The Effects of Being Stranded After Flooding (Hydraulic Disturbance) on Cased Caddisfly Larvae

By

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Declaration

I declare that the worked described in this thesis has been carried out by myself unless otherwise acknowledged. It is entirely of my own composition and has not, in whole or part, been submitted towards any other degree.

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Abstract

The distribution of species of caddisfly larvae within the study stretch of the Whiteadder Water was attributed to three main environmental factors: near-bed water velocity, depth and the amount of Coarse Particulate Organic Matter and species distribution was consistent with previous research. Species of caddisfly that occur within riffles generally have unsynchronised lifecycles, compared to a more synchronised lifecycle in species that occurred in pools, and this more pronounced in the case-less caddisfly larvae.

The incidence of cased caddisfly larvae being stranded in bank-sidebank-side quadrats increased with discharge once a flooding threshold had been exceeded. The incidence of being stranded was dependant on adjacent bank-sidebank-side microhabitat, local topography, and the larval case type. The likelihood of being stranded was not homogeneous, with more individuals being stranded adjacent to riffles than pools, and on gravel substrates than turf substrates. Cased caddisfly larvae with fine mineral cases were the most abundant type found stranded, while species with vegetative cases were rarely found, although they were present in the benthos.

Flume experiments indicated that cased caddisfly larvae were passively deposited on inundated bank-sides, and that they did not actively seek this refuge. The ability of some cased caddisfly larvae to regain the water once stranded varied with case type, and the topography (substrate and slope) of the bank in artificial arenas. Time taken to regain the water was species/case specific with vegetative cased larvae regaining the water fastest and fine mineral cased larvae the slowest. Time taken to regain the water increased with increasing substrate complexity and distance from the water, but decreased with increasing slope.

The incidence of cased caddisfly larvae being stranded by flood disturbance within the Whiteadder Water, while it may be important, did not have a significant negative impact on the assemblage of cased caddisfly larvae. Only (an estimated) 12% of the

vulnerable population of cased caddisfly larvae is lost from the benthic population by being stranded over a year with a typical discharge regimen.

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1 Introduction

Disturbances are characteristic and important features of all natural environments, and may be natural or anthropogenic in origin. The environment can be subjected to many types of disturbance such as, drought, flooding, fire, pollution and the construction of dams, roads and other human structures (see Sousa 1984, 1985; Pickett and White 1985; Pickett *et al.* 1989; Begon *et al.* 1996; Resh *et al.* 1988; Poff and Ward 1989; 1990; Poff 1992). Defining 'disturbance' in ecological terms has been problematic and several definitions have been suggested. Dobson and Frid (1998) defined disturbance as "a discrete event, which removes, damages or impairs the normal function of organisms." Lancaster and Belyea (1997) defined disturbance as "a temporally discrete event that can reduce the fitness of individuals or the population size, or both." Wallace (1990) defined disturbance as "any event that that results in a significant change (positive or negative) in macroinvertebrate community structure (species, abundance, biomass or production) beyond that expected over the annual cycle within a particular habitat." Resh *et al.*, (1988) defined disturbance as "a discrete event that causes significant mortality and changes organism to resource ratios." Hildrew and Townsend (1986) defined disturbance in freshwaters as "any physical processes removing residents from the surface." Sousa (1984) defined disturbance as " a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates opportunity for new individuals to become established." The common theme among all these definitions, is that a disturbance has a negative impact on the individuals or the community that it affects. In the context of this study I will use the definition of disturbance used by Lancaster and Belyea (1997), "a temporally discrete event that can reduce the fitness of individuals or the population size, or both." I use this definition of disturbance as flood events are temporally discrete events in streams and as I will be looking at the negative impact of being stranded by these flood events on the cased caddisfly assemblage.

Disturbances can be classified as either autogenic, those that are generated within the system, or allogenic, those that are generated outside the system (Grimm 1994). Autogenic disturbance are usually biotic, and occur on a generally smaller scale, both temporally and spatially within the ecosystem. The effects of invertebrate grazing on the ecosystem can be viewed as one such example of autogenic disturbance. According to this definition it could be argued that everything an organism does in a system is a disturbance, as anything an organism does will alter its environment at some scale. The usefulness of such a broad definition is, therefore, questionable. Allogenic disturbances (such as floods within freshwater systems) are usually abiotic and generally occur on larger temporal and spatial scales,. In the context of this thesis I will be concerned only with allogenic hydraulic disturbances (floods) caused by storm/rainfall events in a low order temperate stream (see Section 1.2 and Chapters 2 and 4).

1.1 Disturbance as a Structuring Process

In both aquatic and terrestrial ecosystems, the concept of disturbance influencing community structure (i.e. the species present and their relative abundances in the community) has long been established (Connell 1978; Huston 1979; McAuliffe 1984a; 1984b; Pickett and White 1985; Pickett *et al.* 1989; Feminella and Resh 1990; Weigand *et al.* 1998). Historically, this has led to various hypotheses about the role of disturbance in determining community structure and function. Although disturbance is important in the structuring of communities, it must be recognised that other factors such as competition and predation also play an important role. Most communities are probably organised by a mixture of competition, predation and disturbance, but the relative importance of each depends on a number of circumstances (see Connell 1983; Sih *et al* 1985; Gee and Giller 1987).

A classic example of how a top predator can influence community structure has been clearly demonstrated by Paine (1966) on rocky intertidal shores of the Pacific coast of North America. The starfish *Pisaster ochraceus* preys on sessile filter-feeding barnacles and mussels, and on limpets, chitons and small carnivorous whelks. These species, together with a sponge and four macroscopic algae, form predictable associations on the rocky intertidal zone. Paine manipulated a typical piece of the shore by removing all individuals of *P. ochraceus* from an area 8 × 2 m, and excluded them over several years. At intervals, the densites of invertebrates and algal cover was assessed in the experimental area and in an adjacent control site. The control site remained unchanged during the period of the study. The removal of *P. ochraceus* led to a change in the community structure. Within a few months, the barnacle *Balanus glandula* settled successfully. The mussel *Mytilus californianus* eventually replaced the barnacle and all but one of the algal species disappeared, apparently through lack of space and a reduction in browsers. The main influence of the starfish *P. ochraceus* was to create spaces for competitively subordinate species, by removing barnacles and the dominant mussels that would otherwise out-compete other invertebrates and algae for space. Physical disturbance by wave action has an analogous effect by generating gaps that are invaded by rapidly colonizing but competitively inferior species (Paine and Levin 1981).

The importance of physical and biotic factors that varied along a gradient of environmental stress in the sessile communities of rocky intertidal zones was demonstrated by Menge and Sutherland (1976; 1987). In the rocky intertidal zone, predators were mobile and more susceptible to harsh conditions associated with storms and wave action, than their sessile prey (Menge and Sutherland 1987). In 'stressful' environments predators have little effect because they were either absent or inactive, and competition for space is prevented because harsh conditions keep populations densities low. Both mobile and sessile components of the community in these stressful environments are structured by physical factors. In moderate environments, predators are still considered to be ineffective as they were assumed to be more strongly affected by physical conditions than organisms that occur at lower trophic levels. Sessile organisms in these moderate environments occur at high densities, which results in competition for space. In benign environments the community is structured by predation as the predators keep their sessile prey at low density and thus prevent competition space.

The relative roles and interactions associated with competition, predation and disturbance were investigated in communities of North American amphibians in experimental ponds (Wilbur 1987). Four species of amphibians (*Rana utricularia*, *Scaphiopus holbrooki*, *Bufo americanus* and *Hyla chrysoscelis*), were introduced in high densities as hatchling tadpoles to experimental ponds. During the course of the experiment there was a large increase the relative abundance of *S. holbrooki*, while the relative abundances of *R. utricularia* and *H. chrysoscelis* decreased. The presence of the predatory salamander *Notophthalmus viridescens* in experimental ponds did not alter the total number of individuals reaching metamorphosis, but the relative abundance of species was altered, as *S. holbrooki* was selectively eaten. These results demonstrate the importance of predators in mediating the coexistence of species within a community. To simulate disturbance Wilbur subjected the tadpole communities to water loss, which simulated a natural drying regime. Competition had the effect of retarding growth and so increasing the risk of desiccation in drying ponds. *Scaphiopus holbrooki* had the shortest period as tadpoles and constituted a greater proportion of metamorphosed tadpoles at the end of the experiment in which the ponds had dried. The presence of the predator, *N. viridescens* ameliorated the effects of competition, allowing surviving tadpoles of *R. utricularia* and *H. chrysoscelis* to grow rapidly enough to metamorphose before the ponds dried up.

In early studies, communities were considered to exist in a state of equilibrium, and this led to the development of the 'equilibrium model of community structure'. Equilibrium theory assumes a constant environment, and that biotic processes (e.g. competition, predation and parasitism) are the primary determinants of community structure (McIntosh 1985; 1987). If the environment is not constant then species are adapted to a degree of variability and biotic processes predominate (Resh *et al.* 1988). Therefore, in the absence of disturbance, community structure is a direct result of competitive, mutalistic and trophic interactions between species (Resh *et al.* 1988). The equilibrium hypothesis assumes a constant, disturbance-free environment and this is unrealistic for the majority of stream ecosystems. Minshall *et al.* (1985) and Hemphill and Cooper (1983), however found that some small, low order spring-fed streams appeared to have communities that fitted the equilibrium theory. The study by Minshall *et al.* (1985) was carried out in a high elevation mountain stream (Salmon

River, USA), where a spring snowmelt spate occurs regularly each year. During the remainder of the year the flow was relatively constant and the time between 'disturbances', was long enough to allow a quasi-equilibrium to become established. As this spate occurs in a predictable manner it can be argued that it is not really a disturbance, but a normal feature of that system, though Poff (1992) argues that disturbances can be predictable. Poff argues that disturbances are by definition ecological events but if their temporal distribution of disturbance events is "predictable enough", ecological responses may be small because organisms and communities have adjusted to them in evolutionary (historical) terms.

Hemphill and Cooper (1983) observed that the larvae of the caddisfly *Hydropysche oslari* were competitively superior to the larvae of the blackfly *Simulium virgatum* in a Californian stream. The blackfly persisted in the system by exploiting space vacated by *H. oslari* during regular spring spates. The blackfly larvae are opportunistic colonisers, which quickly invade. As the water level drops and stabilises (creating near equilibrium environmental conditions), *H. oslari* became dominant again. The examples discussed so far show that an equilibrium state can exist in stream ecosystems, but only temporarily and is an exception rather than the general rule in such lotic systems. Reice (1985) argued that frequent spates kept stream macroinvertebrate communities in perpetual dis-equilibrium, and high species richness was attributed to disturbance that prevented competitive exclusion. Grossman *et al.* (1982) and Meffe (1984) have shown that disturbances can structure fish communities in a non-equilibrium mode.

There are several hypotheses that describe the role that disturbance plays in structuring communities, such as the intermediate disturbance hypothesis (Connell 1978) and dynamic equilibrium model (Huston 1979). Historically, Connells' (1978) intermediate disturbance hypothesis was proposed to explain the high diversity of coral reefs and tropical rain forests. The hypothesis assumes a competitive hierarchy within the species of the community. In the absence of any disturbance superior competitors replace inferior species, reducing the species richness of the system. The model also assumes that these superior competitors are efficient in occupying space. If disturbances are too frequent or too great in magnitude, the superior competitors are unable to establish and so are removed from the system. The system then becomes dominated by colonising species (inferior competitors), which in turn results in low species richness. Therefore, in an intermediate regime of disturbance, the superior competitors can become established in the system, along with the colonising (inferior competitors) species exploiting areas of disturbance, this in turn results in a high species diversity. In contrast Huston (1979) hypothesised that community structure was a balance between the rates of growth and, competitive exclusion, and the frequency of disturbance events that would reduce populations within the community. If the intervals between disturbance events was shorter than the time required for competitive exclusion, then inferior competitors would remain in the system, and so increase the species richness. If the disturbance occurred at a greater frequency or was severe enough, species in the community with a long life cycle would be removed. Huston (1979) proposed that the community structure was determined by the influence of the environment on the net outcome of species interactions. Elements of these models have been applied to stream communities.

The dynamic equilibrium model (Huston 1979) in which frequent disturbances occur on a relatively short and unpredictable regime can be applied to run-off fed stream systems, that is the stream is not primarily spring fed, but channels water from the landscape after precipitation. Though it must be stated there is no sharp contast between a spring-fed and run-off fed stream, but a continuum (Gee *pers comm.*). In these systems, storms can generate spates and floods within hours, and at any time of the year provided that there is precipitation. It has been proposed that these frequent spates and over-bank floods keep the macroinvertebrate community in a state of continual dis-equilibrium. McAuliffe (1984a; 1984b) showed that the caddisfly *Leucotrichia pictipes* was prevented from developing a competitive monopoly by spate driven rock tumbling. In the absence of disturbance *L. pictipes* appears can establish a competitive monopoly over the larval moth *Paragyractis confusalis* and the chironomid *Eukiefferiella,* which also inhabit the same system, through aggressive territorial behaviour around its retreats. *Leucotrichia pictipes* also has the advantage in that their silken retreats persist from year to year and therefore can be occupied by subsequent generations. In the absence of disturbance, the presence of available retreats for *L. pictipes* confers an advantage over *P. confusalis* whose larvae always build new retreats for each generation. Disturbances such as floods, which rolled rocks in the stream, thus making the previous generations of *L. pictipes* retreats unavailable, allowed the two species to coexist. The coexistence of *Eukiefferiella* was attributed to low stream discharges late in the summer that emersed some of the stones. The emersion of the stones caused some of them to dry out and the *L. pictipes* that cannot abandon their retreats perished as the stones dried. This allowed *Eukiefferiella* to become established as it has several generations in a year and can exploit the ephemeral resources of shallow water stones in the system. This fits the dynamic equilibrium model, as the interval between disturbances is shorter than the time required for competitive exclusion.

Another example of how physical disturbance can modify competitive and predator-prey interactions was shown by Meffe (1984) in two species of fish in Arizona streams. Meffe (1984) studied the predator-prey interaction between an introduced species of mosquitofish *Gambusia affinis* and a native topminnow *Poeciliopsis occidentalis*. *Gambusia affinis* has replaced *Poeciliopsis occidentalis* in most streams in Arizona, streams where the species apparently coexist are all in habitats that are subjected to severe spates. Meffe showed that the coexistence occurred because the prey species (*P. occidentalis*) is less susceptible to downstream removal by large spates than the predator *G. affinis*.

The intermediate disturbance hypothesis (IDH) suggested by Connell (1978) has been supported by various stream studies (Stanford and Ward 1983; Robinson and Minshall 1986). Robinson and Minshall (1986) manipulated the disturbance frequency on experimental brick substrates by turning them over at intervals of 0, 3, 9, 27 and 54 days. The invertebrate species richness and density declined as the frequency of the disturbance was increased. This study did produce some data that were consistent with the intermediate disturbance hypothesis, with the reduced species richness at high frequencies of disturbance, but did not show maximum richness at intermediate disturbance frequencies. While Robinson and Minshall (1986) study appears to support the IDH, it can be argued that manipulating species richness of mobile taxa on individual bricks is not the same as community structure. In contrast Reice (1984) found that species diversity and richness did not change with minor amounts of rock tumbling disturbances. Reice inferred that the intermediate disturbance hypothesis could not be applied to stream systems due to a lack of knowledge of competitive displacements in streams. McCabe and Gotelli (2000) also failed to find any evidence to support the IDH, in experiments that manipulated the frequency, intensity and area of disturbance on benthic macroinvertebrates in a northern Vermont stream. Using rarefied samples, they found that species richness was higher in all disturbed treatments compared to the undisturbed control, with significant increases in species richness for larger areas and greater intensities of disturbance. The increases in species richness in response to disturbance were consistent within patches, amomg patches with similar disturbance histories, ang among patches with differing disturbance histories. Their results while they did not support the IDH, do lend some support Huston's dynamic equilbrium model. In contrast Hart (1985, 1986) and Gawne (1996) have observed competitive interactions among grazers in streams.

1.2 Hydrualic Disturbance in Lotic Systems

The consequences of hydraulic disturbances to benthic communities are well documented (see Sousa 1984; 1985; Fisher *et al.* 1982; Resh *et al.* 1988; Reice *et al.* 1990; Giller *et al.* 1991; Lugthart and Wallace 1992; Death 1996; Gawne and Lake 1996; Bradt *et al.* 1999). But what are the abiotic processes/forces that lead to hydraulic disturbance affecting the benthic community? In this section I will concentrate on the physical nature of flow and the abiotic processes/forces associated with floods that can result in a negative impacts on benthic assemblages of organisms. In streams, storm-related floods are the most frequent causes of hydraulic disturbance, although increases in discharge downstream caused by dam releases is another potential cause. Flow in most rivers in temperate regions of the world flow during periods of no rainfall due to inputs from groundwater or lakes. In low order streams, the flood hydrograph usually consists of a rapid rise to peak discharge and a gradual fall back to base flow once rainfall has ceased. The catchment size, shape, gradient and vegetation all affect the flooding response time of a stream to rainfall. The quicker the water runs off the catchment area the quicker the ascending limb of the flood hydrograph climbs to peak discharge. As a result, small low order streams show more short-term variation in discharge than lowland rivers with a larger catchment area and volume to storm events.

