loose patches). These deposits are commonly associated with either channel boundary irregularities (such as tributary mouths, pool margins, and bank obstructions) or with low velocity zones in the wake of large obstacles (Kondolf *et al.*, 1991, Barta *et al.*, 1994, Schmidt & Gintz, 1995, Rathburn & Wohl, 2003) (Figure 2.3).

These deposits, referred to herein as Loose patches, are likely to be the major source of bedload below the threshold shear stress that disrupts the rest of the unstructured coarse bed (Warburton, 1992, phase I transport). Unlike Structured patches, they are a depositional environment with characteristically low entrainment thresholds. These



	Loose	**Degraded**	**Structured**
Sediment characteristics	Fine particles, loose	Larger particles Pockets - Fine loose particles	Larger boulders, imbricated jammed
Hydrualic forces at Base flow	Low	Variable	High over top, variable to low elsewhere
Environment	Depositional	Erosive	Erosive
Dominant Disturbance mechanism	Particle Movement	Pockets - Particle movement Large particles - Particle Movement Shear stress Abrasion	Shear stress Abrasion
Disturbance frequency	Frequent	Pockets - Frequent Large particles - Particle movement = occasional Shear stress Abrasion = Frequent to occasional	Frequent to occasional
Sediment Transport *	Phase I	Phase I - pockets Phase II - large particle	Phase III

Figure 2.3 General characteristics of each patch type. * Refers to sediment transport phase from Warburton (1992). Phase I = mobilisation of fine particles, phase II = mobilsation of coarse armour layer, and phase III = mobilisation of bedform structures.

patches are found within pool, riffle and rapid units, and in steep streams likely represent the main source of variation in particle entrainment between these channel units.

The potential for dislodgement from particle movement is greatest in Loose patches, as entrainment thresholds are likely to be exceeded more often than in other areas of the streambed, and at relatively low thresholds (Larronne *et al.*, 2000). Lake (2000) suggests that such deposits may represent disturbance-dependent refugia, safe at one discharge, but areas of denudation at high discharges. Brooks (1998) found that deposits downstream of protruding boulders have a rich and diverse fauna, and were hypothised to be refugia. However, during flooding when water rose over the boulders, most fauna was dislodged and removed. If a low flow environment however is maintained throughout the hydrograph, Loose patches may represent areas of accumulation (e.g. Palmer *et al.*, 1996, Winterbottom *et al.*, 1997, Lancaster, 1999). If the hydrograph then reaches a level in which sediment is mobilized and denudation occurs, these patches could have a disproportionately large effect on the total loss of individuals from the stream reach, as accumulated fauna may then be dislodged. The switch from net gain to net loss in such patches may not be a simple process. At high discharge a strong, prominent eddy fence or shear zone can develop which can become anchored on the substrate or bank. Sediment and fauna deposited during lower discharge may be retained and not be flushed out, even though strong eddy currents may continue to mobilize sediment within the patch (Rathburn & Wohl, 2003). Finally, the influence of Loose patches may extend beyond that of the deposit itself. If fine material deposited during low flows is indeed flushed out, it may contribute to an increase in abrasion immediately downstream.

C) Degraded Patches:

The channel within steep streams is often referred to as degraded: poorly sorted sediment dominated by coarse fractions. Fine sediment is usually routed through these systems with little aggradation, and indeed, the majority of the channel bed, excluding discrete deposits of fines (Loose patches), is typically in a degraded state. Thus, where sediment is not imbricated or jammed together, forming Structured patches, the bed can be characterized as poorly sorted with little structural development, i.e. particle imbrication or jamming. I refer to this section of the bed as Degraded, encompassing areas within rapid, riffle and pool units. It differs from Structured in that there is a lack of structural development, and the sediment, while generally poorly sorted, exhibits a variety of small-scale (centimetre to decimetre) patterns in grain size distribution, characterized by interstitial pockets of fine particles (Laronne *et al.*, 2000). The Degraded patches are therefore characteriesed by two sediment types; a) interstitial pockets of fines, herein referred to as the matrix, and b) a poorly sorted coarser fraction.

Particle entrainment may occur over a large range in shear stress (Ryan *et al.*, 2002), depending upon factors such as particle size and shape (Schmidt & Gintz, 1995) and embeddedness (Downes *et al.*, 1998). The initial mobilization of particles from this environment however is likely to be controlled by the presence, areal extent and interconnectedness of the matrix (Laronne *et al.*, 2000). While it may be too small to map, its extent may partly determine levels of abrasion in the surrounding areas of the streambed, as fine particles are winnowed from these pockets during the initial phase of flooding (Warburton, 1992). For organisms that inhabit these pockets, mobilisation may result in dislodgement. As shear stress increases to mobilize the coarser fraction, particle movement may become size selective. That is, the greater the shear stress, the larger the particle mobilized and the greater the area mobilsed. Large embedded boulders, however, may act to disrupt this relationship, as they are restrained by part burial. Their restraint will also allow for the build up of localized high shear stress.

The Degraded environment thus represents the most variable in terms of particle movement thresholds (e.g. Downes *et al.*, 1998), and it is likely that all four mechanisms of disturbance act to dislodge invertebrates. Nonetheless, some general relationships may exist. Jackson (1981) described a two phase sediment transport model for gravel streams in which phase I represents the winnowing of fines and phase II the breakup of the coarse surface layer. Recent studies support the existence of a breakpoint in sediment transport between phase I and II (e.g. Ryan et al., 2002, Lenz, *et al.*, 2004). This breakpoint may also represent a switch in dominant disturbance mechanism on Degraded patches, e.g., from abrasion and shear stress (breakup of matrix, phase I transport), to particle movement (breakup of coarse layer, phase II transport).

2.3 Summary

Structured, Loose and Degraded patches likely have different sediment size distributions and structure, and hydraulic characteristics. Degraded and Structured patches are erosional and have the potential for high shear stress during flooding, whereas Loose patches are depositional environments characterised by small particle sizes. The dominant disturbance mechanism is likely to vary between patch types, from non-scouring mechanisms such as shear stress on Structured patches to particle movement on Loose patches (Figure 2.3).

The possible relationship of discharge with disturbance mechanism, particle movement and shear stress, on each patch type is shown in Figure 2.4a. The switch in mechanism, from shear stress to particle movement on each patch type is hypothesised to correspond to specific phases in sediment transport, i.e. mobilisation of Loose patches and the matrix within Degraded patches (hypothesised to be phase I transport), coarse particles of Degraded patches (phase II transport), and mobilisation of Structured patches (phase III transport). The possible relative discharge at which these switches take place on each patch type is shown in Figure 2.4a. Note, a decrease in shear stress occurs over a patch the moment it is mobilised because there is a sudden reduction in particle resistance. In Figure 2.4a, the mobilisation of the Loose patches and that of the matrix are hypothesised to occur at the same discharge.

The possible relationship of population loss (i.e. dislodgement) with discharge on each patch type is shown in Figure 2.4b. For each patch two relationships are shown,

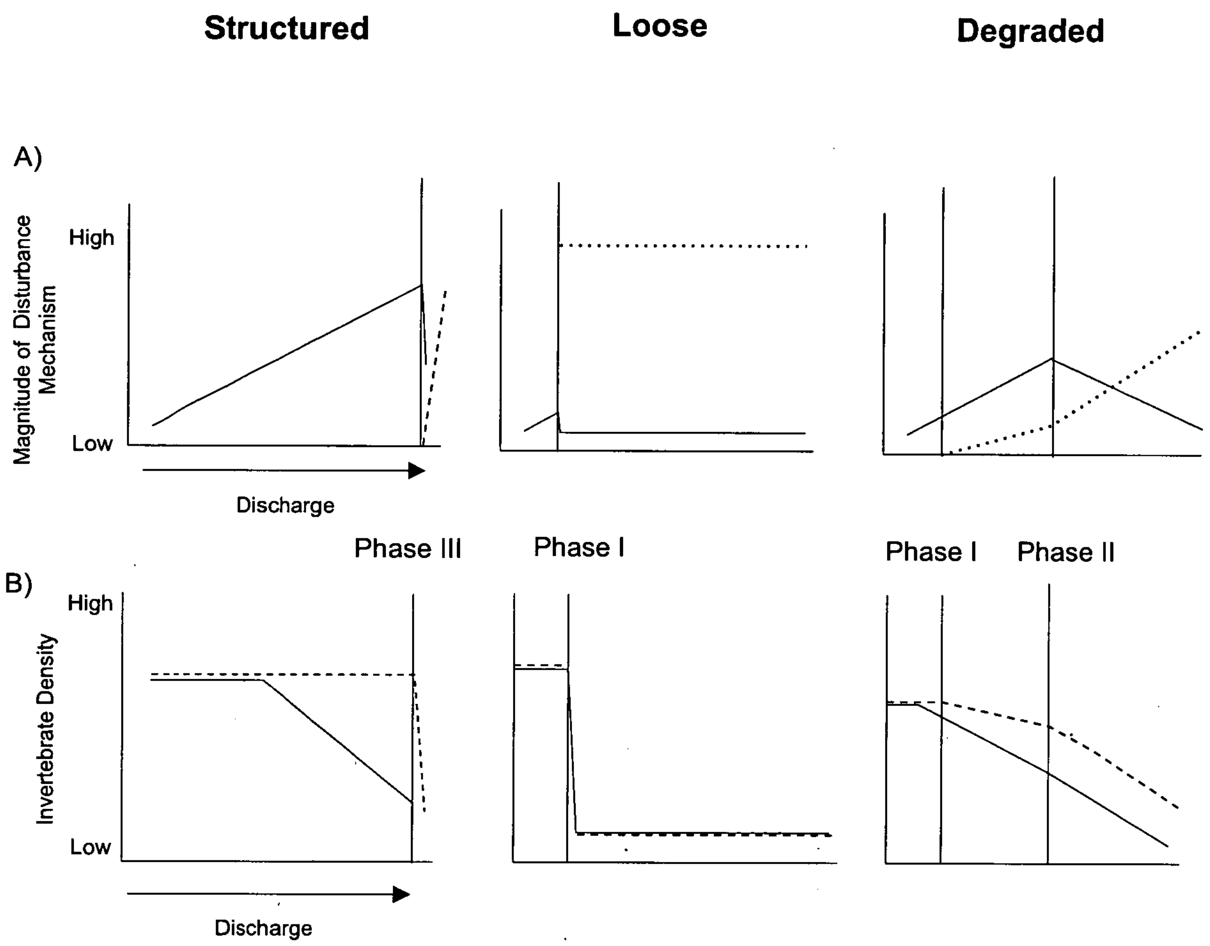


Figure 2.4 A) Potential relationships in the magnitude of disturbance mechanism with increased discharge on each patch type. Solid line indicates shear stress and the dotted line indicates particle movement. B) Potential relationship of invertebrate density on each patch type with increase in discharge for taxa that are susceptible to shear stress (solid line) and taxa that are only susceptible to particle movement (dashed line). In both A and B the vertical lines indicate the initiation of transport phase. Note, these relationships do not include accumulation. See text for explanation.

one corresponding to an organism with traits that concur resistance to high shear stress, e.g. an ability to securely attach to the substrate, and is only dislodged through particle mobilisation. The second relationship corresponds to an organism that is susceptible to dislodgement by high shear stress. On stable particles, as discharge increases more individuals are lost as a greater area is influenced and strong turbulent eddies impinge into areas along the side and around the base of particles.

These relationships represent simple models of change in density on each patch type. They nevertheless illustrate the potential for change in dislodgement brought about by change in sediment transport phase. A change in transport phase during flooding may represent an important process, influencing the extent and spatial distribution of refugia during flooding. These relationships suggest that during phase II transport only Structured patches can act as refugia, and during phase I transport Structured and too a limited extent, Degraded, may act as refugia. These relationships however do not include accumulation. The system could conceivably be rather complex.

The next two chapters focus on the physical aspects of the patch classification. Chapter Three describes the main sediment characterises of each patch type and their location and spatial extent. Chapter Four examines the relationships between particle movement, patch type and transport phase.

Chapter Three Patch Classification in Two Headwater Streams

3.1 Introduction

I studied the physical characteristics of each patch type in two steep headwater streams. According to the patch definitions in Chapter two, Loose patches should be composed of uniformly small particles, Structured patches large imbricated and or jammed boulders, and Degraded patches a wide mix of sediment sizes, but unstructured, i.e. no imbrication. The patches should be unique entities with respect to sedimentological character, and easily identified in the field. Patches with distinctly different sediment character suggests different formative processes, such as particle entrainment and deposition. In this chapter I thus present patch specific distributions and associated parameters, describing the sedimentological character of each patch type. Statistical tests were not performed as the patches were selected on the basis of differences, and of prime importance is clear identification in the field. Information obtained from the grain size distributions is used in Chapter Four to examine patch specific entrainment thresholds.

A second aim of this chapter is to survey and map the streambed, determining the location and size, and proportion of streambed occupied by each patch type. This information is used in Chapters Four, Five and Seven to permit the scaling up of processes (e.g. particle movement, Chapter Four) and patterns (e.g. invertebrate abundance, response to flooding) to the reach scale. Finally, I classify the channel units within each stream reach. This was undertaken to provide a comparison of morphological detail with the patch classification. The patch classification incorporates morphological features at both the channel unit and sub-unit scale, and presumably incorporates a greater amount of morphological detail.

3.2 Study Sites

Scottish Borders

The study was conducted in headwater streams of the Scottish Borders, part of the Southern Uplands, south east Scotland. This is an extensive upland area of broad hills and open valleys. The area is underlain by sedimentary rocks of the Ordovician Gala group, comprising of greywacke and black graptolitic shales. The landscape is characterized by sweeping expanses of moorland, with mixed heather, rough grasslands and tracts of peaty mires. The area is managed for the light grazing of sheep and hill walking.

Two headwater streams were chosen: Talla Water and Cramalt Burn, lying between the small settlements of Talla Linnfoots and Tweedsmuir, 60 km south of Edinburgh. The streams are typical of those in the area, small, steep and bouldery, with a strong coupling to neighboring hill slopes. Mass wasting events are common, as evident from numerous non-vegetated scars on many of the neighboring hill slopes, delivering sediment directly into the stream channel (Figure 3.1a). Precipitation falls mostly as rain, although during mid winter snowfalls are common and partial freezing of the stream surface can occur. Annual rainfall in this area is over 1.5 m.

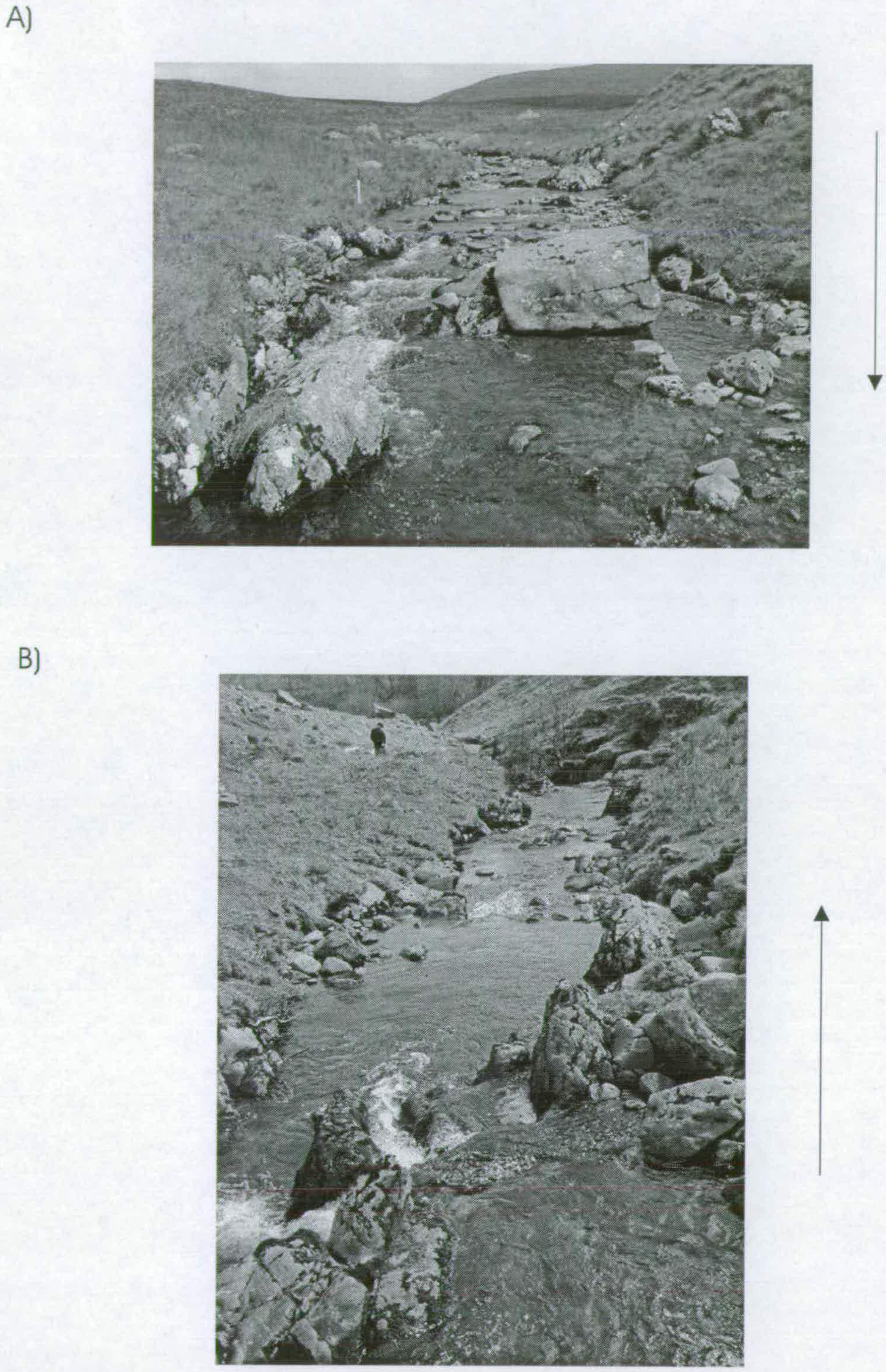


Figure 3.1 A) Study site in the Talla Water B) Study site in the Cramalt Burn. Arrow indicates direction of flow.

Talla Water

The Talla Water is a small stream, 4 km long rising at an altitude of 740 m, and dropping total of 400 m into the Fruid reservoir, in the upper portions of the Tweed Catchment. The upper and mid portions of the stream are characterised by long steep rapid sections with an average gradient of 4 %. The stream in this section has an average width of 5.1 m. The channel is more or less rectangular with well defined banks and only very limited, isolated flood plains. The channel bed is dominated by large boulders, with limited bedrock outcrops and no woody debris. The study was undertaken along a 148 m section of the stream in this portion of the catchment (Figure 3.1a). Below the study reach the stream then enters a small steep gorge characterized by a series of large falls. These falls have provided an effective barrier to fish migration. Fish stocks in the upper portions therefore are low (Edwards, 2005). At the base of the gorge the stream flattens out onto a small flood plain at the head of the Fruid reservoir.

Cramalt Burn

The Cramalt Burn rises at an altitude of 700m in nearby hills, approximately 8 km from the source of the Talla. It is a small steep stream, 3.5 km long, dropping 420 m into the Meggett Reservoir, an average gradient of 12 %. The upper portions of the stream are characterized by long rapid sections, below which the stream steepens into a series of rapid and step / cascade / pool units. The stream in this section has an average width of 4.3 m. The channel shape is similar to that of the Talla, with well defined banks and no flood plain development. The bed is similarly dominated by large boulders with limited bedrock and no woody debris (Figure 3.1b). The study was undertaken along a 100 m section of the stream in the steeper lower portions of the catchment. Below the study site the stream enters a large culvert just above the Megget Reservoir, into which it drains. Fish stocks above the culvert are low (Edwards, 2005).

3.3 Methods

There were two approaches: First, intensive sediment sampling was undertaken to characterise the grain size distributions of each patch type in each stream. Second, a general survey was conducted to map the location of patch types and channel units (after Grant *et al.*, 1990) with respect to the channel boundaries, and describe the location and size of each patch type. The maps allow the patch classification scheme to be placed in a spatial context with respect to the channel unit classification scheme. They also permit estimates of the total area of streambed covered by each patch type. This information will be used in Chapters Four, Five and Seven to allow scaling up of processes and patterns.

3.31 Sediment Sampling

Due to the wide range of sediment textures and occurrence of large boulders in these headwater streams, two sediment-sampling methods were employed, bulk areal sampling and Wolman counts (1954). A surface pebble count (Wolman, 1954) can adequately represent particle sizes between pebbles and large boulders, but may under-represent finer size classes. Conversely, bulk areal samples can be used to determine the distribution of fine classes, but become impracticable in the presence of large boulders.

To obtain a bulk areal sample representative of all size fractions the total mass of sediment required is estimated by the following equation (Church *et al.*, 1987);

$$m = (2.87*D_{max} - 44.8) \qquad \text{Equation (3.1)}$$

where, m (kg) is the total mass of the sample and D_{max} (mm) is the largest particle.

In Degraded patches the largest particle fraction was estimated to be 700 mm (visual observation), and would require sampling at least 1900 kg of sediment for bulk areal sampling. This was clearly beyond the scope of this study given the obvious constraints in removing, sieving and weighing such a sediment load, so the sediment grain size distribution of Degraded patches was determined from a combination of a reduced bulk areal sampling programme, and Wolman (1954) counts.

In Loose patches, the largest particle was estimated to be 90 mm for the Talla and 128 mm for the Cramalt. From equation 1 a maximum total of 213 kg of sediment from each stream was required to be sampled to maintain representative size fractions. This was possible and the preferred bulk areal sampling was therefore undertaken for Loose patches. The grain size distribution of Structured patches was determined using Wolman (1954) counts.

Loose patch - Bulk Areal sampling:

Five Loose patches were sampled from each stream. Only the surface layer from each patch was sampled, defined as the depth of the largest particle. The surface sediment was removed, sieved and classified into phi increments in the field to 16 mm (-4 Phi). All sediment less than 16 mm was bagged and later sieved in the laboratory to > 2.83 mm (-1.5 Phi). A total of 223 kg of sediment was sampled from the Talla Water, and 215 kg from the Cramalt Burn. Bulk sample volume equivalents (sieve by weight) were converted to surface sediment grain size distributions (area by weight) following Kellerhals and Bray (1971);

$$W_{bulk} = W_{surface} / D_m \qquad \text{Equation (3.2)}$$

Where, W_{bulk} is the converted weight of a particular size fraction, $W_{surface}$ is the weight of the size fraction on the sieve and D_m is the geometric mean diameter of that material.

Degraded patch - Bulk Areal sampling / Wolman Counts

In the Talla Water, sediment sampling of Degraded patches was undertaken using a combination of bulk areal sampling and Wolman (1954) counts. In the Cramalt Burn, the grain size distribution was not required for analysis of bedload (Chapter Five), so the distribution was determined from Wolman (1954) counts, which are more practicable, and can adequately represent particle sizes between pebbles and large boulders.

In the Talla Water, three 1 X 1 m areas of the degraded bed were bulk sampled, giving a total of 350 kg of sediment. Only the surface sediment, defined as the depth of the largest particle, was removed and sieved. Barriers were erected upstream from each sample patch to reduce flow and permit the sampling of fines. Sieving procedures followed those for the loose samples. Three Wolman (1954) counts, one each in a pool, riffle and rapid, were carried out within a large channel spanning grid, 70 X 70 cm. The b-axis of particles immediately below each node point of the grid was measured. One hundred particles were selected and measured in each unit. The grid spacing (70 cm) was determined from an estimate of D_{max} (700 mm), and was adopted to reduce the likelihood of re-sampling. The counts from each channel unit permitted some comparison of the grain size distribution between them.

The mean grain size distribution was established by combining the distributions from the bulk areal sample and the three-pooled Wolman (1954) counts, following Fripp & Diplas (1993). The bulk areal sample was converted to a grid-by-number distribution using equation (2) (Kellerhals & Bray, 1971), equivalent to the distribution obtained from the Wolman counts (1954). The two distributions were then combined as follows; I selected the size class (D_i) in which the percent frequencies from each distribution (bulk areal converted, $n\%_{areali}$, and Wolman count, $n\%_{woli}$) were most similar. A scaling factor, F, was then calculated, where;

$$F = (n\%_{wol\,i} - n\%_{areal\,i}) / n\%_{wol\,i} \qquad \text{Equation (3.3)}$$

F was then subtracted from the percent frequency for all size classes below the size class selected (D_i) from the Wolman (1954) count distribution ($n\%_{woli}$). This yielded an adjusted Wolman count distribution for all size classes finer than that initially selected (D_i). The adjusted Wolman (1954) count distribution and the converted bulk areal distribution ($n\%_{areali}$) were then summed. This final distribution was readjusted to 100%, representing the new particle distribution for the combine sample.

In the Cramalt Burn, three Wolman (1954) counts were conducted, each measuring 100 particles. A grid was established for each count as per the Talla, all within rapid sections, the dominant channel unit.

Structured patch - Wolman Counts:

In each stream the b-axis of a total of 202 particles from the Talla, and 189 from the Cramalt Burn, 20 structures in each, was measured. All constituent particles of a particular structure were recorded.

3.32 General Surveying

The location of Loose, Structured and Degraded patches, emergent bars and large boulders (> 1 m) within the channel was recorded and mapped onto sheets. The size of Loose and Structured patches was estimated by taking one measurement of the longest axis (in the case of Structured patches this was the spine of the feature) and three measurements perpendicular to this axis. The size of the Degraded patches was estimated later from detailed maps, as that being all parts of the streambed excluding Loose and Structured patches, large boulders and emergent bars. All patches were classified visually based on the main sedimentological characteristics defined in

Chapter two, such as size, sorting and degree of particle imbrication. Where possible flow characteristics were also used.

Channel units were classified by visual estimates of relative roughness, percentage estimates of area in supercritical flow, and degree of imbrication and step development (after Grant *et al.*, 1990). As a guide, the photographs of Grant *et al.*, (1990) and Halwas & Church (2002) were used during initial field identification. Units were classified into: pool, glide, riffle, rapid, bedrock chute, boulder cascade, bedrock cascade, and isolated step. The location of channel units with respect to the channel boundary and patch types were recorded and mapped onto sheets. All classifications were carried out during low flows by one observer.

3.4 Results

3.41 Sedimentological Characteristics - Loose, Degraded and Structured

Loose patches in both streams were moderately well sorted (after Folk and Ward 1957), consisting of fine gravels and pebbles, with an average D_{50} of 29 mm in the Talla and 32.1 mm in the Cramalt (Table 3.1). Indeed, the average grain size distribution of the Loose patches from both streams was very similar (Table 3.1), and considerably finer than both Degraded or Structured patches (Figure 3.2). Most Loose patches only consisted of two or three dominant size classes and were relatively homogenous throughout (Figure 3.3a). However, if present, the sand component commonly collected in small deposits within the patch, exhibiting some level of intra-patch sorting (Figure 3.3b).

Degraded patches on average were very poorly sorted (Table 3.1) (after Folk and Ward 1957). They consisted of particles ranging in size from < 2.83 mm to over 724 mm (-9.5 Phi) in both streams, encompassing almost the entire range of particle sizes on the stream bed, from the smallest particles within Loose patches to the largest particles within Structured patches (Figures 3.2 & 3.4a). The grain size distribution of Degraded patches from both streams was generally similar, with a D_{50} of 113 and 74 mm in the Talla and Cramalt respectively, both of which were larger than the D_{90} for Loose patches. The finer particle fraction of Degraded patches, the matrix, generally collected within small inter-particle voids (Figure 3.4b), rather than inter-dispersed evenly throughout the patch. While a complete textural analysis of the

Table 3.1 Sediment characteristics from Talla Water and Cramalt Burn

	Loose	*Degraded*	*Structured*
Talla			
D_{90} (mm)	83	396	614
D_{50} (mm)	29	113	265
D_{18} (mm)	14	14	125
Sorting Coefficient	0.988	2.32	0.960
Sorting Classification *	Moderate	Very poor	Moderate
Cramalt			
D_{90} (mm)	71	280	728
D_{50} (mm)	32.1	74	430
D_{18} (mm)	14	29	133
Sorting Coefficient	0.981	2.02	0.991
Sorting Classification *	Moderate	Very poor	Moderate

- * after Folk and Ward (1957)

Sorting Coefficient = $(D_{84} - D_{16})/4 + (D_{95} - D_5)/6.6$

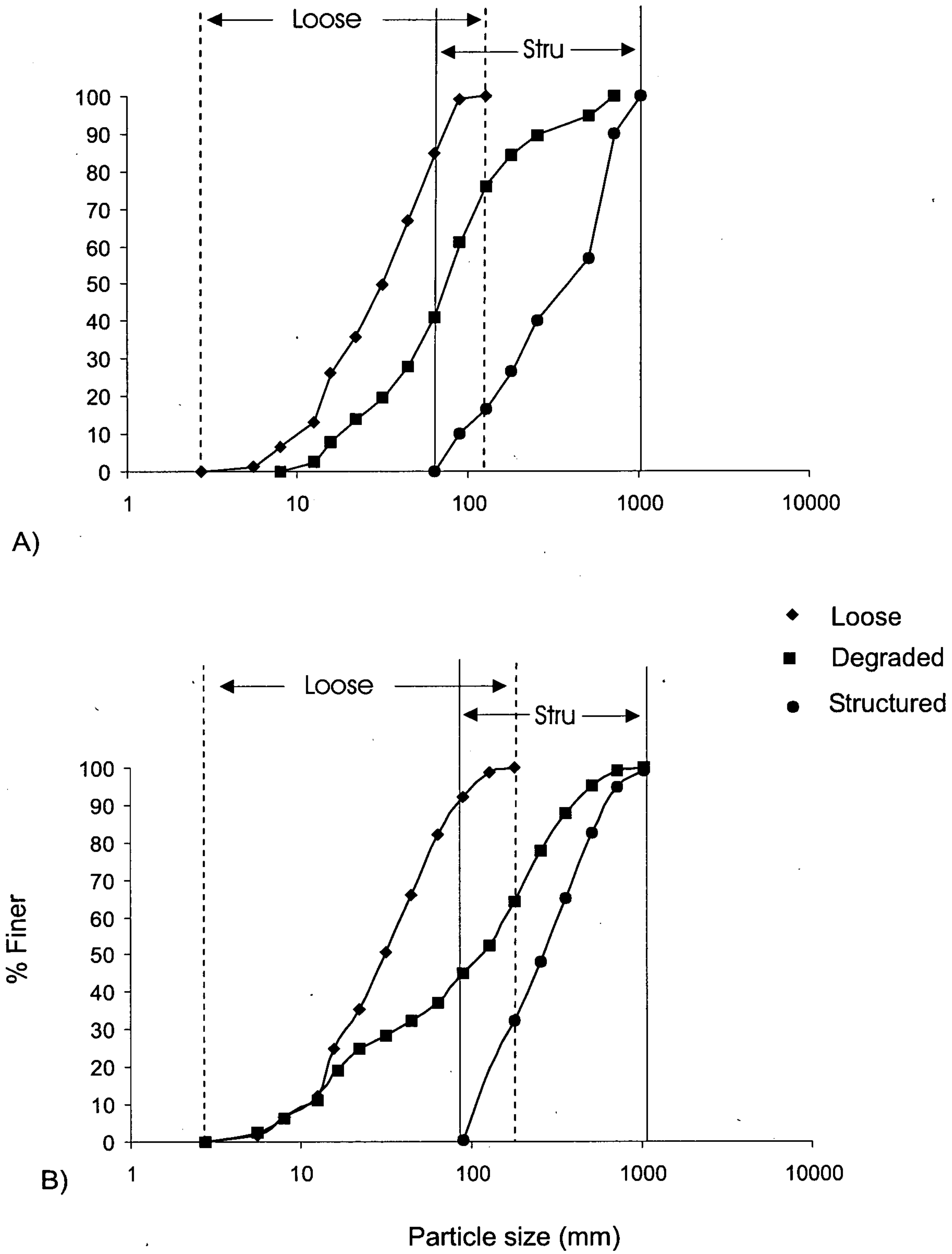


Figure 3.2 Particle size distributions from the three patch types from A) Cramalt Burn and B) Talla Water

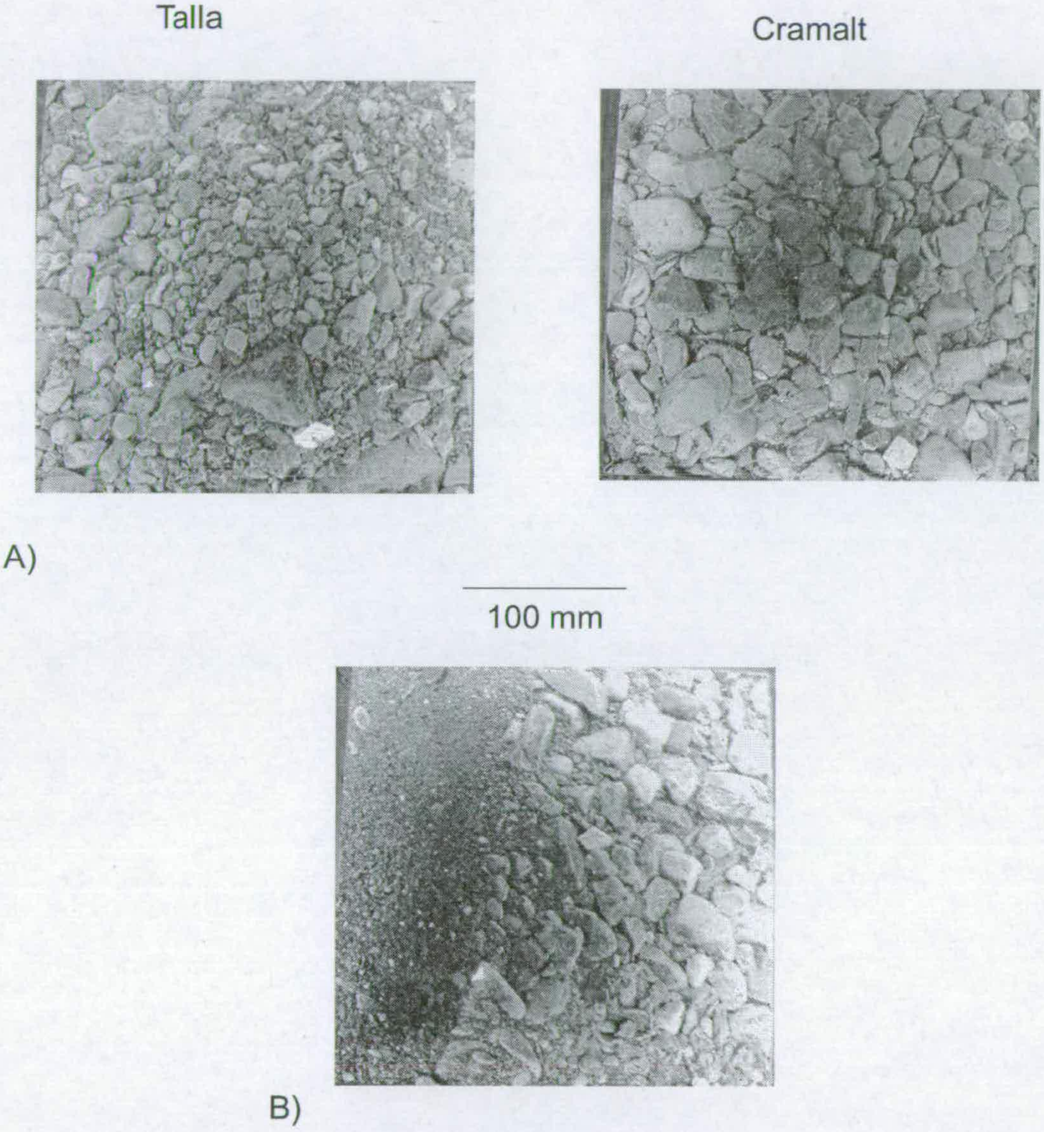


Figure 3.3 A) Loose patches in the Talla and Cramalt. B) Separation of grain sizes within Loose patch. Flow is from top to bottom.

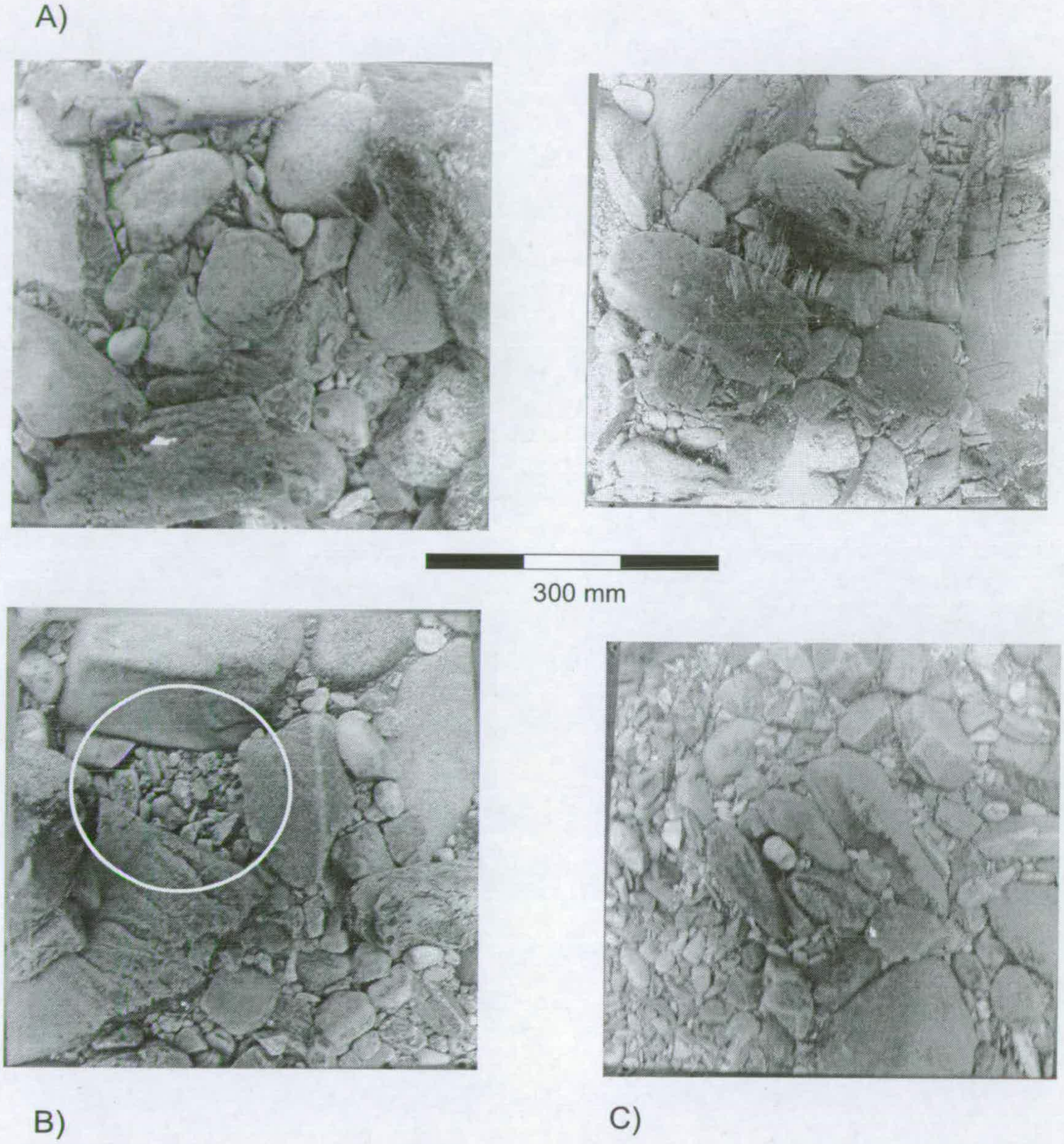


Figure 3.4 A) Typical Degraded patches from the Talla and Cramalt. B) Degraded patch with an inter-particle void full of fines, called the matrix. C) Degraded patch where the matrix is extensive, verging on being categorised as a Loose patch.

sediment within these pockets was not carried out, estimates of size ranges from the areal photographs of the Degraded patches indicate that the general size distribution is similar to that of the Loose patches, although without the coarsest fractions present (64 - 90 mm). In both streams, the Structured patches were composed of the largest particle fractions, consisting of boulders up to 1 m (Figure 3.2). The sediments were generally moderately well sorted, with few particles < 100 mm (Table 3.1). The boulders were usually imbricated or jammed against one another forming a stable collection (Figure 3.5a). Typically the boulders were jammed against either a bedrock protrusion from the bank, or a particularly large immovable boulder (> 1m).

Sediment Distribution with Respect to Channel Unit:

Both Degraded and Loose patches commonly occurred in riffle, rapid and pool units, with Structured patches occurring in rapid units (e.g. transverse steps – sub-unit scale, see Chapter Two) and as whole channel units (e.g. isolated step and cascade). The sediment distributions of Loose and Degraded patch types did not vary considerably between channel units (Figure 3.6). Degraded and Loose patches from riffle, rapid and pool units were reasonably similar, although the Degraded patch was slightly finer in the riffle unit. There was little variation in the grain size distribution of both Loose and Structured patches.

3.42 Surveying and Mapping

The study sites in both streams are characterised by long rapid sections interspersed with short riffle, pool, isolated step, and cascade channel units (Figures 3.7 & 3.8). For both streams, the patch classification resulted in a greater detail of morphological

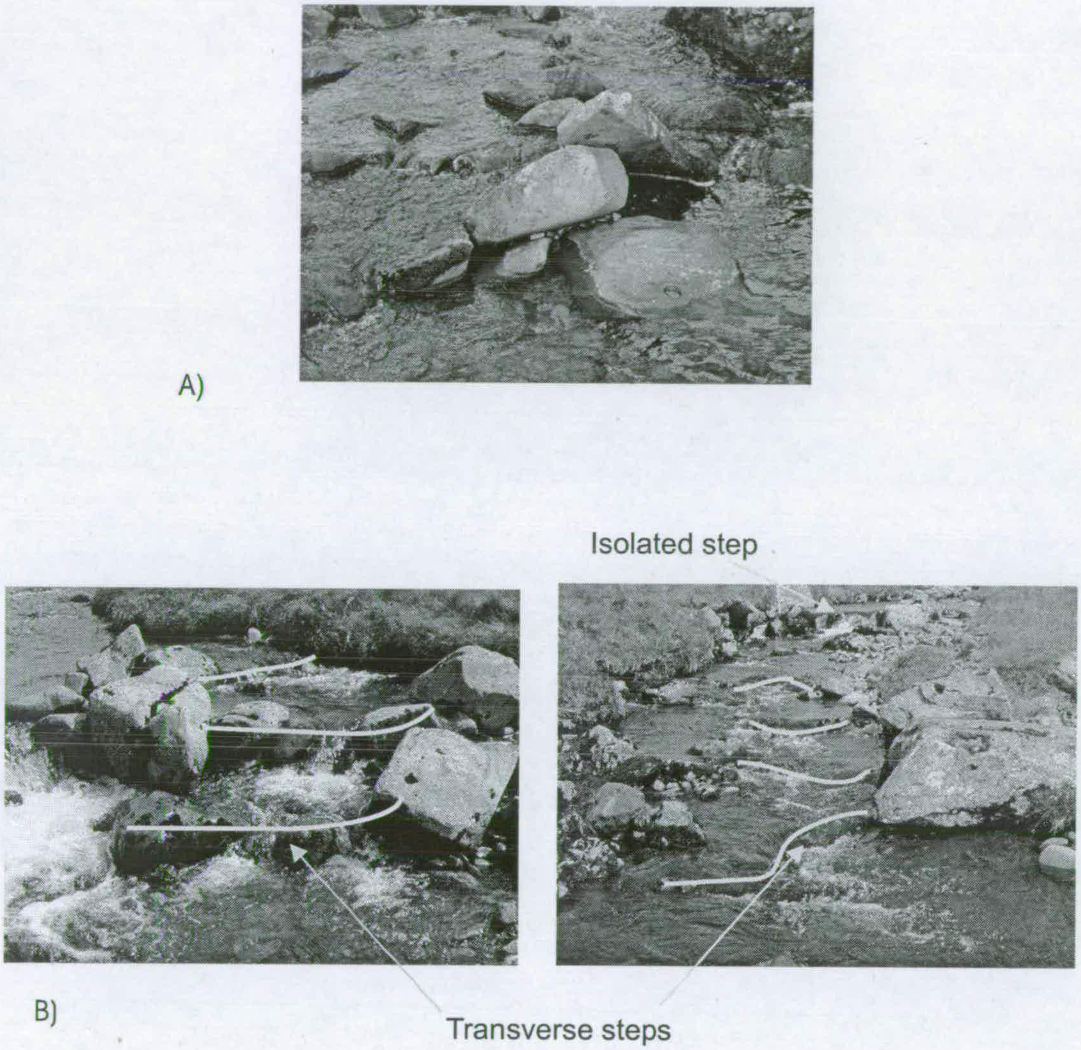


Figure 3.5 A) Particle imbrication typical of a Structured patch
B) Structured patches, semi-emergent and submerged transverse steps. Submerged steps are easily identified by the increased turbulence. White lines indicate transverse steps.

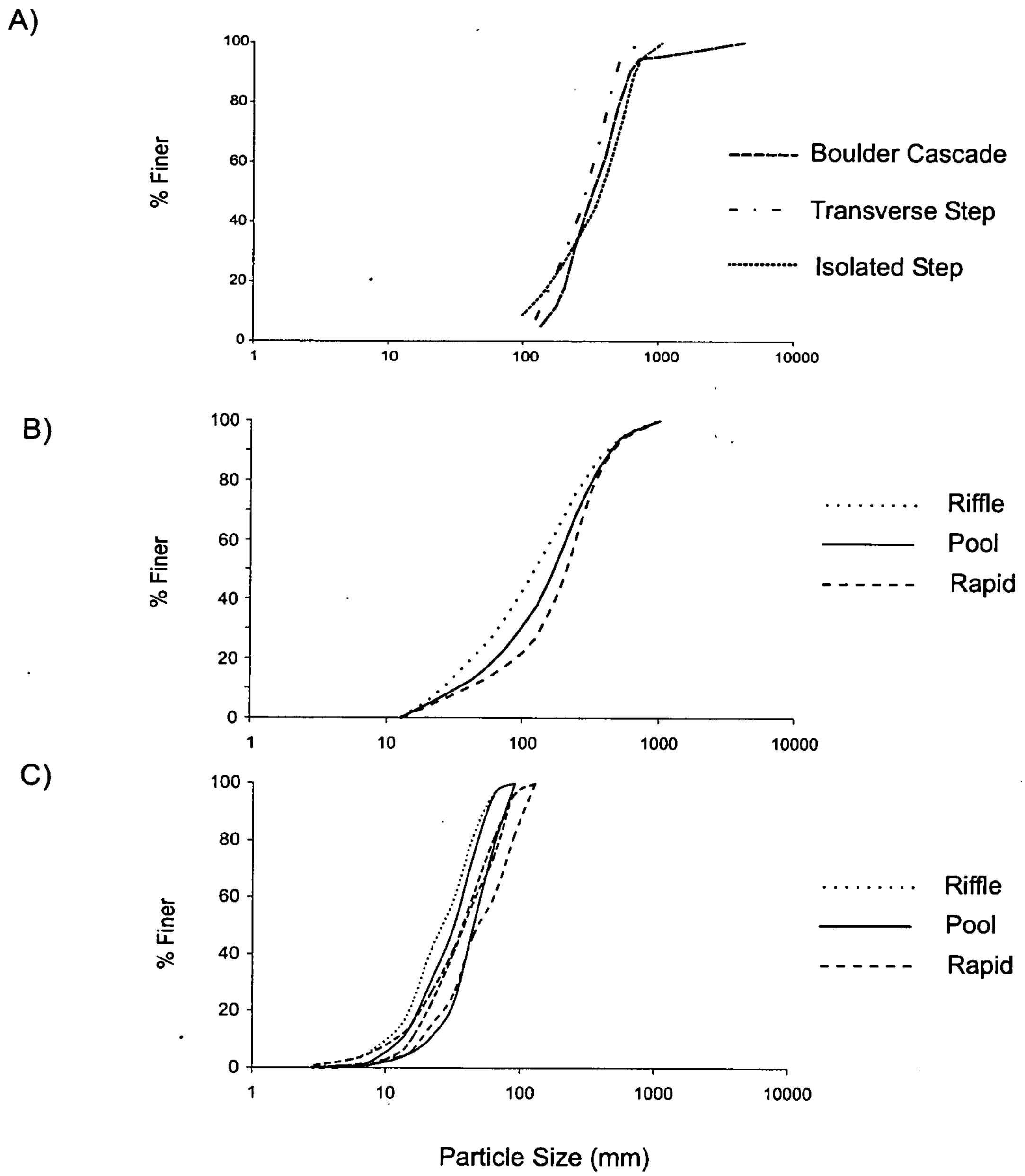


Figure 3.6 Grain size distributions from A) Structured patches, boulder cascade, isolated steps (channel unit) and transverse step (sub-unit), Wolman counts. B) Degraded, Wolman counts, and C) Loose (areal bulk sampling) patches within riffle, pool and rapid units from Talla Water. Note, the grain size distributions of the Structured and Loose patches were obtained from multiple Wolman counts and multiple bulk samples respectively. The grain size distribution of Degraded patches was obtained from one Wolman count.

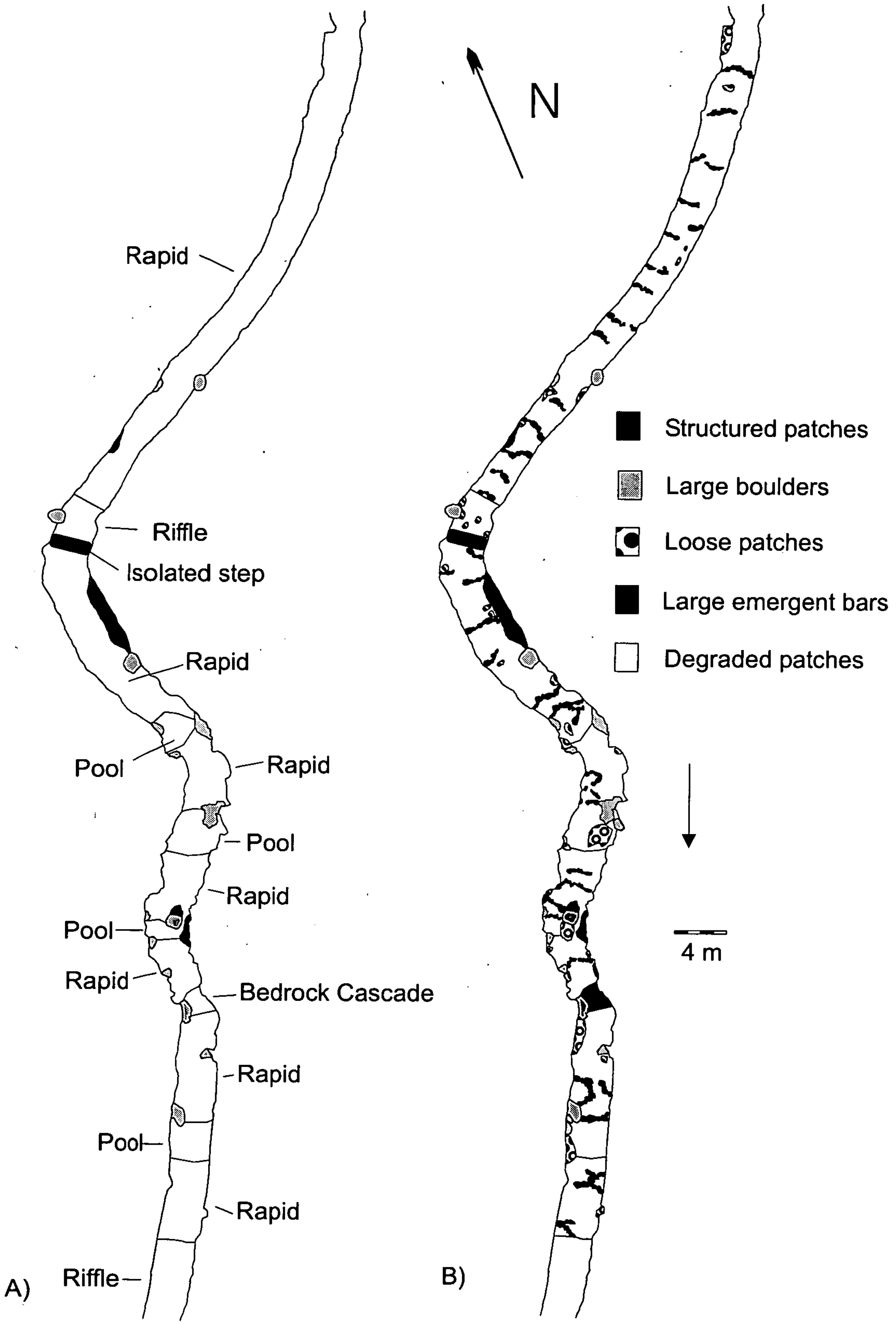


Figure 3.7 Map of the study reach in Talla Water showing A) channel units and B) sedimentological patch types

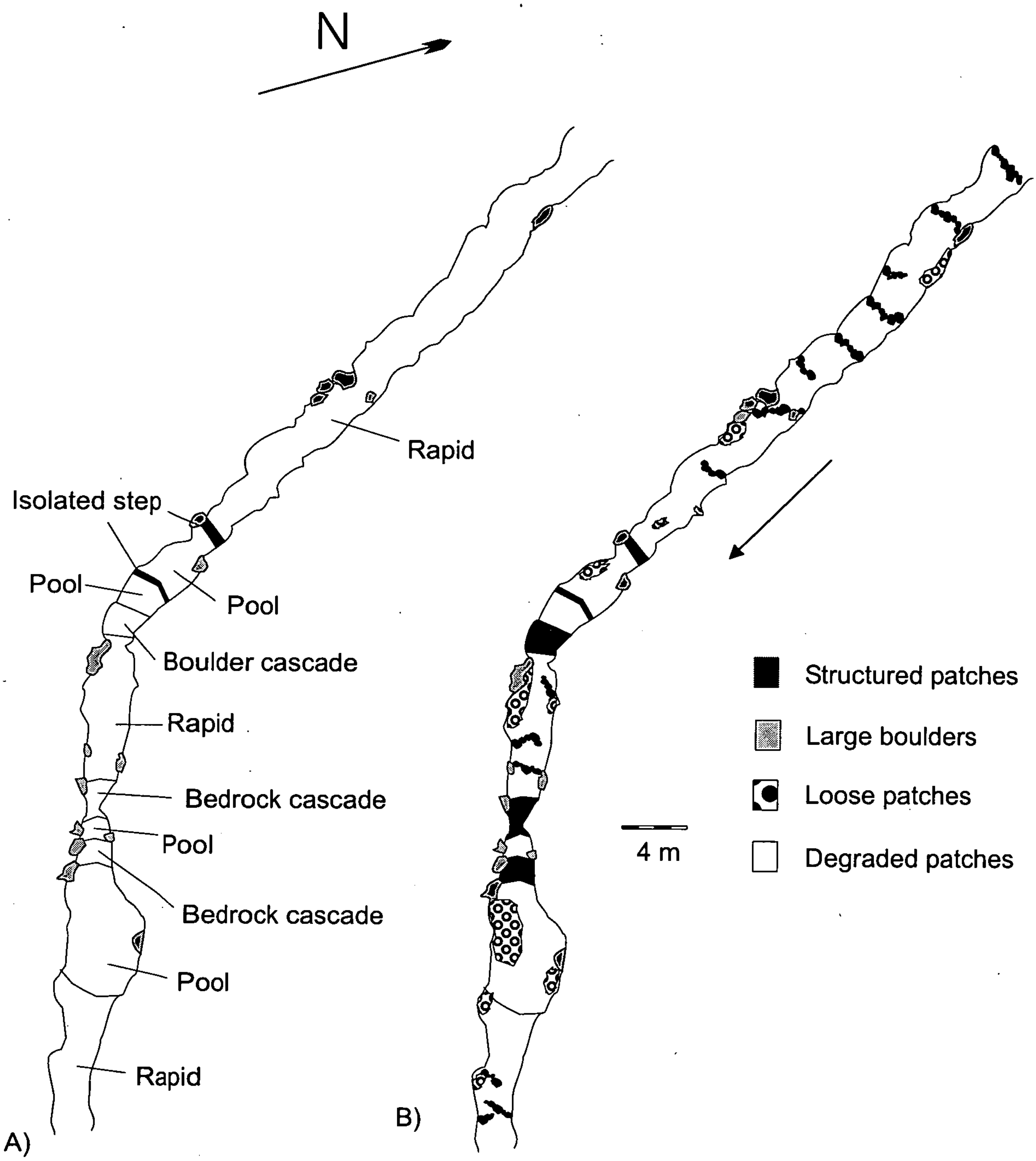


Figure 3.8 Map of the study reach in Cramalt Burn showing A) channel units and B) sedimentological patch types

features than the channel unit classification, where long sections of unbroken streambed are uniformly classified as rapid. The relative dominance in terms of percent area streambed covered by each patch type was similar in both streams. Degraded patches accounted for 64 and 68 % of the total wetted streambed in the Cramalt and Talla respectively, with Structured patches accounting for 31 and 26 % respectively, and Loose patches less than 10 % in both streams.