Several factors the frequency, intensity and severity of can influence its effect on a community,. For example, the geomorphology of a stream could affect how the community is affected by disturbances such as sedimentation. Some depositional areas will be more susceptible to the effects of sedimentation than non-depositional areas such as riffles in fast flowing, shallow, high-gradient reaches (Gurtz and Wallace 1984). At the extreme end of the scale, the eruption of Mt. St. Helens resulted in massive sedimentation that eliminated the majority of stream biota and drastically altered such habitats (Resh *et al.* 1988). The channel form influences the physical attributes of the stream such as, depth, discharge, water velocity, substrate size/character, flooding and stability and bed load sediments. The effect of flood disturbances on streams varies in relation to the substrate and channel form in a predictable way. A moderate increase in discharge will have little effect on a channel that is dominated by boulders or cobbles, whereas a channel dominated by a gravel bed can be moved by a moderate increase in the discharge (Resh *et al.* 1988). So the intensity and frequency of the disturbance is also related to the substrate on which the community resides.

In order to understand how hydraulic forces can affect communities and individuals, the nature and properties of these forces needs to be understood. Flow in stream channels is three-dimensional; each fluid particle may travel longitudinally, laterally or vertically. At the same velocity flow can be either turbulent or laminar (related to the depth and roughness of the substrate) (Gordon *et al.* 1992; Vogel 1996). Laminar, hydraulically smooth flow conditions can exist over solid, smooth surfaces (e.g. mud substrates and flat smooth bedrock). When the flow is laminar the fluid particles move in parallel layers which slide past each other at different speeds but in the same direction. However, pure laminar flow is rare and usually occurs at low velocity. Turbulent, hydraulically rough flow occurs in areas of coarse, uneven substrates and at a higher velocity and involves chaotic eddies in every direction that disrupt orderly laminar flow. Turbulent flow has an important mixing effect on heat, water chemistry and oxygen into areas close to the substrate from above layers.

The nature of flow is also influenced by two other properties: viscosity and inertia. Viscosity is related to how quickly a fluid can be deformed, the resistance due to the coherence of its molecules (Giller and Malmqvist 1998; Vogel 1996). Colder water is more viscous than warmer water. Inertia reflects the resistance of fluid particles or objects in a fluid to accelerate or decelerate when force is applied. Generally, high inertial forces promote turbulence and high viscous forces promote laminar flow (Gordon *et al.* 1992; Vogel 1996). The ratio of inertial forces to viscous forces is known as the Reynolds number (Re). Within a fluid, Re can be estimated for the stream channel or an individual organism. For a fluid, a large Re, where inertial forces dominate, indicates turbulent flow dominates. For example, a small brook with a current of 0.1 m s^{-1} has a Re of 10 000 (Reynolds *et al.* 1991; Reynolds 1994). In contrast, a small Re, where viscous forces dominate, indicates laminar flow, with a transitional range between 500 and 2000 (Vogel 1986). For any given depth flow becomes becomes laminar when velocity decreases such that Re drops well below 2000. Re also indicates the forces that will be experienced by an organism. In general, small organisms close to the stream bed where flow velocity is low have low Re values and therefore will be more subject to viscous forces. Large organisms in greater flow velocity conditions have higher Re values and will be more subject to inertial forces (Statzner and Holm 1989; Vogel 1996).

In a river or stream at a given discharge, the velocity of water at any-one point decreases logarithmically with depth resulting in a velocity gradient (Gee *pers com.*). Velocity gradients are the result of a thin layer of fluid in contact with the substrate being prevented from moving by frictional drag, the 'no slip' condition (Vogel 1996; Gordon *et al.* 1992). At the interface between a stationary solid and a moving fluid, the velocity is zero. This layer is called the boundary layer and is not quite a physically distinct layer (Vogel 1996). The boundary layer can be described as the region from where the fluid contacts a surface (e.g. the stream bed) to where the fluid is no longer significantly influenced by the substrate. The flow above this so called boundary layer is also slowed but the influence of frictional drag diminishes with increasing distance from the substrate and the velocity increases the further it is from the substrate. The thickness of the boundary layer decreases with increasing velocity. The boundary layer contains a viscous laminar sublayer that varies in thickness depending on the substrate. Where flow hits an object (substrate or organism) the front edge is fully exposed to the flow, but on the top and sides there is a thin laminar layer that progressively increases along the object (Statzner *et al.* 1988; Vogel 1994). At the downstream edge, the flow separates and the velocity behind the object is reduced or becomes virtually non-existent creating a 'dead zone'.

Shear stress relates to the force required to dislodge and entrain substrate particles or organisms, and to the energy required to withstand the force. Flow velocity gradients in streams produce shearing forces on the stream bed, the main shearing force is shear stress. Shear stress is the force acting parallel to the surface (i.e. stream bed or organism) per unit area (see Gordon *et al.* 1992; Vogel 1994). As water flows over a solid surface whether it is a substrate particle or an organism it generates lift and drag forces. If the stress force is large enough then the particle or organisms can be dislodged and set in motion. Shear stress is correlated to the square of the current velocity, so high flows (e.g. floods) will exert a greater shear stress on the stream bed. During periods of high discharge the average current velocity and hydraulic stresses (shear stress, lift and drag) can cause scouring and movement of the stream bed that disrupts benthic habitats (Thorup 1970; Matthaei *et al.* 1996, 1999), which in turn can dislodge and kill benthic invertebrates resulting in a reduction in the density of benthic organisms (Anderson and Lehmkuhl 1968; Sagar 1986; Giller *et al.* 1991; Grimm 1994; Matthaei *et al.* 1997). With reductions in benthic population density, gaps may be created that can be invaded by rapidly colonizing but competitively inferior, species allowing a higher species richness (Paine 1966; Paine and Levin 1981).

As a result of the hydraulic forces acting on them benthic organisms in stream have to be able to withstand increases in hydraulic forces or become dislodged transported and potentially killed by the flood event,by becoming crushed and/or hit by the mobilisation of the substrate particles. However, benthic organisms do persist and are resilient to flood events, and this resilience may be achieved by a combination of physiological, morphological and behavioural mechanisms.

1.3 Strategies: Morphology, Behaviour and Life History

How organisms/individuals survive disturbances, and the mechanisms by which this is achieved is vital in the understanding of stream community structure and the interactions between trophic levels. Members of a community that are able to resist or avoid disturbances are at an advantage, over less well-adapted species. Many organisms within stream communities have morphological, physiological and behavioural adaptations that allow them to persist despite the physical stresses of disturbance.

1.3.1 Morphology

Body shape plays an important role in determining how individuals resist dislodgement by the movement of water. Examples of morphological adaptations to resist dislodgement by hydraulic forces found in stream macroinvertebrates are shown in Table 1.3.1. Claws, hooks, suckers and friction pads all allow an organism to remain firmly attached to the substrate and thus it is less likely to be dislodged during a flood. The use of flattening, streamlining and small size also help to prevent the animal being dislodged by reducing drag forces (i.e. friction and pressure drag: see Statzner and Holm 1982; 1989), and by residing in the boundary layer where hydraulic forces are minimal; these adaptations minimise the effects of increased hydraulic forces on individuals.

Stream insects have not evolved an optimal body form for resisting hydraulic forces. The evolution of body shape has been influenced by at least five physical factors: diffusion through boundary layers, corrasion, lift, friction and pressure drag (Statzner and Holm 1982; 1989; Ward 1992). Drag forces on stream invertebrates would vary with size, as drag forces vary as a function of body size (Statzner and Holm 1982; 1989; Statzner 1988a). Therefore different morphologies would be required to minimise drag in small/young or larger/older individuals of the same species (Statzner and Holm 1989; Vogel 1996). Small animals or young individuals live in a world of low Reynolds number (Statzner and Holm 1989; Vogel 1996). In this environment viscousity is more important than inertial forces. Movements are impeded and the rate of gas exchange is reduced, but the flow of water around them is less turbulent and buffeting. Large animals, such as fish, experience higher Re values, which means that inertial forces are much more important, so large animals have relatively few problems with locomotion and gas exchange. The effects of flow therefore change with the body size of a single individual as it grows.

Table 1.3.1 Examples of morphological adaptations exhibited by aquatic insects to resist dislodgement by current (After Ward, 1992).

Adaptation	Function	Lotic Examples
Flattening	Current avoidance (reside in boundary layer or crevices)	Psephenidae (Coleoptera), Heptageniidae (Ephemeroptera)
Small size	Current avoidance	Elmidae (Coleoptera)
Streamlining	Fusiform shape and smooth contours	Baetidae (Ephemeroptera)
Suckers	Firm attachment to substrate	Blephariceridae (Diptera)
Friction Pads	Increased body contact with substrate	*Drunella doddsi* (Ephemeroptera) *Rithrogena* (Ephemeroptera)
Claws/Hooks	Reduce chance of dislodgement	Elmidae (Coleoptera), *Rhyacophila* (Trichoptera)
Silk and sticky secretions	Attachment to substrate in high current areas	Psychomyiidae (Trichoptera) *Petrophila* (Lepidoptera) Simuliidae (Diptera)

Dorsoventral flattening of the body is a characteristic of several groups of stream invertebrates that reside in fast flows, especially in the heptageniid mayflies. Statzner and Holm (1982) analysed the microcurrent regime around the mayfly *Ecdyonurus venosus* (Ephemeroptera: Heptageniidae) using laser doppler anemometry. They found that the boundary layer was thinner than previously thought and that insects may exert some active control over their immediate boundary layer by altering their body posture; a conclusion supported by Smith and Dartnall (1980) and Statzner and Holm (1989). Weissenberger *et al.* (1991) discovered that *Ecdyonurus* spp. could sometimes create negative lift (down force) by lowering its head capsule and using its flattened femurs as spoilers to prevent dislodgement by the current. Another advantage of flattening as well as a mechanism of current resistance, is avoidance of the current flattening enables insects to move into crevices within substrates to avoid the rigours of the current.

Streamlining and a fusiform body shape are found in a few species of beetles (McShaffrey and McCafferty 1987) and bugs as an adaptation for swimming. Streamlining reduces drag and also reduces lift; this reduces the energy an individual has to expend to remain attached to the substrate. In lotic species a fusiform body shape is exhibited only in some baetid mayfly species, which enable them to swimming against a strong current for short distances (Ward 1992).

Suckers and friction pads are also used by several benthic invertebrate groups to provide physical resistance to the current. Among aquatic invertebrates true hydraulic suckers are found only in the net-winged midges (Diptera: Blephariceridae). Blephariceridae inhabit mountain streams and reside on the tops of rocks, they maintain position by the use of ventral suckers applied to the surface of the rocks. Blephariceridae are capable of moving against currents of 2.0 m s^{-1} (Frutiger 1998). The ability to move against such high flows is attributed to the fact that during locomotion the larvae remain attached to the substrate by at least 2 suckers. This minimal number allows maximal mobility and speed, but guarantees mechanical stability and safe attachment (Frutiger 1998). Friction pads are not as efficient as true hydraulic suckers, but increase the frictional resistance by increasing the area of the body in contact with the substrate. Friction pads are used in several heptageniid mayflies, whose gills are enlarged (to increase the area of the body in contact with the substrate), and can direct the current away from the underside of the body. Corbett (1962) reported that a few of the lotic zygopterans residing in fast flowing streams have enlarged caudal lamellae with setae on the margins that act as a kind of adhesive organ.

The use of claws and hooks is a very common adaptation found in lotic invertebrates that enables them to withstand high water flows. The posterior prolegs of the caseless caddisfly *Rhyacophila* spp., and lotic chironomid midges have hooks or hooklets that help the larvae from becoming dislodged into the drift as it moves over exposed substrates (Armitage, P. *et al.* 1995; Hart *et al.* 1991; Giller and Malmqvist 1998).

Adult riffle beetles (Coleoptera: Elminthidae), as their name suggests, are found in fast flowing sections of streams, they possess large and stout tarsal claws that enable them to grip the substrate (Brown 1987; Ward 1992).

Sticky secretions and the production of silk are also used in resisting dislodgement. Silk is a generic term used for all fine, fibrous threads produced by arthropods (though its chemical composition may differ), the strands although flexible and soft have a high tensile strength (Giller and Malmqvist 1998). The properties of silk make it ideal as a lifeline and is utilised by some caddisfly larvae and Simuliid larvae to prevent dislodgement and to enable the individual to regain the substrate if dislodged by the flow (Gallepp 1974; Wotton 1986; Merz *et al.* 1988; Holomuzki and Biggs 2000).

In the cased Trichoptera, the case type itself may act as ballast and may prevent individuals becoming dislodged by hydraulic forces. For example, a heavy case would not become dislodged as easily with increasing discharge. The use of a case as ballast, preventing the individual being displaced into the drift has been proposed for some species such as *Goera calcarata, Silo pallipes* and *Anabolia nervosa* (Dodds and Hisaw 1925; Webster and Webster 1943; Otto and Svensson 1980; Otto and Johansson 1995). For example, *Goera calcarata* in lotic waters has a case that is significantly heavier than those species found in lentic water (Otto and Svensson 1980). Otto and Johansson (1995) found that larval *Silo pallipes* when exposed to varying current regimes, resisted entrance into the drift to a greater degree than larvae that had the lateral ballast stones (integral to the case construction) removed. The role of a heavy case that is used as ballast, however, has been questioned by Otto and Svensson (1980). They argue that some species, such as the larvae of the limnephilid caddisfly *Potamophylax cingulatus* build cases of leaf discs during the winter when flow is high and mineral based cases during the summer when the flow is lower, which is contrary to the ballast hypothesis. Some species such as *Anabolia nervosa* and *Silo nigricornis* have lateral additions to their cases made of sticks or gravel, which are thought to provide a ballast function (Dodds and Hisaw 1925; Webster and Webster 1943; Johansson 1991). Recent work by Statzner and Holm (1989) using Laser Doppler Anemometry (LDA) has shown that the use of lateral materials as ballast in cases of some species (e.g. *Anabolia nervosa* and *Silo nigricornis*) may indeed be questionable.

Though they state that more experimental data is required to draw firm conclusions about ballast function of lateral material to cases. The addition of lateral sticks to the case of *A. nervosa* and lateral stones to *S. nigricornis* increased the relative drag in *Silo nigricornis* and *A. nervosa*. The addition of sticks and gravel on the cases may also influence amount of lift the animal experienced. Bernoulli's principle (higher velocity above an object than below it generates lift) can only be applied: a) along a streamline, b) outside velocity gradients close to a wall and c) when viscousity influences are unimportant (i.e. at a Reynolds number of an animal which is above 100 (Vogel 1996). Though the results obtained Statzner and Holm (1989) did not conform strictly to the assumptions of Bernoulli's principle so no firm conclusions could be made the presence of sticks on the case of *A. nervosa* reduced the velocity above the case, thus potentially reducing the amount of lift per unit area of case. However, because the total area of the case was increased by the sticks, the total lift generated may not have been decreased. In *S. nigricornis* the presence of the lateral gravel additions to the case did not reduce the velocity above the case. Statzner and Holm (1989) suggested that in contrast to *A. nervosa*, the material added laterally to the case did not significantly reduce lift per unit area of case surface, i.e. the gravel increased the total lift (because it increased the total area of the case).

1.3.2 Behaviour

Morphological adaptations by themselves will not function successfully unless used in the proper manner; therefore the behaviour of benthic invertebrates is also an important aspect of their resistance to dislodgement by the current (though it is impossible to untangle the two aspects, morphology and behaviour). There have been several reviews of the behavioural adaptations of aquatic insects to high flow rate (Hynes 1970; Wiley and Kohler 1984; Vogel 1996; Ward 1992; Giller and Malmqvist 1998). Table 1.3.2 shows examples of behavioural adaptations to flow rate in aquatic insects.

Table 1.3.2 Behavioural adaptations of aquatic insects to flow rate (After Ward 1992).

Adaptation	Functions	Lotic Examples
Ballast	Reduced buoyancy	*Silo* (Trichoptera)
Positive rheotaxis	Reduction in accidental dislodgement and counters downstream dislodgement	*Leptophlebia cupid* (Ephemeroptera)
Negative phototaxis	Current avoidance by cryptic behaviour	Heptageniidae (Ephemeroptera)
Current preference	Selection of micro-current habitats active or passive mechanisms	Unknown, suggestion that theremay be a lack of strong flow response curves by benthic invertebrates (Lancaster and Hall 2001 unpublished)

Lotic organisms exhibit various active movements in response to environmental stimuli (taxes), such as flow rate and light intensity, that may directly or indirectly enable individuals to avoid high flow rate. Many benthic invertebrates are positively rheotactic and tend to orientate themselves towards the current. Orientating the body with the current maintains the body in a position least liable to accidental dislodgement into the water column. By presenting a stream lined body form into the flow individuals can lower the hydraulic forces acting on them that could dislodge the organism. Negative phototaxis (active movement away from the light) is exhibited by a number of benthic invertebrates such as some caddisflies species (Elliott 1969; Wagner 1989) and molluscs (Evans 1951). Negative phototaxis among stream invertebrates can indirectly, through cryptic behaviour avoid high currents by residing under rocks or burrowing into the substrate.

1.3.3 Life History

The life histories of the organisms of a system must also be taken into consideration in relation to the frequency and type of disturbance (Stearns 1976, 1977; Lytle 2001). From an evolutionary perspective, disturbances can be categorised as either fine-grained events that affect only part of the population at a time or coarse-grained events that affect the entire population simultaneously (Iwasa and Levin 1995). Fine-grained disturbances include the formation of gaps in forest canopies (Runkle 2000), and flash floods (Fisher *et al.* 1982; Gray 1981; Lytle 2000), and the scouring of marine benthic algae by storms (Airoldi 2000). Coarse-grained disturbances include inter-annual variability in growing season length or annual rainfall (Philippi 1993), or hurricanes that disturb large areas (Lytle 2001).

In the context of this thesis, I will be concerned with fine-grained disturbances caused by hydraulic flooding disturbance within streams. When the environment varies unpredictably over the life span of the individual, then selection may favour the spreading of reproduction over many seasons or concentrate it early in life-depending on the circumstances (Goodman 1979; Ladle and Ladle 1992; Lytle 2001). When recruitment of offspring is unpredictable from year to year, selection is assumed to favour adult survival adult survival at the expense of present fecundity, a strategy that is referred to as 'Bet-hedging' (Stearns 1976). For example in desert streams in the southwestern United States (Fisher *et al.* 1982) flash flooding can eliminate a very large percentage (up to 95%) of the benthic community. Species in these communities have short life histories and overlapping generations, which ensures a rapid recolonisation by adults from the adjacent riparian zone (Fisher *et al.* 1982; Gray 1981; Gray and Fisher 1981). The species in this habitat have adapted over evolutionary time scales to short life cycles and continuous emergence and are well suited to the type of disturbance. So community structure should remain constant in the long term, with little long-term impact from disturbance. The prior exposure, and the frequency and kind of disturbance, influence the species composition and the response of the community to the disturbance. If the species or community have not been exposed to a disturbance before, then there is no evolutionary basis or physiological resistance upon which either a specific or a community response can be framed (Wallace *et al.* 1986). .

1.4 Flow Refugia

Hydraulic disturbances can dramatically reduce the abundance of benthic invertebrates, but communities are usually resilient and recover in a few weeks or months, which is often less than generation time of the organisms (Lake 1990; Sedell *et al.* 1990; Giller *et al.* 1991; Mackay 1992; Matthaei *et al.* 1997). The heterogeneous nature of a stream may allow populations to remain at a higher density than possible through morphological and physiological adaptations alone, through the use of flow refugia (Lancaster and Belyea 1997). It is therefore likely that benthic macroinvertebrates ameliorate the negative impacts of high flow velocity by sheltering in, and re-colonising from, refugia. The term 'refugia' is broadly defined as places (or times) where the negative effects of a disturbance are lower than in the surrounding area (Lancaster and Belyea 1997). During hydraulic disturbances it is expected that organisms most susceptible to the increased hydraulic stresses are most likely to use refugia. Individuals that happen to be present in refugia, or that actively move or are passively deposited in the refugia during disturbances, avoid the negative effects experienced in other parts of the system and subsequently are available to re-colonise the entire habitat. There has been considerable interest in the various kinds of refugia that could reduce population losses of invertebrates after disturbances (see Reice 1980, 1985; Boulton *et al.* 1988, 1992; Giberson and Hall 1988; Palmer *et al.* 1996, 1995; Marmonier and Creuze de Chatelliers 1991; Lancaster and Hildrew 1993a, 1993b; Stanley *et al.* 1994; Lancaster 1996; Lancaster and Belyea 1997; Dole-Olivier *et al.* 1997; Winterbottom *et al.* 1997; Rempel *et al.* 1999; Matthaei and Townsend 2000a; Matthaei *et al.* 1999, 2000).

At the largest spatial and temporal scales, disturbances can affect whole catchments or large sections of river systems and have catastrophic effects on stream communities. An example of such disturbance includes flash floods in desert streams of the USA, as observed by Fisher *et al.* (1982). These disturbance events though large are still only fine-grained disturbance events, as they only affect part of the population at a time. Coarse-grained disturbance events are events that affect entire populations simultaneously such as inter-annual variation in growing season (Lytle

2001).Recolonisation of habitats after such events was primarily by individuals in refugia outside the system, e.g. from other catchments or tributaries, and may have occurred over several generations. Detailed studies on these types of refugia are scarce because of the practical difficulties of carrying out research projects on these scales (see Fisher *et al.* 1982).

At smaller scales, flow refugia may exist within a single stream system, and re-colonisation after disturbance occurs within a single generation. Empirical evidence suggests that refugia for stream benthic invertebrates may exist in the hyporheos (Williams 1984; Dole-Olivier and Marmonier 1992; Dole-Olivier *et al.* 1997; del Rosario and Resh 2000), in debris dams (Palmer *et al.* 1995, 1996), within the main stream channel itself, e.g. in areas of the stream that have a low near-bed flow velocity even during floods (Figure 1.4.1), such as in dead zones (Reynolds *et al.* 1991; Lancaster and Hildrew 1993a; Winterbottom *et al.* 1997) and along the inundated margins (Perry and Perry 1986; Badri *et al.* 1987; Matthaei and Townsend 2000b).

1.4.1 The Hyporheic Zone

The evidence for the use of the hyporheic zone as a flow refugium is equivocal, with some studies showing an increase in invertebrate densities during spates (Dole-Oliver and Marmonier 1992). However, others have shown the opposite with over 50% losses in the density of animals from the hyporheic zone during spates in a sandy bottomed river in Virginia (Palmer *et al.* 1992). During floods, substrate can be scoured (Matthaei *et al.*1999) and moved from the hyporheic zone therefore the hyporheic zone was not a guaranteed refugium from floods.

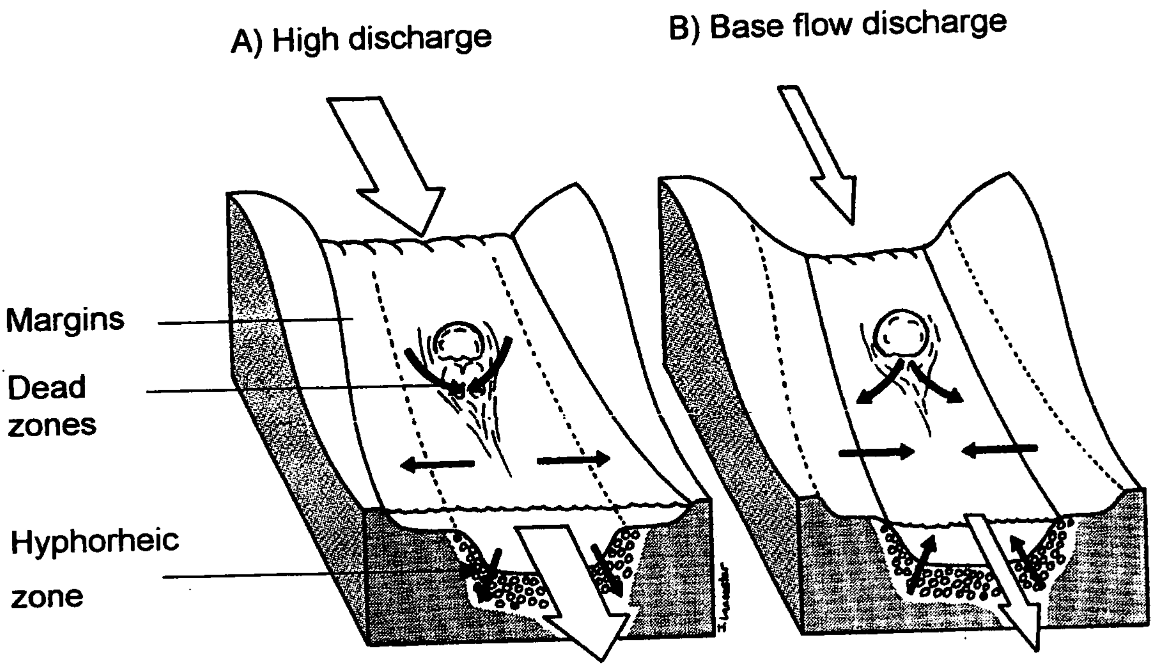


Figure 1.4.1 Diagrammatic representation of potential flow refugia found within a stream at high and base flow discharge. Where the bold black arrows represent the movements of benthic organisms into and out of the potential refugia. The solid black line the water level and the dashed line the stream channel at either high or base flow discharge (Modified from original drawing by J. Lancaster).

1.4.2 Instream Flow Refugia

The heterogeneity of flow within a river or stream channel both laterally and longitudinally can act as a refugium from hydraulic disturbance (Lancaster and Hildrew 1993a). Instream habitats that have the potential to be instream flow refugia include stands of plants, behind or underneath cobbles and boulders (Borchardt and Statzner, 1990; Borchardt 1993) and within dead zones where flow is reduced even during floods. Within streams these areas of low flow can be in the order of several hundred square centimetres and in these low flow patches the flow andassociated hydraulic stress remain low and change little even during flood events (Lancaster and Hildrew 1993a, 1993b). Lancaster and Hildrew (1993b) found that the relative density of several benthic invertebrate taxa (particularly Plecoptera) increased in 'slow' patches over a seven-month period in which discharge and flow events gradually increased. The results were taxa and size specific, small individuals showed no response, whereas large stoneflies exhibited a response. This may be related to how the size of an organism relates to the amount hydraulic forces that acts upon that organism (see section 1.2). Winterbottom *et al.* (1997) demonstrated that macroinvertebrates used artificial flow refugia over short periods of time. This suggested that individuals might have survived disturbances (floods) by moving between different microhabitat types and patches. It was demonstrated that the relative colonisation of refugium cages was greatest during periods of peak flow, suggesting that organisms had used these artificially constructed areas of low flow as a refugium during flood events.

1.4.3 Inundated Margins

The inundated stream margin has been suggested as a potential refugium during floods (Bishop 1973; Poole and Stewart 1976; Perry and Perry 1986; Badri *et al.* 1987; Matthaei and Townsend 2000b). The inundation of floodplains during floods is known to be important for some fish (Schlosser 1991), but the evidence for the role of this habitat for invertebrates is contradictory. In order to be a 'true' refugia from hydraulic disturbance, individuals that utilise the refugium have to be able to return to the base-flow channel after the disturbance. In utilising inundated lateral habitats, there is always the potential to become stranded and perish when the waters recede. Badri *et al.* (1997) found that invertebrates accumulated in a grassy floodplain during a three-week flood in the Rdat, a small Mediterranean stream. The majority of the invertebrates, especially rheophilic species like baetid mayflies and simuliids, followed the slowly receding waters and returned to the base-flow channel. In contrast, the use of the inundated margins was not considered to be 'true' refugia by Perry and Perry (1986). They found that invertebrates were stranded in significant numbers in the near-shore regions following dewatering, during experimental flow reductions in the regulated Kootenai River, Montana USA. Though the rate of flow reduction was rapid (occurring over several hours), it did not exceed the natural rate that can occur in rivers that have a naturally flashy discharge regime (Matthaei and Townsend 2000b).

The use of the inundated margins as flow refugia during floods therefore is an area of research that still needs to be addressed. Whether the inundated margins are , 'true' refugium from floods, in that individuals using the refugium do not become stranded once the water recedes after a flood and perish, has not been established. The research in this study will address these questions. Caddisflies were used as the study species for this research as field observations (Lancaster *pers obs*) have shown that caddisfly larvae are found alive but stranded on the banks after periods of high discharge in the Whiteadder Water.

1.5 The Trichoptera

The Trichoptera, caddisflies, are an order of holometabolous neopteran insects that are closely related to Lepidoptera and were used as study organisms throughout the thesis;. The name Trichoptera literally means 'hairy-winged' from Greek 'trichos' hair and 'pteron' wing. The derivation of the common name is unclear but may be related to the silk secreted by the larvae, as "cadace" refers to a commercial grade silk (Ward 1992). Hickin (1967) suggests an alternative; that the common name may result from the resemblance of cased caddisfly larvae to that of caddice men, vendors who attached their goods (e.g. ribbons and pieces of braid) to their coats like the caddisflies building and covering themselves in material to build their cases. There are nearly 6,000 described species of which over 400 occur in Europe; about 190 of these occur in the United Kingdom (Chinery 1993). While both cased and caseless caddisfly larvae occur in the Whiteadder Water (see Chapter 3) for the purpose of this thesis the tube-case makers or Integrepalpia (Wiggins and Wichard 1989; Frania and Wiggins 1997) is the suborder of caddisflies that will be discussed.

Caddisfly larvae are found in a wide range of habitats and the greatest diversity occurs in cool lotic waters. This habitat is regarded to be the primordial habitat of caddisflies, as these genera exhibit more ancestral characteristics and genera in warm lentic habitats show more differentiation from this ancestral form (Frania and Wiggins 1997). Because of their considerable habitat diversification, caddisflies play an important ecological role in most freshwater systems. Caddisflies are an important dynamic link in stream food webs, playing a functional role in energy flow between the detritus base and higher trophic levels. Whiles *et al.* (1993) demonstrated the importance with *Lepidostoma* spp. in a headwater stream in the USA. After treating two streams with insecticide, *Lepidostoma* spp. colonised the streams rapidly, enhancing the restoration of vital ecosystem processes such as litter decomposition.

1.5.1 Life History

Caddisflies are usually uni- or multi-voltine in that they may have one or more generations each year; or may produce one generation every two or more years (semi-voltinism) (see Elliott 1968, 1969, 1981, 1982). Some genera appear to have a rigid life cycle, such as *Potamophylax* spp., which has a univoltine life cycle throughout its range (Elliott 1968; Higler and Solem 1986). Other species of caddisfly are flexible and alternate between uni- and semi-voltinism such as *Apatania* spp. (Elliott 1968). A shift often occurs from uni- to semi-voltinism in caddisflies found inhabiting lowland to montane areas respectively (Solem and Gullefors 1996). This difference in life histories of species is important when considering how disturbance may effect populations. For example, a species with a two-year life cycle living in a stream would have a higher probability of experiencing a disturbance (i.e. floods) during its life compared to a species with a one-year life cycle. Consequently, a species with a two-year life cycle may have well-developed physiological, morphological and behavioural responses including the exploitation of refugia, that allow it to persist in habitats subject to frequent disturbance such as floods.

1.5.2 Function of Caddisfly Cases

Caddisfly larvae are characterised by their ability to spin silk which can be used to construct cases, nets and retreats. The silk secreted from the tip of the labium is used either by itself or to glue together sand grains or plant material to form a case. The case construction differs widely in design and the materials used, but are relatively consistent at a generic level (Frania and Wiggins 1997) (Figure 1.5.1). Larval Trichoptera can be categorised generally by their case construction and ecological roles, (Table 1.5.1) (Solem and Gullefors 1996). The function of the caddisfly larvae case has been the subject of much speculation (e.g., Dodds and Hisaw 1924; Wiley and Kohler 1984; Williams *et al.* 1987; Dudgeon 1990; Zamora-Munoz and Svensson 1996; Delgado and Carbonell 1997). Three main adaptive functions of the larval case have been suggested: 1) To increase the efficiency of respiration, 2) a protective function and 3) to provide ballast to prevent accidental entry into the drift.

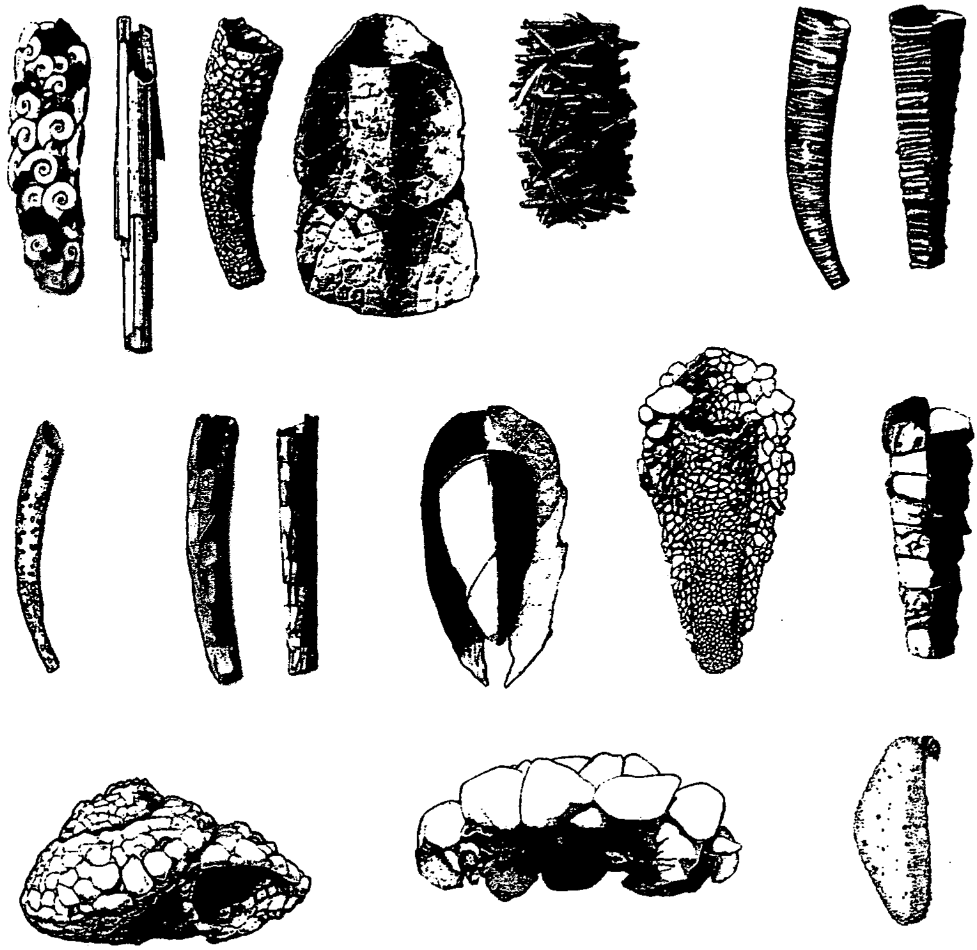


Figure 1.5.1 Examples of the variety of caddisfly case morphology (modified from Merritt and Cummins (1984)).

Table 1.5.1 Classification of larval Trichoptera according to case or retreat construction.