Loose patches occurred in three main locations; a) mid channel deposits in the lee of large clasts or within small pockets, b) along the wetted channel edge and c) the edges of pools (Figures 3.7 & 3.8). All Loose patches, except those within riffle units, were associated with flow separation resulting from an obstruction such as a protruding bank or large boulder, or from flow de-acceleration into a pool unit. At base flows, areas of flow separation were clearly observed and provided a good indication as to the location of many Loose patches (Figure 3.9). Most patches were also easily distinguished from other areas of the streambed by particle size and sorting (compare Figures 3.3a & 3.4a). Boundaries were typically sharp, and rarely did one patch grade into another. Loose patches associated with riffle units however, where not clearly associated with any obstruction, which presented some confusion. In riffle units the collection of fine particles was wide spread, making it difficult to distinguish between a Degraded patch with a large extensive matrix, or a Loose patch with numerous large isolated clasts (Figure 3.4c).

Based on location and association with an obstruction, six types of Loose patch were recognized; pocket (small patch between two large boulders), riffle patch (within a

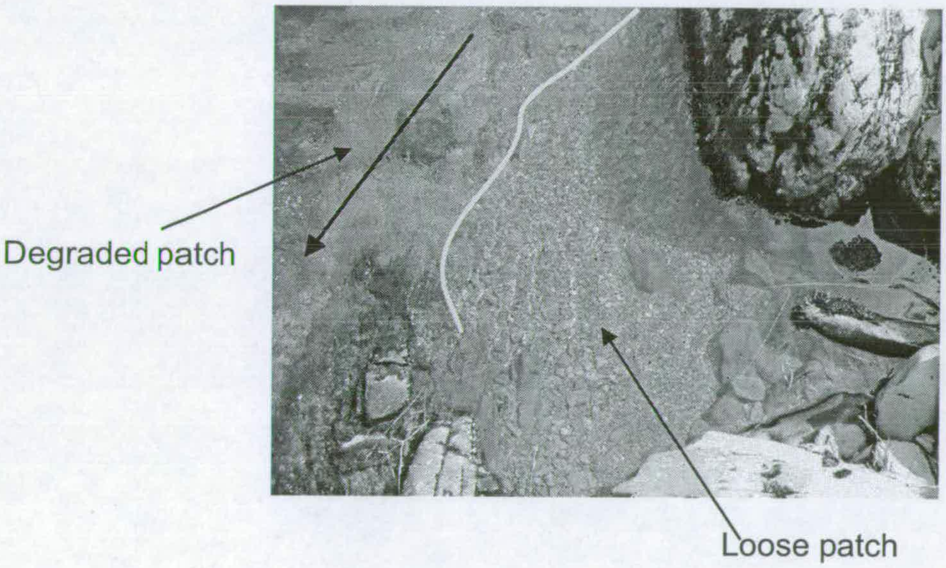


Figure 3.9 Loose patch showing flow separation zone. Arrow indicates flow direction.

riffle unit), boulder patch (lee of a large boulder), lateral patch with no obstruction (located along the channel bank), lateral patch with obstruction (located along channel bank behind a large boulder or bank obstruction), and pool patch (within a pool unit). The distinction between patch types likely reflects formative processes, i.e. particle entrainment (see Chapter Four). They ranged in size from 0.12 m^2 to 3.98 m^2 in the Talla Water, and 0.11 m^2 to 6.89 m^2 in the Cramalt Burn. In both streams, the largest patches occurred on the edges of plunge pools just below large steps or cascades. In general, lateral and pool patches tended to be larger than the mid channel deposits; pocket, riffle and boulder (Figure 3.10). These deposits were typically 2 to 3 times larger in the Cramalt than the Talla.

Degraded patches were extensive in both streams. They formed long continuous areas of streambed, only divided from one another by channel spanning Structured patches such as isolated and transverse steps and boulder cascades (Figures 3.7 & 3.8). The largest unbroken area of Degraded bed was approximately 47 and 36 m^2 in the Talla and Cramalt respectively. The dominant type of Structured patch in both streams was a horizontal step, either partial or channel spanning. These occurred at regular intervals from 1 to 2 channel widths apart in both streams (Figures 3.7 & 3.8). The size of the steps ranged from channel spanning (mean = 2.4 m^2, SE = 0.19) to partial steps typically reaching ½ to ¾ of a channel width (mean = 1.3 m^2, SE = 0.11), both typically no more than 2 particles wide. Boulder and bedrock cascades were not as common, yet far larger, spanning the channel and reaching 1 to 2 channel widths in length (mean = 8.78 m^2, SE = 0.76). The Structured patches were easily separated from the other patch types on the basis of flow, areas of increased

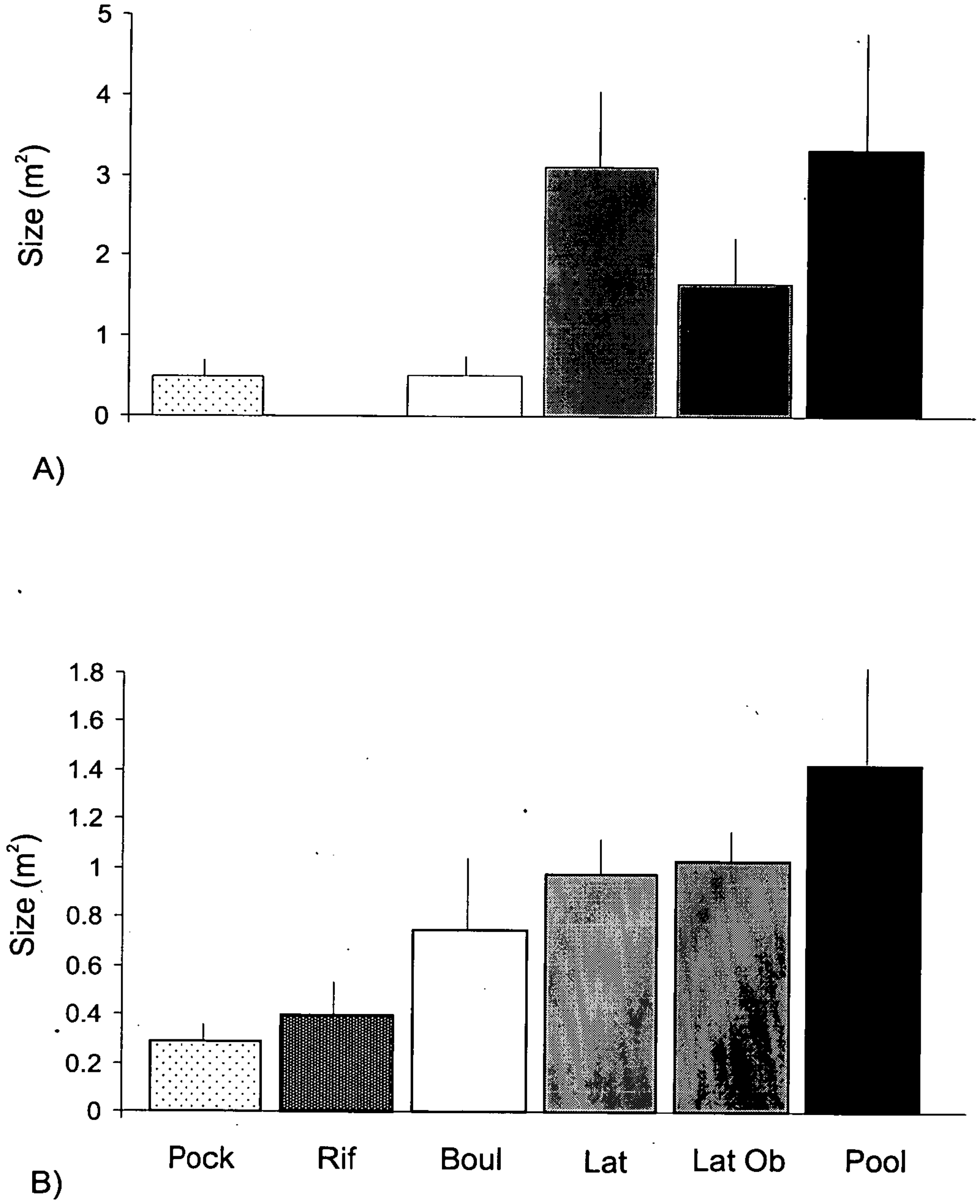


Figure 3.10 Average size (1 SE shown by vertical lines) of Loose patches in A) Cramalt Burn and B) Talla Water. Pock - pocket, Rif - riffle, Boul - boulder, Lat - lateral, Lat Ob - lateral obstruction, Pool - pool. Note different scales on y-axis.

turbulence and aeration (e.g. Figure 3.5b), and relative roughness, i.e. large particle sizes relative to flow depth, and imbrication (e.g. Figure 3.5a).

3.5 Discussion

Patches of streambed of two high gradient streams were classified into three distinct sedimentological types, Structured, Degraded and Loose, based on sediment grain size and degree of structural development. The grain size distributions of the three patch types, their location within the channel and their relative sizes all differed. These differences likely reflect the different formative processes. The location of deposits of fine sediment for example, within pools and behind large obstacles, is in keeping with that observed in other studies (e.g. Kondolf *et al.*, 1991, Barta *et al.*, 1994, Rathburn & Wohl, 2003), where flow separation associated with channel irregularities and roughness elements, such as large boulders, create low energy depositional zones (Rathburn & Wohl, 2003). The size of the deposit was generally reflected by the size of the flow separation zone at base flow, suggesting little change in the hydraulics during flows just competent to transport sediment. During higher flows however, the zone of flow separation may migrate (Rathburn & Wohl, 2003), altering local hydraulics, competence to entrain sediment and presumably the size of the deposit.

The majority of Structured patches, transverse and partial steps, were composed of the largest particle fractions, where collections of boulders were either jammed against one or two extremely large boulders, or bedrock outcrops. This has been observed elsewhere (e.g. De Jong & Ergenzinger, 1995, Church *et al.*, 1998, Zimmerman & Church, 2001,). The large boulders, or bedrock outcrops, are thought to act as immovable seed particles against which other boulders are jammed during extreme flood events (Church *et al.*, 1998). The spacing between the Structured patches in both streams is of the same order, typically 2 to 3 channel widths apart. This is also consistent with that observed elsewhere (e.g. Chin, 1989, Gomi *et al.*, 2003). The spacing between steps is thought to represent an adjustment to maximum channel resistance (Abrahams et al., 1995), with channel gradient related to step spacing. While some have found weak evidence for this (e.g. Chin, 1989, Grant *et al.*, 1990, Wohl *et al.*, 1997), others suggest that step spacing is controlled by the random emplacement of large boulders in the channel (Zimmerman & Church, 2001). The spacing of steps potentially has significance for the drift distance, settlement and accumulation of invertebrates in steep streams (Chapter Six).

The sedimentological characteristics, location and relative extent of each patch type were very similar between the two streams. This however, is not surprising given the similarities of the two streams and the process based foundation of the patch classification, i.e. particle movement. In the least, it suggests that the classification should be generally applicable to steep streams with similar characteristics. For streams of higher gradients than those here, e.g. 10 -20 % (Halwas & Church, 2002) where the step / pool morphology dominates, the classification should still hold, as the morphological features of such channels (Halwas & Church, 2002) can be directly classified as either Structured, Degraded or Loose, and the formative processes remain the same (Grant *et al.*, 1990). One difference between the two streams in this study however, was the size of the Loose patches, which were generally greater in the Cramalt. This may be a reflection of the size of the flow separation zones (i.e. ability to store sediment in the channel), but also the supply of fine sediment to the channel.

For lower gradient streams the classification may be in appropriate as Structured patches are unlikely to exist and patch types not typically present in high gradient streams may be important, e.g. deposits of fine silt and mud, or macrophyte beds. In systems where riffle / pool units dominate, e.g. medium to low gradient systems, the classification may also be unworkable, or require adjustment. The distinction between patch types was generally very easy, however, within the riffle units the distinction between Loose and Degraded patches was not so apparent. While the process of deposition remains the same, there was a lack of clearly defined flow separation zones within the riffle units.

As a whole, the patch types were easily defined in the field, with clearly delineated boundaries. Studies of channel unit classifications however, have indicated the potential for observers to misclassify physical units, resulting in biased, unrepeatable and imprecise estimates of habitat availability (e.g. Poole *et al.*, 1997, Peterson & Rabeni, 2001). The misidentification of channel units has generally been partly put down to the large number of physical units in some classifications (Peterson & Rabeni, 2001) which can incorporate very similar substrate types (e.g. Barmuta, 1989). Some workers have therefore advocated reducing the number of channel unit types as a means of decreasing the influence of observer bias (e.g. Roper & Scarnecchia, 1995). A simple scheme such as that defined in Chapter two, with just three physical types, may represent a scheme in which observe bias, and mis-identification is not great.

By reducing the number of physical units however, care has to be taken that the classification scheme does not incorporate heterogeneity that is of relevance for the biotic community (Peterson & Rabeni, 2001). While the patch classification scheme incorporates a greater amount of sedimentological heterogeneity compared with that of the channel unit classification (after Grant *et al.*, 1990), variation at scales smaller than the patch unit may exist (Downes *et al.*, 1998, Larronne *et al.*, 2000). Minor cluster development (Brayshaw *et al.*, 1993), particle embeddiness (Downes *et al.*, 1998) and intra patch sorting may all lead to intra patch variation in particle movement. This may be significant within Degraded patches due to the large range in sediment size, and the disproportionately large area of bed covered by these patches. Variation in particle movement within patches may lead to variation in invertebrate assemblage and response to flooding.

Variation in particle movement and invertebrate assemblage within and across patch types will be addressed in Chapters Four and Five.

Chapter Four Patch Specific Particle Movement in a Steep Stream

4.1 Introduction

The movement of sediment through steep streams involves the integration of a complex array of processes operating over a wide range of spatial and temporal scales. Collectively these processes transfer sediment from the hillslope to the channel network and then downstream through the watershed, and are known as the sediment cascade. A part of the cascade that has received a lot of attention is the fluvial transport component. This incorporates three processes, entrainment, transport and deposition of sediment. The focus of this chapter is on the entrainment of sediment from the three patch types, Loose, Degraded and Structured.

Entrainment is fundamentally dependent on two requirements; 1) an available supply of sediment and 2) flows capable or competent to transport the available sediment. At large scales sediment supply is limited by stochastic mass wasting events, e.g. land slides, that can deliver large quantities of sediment into the channel. At small scales, sediment supply is influenced primarily by the sedimentological character of the streambed. Bedform features, surface armouring, particle embeddedness, and patch specific sorting and hiding, all act to control the size fractions available for entrainment (Church, 1985, Beschta, 1987, Gomez, 1995, Paola & Seal, 1995). In steep streams these size fractions are typically much smaller than the grain size of the bed surface, i.e. the bedload is most commonly composed of predominantly fine particles (Lenzi *et al.*, 2004). Flows therefore do not usually entrain and transport as much sediment as they are capable or competent to do so (Church, 1985).

The entrainment and transport of sediment in steep streams has been described to occur in phases (e.g. Jackson & Beschta, 1982, Ashworth & Ferguson, 1989, Warburton, 1992, Paola & Seal, 1995) with the entrainment of fine particles (phase I transport) predominating at low discharge until a threshold is reached, above which the entrainment of coarse particles occurs (phase II). Phase I transport has been described variously to consist of overpassing sand (Ashworth & Ferguson, 1989), the flushing out of fines deposited in the channel (Warburton 1992), transport of sediment over a stable armour (Jackson & Beschta, 1982) and re-mobilization of fines deposited in pools and tranquil areas (Ryan *et al.*, 2002). A unifying characteristic is that the bedload associated with phase I transport is finer than the coarse armoured surface layer. Ashworth and Ferguson (1989) extended the phase transport model of Jackson & Beschta (1982) to include a third phase, which occurs at the highest discharges, and has since been observed by Warburton (1992) and Lenzi *et al* (2004). However, while Lenzi *et al.,* (2004) and Ashworth and Ferguson (1989) defined phase III as transport nearing equal-mobility, i.e. the size distribution of particles in transport is the same as that of the bed, Warburton (1992) defined it as the breakup of bed features such as boulder steps and large particle clusters. The three-phase model of sediment transport for steep streams therefore describes three distinct entrainment episodes, that can potentially be linked to morphological features of the streambed, ie different morphological features are entrained in each phase (e.g. Warburton, 1992).

The onset of each sediment transport phase is governed by a suite of different physical characteristics and processes. The availability of fine sediment on the surface of the streambed is undoubtedly the prime determinant of the onset of phase I (Church 1985). It is nevertheless also affected by the spatial arrangement of fine material on the surface of the bed (Laronne *et al.*, 2002) and the degree of hiding provided by obstructions (Barta *et al.,* 1994). Phase II transport occurs at flows strong enough to breakup and entrain the coarse armour layer (Jackson and Beschta 1982). The beginning of this phase is thought to occur on or near bankfull flows (Andrews, 1983), although the threshold is poorly understood (Ryan *et al.,* 2002). The onset of phase II is presumably influenced by the same factors involved in the entrainment of coarse particles in steep streams, such as imbrication and particle clustering (Brayshaw *et al.*, 1983, Church *et al.*, 1998), relative roughness (Church, 1985), particle geometry (Schmidt and Gintz, 1995) and embededness (Downes *et al.,* 1998). Phase III transport likely occurs only during extreme flood events (Grant *et al.*, 1990, Lenzi *et al.*, 2004), and involves the destruction and re-arrangement of the channel morphology (e.g. Warburton, 1992).

Identification of specific sediment transport phases in mountain streams is rare (see Warburton 1992, Ryan *et al.*, 2002, Lenzi *et al.*, 2004), and only Warburton 1992 and Ryan *et al.*, 2002, in part, have related a specific phase to a sediment source, or sedimentological bed feature. Relating sediment transport phase with source is potentially useful because it allows spatial attributes (e.g. location, size of area mobilised) to be assigned to each transport phase. The mapping of sediment sources linked to a specific transport phase potentially provides a map of particle entrainment thresholds. By extending Warburton's (1992) definition of the transport phase model, I speculate that the phase breakpoints can be linked to the mobilization of each patch type. Phase III likely refers to the breakup and mobilization of the Structured patches, phase II the breakup and mobilization of the Degraded patches, and phase I the mobilization of the Loose patches. The mobilization of the fine matrix within the Degraded patches, may either contribute to phase I, which along with Loose patches may represent the initiation of bedload (Laronne *et al.*, 2002), or contribute to phase II once the coarse layer has been disrupted. Determining the existence of such associations is important because it opens up the possibility of using bedload information obtained at a reach scale to provide a spatial description of particle mobilization at much smaller scales, the scale of the source, e.g. Loose patches. The point at which a shift in phase occurs may also define a shift in the dominant disturbance mechanism, and loss of potential refugia. The onset of phase II transport for-example, likely results in a shift in mechanism from that dominated by shear stress (high flows over stable particles) and abrasion (transport of fines over stable particles, phase I transport) to that dominated by particle movement (entrainment of coarse particles) (see Chapter Seven).

Identification of sediment transport phases and their association with particular sediment stores, or morphologies is not a trival task. Particle movement is inherently difficult to measure, especially in steep streams. Where specific phases have been identified, workers have employed bedload samplers (Warburton 1992, Ryan *et al.*, 2002, Lenzi *et al.*, 2004), and used detailed mapping of the streambed before and after flooding to relate phase with sedimentological feature (e.g. Warburton 1992). A change in the character of the sediment load and transport rate with discharge has generally been used to indicate a shift in phase transport. For example, a shift in bedload from that dominated by sand to that of coarse particles. The use of bedload samplers to trap sediment in motion is not without its problems. Few samplers measure the process of sediment transport without at the same time interfering with it (Reid *et al.*, 1980, O'Leary & Beschta, 1981,). The sampling of bedload in steep streams is further complicated by the occurrence of large boulders that can inhibit the emplacement of pit traps sunk into the bed. Over filling can also become a problem in such streams, particularly during large events, leading to sample biases.

In this study I used two different methodological approaches to assess particle entrianment and address the aims of this Chapter, which were; 1) to identify sediment transport phases I, II and III, and their breakpoint discharges, 2) to investigate relations between transport phase and mobilisation of particles within each patch type. While the breakpoint for phase III, and indeed mobilization of Structured patches may not occur during the study period (expected return intervals are likely to be much larger than 3 years, Grant *et al.*, 1990), it may be possible to identify a lower bound on the phase III breakpoint. Photography of the streambed before and after flooding was used to relate particle movement within each patch type to discharge. Identification of transport phases using photography was compared with that obtained from bedload traps, and the potential for bedload data, as derived by computational means, to predict particle transport was explored using equations of shear stress. While the applicability of bedload equations in steep streams is questionable (Chapter One, references therein), recent work by Zimmerman & Church (2001) highlights the potential for some equations to model the entrainment of deposits of fine particles within high gradient streams, thus potentially providing a tool to model the mobilisation of particles at the patch scale.

4.2 Methods

4.21 Hydraulic Parameters

Stage Recorders – estimating peak discharges

Four stage recorders were installed along the length of the study reach in the Talla Water to record peak water height during flood events. Each gauge consisted of a large metal stake driven into the substrate near the bank. A hollow transparent tube was attached to the stake such that one end was buried into the substrate under the water, the other fixed above the water line. Ground cork was placed inside the tube to rest on the surface of the water. During rising water levels the cork was carried up the tube to be deposited on the side as water levels start to recede, thus indicating maximum water depth during peak discharge. This was recorded against a graded tape fixed to the outside of the tube. The height of each gauge above a standard datum point was established using a level and stadia, enabling relative water heights, mean flood depths and wetted widths to be estimated at each gauge station for a given flood event.

A transect across the channel was established at gauge 4, where discharge measurements were taken during a range of flows. Each discharge measurement consisted of a series of velocity and depth readings taken at 0.40 m intervals along the transect. A rating curve, relating gauge height to discharge, was established. The relationship was well described by a straight line on logarthimic scales (Figure 4.1), taking the form of:

$$\text{Log } Q = \log a + b \log (H) \qquad \text{Equation (4.1)}$$

Where Q is discharge, H is stage height, and a and b are coefficients.

4.22 Patch Photography – Measuring Particle Entrainment

Particle movement was monitored in the Talla Burn from December 01 until December 03. While event based monitoring was preferred, it was not always possible due to difficultly accessing the site during mid winter and the time constraints of short daylight hours.

At each stream site, replicates of each patch type (Structured, Degraded and Loose) were selected using a random stratified sampling design. Each replicate of each patch type was chosen in turn, and selected by walking a randomly determined distance upstream and choosing the nearest patch of that particular type. Photographs of the substrate of each replicate patche were taken through a large (0.5 x 0.5m) clear perspex viewing box rested on the water surface (Figure 4.2a). If the patch area was larger than the area of the view box (0.25 m^2), then a portion of the patch was photographed with a digital camera. To reduce glare a three-sided black plastic canopy was attached to the box. Natural lighting was sufficient for all day light conditions.

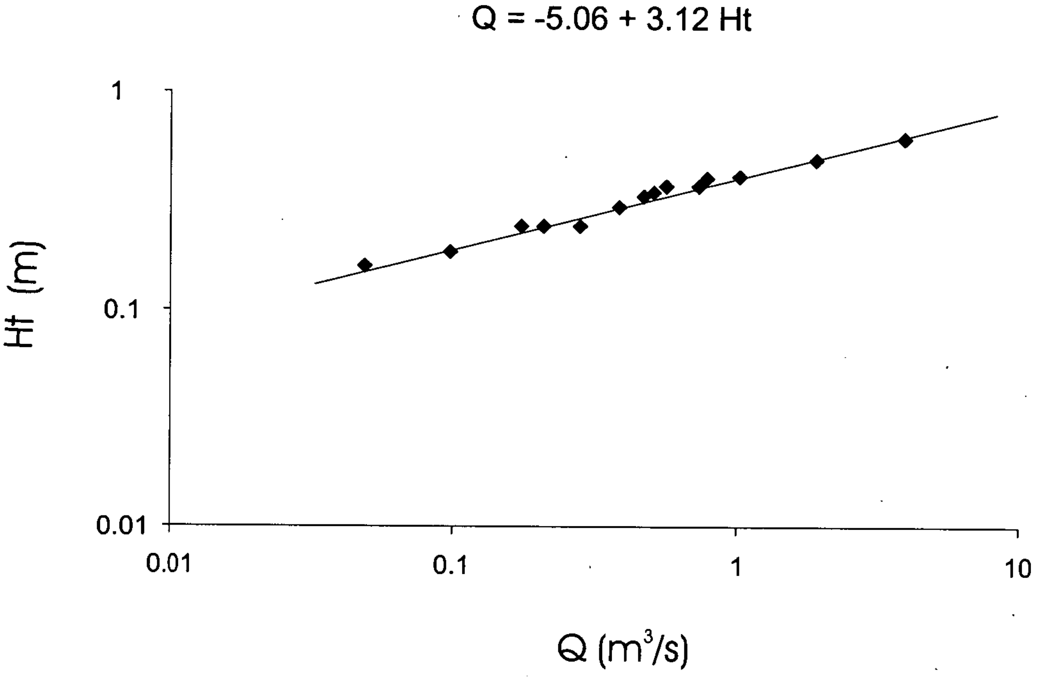


Figure 4.1 Relationship between stage ht and discharge, showing line of best fit. Also shown is the regression equation used to estimate discharge (F = 903.83, P = 0.000, R^2 = 99.2%). Note Ht is shown on the Y-axis and Q on the X-axis for ease of display.

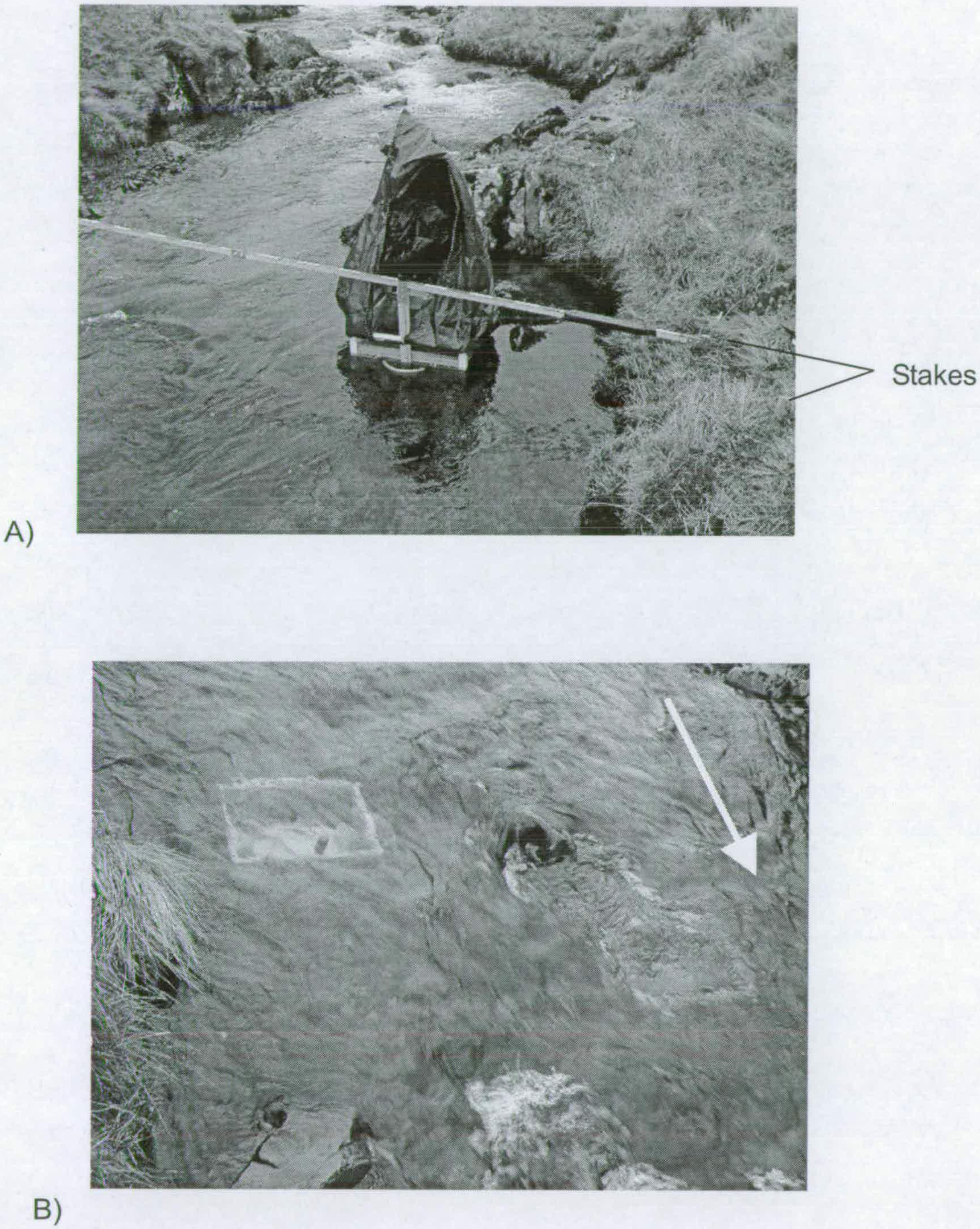


Figure 4.2 A) Viewing box showing position of graded stake and method of patch location. B) Bedload pit traps in the Talla Water.

Each patch was photographed repeatedly during the study period, before and after flooding. To accurately locate the patches and ensure that the same area of streambed was photographed on consecutive visits, a transect was established for each patch. A small wooden stake was driven into the bank nearest to the patch of interest. It was positioned such that the b-axis of the stake pointed along the line of the transect to the downstream edge of the patch of interest. A graded staff rod was attached to the top of the stake so that it ran along the transect to the patch (Figure 4.2a). The patch could then be accurately located (to within ± 1 cm) with reference to the distance along the staff rod. Each stake was colored coded according to patch type and numbered to assist in the location of patch replicates.

For each patch, distance from thalweg, thread of highest flow along the channel, and distance from nearest bank were recorded. For Loose patches, patch size was also estimated by measuring the length of the longest axis of the patch, and three measurements perpendicular to this. The type of Loose patch was also recorded (see Chapter 3 for descriptions). A metal rule was placed onto the substrate in each photograph for scale.

Analysis:

The quality of the digital photographs was too poor for application of image processing software that would allow the computation of grain size distributions (photosieving). The majority of photosieving techniques have been developed for images taken from emergent gravel bars (e.g. Ibbeken & Schleyer, 1985). Such techniques, which rely heavily on accurate thresholding (the detection of boundary edges), are strongly influenced by bubbles entrained under the viewing box, cpom and filamentus algae.

The quality of the photographs was sufficient however, for the direct visual characterization of the sediment and accurate identification of particle location before and after flooding (Figure 4.3a). All photographs were viewed using the graphics package Corel Draw 9, permitting adjustments to contrast, exposure, colour, hue and sharpness allowing for clear images. The location of all particles down to a size of 5 mm was noted visually from each photograph, and assessed before and after flooding to identify mobilized particles.

Particles that had been mobilized were traced and coloured black, the remaining immobilized area was coloured light grey. Using an image processing package (NIH Image, v. 1.61), the total area of the blacked out sections, and total area of the image in pixels were calculated, thus providing an estimate of percentage area mobilized. Figure 4.3 outlines this process. To assist in the location and orientation of smaller particles, their position relative to larger particles, their colour and shape, and any distinguishing features such as crevices, large crystals, or discolourations were used. Using this process a large variation in particle movement could be identified; turning or rolling of the particle *in situ*, small scale transport within the patch, and removal from the patch (Figure 4.4). To simplify the analysis, a particle was considered 'mobilised' only if it had been transported out of the bounds of its original position.

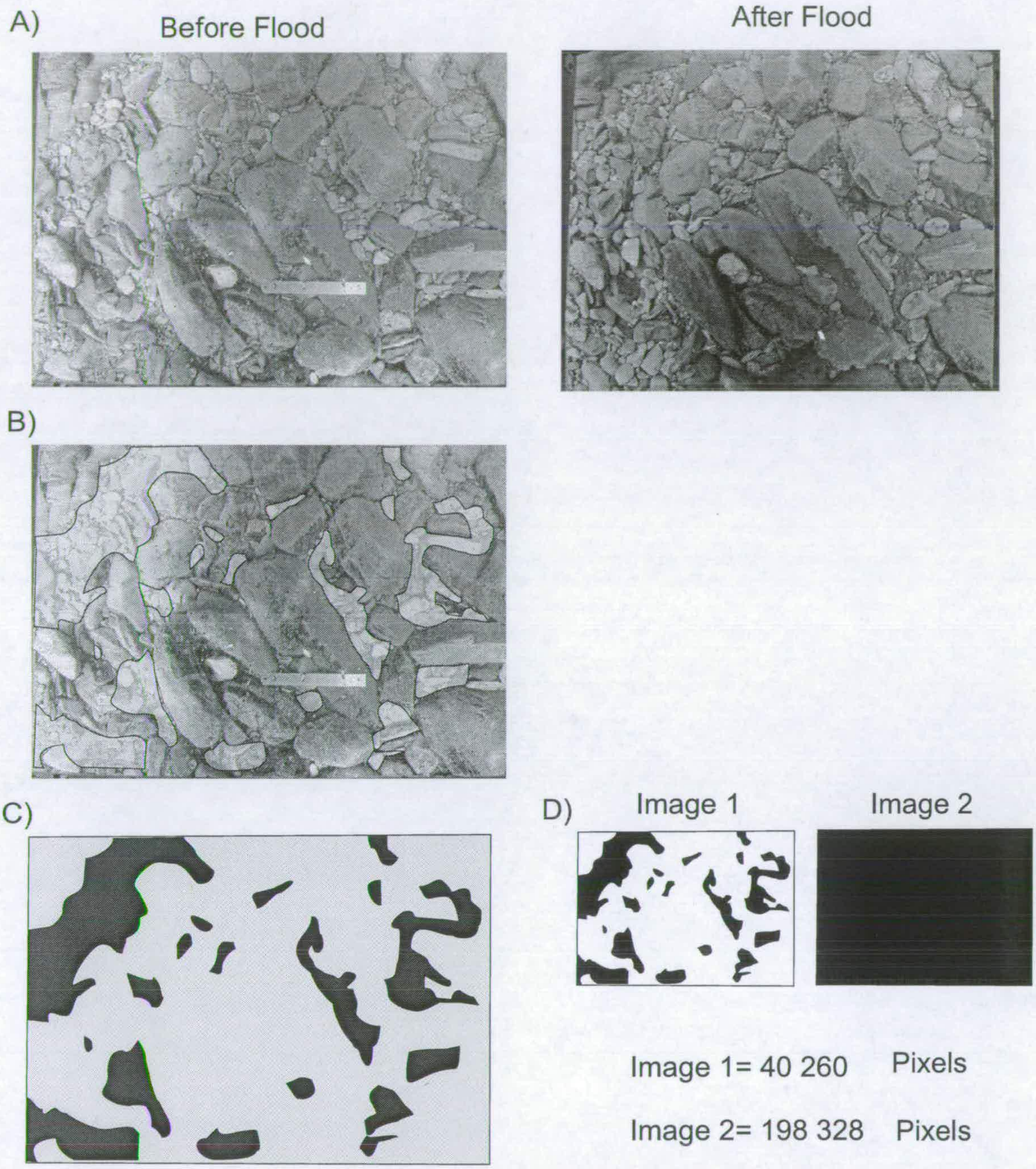


Image 1= 40 260 Pixels

Image 2= 198 328 Pixels

Percent area mobilised = (Image 1 / Image 2) * 100 = 20.3 %

Figure 4.3 Process of estimating percent area mobilised from photographs. A) Photographs of streambed taken before and after flooding. B) mobilsed particles identified and coloured grey. C) Image was transformed into shades of grey, dark grey indicates mobilised area. D) Image transferred to image processing package and number of pixels determined of mobilised area (Image 1) and total area of image (Image 2), allowing percent area mobilised to be calculated.

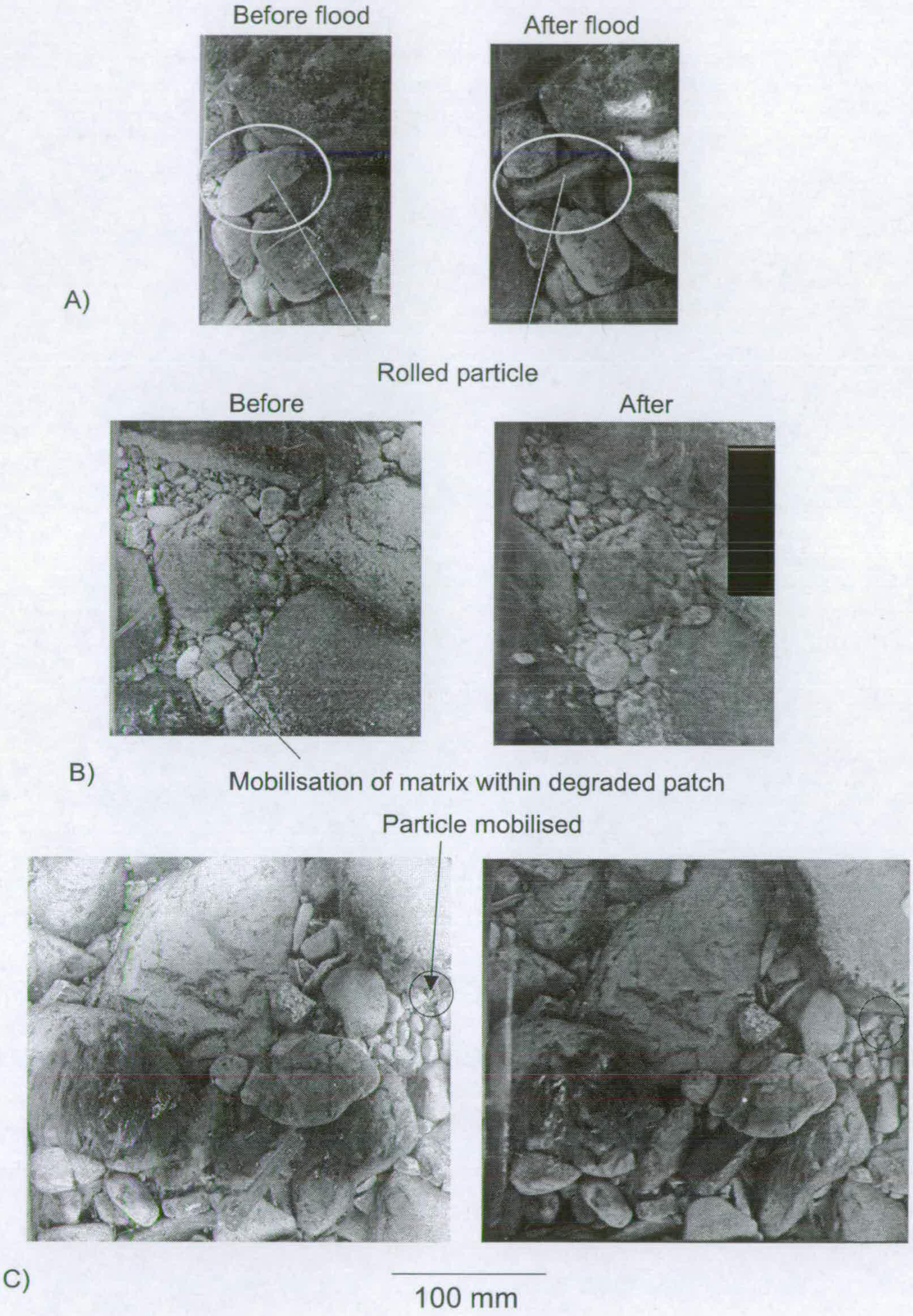


Figure 4.4 Illustrating: A) Rolled particle, still remaining in-situ, and thus not recorded as mobilised. B) Mobilisation of the matrix within a Degraded patch. C) The minimum particle size allowing for accurate analysis for mobilisation.

When no particles could be recognized from one period to the next, no estimates of particle movement was made, and the replicate removed from the analysis. Three scenarios could create this situation; scour and then fill, no scour but fill, and locational error (i.e. miss-read staff or stake location). Where only a portion of the patch had changed, it was possible to determine if it was a result of scour, fill or locational error, by using discolourations, crevices, and algal patches on large particles that had remained stable from one event to the other to determine any change in local level of the surrounding bed (see Figure 4.4). This was possible on almost every Degraded patch and the majority of Loose patches, allowing for some estimate of particle movement.

Using the same imaging process methods as described above (and in Figure 4.3), the percent area of small-scale pockets of fines within each Degraded patch, i.e. matrix, was also calculated.

4.23 Bedload Traps

Pit traps were installed in the channel bed to measure the total mass of bedload moved over a given event, thus providing gross yields rather than instantaneous transport rates (Figure 4.2b). Three traps were installed along a transect across the streambed at the downstream end of the study site. Each trap consisted of a 0.56 x 0.36 x 0.30 m wooden compartment sunk into the bed with the top flush with the surface. A slightly smaller, removable steel compartment fitted snuggly inside (vol = 0.044 m^3). The sediment caught in the traps could be easily emptied by removing the steel compartment and un-loading the sediment before replacing it in its original position. All particles removed from the traps were classified in the field into phi increments using a series of templates and sieves to a size fraction of 16 mm and weighed. The gravel fraction less than 16 mm was returned to the laboratory and dried in an oven at 60 c for 24 hours and then sieved and weighed at phi increments to 2.8 mm.

4.25 Predicting Particle Movement – Equations of Shear Stress

Estimates of particle movement were based on two equations, du Boys formula, based on the water depth / slope product, and the Karman-Prandel-Keulegan (KPK) equation based on velocity and relative roughness.

a) du Boys formula

Two estimates can be derived using du Boys formula, one based on the slope of the entire study site, and the other based only on the gradient of the bed between transverse step features. Du Boys formula assumes a steady uniform flow, which is rarely achieved in natural streams where flow energy is dissipated in jet-driven turbulence as plunging flow over the steps, rather than directed downstream along the channel bed (Chin, 2003). The gradient based only on the bed between the steps, i.e. tread gradient, likely provides a more realistic estimate of reach averaged shear stress acting to entrain particles. A gradient inclusive of steps however, i.e. complete study section, does not represent a true reflection of the energy available for particle entrainment (Zimmerman & Church, 2001). This gradient nevertheless is typically employed in most calculations, and will be used here to provide a direct comparison with the estimates provided by the tread gradient.

Study Section Gradient:

An estimate of mean bed shear stress can be obtained from du Boys formula;

$$\tau_0 = \gamma R_b S \qquad \text{Equation} \quad (4.2)$$

where , γ is fluid specific weight, S is the energy slope, taken as the slope of the water surface at peak discharge over the complete study site, and R_b is the hydraulic radius associated with that portion of the total fluid force carried by the bed (Einstein, 1942). Hydraulic radius is defined as;

$$R_b = w_s d/(2d+w_s) \qquad \text{Equation} \quad (4.3)$$

where, w_s is the water surface width and d is hydraulic mean depth. Stream wetted width and hydraulic mean depth were derived from channel cross sections at each gauge station for each peak discharge (e.g. Figure 4.5).

Tread Gradient Estimate:

In step / pool systems the pool gradient is considered a more realistic gradient for the calculation of the transport capacity of the stream (Zimmerman & Church 2001), as the pool gradient is the lowest gradient in the stream reach through which sediment is transported (Ashida *et al.*, 1981). While the study reach on the Talla is not characteristic of a step /pool system (see Chapter 3), the lowest average gradient within the reach, i.e. the tread between large steps, is used here as a better estimate of the reach averaged energy gradient along which sediment is transported. Because the necessary data to accurately estimate the water surface slope along such sections is not available, the channel bed gradient is used. This is considered as a good surrogate

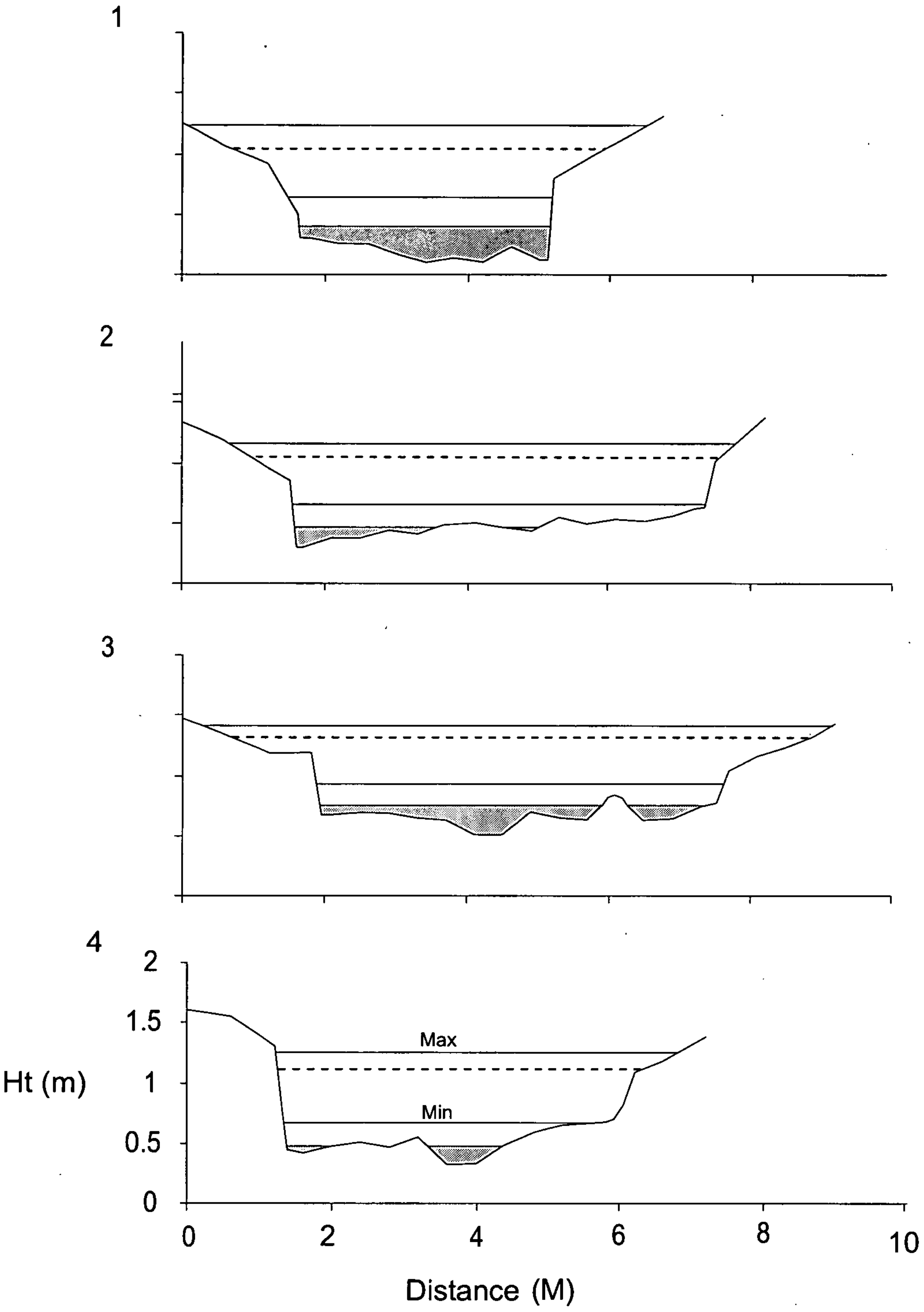


Figure 4.5 Flood heights, showing maximum and minimum ht recorded, and reach average bankfull discharge (dashed line) at gauges 1 to 4, Talla Water..Area shaded grey indicates summer base flow level.

(Chin, 1998). Indeed the largest difference between overall channel gradient and water surface slope at peak discharge in the study reach is only 0.003. Substituting, S_{pb}, the gradient between large steps averaged across all sections within the study reach, for S into equation 4.2, a more realistic estimate of reach averaged shear stress for particle entrainment is obtained.

b) Karman-Prandel-Keulegan (KPK) equation

Mean velocity just above the bed reflects the force balance between the potential energy gradient along the stream and the drag effects derived from the boundary. Flow resistance equations such as the commonly employed Karman-Prandel-Keulegan (KPK) equation expresses this relationship and can be used to derive estimates of mean bed shear stress during peak flows.

The KPK equation can be written as;

$$\mu / \mu^* = (1 / \kappa) \ln (11^* d / k_s) \qquad \text{Equation} \quad (4.4)$$

where μ is mean flow velocity, μ^* is shear velocity, d is flow depth, k_s is roughness length and κ is the von Karman constant (= 0.4). Shear velocity, μ^*, can be expressed as $\sqrt{(\tau / \rho)}$ where ρ is fluid density and τ is shear stress. Equation 4.4 can then be rewritten as;

$$\tau = \mu^2 \rho \kappa^2 / (\ln (11^* d / k_s))^2 \qquad \text{Equation} \quad (4.5)$$

For high roughness, as in that of steep streams it has been suggested that, $k_s \approx D_{84}$ (Wiberg and Smith, 1991, Lee and Ferguson, 2002). Here D_{84} for the degraded environment (313 mm) was used as it forms the majority of the bed surface and encompasses most size classes found in the stream (see Chapter 3). Mean flow velocity was back calculated from cross sectional area and discharge at peak flow, averaged across all gauges.

Equation 4.5, like that of equation 4.2, assumes a semi logarithmic velocity profile, as observed in steady, horizontally uniform flows over beds with small roughness elements, i.e. no large boulders or bed features. In steep mountain streams where roughness elements and bed features are comparatively large, the flow structure may depart significantly from semi-logarithmic estimates (Wohl & Thompson, 2000). Under such conditions Wiberg and Smith (1991) found that the KPK equation takes the form;

$$\tau = \mu^2 \rho \kappa^2 / (\ln (14.4 * d / k_s))^2 \qquad \text{Equation} \qquad (4.6)$$

The constant, 14.4, was derived empirically from steep mountain streams. While equation 4.6 may provide an estimate of shear stress for flows that depart from semi-logarithmic estimates, the generality of the empirical relations developed by Wiberg and Smith (1991) has yet to be fully accepted.

Given an estimate of mean bed shear stress, the largest grain size that can be mobilised by a particular flow may be estimated by using Shield's equation, which can be written as;

$$\tau = \theta g \rho_s D \qquad \text{Equation} \qquad (4.7)$$

where g is gravity, ρ_s is the submerged density of the grains (taken here to be 1650 kg m^{-3}), θ is Shield's number, and D is the grain diameter. Rearranging equation 4.7 we get;

$$D_{max} = \tau / \theta g \rho_s \qquad \text{Equation} \qquad (4.8)$$

where D_{max} is an estimate of the largest grain size that a high flow event is notionally capable of transporting. Equating this grain size with that of D_{90} of each patch type (Chapter 3) gives an estimate of the shear stress predicted to mobilise each patch type.

4.3 Results

4.31 Hydraulics

Discharge on the Talla Burn during the study period ranged from low base flows of approximately 0.21 m^3/s up to a peak discharge from the largest event of 10.16 m^3/s. Average bankfull discharge, that at which the ratio of channel width to channel depth is at a minimum (Wolman 1955), was estimated to be 7.35 m^3/s, breeching the banks at gauges 1 & 3, but contained with the channel at gauges 2 & 4 (Figure 4.5). The minimum level regarded as a 'flood' was well within the channel at all gauge stations. During minor events, the water surface generally extended from bank to bank and submerged small gravel bars that were emergent at low base flows (Figure 4.5). Water surface slope, as established from the gauge stations, remained relatively constant across a large range of flows (0.041 – 0.042) (Table 4.1), and was similar to the overall channel gradient (0.039).

Relative roughness (d/D_{50}) during most flood events was well above 1 over Degraded patches, approaching 6 during the largest events. Over the Structured patches, flow depth was restricted, with a maximum relative roughness (d/D_{50}) of between 1 and 2 during most peak discharges (Table 4.1). Relative roughness for the largest particle fractions within Structured patches, D_{90}, was under 1 for all but two events, the very largest boulders remained emergent. While velocity profiles were not measured, during the highest discharges, the flow structure over Degraded patches may have approached that of a semi-logarithmic profile. Over the step like structures however, where roughness length is approximately 1 or under, velocity

Table 4.1 Maximum discharge and basic hydraulic characteristics at peak flows, including relative roughnes Estimates (d/D_{50}, where d is depth averaged across all four staff gauges, and D_{50} is median particle size), for all sampling dates (bedload and photo-monitoring). Width, depth and area averaged across all four staff gauges.

Date	Q_{max} (m^3/s)	*Slope*	*Width* (*m*)	*Depth (d)* (*m*)	*Area* (m^2)	*Velocity* (*m/s*)	d/D_{50deg}	d/D_{50str}	d/D_{90str}
12-2-02	10.16	0.042	7.04	0.76	5.31	1.97	6.7	2.9	1.2
5-3-02	3.95	0.042	5.34	0.46	2.39	1.68	4.1	1.7	0.7
8-8-02	7.84	0.042	6.36	0.65	4.07	1.99	5.7	2.3	1.1
17-8-02	1.25	0.041	5.24	0.25	1.25	1.05	2.2	0.9	0.4
27-8-02	2.34	0.041	5.11	0.35	1.77	1.34	3.1	1.3	0.6
27-9-02	3.41	0.042	5.28	0.44	2.24	1.55	3.9	1.7	0.7
13-10-02	1.97	0.041	5.06	0.32	1.59	1.25	2.8	1.2	0.5
24-10-02	5.43	0.042	5.90	0.55	3.19	1.76	4.9	2.1	0.9
31-10-02	4.54	0.042	5.69	0.50	2.81	1.67	4.4	1.9	0.8
5-11-02	2.09	0.041	5.08	0.33	1.64	1.29	2.9	1.2	0.5
12-11-02	5.20	0.042	5.83	0.54	3.07	1.74	4.8	2.0	0.9
19-11-02	1.25	0.041	4.99	0.26	1.23	1.05	2.3	1.0	0.4
4-12-02	4.34	0.041	5.59	0.49	2.69	1.66	4.3	1.8	0.8
29-4-03	2.09	0.041	5.07	0.33	1.63	1.3	2.9	1.2	0.5
4-5-03	0.87	0.041	4.90	0.24	1.12	0.83	2.1	0.9	0.4
3-12-03	5.92	0.041	5.93	0.56	3.26	1.87	4.9	2.1	0.9

throughout the water column is likely to depart strongly from any semi-logarithmic estimate (e.g. see Wohl & Thompson, 2000). During higher flows, various hydraulic environments were observed around Structured patches, including plunging flow into downstream pools, tumbling flow over sequential boulders, and supercritical jet flow over the top of the step, or occasionally between two large boulders forming a chute.