Retreat Type	Family	Habitat and feeding ecology
Free living forms	Rhyacophilidae	Lotic predators
Saddle-case makers	Glossosomatidae	Lotic grazers
Purse-case makers	Hydroptilidae	Lentic and Lotic Herbivores
Net spinners and retreat makers	Philopotamidae	Lentic and Lotic Filter feeders, grazers and predators
	Psychomyiidae	
	Ecnomidae	
	Polycentropodidae	
	Hydropyschidae	
	Arcopyschidae	
Tube case makers.	Limnephilidae	Lentic and Lotic
	Goeridae	
	Phryganeidae	
	Brachycentridae	
	Lepidostomatidae	
	Beraeidae	
	Sericostomatidae	
	Odontoceridae	
	Molannidae	
	Leptoceridae	

Respiration

The idea that the case of larval caddisflies aids respiration has been suggest by several researchers (see Dodds and Hisaw 1924; Fox and Sidney 1953; Philipson 1953; Wiley and Kohler 1984; Williams *et al.*1987). It is argued that the mechanical efficiency of moving water past the gills is increased by surrounding the abdomen with a tube against which water can be pushed; this would result in less energy being required to move water over the abdomen. This efficient means of moving water over the gills, it has been suggested, allowed caddisflies to colonise warm lentic waters from their cool lotic ancestral habitats (Ross 1967; Frania & Wiggins 1997).

The hypothesis that caddisfly cases aid respiration is still in debate and has been investigated by several researchers (see Fox and Sidney 1953; Feldmeth 1970; Philipson and Moorhouse 1976; Otto 1983). Observations that rates of abdominal undulations increase with decreasing oxygen concentration (Fox and Sidney 1953; Feldmeth 1970) have also been shown in the family Polycentropodidae that have no case, but do construct silken galleries. Williams *et al.* (1987) compared the oxygen uptake in cased larvae vs. larvae that had been removed from their case. Seven families of Trichoptera (at least one representative of each family), had the uptake of oxygen reduced by the presence of the case, and in two families the oxygen uptake increased. In the Limnephilidae there was no obvious effect of the case on oxygen consumption. However, caddisfly larvae evicted from their cases would be stressed and thus may exhibit an increase in oxygen uptake due to this stress. Whether the presence of a case allows the maximization of oxygen uptake (so larvae would have a lower rate of oxygen uptake if the case was removed) or it optimises the uptake of oxygen is unclear. It is also unclear whether the energetic cost of case construction is balanced by any respiratory advantage gained by having a case. The fact that caddisfly larvae build a variety of case forms using a wide range of materials may argue against a purely respiratory role. If the role were primarily to increase respiratory efficiency then a uniform case structure would be found in all cased caddisflies, but this would occur only if they have finished evolving to this 'optimum' end point. However, at a generic level it may be considered that cased caddisfly larvae have evolved to the 'end-point', (though it is impossible to know or measure the 'end-point' of evolution) as all caddisfly cases do comprise of a hollow tube of some form, with only the materials used and tube design varying between genera.

Protection

The case of caddisflies may also have protective functions: providing resistance to crushing by predators, protection from wounding and damage, increasing their apparent size and camouflaging the larvae against the substrate (Otto and Svensson 1980; Otto 1983; Otto 1987; Williams *et al.* 1987; Rowlands and Hansell 1987; Johansson 1991; Johansson and Johansson 1992; Nislow and Molles 1993). Evidence for the defensive role of the caddisfly case (Otto and Svensson 1980) indicates that larvae with organic cases suffered a higher rate of predation by fish when on sandy sediments than when a substrate of leaves against which they are cryptic. Larvae with cases made of inorganic materials are less vulnerable to predators than those in cases comprised of organic material (such as leaf fragments), because they are more resistant to crushing (Otto 1983). Otto (1983) also showed that larvae inhabiting fragile cases are more likely to abandon them during simulated bird predation than larvae in stout crush-resistant cases. During simulated bird attacks on the larvae of two species, the limnephilid *Trichostegia minor* (that has a fragile case that cannot resist much pressure (crushing), and *Glyphotaelius pellucides* (that has a sturdier mineral case), it was observed that *Trichostegia minor* abandoned its case with greater frequency, than *Glyphotaelius pellucides.*

Though stout inorganic cases are more crush resistant than organic cases they are energetically more expensive to build. Otto and Svensson (1980) observed that *Potamophylax cingulatus* (Limnephilidae) constructed organic cases that are assumed to be energetically less costly when leaf litter was abundant, but switched to inorganic materials when leaf litter is scarce and the pressure from predation was greater. Otto (1982) observed that lotic limnephilids predominately built mineral cases in Scandinavian streams, but lentic species without predation pressures from fish built organic cases. Alternatively, this may be due to differences in the relative abundance of case building materials available within the two different habitats, with organic material found in a greater abundance in lentic systems. Species in fish-free lentic habitats that can build energetically economical cases may be larger than lotic species (Otto and Svensson 1980; Dudgeon 1990). Enlarging the case with structures that extend beyond the case also reduces predation, making them too large to be handled by predators and thus providing a size refuge from predation. This is more common in species with organic cases compared to those with inorganic cases. Otto and Svensson (1980) and Otto (1987) have shown that the removal of these extensions or the artificial shortening of organic cases of caddisfly larvae increases the vulnerability to predators. They also note that despite an adaptive value to species with organic cases, few species that build solely inorganic cases exhibit case enlargement. This, they suggest, may reflect the energetic penalty of dragging a heavy enlarged inorganic case. Studies on the economics of case building and material selection are rare. There must be energetic costs in the construction of cases as has been implied in several studies (Williams and Penak 1980; Otto and Svensson 1980; Stephens 1999). Individuals forced to construct new cases exhibit a decrease in case size when forced to progressively construct a number of cases (Williams and Penak 1980). Costs differ depending on the choice of case building materials. Otto and Svensson (1980) demonstrated that cases built of sand grains have a higher constructional cost than larger particles owing to handling time. The use of silk in the construction of cases is also energetically costly. In a study by Otto (1974), silk used by *Potamophyalx cingulatus* in the construction of cases contributed 12% of the energy expenditure in the final instar.

The case may also protect caddisfly larvae from desiccation during periods of exposure caused by drought or being stranded. In experiments designed to elucidate differential survival under drought conditions in temporary pools, that organic cases held water more efficiently than mineral cases when exposed to air As a result organic cased individuals were considered more resistant to desiccation (Zamora-Munoz 1996).

Cased caddisfly larvae are fairly long-lived organisms and although the case in some instances may help to prevent dislodgement. However, observations of the cased caddisfly larvae on the banks of streams after floods (Lancaster and Dobson *pers obs.*), suggest that they may be poorly adapted to withstand dislodgement by flood disturbances. In low-order streams that are prone to flood disturbances, cased caddisfly larvae should, therefore be expected to be affected by floods (e.g. dislodged) with the possibility of becoming stranded on the banks (see Chapter 4). The observations of stranded caddisfly larvae on the banks after floods lead to the question, 'How do cased caddisflies with apparently poor adaptations to flood disturbances persist in frequently disturbed low-order streams?'

1.6 Aims Of The Study

The main aim of the study was to determine the effects of being strandied after hydraulic disturbance (i.e. floods) on cased caddis larvae. Six main objectives were addressed in this study in order to address this aim.

1. To describe the species of Trichoptera, their microdistributions and life histories in one study site, the Whiteadder Water.
2. To determine the incidence of stranding of cased caddisflies being stranded on the banks of the stream over a year with respect to adjacent instream microhabitat (pool or riffle), bank-side topography (substratum and slope) and case type (coarse mineral, fine mineral, mixed and vegetative).
3. To investigate the relationship between the incidence of being stranded in cased caddisfly larvae and the magnitude of hydraulic disturbances (floods).
4. To determine whether the mechanism by which larvae are stranded occurs is 'active' or 'passive' through the use of flume experiments.
5. To determine the effect of species-specific traits (i.e., case type) and the bank-side topography (substratum and slope) on the ability of cased caddisfly larvae to regain the water when stranded on an artificial bank-side.
6. To investigate whether the incidence of being stranded is a significant source of mortality in populations of cased caddisfly larvae in the Whiteadder Water.

2 The Whiteadder Water: Study Site Description

The study site is in the headwaters of the Whiteadder Water in the Lammermuir Hills of SE Scotland, (NGR: NT 626 668) and it is part of the Tweed catchment (Figure 2.1). Mean annual rainfall was 824 mm a year (for the period 1980 to 1999) at Nunraw Abbey weather station (NGR: NT 594 700), which is 5 km from the study site (data from the British Atmospheric Data Centre). The stream catchment is mainly heather moorland managed for grouse and some sheep grazing. There is no forestation or habitation above the study area.

The surrounding moorland vegetation was principally heather (*Calluna vulgaris* (L.) Hull), bracken (*Pteridium aquilinum* (L.) Kuhn) and purple moor grass (*Molinia caerulea* (L.) Moench) with rushes (*Juncus* spp.) in the wet flushes and along the valley floor. Within the stream aquatic macrophytes were rare, with only sparse clumps of common water starwort (*Callitriche stagnalis* Scop.) and water mint (*Mentha aquatica* (L.)) in slow flowing marginal pools. The aquatic bryophytes, *Hygrohypnum* spp. and *Fontinalis antipyretica*, were found in some riffles at low densities (Lancaster, 2000). The underlying is geology comprised mainly of Silurian greywacke, a coarse substrate of marine origin (Davies, MacAdam and Cameron 1986). The thin overlying cover of peat results in nutrient poor soils.

The study site is comprised of a series of five riffles and pools within a 240 m stretch with each with different bank-side topographies to each other (Figure 2.2). The study stretch is about 4.5 km from the source of the Whiteadder Water, and above the Whiteadder reservoir (NGR: NT 655 635). The riffles and pools where selected visually on their physical appearance of flow and on the bordering bank-side topography, details of which I will discuss in Chapters 3 and 4. The physical dimensions of the stream were surveyed using laser theodolite at 2 m intervals in the centre of the stream and width (m) was measured across this point, this enabled a site map to be constructed (Figure 2.2).

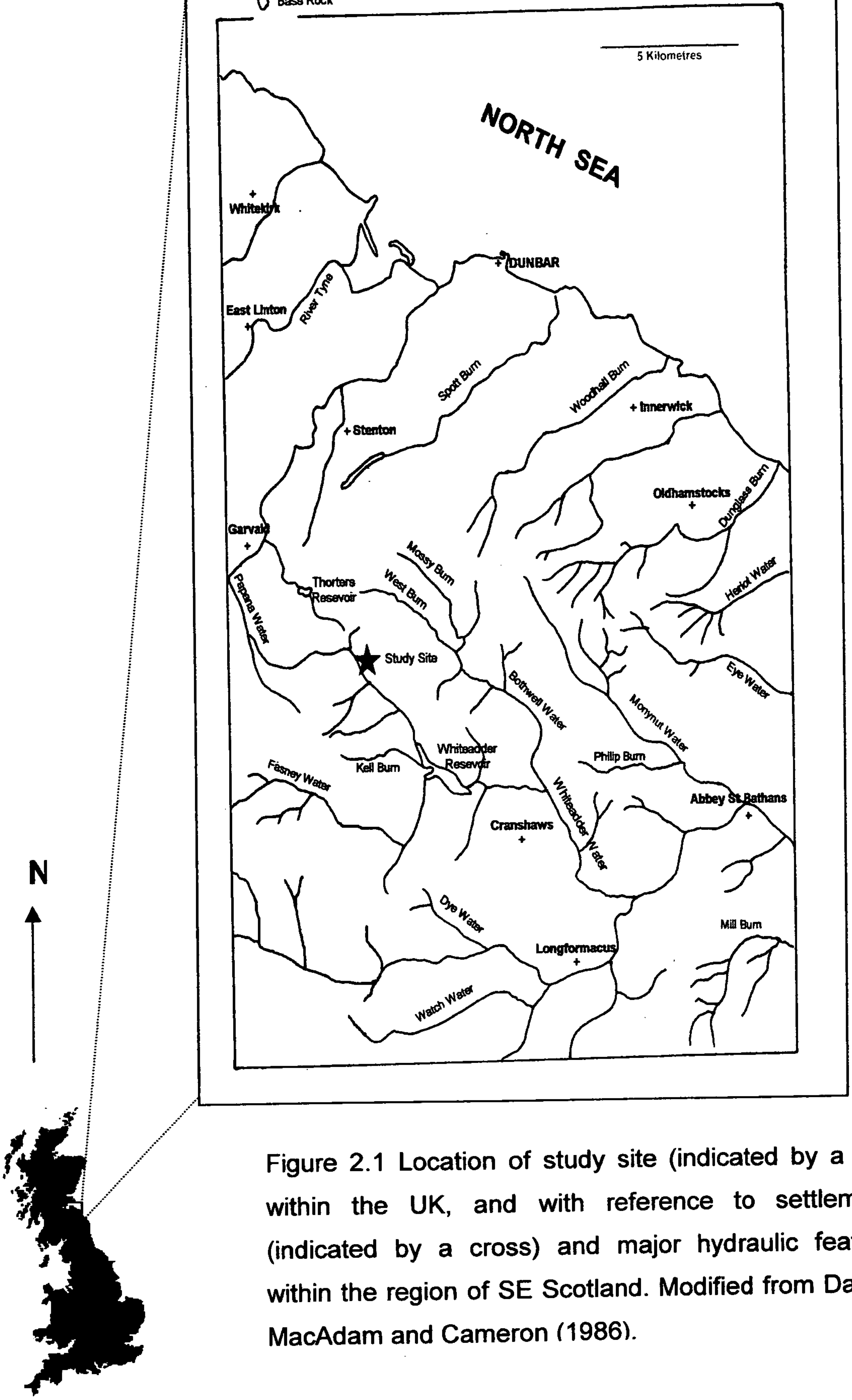


Figure 2.1 Location of study site (indicated by a star) within the UK, and with reference to settlements (indicated by a cross) and major hydraulic features within the region of SE Scotland. Modified from Davies, MacAdam and Cameron (1986).

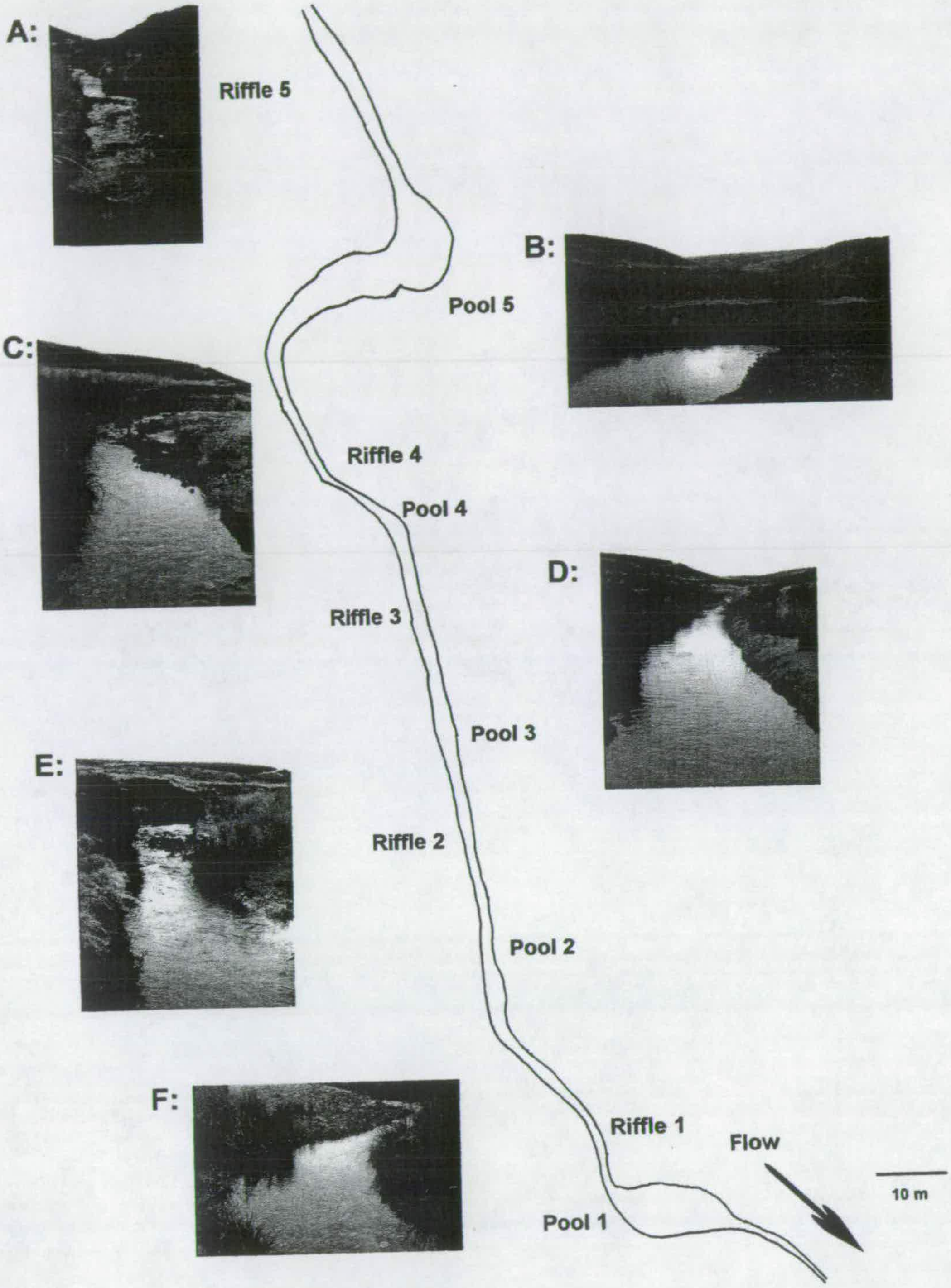


Figure 2.2 Map of study site showing the location and photographs of each pool and riffle; A: riffle 5, B: pool 5, C: riffle 4 (top of photograph) and pool 4 (bottom of photograph), D: riffle 3 and pool 3,E: riffle 2 and pool 2 and F: riffle 1 and pool 1.