4.32 Area Mobilised

The mean percent area mobilized of the three patch types varied considerably across each discharge event. The Structured patches remained stable during the study period, experiencing no particle mobilization (Table 4.2). In contrast, Loose patches experienced almost complete mobilization during the largest flood events, and Degraded patches an intermediate level, on average not exceeding 45 % (Table 4.2).

The Loose and Degraded patches showed different modes of particle mobilization. A breakpoint is suggested for the loose patches at a discharge ≈ 2 m^3/s. There was a rapid shift from almost zero mobilization to almost complete mobilization over a narrow band of discharge (Figure 4.6), suggesting a form of equal mobility transport (EMT). The mobilization of these patches represents the entrainment and transport of the finer particle fractions of the bed, phase I transport. For Degraded patches, % area mobilized increased relatively gradually with discharge (Figure 4.6), suggesting some form of size selective transport (SST). The potential for patch specific transport modes is reflected in the different frequency distributions of percent area mobilized for each patch environment. The Loose patches show a clear bi-modal distribution, suggesting a switch like behaviour from minimal to almost complete mobilization

Table 4.2 Mean percent area mobilized (Mean_{mob}) and standard error (SE) of Degraded and Loose patches for each flood event monitored. Also shown is the mean percent area of matrix (Mean_{mat}) within Degraded patches. Structured patches are not shown as no particles were mobilized during any flood event. NA – missing data.

Date sampled	*Maximum Discharge (m^3/s)*	*Replicate number*		**Patch type**					
				Degraded				*Loose*	
		Deg	Loose	Mean_{mob}	SE	Mean_{mat}	SE	Mean_{mob}	SE
5-3-02	3.95	30	15	18.26	2.96	19.93	2.76	86.22	7.30
8-8-02	7.84	26	14	43.74	5.45	12.36	1.84	NA	
17-8-02	1.25	25	14	7.27	1.97	17.32	2.69	18.8	10.1
27-8-02	2.34	19	10	14.49	2.78	11.2	1.52	62.9	12.6
27-9-02	3.41	19	9	22.34	5	12.68	2.44	86.52	7.79
13-10-02	1.97	17	10	5.57	1.83	12.11	2.85	1.23	0.842
24-10-02	5.43	21	10	41.97	5.99	14.20	2.45	77.2	11.5
5-11-02	4.54	19	10	20.22	5.65	11.66	2.68	NA	
19-11-02	5.20	19	10	35.75	5.10	18.43	1.98	93.68	2.91
13-4-03 to 29-4-03	2.09	18	10	11.23	2.6	16.17	2.08	80.3	10.5
30-9-03 to 3-12-03	5.92	19	10	40.46	6.24	16.08	1.57	99.6	0.209

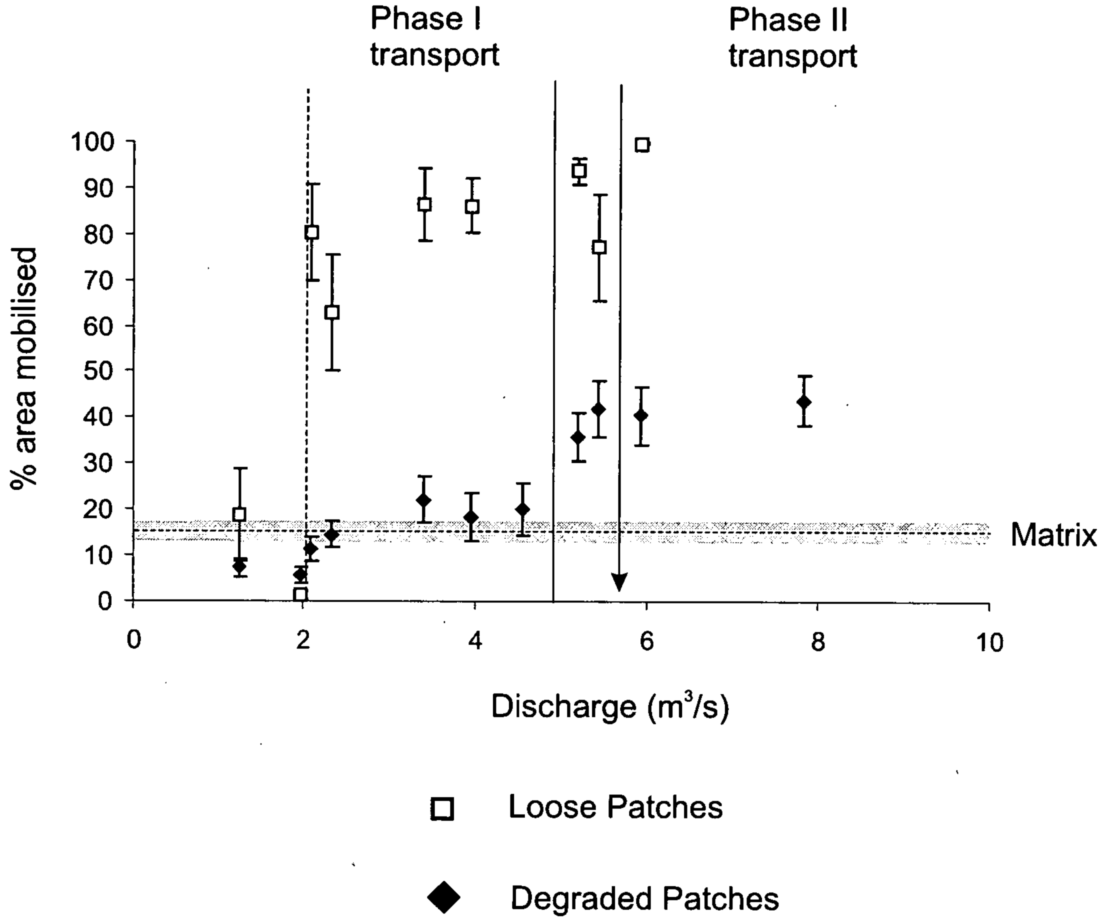


Figure 4.6 Relation between % area mobilised and discharge for Loose and Degraded patches. Structured patches are not shown as no particles were mobilised during the study period. Horizontal dashed line shows mean area of matrix within degraded patches, including 95% confidence interval, shown in grey. Solid vertical line at 5 m^3/s is a break point for the Degraded patches (point at which percent area mobilised is consistently above that of the matrix). Dashed vertical line indicates a breakpoint for the loose patches. Arrow indicates the breakpoint discharge as determined from the D_{90} bedload (see p. 119 and Figure 4.11 for explanation).

(Figure 4.7). In contrast the distribution of percent area mobilized of Degraded patches was unimodal, strongly skewed to the left, reflecting the generally low levels of mobilization.

Phase II transport, entrainment of coarse particles, is suggested at a discharge of approximately 5 m^3/s (Figure 4.6), corresponding to a breakpoint for the Degraded patches. Above 5 m^3/s there was a relatively rapid increase in mean percent area mobilized, to an area greater than that of the matrix. Visual inspection of the photographs confirms this breakpoint as the mobilisation of the larger particle fractions.

The complete mobilization of the matrix within Degraded patches occurred at a discharge similar to that of the breakpoint for the mobilization of Loose patches, suggesting that the matrix, along with the Loose patches contributed to phase I transport (Figure 4.6). A subsequent increase in discharge did not result in any considerable increase in percent area mobilised until the second breakpoint (phase II transport) was reached. This breakpoint (phase II transport) occurred at a discharge approximately 2.5 times greater than that of breakpoint one (phase I transport), corresponding to an increase in mean bed shear stress of approximately 1.5.

Relations between Transport Phases and Patch Characteristics

Degraded Patches:

During phase I transport, below the breakpoint threshold of 5 m^3/s, there was a significant relationship of area of matrix and % area mobilised (Table 4.3). An

Table 4.3 Summary statistics for regression analysis, percent area mobilized vs distance from thalweg, distance from bank and percent area of the matrix for Degraded patches, and distance from thalweg and size of patch for Loose patches (see Figures 5.8 & 5.9). Note, the matrix refers to small pockets of fine particles within Degraded Patches (see Fig 3.4, p. 71).

Degraded				
Phase I	**Df**	**MS**	**F**	**P**
Distance from thalweg	1,42	202.54	2.11	0.154
Distance from bank	1,30	31.9	0.29	0.592
Percent area of matrix	1,66	1467.2	9.24	**0.003**
Phase II				
Distance from thalweg	1,17	3143.9	15.05	**0.001**
Distance from bank	1,13	894.8	1.55	0.235
Percent area of matrix	1,47	901.1	2.36	0.131
Loose				
Phase I				
Distance from thalweg	1,18	203.2	0.38	0.544
Size of patch	1,15	0.1	0.00	0.990

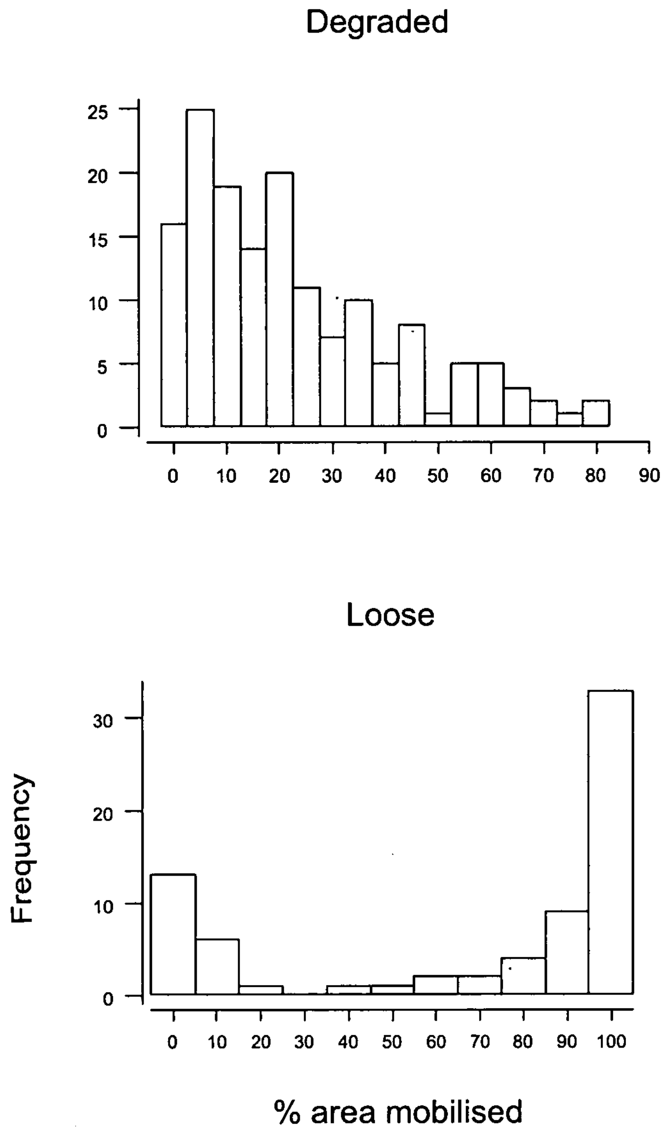


Figure 4.7 Frequency distributions of % area mobilised for loose and Degraded patches across all flood events monitored on Talla Water and Cramalt Burn.

increase in the area of matrix resulted in an associated increase in the percent area mobilized (Figure 4.8, Table 4.3). Position within the channel, as defined by both distance from the bank and distance from the thalweg, did not appear to influence the area mobilized in Degraded patches.

During phase II transport, above the breakpoint threshold of 5 m^3/s, the area of matrix was not associated with the percent area mobilized (Figure 4.8). Position within the channel though, as defined by distance from the thalweg, was negatively associated with area mobilised (Table 4.3, Figure 4.8). The thalweg is the thread of flow within the channel that is the deepest and fastest flowing and, thus, it generally refers to the area that experiences the highest shear stress.

Loose Patches:

During phase I transport, most Loose patches were almost completely mobilized. Consequently, no variable, i.e. size or distance from thalweg, showed any trends (e.g. Figure 4.9a), although there was a tendency for lateral loose patches associated with an obstruction to experience slightly less mobilization (Figure 4.9b). Indeed patches above the breakpoint threshold with little mobilization (< 5%) were associated with a lateral obstruction. Those patches associated with pool units tended to experience the greatest amount of mobilization, indeed greater than 95% in every patch.

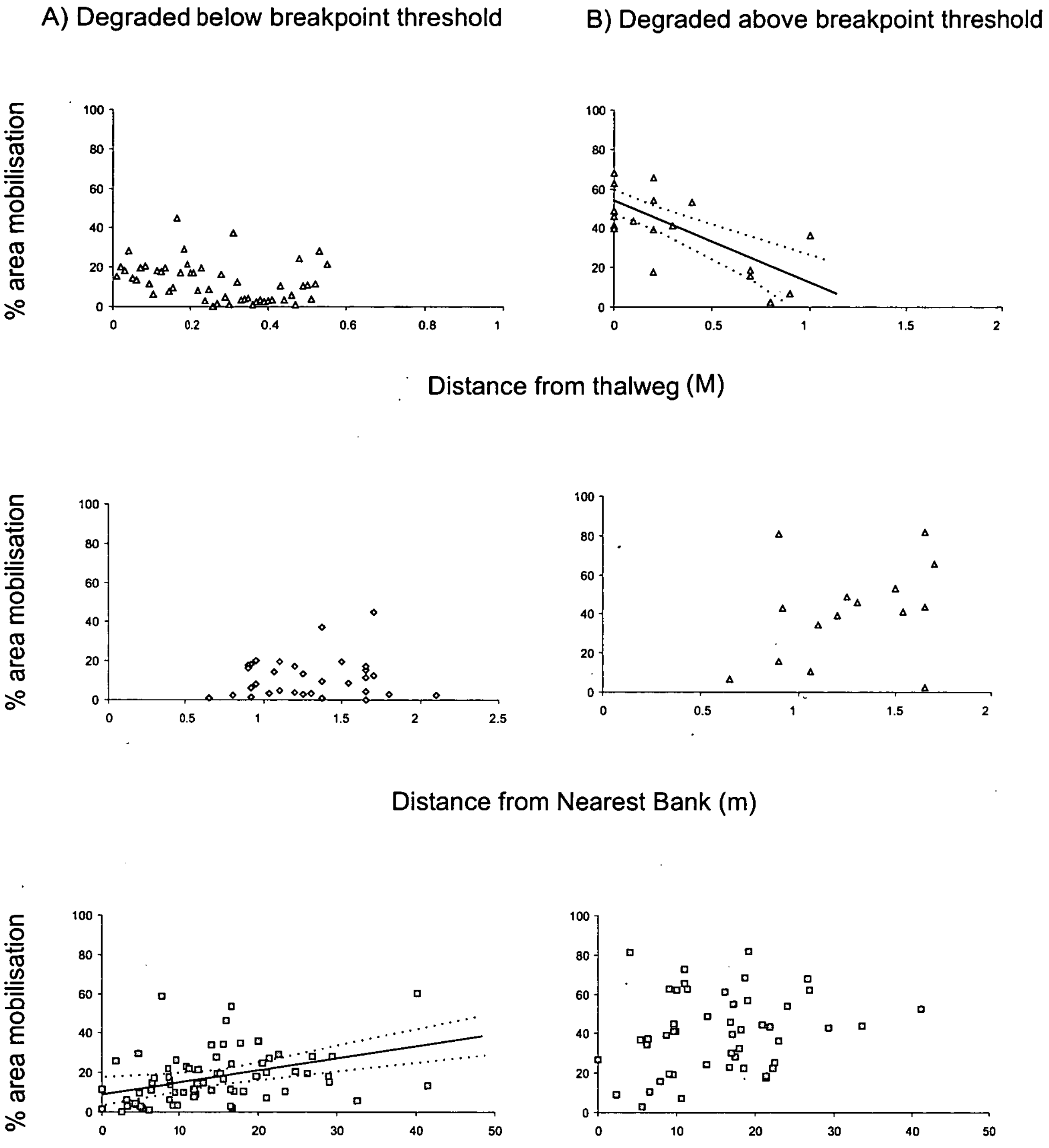


Figure 4.8 Relation between % area mobilised with distance from thalweg, distance from bank, and % area matrix for degraded patches from floods below and above the breakpoint threshold (5 m^3/s). Significant linear regressions are shown as a solid line (line of best fit). 95 % confidence interval is shown as dotted lines. Details of the analysis is shown in Table 4.3.

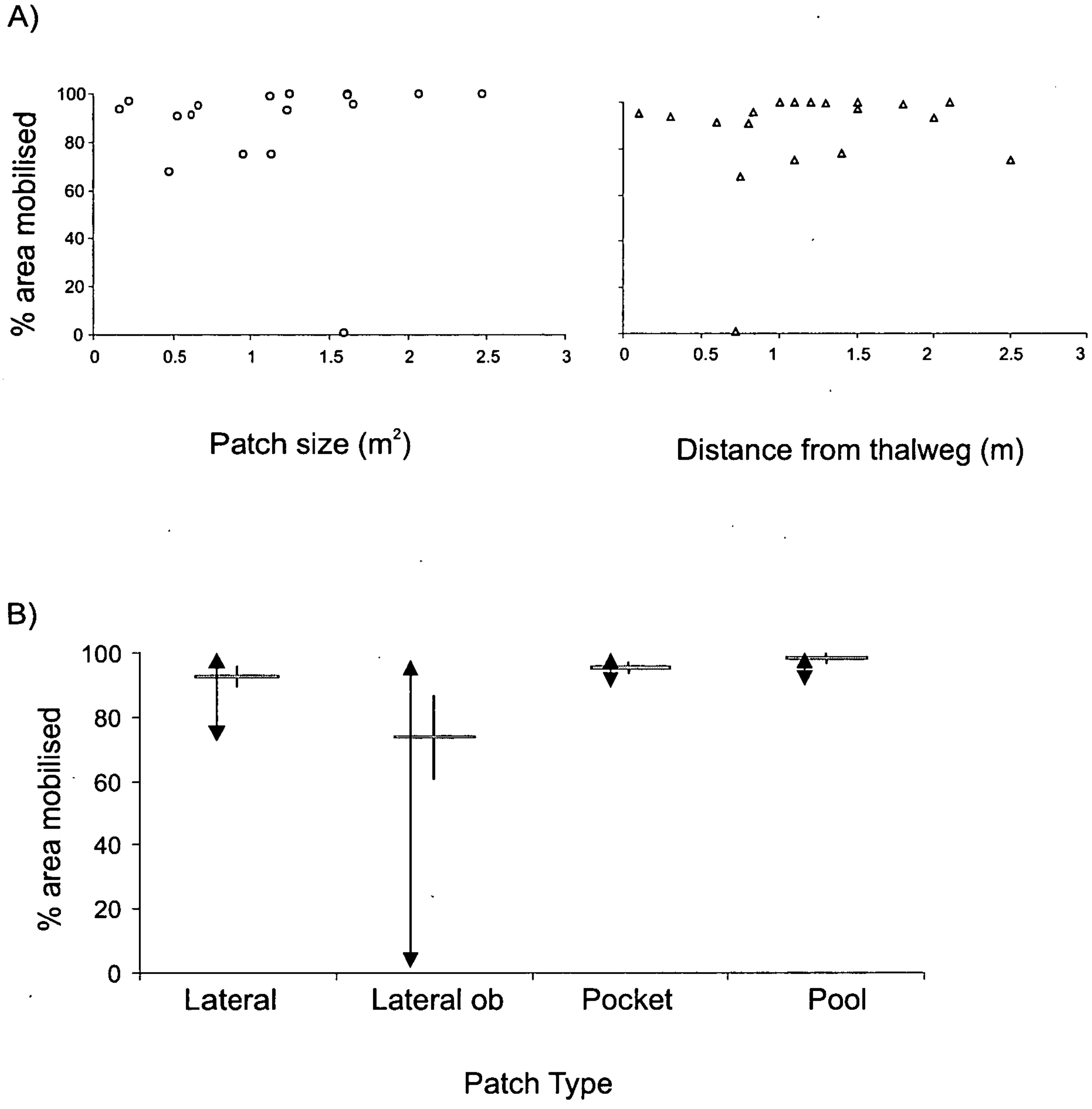


Figure 4.9 A) Relation of percent area mobilised with size of Loose patch and distance of patch from thalweg during phase I transport B) Average percent area mobilised (horizontal bars) for different Loose patch types, from flood events of magnitude greater than breakpoint point threshold (2 m^3/s). Vertical bars show one standard error, arrows show range of maximum and minimum.

4.33 Bedload

In most studies bedload is used to define transport phase (e.g. Warburton, 1992, Lenz *et al.*, 2004 , Ryan *et al.*, 2002). A change in phase is indicated by a change in the character of the load, which is typically expressed as a break in slope of the relation between bedload distribution parameter, e.g. D_{50} or D_{max}, and discharge.

The bedload was collected on eleven occasions during the study period, from floods ranging in peak discharge from 0.87 to 10.16 m^3/s. Very little sediment (< 0.2 kg) was collected below approximately 1.3 m^3/s, and overfilling occurred at discharges greater than 2.1 m^3/s. During the study period a total of 465 kg of sediment was sampled from the traps, encompassing particle sizes < 2 mm to 162 mm. The bedload yield from four flood events can be related directly to a single peak discharge (Table 4.4). On seven occasions however, the total bedload yield in the traps incorporated load from at least two or more flood events, a problem arising because of access difficulties between events (Table 4.4). For such data, the total yield was associated with the largest discharge in all analyses.

Most large flood events (those producing more than 5 kg of sediment in total across all traps) yielded similar uni-modal grain size distributions, with a characteristic dip in the 16 mm size category (Figure 4.10). The two largest events however, were slightly skewed, with an increase in the distribution of the largest size fractions (128 mm and 181 mm), corresponding to fractions approximately equivalent to D_{50} of the Degraded patches. The difference between yields below and above 3-4 m^3/s was marked (Table 4.4), suggesting a large shift in the availability of sediment.

Table 4.4 Characteristics of the total bedload yield (across all traps) on each sampling occasion from the Talla Water. '*' bedload sampled from single flood events (total yield corresponds directly with peak discharge). All other total yields encorporate load from two or more flood events. For such cases the peak discharge shown is that of the largest event. Bedload distributions for all events larger than 5kg are shown in Figure 4.10, page 118. '#' missing data.

Date sampled	*Peak Discharge (m^3/s)*	*Total yield (kg)*	*D_{50} (mm)*	*D_{84} (mm)*	*D_{90} (mm)*	*Largest Particle (mm)*	*$D_{90loose}$ / $D_{90bedload}$*	*D_{90deg} / $D_{90bedload}$*
12-2-02	10.16	108.3	31	98	137	#	0.6	2.89
13-10-02	1.97	1.9	6.8	17.1	22	35	3.7	18
24-10-02	5.43	77.9 *	19	48.4	64.8	99	1.28	6.11
31-10-02	4.54	63.0	15	42	50	97	1.66	7.92
5-11-02	2.09	2.2	9.1	41	50	52	1.66	7.92
12-11-02	5.20	66.5	20.1	54	71	148	1.17	5.58
19-11-02	1.25	0.2 *	12	20	22.3	24	3.72	17.76
3-12-02	4.34	63.5	19.1	58	80	108	1.04	4.95
29-4-03	2.09	2.6 *	21.1	38	41.2	56	2.01	9.61
4-5-03	0.87	0.3	14.3	19.8	21	22.2	3.95	18.86
3-12-03	5.92	79.1 *	23.4	92	126	162	0.66	3.14

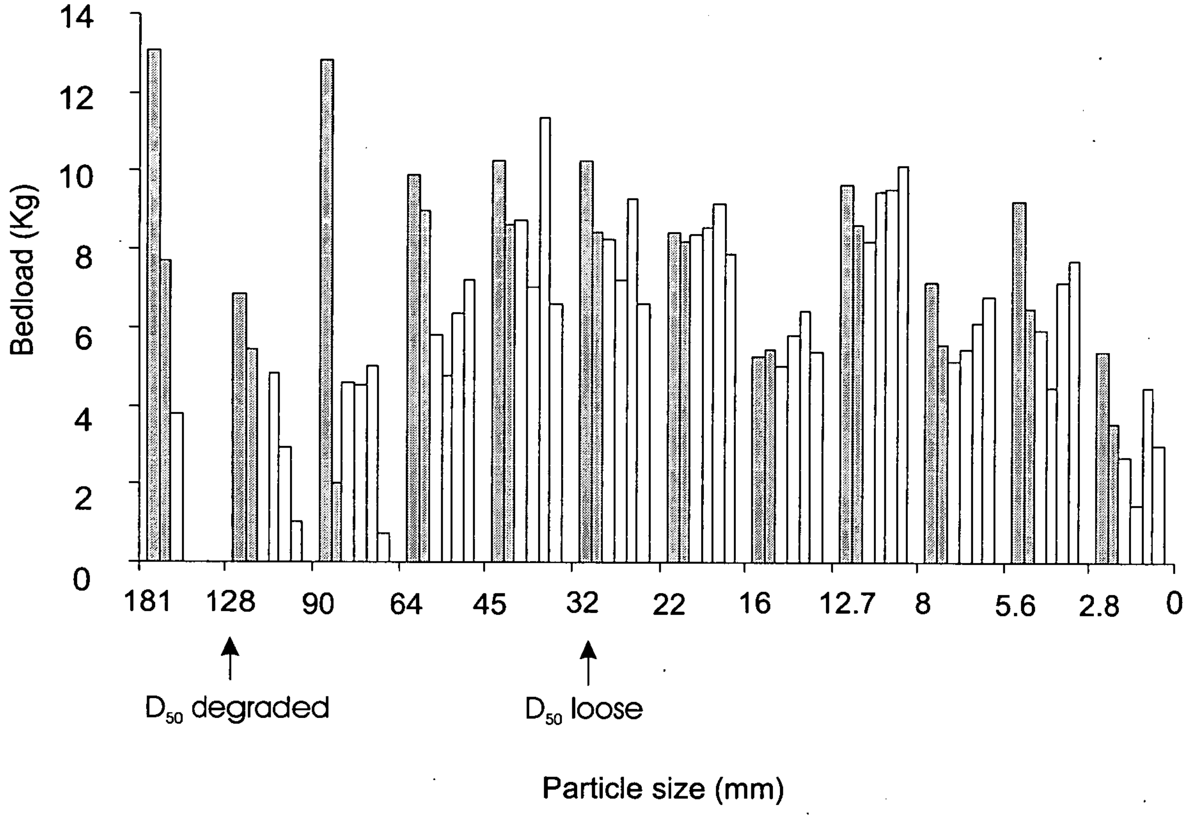


Figure 4.10 Bedload distribution for events that yielded greater than 5 kg. Distributions represented by shaded columns are from the two largest events (see Table 4.4 for bedload characteristics and peak discharge estimates) and show an increase towards the larger particle fraction and slight bi-modality. Note, each bar for a particular particle size represents an individual event.

Transport Phase:

D_{90} bedload shows a large increase in particle size at a discharge of approximately 5.4 m^3/s, mobilising particles significantly larger than those defining the both the matrix and Loose patches (Figure 4.11). A breakpoint from phase I to phase II transport is suggested at this discharge, whereby there is a shift in transport from fine gravels to one of larger particles, > 120 mm. This likely corresponds to the initial break up of the coarse surface layer of Degraded patches (no Structured patches were disturbed during the study period).

Over half the floods analysed occurred at a discharge over 2.1 m^3/s, completely filling the traps. This possibly led to an over representation of fine particles and under representation of coarser particles (e.g. D_{90}) in the load. The breakpoint indicated by D_{90} bedload is therefore likely to be conservative. Indeed, the shift from phase I to phase II transport, as indicated from the photographic data, is at a slightly lower discharge (Figure 4.6), corresponding to approximately 75 per cent of bankfull discharge (7.25 m^3/s).

A comparison of the patch surface grain size distribution and the bedload grain size distribution can be made by forming the ratio of $D_{90surface}$ to $D_{90bedload}$. A ratio of 1 indicates that complete mobilisation occurred, that is every grain size on the surface of the bed is found within the bedload. Ratios are well above one for the Degraded patches for all events (Table 4.4), indicating that complete mobilisation of the Degraded environment was not achieved. This is certainly supported by the photographic data, which shows that even during the largest events, on average only

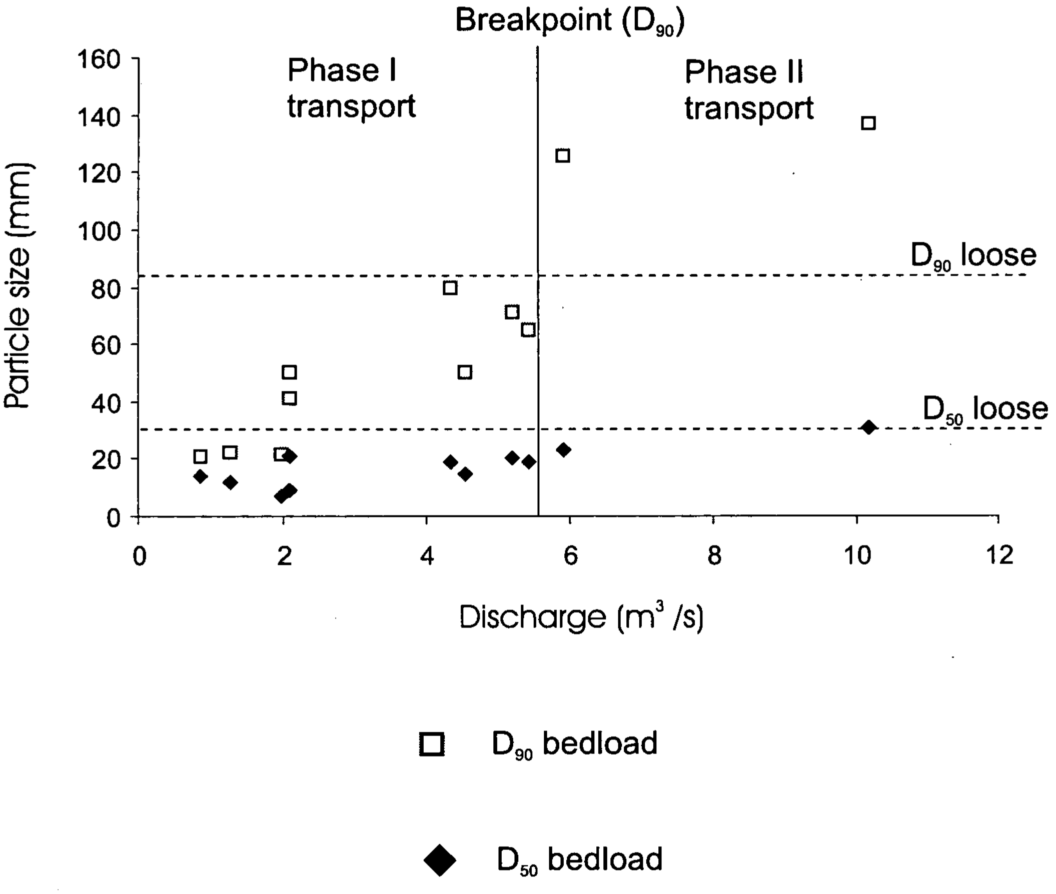


Figure 4.11 Relation between bedload particle size and discharge. Breakpoint is indicated by a break in slope in the D_{90} fraction (see text for explanation). Horizontal lines show D_{50} surface and D_{90} surface of the loose patches.

45 % of the area was mobilised. In comparison, for the two largest events, $D_{90bedload}$ is much greater than the D_{90} of Loose patches (Table 4.4), again supporting that indicated by the photographic data, i.e. near complete mobilisation of this patch type.

4.34 Predicting Particle Movement – bedload equations

The estimated bed shear stresses for peak flows are variable (Table 4.5). Calculations based on du Boys formula (equation 4.2) whole study site gradient, predict shear stresses of the order of 10^2 N/m^2, approaching 330 N/m^2 for the largest flood recorded. Estimates using the tread gradient (0.021) were 50 % lower. The relative estimates of the KPK equation however varied with discharge. During high discharge events, KPK estimates were an order magnitude smaller than those derived from du Boys formula using the tread gradient, and considerably smaller than those derived from the whole study site gradient (Table 4.5). During lower flows KPK and du Boys estimates were reasonably close, particularly that derived using the tread gradient (Table 4.5).

Given an estimate of the mean bed shear stress, the largest particle that can be entrained and transported by a particular flow was estimated from Shield's equation (equation 4.7). Critical Shield's number, θ, is generally accepted to be 0.045 for a loose heterogeneous sediment mix (Komar, 1987), however, where particles are constrained through imbrication, embeddedness, or hidden in the wake of other particles, critical Shield's number can approach 0.1 (Church *et al.*, 1998). Given a particular Shield's number, the largest particle the stream could transport during a flood varies by a factor of approximately 5 between estimates based on, du Boys

Table 4.5 Estimates of shear stress (N/m^2) derived from; du Boys equation $\tau_o = \gamma R_b S$ (see text for terms), where $\tau_{b\,uni}$ is that derived from mean energy slope and $\tau_{b\,btw}$ derived from mean channel slope between steps, and KPK resistance equation where KPK_{log} assumes a logarithmic profile and $KPK_{non\text{-}log}$ assumes non-logarithmic profile.

		Du Boys (N/m^2)		**KPK (N/m^2)**	
Date	*Peak Discharge (m^3/s)*	$\tau_{b\,uni}$	$\tau_{b\,btw}$	KPK_{log}	$KPK_{non\text{-}log}$
12-2-02	10.16	321.59	161.94	71.93	61.44
5-3-02	3.95	201.89	101.66	72.89	60.59
8-8-02	7.84	277.67	139.83	80.91	68.59
17-8-02	1.25	114.63	59.13	46.69	36.96
27-8-02	2.34	154.61	79.76	57.02	46.50
27-9-02	3.41	194.04	97.71	64.07	53.11
13-10-02	1.97	142.67	73.60	53.36	43.21
24-10-02	5.43	238.51	120.11	70.63	59.35
31-10-02	4.54	218.80	110.18	67.89	56.73
5-11-02	2.09	146.69	75.67	55.41	44.98
12-11-02	5.20	234.41	118.04	69.90	58.67
19-11-02	1.25	118.26	61.01	45.04	35.80
4-12-02	4.34	209.39	108.02	68.04	56.78
29-4-03	2.09	146.65	75.65	56.27	45.68
4-5-03	0.87	109.79	56.63	30.30	23.89
3-12-03	5.92	236.58	122.04	78.77	66.26

formula and the KPK equation (Table 4.6). Estimates based on whole study site slope (du Boys formula, equation 4.2) predict boulders up to 0.44 m ($\theta - 0.045$) may be mobilized during the largest flood events monitored, well above D_{50} Structured (0.26 m). Indeed, given higher Shield's numbers, ≈ 0.1, which would generally correspond to the structurally restrained environment more typical of the Structured patches (Church *et al.*, 1998), equation 4.2 still predicts the mobilization of boulders during the larger flood events, approaching D_{50} Structured (Table 4.6). No boulders of this size were mobilised and caught in the traps during these events (Table 4.4). Whole study site slope (du Boys formula, equation 4.2), even with a Shield's number appropriate for a highly structured environment ($\theta \approx 0.1$), continually over estimates the maximum particle size mobilized (compare lines with D_{90} bedload in Figure 4.12). Calculations based on the lower tread gradients (equation 4.2), similarly over estimates particle size at low Shield's numbers (0.045), however for a highly restrained environment (i.e. high Shield's numbers, $\theta - 0.1$), this equation does perform well, showing reasonable correspondence with the D_{90} bedload, particularly for flood events below the breakpoint threshold (< 5 m^3/s, phase I transport) (Figure 4.12). For flood events above the breakpoint threshold (> 5 m^3/s, phase II transport), a Shield's number of 0.06 corresponds more closely to the maximum particle size mobilized. This shift likely reflects a change in transport process.

The velocity-based estimates of shear stress (KPK equation) predict the mobilization of smaller particle sizes, generally within an order of magnitude of those based on tread gradient, equation 4.2 (Table 4.6). At low discharges estimates from these

Table 4.6 Maximum grain size mobilised (m) as derived from Shield's equation and shear stress estimates derived from; du Boys slope / depth equation based on mean energy slope (*Uniform*) and mean between step channel gradient (*Btw step*), and KPK resistance equation, where KPK *log* assumes a logarithmic velocity profile and KPK *non log* assumes a non-logarithmic velocity profile. Critical Shield's numbers (θ) 0.045, 0.06 and 0.1 have been used in the calculation of maximum grain size mobilised. The critical Shield's number is a dimensionless number that reflects the force balance between that promoting entrainment and that resisting entrainment (the higher the number the greater the particle restraint).

		du Boys Equation						**KPK Equation**					
		Uniform			*Btw step*			*KPK log*			KPK non log		
Date	**PeakQ (m^3/s)**	**θ 0.045**	**θ 0.06**	**θ 0.1**	**θ 0.045**	**θ 0.06**	**θ 0.1**	**θ 0.045**	**θ 0.06**	**θ 0.1**	**θ 0.045**	**θ 0.06**	**θ 0.1**
12-2-02	10.16	0.442	0.331	0.199	0.223	0.167	0.100	0.099	0.074	0.044	0.084	0.063	0.037
5-3-02	3.95	0.277	0.208	0.124	0.140	0.104	0.062	0.100	0.075	0.045	0.083	0.062	0.037
8-8-02	7.84	0.382	0.286	0.171	0.192	0.144	0.086	0.111	0.083	0.050	0.094	0.070	0.042
17-8-02	1.25	0.158	0.118	0.070	0.081	0.060	0.036	0.064	0.048	0.028	0.050	0.038	0.022
27-8-02	2.34	0.212	0.159	0.095	0.109	0.082	0.049	0.078	0.058	0.035	0.064	0.047	0.028
27-9-02	3.41	0.267	0.2	0.12	0.134	0.100	0.060	0.088	0.066	0.039	0.073	0.054	0.032
13-10-02	1.97	0.196	0.147	0.088	0.101	0.075	0.045	0.073	0.055	0.033	0.059	0.044	0.026
24-10-02	5.43	0.328	0.245	0.147	0.165	0.123	0.074	0.097	0.072	0.043	0.081	0.061	0.036
31-10-02	4.54	0.301	0.225	0.135	0.151	0.113	0.068	0.093	0.069	0.041	0.078	0.058	0.035
5-11-02	2.09	0.202	0.151	0.090	0.104	0.077	0.046	0.076	0.057	0.034	0.061	0.046	0.027
12-11-02	5.20	0.322	0.241	0.144	0.162	0.121	0.073	0.096	0.072	0.043	0.081	0.060	0.036
19-11-02	1.25	0.162	0.121	0.073	0.084	0.062	0.037	0.061	0.046	0.027	0.049	0.037	0.022
4-12-02	4.34	0.288	0.215	0.129	0.148	0.111	0.066	0.093	0.070	0.042	0.078	0.058	0.035
29-4-03	2.09	0.202	0.151	0.090	0.103	0.078	0.046	0.077	0.058	0.034	0.063	0.047	0.028
4-5-03	0.87	0.151	0.113	0.067	0.078	0.058	0.035	0.041	0.031	0.018	0.033	0.024	0.014
3-12-03	5.92	0.325	0.243	0.146	0.168	0.125	0.075	0.108	0.081	0.048	0.091	0.068	0.040

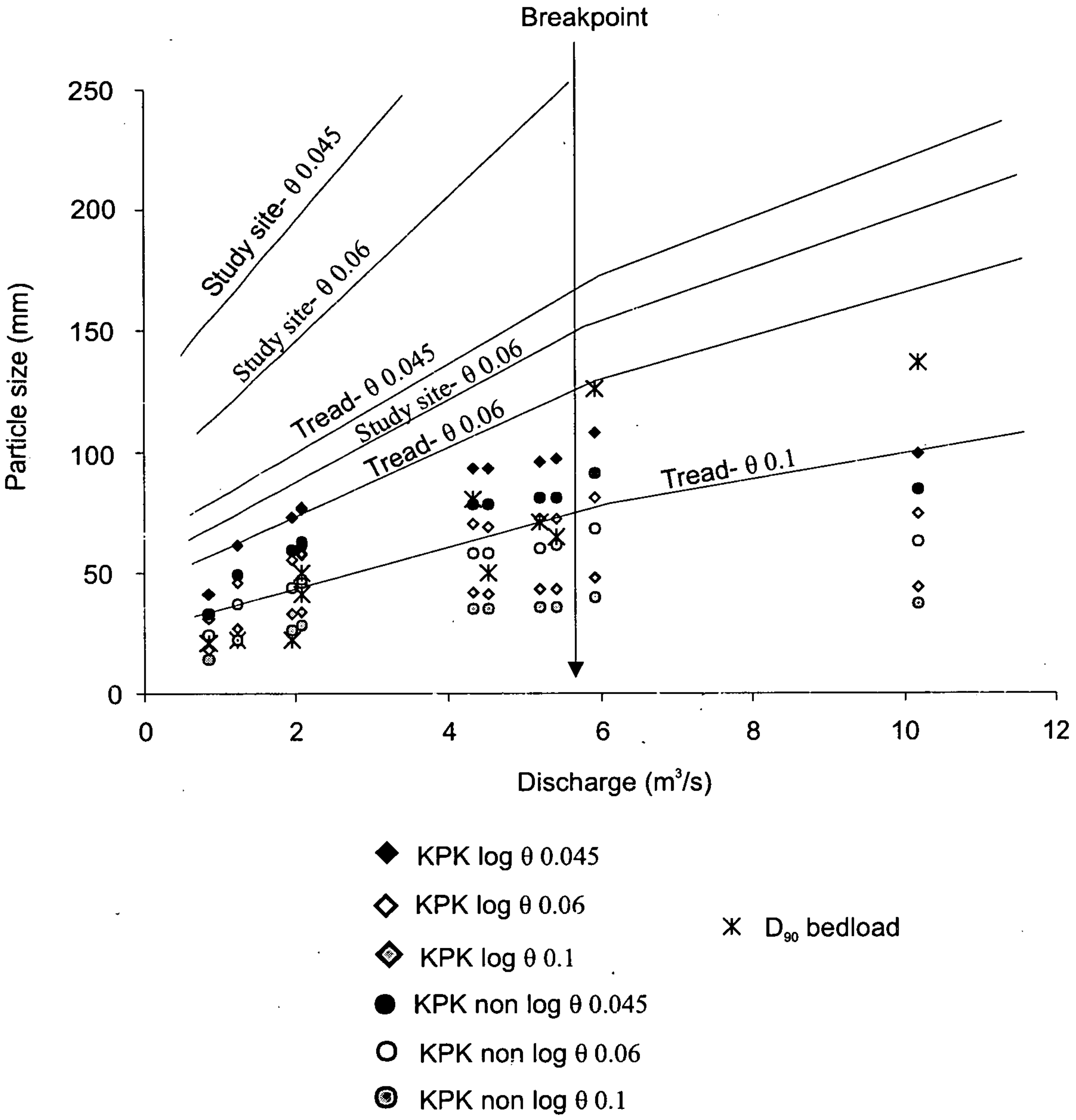


Figure 4.12 Relation between discharge and max particle size estimated from Shields equation (equ 4.7), using different Shields numbers. Lines : estimates from du Boys formula, slope defined as 'study site' is whole study site slope, and 'tread' is average channel slope between steps. Symbols: estimates from KPK resistance equation based on mean velocity. D_{90} bedload is also plotted. Arrow indicates the threshold breakpoint for phase II transport.

equations were similar to observed D_{90} bedload, but tend to underestimate particle size above the breakpoint (phase II transport) (Figure 4.12).

4.4 Discussion

Two phases of bedload transport were identified during the study, phases I and II. Phase III transport did not occur. No Structured patches were mobilised. Indeed, the largest particle sampled from the bedload traps was 162 mm, considerably smaller than D_{90} of both Degraded and Structured. The estimated return interval for the largest flood during the study period was 3.5 years, well under that estimated for the mobilsation of large bedform features such as transverse steps (Grant *et al.*, 1990, etc). Indeed, Lenzi *et al.*, (2004) reported only the beginning of phase III transport in a small steep stream from a flood event with a return interval of approximately 53 years.

The results from this study suggest that transport phases I and II can be related to particular sediment sources. The onset of phase I transport primarily occurred at a discharge equating to the mobilisation of Loose patches. This is in accordance with that described by Ryan *et al.*, (2002), Paola & Seal (1995) and Lisle (1995); as the remobilisation of finer materials deposited from previous transport events in pools and low flow zones. The matrix within Degraded patches however, was also mobilised at a similar discharge as that of the Loose patches, contributing to phase I transport. This is consistent with Larronne *et al.*, (2000), who observed that small pockets of interstitial fines, similar to the matrix in this study, contributed to the first phase of sediment transport in their gravel bed stream. During phase I transport the percent area mobilised of streambed within Degraded patches was influenced by the areal extent of the matrix, as one would expect. The onset of mobilisation of Degraded patches however, i.e. mobilisation of the matrix, may be influenced by the size and interconnectedness of the small pocket voids that make up the matrix (Larronne *et al.*, 2000).

Phase II transport was associated with the break up and mobilisation of coarse particles from Degraded patches. This corresponded to the mobilisation of particles larger than D_{50}, which is in agreement with the general definition of phase II transport, as defined by Jackson and Beschta (1982), and that observed by Warburton (1992). Degraded patches therefore contributed to both transport phases. The beginning of phase II transport is thought to occur at or near bankfull discharge (Parker *et al.*, 1982, Andrews, 1984). The onset of phase II transport in this study occurred at a discharge approximately 70 % of bankfull. This is consistent with that observed by Ryan *et al.*, (2002), who found that the shift from phase I to phase II transport occurred at a discharge of approximately 80% of bankfull. They found that this relationship was surprisingly consistent across a range of channels with varied slope, size, roughness and bed topography.

While the onset of phase I transport generally corresponded to the near complete mobilisation of both the Loose patches and Degraded matrix, the onset of phase II transport only corresponded to the partial breakup and mobilisation of the coarse layer of the Degraded patches. It is likely that the breakpoint for phase II transport in this study represents the threshold for the mobilisation of readily available coarse particles on the surface of Degraded patches, thus representing the initial stages of phase II transport. The force required to mobilize individual particles can vary dramatically, dependent upon factors such as embeddedness and packing (Downes *et al.*, 1997), factors not taken into account by the patch classification scheme (see Chapters Two & Three). During phase II transport however, variation in percent area mobilised of Degraded patches can partly be ascribed to the distance from the thalweg. This is likely related to shear stress, as the thalweg typically represents the line of greatest flow and depth. The complete mobilization of Degraded patches however, may only occur at very high discharges. Indeed, only during an extremely large flood (return interval of 53 years) did Lenzi *et al.*, (2004) observe a well developed phase II, and the beginning of phase III transport.

The onset of phase I transport in the Talla likely results in the dislodgement of invertebrates from Loose patches and the matrix within Degraded patches. Using area estimates of Loose patches and the matrix (Chapter 3), and the bedload data, one could conceivably provide a lower limit of area disturbed (i.e. area where invertebrates have been dislodged) during a discharge that results in phase I transport. That is, bedload data may provide a surrogate measure for area of stream mobilised. Depending on the response of the invertebrate assemblages to increased shear stress and or abrasion (i.e. whether or not dislodgement occurs), this area may not change significantly until the onset of phase II transport. During flooding however, fine sediment can also be derived from sources outside of the stream bed, e.g. banks. The initial onset of phase I transport, as indicated by fines caught in the bedload traps, may therefore, not necessarily relate directly to the mobilisation of the streambed, i.e. represent the passing of fine particles over a stable bed (Ashworth & Ferguson, 1989). In such systems bedload data may not provide a good surrogate measure for area mobilised. The incomplete mobilisation of Degraded patches during phase II transport precludes any estimation of area disturbed using surrogate measures such as discharge or bedload.

Predicting Particle Mobilisation using Bedload Formula:

Bedload formulae, e.g. Shield's equation, have been widely used to quantify the extent of particle movement in streams as a measure of disturbance (e.g. Cobb *et al.*, 1992, Death & Winterbourn, 1995, Scarsbrook, 1995, Muotka & Virtanen, 1995). These equations however, generally do not yield good estimates of initial motion (Gomez & Church, 1989), particularly in steep streams where large clasts disrupt the velocity profile (Wiberg & Smith, 1987). Relationships between discharge and bedload in steep streams are also non-linear, where distinct breakpoints occur with a change in transport phase (e.g. Ryan *et al.*, 2002), as noted in this study.

In an attempt however, to determine what forces act on the bed of a steep boulder-cascade channel, Zimmerman & Church (2001) recently demonstrated that flow competence estimated from Shield's' equation based on a pool gradient, as apposed to the more commonly employed channel gradient, corresponded reasonably well with the likely mobilisation of deposits of fine loose particles (i.e. Loose patches, phase I transport). In this study, as also noted by Zimmerman & Church (2001), Shield's' equation based on the lower gradient (i.e. tread) produced more realistic estimates of particle mobilisation. These estimates however still tended to overestimate the size of the particle mobilised, although better estimates were obtained with a critical Shield's number of 0.06 and 0.1, which is consistent with the notion that the particles within high gradient streams are typically constrained (Church *et al.*, 1998). Estimates based on the KPK equation, with a Shield's number of 0.06 and 0.1, tended to perform slightly better in predicting the maximum particle size mobilised during phase I transport. This equation incorporates channel resistance (i.e. loss of energy over steps and large boulders) and thus may better represent the energy available for particle transport. However, this equaiotn underestimated particle size during phase II transport. The KPK equation cannot be regarded as conservative due to the power relation between τ, and velocity and depth. It is thus sensitive to slight changes in these variables. As mean velocity was derived from estimates of discharge based on the stage discharge-rating curve, confidence in this variable is lower at high discharge estimates, above those actually recorded in the field. The discrepancy between observed and predicted particle size may also be partly due to the inefficiency of the pit traps at high discharges. The larger particle fraction was most probably under-sampled during large flood events due to the overfilling of the traps, thus underestimating the maximum particle size mobilised.

Bedload formulas, such as Shield's equation, represent a very attractive tool for predicting particle movement in streams. Estimates can be derived easily and quickly from a number of sites. However, as demonstrated in this brief analysis they are very sensitive to estimates of mean bed shear stress, which can vary widely depending on the equation used. This brief analysis also demonstrated the sensitivity of Shield's number. Shield's number is a dimensionless number that reflects the force required to entrain particles, and is generally accepted to be 0.045 for a loose heterogeneous sediment (Komar, 1987), and closer to 0.1 for a tightly packed structured bed (Church *et al.*, 1998), i.e. the Talla. The size of particle predicted in the Talla varied by a factor of 2, depending on the Shield's number used. Major advances are still required in bedload formulae if we wish to predict the mobilisation of particles, or indeed transport phase, in steep streams (Martin, 2003). There are however, as noted by Gomez & Church (1989) more bedload formula in existence than there are reliable data to test them.

Patch Classification – Summary of Physical Attributes:

Particle movement in steep streams is a complex phenomenon (Church, 1985). Nevertheless, I identified two distinct transport phases that corresponded largely to patch type.Loose patches, characterised by fine well-sorted particles, are mobilised at relatively low discharges, the same as the matrix within Degraded patches, and both contribute to phase I transport. Phase II transport, mobilisation of the coarse particles within Degraded patches, occurred at a discharge approximately 2.5 times that for phase I transport. Phase III transport, mobilisation of Structured patches, presumably occurs at considerably higher discharges. The general relationships of particle movement with discharge for each patch type, in particular the relative breakpoints in transport phase, are therefore not unlike those in Figure 2.4a. The invertebrate assemblage on each patch type is described in the following chapter.

Chapter Five Invertebrate - Patch Association

5.1 Introduction

The objectives of this chapter are 1) to evaluate the relevance of the patch classification scheme for invertebrates in steep streams, ie are there patch – specific invertebrate assemblages, and 2) characterise the distribution pattern of invertebrates across patch types at base flow, against which post flood samples can be compared (see Chapter Seven).

Species richness and abundance of invertebrates in streams typically vary over several spatial scales (Downes *et al.*, 1993, Li *et al.*, 2001) and are influenced by a variety of ecological processes, such as biotic interactions (e.g. McAuliffe, 1984), dispersal and settlement (e.g. Fonseca & Hart, 2001), resource exploitation (e.g. Negishi, 2002), and physiological requirements (e.g. Feldmeth, 1970). Substratum heterogeneity and flow are major environmental gradients in streams and influence many of these processes (Minshall, 1984, Statzner *et al.*, 1988, Hart & Finelli, 1999). Flow for example may affect a predator's ability to successfully capture and handle prey (Hansen *et al.*, 1991), affect the filtering rates of net spinning Hydropsychidae (Georgian & Thorp, 1992), or alter grazing efficiency in herbivores (DeNicola & McIntire, 1991). It may also affect the distance an organism disperses in the drift (Elliott, 1971) and settlement habitat (Fonseca & Hart, 2001). Substrate size, particle imbrication and embededness can potentially influence availability of refugia (Downes *et al.*, 1998), resource availability, i.e. higher algal biomass on larger stable particles (e.g. Biggs *et al.*, 1999), and even the ability to burrow and access hyporheic substrates (Eriksen, 1964). Spatial variation in faunal abundance is therefore often associated with similar variation in physical variables, in particular substrate and flow (e.g. Downes *et al.*, 1993, Rempel *et al.*, 2001, Rabeni *et al.*, 2002). If ecological processes in steep streams vary in response to these variables, which largely define the classification scheme outlined in Chapter Two, then we may expect to see different assemblages on each patch type.

The strong coupling between flow and substrate in steep streams, i.e. large particles associated with high flow, small particles with low flow (Grant *et al.*, 1990), can make it difficult to identify casual pathways underlying relationships between benthic invertebrate distribution and the physical environment (Hart & Finelli, 1999). It nonetheless may act to strengthen faunal associations with particular substrate / flow conditions, (e.g. Structured patches – large particles and high flow, Loose patches – fine particles and low flow). The occurrence of suspension feeders on large particles (e.g. Malas & Wallace, 1977) for example, may in part be due to the fact that these substrates are typically associated with high velocity and provide for high filtering rates (Georgian & Thorp, 1992). Similarly, some detritivores are more common in sediments with high concentrations of organic particulate matter (Minshall, 1984), which in turn are more likely to occur in habitats of low flow.

The patch types Structured and Loose typify the strong coupling between flow and substrate that is evident in steep streams, characterizing erosional and depositional environments respectively. These environments typically harbour different assemblages, (e.g. Scarsbrook & Townsend, 1993, Lancaster & Hildrew, 1993b).

The inherent stability of structured bedform features (Brayshaw *et al.*, 1983, Grant *et al.*, 1990, Church *et al.*, 1998) provides a stable platform for high algal and bryophyte biomass (Biggs *et al.*, 1999) and the retention of organic matter (Negishi, 2002), and may further contribute to differences in assemble between Structured and Loose patches. Structured bedform features offer a more diverse habitat and richer food resources than surrounding areas of the bed (Biggs *et al.*, 1997).

The unique substrate and flow conditions of each patch type may provide for distinct invertebrate assemblages. If indeed the physical and biotic factors that govern invertebrate distributions in steep streams are strongly influenced by the suite of substrate and flow conditions that characterize each patch type, then a high portion of the spatial variance in the invertebrate community in such streams may be explained by the patch classification. The aim of this chapter is to characterize the invertebrate assemblages on Structured, Loose and Degraded patches, addressing the specific hypotheses: 1) there is no difference in the relative and absolute abundance of invertebrates and taxon richness across patch types. 2) The pattern of assemblage composition among patch types is the same between streams. I expected high taxon richness and density, and an assemblage containing filter feeders and sedentary species on Structured patches, whereas on Loose patches, with reduced bryophyte biomass, low organic matter retention, and the potential for frequently mobilized particles, I expected low taxon richness and density, and an assemblage dominated by one or two highly mobile species, such as *Baetis*. Degraded patches largely represent an intermediate environment between Loose and Structured (Chapter Three), as characterized by substrate and flow. If indeed these two parameters act to influence invertebrate distribution at the scale of the patch classification, then I expect Degraded patches to harbour an assemblage intermediate between those of Loose and Structured.

5.2 Methods

5.21 Invertebrate Sampling

Invertebrates were collected from the Talla Water and Cramalt Burn at base flow condition during early winter (November) and spring (April). A detailed description of the streams and the study site is provided in Chapter Three. Samples were collected bi-annually (early winter and spring); on five occasions from the Talla Water (from November 2001 to December 2003), and on two occasions from the Cramalt Burn (in April 2002 and November 2002). I was unable to collect samples in April 01 due to access problems caused by the foot and mouth outbreak. The early winter sample from the Talla in 2003 was taken in September rather than November. This was necessary to ensure a base line sample before the first major flood event in the last year of study (see Chapter Seven).

A standard Surber sampler (0.09 m^2, 250 μm mesh) was used to take samples from all loose patches. A modified drift net, mouth dimensions of 0.6 m wide and 0.25 m high (250 μm mesh), was used on Degraded and Structured patches, where particle sizes were too large for the standard Surber. The large drift net had moveable side arms, 0.6 m long, hinged at the mouth of the net, enabling invertebrates to be sampled from a wide range in particle sizes, including boulders, whilst also ensuring all invertebrates are funnelled into the net. The distance between the ends of the arms was measured after each sample to estimate the total area enclosed. The minimum area sampled using this sampler was 0.30 m^2, and occurred when the arms were parallel. The largest area sampled was 0.46 m^2. Substrate within the sample area was disturbed to the depth of the largest particle, rolling over all particles four times. Samples were preserved in the field in 80% alcohol. On each sampling occasion, between five and ten samples were taken from replicate patches of each type in each stream. All samples were taken from different patches, one sample per patch, except those from Degraded. This was unavoidable due to the extensive nature of the Degraded patches (i.e. many patches were > 20 m^2). However, to ensure independence between seasons (factor analysed), all samples taken over the course of a year were taken from different patches. The following year, if patches were re-sampled, then the sample was taken from a different area.

Samples were rinsed through a set of sieves (5 mm, 1 mm and 250 μm) in the laboratory. All invertebrates caught on each sieve were picked out and placed into separate vials. Where possible, all invertebrates were identified to species level. All CPOM and moss was removed from the surface of the sieves, dried separately for 24 hours at 80 °C and then weighed.

5.22 Environmental Parameters

Three spot measurements of depth and current velocity were obtained from each sample patch. Near-bed velocity was measured using an electromagnetic flow meter, Valeport Model 801 fitted with a single axis flat sensor. A 15 s average was used for each reading, at a frequency of 2 Hz. Depth was measured to the nearest centimetre at each velocity point. After invertebrate sampling, all surface particles within the sample area were removed from the streambed. Particles from Degraded and Structured patches were sorted into phi classes on the stream bank using a template and ruler, weighed and counted. Particle sizes below 64 mm were ignored, as they could not be collected with precision given the flow rates encountered and obscured vision. Surface particles from Loose patches were collected and bagged in the field, and dried and sorted into phi classes and weighed in the laboratory. These patches commonly occurred in shallow slow flow environments, so fine gravel particles coulde be sampled. A list of all environmental variables is shown in Table 5.1.

5.23 Data Analysis

Standardising Invertebrate Abundance and Species Richness

Invertebrate Abundance:

Abundance generally increases with total area sampled. So samples collected using samplers of different sizes required standardization. Abundance is commonly standardized in relation to sample area (i.e. density), in which area is typically the product of sampler length and width. Where particle sizes differ markedly between sample units however, e.g. Structured and Loose patches (see Chapter 3), some error maybe introduced as the three dimensional nature of the environment is not accounted for.

A simple calculation demonstrates the potential for bias in area estimates where particle sizes differ. The average D_{50} of the Loose, Degraded and Structured patches

Table 5.1 Description of environmental variables for each patch type

Variable	Description	Units
CPOM	Dried weight of sample	g /m ^{2}
Moss	Dried weight of sample	g /m ^{2}
Depth	Average of 3 readings	m
Depth variance	Variance / Mean	
Velocity	Average of 3 readings	m/s
Velocity variance	Variance / Mean	
Max Velocity	Maximum velocity	m/s
Dmax	Maximum particle size	m
D_{50}	Median particle size	m

(Chapter 3), and the surface area of a sphere, $4\pi R^2$, where R is radius, were used to test for potential bias between samples from different patch types (see Table 5.2 for calculations). Estimates of density as calculated from sample area (sampler length * width) and those accounting for the difference in average particle size, provided the same relative comparisons between Loose, Degraded and Structured patches, with no bias regarding particle size (Table 5.2). When the interstitial area between particles is also accounted for, total surficial area (interstitial and particle size accounted), is approximately twice that of the sample area (Table 5.2). This simple calculation demonstrates that by standardizing abundance by sample area, very little bias is produced between samples taken from areas with different particle sizes. For all analyses therefore, density was standardized by sample area (sampler length * width). However, one must consider that density estimates may be overestimated. A note of caution though, this simple calculation does not take into account degree of particle imbrication or embeddedness.

Taxon Richness:

Taxon richness was standardized per unit count, i.e. as the number of taxa per count. This is sensitive to the relative abundance of individuals and is a good indicator of taxon richness for comparative purposes (Larsen and Herlihy, 1998), especially where standarisation by sample area may be difficult.

Rarefaction is a statistical method for estimating the number of species expected E(Sn) per unit count (n) (Hurlbert, 1971);

$$E(S_n) = \sum_{i=1}^{s}\left\{1-\frac{\binom{N-n_i}{n}}{\binom{N}{n}}\right\} \qquad \text{Equation (5.1)}$$

Where $\binom{N}{n}$ is the number of combinations of n individuals chosen from a set of N individuals, i.e.,

$$\binom{N}{n}=\frac{N!}{n!(N-n)!}$$

Rarefaction curves were produced for each patch from each stream. For each sample, Es was estimated for a range in unit count (n) from 10 to 2800 (just under the largest sample) using the program Mathematica v5.0. Calculations were halted when n was greater than the sample total. Rarefaction tends to overestimate the expected number of species per unit count. The degree to which it does though depends in part on the relative abundance of individual species (Simberloff, 1972). As species abundance from all three patches was highly skewed (i.e. abundance dominated by a few taxa) comparisons between patch types should be valid.

Analysis:

Total invertebrate density and taxon richness were compared among patch type and sampling date using a two way ANOVA (factors: date and patch, both fixed) using the General Linear Model procedure in the statistical package SPSS 9. Homogeneity

Table 5.2 Summary of calculations to correct for different particle sizes between patch types. Area 1 is the areal sample area (sampler length * width). Area 2 is standardized by particle size. For purpose of calculation particles are assumed to be abutting one another with no imbrication, and buried within the substrate so that half of the sphere only is available for colonization. Hence in the calculation for Area 2, the factor A is divided by 2. Area 3 incorporates the area of the interstitial spaces between the spheres $= 1 - (B * 2\pi R)$, where R is sphere radius. D_{50} of each patch type is obtained from Chapter 3, see Table 3.1, page 68.

Patch Type	D_{50} (mm)	A = Surface area of D_{50} (m^2)	B = # of D_{50} particles per m2	Area 1 = 1 (m^2)	Area 2 = (A*B)/2 (m^2)	Interstitial space $= 1 - (B * \pi D_{50})$	Area 3 = Area 2 + Interstitial space
Loose	29	0.00264	1190.25	1	1.571	0.609	2.18
Degraded	113	0.04011	77.44	1	1.548	0.609	2.157
Structured	265	0.22061	14.21	1	1.563	0.609	2.172

of variance was tested using Levens test, and the Anderson-Darling Normality test was used to test deviation from normality. Taxon richness data did not require transformation, but density was log (x + 1) transformed, to satisfy assumptions of homogeneity of variance and normality. The same univariate analyses were carried out on the density of each common taxon (i.e., > 5 % of the total).

Species and Sample Associations

Species associations with patch type were examined using a multidimensional scaling technique (SSH – Semi Strong Hybrid multidimensional scaling) using the program PATN (Belbin, 1991). Multidimensional scaling is a technique whereby the original species composition data is replaced by a matrix of dissimilarity values, from which the ordination diagram is obtained. The 'hybrid' approach (Faith *et al.*, 1987) accounts for the fact that the relationship between the dissimilarity matrix and inter-object distance is typically non-linear for large dissimilarities, those at the ends of long ecological gradients, and linear for small dissimilarities. This is achieved by combining two matrices, one accounting for the non-linear relationships and the other accounting for the linear relationships, in a manner that minimizes overall stress, the measure of agreement between matrix and inter-object distance. The overall effect is to reduce the effect of arching which is common in some ordination methods. SSH also permits flexibility in choice of dissimilarity index. For all analyses, the Bray-Curtis index of dissimilarity was used because it is considered to be robust for ecological data, while also permitting further analysis directly on the matrix scores (Faith *et al.*, 1987). This is discussed in more detail later.

Species that represented < 0.05 % of the total number of individuals were considered to be rare and were eliminated from all analyses to help reduce 'noise' (*sensu* Gauch, 1982) and aid interpretation of results. Species abundances were also log $(x + 1)$ transformed prior to analysis to prevent high values unduly influencing results. For all ordinations, three dimensions (axes) were used. The stress function, a measure of how well the distance in the ordination space corresponds to the dissimilarity values, was below 0.15 for all ordinations, a value recognized as an upper limit for caution (Belbin, 1991). Principal axis correlation (PCC) in PATN was used to examine the association of species with the ordination plot and each patch type. PCC is essentially a multiple-linear regression program designed to see how well a set of attributes, in this case species, can be fitted to the ordination, by finding the location of the best fitted vector in ordination space. The significance of the correlation was determined by running 1000 Monte-Carlo randomizations of the original ordination (MCAO procedure in PATN), and fitting each attribute (species) to each randomization. Significance was corrected for the total number of contrasts (species) made using the Bonferroni technique. The same procedure was used to find the location of the best fitted vector for each environmental variable in ordination space, thus allowing a comparison of species and environmental gradients in relation to patch type.

The ordination diagrams from SSH provide a visual documentary of assemblage variation between the patch types and associations with environmental gradients (after PCC). Samples closer together in ordination space are more similar. All analyses were undertaken using quantitative data, so variations in abundance, rank order and the presence and absence of taxa between samples can all influence the distance between sample points in ordination space. The ordination however, only represents a qualitative analysis in two dimensions (axes). Variation in patch assemblage along the third dimension (axis) is not shown. A quantitative estimate of the variation between samples that accounts for all dimensions can be obtained by computing the average Bray-Curtis dissimilarity scores between samples. The dissimilarity scores can be obtained directly from the dissimilarity matrix that is used to produce the ordination.

A quantitative estimate of the difference in invertebrate assemblage between patch types was therefore obtained by averaging the dissimilarity scores between all sample pair combinations from different patch types. This was used to provide a comparative measure of assemblage difference between patch types, across streams and season. The larger the average score the more dissimilar the patch types. Average dissimilarity between sample pairs within each group can also be used to provide a measure of assemblage variation within each patch type. Again the larger the score the greater the variation.

Partitioning of Variance

Multivariate (partitioning community variance):

To partition out the variation in species assemblages ascribed to stream, patch type, and environment (velocity, depth, CPOM, moss, substrate) I used a form of canonical correspondence analysis (CCA) in CANOCO 4.5 (ter Braak & Smilauer, 2002). This allowed me to quantify what proportion of variance in the invertebrate assemblage could be attributed to environmental variables, patch type, and stream. Decomposition of the variance was achieved by performing a series of partial CCAs, in which a CCA is computed after removing, by multiple linear regression, the effects of a known variable or group of variables, referred to as covariables. This procedure was introduced in ecology by Borchard *et al.* (1992) to decompose the variance explained by environmental as opposed to spatial variables, and has since been applied to other ecological problems (e.g. Robertson *et al.* 1997). The data set in this analysis was constructed from the Cramalt and Talla, permitting a decomposition of the spatial variance (stream and patch), from environmental variance (velocity, substrate, and depth parameters, CPOM, moss,) in the species assemblages.

Univariate (partitioning individual species variance):

For abundant species (> 5% of the total) an analysis of variance model (ANOVA) was used to decompose the variance in data of individual species density, total invertebrate density and taxon richness ascribed to stream, patch type, and sample. Each data set, Cramalt and Talla combined, was fitted to a two way mixed factorial model using the General Linear Model procedures in the statistical package SPSS 9. The model incorporated factors, stream and patch type, as fixed. The variance components were calculated using type III expected mean square following Quinn & Keough (2002). All data were log (x+1) transformed and homogeneity of variance tested using Levens test. The Anderson-Darling test was used to test deviation from normality. After transformations, assumptions of homogeneity of variance and normality were met.

Environmental Variables

To compare environmental variables between patch types, sampling date and stream, a three way factorial ANOVA using the General Linear Model procedures in the statistical package SPSS 9 was used. All data was log (x+1) transformed. After transformations, assumptions of homogeneity of variance and normality were met.

Stream as a Fixed Factor

Ideally, the factor 'stream' would be a random factor, but I specified it in all ANOVA as a fixed variable. When sample sizes are different, as they were here, there is no reliable method for estimating the variance components of random factors (Quinn & Keough, 2002). For consistency this was maintained across all ANOVAs. While it does not inhibit comparisons between the Talla and Cramalt, it does limit the ability to generalize to steep headwater streams.

5.3 Results

5.31 Environmental Variables

Dry weight of CPOM and moss was significantly higher on Structured patches in both Cramalt and Talla (Tables 5.3 & 5.4). CPOM and moss also varied between streams, influenced largely by relatively low values in the Structured patches of the Cramalt compared with those of the Talla (Tables 5.3 & 5.4). Loose patches had the least CPOM and no moss cover in both streams. Substrate size, as defined by both D_{max} and D_{50}, also varied significantly between patch types (Tables 5.3 & 5.4). There was a strong correspondence between the particle size distribution of each patch type, as characterized in Chapter Three, and that from invertebrate samples (Figure 5.1). Only substrates with particularly large boulders, >600 mm, were avoided.

All velocity parameters (average, max, variance scaled, min) differed significantly between patch types (Tables 5.3 & 5.4). In both streams, the Loose patches had the lowest velocity, averaging 0.21 m/s and 0.27 m/s in the Talla and Cramalt respectively (Tables 5.3 & 5.4). The Structured patches had the highest velocity in the Talla (average & max), approaching 1.5 m/s on top of some steps, although in the Cramalt velocity was slightly higher over Degraded patches (Tables 5.3 & 5.4). Variation in velocity was greatest on the Structured patches, reflecting the high velocity on top and low velocity commonly recorded immediately downstream (Tables 5.3 & 5.4). Indeed, negative velocity (flow back towards the step) was recorded downstream from several Structured patches in both streams (see Chapter Six for a detailed characterization of the typical velocity structure over a step).

Table 5.3 Summary statistics of environmental variables for each patch type in the Cramalt and Talla. Depth variance (Depth var) and velocity variance (Vel var) have been scaled by the mean. See Table 5.4 for ANOVA summary statistics.

Talla		**Cpom (g)**	**Moss (g)**	**Depth (m)**	**Depth var**	**Vel (m/s)**	**Vel var**	**Max vel (m/s)**	**Min vel (m/s)**	**D_{max} (mm)**	**D_{50} (mm)**
Structured	Mean	2.63	1.87	0.13	0.018	0.44	0.32	0.73	0.10	335.35	271.32
	SE	0.26	0.4	0.01	0.003	0.04	0.07	0.06	0.02	21	24
Degraded	Mean	1.00	0.32	0.21	0.009	0.30	0.08	0.42	0.17	246.7	143.34
	SE	0.15	0.3	0.01	0.002	0.03	0.03	0.06	0.01	22	23
Loose	Mean	0.47	0	0.13	0.009	0.21	0.03	0.26	0.16	79.18	38.43
	SE	0.04	0	0.02	0.003	0.05	0.05	0.08	0.01	18	15
Cramalt											
Structured	Mean	1.37	0.34	0.09	0.021	0.34	0.13	0.53	0.14	339.21	264.07
	SE	0.40	0.09	0.01	0.003	0.03	0.02	0.05	0.02	27	23
Degraded	Mean	1.08	0.18	0.16	0.003	0.39	0.08	0.54	0.23	243.05	137.48
	SE	0.31	0.06	0.01	0.003	0.03	0.02	0.05	0.02	27	21
Loose	Mean	0.82	0	0.17	0.002	0.27	0.03	0.33	0.20	70.45	38.74
	SE	0.10	0	0.01	0.003	0.04	0.02	0.05	0.01	32	24

Table 5.4 Summary statistics for ANOVA of environmental data. See Table 5.3 for values.

	Df	MS	F	P
CPOM				
Stream	1	14.48	16.5	**0.000**
Season	1	0.00	0.00	0.968
Patch	2	5.44	6.21	**0.004**
Stream*season	1	0.00	0.00	0.977
Stream*patch	2	4.06	4.63	**0.014**
Season*patch	2	0.46	0.53	0.594
Error	57	0.87		
Moss				
Stream	1	0.42	8.65	**0.005**
Season	1	0.37	7.60	**0.008**
Patch	2	0.80	16.5	**0.000**
Stream*season	1	0.02	0.57	0.455
Stream*patch	2	0.14	3.07	0.054
Season*patch	2	0.12	2.57	0.085
Error	57	0.04		
Depth				
Stream	1	0.00	4.45	**0.039**
Season	1	0.00	0.00	0.945
Patch	2	0.05	25.9	**0.000**
Stream*season	1	0.00	3.50	0.067
Stream*patch	2	0.01	8.28	**0.001**
Season*patch	2	0.00	1.50	0.233
Error	57	0.00		
Depth variance				
Stream	1	0.00	1.27	0.264
Season	1	0.00	1.57	0.215
Patch	2	0.00	17.7	**0.000**
stream*season	1	0.00	0.12	0.730
stream*patch	2	0.00	0.76	0.471
season*patch	2	0.00	0.26	0.769
Error	57	0.00		
Mean Velocity				
Stream	1	0.00	0.00	0.993
Season	1	0.02	0.88	0.351
Patch	2	0.15	5.95	**0.005**
Stream*season	1	0.05	2.24	0.140
Stream*patch	2	0.09	3.44	**0.039**
Season*patch	2	0.01	0.50	0.611
Error	57	0.02		

Table 5.4 cont.

	Df	MS	F	P
Velocity Variance				
Stream	1	0.26	4.91	**0.031**
Season	1	0.02	0.38	0.539
Patch	2	0.48	9.02	**0.000**
stream*season	1	0.00	0.01	0.926
stream*patch	2	0.20	3.86	**0.027**
season*patch	2	0.00	0.01	0.986
Error	57	0.05		
Velocity Max				
Stream	1	0.05	1.09	0.294
Season	1	0.01	0.92	0.538
Patch	2	0.84	18.58	**0.000**
stream*season	1	0.16	3.62	0.062
stream*patch	2	0.29	6.47	**0.003**
season*patch	2	0.07	1.75	0.183
Error	57	0.04		
Velocity Min				
Stream	1	0.00	1.12	0.284
Season	1	0.02	0.38	0.538
Patch	2	0.00	1.38	0.223
stream*season	1	0.07	2.62	0.124
stream*patch	2	0.14	4.47	**0.028**
season*patch	2	0.01	0.56	0.524
Error	57	0.03		
Dmax				
stream	1	0.00	0.16	0.687
season	1	0.00	0.66	0.419
patch	2	0.41	121	**0.000**
stream*season	1	0.00	0.62	0.436
stream*patch	2	0.00	0.10	0.903
season*patch	2	0.00	0.71	0.496
Error	57	0.00		
D_{50}				
Stream	1	0.00	0.00	0.954
Season	1	0.00	0.24	0.628
Patch	2	0.29	317	**0.000**
Stream*season	1	0.00	0.77	0.382
Stream*patch	2	0.00	0.02	0.982
Season*patch	2	0.00	0.98	0.380
Error	57	0.00		

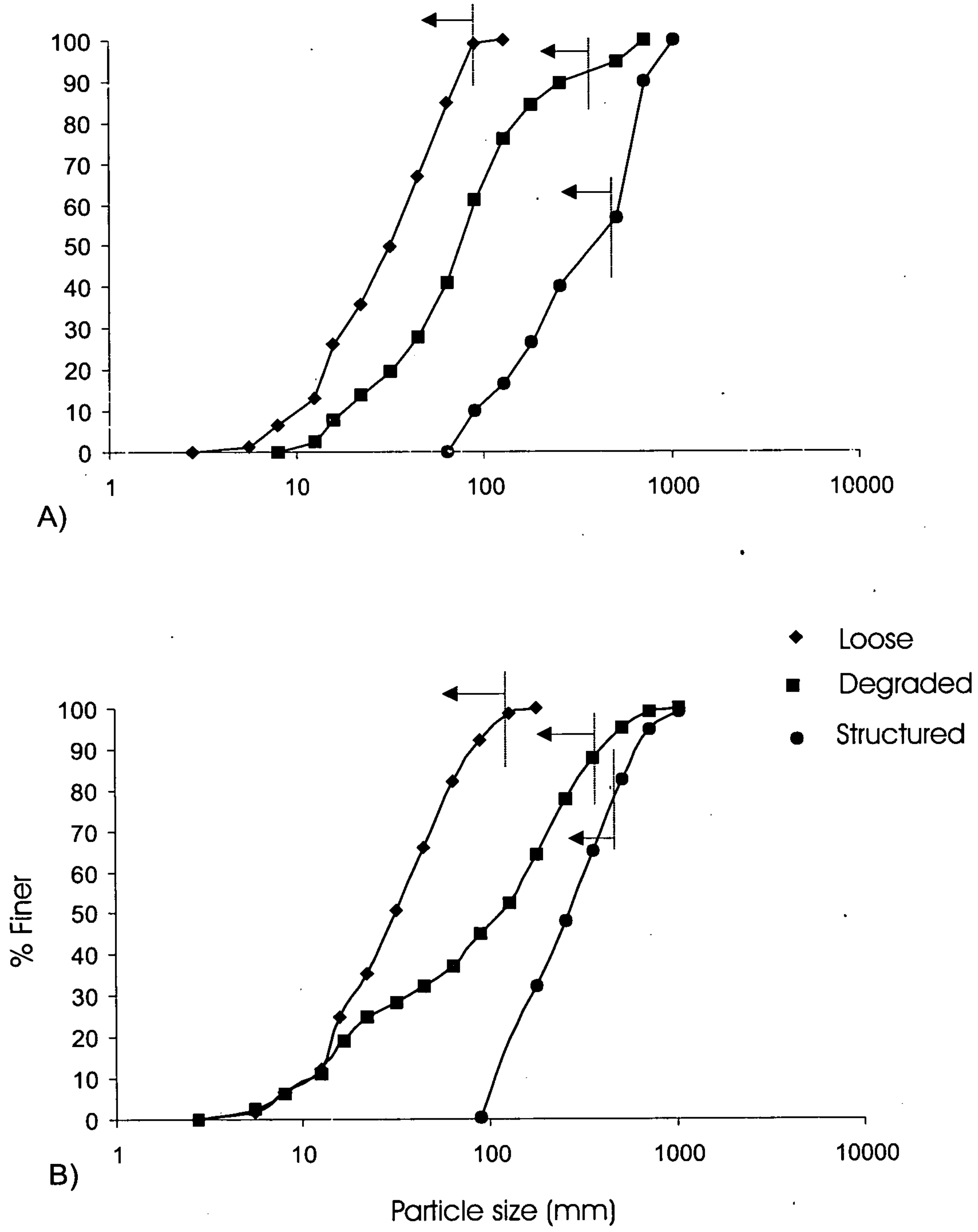


Figure 5.1 Particle size distribution for each patch type from A) Cramalt and B) Talla. The dotted vertical lines indicate the maximum particle size from the invertebrate samples.

Average depth and depth variance also varied significantly between patch types (Tables 5.3 & 5.4), although the range in depths recorded during sampling was small. Only moss showed a significant seasonal effect.

5.32 Invertebrate Species, Density and Taxa Richness

During the sampling programme, 49 taxa in total were sampled, 47 from the Talla and 42 from the Cramalt. Many of the species were widespread, occurring in both streams, and on all sampling occasions (Table 5.5). Some species appeared to be restricted to a particular stream, for example *Philopotamus montanus* was sampled on every occasion from the Talla but not found in the Cramalt. Six other taxa were also sampled from the Talla and did not occur in the Cramalt (Table 5.5). Conversely, only two species were sampled from the Cramalt, *Nemoura cambrica* and *Drusus annulatus*, that did not occur in the Talla (Table 5.5), although this may be an artefact of the reduced sampling effort in the Cramalt (see page 134).

Density and Taxon Richness

In both streams, average invertebrate density on Structured patches was significantly greater than that on Degraded and Loose patches (Figure 5.2, Table 5.6). Density varied significantly between sampling dates in both streams, however there was no significant interaction term between sampling date and patch (Table 5.6). In the Cramalt, taxon richness was significantly higher on Structured patches than Degraded and Loose (Table 5.6), although this was largely driven by November 02 (Figure 5.3). Indeed, there was a significant seasonal response in taxon richness in the Cramalt, and a significant interaction term, Date X Patch (Table 5.6). There

Table 5.5 List of taxa from the Talla and Cramalt on sampling dates. In the Coleoptera, 'A' refers to adults; 'L' to larvae

	Talla					Cramalt	
Taxa	Nov 01	Apr 02	Nov 02	Apr 03	Sept 03	Apr 02	Nov 02
Ephemeroptera							
Baetis sp	+	+	+	+	+	+	+
Ecdyonurus sp	+	+	+	+	+	+	+
Rhithrogena semicolorata	+	+	+	+	+	+	+
Ephemerella ignita	-	+	-	-	+	-	-
Paraleptophlebia submarginata	-	+	-	-	+	-	-
Caenis sp	-	+	-	-	+	-	-
Plecoptera							
Leuctra sp	+	+	+	+	+	+	+
Amphinemura sulcicollis	+	+	+	+	+	+	+
Brachyptera risi	+	+	-	+	-	+	+
Protonemoura praecox	+	+	+	+	+	+	+
Nemoura cambrica	-	-	-	-	-	+	-
Isoperla grammatica	+	+	+	+	+	+	+
Perlodes microcephala	+	+	+	+	+	+	+
Dinocras cephalotes	+	+	+	+	+	+	+
Capnia bifrons	+	-	-	-	-	-	-
Siphonoperla torrentium	+	+	+	+	+	+	+
Trichoptera							
Philopotamus montanus	+	+	+	+	+	-	-
Odontocerum albicorne	+	+	+	+	+	+	-
Sericostoma personatum	+	-	-	-	-	-	+
Rhyacophila dorsalis	+	+	+	+	+	+	+
Plectrocnemia geniculata	+	+	+	+	+	+	+
Hydropsyche siltalai	+	+	+	+	+	-	+
Drusus annulatus	-	-	-	-	-	+	-
Halesus radiatus	+	+	+	-	+	+	+
Diptera							
Dicranota sp	+	+	+	+	+	+	+
Simulium sp	+	+	+	+	+	+	+
Chironominae	+	+	+	+	+	+	+
Tanypodinae	-	+	-	+	+	+	+
Orthocladiinae	+	+	+	+	+	+	+
Athericidae	-	+	-	+	+	-	-
Empididae	+	+	+	+	+	+	+
Dixa sp	+	-	+	-	+	+	+
Coleoptera							
Elmis aenea A	+	+	+	+	+	+	+
Elmis aenea L	+	+	+	+	+	+	+
Limnius volckmari L	+	+	-	+	+	+	+
Limnius volckmari A	+	+	+	+	+	+	-

Esolus paralellepipedus L	-	+	+	+	+	+	-
Esolus paralellepipedus A	-	+	-	+	+	+	-
Oreodytes sanmarkii L	-	+	-	-	+	-	-
Oreodytes sanmarkii A	-	+	-	-	-	+	-
Hydraena gracilis	+	+	+	+	+	+	+
Helodidae	+	+	+	+	+	+	+
Isotonurus palustris	+	+	+	+	+	+	+
Mite							
Hydracarina sp	+	+	+	+	+	+	+
Worm							
Oligochaetea	+	+	+	+	+	+	+
Ampipoda							
Gammarus pulex	+	+	+	+	+	+	+
Triclad							
Turbellaria Planariidae	+	+	+	+	+	+	+
Mollusca							
Ancylus fluviatilis	+	-	+	-	-	-	+
Pisidium sp	-	+	-	-	-	-	+

Table 5.6 Summary statistics of ANOVA for total invertebrate density and Taxon richness (standardized for 120 individuals) for Talla and Cramalt. Factor Patch has three levels (Structured, Loose, Degraded) and Date two (April 02, Nov 02).

	DF	MS	F	P
Talla				
Total Density				
Patch (P)	2	10.68	55.8	**0.000**
Date (D)	4	1.39	7.29	**0.000**
D * P	8	0.21	1.13	0.355
Error	80	0.19		
Taxon richness				
Patch (P)	2	5.65	3.17	0.085
Date (D)	4	2.19	1.23	0.306
D * P	8	5.47	3.07	0.061
Error	80	1.78		
Cramalt				
Total Density				
Patch (P)	2	1.94	10.7	**0.001**
Date (D)	1	1.33	7.40	**0.012**
D * P	2	0.08	0.46	0.636
Error	24	0.18		
Taxon Richness				
Patch (P)	1	13.03	2.19	0.152
Date (D)	2	32.99	5,54	**0.011**
D * P	2	27.77	4.66	**0.019**
Error	24	5.95		

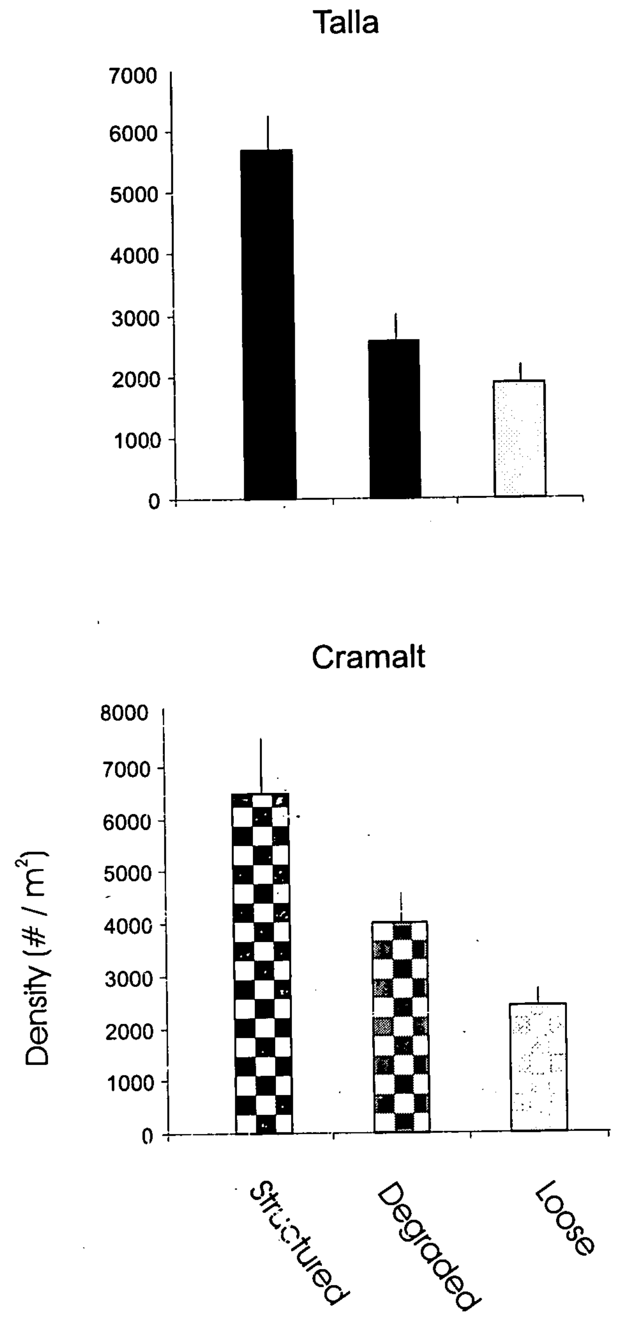


Figure 5.2 Average total density of invertebrates in each patch in the Talla (solid bars) and Cramalt (check bars). Averaged across all months. Each month shows a similar pattern. One standard error is shown by vertical line.

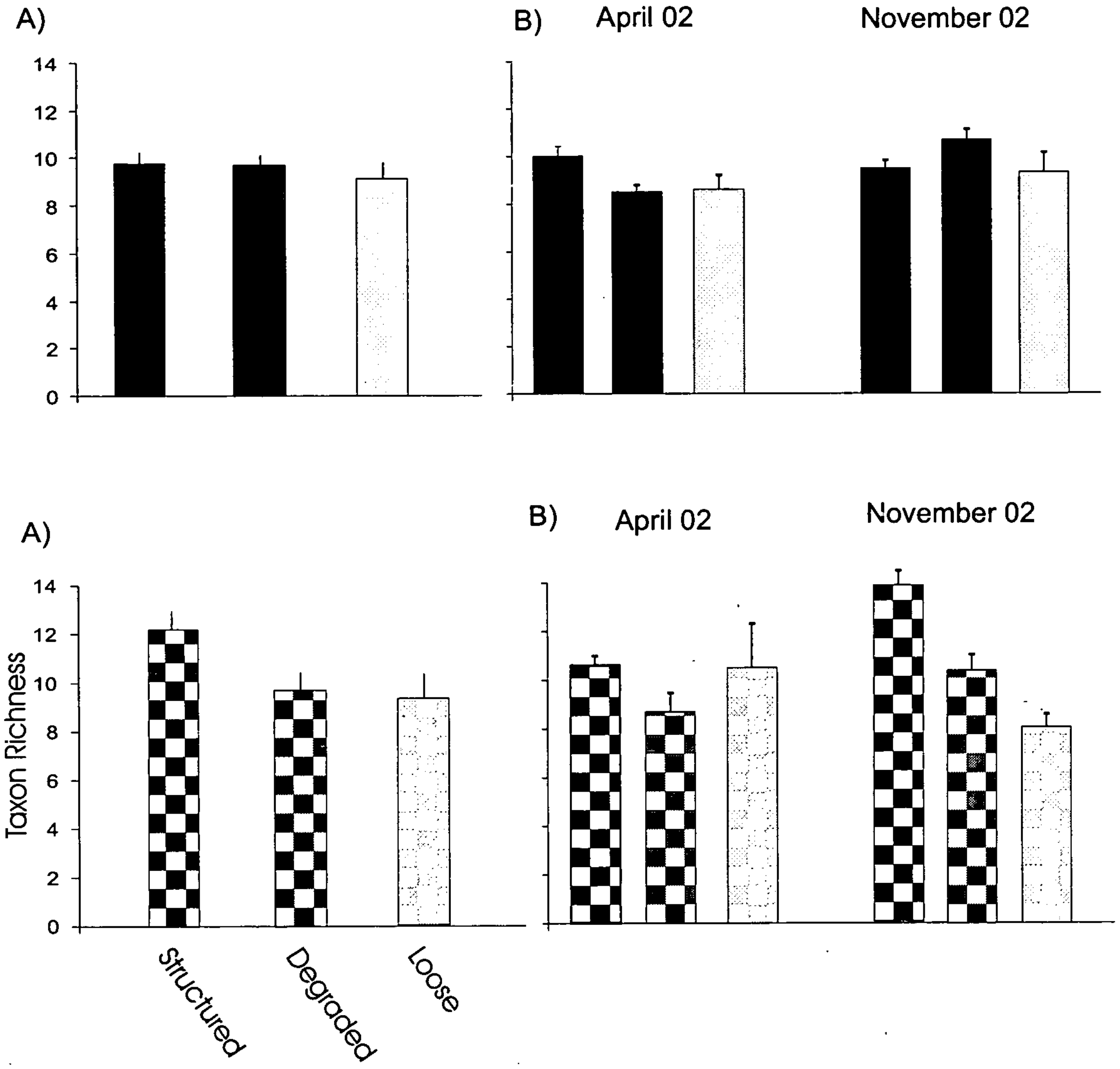


Figure 5.3 Taxon richness, standardised per count of 120, for each patch type in the Talla (solid bars) and Cramalt (check bars). A) Averaged across all months. B) Averaged across replicates within sample date. Nov 01, April 03 and Nov 03 not shown for Talla. No significant differences were found. One standard error is shown by vertical line.

was no significant difference in taxon richness between patch types in the Talla, and no seasonal response.

The high taxon richness on the Structured patches in the Cramalt is reflected in the species richness curves (Figure 5.4). The difference between Structured and Degraded curves in this stream illustrates the consistently higher taxon richness found on Structured patches. In the Talla however, there is little difference between the curves. For both streams there is a levelling off in taxon richness on Degraded and Structured patches at approximately 350 individuals. However, neither curve reaches an asymptote. Even after 2000 individuals, a new taxon is added every 700 to 800 individuals on Structured patches. On Loose patches the curve appears to level off at a similar sample size to that of the other patch types in the Talla, however in the Cramalt there is no apparent levelling off in taxa richness.

5.33 Faunal Associations with Patch type

Associations of Abundant Taxa with Patch Type

Of the 49 taxa sampled from the Talla and Cramalt, only *Simulium* sp, *Baetis* sp, *Leuctra* sp, *Siphonoperla torrentium, Rithrogena semicolorata* and Orthocladiinae were abundant enough for univariate analysis (> 5 % of the total sampled). Of these taxa, *Simulium* sp, *Baetis* sp, *Leuctra* sp and Orthocladiinae all had significantly higher densities on Structured patches in both the Talla and Cramalt (Figure 5.5, Table 5.7 & 5.8). *Siphonoperla torrentium* and *Rithrogena semicolorata* in contrast were found in significantly higher densities on Loose patches, but only in the Cramalt (Figure 5.5, Table 5.7 & 5.8). In the Talla these species occur on all patch

Table 5.7 Summary statistics for ANOVA of abundant taxa, Talla. See Figure 5.5 for summary data.

	DF	MS	F	P
Siphonoperla torrentium				
Patch (P)	2	1.88	1.32	0.273
Date (D)	4	7.49	5.25	**0.001**
D * P	8	2.85	2.01	0.056
Error	80	1.42		
Simulium sp				
Patch (P)	2	230.98	224	**0.000**
Date (D)	4	9.53	9.28	**0.000**
D * P	8	1.74	1.70	0.111
Error	80	1.02		
Baetis sp				
Patch (P)	2	18.34	53.5	**0.000**
Date (D)	4	4.5	13.1	**0.000**
D * P	8	0.30	0.89	
Error	80	0.34		
Rithrogena semicolorata				
Patch (P)	2	0.02	0.04	0.965
Date (D)	4	3.31	4.12	**0.004**
D * P	8	0.86	1.07	0.392
Error	80	0.80		
Leuctra sp				
Patch (P)	2	29.69	51.0	**0.000**
Date (D)	4	6.18	10.6	**0.000**
D * P	8	0.34	0.59	0.784
Error	80	0.58		
Orthocladiinae				
Patch (P)	2	90.10	82.4	**0.000**
Date (D)	4	69.27	63.4	**0.000**
D * P	8	1.99	1.86	0.084
Error	80	1.09		

Table 5.8 Summary statistics for ANOVA of abundant taxa, Cramalt
See Figure 5.5 for summary data.

	DF	MS	F	P
Siphonoperla torrentium				
Patch (P)	2	1.78	4.44	**0.023**
Date (D)	1	0.00	0.00	0.980
D * P	2	2.58	6.44	**0.006**
Error	23	0.40		
Simulium sp				
Patch (P)	2	63.40	35.5	**0.000**
Date (D)	1	33.23	18.61	**0.000**
D * P	2	2.45	1.37	0.273
Error	23	1.78		
Baetis sp				
Patch (P)	2	4.73	13.8	**0.000**
Date (D)	1	3.51	10.2	**0.004**
D * P	2	0.11	0.35	0.709
Error	23	0.34		
Rithrogena semicolorata				
Patch (P)	2	1.62	7.35	**0.003**
Date (D)	1	2.37	10.6	**0.003**
D * P	2	0.01	0.07	0.933
Error	23	0.22		
Leuctra sp				
Patch (P)	2	1.29	6.92	**0.004**
Date (D)	1	0.12	0.67	0.422
D * P	2	0.28	1.52	0.240
Error	23	0.18		
Orthocladiinae				
Patch (P)	2	51.10	67.9	**0.000**
Date (D)	1	30.74	40.8	**0.000**
D * P	2	0.50	0.67	0.522
Error	23	0.75		

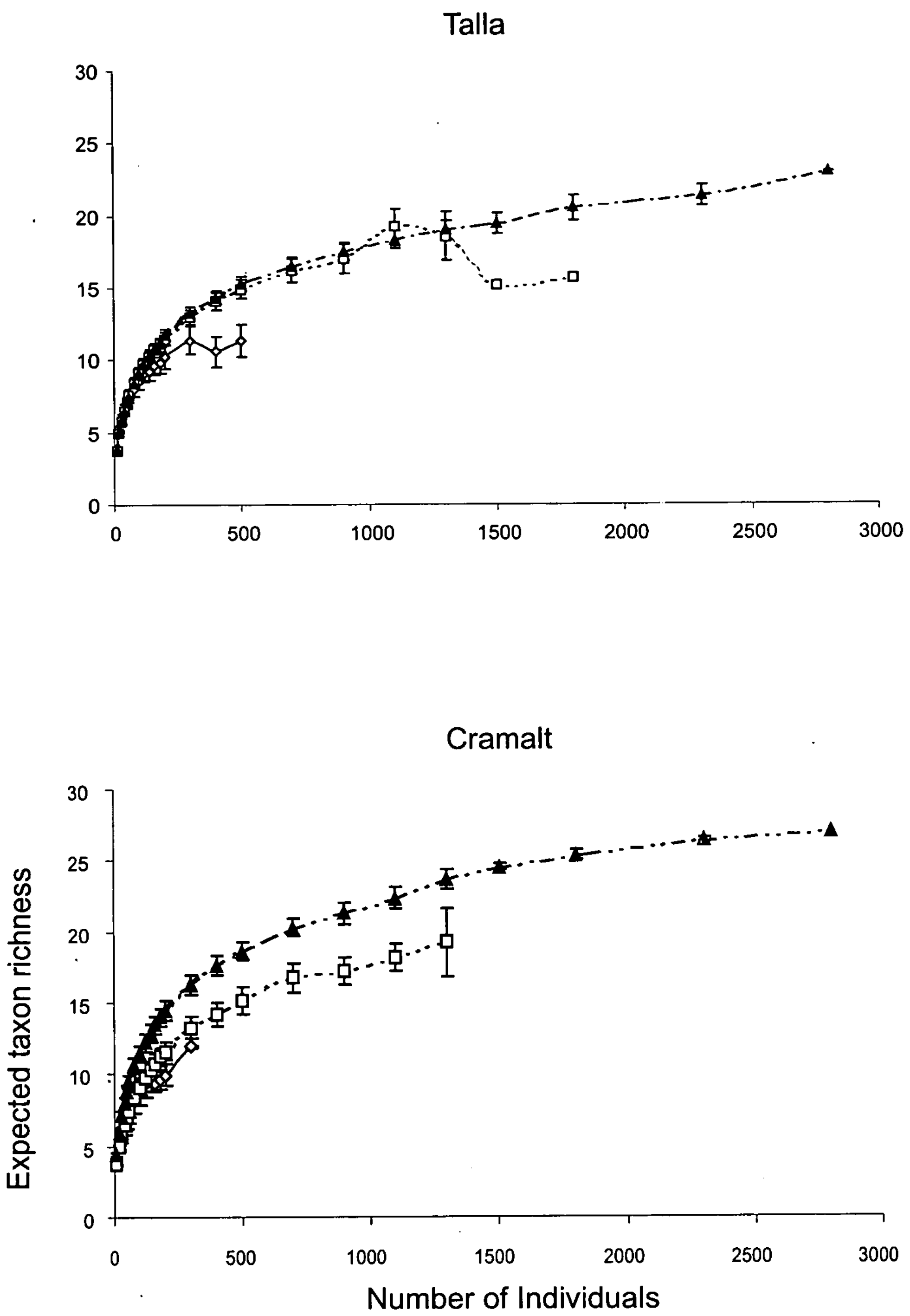


Figure 5.4 Taxon richness curves for Structured (black triangles) Degraded (open squares) and Loose (grey diamonds) inTalla and Cramalt. One standard error is shown by bars.

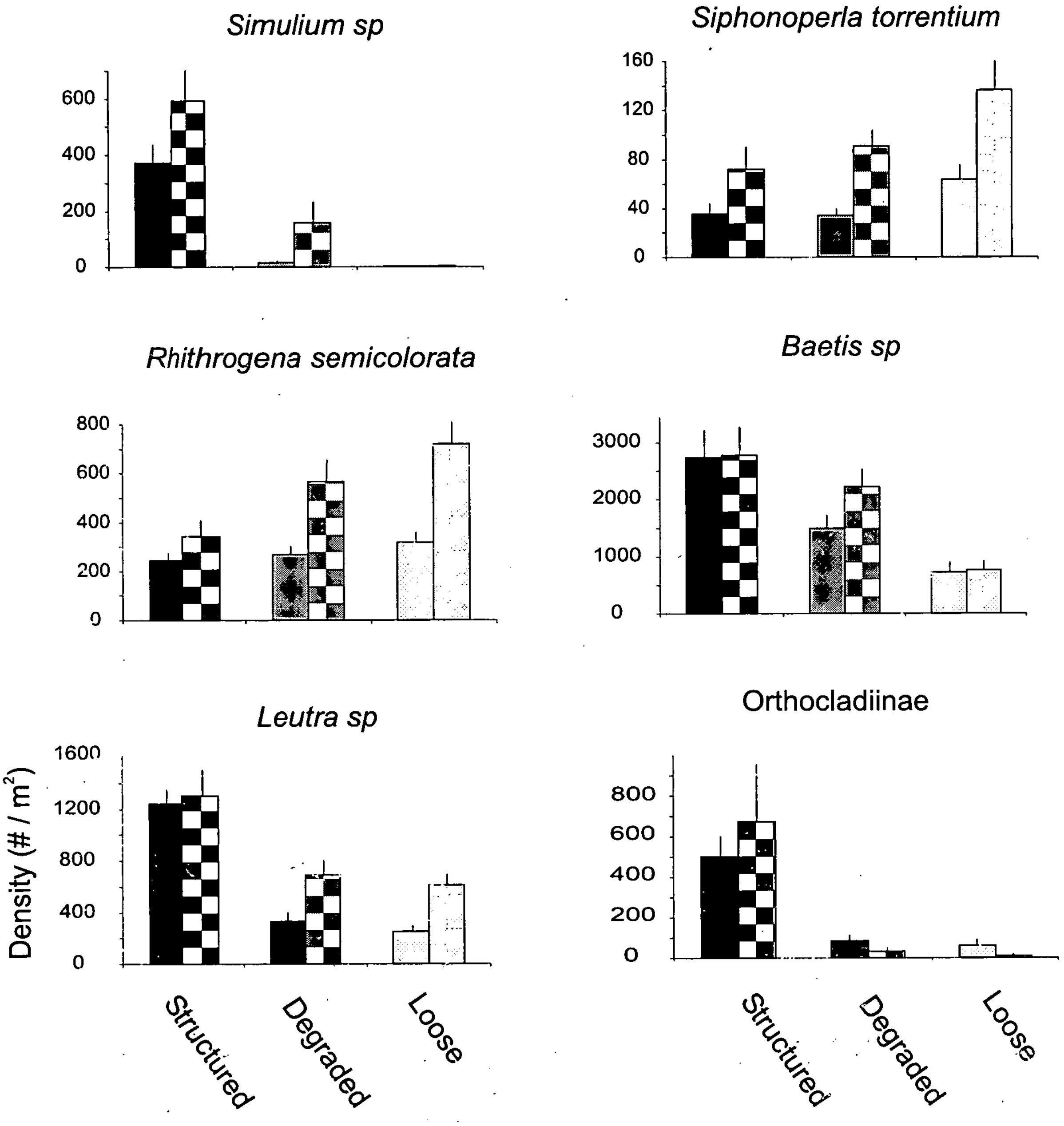


Figure 5.5 Average density (#/m^2) of abundant taxa for each patch type. Solid bars show Talla, checked bars Cramalt. One standard error is shown by vertical line, See Tables 5.7 & 5.8 for summary statistics of ANOVA.

types in relatively even densities. For most taxa, densities on Degraded patches represented an intermediate between those on Structured and Loose patches (Figure 5.5).

In the Talla, the density of all abundant taxa varied significantly with sample date (Table 5.7). In the Cramalt however, only density of *Rithrogena semicolorata, Simulium* sp and *Baetis* sp. varied with sample date (Table 5.8). *Siphonoperla torrentium* however exhibited a change in the pattern of density with season (significant interaction term, Patch X Date, Table 5.8). In April 02, the density on Loose patches was 5 times that on Structured, however in November 02 the densities on Loose and Structured were comparable. There was no significant interaction term in the Talla.

Assemblage Associations with Patch Type

Ordination of the samples, using all but rare taxa (< 0.5 %), shows clear differences in community assemblages on each patch type, based on density of individuals. These differences were maintained across season (winter and spring), year and stream (Figures 5.6 & 5.7). In most ordinations, the Degraded patches sit as an intermediate assemblage between Loose and Structured (exception, Talla April 02, Figure 5.6), reflecting the average densities of the abundant taxa (Figure 5.5). The ordinations in Figures 5.6 & 5.7 show sample plots on the two axes that show the greatest distance between patch types. When plotted with the third axis, separation between one or more of the patch type groups was still evident for most ordinations,

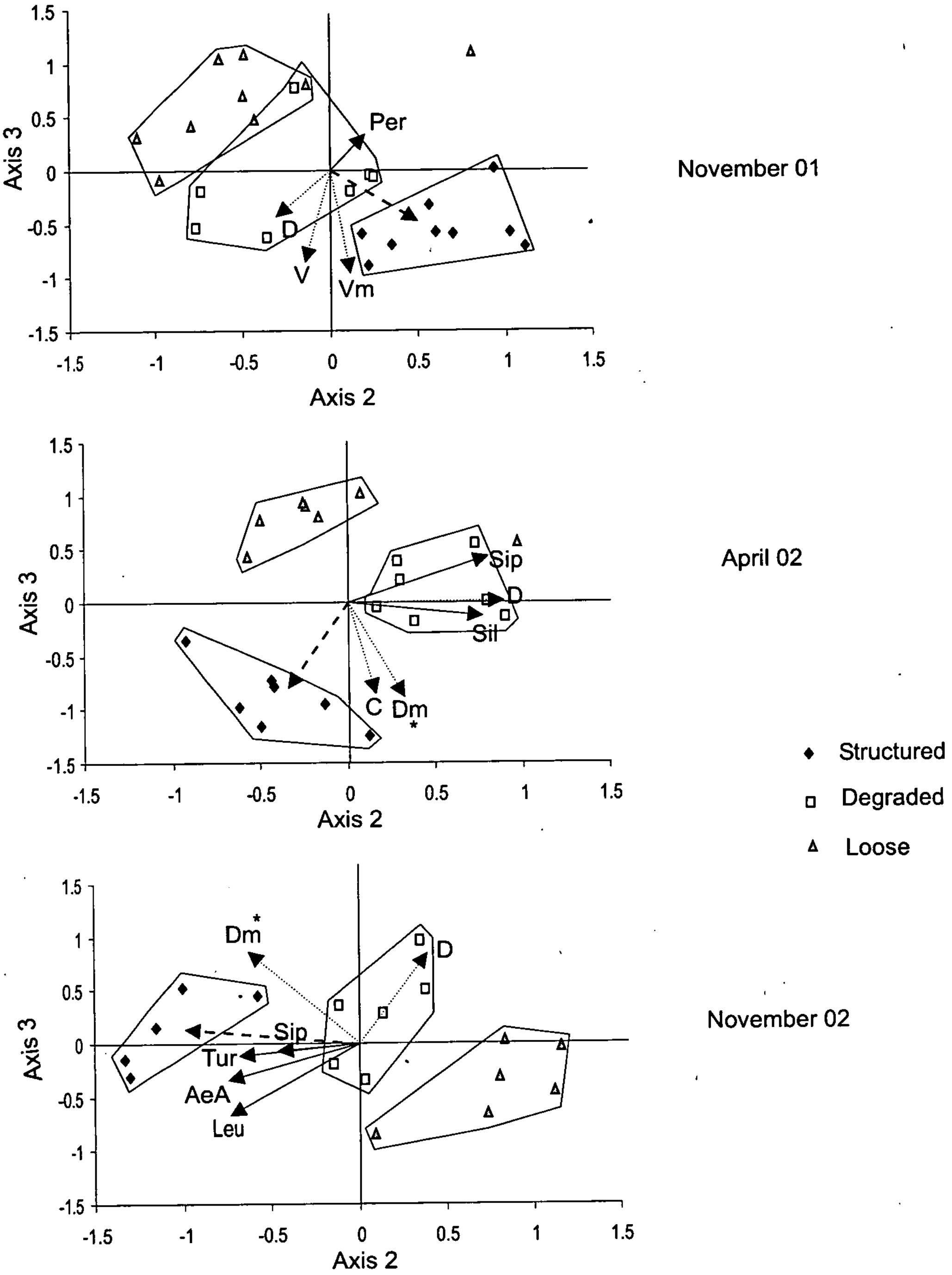


Figure 5.6 Sample hybrid multi-dimensional scaling (HMDS) ordination plots using all but rare taxa from the Talla, all sampling dates shown. The choice of axes was determined by the plots which showed the clearest separation in patch types. Superimposed on the ordinations are the species vector plots of those species that are significantly correlated with the ordination in a direction other than that towards the Structured patches, and the environmental variable plots (dotted line), significance shown by *. To enhance clarity, the dashed vector shows the main direction of all species and environmental variables associated with the structured samples. See Tables 5.9 (p. 168) & 5.11 (p. 173) for a list of species and environmental variables and their letter codes.