The mean physical dimensions of the stream within the study stretch can be seen in Table 2.1. Within the study stretch pools covered a total area 186.2 m^2 and riffles an area of 183.2 m^2.

Cross-sections of the each replicate pool and riffle were surveyed at 0.4 m intervals across the centre of the pool or riffle to provide a depth profile (Figure 2.3). Riffles were generally shallower and narrower than pools. The streambed was composed primarily of fairly stable mineral substrates, which range in maximum dimension from 1 to 35 cm with a median maximum dimension of 9.5 cm. The substrate characteristics (e.g. granulometry and stability) of riffles and pools are discussed in detail in Chapter 3.

The pH was measured using a Hanna HI 9023C pH and temperature meter during monthly sampling. The stream water pH is neutral to alkaline with values ranging from pH 7.0- 8.4, (Figure 2.4) with a mean value pH of 7.8 (SD = 0.38). These pH values are attributable to the underlying geology rather than the overlying soils, due to the calcareous nature of the substrata (i.e. the Silurian greywacke), which buffers the acidic runoff from the overlying peat. Water temperatures were recorded with a maximum / minimum thermometer submerged in the stream within pool 3, which was reset after each reading. Water temperatures varied seasonally and ranged from 3 to 16 °C with seasonal variation (Figure 2.5). The pH and water temperature were assumed to be homogeneous throughout the short study stretch of the Whiteadder Water, thus only one point reading was taken.

The riparian zone of the stream varies in its topography with both areas of vegetation and exposed gravel on a range of gradients from flat (gentle) to vertical banks. The predominant vegetation/substrata types were grass and *Calluna* spp. (Table 2.2). Banks were classified at each of the 2m intervals surveyed with the laser theodolite, and were classified as either gentle / no obvious slope (0-10°), moderate (11-44°), steep (>45°) and cliff (vertical bank face). The majority of the banks were visually classified as steep along the study stretch, with only a small percent classified as gentle (Table 2.3).

Table 2.1 Physical dimensions of the Whiteadder Water study site from data recorded at intervals along the study stretch, all measurements in metres.

	n	Mean	SD
Stream width	156	2.18	0.70
Stream depth	156	0.20	0.11
Riffle width	52	1.85	0.60
Riffle depth	52	0.12	0.07
Pool width	61	2.45	0.88
Pool depth	61	0.27	0.13

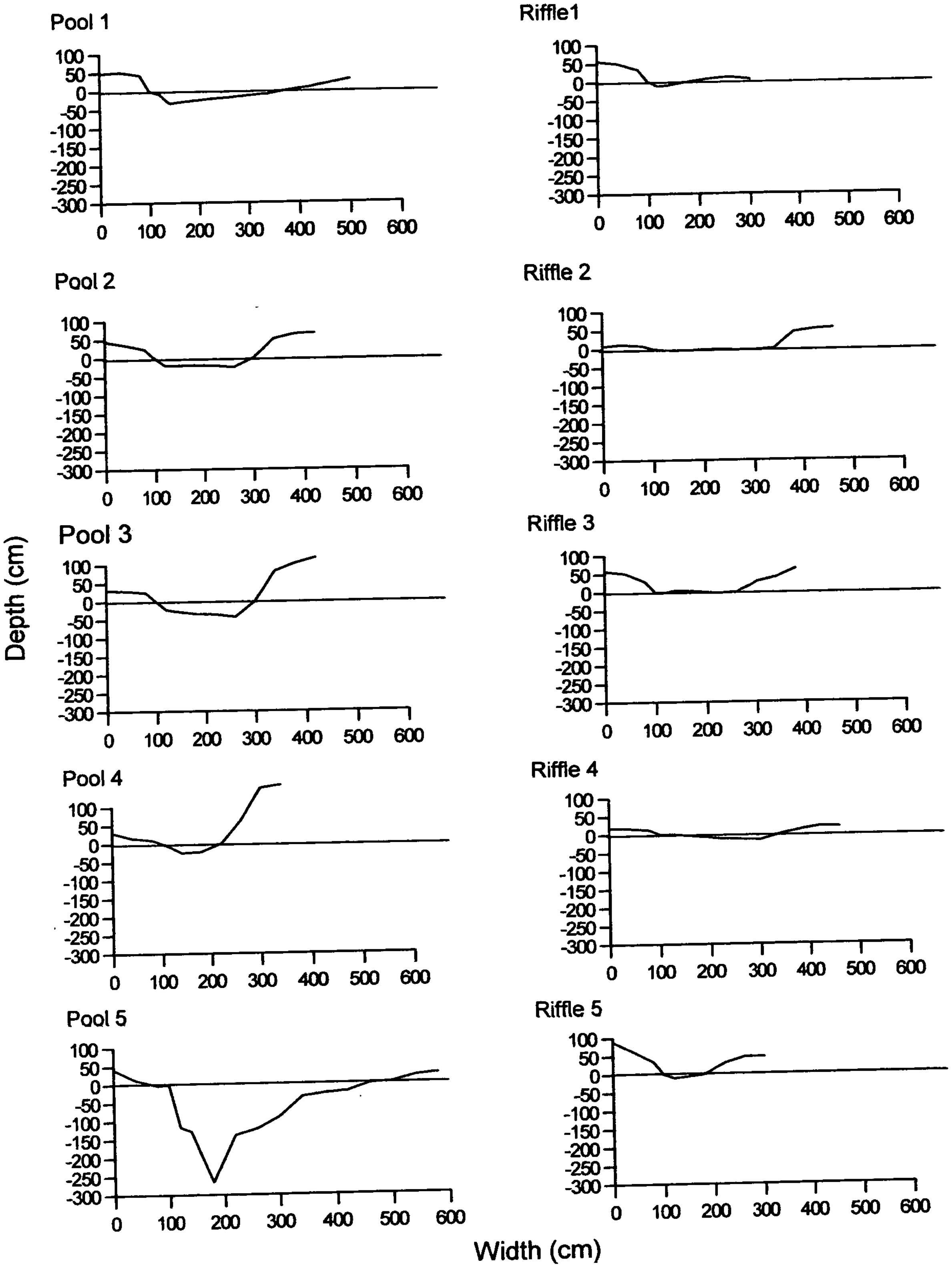


Figure 2.3 Cross sections of water depth (measured at 40 cm intervals) with pools and riffles in the study stretch on the 16th January 1999. Water level is indicated by the horizontal black line at zero depth.

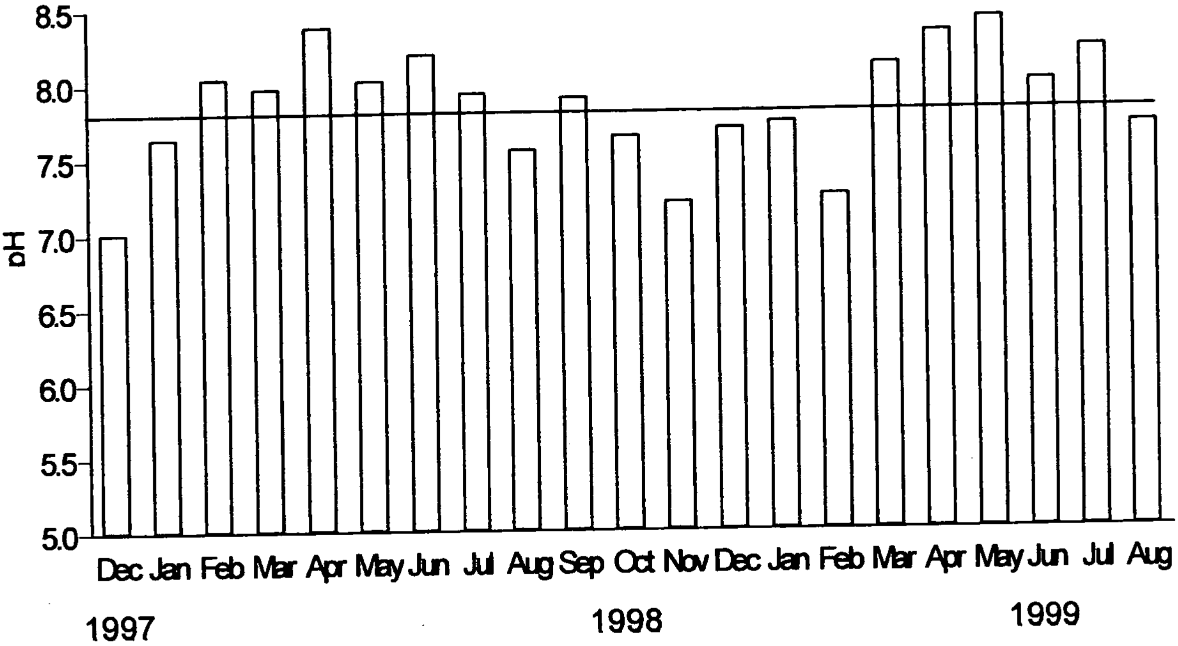


Figure 2.4 Stream water pH from December 1997 to August 1999. The solid black line indicates the mean pH for the study period.

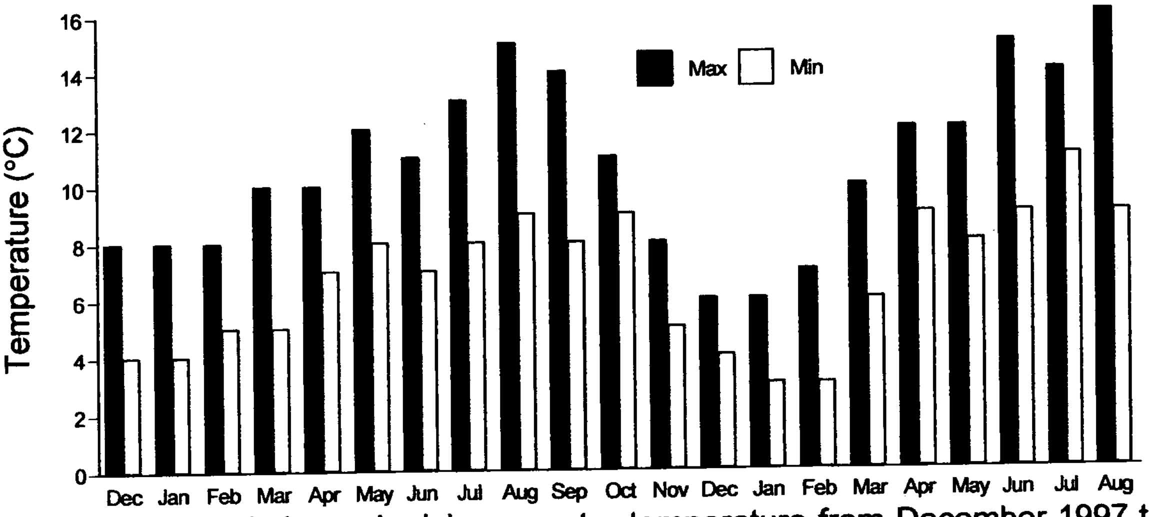


Figure 2.5 Maximim and minimum water temperature from December 1997 to August 1999.

Table 2.2 Percentage compositions of bank-side vegetation and substratum along the 240 m study stretch. The riparian vegetation and substrates were classified into five visually distinct groups determined by the dominant vegetation or substrate type where: *Calluna* spp.= CA, grass= G, *Juncus*= J, grass and *Juncus* =GJ, no vegetation or bare earth= NV and gravel= GR.

Vegetation/substrate	Right Bank (%)	Left Bank (%)	Mean Bank Value (%)
CA	16	26	21
G	26	41	34
J	17	17	17
GJ	18	8	13
NV	7	5	6
GR	16	3	9

Table 2.3 Percentage compositions of bank-side slopes along the 240 m study stretch. The slope (gradient) of the banks, was divided into four visually distinct categories where: gentle= G, moderate= M, steep= S and cliffs with a vertical face= C.

Slope	Left Bank (%)	Right Bank (%)	Mean Bank Value (%)
G	12	17	14
M	29	22	26
S	46	39	42
C	13	22	18

3 Microhabitat Distribution Patterns and Life Histories of Some Trichoptera

3.1 Introduction

In order to address the main aim of this thesis, 'to determine the effects of being stranded after hydraulic disturbance (i.e. floods) on the populations of cased caddis larvae', firstly I needed to establish the species composition, the density and the distribution of caddisflies. The distribution patterns of caddisfly larvae were examined at a fine-grained scale within different instream habitats (i.e. pool and riffle). The rationale behind this approach is that riffles and pools are affected in different ways during hydraulic disturbances. The distribution patterns of cased caddisfly larvae were also examined at a fine-grained scale along environmental gradients (e.g., near bed flow velocity, depth and amount of detritus). The data on the density and distribution of cased caddis were used in conjunction with the data from subsequent chapters to calculate the impacts of being stranded by floods on the cased caddisfly assemblage of the study stretch of the Whiteadder Water (see Chapter 7). It is also important to ascertain when species occur in the stream (their life-history), as hydraulic disturbances are unpredictable in the short-term (e.g., days or weeks) but do show seasonal trends (e.g. greater frequency of high rainfall leading to floods during the winter). Species may have adapted their life-cycles to avoid periods when there is a greater chance of disturbance by flooding and potential for being stranded, by either being absent from the stream (e.g. terrestrial adults) when flood risk is high, or by being at a stage of the life-cycle where the effects of disturbance are minimal (e.g. as eggs or small size/ early instars). The data collected on the life histories of the caddisfly larvae (i.e. when and at what size/stage of their lifecycle that they occur in the study stretch) were also needed to determine the impacts caused by being stranded on the assemblage.

River systems are hierarchically organised systems, with levels nested at successively smaller spatio-temporal scales (Minshall, 1988) ranging from complete drainage basins to a single substratum particle. For example, the riffle-pool sequence is determined by higher order characteristics such as the slope of the whole reach, water runoff and sediment inputs from the catchment. In this study I am concerned with the small spatial scales of this hierarchy i.e., the pool/riffle system, with an approximate linear spatial scale of 10^0 m and the microhabitat system (10^{-1} m) as described by Ward (1989). Some of the factors that influence the distribution of stream insects on large scales, such as temperature and water chemistry, can be ignored when assessing microhabitat preferences within a single stream stretch as they are assumed to be homogeneous over the entire stretch (see Chapter 2). In this chapter, I will focus upon abiotic variables such as near-bed flow velocity, substrate type, substrate stability and the amount of available resources (e.g., detritus), which can vary widely across small spatial scales and affect the distribution patterns of the benthos.

Benthic organisms do not occur evenly over the streambed (Linduska 1942; Scott 1958; Cummins 1964; Egglishaw 1964, 1969; Hynes 1970; Rabeni and Minshall 1977; Otto 1982; Culp *et al.* 1983; Ormerod 1988; Barmuta 1989; Bacher and Waringer 1996; Pardo and Armitage 1997), and the impacts of hydraulic disturbance are not uniform across the stream spatially or temporally. Thus, the potential for caddisflies present in different stream habitats to be affected by hydraulic disturbances and for individuals to become dislodged and potentially stranded in margins is not uniform. Documenting the patchy distribution patterns of caddisflies in the Whiteadder Water is not especially interesting in itself, but such data are essential in order to scale-up and estimate the population-level impacts of floods. The patchy distribution of the individuals on the stream bottom may be determined by either or both of two factors: (1) environmental (abiotic) factors or gradients within the stream, such as substrate, flow velocity and resources (e.g., organic debris), (2) biotic factors, such as adult dispersal patterns, predator avoidance and interspecific competition. The terrestrial adults of species with aquatic larvae have an uneven pattern of dispersal and oviposition. For example, larval aggregations may be the result of the eggs being deposited by the adult in clumps (as in most Trichoptera), rather than broadcast and scattered throughout the stream (as in some Odonata and Plecoptera). However, in the caddisflies all species lay egg masses rather than by broadcasting eggs into the stream, resulting in a clumped distribution of eggs and early instar larvae (Hickin 1967

Hildrew and Wagner 1992). Obviously, many of the environmental gradients (factors) are interrelated, e.g., water velocity largely controls the substratum particle distribution within a stream, however, for convenience, they are discussed separately in the following sections of this chapter.

3.1.1 Hydraulic factors

The flow of water and variations in flow velocity are considered to be among the most important environmental gradients in determining distribution patterns of benthic organisms (Statzner and Higler 1986; Hildrew and Townsend 1987; Poff and Allan 1995; Poff 1997; McCabe and Gotelli 2000). The flow of water encompasses two main components: (1) discharge, which is the volume of water moving through the stream or river channel (m^3 s^{-1}) and is related to the width, depth and current velocity and 2) velocity or current speed (m s^{-1}), which is the actual speed at which the water is moving. The movement of water creates associated hydraulic forces (such as drag, lift, turbulence and shear stress) that act on the substrate and organisms. It is these hydraulic forces, (i.e. drag, lift, shear stress and turbulence) which benthic organisms experience directly and which they have to resist to prevent dislodgement from the substrate.

Floods increase the velocity of the water and therefore the associated hydraulic forces such as shear stress also increase, but this change is not uniform across the stream. Shear stress is defined as the force acting parallel to the surface per unit area of streambed. As water flows over a solid surface it generates lift and drag forces and, if the stress is large enough, then particles on the streambed (mineral or biological) are set in motion. In general terms, the magnitude of shear stress increases with the depth of water and is also correlated with the square of current velocity, so during high flows (increased depth and current velocity) a large force can be exerted on the particles on the stream bed, though real streams may not necessarily behave in this way. In this study direct measurements of the hydraulic forces (e.g. shear stress) were not taken, near bed flow velocity was used as a surrogate for the hydraulic forces due to its close relationship with the hydraulic forces that act on benthic organisms (Morisawa 1985; Gordon *et al.* 1992).