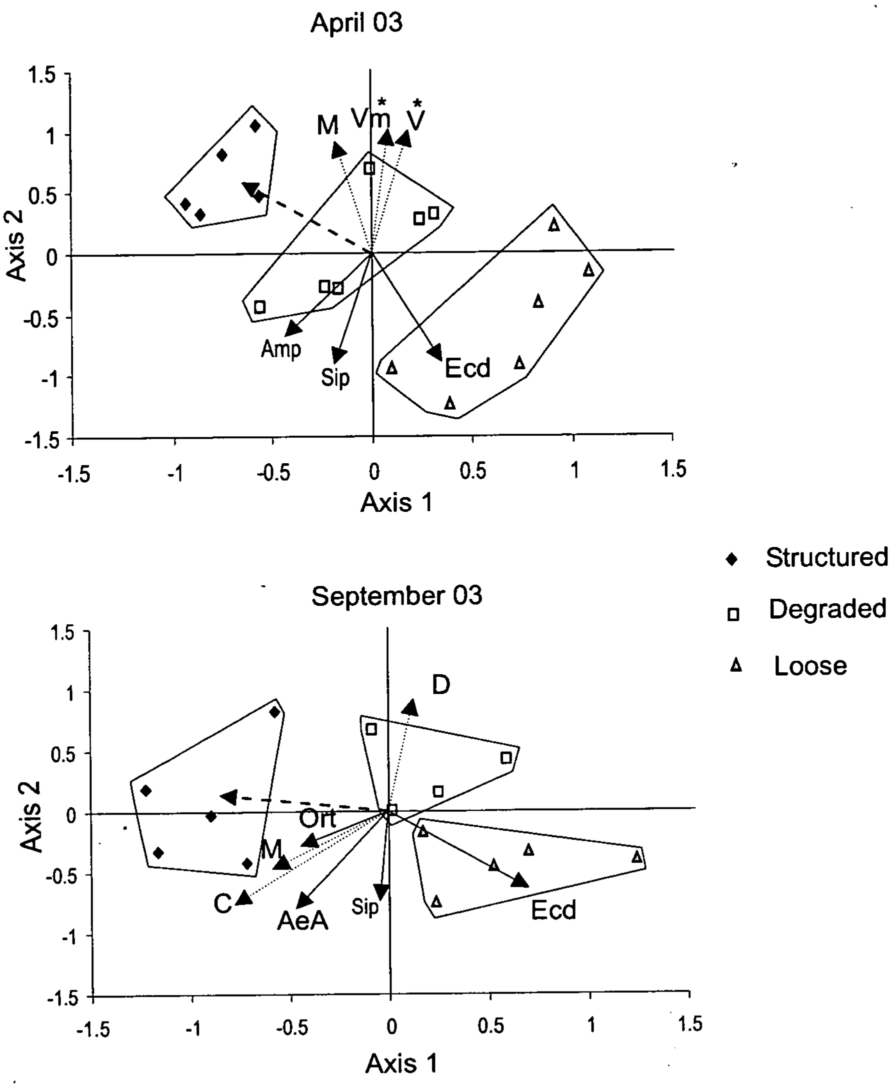


Figure 5.6 cont'

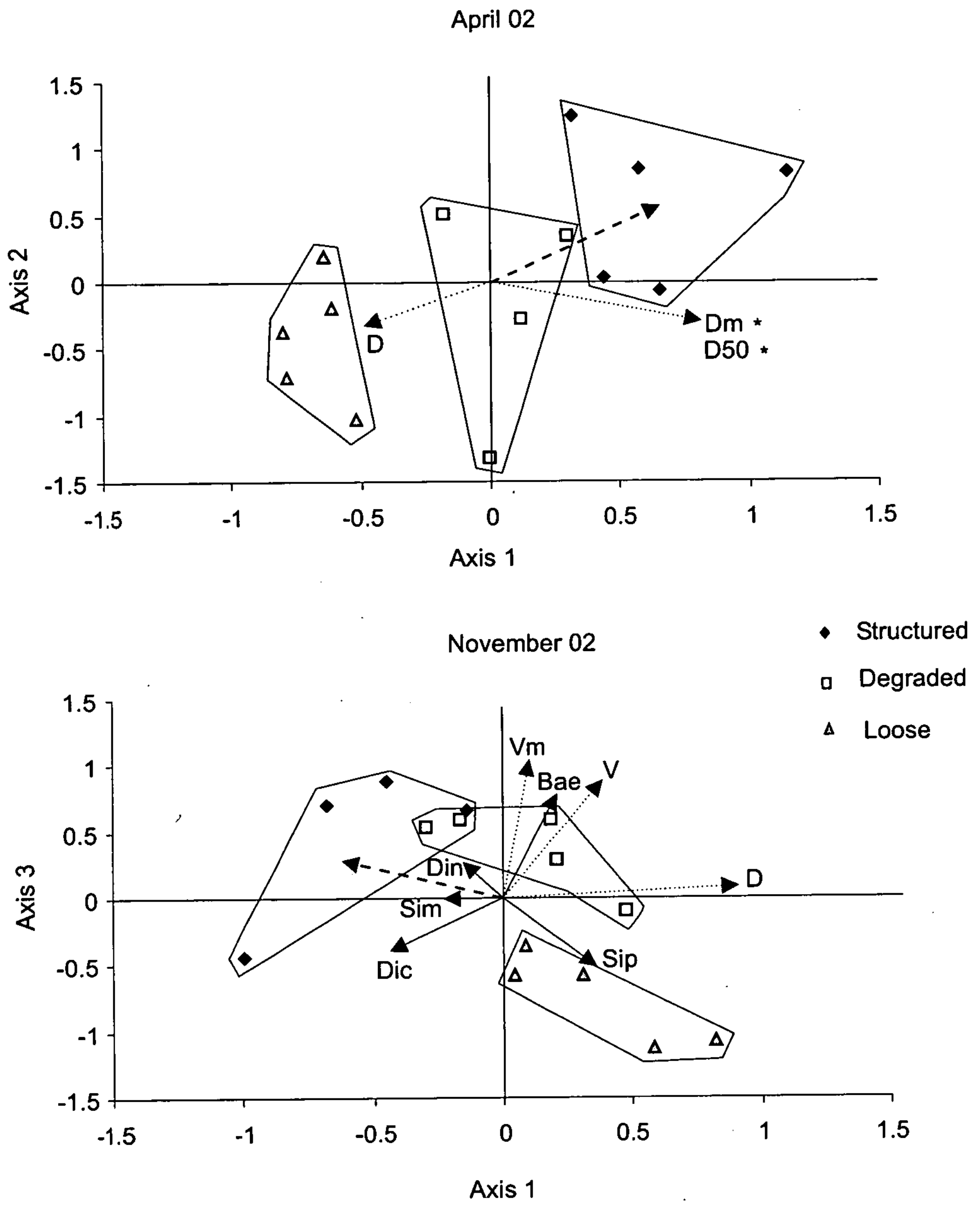


Figure 5.7 Sample hybrid multi-dimensional scaling (HMDS) ordination plots using all but rare taxa from the Cramalt, all sampling dates shown. The choice of axes was determined by the plots which showed the clearest separation in patch types. Superimposed on the ordinations are the the species vector plots of those species that are significantly correlated with the ordination in a direction other than that towards the Structured patches, and the environmental variable plots, significance shown by *. To enhance clarity, the dashed vector shows the main direction of all species and environmental variables associated with the structured samples. See Tables 5.10 & 5.11 (p. 173) for a list of species and environmental variables and their letter codes.

although not as distinct. Note, the reference to the third axis does not necessarily mean axis 3, it is simply a reference to the axis not included in the Figure of interest.

Species Specific Associations:

A) Structured

Several species in the Talla, *Simulium sp, Baetis* sp, *Leuctra* sp, *Philopotamus montanus* and *Rhyacophila dorsalis* were significantly correlated (after PCC and Monte Carlo randomizations) with the ordination plots, with vectors along the main gradient from Loose to Structured (Figures 5.6 & 5.7, Table 5.9). These vectors indicate an increase in density towards the Structured patches, largely supporting the results of the ANOVA (Table 5.7) and that shown in Figure 5.5 for *Simulium* sp, *Baetis* sp, and *Leuctra* sp. *Philopotamus montanus* and *Rhyacophila dorsalis*, whilst not occurring in such high densities in the Talla, either occurred almost exclusively on Structured patches (*P. montanus*), or had densities on average four times that on Degraded, and up to 10 times that on Loose (*R. dorsalis*) (Figure 5.8).

In the Cramalt, the associations with patch type were weaker than in the Talla and varyied between seasons. In April 02, only *Baetis* sp was significantly correlated with the ordination plot (Table 5.10). The vector position of this species confirms that indicated by Figure 5.5, that the average density of this species was greatest on Structured patches. In November 02, Orthocladinae, *Leuctra* sp, *Rhyacophila dorsalis* and *Protonemoura praecox* were all significantly correlated with the ordination plot indicating increased abundance towards Structured patches

Table 5.9 List of taxa from the Talla whose vector plots are significantly correlated (after PCC and monte-carlo randomizations) with the ordination plots. * indicates that the direction of the vector is either towards a patch type (Structured or Loose – 'L'se'), or no clear association with patch type (other – 'Oer'). The three letter code is shown after each taxa name.

Taxa	*Nov 01*			*April 02*			*Nov 02*			*April 03*			*Sept 03*		
	Stru	L'se	O'er	Stru	L'se	O'er	Stru	L'se	O'er	Stru	L'se	O'er	Stru	L'se	O'er
Baetis sp Bae	*			*			*			*			*		
Ecdyonurus sp Ecd											*			*	
Leuctra sp Lau	*			*					*	*			*		
Amphinemura sulciollis Sul				*			*			*					
Brachyptera risi Ris				*											
Protonemoura praecox Pra										*			*		
Perlodes microcephala Per			*												
Dinocras cephalotes Din							*								
Siphonoperla torrentium Sip						*			*			*			*
Philopotamus montanus Mon	*			*			*			*			*		
Rhyacophila dorsalis Dor	*			*			*			*			*		
Hydropsyche siltalai Sil						*							*		
Simulium sp Sim	*			*			*			*			*		
Orthocladinae Ort	*			*			*			*					*
Elmis aenae (A) AeA															*
Elmis aenae (L) AeL	*								*						
Helodidae Hel				*			*								
Gammarus pulex Amp												*			
Turbellaria Planariidae Tur									*						

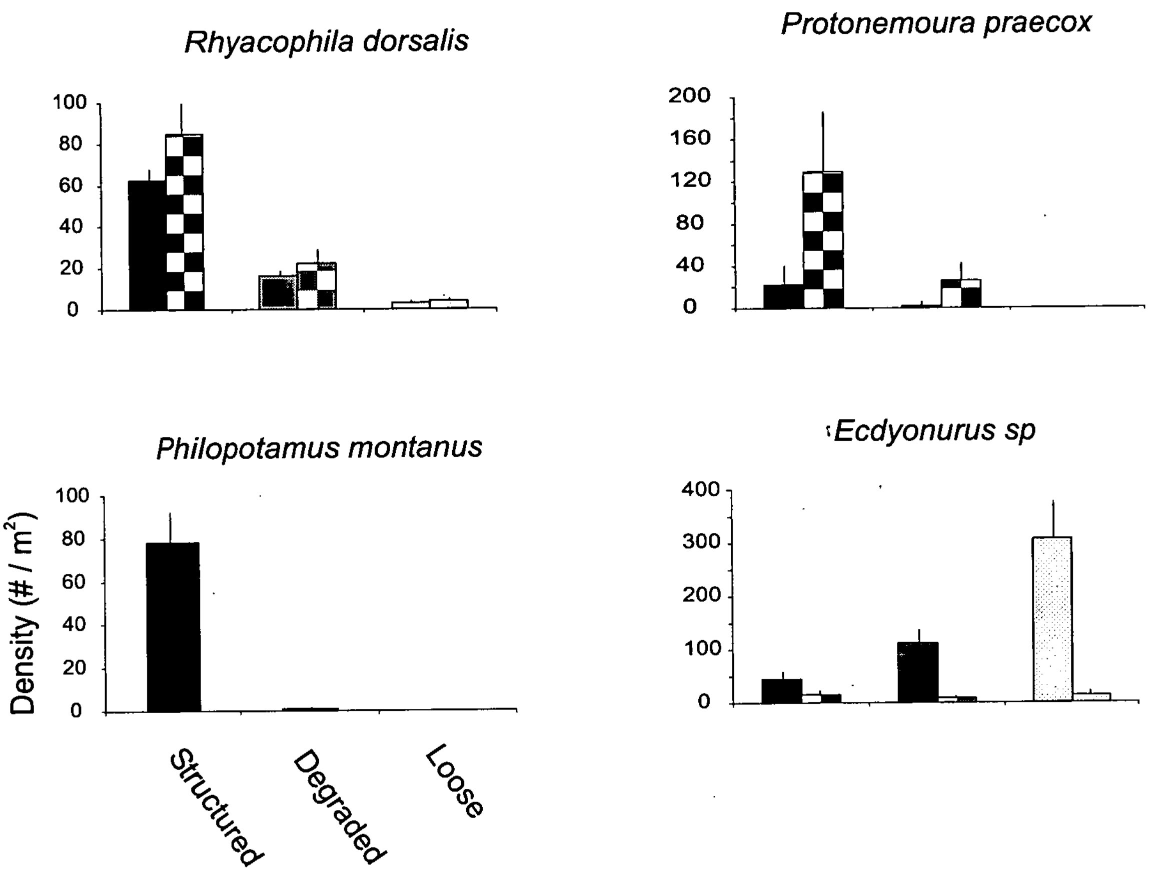


Figure 5.8 Average density (#/m^2) of taxa showing preference for each patch type. Solid bars show Talla, checked bars Cramalt. One standard error is shown by vertical line.

(Figure 5.7, Table 5.10). Indeed, density of both *Rhyacophila dorsalis* and *Protonemoura praecox* was approximately five to ten times higher on Structured patches than Degraded and Loose respectively (Figure 5.8).

B) Loose

In the Talla only *Ecdyonurus* sp was significantly correlated with the ordination plots along vectors showing an increase in abundance towards Loose patches (Figure 5.6, Table 5.9). This species was scarce in the Cramalt, however in the Talla, density of *Ecdyonurus* sp on Loose patches was up to three times that on Degraded patches, and over six times that on Structured patches (Figure 5.8). In the Cramalt, *Siphonoperla torrentium* was significantly correlated along vectors showing an increase in abundance towards the Loose environment, but only in November 02 (Figure 5.7, Table 5.10). While this species occurred in high densities in both streams, in the Talla there was little difference in average density across patch types, whereas in the Cramalt densities on the Loose patches were approximately twice that on Degraded and Structured (Figure 5.5).

C) Taxa with no Associations with Patch Type

Several taxa had vector plots that were significantly correlated in ordination space, but in a direction other than towards either Structured, Loose and Degraded patches (Figures 5.6 & 5.7, Tables 5.9 & 5.10, under the heading 'Other'). In the Talla these species included *Siphonoperla torrentium*, *Gammarus pulex*, and *Elmis aenea* (Adult), although only *Siphonoperla torrentium* was significantly correlated with more than one plot (Figure 5.6, Table 5.9). *Dinocras cephalotes*, *Dicranota* sp, *Baetis* sp and *Simulium* sp were the only species in the Cramalt that were significantly correlated with an ordination in a direction other than towards Structured or Loose.

To examine the possible cause of this variation, the vectors of the environmental variables were plotted onto the ordinations. The gradient for the majority of variables, as suggested in Tables (5.3 & 5.4), is towards the Structured patches (Figures 5.6 & 5.7, Table 5.11). The vector plots for some environmental variables however are not aligned with this gradient in every ordination plot. These vectors however do not align along the same gradient as that of the vectors of the taxa listed above in section C (Figures 5.6 & 5.7). Only *Baetis* sp appears to be consistently associated with an environmental variable, but only in the Cramalt. In this stream *Baetis* sp was closely associated with the velocity gradient, as characterized by both average and maximum velocity, on both sampling occasions (Figure 5.7, Table 5.10). Note, in Figure 7.2 the dashed line in the April 02 ordination represents the vector of both *Baetis* sp and velocity, average and maximum (see Tables 5.10 & 5.11).

Quantitative estimates of Variation in Patch Assemblage:

Variation between Patch Types:

The ordination plots provide a qualitative study of the variation in patch assemblage. A quantitative estimate however can be obtained by averaging the dissimilarity scores (Bray-Curtis) across all sample pairs between patch types. The higher the average the more dissimilar the assemblage. Average dissimilarity between samples was greatest between the Loose and Structured patches across all seasons and streams (Figure 5.9). Assemblages on these two patch types were consistently the most different. Average dissimilarity between patch types however was generally greater in the Cramalt than the Talla (Figure 5.9), suggesting that the patch specific assemblages in the Cramalt were slightly more distinct than those in the Talla. The difference between patch assemblages also varied with season and year (Figure 5.9), although always maintaining the general pattern of greatest difference between Structured and Loose.

Variation within Patch Types:

The Talla and Cramalt exhibited slightly different patterns of within patch sample variation. For both streams the Degraded patch type exhibited an intermediate level of variation between that of Loose and Structured, as indicated by the dissimilarity score averaged across all pair samples within the patch type (Figure 5.10). In the Talla however, the Loose patches had the highest variation and the Structured the least, whereas in the Cramalt, the converse occurs, with the Loose patches exhibiting the lowest variation.

5.34 Partitioning effects of Environment, Patch, and Stream

A series of partial canonical correspondence analysis (CCA) of combined data from both streams quantified the variation in invertebrate assemblage that was explained by environmental variables (velocity, depth and substrate parameters, CPOM, moss), patch type and stream. Summary statistics for the CCA containing all parameters is shown in Table 5.12. The classification 'patch' accounted for 7 % of the total variance in April 02 and 5 % in November 02 in the combined (both streams) data

Table 5.10 List of taxa from the Cramalt whose vector plots are significantly correlated (after PCC and monte-carlo randomizations) with the ordination plots. * indicates that the direction of the vector is either towards a patch type (structured or loose), or no clear association with patch type (other). Three letter code is shown after each taxa name.

Taxa	*April 02*			*Nov 02*		
	Stru	Loose	Other	Stru	Loose	Other
Baetis sp Bae	*					*
Leuctra sp Leu				*		
Dinocras cephalotes Din						*
Siphonoperla torrentium Sip					*	
Rhyacophila dorsalis Dor				*		
Dicranota sp Dic						*
Simulium sp Sim						*
Orthocladinae Ort				*		

Table 5.11 Environmental variables whose vectors are in a direction towards structured patches are shown by #. * indicates variables that are significantly correlated (after PCC and Monte Carlo randomizations) with the ordination plots. For all variables whose vectors are not in a direction towards Structured patches, the vector is plotted in ordination space (see Figures 5.6 & 5.7).

		Talla					**Cramalt**	
		Nov 01	April 02	Nov 02	April 03	Sept 03	April 02	Nov 02
CPOM	C	#	*	#	#*	#	#	#
Moss	M	*	#	#		#	#	#
Depth av	D	#		#	#			
Depth var	Dv	#	#	*	#*	#	#	#
Vel av	V			#	*	#	#	
Vel var	Vv	#	#	#*	#	#	#	
Vel max	Vm		#	#*	*	#*	#	#
D max	Dm	#*	*	*	#*	#	*	#*
D$_{50}$	D50	#*	#*	#*	#*	#*	*	#*

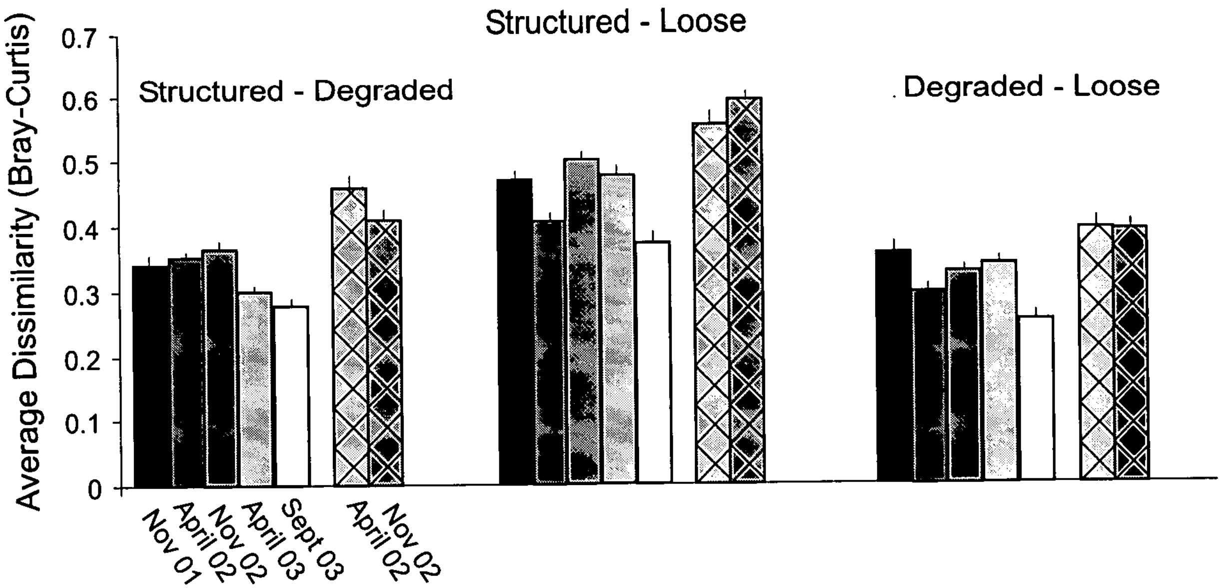


Figure 5.9 Average dissimilarity of all sample pair combinations between all patch type combinations (i.e. Structured-Degraded, Structured-Loose, Degraded-Loose) for each sample date in the Talla (solid bars) and Cramalt (Crossed bars). One standard error is shown by vertical lines.

Table 5.12 Summary of statistics for canonical correspondence analyses of combined invertebrate data from Cramalt and Talla each sample season. Percent variance in species data among the environmental variables was determined by a series of partial CCAs on each data set (see Figure 5.11).

April 02 Talla & Cramalt data sets combined

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.160	0.067	0.044	0.030	0.737
Species-environment correlations	0.976	0.892	0.883	0.831	
Cumulative percentage variance					
of species data	21.7	30.8	36.8	40.9	
of species-environment relation	45.1	64.2	76.6	85.1	
Sum of all canonical eigenvalues					0.354

November 02 Talla & Cramalt data sets combined

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.150	0.099	0.034	0.032	0.671
Species-environment correlations	0.965	0.971	0.917	0.828	
Cumulative percentage variance					
of species data	22.4	37.1	42.2	47.0	
of species-environment relation	39.8	65.9	75.1	83.7	
Sum of all canonical eigenvalues					0.377

Table 5.12 Summary of statistics for canonical correspondence analyses of invertebrate data from Cramalt and Talla in each sample season. Percent variance in species data among the environmental variables was determined by a series of partial CCAs on each data set (see Figure 5.11).

Cramalt April 02

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.183	0.081	0.067	0.047	0.664
Species-environment correlations	0.979	0.952	0.939	0.919	
Cumulative percentage variance					
of species data	27.6	39.7	49.8	56.9	
of species-environment relation	39.0	56.1	70.4	80.4	
Sum of all canonical eigenvalues					0.470

Cramalt November 02

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.129	0.053	0.033	0.026	0.430
Species-environment correlations	0.996	0.946	0.836	0.932	
Cumulative percentage variance					
of species data	30.1	42.4	50.0	56.0	
of species-environment relation	43.6	61.4	72.5	81.2	
Sum of all canonical eigenvalues					0.297

Talla April 02

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.195	0.067	0.047	0.035	0.721
Species-environment correlations	0.980	0.958	0.776	0.907	
Cumulative percentage variance					
of species data	27.1	36.4	43.0	47.8	
of species-environment relation	45.3	60.8	71.8	79.8	
Sum of all canonical eigenvalues					0.432

Talla November 02

CCA axis	1	2	3	4	Total inertia
Eigenvalues	0.220	0.063	0.043	0.038	0.646
Species-environment correlations	0.985	0.904	0.836	0.930	
Cumulative percentage variance					
of species data	34.1	43.8	50.5	56.3	
of species-environment relation	50.4	64.8	74.7	83.3	
Sum of all canonical eigenvalues					0.437

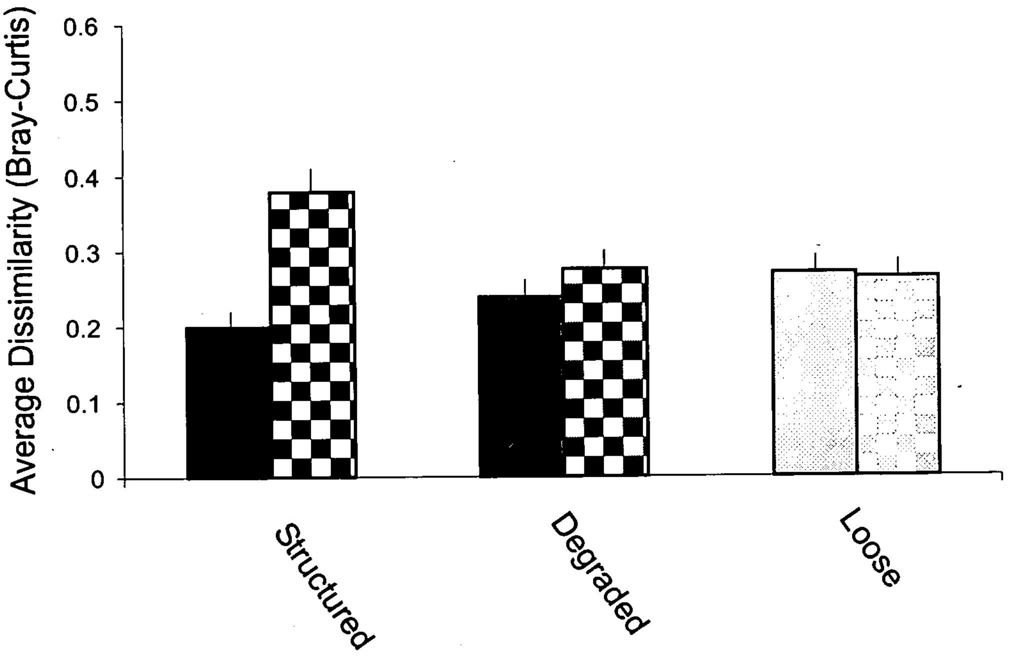


Figure 5.10 Average Bray-Curtis dissimilarity of sample pairs within each patch type for Talla (solid bars) and Cramalt (check bars), averaged across all seasons.

set (Figure 5.11). A similar amount of variance was explained at the stream scale, 7 % over both months. The environmental variables accounted for the greatest amount of variance in the data, 13 % in April 02 and 18 % in November. A large portion of variance however was shared between parameters (Figure 5.11).

When the data sets from each stream were analyzed separately (summary statistics Table 5.12), the amount of variance explained by the patches increased in both streams, to 12 % in both months in the Talla, and 13 % (April 02) and 10 % (November) in the Cramalt (Figure 5.11). The proportion of variance explained by the environmental variables also increased, explaining up to 40% in the Cramalt (Figure 5.11). A large portion of variance was again shared, reflecting the strong association of environmental variables with patch classification.

For all taxa, except *Rhithrogena semicolorata* in November 02, more variation was explained by patch type than differences between stream (Tables 5.13 & 5.14). Indeed, for *Simulium* sp in November 02, and Orthocladiinae and *Baetis* sp in April 02, this variation was greater than that explained by the residual variance. For total density, the patch also explained a greater amount of variation than either that of stream or sample. For species richness however, the sample explained a greater amount of variation, more than stream or patch, although in November 02 the interaction term (stream*patch) explained the greatest amount.

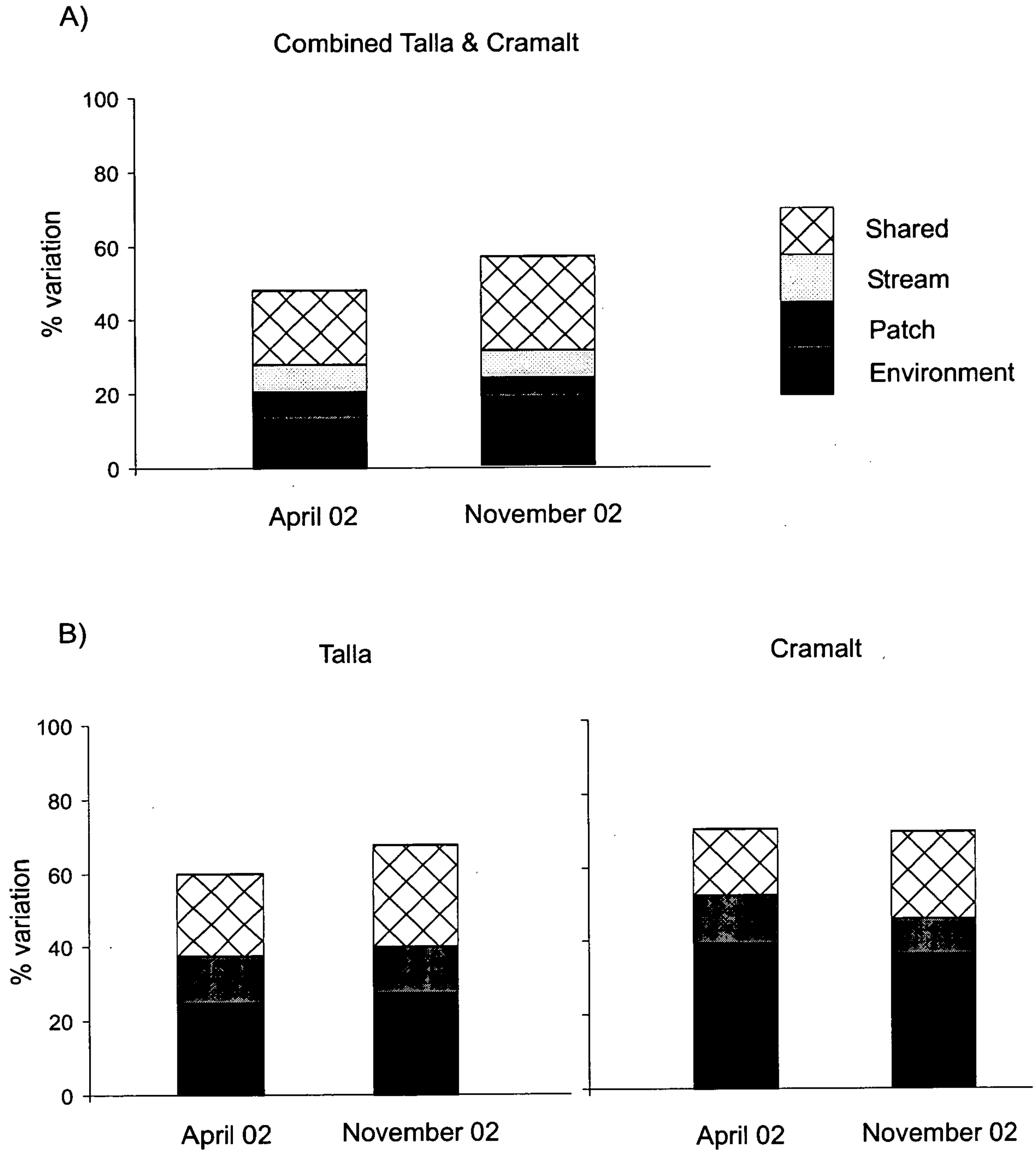


Figure 5.11 Percent variance explained in species data partitioned among A) environmental variables, patch and stream and B) environmental variables and patch, as determined by a series of partial CCAs. See Table 5.12 for summary statistics. 'Shared' category is the percent variance explained by that is shared among all variables in the analysis (e.g. in the within each stream (A) it is that shared between both 'patch' and 'environment'.

Table 5.13 Summary statistics of two way factorial ANOVA (stream – fixed, patch –fixed) for abundant taxa in November 02, showing percent variance explained by each factor.

	DF	MS	F	%
Rhithrogena semicolorata				
Stream (S)	1	1.87	8.99	58
Patch (P)	2	0.09	0.46	0
S*P	2	0.21	3.89	10
Sample	26	0.05		32
Baetis sp				
Stream (S)	1	0.01	0.11	0
Patch (P)	2	0.71	4.79	45
S*P	2	0.15	2.9	8
Sample	26	0.05		47
Leuctra sp				
Stream (S)	1	0.95	4.43	19
Patch (P)	2	1.08	5.01	33
S*P	2	0.21	2.67	10
Sample	26	0.08		38
Simulium sp				
Stream (S)	1	1.54	4.22	3
Patch (P)	2	18.30	50.04	80
S*P	2	0.36	1.23	1
Sample	26	0.29		16
Total				
Stream (S)	1	0.30	2.74	10
Patch (P)	2	0.70	6.26	45
S*P	2	0.11	3.21	11
Sample	26	0.03		34
Sp Richness				
Stream (S)	1	0.02	0.94	0
Patch (P)	2	0.04	1.92	24
S*P	2	0.02	8.53	39
Sample	26	0.00		37

Table 5.14 Summary statistics for two way factorial ANOVA (stream – fixed, patch –fixed) for abundant taxa in April 02, showing percent variance explained by each factor.

	DF	MS	F	%
Rhithrogena semicolorata				
Stream (S)	1	0.21	3.15	10
Patch (P)	2	0.18	2.67	12
S*P	2	0.07	1.09	1
Sample	29	0.06		77
Baetis sp				
Stream (S)	1	0.08	6.35	2
Patch (P)	2	1.45	119.99	58
S*P	2	0.01	0.15	0
Sample	29	0.08		40
Leuctra sp				
Stream (S)	1	1.07	3.47	21
Patch (P)	2	0.80	2.61	21
S*P	2	0.31	4.31	20
Sample	29	0.07		38
Siphonoplera torrentium				
Stream (S)	1	0.24	8.26	6
Patch (P)	2	1.38	47.48	55
S*P	2	0.02	0.34	0
Sample	29	0.08		39
Orthocladiinae				
Stream (S)	1	0.20	8.84	1
Patch (P)	2	9.74	431.52	82
S*P	2	0.02	0.14	0
Sample	29	0.16		17
Total				
Stream (S)	1	0.16	11.72	9
Patch (P)	2	0.57	40.27	48
S*P	2	0.01	0.35	0
Sample	29	0.04		43
Spec. richness				
Stream (S)	1	0.03	0.97	0
Patch (P)	2	0.04	1.21	2
S*P	2	0.03	0.89	0
Sample	29	0.04		98

5.4 Discussion

The results from this study suggest a strong association of invertebrate assemblage with patch type as outlined in chapter two. The propensity for some species to be restricted to a single patch type, e.g. *Philopotamus montanus*, and the strong patch specific patterns of some abundant taxa, e.g. *Simulium* and Orthocladiinae, drive the assemblage-patch relationship in both streams. It is consistent with the idea that lotic benthos, in some systems, can be viewed as consisting of a series of more or less discrete assemblages occupying particular habitat types (Reice, 1974).

In both streams, samples within each type patch were more closely related than between patch types, on every sampling occasion. These results suggest a uniqueness of the structure of the fauna of each patch type. Indeed, some taxa sampled in high abundance from Structured patches were rarely found on Loose patches, e.g. *Simulium*, whereas other taxa only occurred in high densities on Loose patches, e.g. *Ecdyonurus torrentis*. The density of many taxa formed a gradient from low density in Loose to high density in Structured, with intermediate density in Degraded patches. This gradient undoubtedly contributes to the observed assemblage-patch relation, and is largely echoed by a similar gradient in the majority of environmental variables, e.g. velocity, substrate size, moss cover and CPOM. The underlying uniqueness of the patch specific assemblages is likely, in part, due to the unique physical character of the patch types. Indeed, for the most part, strong biological analogues to physical habitat classifications have been found where habitats have been based on very different substrate types (e.g. Angradi, 1996, Pardo & Armitage, 1997). Underlying similarities in fauna however have been associated with habitat units based on similar substrates (e.g. Rabeni *et al.*, 2002) or where units form part of a gradation from depositional to erosional environments (Barmuta, 1989).

Structured patches largely drive many of the biotic patterns observed in both streams, harboring the highest density of most taxa, and in the Cramalt, the highest taxon richness. They are undoubtedly an important habitat. Indeed, the over-all contribution of Structured patches to invertebrate density is much greater than their areal extent suggests. In the Talla for example, Structured patches only account for 26 % of the surface of the streambed (see Chapter Three), yet they support approximately 43 % of the total population. In the Cramalt they support approximately 41 %, while only occupying 31 % of the surface of the streambed. In this study, only transverse and partial steps were sampled. Boulder cascades and large isolated steps were present also, and exhibited similar physical features (strong gradients in velocity, large substrate and high moss cover). Invertebrates are likely to be abundant in these structures also. Indeed, while a diverse bedform nomenclature exists in steep streams (see Grant *et al.*, 1990, de Jong *et al.*, 1995), bedform features may be biological very similar. The high taxon richness and density on transverse steps for example is consistent with that of Biggs *et al.*, (1997) on micro-bedform clusters.

The mechanisms underlying many of the associations of invertebrate density with patch type are likely to be complex and varied, and at least partly relate to the unique physical characteristics of the patch type. The preference of filter feeders for example, for large particles (e.g. Wallace, 1975), high velocity (e.g. Wetmore *et al.*, 1990, but see Edington, 1968) and moss cover (e.g. McAuliffe, 1984) may explain the strong association of *Simulium*, *Philopotamus montanus* and *Hydropsche siltalai* with Structured patches. Environmental variables alone nevertheless do not explain the entire variance observed in invertebrate density. While a large portion in variance is shared, the patch classification still accounts for a portion of variance not already explained by the environmental variables. The patch classification likely incorporates a number of factors that can potentially affect invertebrate distribution, but are traditionally difficult to quantify, such as disturbance history (Matthaei & Townsend, 2000), and drift settlement (Hart & Finelli, 1999, see Chapter Six). The low density of sedentary species and filter feeders, and dominance of mobile Ephemeroptera on Loose patches for example, is consistent with the notion that these patches are mobilized, and hence likely disturbed (see Chapter Seven), more often than Degraded or Structured patches (Scarsbrook & Townsend, 1993).

One concern raised in Chapter Three was the potential for high variation in invertebrate assemblages on Degraded patches relative to the other patch types. The Degraded patch describes the majority of the streambed, including rapid, riffle and pool units, and incorporates a wide range of sediment size and velocity. This physical variation was not, however, reflected in the invertebrate assemblage. The assemblage on this patch type was no more variable than that of Loose patches in the Talla, and Structured patches in the Cramalt. Indeed, in the Cramalt Structured patches were twice as variable, as defined by paired average Bray-Curtis dissimilarity score, as those in the Talla. This was consistent across season, and is somewhat intriguing as sediment size and structure was similar between the two streams, and indeed replicate patches. The Structured patches in the Cramalt however were more variable with respect to CPOM, potentially an important resource for detritivores and some suspension feeders (Suren & Winterbourn, 1992, Allan, 1995, Nikora *et al.*, 1998). While substrate may be of prime importance in the local distribution of invertebrates (Minshall, 1984), and indeed may be an important determinant of distribution across patch types here, at smaller scales, between patch replicates, other factors maybe more important, such as CPOM.

For some taxa, factors operate at different spatial scales to that of the patch classification, influencing their distribution. *Philopotamus montanus* for example, while it showed very strong patch specific distributional patterns in the Talla, it was limited to this stream. Indeed, stream differences and patch classification accounted for a similar amount of variance in invertebrate assemblage. In a study of the spatial variation in the distribution of stream invertebrates, Downes *et al.*, (1993) clearly showed that not all species abundances varied over similar spatial scales, supporting the view that no single 'patch size' exists for the whole invertebrate assemblage (Pringle *et al.*, 1988). Indeed, while strong patch specific associations were found, the results of this study are in general support of this. The distribution of some taxa between patch types and stream however, suggests that the factors responsible for distribution at one scale, i.e. patch, may not be consistent across streams. *Rhithrogena semicolorata* and *Siphonoperla torrentium* occurred in both streams, but only exhibited patch specific patterns in density in one; higher densities on Loose patches in the Cramalt. The pattern of taxon specific density on Structured and

Degraded patches was remarkably consistent between streams. For taxa such as *Rhithrogena semicolorata* and *Siphonoperla torrentium* however, the generality of the patch classification is questionable.

The overriding pattern of faunal density within this study nevertheless suggests a strong biological analogue to the patch classification of these two streams, which is largely driven by the Structured patches. One of the possible mechanisms, constrained settlement from drift dispersal, is investigated in Chapter Six. The high density of individuals on Structured patches may partly be a result of the unique hydraulic environment, which may promote settlement from the drift immediately downstream of the feature in the re-circulation zone (i.e. flow back towards the step), effectively 'trapping' the drift. As these features can span the width of the channel, all flow and drift is likely to encounter the hydraulic environment associated with Structured patches. The distribution may also reflect disturbance history. Flooding in these high gradient streams occurs frequently, indeed, it is estimated in the Talla the Loose patches are mobilised every 3 to 4 weeks by minor events, which presumably result in increased shear forces on Structured patches, and mobilisation of the matrix within Degraded patches (Chapter Four). Some of the fauna on Structured patches appear to be well adapted to living in high flows, e.g. *Simulium* sp, and may be able to resist dislodgement on these patches during minor events. The patch specific response to flooding is examined in Chapter Seven.

Chapter Six Influence of Transverse Steps on Drift and Settlement of Invertebrates

6.1 Introduction

This chapter focuses on the influence of transverse steps on drift and settlement. For the majority of taxa in the Talla and Cramalt (with the exceptions of *Ecdyonurus sp*, *Rhithrogena semicolorata* and *Siphonoperla torrentium*) transverse steps harboured a greater density than other areas of the streambed. While many factors may drive such distributions (see Chapter Four and references therein), one possible mechanism is the constraint imposed on drifting and settling invertebrates by the unique hydraulic character of the step environment (see Fonseca & Hart, 2001). Although a lot work has been done on the settlement constraints imposed by hydraulic forces on marine larvae (see review, Downes & Keough, 1998), this is a relatively new idea for lotic systems and warrants much more consideration.

In streams, downstream movement of invertebrates in the water column, or drift, is a prime mechanism of larval dispersal for many taxa (Bilton, *et al.*, 2001). It provides a supply of immigrants to newly available substrates (Townsend & Hildrew, 1976), can directly affect the local distribution of some taxa (Fonesca & Hart, 2001), and alter local assemblages via influx of new species (Palmer *et al.,* 1995). Many studies of invertebrate dispersal in streams have focused on factors that influence the initiation, composition and abundance of drift, such as hydraulic disturbances (Tockner & Waringer, 1997, Gayraud *et al.*, 2000, Imbert & Perry, 2000), and density dependent effects such as reduced feeding rates (Fonesca & Hart, 1996), predation (Lancaster, 1990), and diurnal cycles (Waters, 1965, Elliott, 1969). Although many factors that influence the initiation of stream drift are well documented, the factors that determine when and where a drifting invertebrate will return to the substrate are poorly understood, but no less important. The distance invertebrates drift and their settlement habitat ultimately influence the supply of immigrants to the substrate; and hence potentially influences local population dynamics, assemblage composition and instream distribution patterns.

Where there is a strong uni-directional flow of water, velocity provides a strong control on drift distance (Elliott, 1971). Distance generally increases with current velocity, and the nature of this relationship varies with the behaviour of the organism (Ciborowski & Corkum, 1979, Cambell, 1985, Allen & Feifarek, 1989). At moderate to high velocity, for example, swimming towards the substrate can reduce drift distance (Elliott, 1971, Allen & Feifarek, 1989); at low velocity, swimming up into the water column or splaying of the legs and increasing surface area can prolong drift and increase distance travelled (Campbell, 1985, Allen & Feifarek, 1989).

Traditionally, most drift studies consider only the stream-wise component of velocity, lateral and vertical flows have received less attention. The fluid environment in streams is complex and three dimensional, and although the net direction of flow is downhill, parcels of water may not always flow at the same rate, or same direction. Complex flow patterns can potentially influence the distance an invertebrate may drift. Lancaster *et al.*, (1996) related drift distance with mean hydraulic dead zone volume of a stream channel, a reach-averaged measure of departure from the stream-wise velocity component. They found that drift distance for most invertebrate species was inversely correlated with dead zone volume, and was roughly independent of average stream-wise velocity. However, drift distance was not related simply or only to dead zone volume, or indeed stream-wise velocity. There potentially exists a complex set of interactions between hydraulic environment, invertebrate behaviour, drift distance and settlement location. To understand fully the causes and consequences of drift, we need to tease apart these interactions.

The hydraulic environment in streams is largely influenced by channel morphology and thus the characteristics of invertebrate drift and settlement may also vary between channels that differ in geomorphology. In steep streams, channel-spanning steps are ubiquitous and typically consist of several large boulders jammed together to form a small isolated fall (Chin, 1989). They create a distinctive hydraulic environment characterized by a re-attachment point downstream, where the flow over the step is forced down towards the bed, and a re-circulation zone between the step and re-attachment point, where flow runs up towards the step (Keogh & Addison, 1996). A shear layer of high turbulence is created downstream of the step as the faster main channel flow shears across the top of the slower fluid contained within the re-circulation zone. Drift over a step is potentially influenced by all three hydraulic characteristics; downward forced flow to the re-attachment point, upstream flow within the re-circulation zone, and increased turbulence. The hydraulic influence of the steps can exist up to 10 step heights downstream (Keogh & Addison, 1996), and the turbulent effects of the shear layer can extend considerably further (Bradshaw & Wong, 1972). So, a 20 cm step could alter local flow dynamics for > 2 m, a long distance for a drifting invertebrate. Channel spanning steps clearly have the potential to affect invertebrate drift as all surface flow, and hence drifting invertebrates, is forced over the structure. Furthermore, the potential for upstream drift within the re-circulation zone could be significant in steep streams where sequential steps can be common and closely spaced (Chin, 1989).

I investigated the small-scale interactions between invertebrate behaviour and hydraulics that may influence dispersal distance and settlement. Specifically, I tested whether drift distance and time spent in the drift were altered by the hydraulic environment associated with a channel spanning step, a typical Structured patch in steep streams. The experiment was carried out in a large flume where I could manipulate and measure in detail the hydraulic environment, and observe the drift and settlement of invertebrates. For invertebrates that drift primarily as passive particles, or have little behavioural control, such as swimming, (e.g. many larval Diptera and Trichoptera) I predict that drift distance and drift time will be lower over a step than over a plan bed. Increased turbulence downstream of the step can promote rapid descent to the substrate (McNair, 2000) and entry into the re-circulation zone, allowing for settlement on or near the step. For taxa that are more active in the drift however (e.g. nymphal Ephemeroptera), I predict that behaviour, as defined by swimming and posturing, could either increase or decrease drift distance and drift time depending on species-specific behaviour. Marine studies suggest that increased turbulence can increase swimming activity in some invertebrate species, and decrease it in others as a result of an inability to maintain geotatic responses and orientation (Pawlik & Butman, 1993,Tankersley *et al.*, 2002, Forward *et al.*, 2003). If an increase in swimming activity over the step results in an individual entering the re-circulation zone, then the net effect of the step will be to decrease drift distance, independent of stream-wise velocity. However, if increased swimming activity results in drift high in the water column, or indeed a reduction in swimming activity high in the water column, then there is likely to be an increase in drift distance, by passing the re-circulation zone. If indeed the hydraulic environment associated with the transverse step constrains the settlement of drifting larvae, it may influence their distribution (e.g. Fonseca & Hart, 2001). The results of this study may help explain some of the patch specific density patterns observed in Chapter Five.

6.2 Method

6.21 Experimental Design

Experiments were carried out in a laboratory flume in which I could measure drift distance and drift time, and record drift behaviour within controlled hydraulic environments. In 2 X 2 balanced factorial experiments, I manipulated bed topography (step vs plane bed) and the ability of individuals to respond behaviourally (dead vs live animals). An interaction between the two factors would indicate a change in behaviour with an associated change in hydraulics.

In a horizontal glass paneled flume (10 m long, 0.3 m wide and 0.4 m deep) (Figure 6.1a), mains water was circulated by a pump and maintained at 10 to 12 °C (within the range of water temperature in surrounding streams, Loughborough). Maximum discharge was 0.03 m^3/s, equating to a free stream velocity of approximately 1 m/s at 0.1 m depth. Discharge was controlled via the outlet valve on the pump; and water velocity and depth were controlled by a tailgate at the end of the flume. During operation, water was pumped from the storage tanks, up a water tower at the head of the flume, where it then flowed through a collimator and into the working channel, producing a steady flow. For all experiments discharge was maintained at 0.02 m^3/s, at a mean water depth of 28 cm and mean stream-wise velocity of 0.20 m/s, 11 cm above the plane bed.

6.22 Topography

Washed river gravels were used as the base substrate for both topography treatments, plan bed and step. The gravel was glued using a slow curing epoxy resin to

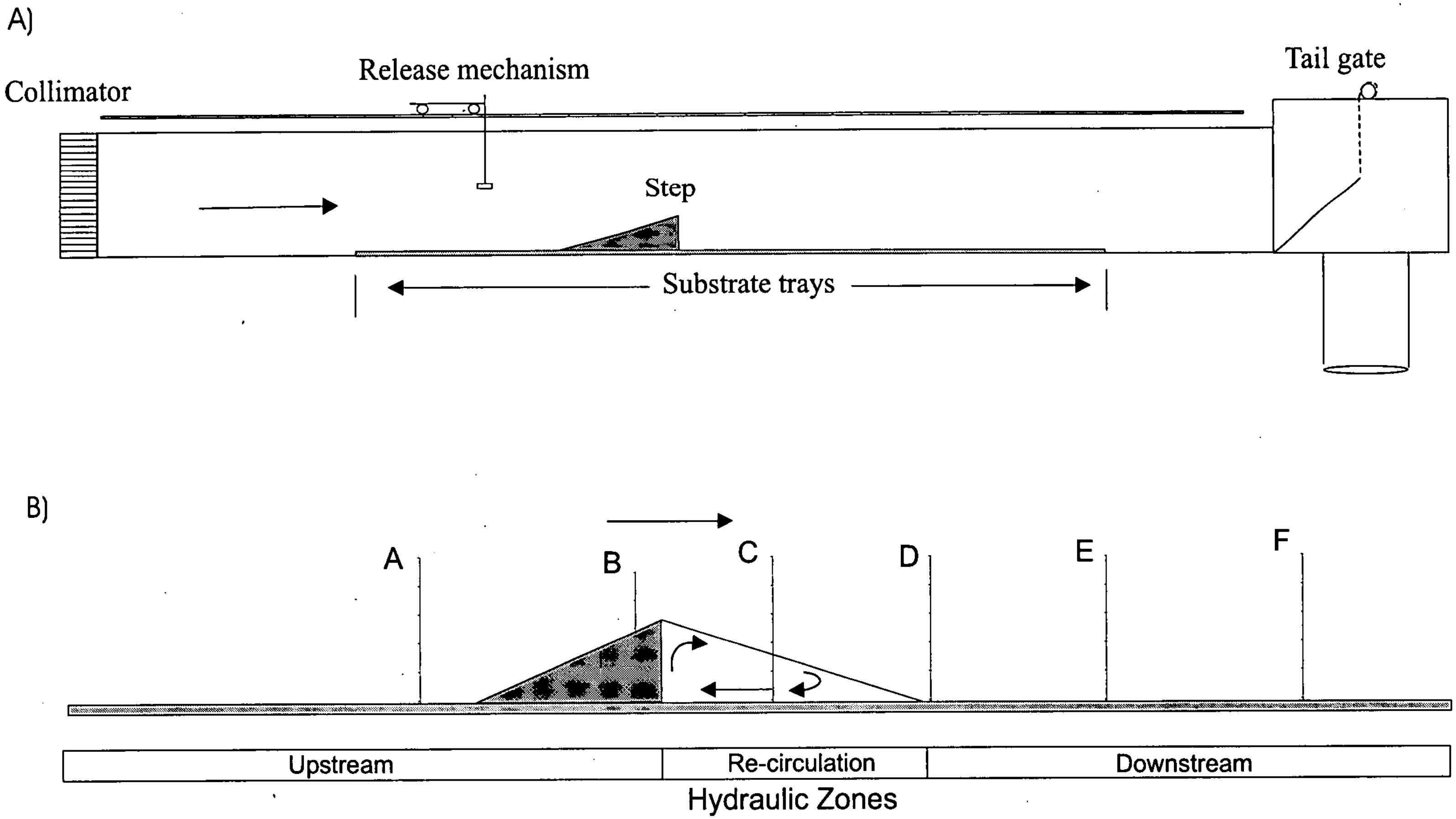


Figure 6.1 A) Schematic of the flume showing position of the trays and step in relation to the release point and flume inlet and outlet pipes B) Step bed showing positions of the velocity and turbulence profiles shown in Figure 6.2. The relative positions are the same over the plane bed. Also shown are the main hydraulic zones, 'upstream', 're-circulation' and 'downstream' (see Table 6.1 for basic hydraulic characteristics of each zone).

prefabricated aluminium trays (0.3 X 1.0 m) that rested on the bottom of the flume. Identical grain size sediment distributions were established for each aluminum tray by sieving, weighing and mixing set proportions of the following particle sizes, 45, 32, 22, 16, 10 and 5 mm in aliquots of 0.28, 0.46, 2.36, 3.25, 0.68 and 0.2 kg respectively. This distribution gave a $D_{50} = 15$ mm.

In the plan bed treatment, seven substrate trays were placed end to end along the flume, the upstream-most tray being 1.5 m downstream from the collimator; the downstream-most tray 1.5 m above the flume tail gate, giving a working length of 7 m. For roughness to generate a boundary layer upstream of the experimental arena, concrete hemispheres (5 cm diameter) and pebbles (b-axis of ~40 mm) were placed between the collimator and the edge of the first tray.

In the step treatment, a simple, ramped step was created in the flume (Figure 6.1b). Step height (17 cm) was constrained by the size of the flume, but was large enough to mimic the main hydraulic characteristics invertebrates may encounter in the field (e.g. steps of 10 – 40 cm are typical of local upland streams). Step shape was designed to create a hydraulic environment downstream of the step characterized by a strong turbulent shear layer, a re-circulation zone, and a re-attachment point. The step consisted of a vertical face and an upstream ramp (Figure 6.1b). The vertical face was a wooden block 17 cm high, 2 cm thick, extending across the flume width. The ramp consisted of an aluminum tray (10 x 30 cm) with one end attached to the top of the wooden block, the other resting on the floor of the flume. The choice of ramp length was guided by surveying natural steps in the field, which were commonly characterized by a wedge of sediment against the upstream face of the step, at an angle of 10 to 15 degrees. Sediment of a similar size distribution to that on the plane-bed trays was glued to the ramp. Taking a datum equivalent to the D_{50} of the substrate sediment on the trays (15 mm), the effective step height was 16 cm. The step was positioned in the flume by replacing the third plan bed tray from the upstream end with step face and ramp, effectively giving 4 m of plane-bed downstream and 2 m upstream.

6.23 Hydraulics

Velocity was measured using an Acoustic Doppler Velocimeter (ADV) mounted on a moveable trolley above the flume. In a non-intrusive manner, the ADV recorded the streamwise, lateral and vertical velocity components to within 0.5 mm of the bed at a rate of 25 Hz. Eleven velocity profiles were obtained over the plane-bed along the centerline of the working length, with eight or nine point measurements in each profile and a 30 s average recorded for each point. With the step in place, 31 velocity profiles were collected along the flume, again using 30 s averages at up to ten points per profile. Fewer measurements in the vertical were collected in the shallow water over the ramp. Profiles were concentrated around the step to provide a detailed characterization of the hydraulic environment.

At each point on each profile, the 30 s time-series were used to estimate the intensity of turbulent fluctuations. For example, in the streamwise direction fluctuating turbulent velocities u', were calculated as

$$u' = u - \bar{u} \qquad \text{Equation} \quad (6.1)$$

where $\bar{u}$ is the mean velocity for the time series and u is an individual velocity measurement. Similar fluctuations for the vertical and lateral components are v' and w'. The intensity of the fluctuations was characterized by the standard deviation of the velocity series or the root mean square (Clifford, 1993); for example,

$$RMS_u = \sqrt{((\sum u'^2)/n)} \qquad \text{Equation} \quad (6.2)$$

An index of total turbulent intensity is then provided by the turbulent kinetic energy, TKE (cm^2/s^2),

$$TKE = 0.5\rho(RMS_u^2 + RMS_v^2 + RMS_w^2) \qquad \text{Equation} \quad (6.3)$$

where ρ is water density.

The hydraulic conditions along the working length of the flume were steady and uniform over the plane-bed, with well-established semi-logarithmic streamwise velocity profiles throughout the entire working section (Figure 6.2b). Three different hydraulic zones were established over the step bed: (i) a zone "upstream" of the step with hydraulics similar to those of the plane-bed but with a steady increase in velocity, (ii) a "re-circulation" zone from the edge of the step to the re-attachment point, and (iii) a zone "downstream" from the re-attachment point (Figures 6.1b & 6.2a, Table 6.1). Upstream of the ramp (profile A in Figures 6.1b & 6.2a) the

Table 6.1 Summary hydraulics over the plane bed (mean velocity and turbulence) and step bed (Max – Min velocity and turbulence within each hydraulic zone, see Figure 6.1).

	Streamwise Velocity (m/s)		**Turbulence (cm^2/s^2)**	
Plane Bed	Uniform	0.24	Low	3-5
Step Bed				
Upstream	Steady increase	0.24 – 0.60	Low	3-5
Re-circulation	Highly variable	-0.20 – 0.80	High	10-35
Downstream	Variable decrease	0.45 – 0.28	Slow dissipation	30-9

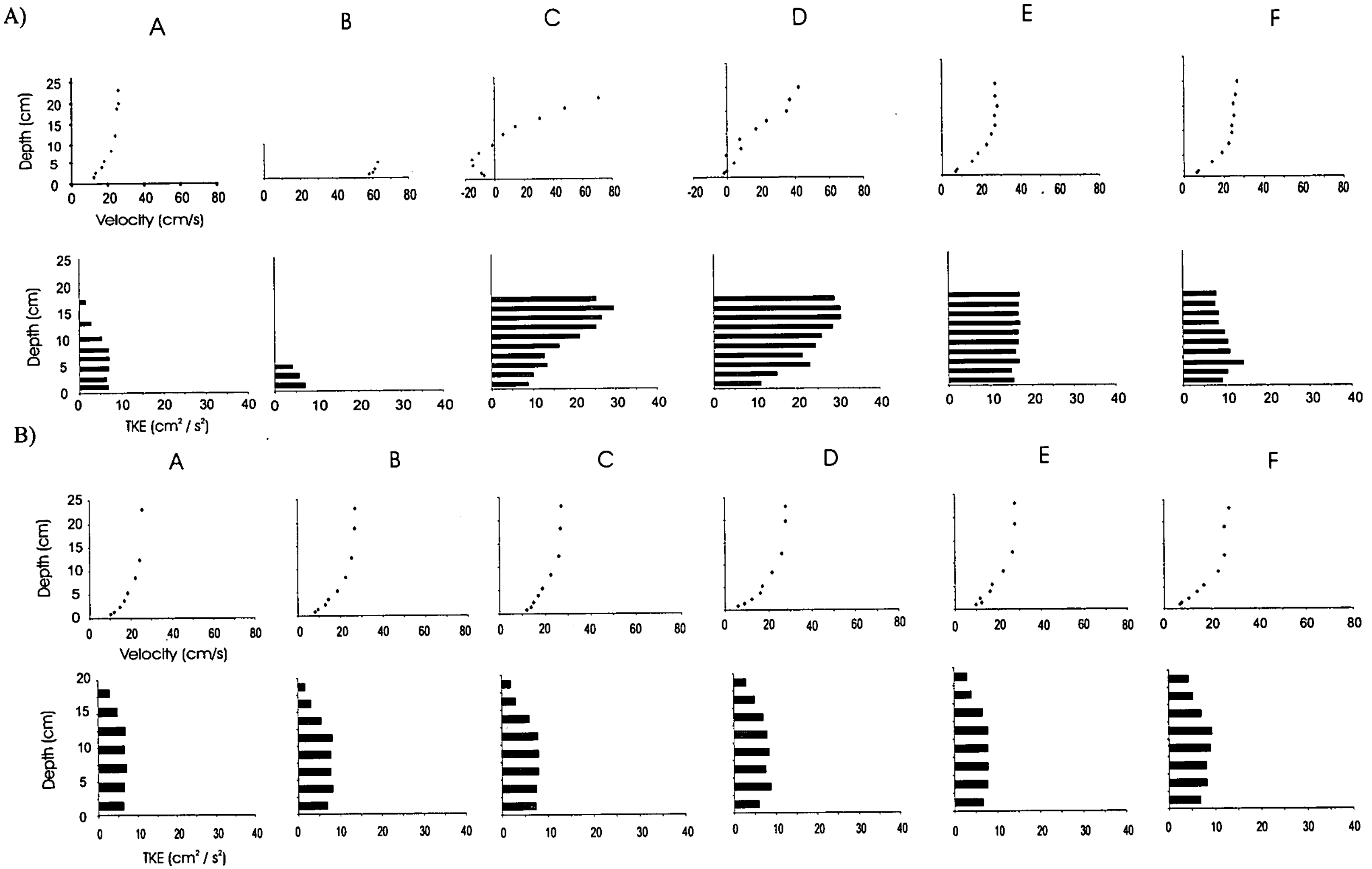


Figure 6.2 Downstream velocity and turbulence profiles over A) step bed and B) plane bed. See Figure 6.1 for the position of each profile (A-F). The profiles were chosen to illustrate the main velocity and turbulence characteristics of each hydraulic zone over the step bed (See Figure 6.1). ‘Depth’ is the water depth above the substrate.

downstream velocity component at the height of invertebrate release (19 cm above the substrate) downstream velocity component at the height of invertebrate release (19 cm above the substrate) changed rather little (an increase from 0.25 m /s to just over 0.26 m /s), but it then increased rapidly to over 0.60 m /s towards the edge of the step (profile B in Figure 6.2a). The dominant velocity component in this upstream section was in a downstream direction, with little vertical or lateral component. Despite this large increase in velocity up the ramp, there was little change in TKE (profile B Figure 6.2a). Indeed, TKE upstream of the step face was very similar to that over the plane-bed, with the most intense turbulence close to the rough bed.

The re-circulation zone (Figures 6.1b & 6.2a) had a re-attachment point 1.42 m downstream from the step, where the turbulent shear layer reaches the substrate and mean streamwise velocity near the bed approaches 0. The re-attachment point is close to profile D in Figures 6.1b and 6.2a. The exact location was determined from the series of 31 velocity profiles taken along the length of the flume over the step bed. The distance downstream to the re-attachment point, approximately 9 step heights, is in general accordance with other studies (Keogh and Addison, 1996). Velocity within the re-circulation zone (profile C Figure 6.2a), upstream of the re-attachment point, reached almost 0.20 m/s in an upstream direction 5 cm above the bed. The streamwise velocity above the re-circulation zone however peaked at approximately 0.80 m/s in a downstream direction, 19 cm above the bed, giving a net change in velocity of almost 1 m/s from the bed to the surface. Turbulence within this area was 6 to 7 times higher than at the same height above the plane bed, or upstream of the step. At the re-attachment point, TKE close to the bed increased as the shear layer separating the re-circulation zone and the more turbulent upper layer reached the substrate (profile D Figure 6.2a). In the downstream zone, TKE slowly dissipated, but was maintained throughout the entire water column at levels greater than over the plane bed (profile E Figure 6.2a). Towards the end of the working section of the flume (6.7 m), both velocity and TKE had fallen back to levels approaching that over the plane-bed (profile F, Figure 6.2a). The overriding effect of the step was an increase in velocity associated with a plume of high turbulence propagating downstream, initially confined to the upper portions of the water column before extending throughout (Figure 6.3).

6.24 Experimental Procedures

I used four species of aquatic insect larvae that are common in medium to high gradient streams, encompassing a range in body morphology, size and swimming ability. *Ecdyonurus torrentis* (Heptageniidae, Ephemeroptera) is strongly dorso-ventrally flattened and commonly inhabits fast flowing riffle sections of rivers and streams. It is a competent swimmer, using dorso-ventral undulations to propel itself through the water. *Baetis rhodani* (Baetidae, Ephemerpotera) is a strong swimmer and also uses dorso-ventral undulations for propulsion. Unlike *E. torrentis,* however, it has a cylindrical body shape, with only minor dorso-ventral flattening towards the end of the abdomen. *Hydropsyche pellucidula* (Hydropsychidae, Trichoptera) is largely incapable of swimming, but does occasionally display a wiggling motion of the abdomen whilst in the water column, although this provides little if any propulsion. *Simulium* sp. (Simuliidae, Diptera) are cylindrical animals with no

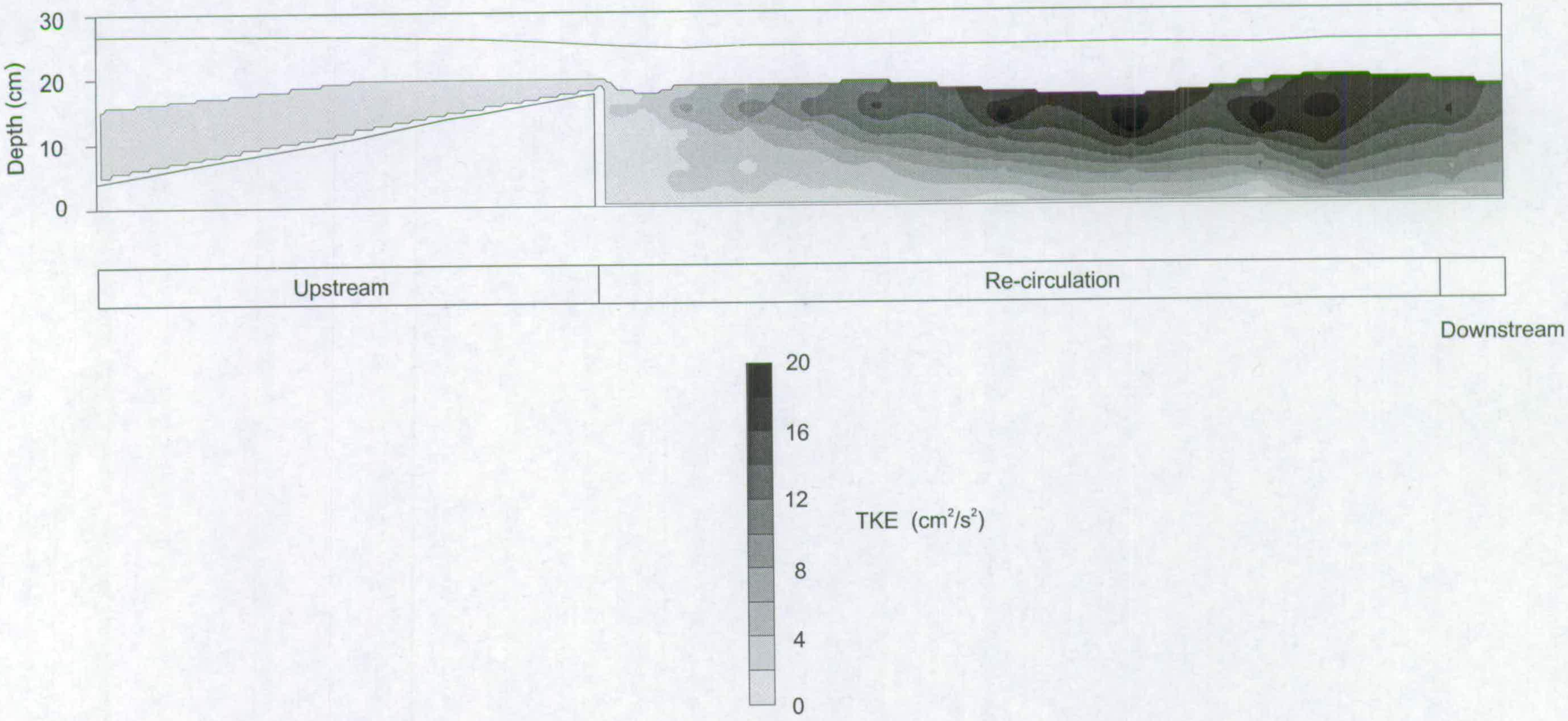


Figure 6.3 Plume of turbulence in re-circulation zone downstream of step

functional legs and no active ability to swim or maneuvre in the water column. They attach to hard substrates by means of posterior hooks anchored in a silk pad, but they are not sessile and often drift (Fonseca and Hart 1996). The role of silk thread in the drift is largely unknown, although anecdotal evidence suggests that trailing threads can snag particles, facilitating re-attachment (Elliott, 1971). In the context of this study, this is not regarded as behaviour per se; whether or not a thread is snagged is likely to be beyond the control of the animal.

Invertebrate species were collected from Wood Brook, on the outskirts of Loughborough, Leicestershire, UK, and maintained in the laboratory in large (5 l) plastic buckets filled with stream water, aerated and maintained between 10 and 12 °C. Nymphs were held for no more than 12 hours before being used in the experimental trials. All invertebrates used in 'dead' trials were killed by being placed in 80% ethanol for 30 s, then placed in water to wash off all alcohol before being placed in the flume. All individuals of each species were of a similar size. Mean (min - max) head capsule width was 1.14 mm (1.1 - 1.2 mm) for *Baetis rhodani*; 3.08 mm (2.8 - 3.4 mm) for *Ecdyonurus torrentis*; 1.62 mm (1.5 – 1.7 mm) for *Hydropsyche pellucidula*; 0.82 mm (0.8 - 0.9 mm) for *Simulium* sp.

For each treatment combination (topography x behaviour) there were 20 trials for each of *Ecdyonurus torrentis*, *Baetis rhodani* and *Simulium* sp., and 10 trials for *Hydropsyche pellucidula*. Each trial involved the release of one individual into the water column, and the tracking of their drift. Each invertebrate was removed from the flume before the commencement of the next trial. The invertebrate release mechanism was positioned 0.4 m upstream from the ramp; 1.4 m upstream of the step (Figure 6.1a). Hydraulic conditions at the point of invertebrate release were the same for both topography treatments (i.e. released 19 cm above the substrate in a total water depth of 28 cm and velocity of 0.24 m/s). Invertebrates were therefore released into the same immediate hydraulic conditions. The release method was designed to be passive, with minimal handling of organisms. I used a method similar to Elliott (1971), in which invertebrates were placed into a container suspended above the bed and released, or swept, into the water column by opening a hatch facing downstream. A 1 mm mesh net covered the upstream end of the container, allowing water to flow once the hatch was opened. To minimize flow disruption in the flume, the container was as small as possible, but large enough to house the study species unimpeded. The container consisted of a 2 cm long section of square tubing (1 x 1 cm) with mesh over one end and the release mechanism (trap door) at the other end (Figure 6.4). The container was suspended from a moveable trolley on top of the flume, 19 cm above the bed (Figure 6.1a). All invertebrates, except *Simulium* sp., were easily coaxed into the open container, or swam into it when placed in the bucket, without direct handling. The container was then removed from the bucket, the trap door closed and the whole unit placed into the water column and suspended from the trolley. *Simulium* sp. larvae were carefully picked up with forceps and placed in to the container. Once in the water column, the trap door was released by pulling a cord attached to its top edge. Most individuals were swept passively into the water column. For those few individuals that clung onto the container, a light tap on the support arm was enough to elicit release and entry into the drift. For each trial of dead and live organisms, distance and time to first substrate contact were

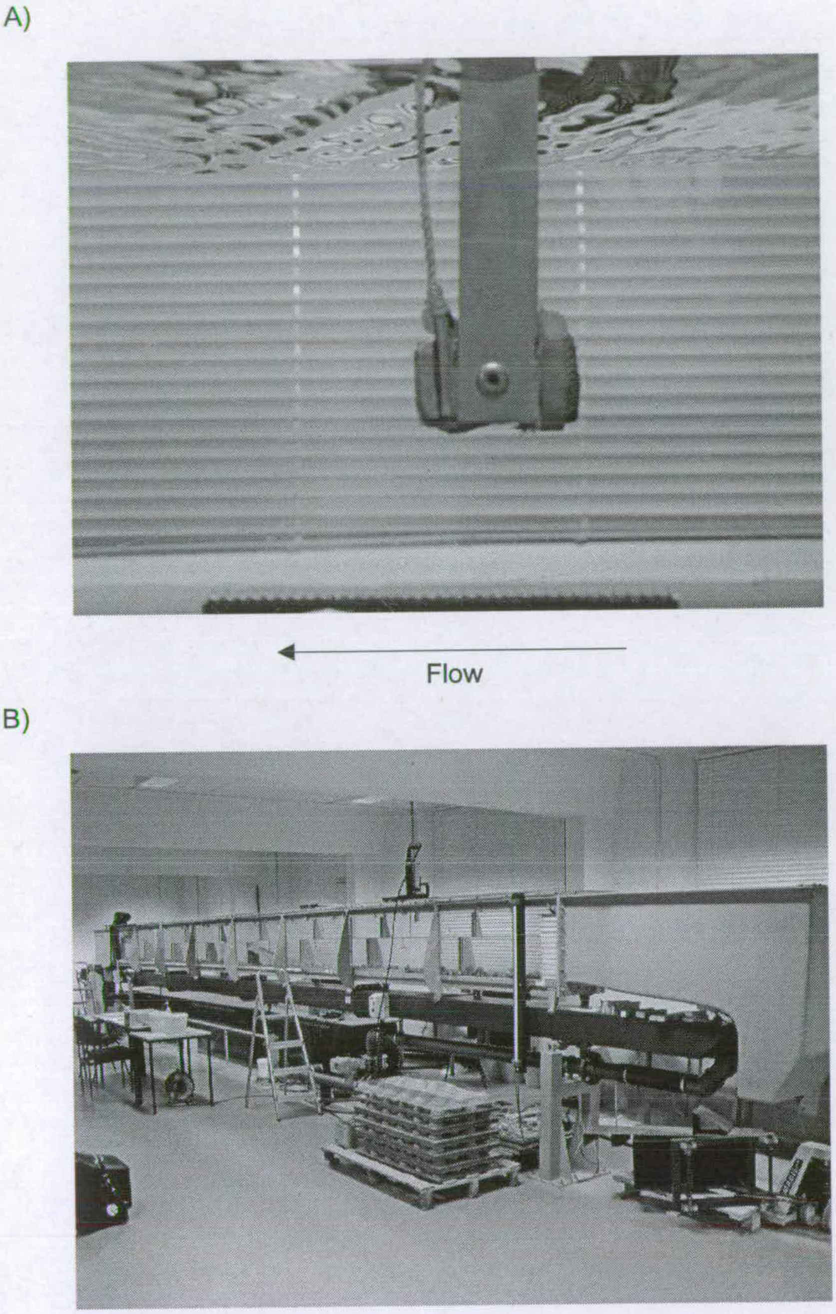


Figure 6.4 A) Release mechanism B) Flume with ADV velocity meter in position in top.

measured. Time was recorded to the nearest second from the moment the organism left the container to first contact with the substrate. At the end of each trial, insects were preserved in 70% alcohol.

Invertebrate Behaviour

Live invertebrates were filmed for the length of their drift using a digital video camera mounted onto a moveable trolley alongside the flume. The aim was firstly, to characterise drift behaviour over the plane bed, observing body orientation (i.e. whether the individual was tumbling or rolling), posture (i.e. position of legs, abdomen and thorax relative to each other) and swimming style; and secondly, to record any changes in drift behaviour associated with the change in hydraulic environment over the step. Drift behaviour was analysed using the video editing program, Media 100. This permitted slow motion tracking of swimming behaviour, and frame by frame analysis of body orientation and posture along a time series. For each hydraulic zone (i.e. upstream, re-circulation, downstream) the amount of time spent with a particular drift behaviour was recorded. At 25 frames per second, this gave a resolution of 0.04 s. The average length of swimming burst and number of swimming bursts for each mayfly species were also calculated for both topographies.

Statistical Procedures

A negative exponential relationship was fitted to the drift data to describe the number of animals in the drift with respect to the distance from release point, as has been established in previous studies (e.g. McLay, 1970; Elliott, 1971; Allan & Feifarek, 1989; Lancaster *et al.,* 1996);

$$N = N_0e^{-bx}$$

where N is the number of animals in the drift, N_o is a constant representing the number in the drift at distance 0, x is the distance of point of contact, and b is the rate of return, or settling coefficient. Regression equations were calculated for each set of 'live' and 'dead' trials for both topography treatments using non-linear curve fitting. This allowed for a comparison of the return rates over the plane bed and step bed for each species.

Drift distance and drift time were analysed by two-way analysis of variance using the statistical package SPSS 9; topography (step and plane bed) and behaviour (live and dead) were the two factors, each having two levels . All data were tested for violations in normality using the Kolmogorov-Smirnov test, and for homogeneity of variance using Levene test. Drift distance data were not transformed, time data were log (x + 1) transformed. The factor 'topography' allowed for an overall evaluation of the effect of the step on drift distance and time, the factor 'behaviour' allowed for an evaluation of the effect of drift behaviour (i.e. swimming and posturing). The main interest was in the interaction term, topography X behaviour, which indicates whether behaviour changes with hydraulic environment.

A three factor, split plot design ANOVA was used to test for a change in behaviour (e.g. swimming or posturing) of *Baetis rhodani* and *Ecdyonurus torrentis* between the upstream zone and the re-circulation zone over the step bed, and that equivalent over the plan bed, using the time series data obtained from the analysis of the films. Topography (plane bed and step) and hydraulic zone (upstream and re-circulation) were fixed factors with two levels. The factor hydraulic zone was nested within the factor topography. Each individual trial was a random factor. The response variables were proportion of time in posture and swimming, and were arcsin√ transformed before analysis. While each hydraulic zone did not occur over the plan bed per se, an equivalent distance was used to partition the plan bed into the two equivalent zones. The analysis therefore accounts for any potential changes in behaviour along the flume length that are independent of topography, e.g. due to exiting the release mechanism. The interest was therefore in the interaction between the two factors, 'topography' and 'hydraulic zone', which indicates that the change in activity from one zone to the next is different from the plane bed to the step.

A two way ANOVA was used to test for a difference in the length of swimming burst, and number of swimming bursts between species over the plan and step beds; the factors being mayfly species (*Baetis rhodani* and *Ecdyonurus torrentis*) and topography (plane bed and step). Length of swimming burst data was log (X+1) transformed. Number of swimming bursts was standardised to per 10 seconds. Transformation was not required.

6.3 Results

6.31 Drift distance and Time

The negative exponential model of invertebrate drift described drift distance for all taxa, in all treatments, i.e. all regression models were statistically significant and R^2 values high (Table 6.2). Return rate, (b), however, was highly variable (Table 6.2) with large differences between species, dead and live treatments, and plane and step bed.

Based on live trials, species fell into one of two groups with respect to drift and settlement patterns. (i) *Baetis rhodani* and *Simulium* sp were largely unaffected by the step. On plane and step beds, return rate was similar (Table 6.2) as was average drift distance (Table 6.3, Figure 6.5), average drift time (Table 6.3, Figure 6.5), and distribution of drift distance (Figure 6.6). Both species settled within all three hydraulic zones over the step, upstream, re-circulation and downstream (ii) *Ecdyonurus torrentis* and *Hydropsyche pellicuda* were affected by the step. Both species drifted further over the step than plan bed, and *Ecdyonurus torrentis* drifted for significantly longer (Table 6.3, Figure 6.5). The return rates of both species were lowest over the step (Table 6.2), and few individuals settled in the re-circulation zone, but were carried on to the downstream zone, affecting distribution of drift distance compared with that over the plane bed (Figure 6.6).

Some animals were able to influence both drift distance and time through behavioural modifications, as suggested by the effect of 'behaviour' (live vs dead). The exception was *Simulium* sp., for which both 'behaviour' and interaction effect

Table 6.2 Summary statistical analyses (regression fitted to model $Y = ax^{-b}$) used to describe drift distances of each species over the plane bed and step bed.

Species	**Treat**	**df**	**F**		**R^2**		**-b**		**P**	
			live	dead	live	dead	live	dead	Live	dead
B. rhodani	Plane	1,18	963	1362	0.982	0.987	0.581	1.060	**0.000**	**0.000**
	Step	1,18	454	191	0.962	0.918	0.611	0.550	**0.000**	**0.000**
E. torrentis	Plane	1,18	540	297	0.968	0.943	1.627	1.064	**0.000**	**0.000**
	Step	1,14	33.6	210	0.706	0.921	0.378	0.711	**0.000**	**0.000**
H. pellucidula	Plane	1,8	320	36.1	0.976	0.819	2.145	1.575	**0.000**	**0.000**
	Step	1,8	244	45.5	0.968	0.851	0.637	0.591	**0.000**	**0.000**
Simulidae	Plane	1,17	186	474	0.916	0.963	0.613	0.819	**0.000**	**0.000**
	Step	1,17	162	551	0.905	0.968	0.626	0.630	**0.000**	**0.000**

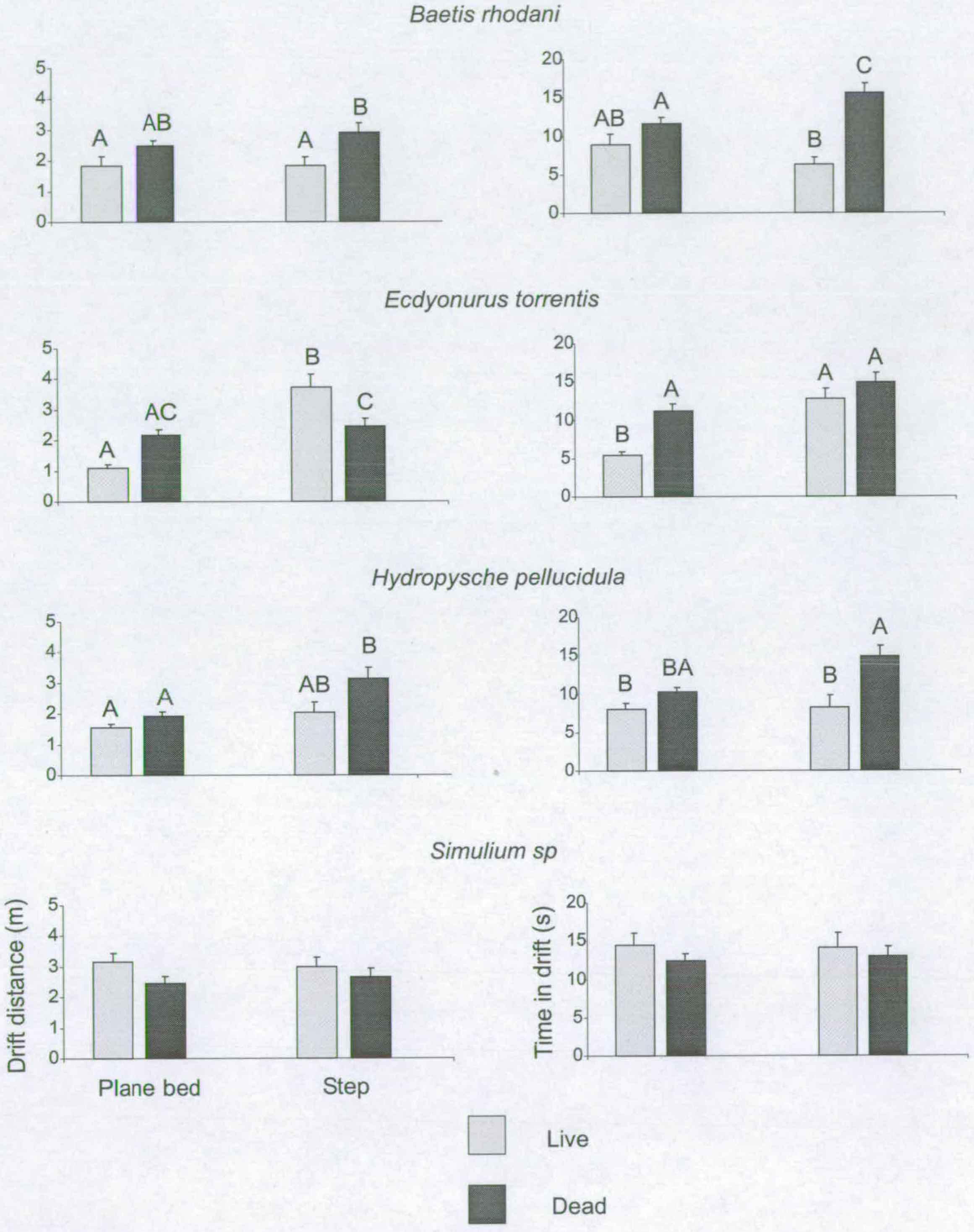


Figure 6.5 Average distance travelled (left panels) and time in drift (right panels) for each species over the plane and step beds with live and dead individuals. One standard error shown. Bars with different letters are significantly ($p < 0.05$) different. See Table 6.3 for statistical summary of ANOVA.

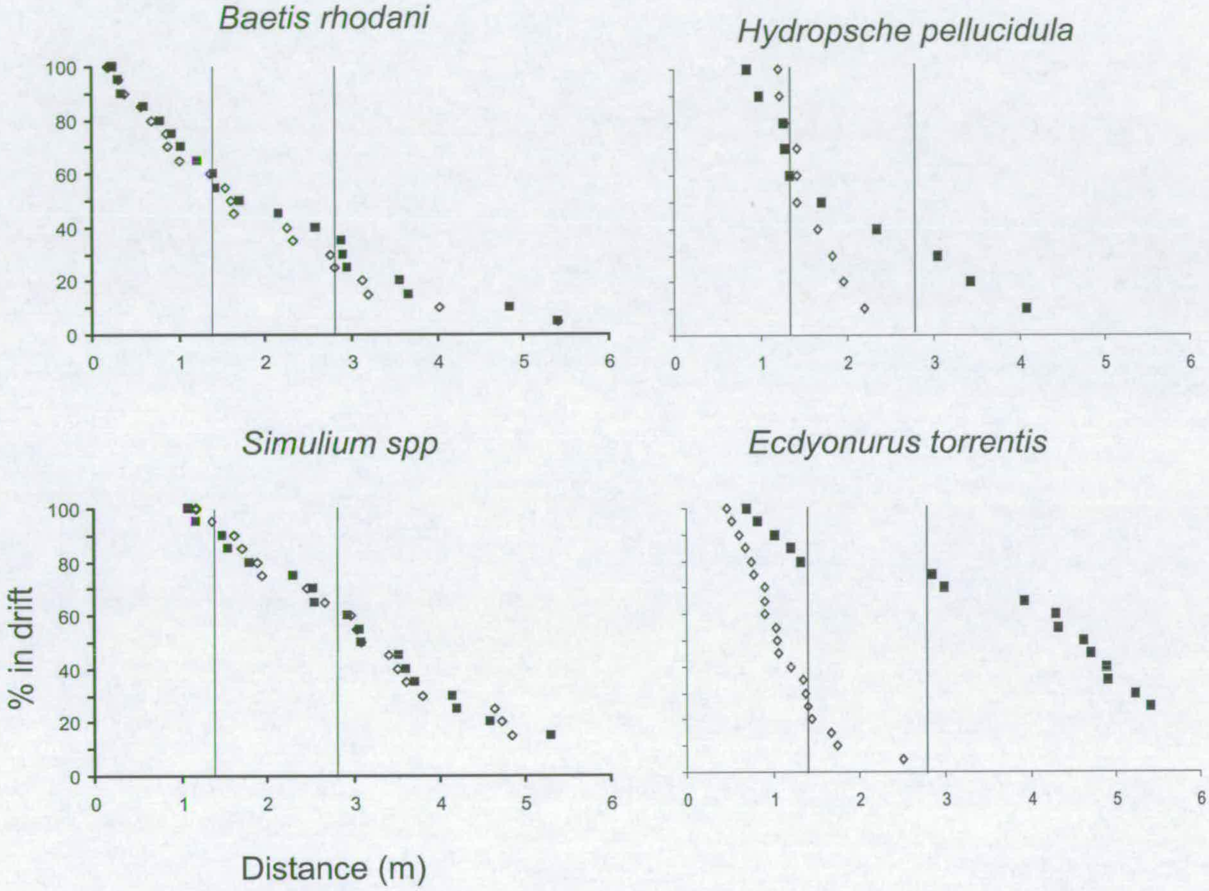


Figure 6.6 Relationship between % of individuals remaining in drift and distance downstream from release point for each species over the plane bed (open diamonds) and step beds (black squares). Only 'live' treatments shown. Coefficients in the fitted model $N = N_0e^{-bx}$ are shown in Table 6.2. Vertical lines show limits of upstream, re-circulation and downstream zones.

(behaviour X topography) were not significant for drift distance or time (Table 6.3, Figure 6.5). For *H. pellucidula* and *B. rhodani* there was a significant effect of 'behaviour' on both drift distance and time (Table 6.3); i.e. dead individuals drifted further than live and spent longer in the drift (Figure 6.5). For *B. rhodani* there was also a significant interaction between 'behaviour' and 'topography' for time (Table 6.3). Over the step bed, live individuals settled considerably quicker than dead, relative to that over the plan bed (Figure 6.5). Over the step bed, dead individuals of *B. rhodani*, and indeed also *E. torrentis*, were held in suspension for long periods of time within the re-circulation zone (Figure 6.7). Live individuals of *B. rhodani* however were able to settle quickly. For *E. torrentis*, 'behaviour' was only significant for drift time (Table 6.3), live individuals settled quicker then dead. There was however a significant interaction between 'behaviour' and 'topography' for distance (Table 6.3); i.e. dead individuals drifted further than live over the plan bed, whereas live drifted further over the step bed (Figure 6.5).

While *B. rhodani* was placed in group (i) (i.e. no recorded difference in drift distance and time between plan and step bed) the significant interaction term between 'behaviour' and 'topography' for time suggests an effect of the step on behaviour. The interaction term (behaviour x topography) for distance drifted by *E. torrentis* similarly suggests an effect of the step on behaviour. Both species appear to modify their behaviour in response to the immediate hydraulic environment. While *H. pellucidula* showed a behavioural effect, the interaction term between 'behaviour' and 'topography' was not significant. The behaviour of these species in the drift, and

Table 6.3 Summary statistics of two-way ANOVA for each species. Each factor has two levels. 'Behaviour' – Dead, Live. 'Topography' – Plane bed, Step bed.

		Distance			Time		
	DF	MS	F	P	MS	F	P
B. rhodani							
Behaviour	1	2.11	14.09	**0.000**	727.0	27.99	**0.000**
Topography	1	0.35	0.23	0.631	8.4	0.32	0.572
Interaction	1	0.27	0.18	0.670	214.3	8.25	**0.005**
Error	76	0.15			26		
E. torrentis							
Behaviour	1	0.11	1.09	0.299	303.8	13.68	**0.000**
Topography	1	3.28	32.35	**0.000**	612.7	27.58	**0.000**
Interaction	1	2.20	21.71	**0.000**	65.5	2.95	0.090
Error	76	0.10			22.2		
H. pellucidula							
Behaviour	1	0.55	8.93	**0.005**	165.1	12.22	**0.001**
Topography	1	0.48	7.67	**0.009**	40.1	2.96	0.094
Interaction	1	0.10	1.63	0.210	33.5	2.48	0.124
Error	36	0.06			13.5		
Simulidae							
Behaviour	1	0.53	2.68	0.106	0.06	0.31	0.582
Topography	1	0.00	0.01	0.916	0.02	0.10	0.755
Interaction	1	0.05	0.27	0.602	0.061	0.30	0.583
Error	76	0.20			0.20		

Table 6.4 Summary statistics of two-way ANOVA for number of swimming bursts and swimming burst length for both mayfly species. Factors have two levels. 'Species' – *Baetis rhodani*, *Ecdyonurus torrentis*. 'Topography' – Plane bed, Step bed.

	# of bursts per 10 seconds				Burst length			
	DF	MS	F	P	DF	MS	F	P
Species	1	7.22	2.78	0.108	1	6.15	13.99	**0.001**
Topography	1	1.88	0.72	0.404	1	0.65	1.48	0.230
Spec * Topo	1	0.03	0.01	0.922	1	5.77	13.12	**0.001**
error	25	2.60			46	0.44		

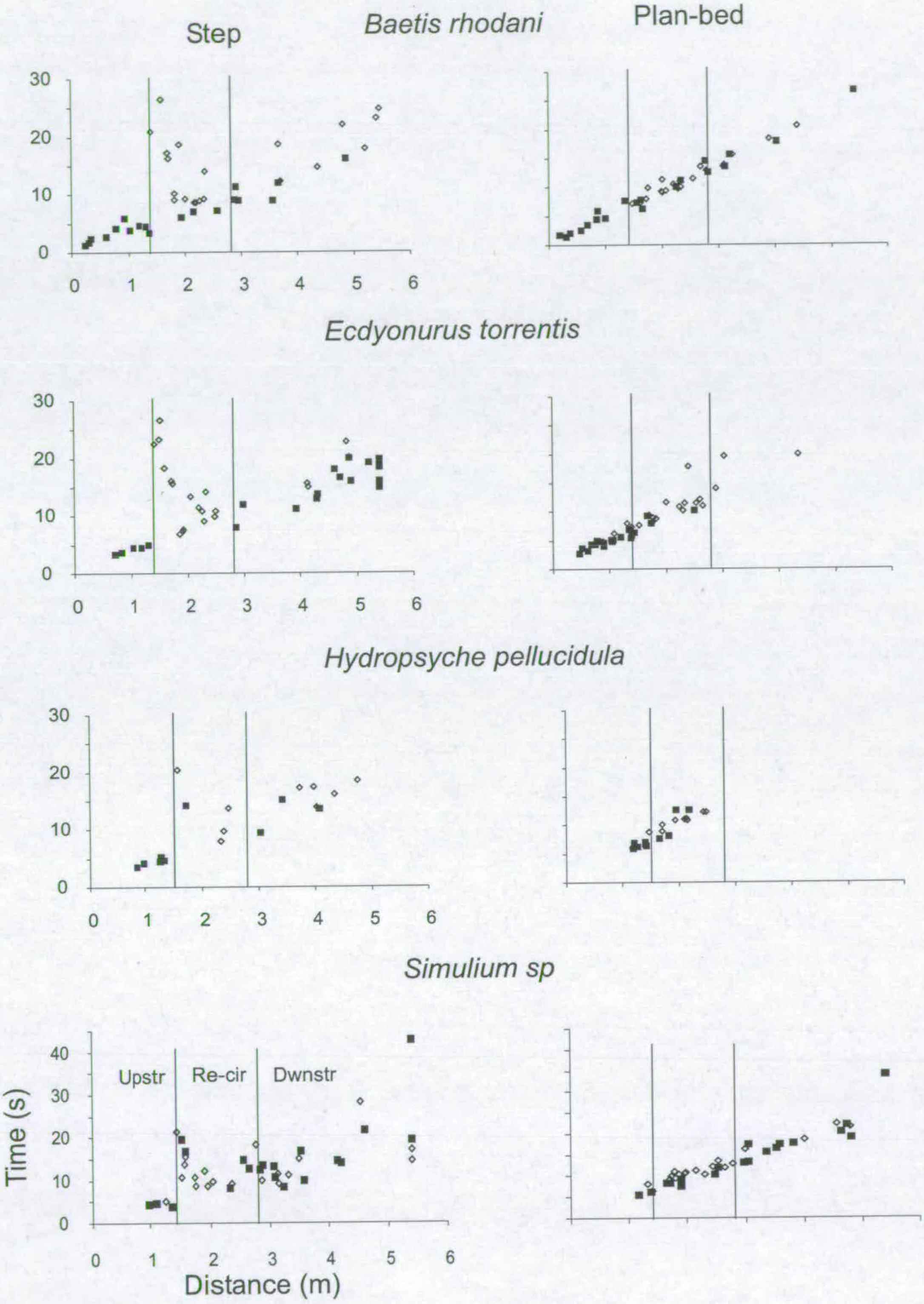


Figure 6.7 Relationship between time in the drift and distance to point of contact from release point over step bed (left panel) and plane bed (right panel) for live (black squares) and dead (open diamonds) individuals. Vertical lines show the position of the three hydraulic zones. See Figure 6.5 for average distance travelled and time spent in the drift, and Table 6.3 for statistical summary of ANOVA.

how it contributes to drift distance and drift time is explored in detail in the next section. *Simulium* sp is not included in the following analysis, as it did not ‘behave’.

6.32 Drift & Settlement Behaviour

B. rhodani, E. torrentis and *H. pellucidula* all exhibited posturing and or swimming behaviours. *Hydropsyche pellucidula* did not swim, but showed two distinct postures: curled up into a ball or stretched out. Over the plane bed, individuals spent most of the time curled into a ball (Figure 6.8), only opening out when they approached the substrate. Over the step bed, there was no dominant behaviour in the upstream zone, with equal amounts of time spent curled into a ball and stretched out (Figure 6.8). Some individuals however, opened out when they came into contact with the substrate towards the end of the ramp, bouncing in an opened position, but unable to re-gain the subsrate. In the re-circulation zone, however, individuals spent on average 70 % in the open position and only 30 % curled into a ball. In the downstream zone, there was a further change and individuals of *H. pellicudula* appeared to revert back to a pattern similar to that over the plan-bed.

When not swimming, the mayfly species, *B. rhodani* and *E. torrentis,* adopted similar drift postures with the abdomen arched backwards and the legs splayed in a ‘parachute’ like position. Whilst posturing, they maintained their body orientation, the head and thorax generally parallel to the water surface. Both species swam using rapid dorso-ventral undulations (e.g., see Kutash and Craig, 1998, for illustrations of *Baetis*). The pattern of swimming however, as defined by the duration and number of swimming bursts, differed between species (Figure 6.9). *Baetis rhodani* swam using

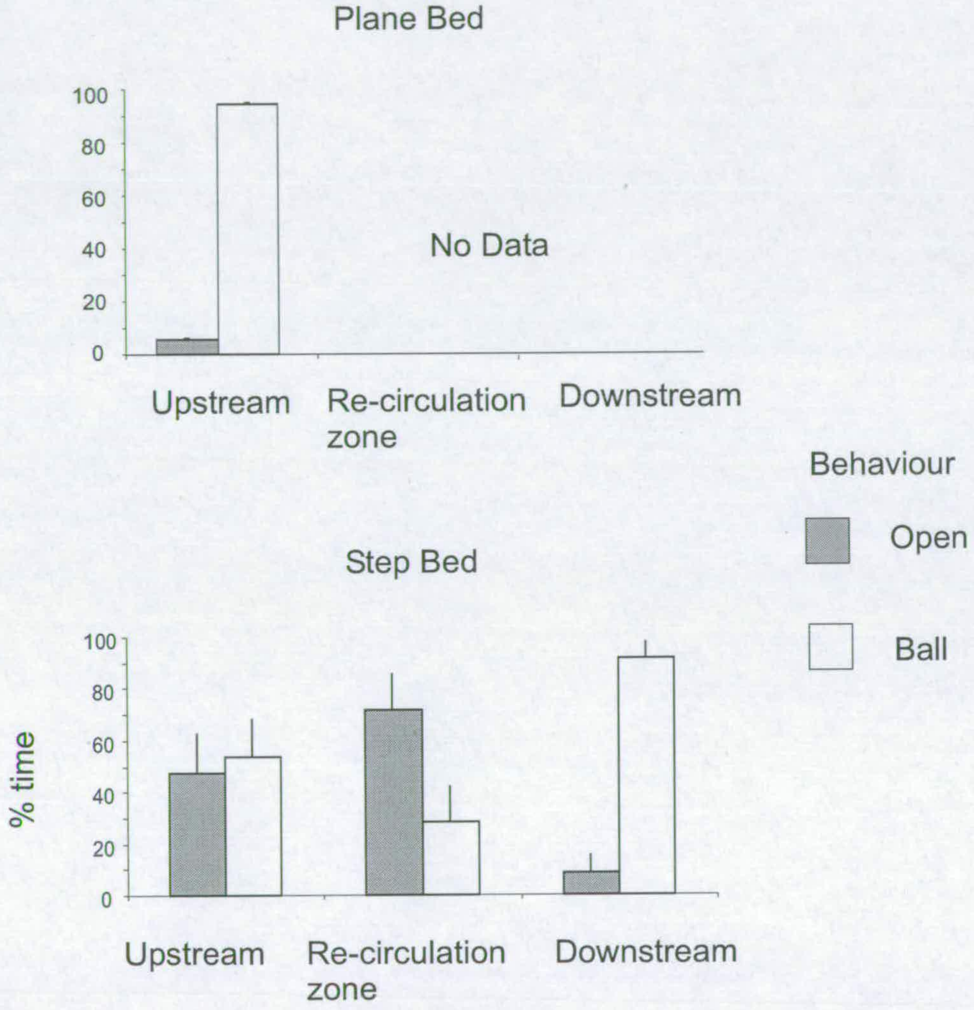


Figure 6.8 Average time (± SE) spent on each posture over the plane and step beds for *Hydropsyche pellicudula*.There are no data in the equivalent re-circulation zone or downstream zone of the plane bed because all individuals settled out in the upstream section. See text for a description of behaviours.

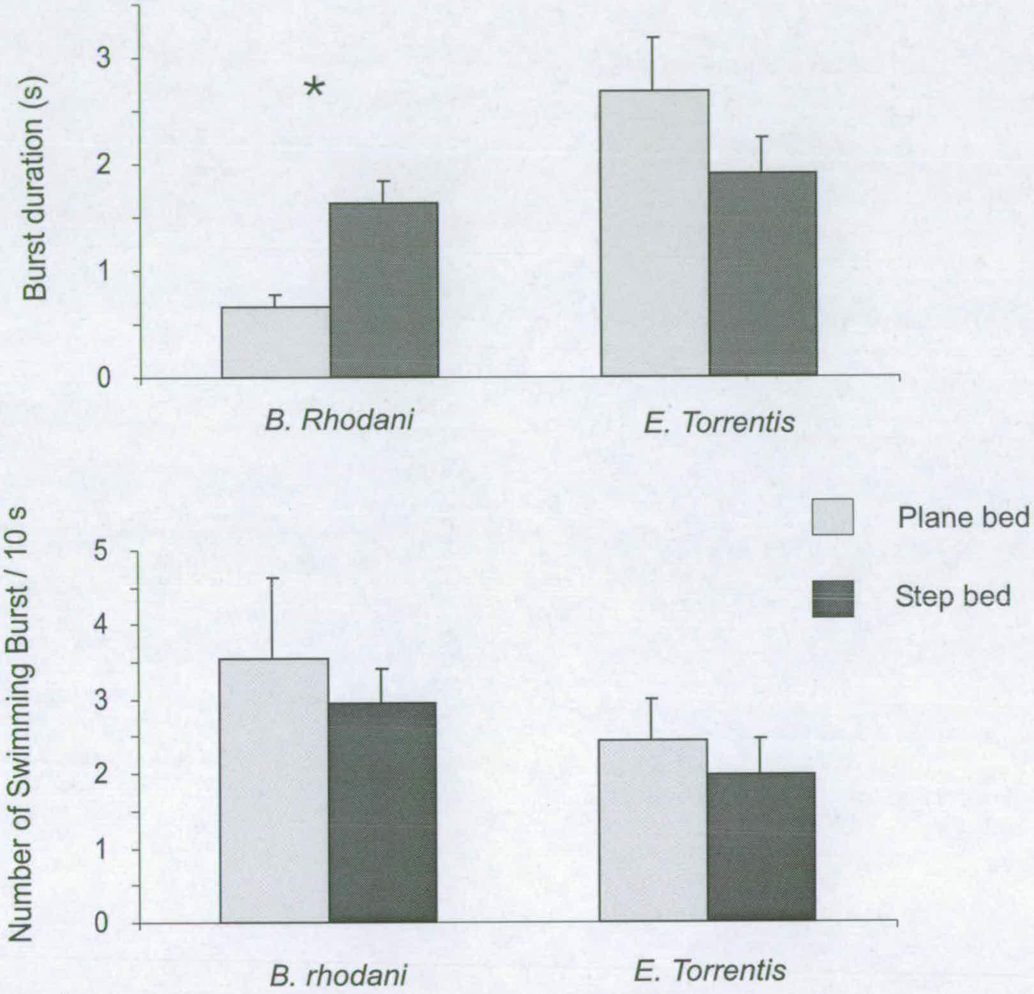


Figure 6.9 Average length of swimming burst and average number of burst per 10s over the plane and step beds for *Baetis rhodani* and *Ecdyonurus torrentis*. * indicates significant difference between bars (Table 6.4).

shorter bursts, although more frequently than *E. torrentis* (Figure 6.9). Across all trials, the longest sustained swimming burst of *B. rhodani* and *E. torrentis* was 3.1 and 5.6 s, respectively. Individuals of both species were observed swimming in all directions in the vertical and horizontal planes, but the most common and possibly most efficient way of returning to the substrate was by turning upstream and swimming downwards at an acute angle.

Over the step bed, swimming bursts of *B. rhodani* were significantly longer in duration compared with that over the plane bed (Figure 6.9). *E. torrentis*, however, had shorter swimming bursts (Figure 6.9) and, although not significant, the two species did respond in a significantly different manner (Table 6.4, significant interaction). There was no apparent change in the frequency of swimming bursts for either taxa over the step bed compared with that over the plan bed.

The longer swimming burst over the step bed exhibited by *B. rhodani* was accompanied by a significant increase in the overall time spent swimming (Figure 6.10, Table 6.5). The significant interaction between topography and hydraulic zone (Table 6.5) reflected the much longer swimming time in the re-circulation zone over the step, compared with the equivalent over the plan bed (Figure 6.10). This was accompanied by a reduction in the time spent posturing (Figure 6.10). While the overall time spent swimming or posturing by *E. torrentis* did not significantly differ between step and plan bed (Table 6.5, Figure 6.10), it did appear to have difficulty maintaining orientation downstream of the step and spent less time swimming. Indeed, *B. rhodani* similarly had trouble maintaining orientation, although not to the

Table 6.5 Summary statistics for three factor split-plot ANOVA describing change in behaviour as defined by proportion of time spent swimming or in posture for *Baetis* and *Ecdyonurus*. Factor 'Topography' = plane bed / step bed, 'Hydraulic zone' = upstream / re-circulation zone. Each individual trail is a random factor.

		Proportion of time swimming			**Proportion of time in posture**		
	df	MS	F	P	MS	F	P
Baetis							
Topography	1	2.10	18.43	**0.001**	0.79	5.89	**0.034**
Hydraulic zone	1	2.38	36.86	**0.000**	0.13	16.27	**0.002**
Topo * zone	1	1.17	18.22	**0.001**	0.42	7.53	**0.019**
Trial	11	0.11			0.13		
Ecdyonurus							
Topography	1	0.73	2.51	0.141	0.00	0.00	0.949
Hydraulic zone	1	0.14	1.27	0.283	0.37	0.35	0.094
Topo * zone	1	0.13	1.12	0.312	0.27	2.36	0.153
Trial	11				0.33		

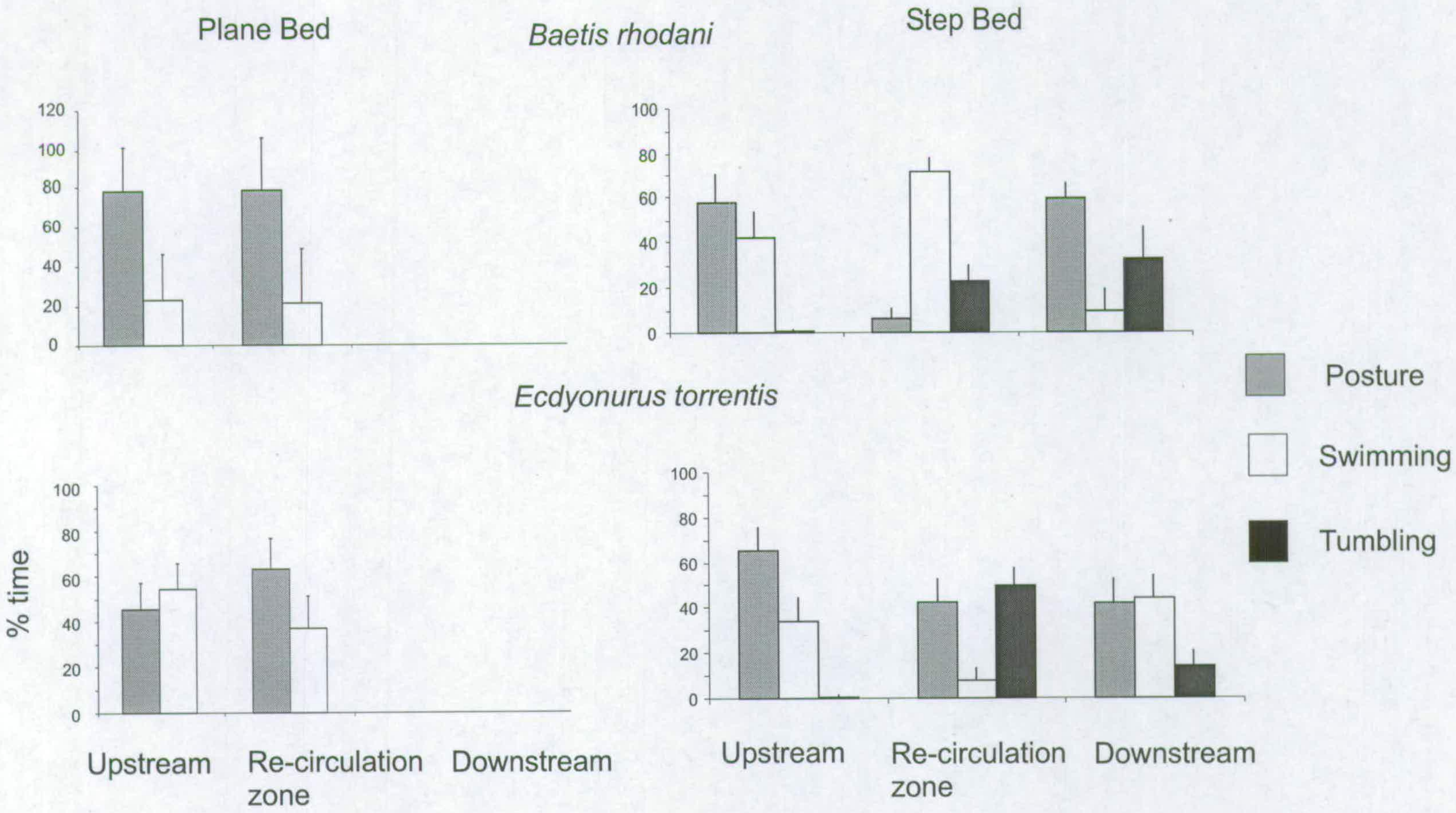


Figure 6.10 Average percentage of time (± SE) spent on each behaviour over the plane bed (left panel) and step bed (right panel) in each hydraulic zone for *Baetis rhodani* and *Ecdyonurus torrentis.* There are no data in the downstream zone equivalent over the plane bed because no individuals drift this far. See text for explanations of behaviour. No individuals experienced tumbling behaviour over the plane bed. See Table 6.5 for a summary of the ANOVA statistics.

extent of *E. torrentis*. Over the plane bed and the upstream section of the step bed, both species were able to control their orientation and remain dorsal surface up. Within the re-circulation zone, however, both species tumbled, i.e. individuals rolled, flipped end to end, or otherwise tumbled in an erratic manner. This was most pronounced for *E. torrentis* (Figure 6.10), and was associated with the drop in swimming activity.

The effect of increased turbulence on both mayfly species downstream of the step is summarized in Figure 6.11. *E. torrentis* were unable to control settlement within the highly turbulent re-circulation zone, often approaching the substrate surface only to be drawn back up into the water column by eddies. *B. rhodani* however were able to maintain smooth trajectories, swimming directly to the substrate surface in many cases.