As flow rate varies, then species often vary in abundance along the hydraulic gradient in a species-specific way. The microdistribution of benthic invertebrates in relation to flow rate has been studied by many (Linduska 1942; Scott 1958; Rabeni and Minshall 1977; Cummins 1964; Otto 1982; Boukaert and Davis 1998; Quinn and Hickey 1994; Mobes-Hansen and Waringer 1998; Lancaster and Mole 1999; Rempel *et al.* 2000). The flow of water is important to benthic organisms for a number of physical and physiological reasons: the hydraulic forces associated with high flow rate can dislodge individuals from the substrate (Waringer 1989, 1993; Statzner and Holm 1989; Otto and Johansson 1995), the movement of water maybe required for respiration (Dodds 1924; Philipson 1953, 1975; Feldmeth 1970) and the flow of water can also alter the feeding efficiency of organisms (Townsend and Hildrew 1979; Tachet *et al.* 1992). The flow of water is also interrelated with the composition of the substrate, (Rempel *et al.* 2000) and with the availability of food (Dobson *et al.* 1992; Dobson 1994; Lancaster 1996). How these factors influence the microhabitat patterns of the benthos is discussed in Sections 3.1.2 –3.

Spatial variation in flow is a main characteristic of streams. In a single stretch, changes in gradient and water depth lead to the development of fast flowing riffles and slower flowing pools over a short distance. At very small spatial scales, such as that of a single cobble or boulder, variations in flow can also occur that can change the current velocity and direction of flow (Hart *et al.* 1996; Bouckaert and Davis 1998). Scott (1958) studied the micro-distribution of caddisflies in a small stony bottomed reach of the River Dean, Cheshire. He concluded that the patterns were a reflection of the interactions of current, substrate and food distribution. For the larvae of *Glossosoma boltoni* (Trichoptera: Glossosomatidae) the current appeared to be associated with the microhabitats it inhabited. *Glossosoma boltoni* usually inhabited exposed microhabitats with current velocities between 0.2-0.4 m s^{-1} on all faces of the stone except the ventral face. *Glossosoma boltoni* then moved to the sheltered ventral faces of stones as the velocity increased (Scott, 1958). Scott (1958) also found that the distribution of caddisfly pupae generally resembled larval distributions in the River Dean, with exception of *G. boltoni* and *Silo pallipes*. In these species pupae occurred in microhabitats with a higher velocity than the larvae, suggesting that final instars moved to faster water to pupate, or that they moved to a different habitat where the water velocity increased and they could not move out of the area like mobile larvae.

3.1.2 Substrate

Among the factors that are associated with the distribution of benthic macroinvertebrates of lotic waters, substrate type (sand, gravel, bedrock, organic debris and vegetation), size and stability are important. The relationship between the substrate and the microdistribution of aquatic insects has been documented in many studies (Percival and Whitehead 1929; Linduska 1942; Scott 1958; Minshall 1984; Holomuzki and Messier 1993; Bouckaert and Davis 1998; Walde *et al.* 1983; Cummins and Lauff 1969; Lancaster and Mole 1999; Malmqvist and Otto 1987; Matthaei *et al.* 2000; Matthaei and Townsend 2000).

Size, stability and heterogeneity

Different substrates support different benthic assemblages, and cause variation in the invertebrate density, diversity and biomass (Mackay and Kalff 1969; Wise and Molles 1979). As a general rule, the diversity and abundance of benthic organisms in streams tends to increase with the stability of the substrate (which in turn increases with mean particle size), and with the availability of resources such as organic debris. Sandy substrates generally support the poorest communities of organisms, presumably due to their inherent instability and tiny interstitial spaces. Riffles with stony substrates usually have more species than pools with a fine organic and silty substrate. However, if both riffles and pools have substrates comprised of mainly gravels then differences in the abundance of organisms and assemblages of benthic organisms present may be reduced. As the median particle size increases, the physical complexity of the substrate will also increase. Minshall (1984) suggested that the diversity of species declines with substrates above the size of cobbles (> 64 mm), as found in experiments where a greater density and diversity of organisms was found in cages filled with pebbles (16 to 63 mm) compared to those filled with cobbles (Minshall and Minshall 1977; Wise and Molles 1979). Heterogeneous substrates are expected to have a greater diversity and abundance of benthic organisms. A heterogeneous substrate would provide a greater range of surfaces, and the size range and extent of pores in the substrate also increases. The more divided the habitat, the greater the habitat area that becomes available for smaller organisms, thus increasing the diversity and abundance of organisms. This explanation of the more divided the habitat, the greater diversity and abundance of organisms is also thought to account for the high species diversity of soils (Giller 1996).

The association of benthic taxa with a particular substrate type, size or roughness has also been documented (Cummins and Lauff 1969; Brusven and Prather 1974; Khalaf and Tachet 1980; Vaughan 1987; Fuller and Rand 1990; Holomuzki and Messier 1993; Quinn and Hickey 1994; Way *et al.* 1995). Cummins and Lauff (1969) showed associations between specific substrates and some species of benthic invertebrates in laboratory experiments. They found that substrate size was a primary factor in habitat selection for the riffle beetle *Stenelmis crenata*, the stonefly *Perlesta placida* and the caddisflies *Pycnopsyche guttifer* and *Pycnopsyche lepida*. Brusven and Prather (1974) also demonstrated a preference for substrates of a particular size in five species of benthic macroinvertebrates, again under laboratory conditions. They found that the caddisfly *Arctopsyche grandis* and the stonefly *Pteronarcys californica* preferred a coarse mineral substrate of large pebbles (12-25 mm) over a substrate comprised of small pebbles (6-12 mm), coarse sand (2.5-6 mm) and fine sand (1-1.5 mm). The mayfly *Ephemerella grandis* and the caddisfly *Brachycentrus* spp. showed a preference for large and small pebbles over substrates of coarse or fine sand. The dipteran *Atherix variegata* however, showed little preference to one size of substrate. Holomuzki and Messier (1993) found that the habitat distribution of the mayfly *Paraleptophlebia guttata* (McDunnough) was related to substrate size/coarseness. The larvae of *Paraleptophlebia guttata* occurred at a higher density in riffles and runs compared to pools. The density of *Paraleptophlebia guttata* was positively correlated to the percentage of coarse substrate (gravel, pebbles and cobbles) in the microhabitat, but was not correlated with the flow velocity, the presence of predatory fish or the quantity of fine particulate organic matter (FPOM) in the riffles, runs and pools. The relationship between density of *Paraleptophlebia guttata* and substrate coarseness was further demonstrated by using an in situ colonisation experiment where densities of the mayfly were greater in coarse, compared to fine, substrates, i.e., sand and silt.

The stability of the substrate (its resistance to being moved by the water current) has been shown to influence microhabitat selection and therefore the microdistribution patterns of benthic organisms in streams (Moon 1940, 1956; Chutter 1969; Malmqvist *et al.* 1978; McAuliffe 1984a, 1984b; Cobb and Flannagan 1990; Cobb *et al.* 1992; Death and Winterbourn 1995; Matthaei *et al.* 2000). Small rocks are disturbed more frequently than large rocks and stability is often inversely related to the size of the substrate particle, i.e., small particles are often less stable than large particles and are therefore disturbed more readily (Connell 1978; Stanford and Ward 1983; Malmqvist and Otto 1987). When the substrate is dislodged and beings to move, it can become entrained in the water column if the hydraulic forces acting on the substrate particles are great enough or it can simply roll along the bed. In both cases, the moving substrate particles have the potential to crush benthic invertebrates and entrained particles can scour the surface of the bed dislodging attached organisms. McAuliffe (1984a) showed that the purse-case caddisfly *Leucotrichia pictipes* is restricted to unstable substrates, where moss is unable to colonise the rocks and prevent the occurrence of the larvae by overgrowing colonisation sites. On stable substrates with moss coverage, the assemblage changes from one dominated by *Leucotrichia* spp. to one dominated by *Hydropysche* spp., a filter feeding caddisfly larvae. Cobb and Flannagan (1990) found that the species diversity of caddisflies in areas with stable substrates was approximately double that found in unstable substrates surveyed in the Ochre River.

3.1.3 Presence of Organic Debris

The presence and amount of detritus and vegetation modify the influence of the substrate on the benthos (Egglishaw 1964, 1969; Reice 1980; Dobson and Hildrew 1992;). Leaf packs and accumulations of other organic debris against instream obstacles generally support a greater abundance and diversity of benthic organisms (Reice 1980; Dobson and Hildrew 1992). Within stony streams the microdistribution of the benthos has been partly explained by the heterogeneous distribution of organic detritus. Egglishaw (1964, 1969) found variation in the amount of detritus found within a single riffle and a positive correlation between the abundance of some species and the amount of detritus. However, in field manipulations, Culp *et al.* (1983)

showed that standardising the source and quantity of detritus resulted in no relationship between the abundance of detritivores and the mineral substrate composition. Reice (1980) showed this also where some of the benthos colonised leaf packs irrespective of the size of the underlying mineral substrates of gravel, pebble or cobble. This indicates that the presence of organic material is more important than the substrate size in determining the distribution patterns of detritivorous organisms.

Accumulations of organic debris, such as natural leaf packs can be utilised in three ways by benthic organisms: as food, as a microhabitat and as building materials. Natural leaf packs in streams may provide food for many species of macroinvertebrates either directly or indirectly by accumulating fine particulate organic matter (FPOM) (Richardson 1991; Richardson and Neill 1991). The densities of macroinvertebrates are usually higher in leaf packs than in the surrounding substrate (e.g., Egglishaw 1964; Mackay and Kalff 1969, 1973; Drake 1984; Dobson and Hildrew 1992; Richardson 1992) and it is often assumed that the leaf packs act as a food source. Not all macroinvertebrates directly consume leaf tissue; leaf packs may provide shelter from the water current, space and attachment sites and protection from predators. Richardson (1992) showed that leaf packs were primarily colonised for their food value rather than as a microhabitat in experiments using natural leaf packs of red alder leaves and artificial leaf packs of leaves of polyester cloth (with no nutritional value). He found that the artificial leaf packs had low rates of colonisation compared to natural leaf packs suggesting that the use of leaf packs as a habitat may be incidental to their use as a food source.

3.1.4 Environment and Life history

The environment plays an important role in the timing of various life cycle processes. Variation in the life history patterns (traits) of aquatic organisms can be attributed to extrinsic and intrinsic factors. Intrinsic factors include factors such as physiology, morphology and behaviour, which tend to restrict life history traits within certain genetically and phylogenetically determined ranges. Extrinsic factors such as temperature, food availability (nutrition), degree of habitat permanence and biotic interactions can also influence life history parameters. It has been speculated that diverse life history patterns may have evolved to enable species to exploit seasonally available food resources and to evade unfavourable conditions such as drought or floods (Wallace and Anderson 1996), though I must emphasize that this is purely speculation as the driving forces behind evolution are unknown and unknowable!

The close association between the environmental conditions and the life history of aquatic insects is most clearly seen in aquatic insects that reside in temporary running waters, where the timing of the life history is important in order to maintain populations. Jacobi and Cary (1996) documented that stoneflies in seasonal (temporary) streams of New Mexico, deposited eggs when the stream was flowing, but the eggs remained in the substrate when the stream dried, and resumed development when the water began to flow again, thus maximising the period for hatching and development. Dietrich and Anderson (1995) also observed that mayflies and stoneflies in seasonal western Oregon streams had life histories that closely followed environmental conditions. They found that mayflies began to hatch in late autumn with the onset of flow in the temporary stream, but the period of hatching was prolonged and development lasted between five to seven months. Mayfly larvae that delayed hatching until spring were able to survive the summer drought in a few permanent pools. The emergence of adult mayflies was also prolonged, with peak emergence preceding the summer drought, when there was still available habitat for egg laying. The stoneflies of these streams had a semi-voltine life history. They were winter active but entered diapause for several months when the stream dried. Growth of the stoneflies only resumed in late autumn when water levels recovered, and they emerged as adults the following spring. It was noted that during this period mortality was high, thus stressing the importance of dormancy in the life cycle under such extreme environmental conditions.

Life history traits in frequently disturbed systems

Under conditions that are more benign than those that occur in temporary streams, life histories still have to be temporally adjusted for seasonal variations in temperature, food resources, optimal conditions for reproduction and dispersal and the unpredictable nature of hydraulic disturbances. The life history traits of benthic organisms in different streams may vary with the type, magnitude and frequency of disturbance that may affect the stream. Life history traits may be further associated with the previous disturbance history of the habitat (Gray 1981; Gray and Fisher 1981; Fisher *et al.* 1982; Wallace *et al.* 1986; Wallace 1990; Matthaei 1999; Matthaei and Townsend 2000; Lytle 2001).

Connell and Sousa (1983) suggested that in more frequently disturbed habitats, populations that can colonise and grow rapidly and that have the ability to recover between disturbances would predominate. Fisher and Gray (1981) observed this pattern after a flash flood in a stream in the Sonoran Desert. They found that up to 95% of the aquatic organisms perished due to the flood, but recovery of the invertebrate biomass was rapid and occurred within approximately two months. This rapid recovery was attributed to chronic exposure to flooding, combined with a warm thermal regime (promoting growth and development), which may have selected life history traits for rapid development, continuous emergence, and diapausing eggs.

The occurrence of frequent but unpredictable disturbances poses a significant problem for life-history adaptations. Scrimgeour and Winterbourn (1989) found that the resilience of the mayfly *Deleatidium* spp. in the frequent but unpredictably disturbed Ashley River, New Zealand, could be attributed to a highly developed refuge-seeking behaviour, and the occurrence of a non-synchronised and flexible life history that enabled *Deleatidium* spp. to colonise previously disturbed substrates rapidly. They suggested that the non-seasonal or poorly synchronised annual cycles reported for many common New Zealand streams (Towns 1983) may be related to the unpredictable nature of hydrologic disturbance. The unpredictability in the flow patterns of many New Zealand streams may have favoured the selection of flexible life histories, which spreads the risk of larval cohort loss due to hydraulic disturbance by having poorly synchronised life histories. This flexibility highlights the importance and major role that prior exposure to a particular disturbance plays in shaping community structure and the response of the community to the disturbance event. Without prior exposure to disturbances, there is no evolutionary basis, for adaptations such as variation in life history traits, morphology and physiology upon which either a community or species-specific response can be framed (Wallace *et al.* 1986; Wallace 1992).

The objective of this chapter was to provide data on the distribution patterns and life histories of the cased caddisfly larvae found with the study stretch. In order to address this objective a number of questions need to be answered. 1) What are the physical characteristics (e.g. near bed flow velocity, depth, amount of CPOM, substrate size and stability) of the visually determined riffle and pool habitats? 2) Does the assemblage of caddisfly larvae differ between riffle and pool habitat types? If there are differences in the assemblage of caddisfly larvae between riffle and pool habitats then the potential impacts by being stranded caused by floods will also differ as pools and riffles, will be affected differently by floods. Therefore data on the caddisfly assemblages of the two habitat types (riffle and pool) were essential in the calculation of population-level impacts. 3) What are the relationships between environmental factors (gradients) and the distribution patterns of larval caddisflies within the study stretch? Using the physical data acquired to answer Question 1, the fine scale associations between species and important environmental factors (gradients) in the study stretch were determined and used in the calculations of Chapter 7. 4) What are the life histories of the common cased caddisfly larvae in the study stretch and are they synchronised to minimise the impacts of by hydraulic disturbance (i.e. are they present and at what size when there is a high possibility of floods occurring)? Using life history data it was possible to determine when and at what stage (size) of the life cycle the larval caddisflies are present in the study stretch. Life history data will be used in conjunction with data from this chapter in Chapter 7. In order to address these questions a monthly, one-year benthic survey of the Whiteadder Water was undertaken.

3.2 Materials And Methods

3.2.1 Benthic survey

Samples were collected once a month from November 1997 to December 1998.

Physical characteristics of microhabitats

Prior to the sampling of the benthic organisms, water depth, near-bed flow velocity, presence/absence of filamentous/flocculent algae, moss and overhanging vegetation were estimated/measured at each sample point. Near bed current velocity at each sampling point was measured 2-3 cm above the substrate, using a mini-bucket wheel velocity meter (5 cm bucket wheel diameter). The velocity meter was fitted with a photo-fibre optic sensor to minimise friction at low velocity, thus ensuring accurate measurement of low velocity. The dominant substrate type at each sample point was visually classified as coarse (large cobbles and boulders), medium (large pebbles and gravel) and fine (fine gravel, sand and silt).

Discharge was estimated on each sampling date. Discharge was estimated in a roughly rectangular section of the study stretch, between pool 3 and riffle 3 (see Chapter 2) using the velocity area method (Gordon *et al.* 1992). Discharge was calculated as:

$$Q = VA$$

Where Q = discharge ($m^3\ s^{-1}$), V = mean velocity ($m\ s^{-1}$) and A = cross-sectional area of water (m^2). Water velocity was measured using the same mini bucket wheel flow meter used to obtain near bed flow velocity measurements. Discharge was estimated as the average of five transects on each visit. Each transect across the stream comprised of 5 points equally spaced along each transect. Velocity measurements at each point were taken at approximately 0.4 the depth at that point, in accordance with Gordon *et al.* (1998).

Coarse particulate organic matter (CPOM) >1 mm diameter was collected from the benthic samples by sequential sieving in the laboratory, with three stacked sieves with decreasing mesh sizes of 10, 2 and 1 mm. Once the CPOM was manually removed from the benthic sample it was placed in a metal tray and oven dried for 48 hrs at 80 °C.

Substrate particle size and stability in pool and riffle microhabitats

Substrate particle size and stability was assessed twice in each riffle and pool using Wolmans' (1952) 100 random particle method. Substrate was measured in summer 1999 and winter 2000 to highlight the extremes of seasonal variation in substrate particle size and stability. In each replicate riffle and pool, 100 stones were picked from the substrate at random by wading across the microhabitat and picking the stone that was immediately below the left big toe after a random period of time. The disturbance of the particles by the samplers left big toe has been found to not to to alter the relationship of that particle to other particles in the stream (Wolman 1952). Each stone was measured across its three dimensions, the A axis (long axis), the B axis (intermediate axis) and the C axis (the shortest axis) (Figure 3.2.1). The C axis on a tabular pebble was the easiest to define, as it is the shortest axis on the substrate particle. The B axis was defined as the shortest axis of the maximum projection plane (the plane of largest area, perpendicular to the C axis, the A axis is then defined as the longest axis perpendicular to the B axis. Particle size (granulometry), for comparison between sites was determined from the (B) median diameter (mm) (Figure 3.2.1). The B axis was used as it most closely approximates the results that would be obtained if a sieve were used, because it is the B axis which determines whether or not an individual pebble falls through a given mesh size and therefore makes results using the two methods comparable (Morisawa 1985; Gordon *et al.* 1992).

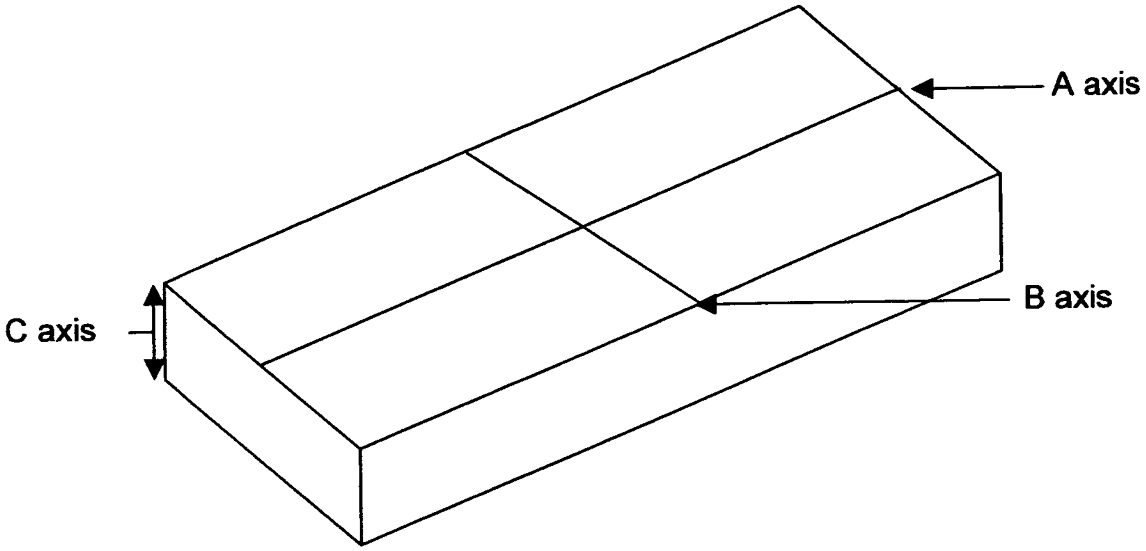
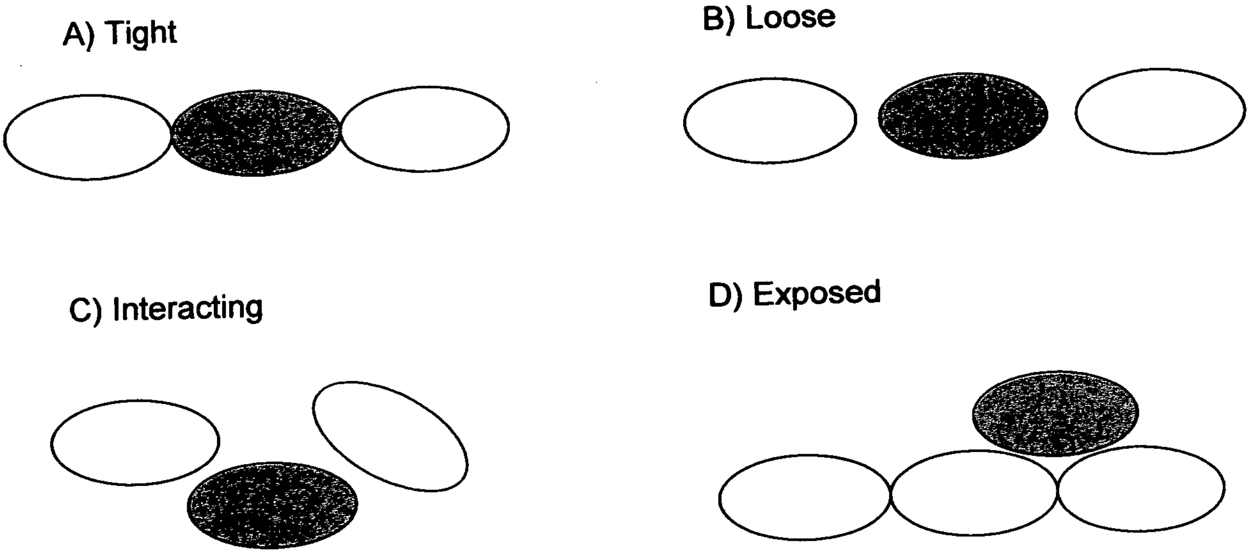


Figure 3.2.1 Axes on a tabular pebble used for measurement substrate particle size determination (modified from Gordon *et al.* 1992).

The phi number (ϕ) is traditionally used by sedimentologists in granulometry and is the negative logarithm (in base two) of the particle size, as indicated by axis B, in millimetres (Table 3.2.1). The advantage of using phi is that it eliminates the inconvenience of unwieldy numbers for small particles and it also overcomes the problem with using mean values in assessing the substrate particle sizes. The problem with using the mean value for describing sediment size is that a few particularly large rocks will bias the mean heavily towards the coarse end of the scale. The preferable approach is to use the mean of the phi values on the assumption that the particle sizes are log-normally distributed (Gordon *et al.* 1992). Substrate particles were also classified as tight or loose to remove from the bed and whether they were exposed or interacting with other substrate particles (see Figure 3.2.2). However, a criticism of the Wolman method that the selection of the particle under the left big toe may disturb the particle sampled so that its relationship with other particles is altered has to be acknowledged. The substrate stability per pool and riffle was estimated as the ratio of stable particles (tight or interacting) to unstable particles (loose or exposed).

Table 3.2.1 Grade scales for substrate particle size (adapted from Gordon *et al.* 1992).

Class (Wentworth)	Particle size along B axis (mm)	ϕ (phi)
Large cobble	256 to 128	-8 to -7
Small cobble	128 to 64	-7 to -6
Very coarse gravel	64 to 32	-6 to -5
Coarse gravel	32 to 16	-5 to -4
Medium gravel	16 to 8	-4 to -3
Fine gravel	8 to 4	-3 to -2
Very fine gravel	4 to 2	-2 to -1
Very coarse sand	2 to 1	-1 to 0


A) Tight

B) Loose

C) Interacting

D) Exposed

Figure 3.2.2 Classification of the stability of substrate particles within the stream as seen from a cross-sectional perspective through the stream bed. Gray ovals represent the substrate particle sampled in relation to other substrate particles in the stream bed (represented by white ovals). Where the sampled particle is A) tight = difficult to remove from the bed, B) loose = no resistance to withdrawal from bed, C) interacting = loose but semi-hidden by other particles and D) exposed = loose and exposed above the stream bed.

Macroinvertebrates

In each of the five riffles and pools, benthic samples were collected monthly from November 1997 to December 1998. A large flood precluded sample collection in December 1997. Within each riffle and pool, six semi-random samples of the benthos were collected with a Surber sampler (0.1 m^2, 250 μm mesh): two near to the left, two near to the right bank and two in the centre of the stream channel. The use of a semi-random design ensured that samples were not always taken from a similar position within the pool and riffles in the study stretch (e.g. mid channel) and so increased the chance that all environmental conditions within the pool and riffle were sampled. Benthic samples were preserved immediately in 70% industrial methylated spirit (IMS). In the laboratory all caddisflies were identified and enumerated with the aid of a binocular dissecting microscope. Head capsule width (HCW) was measured to the nearest 0.01 mm with an eyepiece micrometer and case type (if present) was recorded for each individual. Head capsule width was taken as the width of the head capsule at its widest point, excluding the eyes if they protruded beyond the outline of the head (Wallace *et al.* 1990). Head capsule width was used to determine the age (instar) of individuals, which was used to determine the life history of species within the study reach. For cased larvae, the instar was determined using HCW data tables from Wallace *et al.* (1990). For the case-less species HCW data tables from Edington and Hildrew (1995) were used to calculate larval instars.

3.2.2 Data Analysis

Physical characteristics of riffles and pools

The physical attributes of riffles and pools were described by near-bed velocity, depth and CPOM on each sampling date and were analysed by two-way Analysis of Variance (ANOVA) in the Datadesk computer package (Version 6.0). Measurements were nested within riffles and pools habitats. Flow velocity and depth met the assumptions for homogeneity of variance at $p=0.05$, while CPOM did not meet the assumptions. Homogeneity-of-variance was tested using the Levene statistic to test for the equality of group variances using SPSS version 9.0. when data for CPOM were log transformed they then met the assumptions of homogeneity of variance. Two-way ANOVA was then carried out on the transformed data for CPOM. Pair wise *post-hoc* comparisons between treatments of pool and riffle habitats were analysed using the Scheffé test

Comparisons between qualitative measurements of the physical environment, such as the presence or absence of moss, filamentous or flocculent algae, over-hanging vegetation and the frequency of substrate types (coarse, medium and fine), were made using G-tests (Sokal & Rohlf 1981; Fowler *et al.* 1998). The G-test is an alternative to the chi-square test for analysing frequencies, but it is more robust (Fowler *et al.* 1998). The data for each riffle and pool type were pooled to give the total number of samples that contained, or did not contain the environmental variable being analysed. Summing the data in this manner increases the confidence that the patterns observed are real rather than occurring by chance. Summing the data also has an advantage in reducing the number of cells in the matrix with low values, which can affect the G-statistic (Lancaster 1999a; 1999b).

The physical attributes of riffle and pool habitats may be affected differently by the same discharge, and therefore during high discharge (i.e. floods) the physical conditions will also vary. For example in a riffle a slight increase in discharge may increase the near-bed flow velocity and depth considerably more than in a pool for the same discharge and this in turn will have an impact on the forces acting on the biota. To determine the relationship between discharge (Q) and the mean near-bed flow velocity and mean depth of pools and riffles on a sampling date, linear regressions were performed.

Substrate particle size and stability

Comparisons between the mean particle size (expressed as phi (ϕ)) per riffle and pool and the season (summer or winter) were analysed using a two-way ANOVA. The data met the assumptions for homogeneity of variance at $p=0.05$. Homogeneity-of-variance was tested for using the Levene statistic to test for the equality of group variances using the SPSS (version 9.0) computer package.

The phi quartile skewness and deviation for each replicate riffle and pool microhabitat for summer and winter surveys were also calculated according to the formulae:

Skewness: $Skq\phi = (Q3\phi + Q1\phi - 2Md\phi)/2$ (Krumbein, 1941)
Deviation: $QD\phi = (Q3\phi - Q1\phi)/2$ (Briggs, 1977)

Where $Q3\phi$ = upper quartile phi, $Q1\phi$ = lower quartile phi and $Md\phi$ = the median phi value.

The phi quartile skewness indicates how evenly the particles are sorted in terms of size and indicates the variation in grain sizes at either end of the size scale. Therefore, if large particles are sorted better than small particles, there is a greater range in size amongst the small particles compared to the large particles.

If $Skq\phi = 0$, the small and large particles are sorted equally.
If $Skq\phi > 0$, the large particles are sorted better than the small.
If $Skq\phi < 0$, the small particles are sorted better than large.

The phi quartile deviation ($QD\phi$) shows the general variation in particle size. If the value is high there is some variation, if the value is low there is little or no variation in substrate particle sizes within the microhabitats (pool or riffle). The pool and riffle microhabitats were classified according to their phi quartile deviation (QDϕ); where QDϕ <0.35 = very low variation, 0.35 to 0.50 = low variation, 0.50 to 1.00 = moderate variation, 1.00 to 2.00 = high variation and >2.00 = very high variation (Gordon *et al.* 1992).

To determine if the proportion of stable (tight or interacting) substrate particles in the two microhabitats (pool and riffle) changed between seasons (winter and summer), a 2 x 2 G-test was performed (Fowler *et al.* 1998). The data were pooled across sample points within each riffle and pool. No comparison between the frequencies of unstable substrates was undertaken, because particles can only be classified as stable or unstable so one category will automatically be accompanied by the other.

Macroinvertebrates

The mean density of caddisflies (number of individuals/0.1m^2) was compared between pools and riffles (with replicates nested within habitats), sample date and case type (uncased or cased) using a three-way ANOVA (Datadesk version 6.0). Prior to analysis the data was checked to ensure it met the assumptions for homogeneity of variance at p=0.05. Homogeneity-of-variance was tested for using the Levene statistic to test for the equality of group variances using the SPSS (version 9.0) computer package. It was found that the data met the assumptions for homogeneity of variance and were therefore not transformed.

Multivariate Analysis

The relationships between species of caddisfly and the various environmental factors were analysed using multivariate techniques that relate species to environmental gradients using CANOCO for Windows (version 4) computer package (ter Braak 1998). Multivariate analysis is a useful tool for ecologists as it allows the relationships between variations in species abundance (density) and environmental factors (difficult to isolate experimentally) to be investigated. Therefore, it is ideal to use in determining the important environmental factors that may be associated with the spatial distribution patterns of caddisfly larvae in the Whiteadder Water. Preliminary analysis using detrended correspondence analysis (DCA) revealed gradient lengths greater than 4 s.d. (standard deviations) in the species data and indicated that a unimodal technique (CCA) was the most appropriate form of gradient analysis (see ter Braak and Smilauer 1998). Species density was ln(x+1) transformed to normalise the data, species density was related to environmental variables by partial canonical correspondence analysis (partial CCA) the reasons for choosing partial rather than total CCA are discussed later.

Out of the 13 environmental variables two variables, pool and riffle were highly correlated with the other environmental variables as indicated by a large variance inflation factor (VIF), and therefore had no unique contribution so were removed from the partial CCA in accordance with ter Braak and Simlauer (1998). In the final analysis a subset of the original variables was used that included; near-bed flow velocity (m s^{-1}), CPOM, depth, presence/absence of moss, filamentous and flocculent algae, over-hanging vegetation, visually determined substrate size (coarse, medium and fine) and the position of the sample (sides or mid-channel). Near-bed flow velocity, CPOM and depth were continuous variables and all others were entered as nominal variables. The sample date (month) was entered into the analysis as a covariable.

Data on species density and environmental factors were collected monthly over the study period. It is therefore likely that there was considerable variation in the biological assemblage and the environment over this period. This seasonal variation was not the prime research question, as I wished to relate the species to the physical environmental gradients, and therefore the season (month) should not be part of defining the synthetic ordination gradients (ter Braak and Verdonschot, 1995). This was achieved by using a partial CCA with month defined as a covariable. Covariables are defined as a concomitant variable, background variable, an explanatory variable corresponding to incidental or nuisance parameters, or a block factor in an experimental design (ter Braak and Smilauer 1998). A partial CCA amounts to a normal CCA, but with the extra requirement that each axis must be uncorrelated with the covariables (ter Braak and Verdonschot 1995). In statistical terms, the covariables are explanatory variables that are fitted to the species data before the actual ordination. The ordination is then applied to the residual variation. In direct gradient analysis, the environmental variables are the explanatory variables of prime interest, whereas the covariables are background explanatory variables (nuisance variables), which I am not considering in terms of the overall pattern of caddisfly microdistribution (ter Braak and Smilauer 1998).

The statistical significance of the relationships between species and the whole set of environmental variables, given the covariables, was evaluated using Monte Carlo permutation tests. A Monte Carlo permutation test is a test of statistical significance of the ordination axes obtained by repeatedly shuffling (permuting) the samples. The validity of Monte Carlo tests hinges on the permutation type (how the samples are shuffled) and the generation of new data sets that are equally likely under the null hypothesis: that the species data are unrelated to the environmental data, and the alternative hypothesis; that the species respond to the environment. In CANOCO, new data sets are generated by randomly permuting samples in the species data (the response data) while keeping the environmental (and covariable data if present) fixed (ter Braak and Smilauer 1998). If samples are independent or exchangeable under the null hypothesis then the data can be obtained by completely random permutations, however completely random tests yield invalid tests if the samples show additional structure in the way they are collected, i.e. a stratified sampling design (ter Braak and Smilauer 1998). As the data collected had this additional structure (i.e. samples were not completely random) in the partial CCA, 199 unrestricted, reduced model random permutations occurred within each covariable (month) and not across all the dates (*sensu* Ruse 1994; ter Braak and Verdonschot 1995; ter Braak and Smilauer 1998). The number of permutations used (the number of times the data are shuffled) determines the power of the test, for a test at the 5% significance level, a minimum of 19 permutations is required (ter Braak and Verdonschot 1995; ter Braak and Smilauer 1998). The power of the test increases with the number of permutations, but only slightly after 199 permutations (ter Braak and Smilauer 1998). In CANOCO by default, the residuals from the reduced model ('null model') are permuted, which better maintains Type I errors (ter Braak and Smilauer 1998). Anderson and Legendre (1999) stated that the result observed by using the full model gives a slightly lower

Type II error, and that it is best to use the default reduced model permutation as permutation of data under full and reduced models are generally asymptotically equivalent. Accordingly, I applied the default (reduced model) permutation to the analysis.