The downstream zone was not included in the spilt plot analysis of behaviour of these two species, as too few individuals settled in this zone over the plan bed. However, a general pattern emerges in that within the downstream zone over the step, both species appear to revert back to a behavioural pattern of swimming and posture similar to that over the plane bed (Figure 6.10), although with increased tumbling.

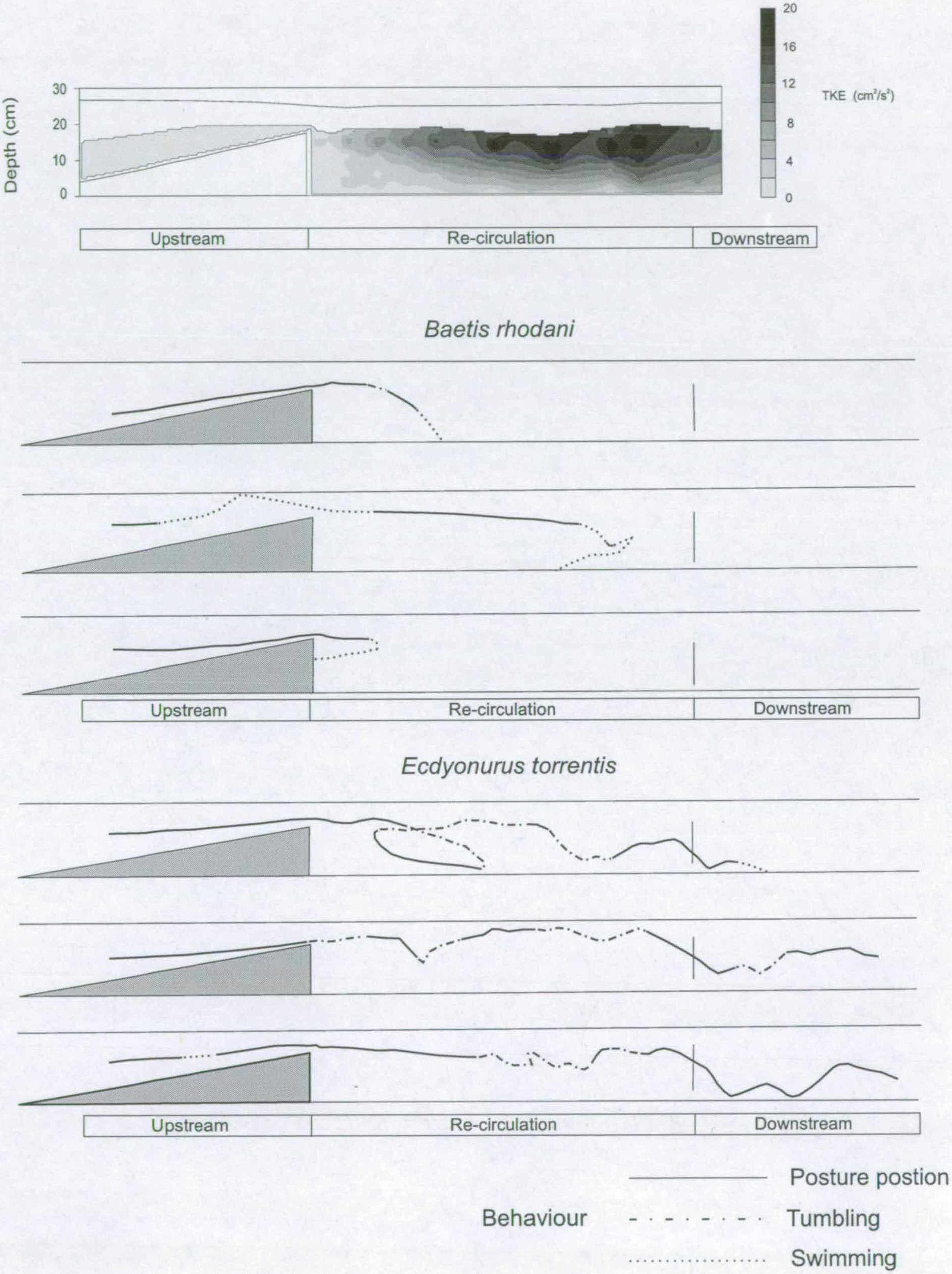


Figure 6.11 Typical trajectories for drifting *B. rhodani* and *E. Torrentis* over the step bed. Also shown is the turbulence plume immediately downstream of the step.

6.4 Discussion

The results from this study are consistent with the view of Lancaster *et al*., (1996), that channel morphology can influence the drift distance and settlement habitat of invertebrates in streams. The channel spanning step resulted in a very different hydraulic environment to that over the plan bed, significantly affecting the drift distance and time in the drift in two of the four species, *E. torrentis* and *H. pellicudula*. The remaining two species, *B.rhodani* and *Simulium* sp., showed no change in drift distance, despite the four fold increase in velocity and six fold increase in turbulence over the step. The response of *E. torrentis* is consistent with the view of Fonesca & Hart (2001), that hydraulic constraints imposed by channel morphologies on drifting invertebrates can affect local distributions. The distribution of this species was restricted over the step. Individuals always settled downstream of the re-attachment point, no individuals settled within the re-circulation zone. This general pattern partly conforms to that observed in the Talla; on transverse steps (Structured patches) this genus was found in very low density relative to other areas of the streambed (Chapter Five, see Table 5.9 and Figure 5.8).

This study is among the first to examine the complex interactions between drift behaviour, hydraulic environment and drift distance and settlement. The complexity of the study necessitated the use of a large-scale flume. The ability to set and measure precise hydrological conditions and census the specific behaviour of drifting individuals, allowed for the quantification of hydraulic effects on drift behaviour, distance and time. While flume systems can lack ecological realism, this was minimized by simulating the main hydrodynamic features of a channel-spanning step, under flow conditions that are not unlike those encountered in the field, i.e. velocities from 20 – 80 cm/s and depths from 5 – 28 cm (compare with Table 5.3). The negative exponential drift model first proposed by McLay (1970) proved a reasonable description of the return of drifting invertebrates, with return rates not unlike those obtained in other studies under similar velocities, both in the flume (e.g. Ciborowski, 1983, Allan & Feifarek, 1989) and field (e.g. Elliott, 1971, Lancaster *et al.*, 1996).

By comparing the distances travelled by live vs. dead larvae, Elliott (1971), Ciborowski (1983), Campbell (1985), Otto & Sjostrom (1986), and Allen & Feifarek, (1989) demonstrated that some invertebrates actively exit the drift by swimming or posturing. The results of this study demonstrate that some invertebrates also have the ability to alter their behaviour in response to the immediate hydraulic conditions, thereby affecting the distance they drift and time spent in the drift. Invertebrates may alter their behaviour in response to velocity, decreasing drift time at high velocity (Allen & Fiefarek, 1989) and increasing time at low velocity (Minshall & Winger, 1968, Poff & Ward 1991). For species that can not control their drift, distance generally increases with current velocity (Elliott, 1971). The results of this study suggest that turbulence may also be important in eliciting a change in behaviour, as demonstrated in the marine environment (e.g., Pawlik *et al.*, 1991, Fingerut, 2003, Forward *et al.*, 2003), thereby affecting drift distance and time. It may also influence the drift distance and time of passive drifters, independent of velocity (McNair, 2000). The species-specific drift response in this study highlights the potential influence of behaviour and hydraulics, but also the interaction between the two.

Exactly what mechanisms underlie the species-specific drift response of invertebrates observed in this study? Body morphology and behavioural response to the immediate hydraulic environment appear to influence the way in which velocity and turbulence together affect drift and settlement over the step. Under conditions of minimal turbulence (i.e. over the plane bed) all individuals of both mayfly species were able to maintain their body orientation in the water column and did not tumble. Under conditions of increased turbulence (i.e. the re-circulation zone) I observed a divergence of behaviour in the two mayfly species, similar to that observed in marine invertebrates (e.g., Pawlik *et al.*, 1991, Fingerut, 2003, Forward *et al.*, 2003). The response of *E. torrentis* was a decrease in swimming activity within the re-circulation zone and a corresponding increase in tumbling. In some marine invertebrates, increased turbulence induces tumbling which, in turn, results in cessation of swimming activity, as larval orientation and geotatic responses become disrupted (Eckman *et al.*, 1994). In essence, directional swimming becomes ineffectual at high turbulence (Fingerut 2003). The inability of *E. torrentis* to maintain body position may have contributed to the reduction of swimming activity. In contrast, *B. rhodani* increased its swimming activity and although maintaining body orientation within the re-circulation zone was difficult, it spent less time tumbling than *E. torrentis*. *Ecdyonurus torrentis* presents a larger surface area in the dorso-ventral plane than *B. rhodani* and is therefore likely to be more susceptible to being buffeted by turbulent eddies. For such body shapes, swimming may cease to be energetically favourable (Pitchford *et al* 2003), or indeed effectual (Fingerut 2003), in conditions of high turbulence. In comparing the typical trajectories of the two species in the turbulent zone, *E. torrentis* was typically buffeted throughout the entire water column, whereas *B. rhodani* were able to maintain a smooth trajectory.

The direction of swimming is important as it influences the time spent and distance travelled by drifting nymphs. By swimming up into the water column for example, a nymph may remain in suspension longer and travel further (Minshall & Winger 1968), whereas swimming directly towards the bed results in a reduction in both time spent and distance travelled (Allen and Feifarek, 1989). Depending on immediate hydraulic conditions, an organism may actively prolong time spent in the drift when conditions are unfavourable (Forward *et al.*, 2003), or reduce time in the drift, thus increasing the chance of remaining in a suitable habitat and reducing risk of predation from fish (Waters, 1961). *Hydropsyche pellicudula* has little ability for directional swimming, but does have some behavioural control over descent time and settlement habitat. The drift posture of curled into a ball likely reduces resistance and increases fall velocity compared with a stretched out posture. Under conditions of high turbulence, *H. pellicudula* tended to spend more time stretched out, possibly leading to the increased travel distance, and reducing the probability of settlement within the re-circulation zone. Indeed, while the transverse step may represent a suitable habitat for filter feeders (Chapter Five), the low flows within the re-circulation zone, and turbulent flows downstream of the re-attachment point may not represent optimal feeding conditions for many filter feeders (Georgian & Thorp, 1992), and as such may not represent a suitable habitat.

This study was carried out under one flow regime using two topographies. Understanding how a change in drift behaviour in response to hydraulics affects not only the dispersal potential of the individual, but also local population dynamics, requires combining both detailed flume and field studies. The next step is to see if the behavioural responses to turbulence and velocity, and the dispersal outcome observed in this study are repeatable under different flow regimes and topographies. The lack of response in drift distance of *Simulium* sp over the step bed for example, while intriguing, may be an artefact of the position of the step within the flume relative to the release point. This species has no obvious ability to maintain body orientation or manoeuvre itself through the water column (Fonseca & Hart, 2001), yet its drift distance and time over the step bed was similar to that over the plan bed, despite the large increase in velocity and turbulence. It is possible that the increased velocity up the ramp and turbulent eddies downstream of the step combined uniquely to produce drift distances not unlike that over the plan bed. *Simulium* sp on the other hand may actually have some level of indirect control over their drift. Elliott (1971) noted that individuals at one stream site, dominated by macrophytes, returned to the bottom at a faster rate and drifted shorter distances than at another site, despite similar water velocity. He observed the silk threads of drifting larvae caught on the macrophytes, which the larvae then used to crawl up and to attach to the substrate. Such chance checkings may have permitted *Simulium* sp to settle in areas over the step, such as the re-circulation zone, in perhaps greater numbers than would otherwise be possible.

Implications for Drift, Settlement and Flow Refugia:

Bedform structures, such as transverse steps, are common features in steep streams. The spacing of these steps may have important consequences for species such as *E. torrentis*. If spaced close together, for example through a step / pool reach (Grant *et al.*, 1990), *E. torrentis* entrained into the drift could conceivably travel the length of a reach, held in suspension by the increased turbulence over each step. A further consequence of this is the potential for limited access to large portions of the bed through the hydrological constraints imposed by the closely spaced steps. In the Talla and Cramalt transverse steps occurred at regular intervals, 1 to 2 channel widths apart (≈ 4 – 8 m apart) (Chapter Three). Given the average D_{50} (approx. 300 mm, Chapter Three) of these steps, the re-circulation zone may extend up to 3 m downstream (10 step heights, Keogh & Addison, 1996), potentially limiting the access of *Ecdyonurus* to up to ¾ of the bed. While *Ecdyonurus* sp was indeed sampled from Degraded patches downstream from steps, densities were far lower than in Loose patches. The results of this study however also have potential significance for drift dispersal beyond that of a channel spanning step and steep streams. Increased turbulence is also commonly associated with other sedimentary features such as isolated boulders and particle clusters (Bouckaert & Davis 1998, Buffin-Belanger & Roy 1998). These features create a small pocket of dead water zone in their wake, similar to the re-circulation zone. Their spacing and reach averaged proportion, similar to that of step spacing, may influence drift distance (Bond *et al.,* 2000a), if indeed animals can enter these dead zones.

The results suggest that the ability of animals to utilize such dead zones, including access to the re-circulation zone below steps, is dependent on species-specific response to the turbulence associated with such features. Circumstantial evidence suggests that there may exist a turbulence threshold, above which a species, such as *Ecdyonurus torrentis*, ceases to swim. Similar thresholds appear to exist for some marine invertebrates (e.g. Pawlik *et al*. 1991, Fingerut, 2003). This potentially has an important implication for access to in-stream flow refugia during spates. Paradoxically, as flood waters and turbulence increase, species such as *E. torrentis* may be unable to access flow refugia from the drift if the only refugia lie behind large boulders, bedform clusters and steps. Species-specific accumulation from the drift during flooding in low flow zones behind obstacles has been recorded before (Palmer *et al.,* 1996), although the mechanisms behind the species-specific nature of such accumulations are unclear.

Chapter Seven

Patch-Specific Response to Flooding

7.1 Introduction

The patch classification defined in Chapter Two was based primarily on particle size and structure. Patch types differ in the entrainment potential of particles (Chapter Four), have distinctly different biotic assemblage at low flows (Chapter Five), and influence drift and settlement (Chapter Six). These three aspects, particle entrainment, assemblage structure, and drift and settlement, influence whether a patch acts as a flow refugium (where invertebrates remain unaffected and or accumulate during floods), or represents an area of dislodgement and reduction in abundance. The patch classification may therefore discriminate on the basis of disturbance, allowing for the identification of refugia and disturbed patches. This represents the focus of Chapter Seven.

Floods in streams occur over a large scale, from small headwater tributaries to entire catchments, incorporating many patch types which may be differentially influenced by flow disturbances (Pringle *et al*,. 1988). Benthic invertebrates may fare better in some patch types than others, dependent on the susceptibility of the patch to physical processes, such as particle movement (e.g. Matthaei *et al* 2000) and shear stress (e.g. Bond & Downes, 2000b), but also on species-specific traits that may confer resistance, such as specialized structures that permit attachment to the substrate and maintenance of position under high shear stress (e.g. Frutiger, 1998). Clumps of particles on the streambed may be scoured, and or mobilised during flooding, dislodging invertebrates (e.g. Palmer *et al*., 1995, 1996, Matthaei *et al*., 2000, Strayer, 1999,), and removing algae and bryophytes (e.g. Biggs *et al*., 1999). Dislodged invertebrates may accumulate in low flow zones, (Palmer *et al*., 1995, 1996, Lancaster, 2000), producing a mosaic of patches on the streambed; some depleted of biota, others where organisms remain largely unaffected, and some where accumulation may take place.

Habitats where the negative effects of disturbance are lower than in the surrounding area, and invertebrates remain in unaffected, have commonly been referred to as refugia (e.g. Hildrew & Giller 1994, Roberston *et al*., 1995, Lancaster and Belyea, 1997). A variety of mechanisms and processes at different spatial and temporal scales may be incorporated under the term refugia (Lancaster and Belyea, 1997), however in this study I use the term to mean within-habitat refugia (sensu Lancaster and Belyea, 1997), that is, all parts of the streambed, including the hyporheic zone, that are hydrologically contiguous within the channel. Several studies have shown that flood refugia in streams can be related to specific morphological features of the streambed, such as clusters of boulders (Francoeur *et al*., 1998, Biggs *et al*., 1999), debris dams (Palmer *et al*., 1996) and the hyporheic zone (Dole-Oliver *et al*., 1997), providing shelter for resident organisms during peak flows and areas for accumulation (e.g. Palmer *et al*., 1996). If the impact of disturbance differs among patches, and morphological features such as debris dams provide refugia, then the abundance and size of such features, as well as the dispersal capabilities of the fauna, may determine population persistence (Lancaster and Belyea, 1997).

In steep streams, the classification scheme outlined in Chapter Two may provide a framework from which to assess the abundance and size of both depleted patches and refugia. The classification discriminates largely on particle movement. Loose patches are almost completely mobilized at relatively low discharges, whereas Structured patches remain stable, even during large flood events (see Chapter Four). Loose patches may therefore represent areas of depleted biota after flooding (e.g. Brooks, 1998), and Structured patches areas of refugia, if only for organisms with traits that confer resistance to high shear stress, e.g. *Simulium* (Eymann, 1988). The flow dynamics associated with each patch type may also affect the potential for accumulation of drifting organisms. While Structured patches remain stable, potentially providing refugia for many taxa, they may provide a poor habitat for accumulation via the drift (see Chapter Six). Loose patches however, while somewhat counterintuitive, may represent areas where accumulation can occur, particularly when flow levels subside and the environment turns from erosive to depositional (Wohl & Thompson, 2000). Brooks (1998) for example suggested that areas downstream of large protruding boulders (cf. boulder type Loose patches) may represent 'disturbance-dependent refugia', safe at one discharge and areas of accumulation (e.g. Palmer *et al.*, 1996), but sites of great turbulence and scouring at another. The switch-like nature from depositional to erosional is indeed suggested from the results in Chapter Four. The potential for Degraded patches as refugia may also be discharge dependent, as a greater area of the patch was usually mobilised as discharge increased. Particle mobilisation on Degraded patches however was complex, and despite the occurrence of an observed breakpoint for phase II transport (i.e. mobilisation of the coarse surface layer) percent area mobilised was generally highly variable (Chapter Four). Refugia, and indeed disturbance, may be equally variable on Degraded patches, and is potentially determined by a complex interaction of the biota with particle movement and shear stress. The potential response of biota to flooding on Degraded patches is discussed in more detail below.

Persistence of populations and communities subject to repeated physical disturbance from flooding depends on the relative proportions of both disturbed patches and refugia, but also on the movement of invertebrates between such patches (Lancaster & Belyea, 1997). During flooding Loose, Degraded and Structured patches may show a reduction in invertebrate abundance (disturbance), no change (refugia) or accumulation (refugia). The relative proportion of each patch type, and the patch-specific biotic responses, are important for the stream-wide persistence of populations. Lancaster and Belyea (1997) developed a series of models based on such criteria, i.e. relative proportions of and movement of organisms into and out off refugia, to help explain how species may exploit environmental heterogeneity to persist in an environment subject to frequent disturbance. In the baseline situation, with no in-stream refugia, the reach is evenly disturbed and a constant proportion of the population is lost (Model A). This model however, is unlikely to apply in steep streams where particle movement, an important disturbance mechanism, is highly variable (Chapter Four). If however the survival of individuals is higher in some habitats than others, a more likely outcome (e.g. Palmer *et al.*, 1995, 1997, Strayer, 1999, Matthaeii *et al.*, 2000), then models B, C, and D may apply. Model B is when no invertebrate movement into and out off patches occurs, i.e. no accumulation. Model C is similar, but incorporates movement out of refugia after flooding, i.e. a re-distribution, while Model D incorporates both accumulation during flooding and a re-distribution after. While all models can maintain a viable population, their efficacy depends primarily on the total area of refugium patches, but also on the movement of organisms into and out of such patches.

The application of Lancaster & Belyea's models however, is problematic if refugia are discharge dependent (e.g. Brooks, 1998), loss at one discharge but accumulation at another, a situation not accounted for in the models, or if the response of the invertebrates is variable within the sampling unit (i.e. patch). The Degraded patches may therefore present a problem because of the large variation in particle movement (Chapter Four). One area of the patch may remain stable and act as a refugium, another may be mobilised and result in a loss. Degraded patches simply may not classify as either refugia or disturbed. If indeed this is the case, then we may expect a continuous relationship rather than a binary response, as indicated by Response A in Figure 7.1. That is, there is a direct impact of disturbance mechanism (e.g. % area mobilised) on invertebrate density, i.e. the greater the % area mobilized the more individuals lost. If however, particle movement is not the only disturbance mechanism to act on benthic invertebrates, and other mechanisms such as shear stress or abrasion are important, then we may not expect a gradational response with particle movement, but a response similar to that of Response B (Figure 7.1). That is, invertebrate loss may occur across the entire Degraded environment. Under such circumstances the patch classification may still be appropriate for Lancaster & Belyea's Models (i.e. Model A). During flooding however, accumulation in one or more patch types may occur (e.g. Palmer *et al.*, 1996). With no dispersal constraints between the patches, three other response types are possible (Figure 7.1). Response C, indicates an influx of individuals (i.e. accumulation), masking any possible relationship between disturbance mechanism (e.g. particle movement) and response variable. That is a loss may or may not have occurred before the accumulation. Response D, indicates an influx of individuals, and the influx may be related to disturbance mechanism via an abiotic process, such as flow dynamics (e.g. hydraulic constraints on drift, see Chapter Six), or related to an ecological process, such as colonisation of recently opened up space. Finally, response E indicates an influx of individuals after loss via the direct impact of disturbance mechanism (i.e. response A). Responses C to E may occur when the influx (accumulation) into a patch is greater than loss. Responses A and B may occur when loss from the patch is greater than any influx of individuals into the patch.

In this Chapter I examine the change in assemblage structure on each patch type, Loose, Degraded and Structured, after flood events of different magnitudes. I aim to address the following questions; 1) Does the response of the invertebrate assemblage to flooding differ across Loose, Degraded and Structured patches? 2) If so, is it related to particle movement, i.e. loss on Loose > Degraded > Structured? 3) Do invertebrates accumulate in one or more patch types, i.e. post flood abundance > pre flood abundance? While I did not testing directly the Models of Lancaster and Belyea (1997), as I did not attempting to link invertebrate response to population persistence, the results of this study may be consistent with one or more of their models. I also examined the response of invertebrates to both particle movement and shear stress on Degraded patches, testing the response models in Figure 7.1.

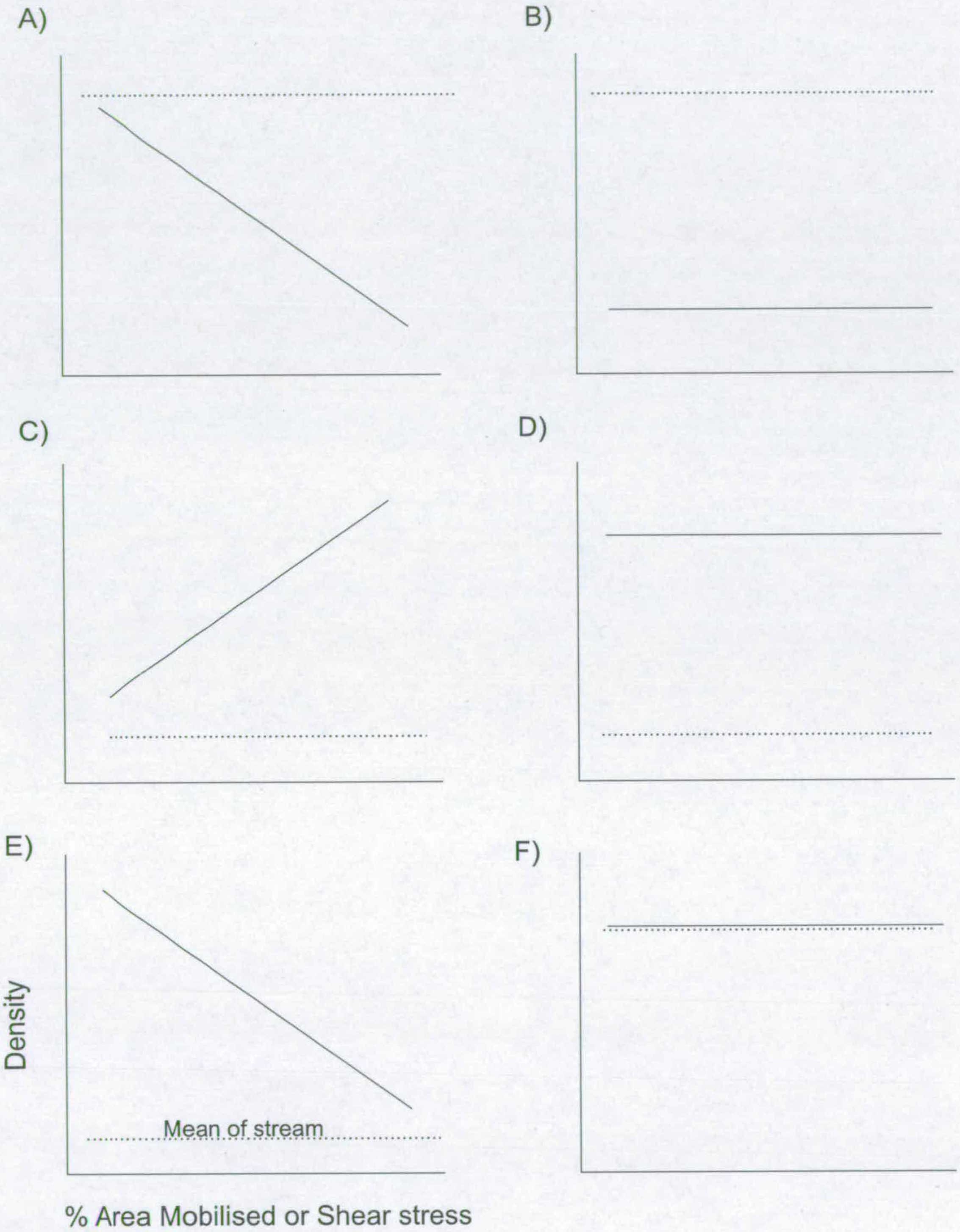


Figure 7.1 Potential relationships of invertebrate density (solid line) with % area mobilised and shear stress in relation to a pre flood mean (dotted line).
A - B: loss > influx of invertebrates. C - E: influx > loss of invertebrates.
F = no difference between pre-flood and post flood.

7.2 Method

To address the objectives, baseline information on the Talla Water from Chapters Four and Five is required. Using invertebrate baseline samples (Chapter Five) and the photographic record of the streambed (Chapter Four) it is possible to relate the impact of each flood event on invertebrate assemblage in each patch type to particle movement, and for Degraded patches, also shear stress (note, only for the Talla Water). That is, samples can be taken from an area of the streambed with a detailed history of particle movement (and shear stress in Degraded patches) and assemblage structure, permitting a comparison of the assemblage before the flood to that after in each patch type. Invertebrate sampling was carried out as soon as was practically possible, usually within 36 hours, after the flood peak of three events, two in the autumn / winter period, 24-10-02 and 4-12-03, and one in the spring period, 29-4-03. Herein these floods are referred to as Flood 1 (29-4-03, peak discharge - 2.9 m^3/s), Flood 2 (24-10-02, peak discharge - 5.4 m^3/s) and Flood 3 (4-12-03, peak discharge - 5.9 m^3/s) in order of increasing peak discharge. The baseline (i.e. pre flood) samples for Floods 1 and 3 were collected on 7-4-03 and 29-09-03 respectively. No flood events occurred between these samples and the floods of interest. No baseline samples however were collected prior to Flood 2. This flood occurred before the early winter baseline sample could be taken. As a result, data from the baseline samples collected on 9-11-01, one year earlier, and on 19-11-02, one month after the flood was combined to produce a pseudo baseline sample for Flood 2. By combining the post flood sample, where recovery may not be fully completed, the combined baseline sample is regarded as conservative. The photographs of the stream bed pre flood were taken on 13-4-03 (16 days before Flood 1), 13-10-02 (11 days before

Flood 2) and 29-9-03 (2 months before Flood 3). No floods occurred between these dates and the flood events of interest.

The location of invertebrate samples after flooding was restricted to areas of the streambed that had previously been photographed. Immediately after flooding a sub set of these patches was selected at random (stratified random sampling, using random number tables, each photographed patch was number, see Chapter Four) for invertebrate sampling. Prior to sampling, the patch was photographed using the same technique as described in Chapter Four. Five Structured patches, six to seven Loose patches and up to ten Degraded patches were photographed and sampled after each flood (see Table 7.1). Sampling, sorting and identification were carried out using the same methodologies and equipment as for the baseline sampling described in Chapter Five. All CPOM and moss collected during sorting was dried and weighed as per baseline samples.

After Flood 3, a sample from the hyporheic zone from each of the replicate Loose patches was taken. The surface substrate was first removed to a depth of 10 centimetres (equivalent to the surface sample). A Surber sampler was then placed on the freshly exposed substrate, which was then disturbed to a depth of 10 centimetres (i.e. 10 cm within the hyporheic zone, 20 cm from the original surface). The sample was then processed as per a surface sample. A baseline hyporheic sample, to compare the response after flood 3, was taken in September 03, the same time as the baseline (pre-flood) surface samples (Chapter Five), two months early.

Table 7.1 Summary statistics of % area mobilized, maximum particle mobilized and shear stress over sampled Degraded Patches during flooding, and % area mobilized over Loose patches. All Structured patches remained stable, i.e. no particle movement.

	Max	Min	Av	SE
Flood 1				
Degraded n = 8				
% Mobilised	28.44	0.97	11.23	2.6
Max part. Size (mm)	79.2	21.3	45.3	7.97
Shear stress (N/m^2)	57.63	15.72	32.96	5.8
Loose n = 6				
% Mobilised	100	1.18	80.3	10.5
Flood 2				
Degraded n = 10				
% Mobilised	81.99	2.65	41.97	5.99
Max part. Size (mm)	242.4	52.8	122.4	17.6
Shear stress (N/m^2)	176.38	38.84	87.66	14.1
Loose n = 7				
% Mobilised	100	8.65	77.2	11.5
Flood 3				
Degraded n = 8				
% Mobilised	90	22.8	47.35	6.24
Max part. Size (mm)	144.15	46.5	106.56	11.4
Shear stress (N/m^2)	104.89	33.84	77.54	8.29
Loose n = 6				
% Mobilised	100	98.55	99.6	0.21

7.21 Data Analysis

Univariate (Invertebrate Response on each Patch Type; total density, taxon richness and abundant taxa):

For total density, taxon richness and density of abundant species (those accounting for > 5% of the total) a two way analysis of variance (ANOVA) was performed using the General Linear Model procedure in SPSS 9, to compare density and species richness before and after flooding on each patch type. The two factors, Patch (Loose, Degraded, Structured) and Flood (Before, After) were both fixed. Each flood was analyzed separately as no Structured patches were sampled after Flood 2. Flood 2 occurred mid way during the study, after which there was a concern about the limited number of Structures available for future sampling. A decision was therefore taken not to sample this patch type, in favour of sampling from future larger events (i.e. Flood 3). The critical statistic for each analysis was the Flood x Patch interaction term since it would indicate that a change in faunal abundance during the flood varied among patch types. All density data was log (x+1) transformed. Homogeneity of variance was tested using Levens test, and the Anderson-Darling Normality test was used to test deviation from normality. After transformations, assumptions of homogeneity of variance and normality were met. Taxon richness was standardized by number using the rarefaction method (see Chapter Four for description). Each sample was standardised to 60 individuals. This differs from that employed in Chapter Four (baseline samples) where a standardisation of 120 individuals was used. The lower standardisation number was used because abundance was low in most post flood samples. To permit comparison with pre flood baseline samples, these were also standardised to 60 individuals for all analysis carried out in this chapter.

Multivariate (Response of Assemblage on each Patch Type):

Invertebrate assemblages on each patch type before and after flooding were examined using multivariate analyses, specifically multidimensional scaling ordination by SSH (semi strong hybrid multidimensional scaling) in PATN. This ordination technique is described in detail in Chapter Five. Essentially, it is based on a dissimilarity matrix that accounts for arching effects that can result in misinterpretation of ordination plots. The technique also allows further analysis directly on the dissimilarity scores within the dissimilarity matrix. In analyses the Bray Curtis dissimilarity score was used. Data preparation and transformation was carried out as described in Chapter Five.

The ordination diagrams provided a visual documentary of variation between pre and post flood assemblages from each patch type. For each patch type, pre and post flood, the replicate samples were grouped in ordination space. The centroid of each group was calculated as the median of ordination scores on each axis of all samples within the group. Distance between centroids of each pre and post flood set of samples (e.g. Loose, Degraded, Structured) was used to estimate the degree of change in the assemblage (e.g. absolute and relative density, and presence / absence of species) from pre flood to post flood (e.g. Boulton *et al*,. 1992). Trajectories from pre to post assemblages for each patch type are shown in each ordination by linking the centroids.

Principal axis correlation (PCC) in PATN (see Chapter Four for description) was used to examine the correlation of each species with the ordination plot. Correlations along assemblage trajectories from pre to post flood would suggest a response to flooding. The significance of each correlation was determined by running 1000 Monte-Carlo randomizations of the original ordination (MCAO procedure in PATN), and fitting each attribute (species) to each randomization. Significance was corrected (Bonferroni correction) for the total number of contrasts made.

A quantitative estimate of the degree of change in assemblage from pre to post flood, incorporating all ordinations axes (dimensions), can be obtained by computing the average dissimilarity scores between sample pairs directly from the dissimilarity matrix. This methodolodgy was used in Chapter Five to provide a quantitative estimate of the difference in assemblage between each patch type (see Chapter Five for full description). Here I calculated the average dissimilarity scores between sample pairs from each patch type, pre and post flood. This allows a quantitative comparison of the degree of similarity between patches before and after flooding.

Effect of Particle movement and Shear Stress on Invertebrates from Degraded patches (Testing Response Models – Figure 7.1):

To test the response models of Figure 7.1, I characterised the relationship between the % area mobilized and peak shear stress with invertebrate abundance and species richness on Degraded patches for each flood event. Only Degraded samples were used in this analysis as neither Loose nor Structured patches showed much variation in % area mobilized (see Chapter Five).

The percent area mobilized in each sample patch was calculated using the methodology outlined in Chapter 4 (see, Figure 4.3). Briefly, this involved comparing photographs of the streambed before and after flooding to identify the movement of individual particles. Particles that had moved were filled in black and the cumulative blacked out area of each pre-flood photograph calculated using an image-processing package (NIH v. 9.0). Maximum shear stress (τ) experienced during peak flooding over each Degraded sample was estimated using Shield's equation;

$$\tau = \theta g \rho_s D \qquad \text{Equation (7.1)}$$

where g is gravity, ρ_s is the submerged density of the grains (taken here to be 1650 kg m^{-3}), θ is Shield's number (0.045), and D is diameter of the largest grain mobilised. D was estimated from the photographs taken before each flood event. A metal rule placed on the substrate in each photograph was used as a scale (see Chapter 4 for description of photographic methods). Shield's number (θ) is a dimensionless number that reflects the force required to entrain a particle. A Shield's number of 0.045 was adopted as it is generally accepted as the force balance for a heterogeneous sediment mix with little imbrication (Komar, 1987), i.e. Degraded patch. As less than 50 % of each Degraded patch was generally mobilised, even during large events, and with only those large particles sitting proud of the bed entrained, and no imbricated patches mobilised (i.e. Structured) (Chapter 4), a Shield's number of 0.045 was appropriate.

Defining Response models:

Least squares regression analysis was used to examine the relationship of invertebrate response variable (density of abundant taxa, total density and species richness) with percent area mobilized and with maximum shear stress. Significant regression constants, slope (b) and y-axis intercept (a), were used to define the type of response model (Figure 7.2). For all regressions an alpha level of 0.1 was adopted. While this is less conservative than the usually accepted 0.05 level, it was adopted here as this analysis is considered exploratory, highlighting the potential for various relationships between invertebrate response and disturbance mechanism.

For all analyses, a linear relationship is assumed. While this is likely the case for % area mobilised, as, in general the greater the area of substrate disturbed the greater the loss, the relationship with shear stress is more likely to have a breakpoint, representing a critical threshold for invertebrate dislodgement (e.g. Borchardt, 1983). The relationship of invertebrate density with shear stress is therefore unlikely to be linear. However, as only ten samples were analysed per flood, an analysis of potential breakpoints was beyond the scope of this study, and so a linear relationship was assumed for simplification.

Finally, because the movement of a particle (max particle mobilised) was used in the estimation of peak shear stress, a level of dependence exists between the two

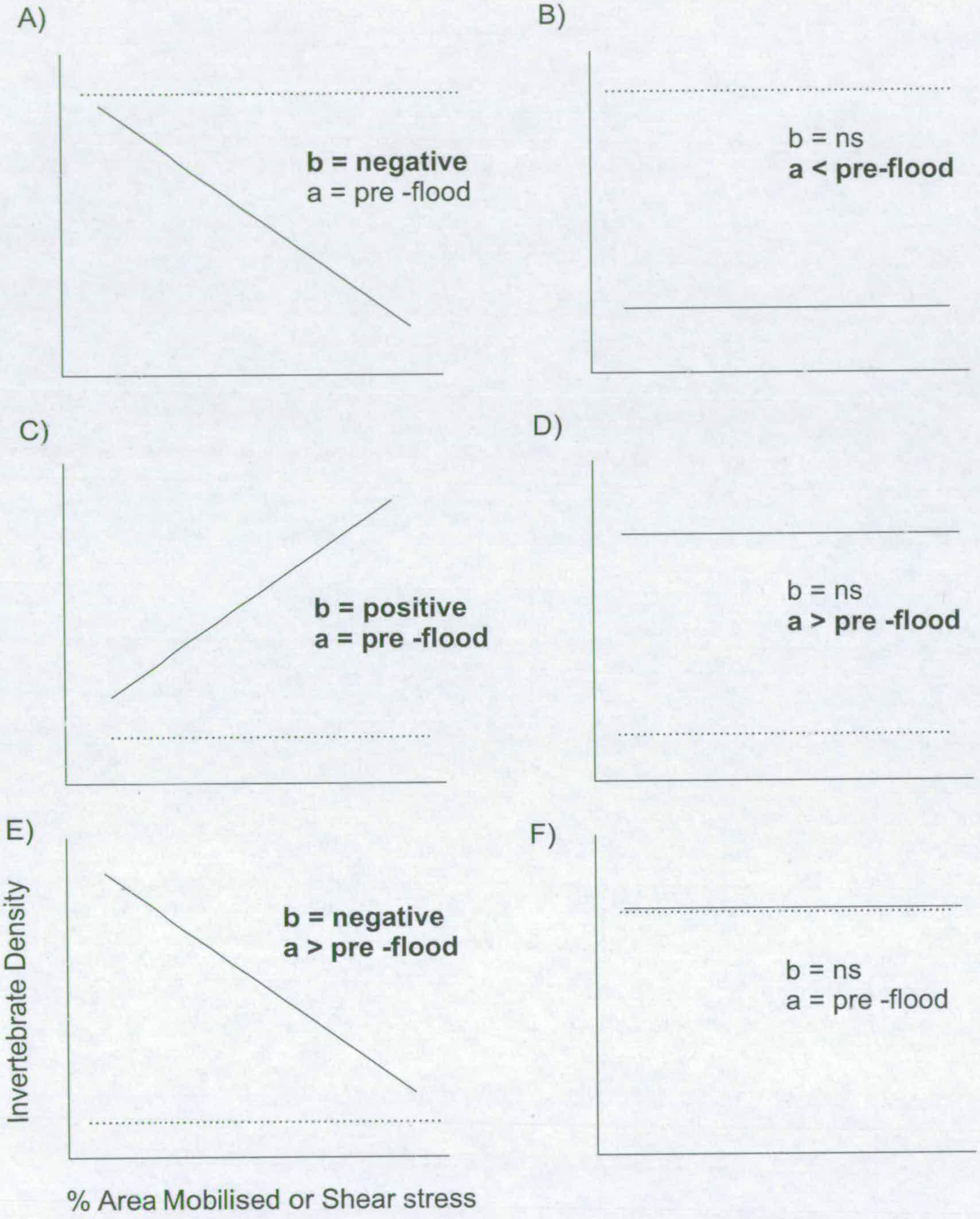


Figure 7.2 Relationships (solid line) of invertebrate density with % area mobilised and shear stress in relation to a pre flood mean (dotted line). A - B: loss > influx of invertebrates. C - E: influx > loss of invertebrates. F = Ho - no difference between pre-flood and post flood invertebrate density. The constants a and b are derived from the regression equation y = a + bx (see table 7.4. Models are only accepted where the appropriate constants are significant, shown in bold.

parameters beyond that of a simple force relation, i.e. they are not independent. While they are not used in the same analysis, a certain level of caution has to be applied when comparing the relative effect of the two parameters on the response variables. For some species, for example those less susceptible to dislodgement by shear stress (e.g. *Simulium*, Eymann, 1988), we may expect different relationships between density and particle movement, and density and shear stress. Due to the dependence between the two parameters however, the chance of detecting any differences is reduced.

7.3 Results

7.31 Flood Magnitudes and Mechanisms of Disturbance

Mean velocity through the study reach (estimated as Velocity = Discharge / Cross sectional area) during peak discharge was 1.30, 1.76 and 1.87 m/s during Floods 1, 2 and 3 respectively. Floods 2 (5.43 m^3/s) and 3 (5.92 m^3/s) occurred at a discharge higher than the estimated breakpoint threshold for Degraded patches, and that for mobilization of the coarse surface armour (Chapter 5). Flood 1 (2.09 m^3/s) however occurred at a discharge below the breakpoint threshold for Degraded patches, although above that necessary for the mobilization of the Loose patches (Table 7.1). No Structured patches were mobilised during any flood.

The percent area mobilized of Degraded patches from Floods 2 and 3 ranged from 2 to 90 % (mean > 40 %). This included the mobilization of coarse particles up to a diameter of 240 mm. The percent area mobilized of Degraded patches from Flood 1 however only ranged from 1 % (i.e. almost completely stable) to 28 %, with a mean of only 11 %, a quarter of that from Floods 2 and 3 (Table 7.1). During this flood, particle mobilization was confined almost entirely to the fine matrix of Degraded patches. The percent area mobilised of Loose patches however was on average greater than 75 % for all three flood events (Table 7.1), although only during the largest event, Flood 3, were all replicate patches completely mobilised (> 98 %). During Floods 1 and 2 at least one patch remained almost completely stable (< 10 % mobilisation, Table 7.1).

Estimates of shear stress over Degraded patches ranged by approximately five fold within each flood event (Table 7.1). Estimates derived from Floods 2 and 3 were approximately 2 to 3 times higher than those derived from Flood 1. The correlation between % area mobilized and peak shear stress over Degraded patches for all flood events was very good (correlation coefficient > 0.998 for all events) (Figure 7.3).

7.32 Impact of Floods on Invertebrate Density, Taxon Richness and Assemblage on Structured, Loose and Degraded Patches

Impact on Total Density and Species Richness:

The impact of the three floods on invertebrate density was similar, with an average reduction in density of 30.0 %, 32.8 % and 34.6 % from Floods 1, 2 and 3 respectively, averaged over three patch types. For all floods this represented a significant reduction in total density (Table 7.2a, b & c). There was a net loss of invertebrates from all patch types during every event (Figure 7.4). Note for graphical purposes, net change is expressed as a percentage, standardised by the mean, whereas statistical analyses use density data). While the decline in abundance varied among patch types, there was no obvious pattern (Figure 7.4), i.e. no one patch type experienced the greatest loss from all flood events. Total density on Loose and Structured patches however showed a trend with discharge. The magnitude of loss on Loose patches increased with discharge, from less than 5% after Flood 1 to over 60 % after Flood 3 (Figure 7.4). The response on Structured patches shows the converse, with a greater loss experienced during Flood 2 compared with Flood 3; there was no data from Flood 1 (Figure 7.4). The trend in total density on these two patch types was largely independent of particle movement (for all floods the majority

Table 7.2a Flood 1, summary statistics for two-way ANOVA (Flood; pre /post, Patch; Loose, Degraded, Structured, both fixed) of density of abundant (< 5 %) taxa.

	DF	MS	F	P
Ecdyonurus sp				
Flood	1	0.014	0.152	0.700
Patch	1	0.559	5.689	**0.025**
Flood * Patch	1	0.229	2.329	0.140
Error	24	0.098		
Rithrogena semicolorata				
Flood	1	0.690	9.878	**0.004**
Patch	1	0.011	0.155	0.697
Flood * Patch	1	0.085	1.229	0.279
Error	24	0.069		
Baetis sp				
Flood	1	0.262	4.722	**0.040**
Patch	1	0.554	9.988	**0.004**
Flood * Patch	1	0.146	2.625	0.118
Error	24	0.055		
Leuctra sp				
Flood	1	0.345	5.357	**0.030**
Patch	1	0.355	5.514	**0.027**
Flood * Patch	1	0.049	0.772	0.388
Error	24	0.064		
Siphonoperla torrentium				
Flood	1	0.076	0.654	0.427
Patch	1	2.023	17.30	**0.000**
Flood * Patch	1	0.512	4.380	**0.047**
Error	24	0.117		

	DF	MS	F	P
Simulium sp				
Flood	1	2.687	7.607	**0.011**
Patch	1	7.842	22.20	**0.000**
Flood * Patch	1	0.229	0.649	0.428
Error	24	0.353		
Orthocladiinae				
Flood	1	0.117	1.012	0.325
Patch	1	0.314	2.714	0.112
Flood * Patch	1	0.998	8.635	**0.007**
Error	24	0.116		
Elmis aena				
Flood	1	0.253	1.180	0.288
Patch	1	2.804	13.06	**0.001**
Flood * Patch	1	1.339	6.237	**0.020**
Error	24	0.215		
Total				
Flood	1	0.152	4.978	**0.035**
Patch	1	0.205	6.714	**0.016**
Flood * Patch	1	0.106	3.464	0.075
Error	24	0.030		
Taxon Richness				
Flood	1	0.009	3.07	0.092
Patch	3	0.000	0.07	0.796
Flood * Patch	3	0.001	0.04	0.531
Error	24	0.003		

Table 7.2b Flood 2 summery statistics for two-way ANOVA (Flood: pre / post, Patch: Loose, Degraded, Structured, both fixed) of density of abundant (< 5 %) taxa.

	DF	MS	F	P
Ecdyonurus sp				
Flood	1	0.572	1.920	0.171
Patch	2	0.944	3.170	**0.050**
Flood * Patch	2	0.167	0.560	0.575
Error	56	0.298		
Rithrogena semicolorata				
Flood	1	5.426	23.52	**0.000**
Patch	2	0.326	1.416	0.251
Flood * Patch	2	0.382	1.656	0.200
Error	56	0.231		
Baetis sp				
Flood	1	0.076	1.424	0.238
Patch	2	0.848	15.71	**0.000**
Flood * Patch	2	0.073	1.362	0.264
Error	56	0.053		
Leuctra sp				
Flood	1	2.502	23.50	**0.000**
Patch	2	3.229	30.33	**0.000**
Flood * Patch	2	0.161	1.516	0.229
Error	56	0.106		
Siphonoperla torrentium				
Flood	1	8.119	23.08	**0.000**
Patch	2	0.578	1.642	0.203
Flood * Patch	2	0.550	1.564	0.218
Error	56	0.352		

	DF	MS	F	P
Simulium sp				
Flood	1	0.020	0.008	0.927
Patch	2	16.71	69.91	**0.000**
Flood * Patch	2	0.725	3.034	**0.056**
Error	56	0.239		
Orthocladiinae				
Flood	1	0.135	0.486	0.489
Patch	2	10.34	37.30	**0.000**
Flood * Patch	2	0.087	0.316	0.731
Error	56	0.277		
Elmis aena				
Flood	1	5.383	22.20	**0.000**
Patch	2	5.935	24.47	**0.000**
Flood * Patch	2	0.405	1.672	0.197
Error	56	0.242		
Total				
Flood	1	0.332	9.670	**0.003**
Patch	2	1.052	30.61	**0.000**
Flood * Patch	2	0.016	0.482	0.620
Error	56	0.034		
Taxon Richness				
Flood	1	0.011	3.84	0.058
Patch	2	0.016	5.44	**0.009**
Flood * Patch	2	0.045	14.78	**0.000**
Error	56	0.003		

Table 7.2c Flood 3, summary statistics for two-way ANOVA (Flood; pre / post, Patch; Loose, Degraded, Structured, both fixed) of density of abundant (< 5 %) taxa.

	DF	MS	F	P
Ecdyonurus sp				
Flood	1	4.000	62.82	**0.000**
Patch	3	0.743	11.65	**0.000**
Flood * Patch	3	0.452	7.083	**0.001**
Error	39	0.064		
Rithrogena semicolorata				
Flood	1	0.012	0.075	0.786
Patch	3	5.090	30.02	**0.000**
Flood * Patch	3	0.294	1.735	0.176
Error	39	0.169		
Baetis sp				
Flood	1	0.592	7.160	**0.011**
Patch	3	4.166	50.42	**0.000**
Flood * Patch	3	0.007	0.087	0.967
Error	39	0.082		
Leuctra sp				
Flood	1	0.939	4.395	**0.043**
Patch	3	4.625	21.63	**0.000**
Flood * Patch	3	0.112	0.522	0.670
Error	39	0.214		
Siphonoperla torrentium				
Flood	1	0.670	2.421	0.128
Patch	3	0.105	0.378	0.769
Flood * Patch	3	0.243	0.876	0.462
Error	39	0.277		

	DF	MS	F	P
Simulium sp				
Flood	1	0.216	0.866	0.358
Patch	3	13.86	55.66	**0.000**
Flood * Patch	3	0.537	2.157	0.109
Error	39	0.249		
Orthocladiinae				
Flood	1	24.78	110.3	**0.000**
Patch	3	5.615	25.04	**0.000**
Flood * Patch	3	0.739	3.295	**0.030**
Error	39	0.224		
Elmis aena				
Flood	1	5.465	24.07	**0.000**
Patch	3	1.752	7.719	**0.000**
Flood * Patch	3	0.965	4.252	**0.011**
Error	39	0.227		
Total				
Flood	1	0.779	22.13	**0.000**
Patch	3	1.680	47.76	**0.000**
Flood * Patch	3	0.065	1.875	0.150
Error	39	0.035		
Taxon Richness				
Flood	1	0.012	2.91	0.099
Patch	3	0.023	5.52	**0.009**
Flood * Patch	3	0.011	2.64	0.089
Error	39	0.004		

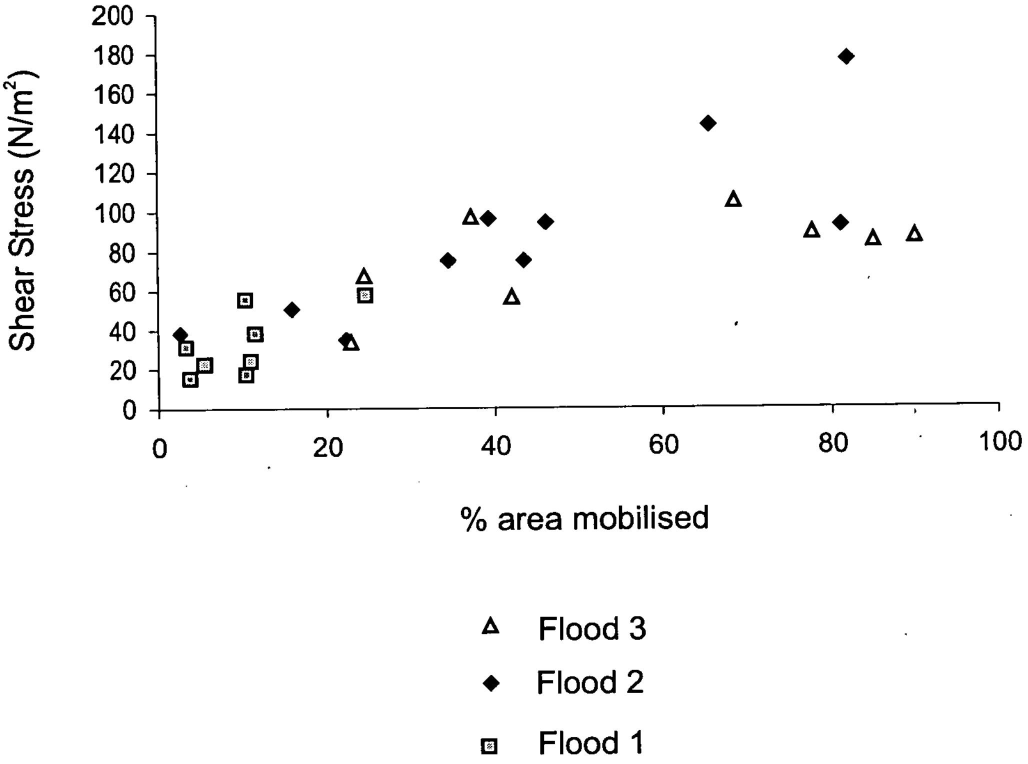


Figure 7.3 Relation between peak shear stress and % area mobilised for Degraded patches for each flood event.

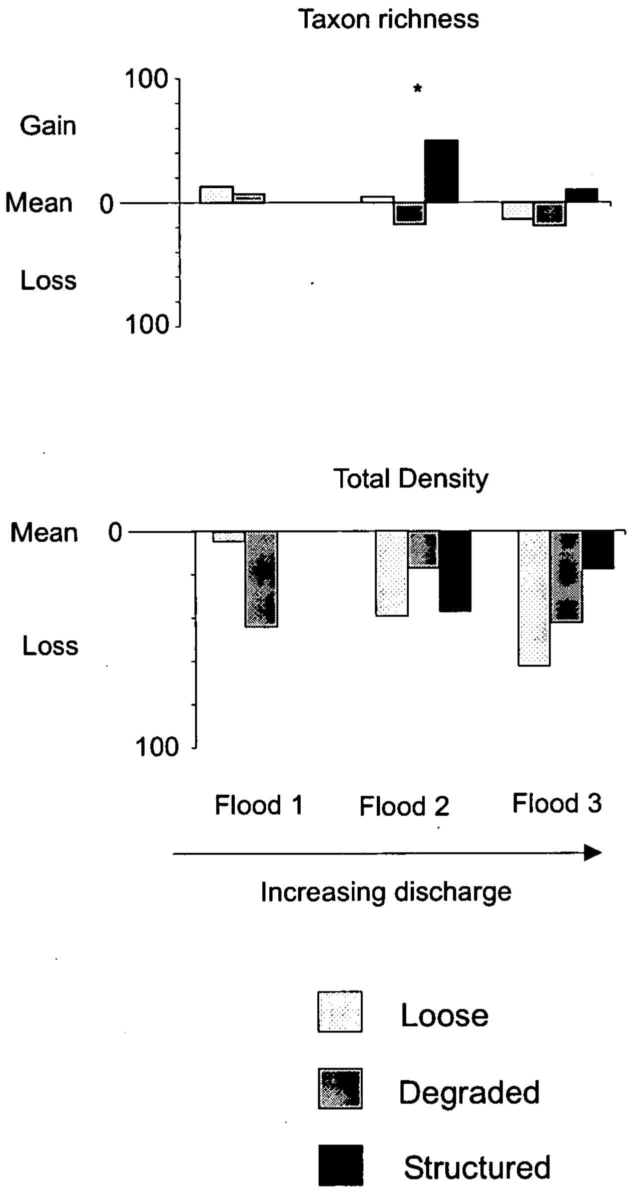


Figure 7.4 Mean change in total density and taxon richness from pre-flood mean on each patch type after each flood event (> 5 %), expressed as percent change from mean. Breakpoint threshold (phase II) was exceeded in Floods 2 and 3, but not in Flood 1. No Structured patches were sampled after Flood 1.'*" Indicates significant interaction between pre and post flood taxon richness with patch type (Table 7.2b).

of Loose patches experienced almost complete mobilization, with little change in average % area mobilized, Table 7.1, and all Structured patches remained stable). For all floods there was no significant Patch X Flood interaction term for total density.

On all patch types taxon richness was largely unaffected by Floods 1 and 3 (Figure 7.4, Table 7.2 a, b & c). There was however a large increase in taxon richness on Structured patches (> 40 %) after Flood 2 (Figure 7.4), with a corresponding decrease, although slight, on Degraded patches. The interaction term (Flood X Patch) for this Flood was significant (Table 7.1 a , b & c).

Impact on Assemblage:

The ordinations in Figure 7.5 show the movement of each patch centroid (median of ordination scores on each axis) in two dimensions. In most cases the change in assemblage structure was in a similar direction (in ordination space) for all patch types. Exceptions are the Structured patches from Flood 3, and the Loose and Degraded patches from Flood 1. The distance between centroids was greatest for Flood events 2 and 3 (above breakpoint threshold), suggesting the greatest change in assemblage (absolute and relative density, and presence / absence) on each patch type occurred during these floods. In general, the distance between centroids was greatest for Loose patches, suggesting the greatest change in assemblage occurred on this patch type, with the hyporheic centroids from this patch environment being the furthest apart after Flood 3 (Figure 7.5).

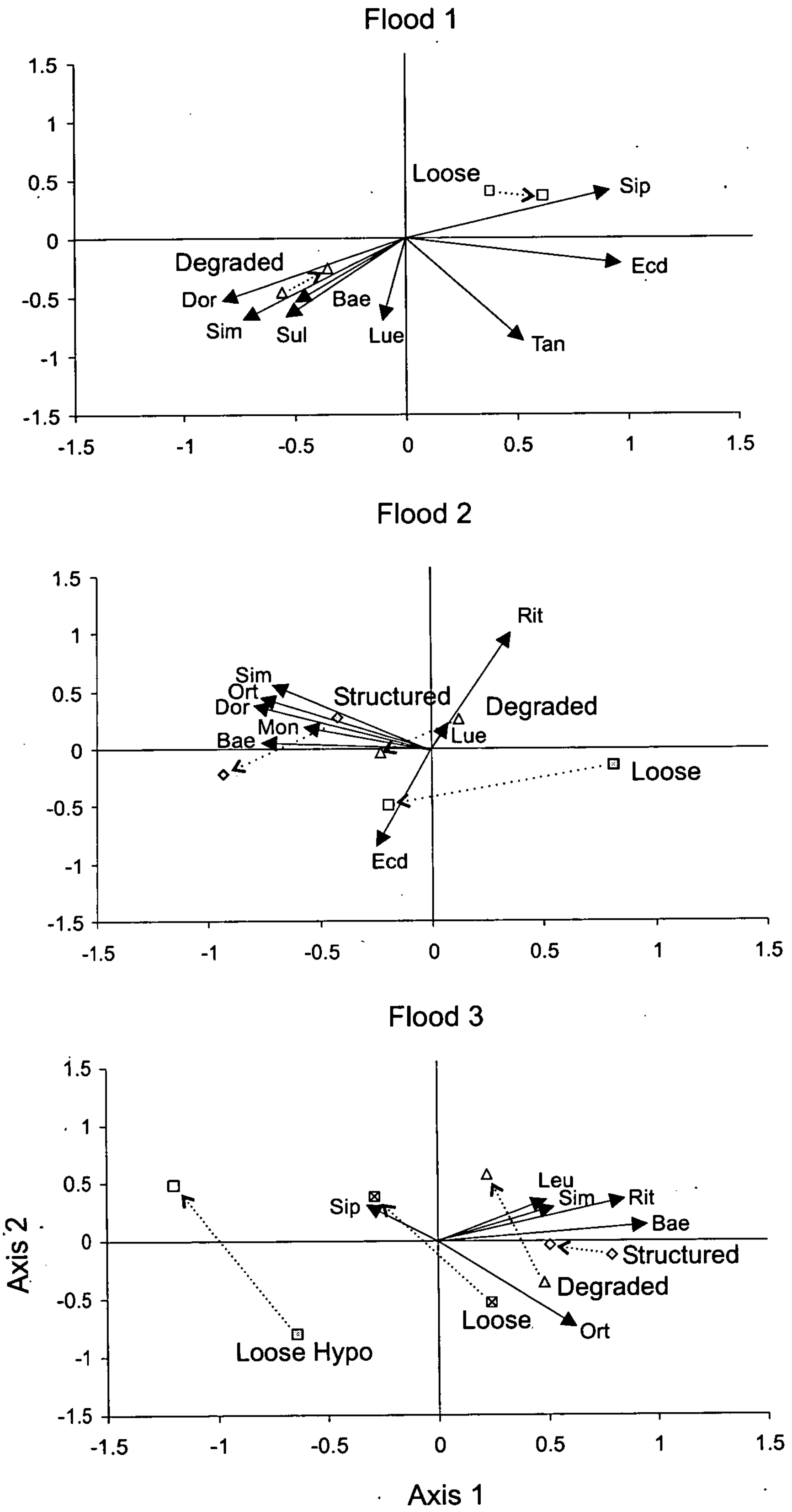


Figure 7.5 Centroids of the samples from each patch type before (closed symbols) and after (open symbols) flooding. The trajectory for each patch type is shown by stippled lines. Also shown are vector plots for each taxon significantly correlated with the ordination plots. See Table 5.9, Chapter Five for letter codes.

Superimposed on these ordinations are vectors, showing direction of increased density for each taxon that was significantly correlated with the ordination plot. Most of the species associations with particular patch types that were observed in the pre flood samples, for example the association of *Baetis* with Structured patches (Chapter 5, Figures 5.6 & 5.7, Tables 5.9 & 5.10), are also evident in these ordinations.

The response of the invertebrate assemblage on each patch type differed between floods below (Flood 1) and above breakpoint threshold (Floods 2 & 3). The average pair wise dissimilarity scores between the same patch types before and after flooding, was greatest for the two floods above the breakpoint threshold (Figure 7.6), and was most pronounced in the Loose patches. This is the same pattern suggested by the ordination plots, i.e. a greater change in assemblage on all patch types after Floods 2 and 3 compared with that after Flood 1, with the assemblage on Loose patches exhibiting the greatest change (as indicated by the higher average pair wise dissimilarly scores, Figure 7.6). Indeed, four taxa were found in the Loose patches after flooding that had not previously been sampled from this patch type on any occasion during the 3 year baseline sampling programme (Table 7.3). The majority of these were found in low abundance after the two flood events above the breakpoint threshold. No taxa were sampled from either the Degraded or Structured patches after flooding that had not previously been sampled there. A large change in assemblage after flooding was also observed in the hyporheic zone of the Loose patches, again confirming patterns in the ordination (Figures 7.6 & 7.5). Taxa were also sampled from this environment after flooding that had not previously been

Table 7.3 List of taxa occurring in Loose patches after flood events that were not sampled from this patch type prior to flooding, indicated by '*'. Str indicates taxa that are characteristic of Structured patches.

Flood	**1**	**2**	**3**
Surface Sample			
Protonemoura praecox (Str)		*	*
Dinocras cephalotes (Str)		*	
Helodidae (Str)			*
Drusus annulatus	*		
Hyporheic Sample			
Simulium			*
Limnus volckmari			*
Odontocerum albicorne			*

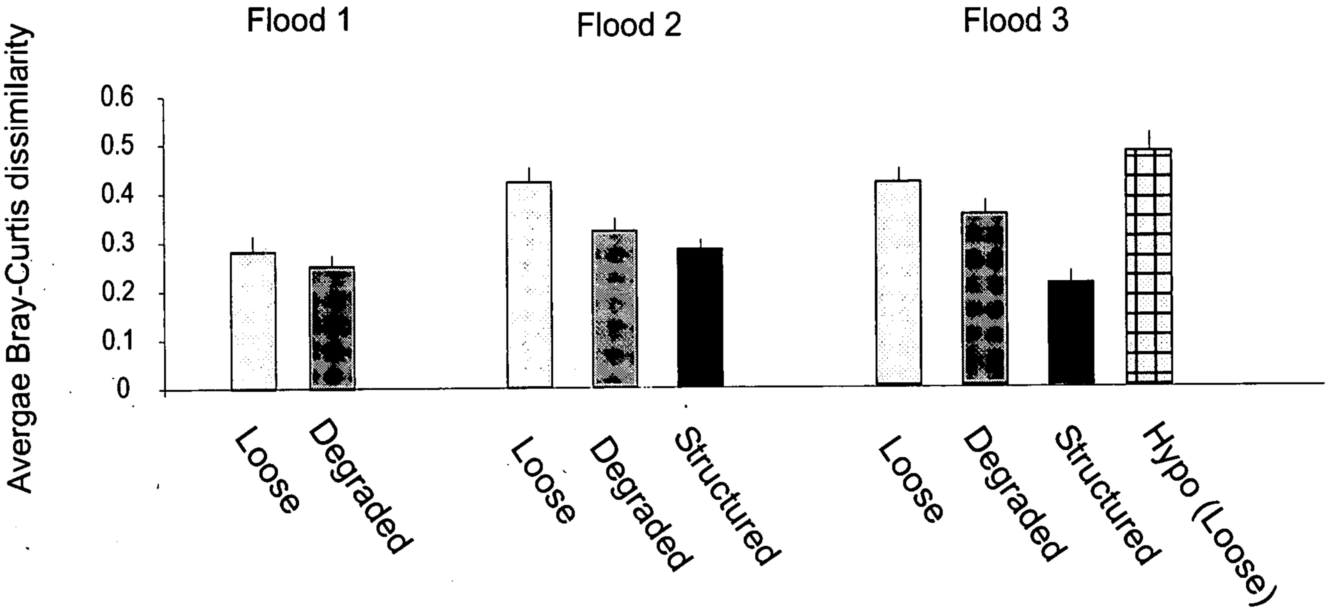


Figure 7.6 Average (SE) dissimilarity (Bray-Curtis) between all sample pairs from pre-flood and post-flood patches

found there, e.g. *Simulium* (Table 7.3). Assemblages on Structured patches showed the least change, with an average dissimilarity score almost half that of the Loose patches (Figure 7.6). The Degraded patches showed an intermediate level of change in assemblage between that of Loose and Structured.

For the floods above breakpoint threshold, the difference in assemblage (average dissimilarity) between patch types, i.e. Loose - Structured, was generally greater after the flood event than before (Figure 7.7). That is, the assemblages were more different from one another after the flood event, suggesting different relative responses on each patch type. For Flood 2 however, the difference between patch assemblages (average dissimilarity) was the same after the flood as before (Figure 7.7).

Taxon Specific Responses:

Most species showed patch specific responses, i.e. an increase in density on one patch type and decrease on another (*Rithrogena semicolorata*, *Ecdyonurus sp*, *Elmis aenea,* Orthocladiine and *Simulium*) (Figure 7.8). Only *Simulium* and *Elmis aenea* (l) however showed a similar pattern after each flood event, an increase in density on Degraded and Structured patches respectively (Figure 7.8). The greatest number of patch specific responses occurred after Flood 1, below breakpoint threshold. Indeed, after this flood three taxa, Orthocladiinae, *Elmis aenea*, and *Siphonoperla torrentium*, had significant flood x patch interaction terms (Table 7.2b), showing a decrease in density on Degraded patches but an associated increase on Loose patches (Figure 7.8).

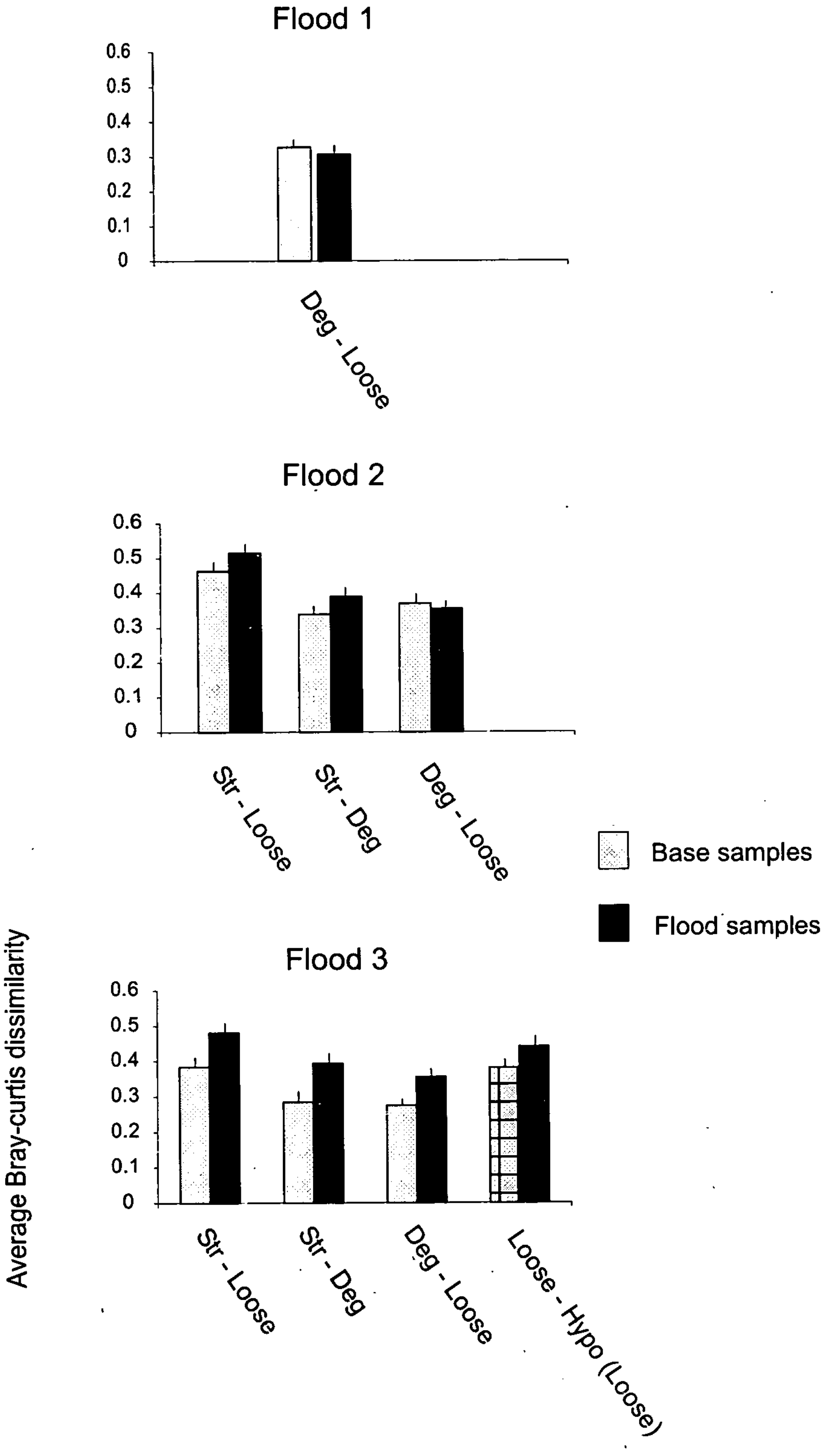


Figure 7.7 Average (SE) dissimilarity (Bray-Curtis) between all sample pairs from different patches, pre and post flood.

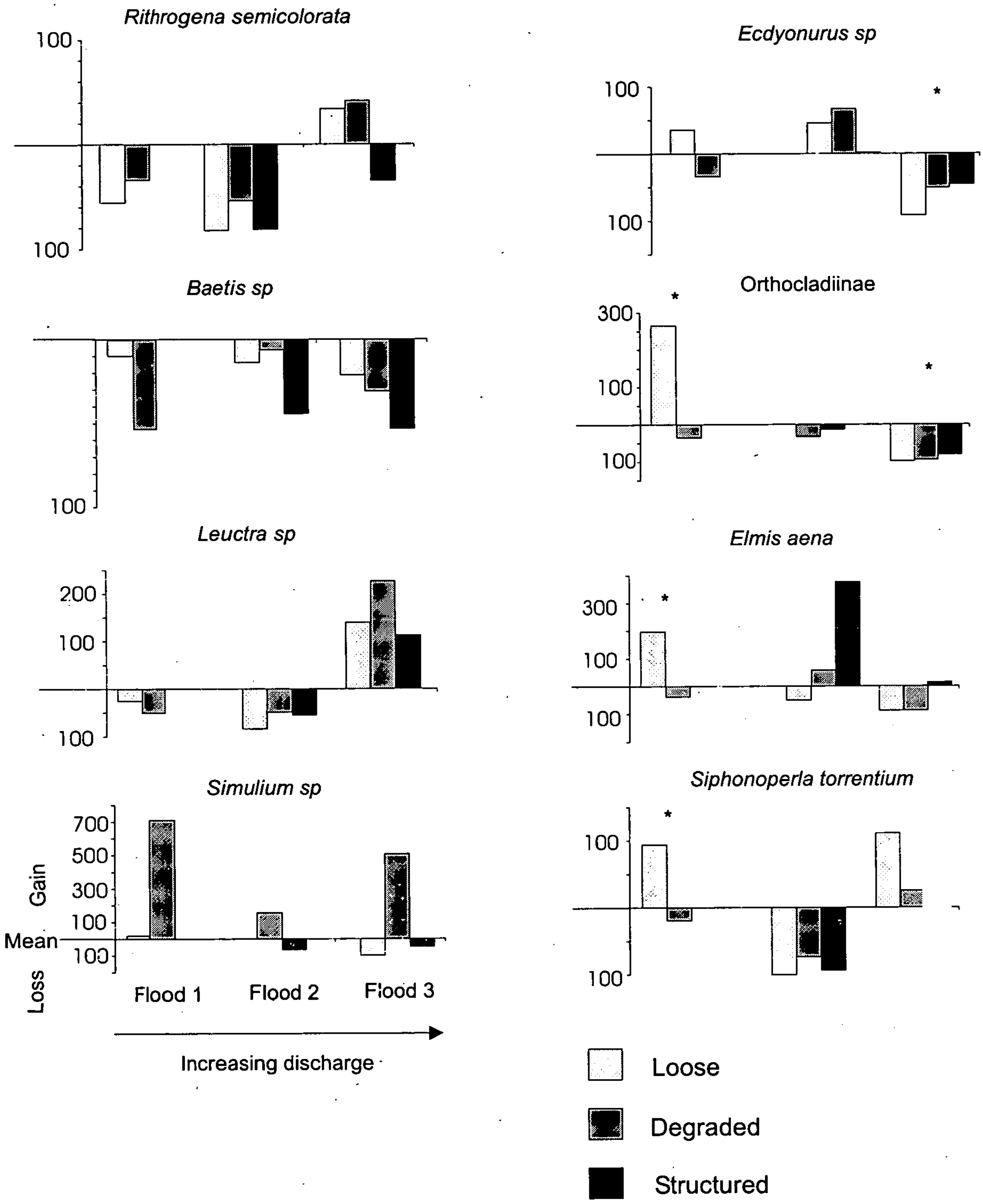


Figure 7.8 Mean percentage change in density from pre-flood mean on each patch type after each flood event for abundant taxa (> 5 %). '*' Indicates significant interaction between pre and post flood densities and patch type (Tables 7.2a, b & c).

For some taxa, their response varied between flood events. The density of *Leuctra* for example, significantly decreased on all patch types after Floods 1 and 2, but significantly increased on all patch types after Flood 3 (Table 7.2 a, b & c, Figure 7.8). *Rithrogena semicolorata* and *Siphonoperla torrentium* also showed a similar pattern (Figure 7.8). Only *Baetis* decreased in density after all flood events on all patch types.

Net change Scaled to the Reach:

Most taxa showed a large net change in density from pre-flood mean, scaled to the reach (i.e. incorporating the relative proportions of each patch type) (Figure 7.9). All taxa incurred a net loss during one or both of the floods. Only Floods 2 and 3 are shown, as no Structured patches were sampled after Flood 1. A net loss was also incurred for total density.

7.33 Response of Invertebrates to Particle Movement and Shear Stress on Degraded Patches (Response Models)

After Flood 1, below breakpoint threshold, total invertebrate density decreased significantly with both % area mobilized and peak shear stress (Figure 7.10, Table 7.4b), corresponding to response model A (Figure 7.1) Density decreased from levels approximating baseline average, for samples that had experienced minimal particle mobilization (3 %) and low shear stress (15 N/m^2), to approximately 20 % of the baseline average, for samples that had experienced greater particle mobilization (25 %) and shear stress (60 N/m^2), suggesting that percent area mobilised and or shear stress had a negative effect on invertebrate density.

Table 7.4a Flood 1 summary statistics of linear regression (y = a + bx) for % area mobilized and shear stress (Degraded) with invertebrate density. '*' indicates significant constant (a, b). See Figure 7.2 for a description of the response model, as indicated by significant constant.

	Df	F	P	R^2 %	a	b	Model
% area mobilised							
Rithrogena semicolorata	1,6	2.48	0.166	29.3	ns	ns	Null
Baetis sp	1,6	2.93	0.138	32.8	*	ns	**B**
Leuctra sp	1,6	4.36	**0.082**	42.1	ns	*	**A**
Siphonoperla torrentium	1,6	0.64	0.453	9.7	ns	ns	Null
Simulium sp	1,6	3.01	0.134	33.4	*	ns	**D**
Ecdyonurus sp	1,6	0.13	0.727	2.2	ns	ns	Null
Orthocladiinae	1,6	2.98	0.135	33.2	ns	ns	Null
Elmis aenea (L)	1,6	0.82	0.401	12	ns	ns	Null
Taxon Richness	1,6	0.01	0.922	0.2	ns	ns	Null
Total Density	1,6	5.45	**0.058**	47.6	ns	*	**A**
Shear stress							
Rithrogena semicolorata	1,6	1.48	0.269	19.8	ns	ns	Null
Baetis sp	1,6	12.26	**0.013**	67.1	*	*	**B,A**
Leuctra sp	1,6	3.84	**0.098**	39.0	ns	*	**A**
Siphonoperla torrentium	1,6	1.55	0.259	20.5	ns	ns	Null
Simulium sp	1,6	1.72	0.238	22..2	*	ns	**D**
Ecdyonurus sp	1,6	0.12	0.737	2.0	ns	ns	Null
Orthocladiinae	1,6	1.09	0.338	15.3	ns	ns	Null
Elmis aenea (L)	1,6	2.47	0.167	29.2	ns	ns	Null
Taxon Richness	1,6	1.74	0.235	22.5	ns	ns	Null
Total Density	1,6	8.68	**0.026**	59.1	ns	*	**A**

Table 7.4b Flood 2 summary statistics of linear regression (y = a + bx) for % area mobilized and shear stress (Degraded) with invertebrate density. '*' indicates significant constant (a, b). See Figure 7.2 for a description of the response model, as indicated by significant constant.

	Df	F	P	R^2 %	a	b	Model
% area mobilised							
Rithrogena semicolorata	1,7	4.48	0.201	19.8	*	ns	**B**
Baetis sp	1,7	0.00	0.950	0.1	ns	ns	Null
Leuctra sp	1,7	0.29	0.604	3.5	*	ns	**B**
Siphonoperla torrentium	1,7	1.90	0.206	19.2	*	ns	**B**
Simulium sp	1,7	3.65	**0.093**	31.3	ns	*	**C**
Ecdyonurus sp	1,7	9.63	**0.015**	54.6	*	*	**E**
Orthocladiinae	1,7	0.00	0.949	0.1	ns	ns	Null
Elmis aenea (L)	1,7	1.69	0.230	17.4	ns	ns	Null
Taxon Richness	1,7	1.81	0.215	18.5	ns	ns	Null
Total Density	1,7	0.04	0.855	0.4	ns	ns	Null
Shear Stress							
Rithrogena semicolorata	1,7	0.43	0.430	5.1	*	ns	**B**
Baetis sp	1,7	0.49	0.504	5.8	ns	ns	Null
Leuctra sp	1,7	0.06	0.815	0.7	ns	ns	Null
Siphonoperla torrentium	1,7	1.57	0.246	16.4	ns	ns	Null
Simulium sp	1,7	0.42	0.533	5.0	ns	ns	Null
Ecdyonurus sp	1,7	2.91	0.127	26.7	*	ns	**D**
Orthocladiinae	1,7	0.05	0.823	0.7	ns	ns	Null
Elmis aenea (L)	1,7	2.93	0.125	26.8	*	ns	**D**
Taxon Richness	1,7	1.42	0.267	15.1	ns	ns	Null
Total Density	1,7	0.30	0.597	3.7	ns	ns	Null

Table 7.4c Flood 3 summary statistics of linear regression (y = a + bx) for % area mobilized and shear stress (Degraded) with invertebrate density. '*' indicates significant constant (a, b). See Figure 7.2 for a description of the response model, as indicated by significant constant.

	Df	F	P	R^2 %	a	b	Model
% area mobilised							
Rithrogena semicolorata	1,7	0.04	0.855	0.6	ns	ns	Null
Baetis sp	1,7	0.19	0.680	3.0	ns	ns	Null
Leuctra sp	1,7	0.28	0.617	4.4	*	ns	**D**
Siphonoperla torrentium	1,7	0.02	0.892	0.3	ns	ns	Null
Simulium sp	1,7	0.13	0.735	2.0	ns	ns	Null
Ecdyonurus sp	1,7	2.61	0.158	30.3	ns	ns	Null
Orthocladiinae	1,7	0.08	0.793	1.2	*	ns	**B**
Elmis aenea (L)	1,7	1.45	0.274	19.4	*	ns	**B**
Taxon Richness	1,7	0.38	0.561	5.9	ns	ns	Null
Total Density	1,7	0.55	0.487	8.4	ns	ns	Null
Shear Stress							
Rithrogena semicolorata	1,7	39.5	**0.094**	39.7	ns	*	**C**
Baetis sp	1,7	1.95	0.212	24.5	ns	ns	Null
Leuctra sp	1,7	0.90	0.380	13	ns	ns	Null
Siphonoperla torrentium	1,7	2.06	0.201	25.5	ns	ns	Null
Simulium sp	1,7	2.84	0.143	32.1	ns	ns	Null
Ecdyonurus sp	1,7	3.27	0.121	35.3	ns	ns	Null
Orthocladiinae	1,7	0.76	0.417	11.3	*	ns	**B**
Elmis aenea (L)	1,7	8.19	**0.029**	57.7	*	*	**B,A**
Taxon Richness	1,7	7.39	**0.035**	55.2	ns	*	**A**
Total Density	1,7	0.71	0.433	10.5	ns	ns	Null

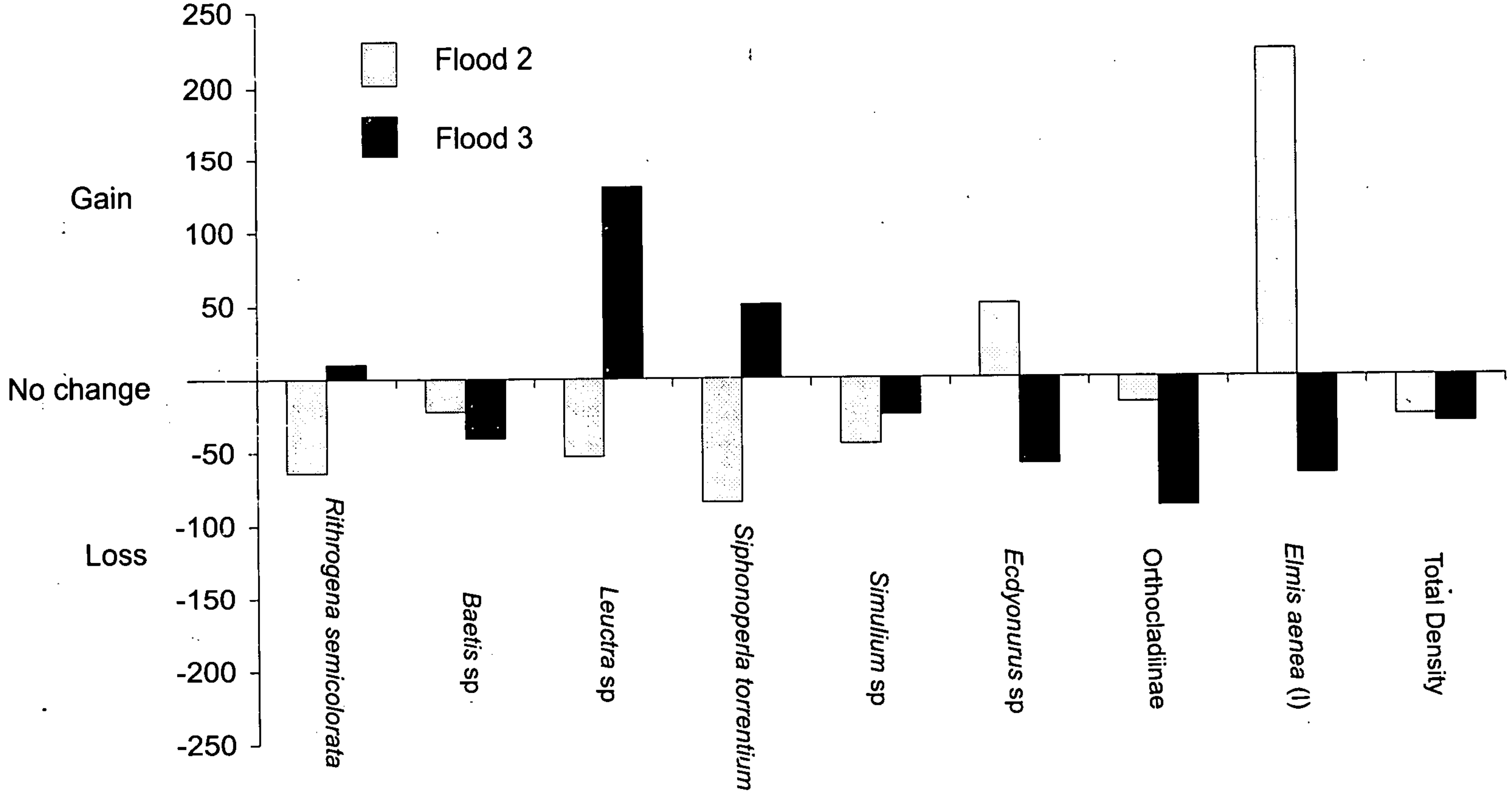


Figure 7.9 Percentage change in density from pre-flood mean, scaled to the study reach (i.e. incorporating the percent area of each patch type in the study site). Flood 1 is not included because no Structured patches were sampled, so could not scale up to the reach.

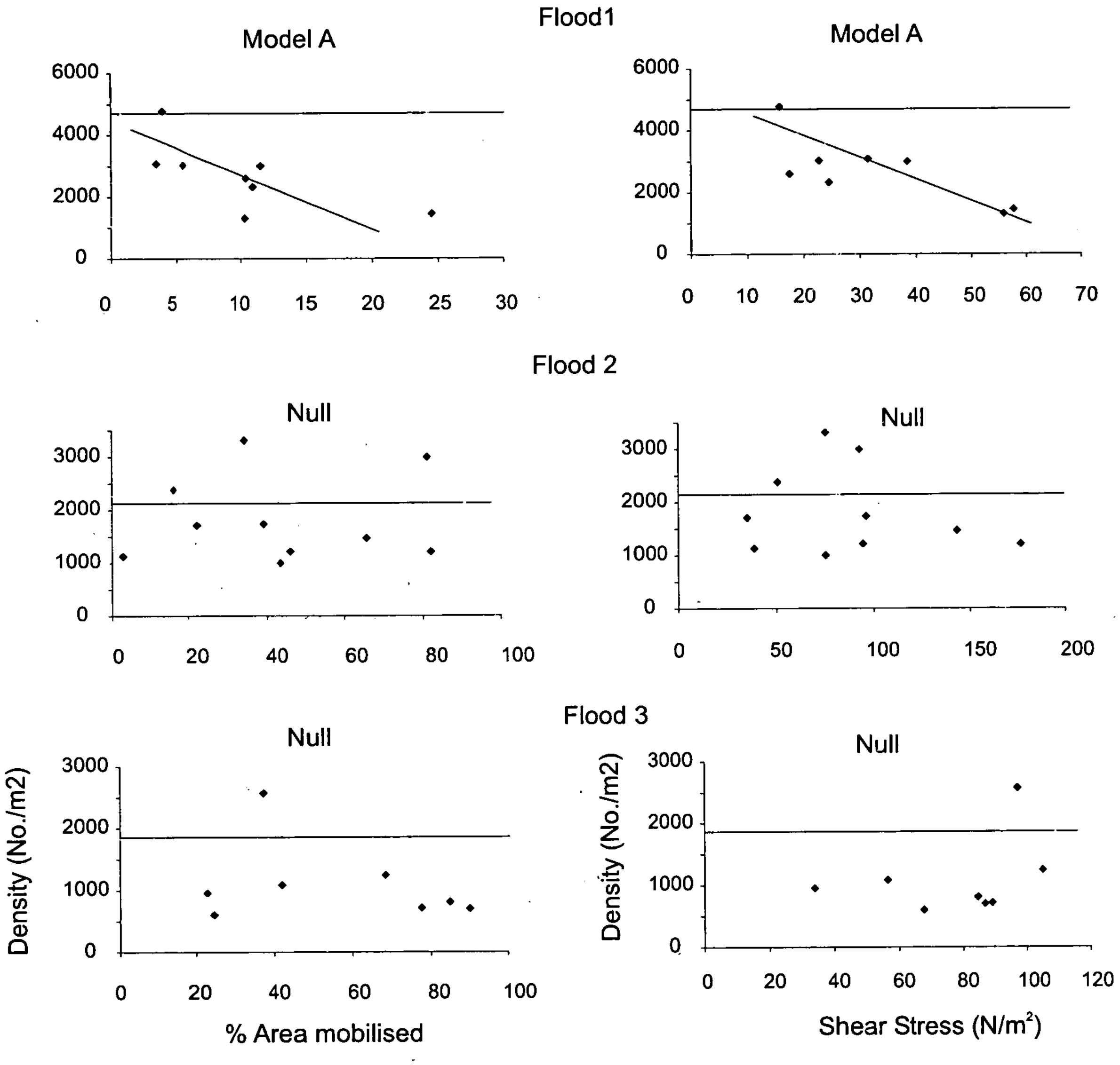


Figure 7.10 Relation between total density with shear stress and % area mobilised for Degraded patches for each flood. Pre-flood mean is shown by the horizontal line. A best fitted line is shown for significant regressions (Table 7.4). The model that best described the response is shown. See Figure 7.2 and text (p. 234, 235) for a description.

For both floods above breakpoint threshold (Floods 2 & 3) however, there was no significant relationship between total density and percent area mobilized or shear stress (Table 7.4 b & c, Figure 7.10). However, for Flood 3, the majority of samples had invertebrate densities of between 40 and 60 % of the baseline average, and while the constant 'a' is non significant (Table 7.4c), the response does appear similar to that of response model B (Figure 7.10). The samples after Flood 2 however, while encompassing a similar range in percent area mobilized as those from Flood 3, showed little reduction in density compared with the baseline average (Figure 7.10).

There was no relationship of species richness with % area mobilized or shear stress for either Floods 1 and 2 (Figure 7.11). For Flood 3, above breakpoint threshold, species richness significantly decreased with increasing shear stress (Table 7.4c, Figure 7.11), corresponding to response model A. No significant relationship however was found with % area mobilised.

For most of the abundant taxa, there was no significant relationship between density and % area mobilised or shear stress across all three floods (Table 7.4 a, b & c). Indeed, only *Leuctra* sp responded to all flood events. For Floods 1 and 2, this response corresponded to models A and B respectively (Figure 7.1), indicating loss on Degraded patches was greater than any influx into this patch environment. However for Flood 3, the response corresponded to that of model D, indicating an influx of individuals into Degraded patches. While no taxa exhibited the same response model between any two flood events, there was some consistency with net

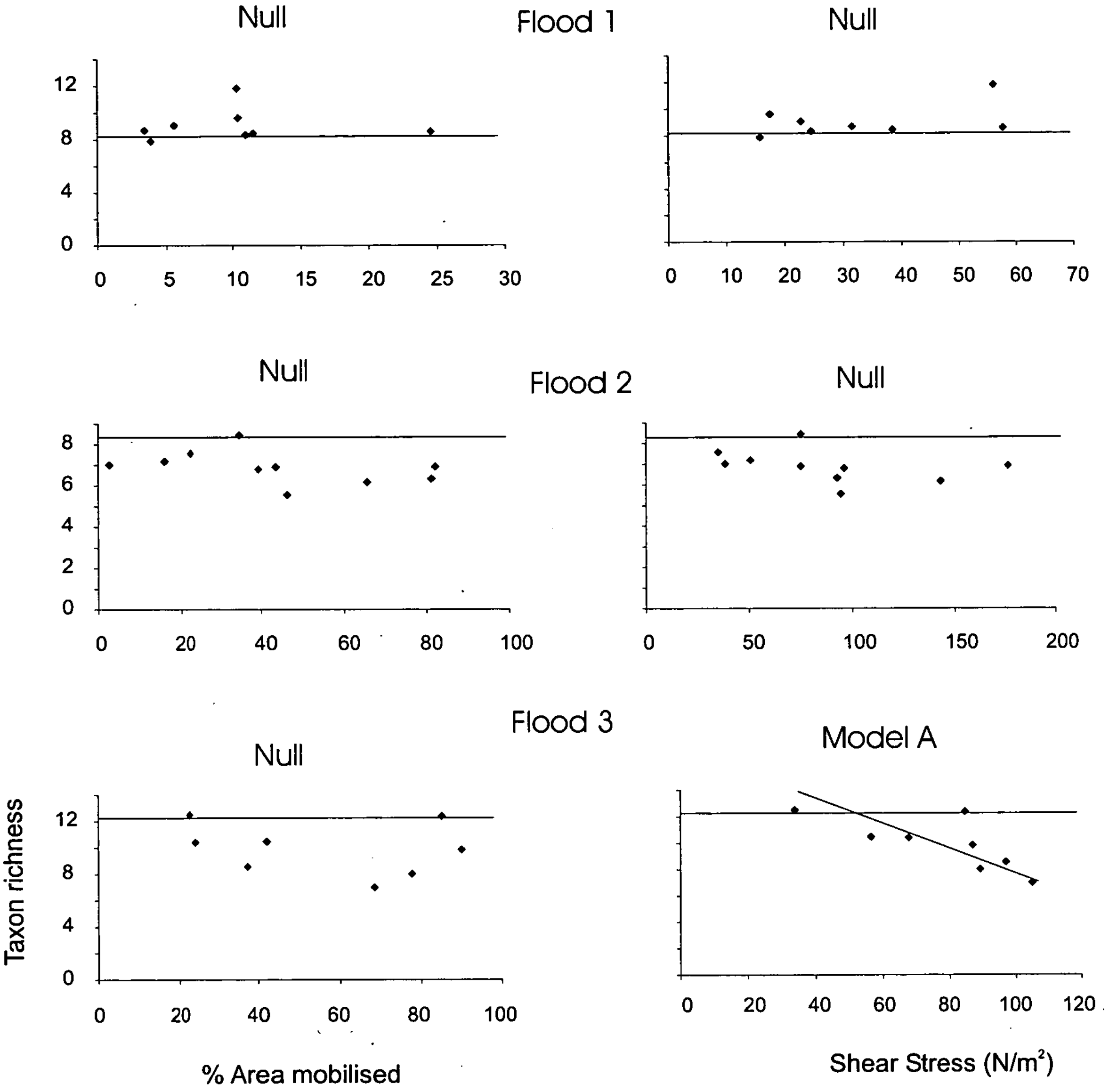


Figure 7.11 Relation between taxon richness with shear stress and % area mobilised for Degraded patches for each flood. Pre-flood mean is shown by the horizontal line. A best fitted line is shown for significant regressions (Table 7.4). The model that best describes the response is shown. See Figure 7.2 and text (p. 234, 235) for description.

gain or loss. *Simulium* sp for example exhibited a net gain from both Floods 1 and 2, models D and C respectively for % area mobilised (Table 7.4, a, b & c).

For Flood 1, below breakpoint threshold, the response to % area mobilised and shear stress was the same for all taxa except *Baetis* sp (Table 7.4a). For Floods 2 and 3 however, above breakpoint threshold, all taxa that exhibited a response, except Orthocladiinae, responded differently to % area mobilised and shear stress (Table 7.4 b & c). Further, above breakpoint threshold, no taxa corresponded to response model A, whereas below breakpoint threshold, no taxa corresponded to models C or E (Figure 7.2).

7.4 Discussion

The results of this chapter are broadly consistent with other studies that have shown that flooding in streams can produce a mosaic of invertebrate patches on the streambed, whereby some animals may fare better in one habitat than another (Cobb *et al.*, 1992, Robertson *et al.*, 1995, Palmer *et al*,. 1995, 1996, Strayer 1999, Matthaei *et al.*, 2000), or accumulate in one habitat compared with another (Palmer *et al.*, 1996). Indeed, the effect of flooding on the invertebrate assemblage varied among patch types, Loose, Degraded and Structured, although the results were complex and do not relate directly to degree of particle movement. Overall, there was a net loss of individuals after each flood event.

The results of this study are in general in contrast with that of Palmer *et al.*, (1996), and Strayer (1999) and Matthaei *et al.*, (1997) who found a good match between biotic response and underlying physical processes, such as particle movement and flow. Indeed, where particles have remained stable after a flood, invertebrate abundance has generally been higher than on mobilised sediment (e.g. Strayer, 1999, Matthaei *et al.*, 1997, 2000, but see Bond & Downes, 2000b). We may therefore have expected for example, a proportionately far greater loss of individuals on Loose patches compared with that on Structured patches. This was only observed however, after the largest flood event. Nevertheless, while no patch type consistently provided refugia for all taxa (i.e. retained residents *in situ*, with or without accumulation of individuals), the assemblage on Structured patches was generally the most resistant. Francoeur *et al.*, (1998) similarly found that bedform clusters conferred increased resistance to periphyton assemblages during flooding, compared with other areas of the streambed. Algal species on such features are most likely to be well adapted to living in areas of high flow (Biggs *et al.*, 2000), with secure attach points and low profiles (Biggs & Thomsen, 1995). Structured patches however, did provide refugia for some taxa, such as *Elmis aenea* larvae. This species generally occurred in high densities on Structured patches, and may be adapted to surviving in an environment of high flows. It is small (typically > 3-4 mm), and may have found refuge from the hydraulic forces during flooding within the moss (e.g. Nikora *et al.*, 1998) or underneath the large particles in small interstitial spaces (e.g. Holomuzki & Biggs, 2000). Other species however, that were generally found in high densities on Structured patches, e.g. *Baetis* sp, were greatly reduced on this patch type after flooding, presumably by non-scouring mechanisms of disturbance, such as shear stress. *Baetis* is a highly mobile species and likely have a different strategy to surviving than species such as *Elmis aenea*, and may have sought other refugia.

Counterintuitively, on Loose patches densities of some taxa were higher after flooding than before, suggesting individuals accumulated during flooding, despite almost complete mobilisation. This included taxa that were abundant in Loose patches pre-flood, such as *Ecdyonurus* and *Siphonoperla torrentium.* However, it also included taxa characteristic of Structured patches, such as *Elmis aenea* and Orthocladiinae, and taxa never before sampled from these patches, such as *Protonemoura praecox*, suggesting the movement of individuals among patch types during flooding (e.g. Palmer *et al.*, 1995). Accumulation may have been active for some species, but passive for others, such as *Protonemoura praecox* and *Elims aenea*, species that are not good swimmers and not typically found in Loose patches in high densities. Individuals need not move actively into a patch however for it to serve as refugium. However, damage and of course mortality during dislodgement from the substrate (e.g. Holomuzki & Biggs, 1999) and or whilst in the drift during flood waters, which can have negative consequences such as predation and starvation (Palmer 1988, Allan 1995), could negate the refuge effects (Palmer et al., 1996). Direct measurement of mortality during flooding however is difficult, as the fate of individuals is not tractable. It nevertheless may have important consequences for post-flood recovery.

Instream refugia have generally been characterized as patches that experience relatively low hydraulic stress during floods (e.g. Lancaster and Hildrew, 1993a & b, Palmer *et al*, 1996), or assumed to be locations where particles on the streambed remain stable (e.g. Strayer, 1999, Matthaeii *et al.*, 2000). One of the important attributes of refugia is that they represent patches that confer spatial or temporal resistance or resilience to biotic communities (Lancaster and Beylea, 1997). While Loose patches may not confer resistance, they may confer resilience, providing a source for subsequent colonization of denuded substrates after flooding. Despite the net accumulation of some taxa on Loose patches, the pre-flood resident fauna may actually have been dislodged by particle movement. Individuals caught in post-flood samples may actually represent individuals that have entered these patches at a later stage, such as the falling limb of the hydrograph (i.e. the post flood assemblage likely represents accumulated fauna, i.e. refugees, rather than residents). While migrations into the hyporheos of Loose patches was recorded after Flood 3 (i.e. taxa that had not previously been sampled from this zone before), the abundance of benthic fauna within this zone after flooding was very limited. Furthermore, many Loose patches were scoured after the large flood events, potentially dislodging the hypotheos (e.g. Palmer *et al.*, 1992). It is unlikely that the resident fauna of Loose patches migrated downward during flooding, to subsequently re-colonise the surface after.

In low gradient streams low flow zones act as refugia and can accumulate individuals (Lancaster & Hildrew, 1993a & b, Palmer *et al.*, 1995, 1996). In the Talla however, accumulating in Loose patches (low flow environment during base flows and minor flood events) too early in the hydrograph may not be a good strategy. Indeed, if accumulation does take place before the mobilisation of the patch (and dislodgement occurs), then Loose patches may actually have a disproportionately large effect on dislodgement and potential loss from the reach. Indeed, during flooding Brooks (1998) found that areas of low flow in the wake of boulders were refugia at one discharge, but zones of high turbulence, scour and denudation at another. In a field experiment using artificial cages as flow refugia (low flow zones), Winterbottom *et al.* (1997) found that in a torrential upland stream similar to the Talla, invertebrates did not to utilise the low flow cages as refugia. In comparison however, in a low land stream with abundant natural low flow refugia, invertebrates utilised the artificial cages, and accumulated during flooding. The invertebrates may have been utilising other forms of refugia in the upland stream, such as stable particles and interstitial spaces (Winterbottom *et al.*, 1997). Given the potential for particle mobilisation within Loose patches, this may represent a better strategy in steep streams.

In the Talla the dynamic between dislodgement and accumulation may be potentially complex, and not just restricted to Loose patches. Accumulation also occurred on Degraded patches, independent of percent area mobilised or shear stress (i.e. Response Model D, similar to Loose patches). Some taxa however, appeared to show a relationship of accumulation on Degraded patches with percent area mobilised and or shear stress (i.e. Response Models C & E). Indeed, Response Model E suggests an initial loss that is directly related to percent area mobilised and or shear stress, followed by an influx of individuals. Response Model C, on the other hand suggests that the influx may be directly linked to the process of particle mobilisation and or shear stress. These response models however, were only noted after the two large flood events (Floods 2 & 3), or phase II transport. The predominant Response Model after these floods was Model B, suggesting a loss on Degraded patches independent of particle movement, i.e. another mechanism of disturbance was likely operating. That is, in areas with low mobilisation (i.e. 20 %) during transport phase II, just as many individuals were lost as that from areas with maximum mobilisation (i.e. 80 %).

In contrast, the predominant Response Model after Flood 1, i.e. transport phase I, was Response Model A (including that for total density), suggesting a direct loss of individuals with either particle mobilisation and or shear stress. That is, with minimal mobilisation (i.e. 5 %), Degraded patches were able to maintain their resident fauna, and act as refugia. However, with 20 % mobilisation, a maximum during phase I transport, a large loss was incurred. This tends to suggest that either a change in transport phase from I to II may represent a change in disturbance mechanism on

Degraded patches, at a mobilisation of 20 % or more, or the shear stress necessary for this, represents a threshold above which dislodgement likely occurs. It also suggests that accumulation is more prevalent on Degraded patches during transport phase II compared with that from transport phase I. This, similar to Loose patches, is again somewhat counterintuitive, as particle mobilisation was greater.

Patch Classification – Refugia Use:

The results of this study generally do not conform to the simplified models of Lancaster & Belyea (1997). Patch-specific responses were complex and species specific, with scenarios such as loss and accumulation not accounted for in the models of Lancaster & Belyea (1997). Despite the strong association of particle mobilisation (Chapter Four) and invertebrate assemblage (Chapter Five) with patch type, the classification only weakly relates to refugium potential for the majority of taxa. Indeed, if we scale the response of the most abundant taxa to the study reach, incorporating the relative proportions of each patch type, there was a net loss after both large flood events (response could not be scaled after Flood 1 because Structured patches were not sampled) for *Baetis*, *Simulium* and Orthocladiinae, and indeed total number of individuals. Recovery was not monitored, so it is difficult to speculate as to how such organisms may persist in the Talla, however, other refugia may exist not incorporated in the patch classification, such as the hyporheic zone within Degraded patches or the lateral margins of emergent bars. Both types of environment have been shown to provide refugia during flooding (e.g. Dole-Oliver *et al.*, 1997, Rempel *et al.*, 2000). Some taxa, such as *Elmis aenea* (l) and *Leuctra*, also showed a net gain into the study reach after at least one of the flood events (on more than one patch type), suggesting accumulation, and refugium use, on scales larger than the patch classification.

A combination of physical habitats within the stream environment, from reach to particle, may act as refugia for invertebrates during flooding, with the possible combination of a number of mechanisms of refugium use, such as surviving *in situ*, or accumulating to re-colonise denude patches after.

Chapter Eight Conclusion

In streams that experience frequent flooding, the persistence of benthic invertebrate populations is reliant on the existence of refugia (Lake, 2000). Post-flood recovery, indeed persistence, can be dependent on the size and spacing of refugia, and the mechanisms of refugium use (e.g. whether organisms accumulate in refugia during flooding and re-distribute after) (Lancaster & Belyea, 1997). The patch classification was proposed as a framework that may allow refugia to be easily identified in steep streams, and allow for the characterisation of the spatial attributes of refugium and non-refugium patches. While it was based primarily on particle movement, the patch classification also incorporated variation in general flow pattern.

Despite the strong association of particle mobilisation (Chapter Four) and invertebrate assemblage (Chapter Five) with the patch classification, it only weakly related to refugium potential, with all patch types incurring a net loss of invertebrates after every flood event. Species specific patterns were evident, although were generally not consistent between flood events. It seems apparent that the process of particle movement in steep streams, as defined and measured in this study, may only be weakly linked with the processes that are responsible for the post-flood pattern of invertebrates. The patch classification likely does not discriminate on the basis of these processes, and may therefore not provide a useable framework to characterise size and spacing of refugia in steep streams.

Some caution should be applied however, when comparing pre and post flood assemblages due to the inevitable time lag between sampling. A large time lag of a few months, particularly over recruitment periods, can lead to an erroneous interpretation, for example recruitment may be misinterpreted as accumulation post flood. If recruitment is restricted to a particular habitat type with minimal egg dispersal, for example oviposition on large emergent boulders, then this can lead to a conclusion of patch specific accumulation. This however, is unlikely to have represented a problem here, as pre and post flood sampling was not conducted over recruitment periods, as evident by a lack of first instars in most samples. Over shorter time scales (~ minutes) however, the continual re-distribution of mobile invertebrates, such as *Baetis*, may interfere with post flood patterns. This is a problem encountered in all field studies on flood disturbance, and is not easily reconciled. Over the last decade an increasing number of flume studies have demonstrated short term movements in freshwater invertebrates (e.g. Richardson, 1992, Lancaster, 1999a, Holomuzki & Biggs, 1999, 2000) however, no work to date has detailed small scale (cm), short term (s), movement patterns in natural streams, especially when associated with flood response.

The evident loss of invertebrates from stable Structured patches nevertheless, and the lack of a clear relationship between particle movement and invertebrate abundance on Degraded patches, suggests hydraulic processes, such as shear stress and abrasion (rather than particle movement) may have influenced the post-flood distribution in the Talla. Indeed, the results from Chapter six illustrate the potential for the hydraulic environment to influence invertebrate instream transport and settlement, although individuals did not accumulate over the step, as hypothesised, rather they were either carried further downstream, or their settlement distribution remained unaffected relative to the simple hydraulics over the plane bed. In a natural stream Fonseca & Hart (2001) found that the hydraulic environment can indeed constrain the dispersal and settlement of invertebrate larvae, and create patches of accumulation. The importance of the hydraulic environment for invertebrate dislodgement, instream transport and settlement can not be over stated (Hart & Finelli 1999), and can clearly have an impact on the post flood pattern of invertebrates (e.g. Lancaster & Hildrew, 1993b). The patch classification however, does not appear to clearly discriminate on the basis of hydraulics at scales relevant to the processes involved in the post flood pattern of invertebrates in the Talla. The loss of invertebrates on Structured patches for example was not consistent between flood events; nor was accumulation on Loose patches.

The hydraulic environment of steep streams is extremely complex and can vary considerably over a large range of spatial and temporal scales, from small turbulent bursts in the order of seconds to extensive flood peaks. The patch classification appears to be too simplistic to capture the necessary variation in hydraulics at scales appropriate for benthic invertebrates. Understanding the links between flood hydraulics, invertebrate response and ultimately post flood distribution, refugium use and persistence represents a significant set of challenges. Foremost, we need a better understanding of instream transport of invertebrates and invertebrate settlement. In particular, how these two processes vary under differing hydraulic environments. More experiments similar to that in Chapter Six are required, but under a greater variety of hydraulic conditions. It is necessary however to also scale up to the stream system. Studies such as that of Fonseca & Hart (2001) start to address this; by examining how the hydraulic environment can constrain settlement in a natural stream. Predictions obtained for flume experiments can be tested in a similar way. In conjunction, future work should also focus on the relationships between streambed morphology and hydraulics, in particular how the relationships change during flooding. This is particularly challenging in steep streams where discharge events can be rapid and access difficult during peak flows.

While the patch classification system derived in this thesis may not provide a workable framework to characterise the size and spacing of refugia in steep streams, the study of patch assemblages did highlight the potential importance of geomorphic features for the invertebrate community. Structured patches for example, while they may not act as refugia for most taxa, do represent an important habitat, accounting for a disproportionately large portion of the total invertebrate abundance in both the Cramalt and Talla, and providing a key habitat for some species, e.g. *Philopotamus montanus*. Collections of large boulders, in the form of Structured patches, may thus represent an important restoration feature for modified and channelised streams. Indeed, Negishi *et al.* (2002) found that artifical collections of boulders, in the form of isolated clusters (Brayshaw, 1984), provided a habitat for increased CPOM retention and detritivore abundance in a stream section that was otherwise devoid of such structures. The distinct invertebrate assemblages associated with each patch type, Loose, Degraded and Structured, also highlights the need to adopt a sampling strategy that incorporates all geomorphic habitats in steep streams, especially when attempting to characterise the invertebrate community. Large imbicated boulders are difficult to sample, however ignoring such features may result in an erroneous estimation of invertebrate density, and omission of key species.

It is now realised that descriptors of physical habitats must be specific enough to be both geomorphologically and ecologically meaningful (Thomson *et al.*, 2001). The patch classification represented in this thesis provides a reasonable stratification of physical variables in steep streams, such as current velocity and substrate size, which are useful in classifying benthic invertebrate assemblages.

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