Life Histories

In order to determine the life history of caddisfly larvae in the Whiteadder Water, life history tables were constructed for all the species of caddisfly larvae that accounted for ≥ 1% abundance. The micro-caddis species, *Hydroptila* spp., were excluded from life history analysis as instars I-IV were very small and the change in head capsule width (HCW) used to determine instar size for instar I-IV (though I cannot be sure that instar I larvae were even sampled due to their very small size) either changed very little or was beyond the resolution of the microscope. Instar V *Hydroptila* spp. are morphologically different from earlier instars (and therefore easy to distinguish) and have a larger HCW. Adult caddisflies were not collected as part of the survey, so the presence of adult caddisflies and the subsequent emergence and flight periods of adults were excluded from the life-history tables. Limnephilid caddisfly species up to the third instar are difficult to identify to species, as many of the morphological differences are absent (Wallace *et al.* 1990). Consequently, I, II and III were grouped together as limnephilid spp., (see Table 3.3.5) and are not included in the life history tables. The presence or absence of species in monthly samples, including those that are not abundant enough to have detailed presentation of instar-specific patterns (i.e., <1% abundance) and those species excluded for reasons outlined above, were tabulated to show the seasonal distribution of caddisfly larvae in the Whiteadder Water.

3.3 Results

3.3.1 Physical variables

The mean near-bed flow velocity was significantly different between pools and riffles for all sampling dates (Figure 3.3.1A Table 3.3.1A); flow velocity within pools was less than in riffles. Mean depth was greater in pools than riffles (Figure 3.3.1B and Table 3.3.1B). The mean amount of CPOM was greater in riffles than pools (Figure 3.3.1C and Table 3.3.1C). There was a significant difference in all physical variables (near-bed flow velocity, depth and CPOM) for also for date (Table 3.3.1). In both riffle and pool microhabitats there were significant positive linear relationships between mean near-bed flow velocity and mean depth with increasing discharge (Figure 3.3.2 and Table 3.3.2). There was no significant relationship between mean amount of CPOM and discharge in either pool or riffle microhabitats over the study period (Table 3.3.2).

In both pools and riffles the medium substrate type was the most common, and the fine substrate type was the least common (Figure 3.3.3A). Coarse substrates were considerably more abundant in riffles than pools (Figure 3.3.3A). The proportions of the three-substrate types between pool and riffle microhabitats were significantly different (G_{adj}= 292.35, d.f. =2 p=0.01). A significantly greater proportion of moss occurred in riffles in comparison to pools (G_{adj} = 2318.13, d.f. = 1, p = 0.01) (Figure 3.3.3B). Pools had a significantly greater proportion of samples with filamentous/flocculent algae present (G_{adj} = 13.78, d.f. = 1, p = 0.01) (Figure 3.3.2B). The presence of over-hanging vegetation was significantly higher in pool microhabitats than in riffle microhabitat samples (G_{adj}=463.77, d.f. =1 p=0.01) (Figure 3.3.3B).

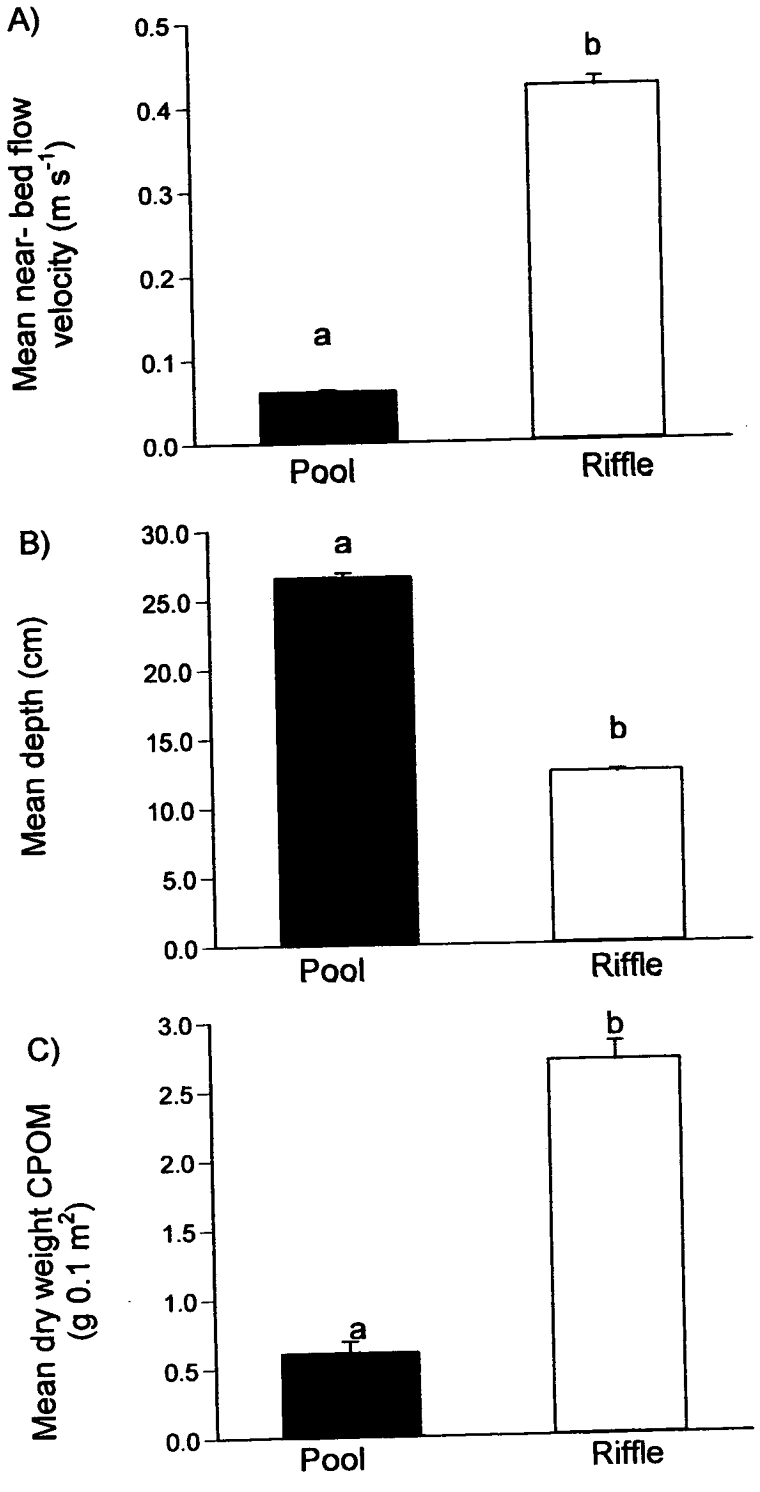


Figure 3.3.1 Mean (± SE) A) near-bed flow velocity, B) depth and C) amount of CPOM present in pools and riffles for all sample dates. Bars with the same letter are not statistically different using Scheffé post-hoc pair-wise comparison tests ($p=0.05$).

Table 3.3.1 Summary tables of the results of two-way ANOVA comparing the mean of physical variables between sample date and habitat (riffle or pool) where A) mean nearbed flow velocity (m s^{-1}), B) depth (cm) and C) CPOM (g/0.1 m^2).

A) Mean near bed velocity (m s^{-1})

Source	d.f	MS	F-ratio	p
Date	12	0.08	11.706	≤0.001
Habitat	1	3.86	573.59	≤0.001
Date x Habitat	12	0.03	4.8551	≤0.001
Error	104	0.01		
Total	129			

B) Mean depth (cm)

Source	d.f	MS	F-ratio	p
Date	12	61.958	6.6368	≤0.001
Habitat	1	6576.4	704.45	≤0.001
Date x Habitat	12	8.8133	0.9440	0.507
Error	104	9.3356		
Total	129			

C) CPOM (g/0.1m^2)

Source	d.f	MS	F-ratio	p
Date	12	2.0047	2.5948	0.004
Habitat	1	8.8557	11.463	0.001
Date x Habitat	12	0.5102	0.6604	0.785
Error	104	0.7725		
Total	129			

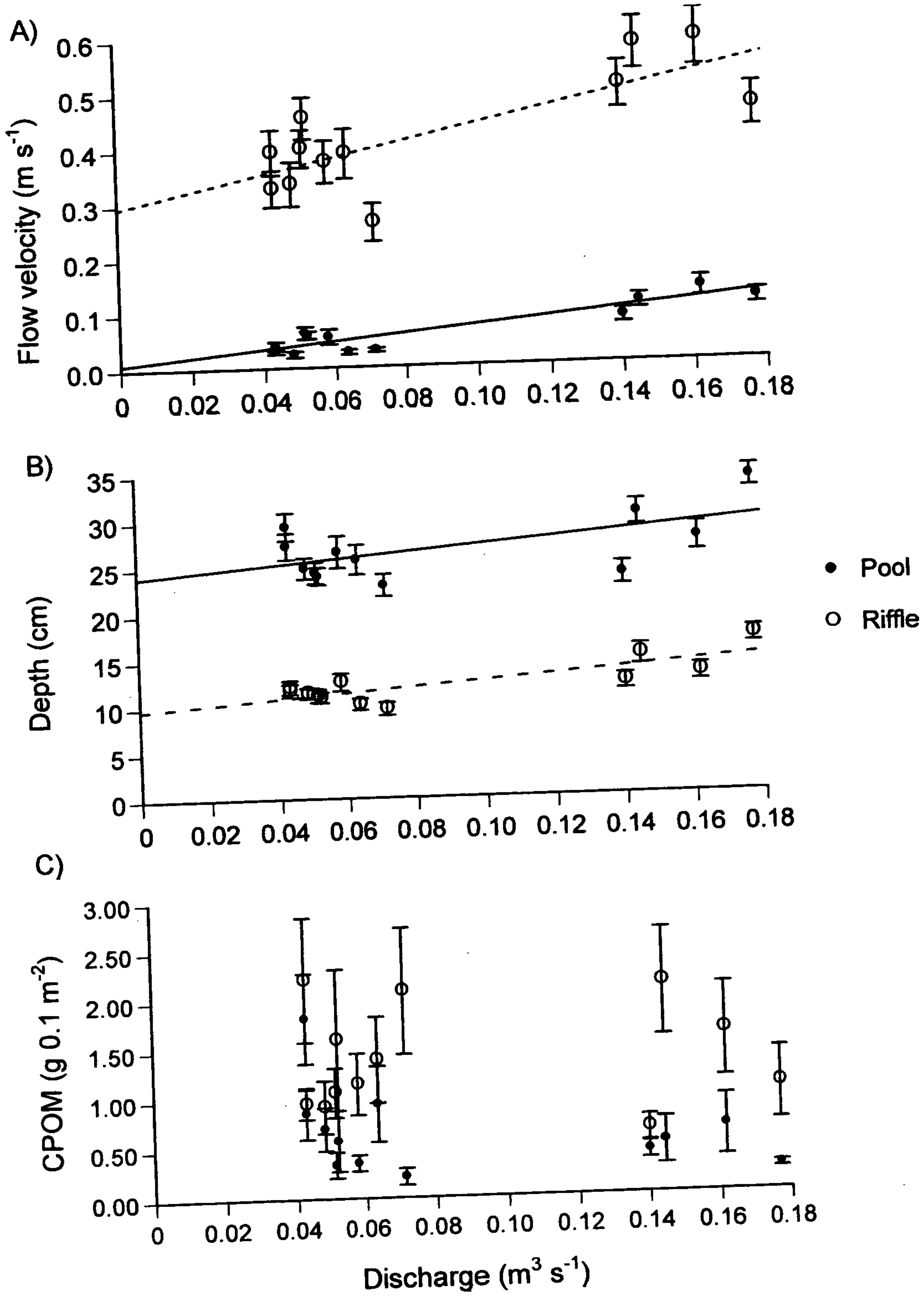


Figure 3.3.2 Relationship between discharge and the mean (±SE), A) near-bed flow velocity, B) depth and C) CPOM in pool and riffle microhabitats. Significant linear regressions (p=0.05) are shown by a dashed line (riffle) and solid line (pool).

Table 3.3.2 Summary of linear regressions of the relationship between mean near-bed flow velocity (m s^{-1}), mean depth (cm) and mean CPOM (0.1 m^2) and discharge (m^3 s^{-1}) in pool and riffle microhabitats. See Figure 3.3.3 for illustration.

	Microhabitat	N	df	F	p	R^2 (adjusted)
Near-bed flow velocity	Pool	12	1,10	35.90	0.001	78.2
	Riffle	12	1,10	12.00	0.006	64.23
Depth	Pool	12	1,10	3.58	0.046	49.23
	Riffle	12	1,10	12.30	0.006	57.2
CPOM	Pool	12	1,10	1.890	0.199	7.5
	Riffle	12	1,10	0.021	0.887	0.8

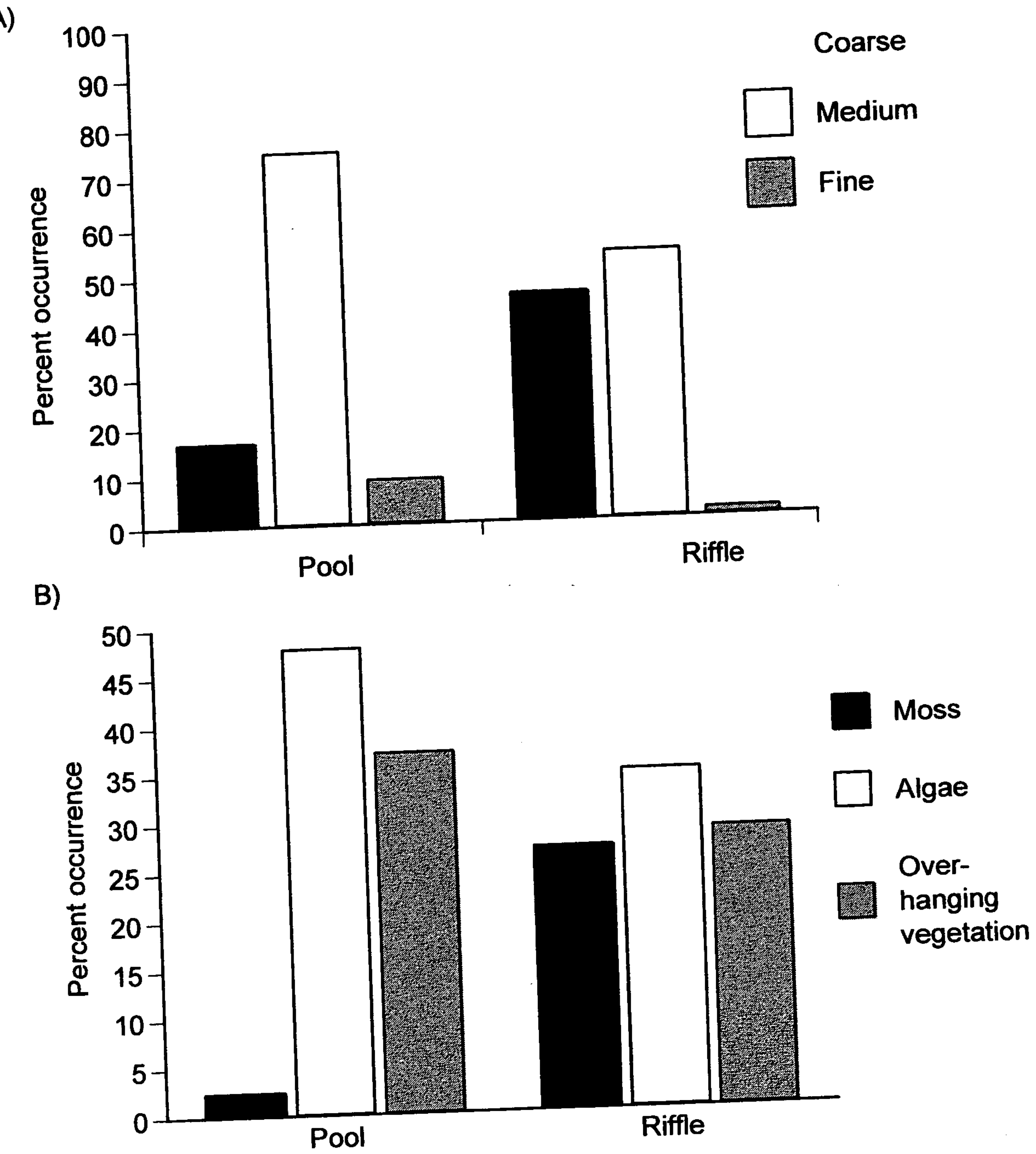


Figure 3.3.3 Percent occurrence in pools and riffles of A) three visually distinguished substrates types (coarse, medium and fine) and B) moss, algae and over-hanging vegetation over all sampling dates.

Substrate particle size and stability

Mean particle size was significantly larger in riffles than the mean particle size in pools in both seasons (summer and winter) (Figure 3.3.4A and Table 3.3.3). There was no significant variation in particle size within pools between seasons, but there was a slight decrease in the mean particle size found within riffles in winter compared to the summer though this was not statistically significant. All the riffles and pools had a low skewness value indicating that small and large particles were equally sorted (Figure 3.3.4B). Pools tended to be more skewed than riffles. All sites had low or moderate variation in particle size as indicated by the phi quartile deviation (QDϕ) (Figure 3.3.4C). The substrate of both riffles and pools is classified as unstable with quotients below 1 (a quotient >1.0 indicates a site with a greater proportion of stable substrate particles, and a quotient <1.0 indicates a greater proportion of unstable substrate particles at a site) (Figure 3.3.5). Two-way G-tests indicated that there was no significant difference in the proportion of stable substrate particles between microhabitats (pool and riffle) and season (G_{adj}=0.583, d.f=1, p=0.05).

3.3.2 Macroinvertebrates

A total of 24 species of caddisfly were identified within the study stretch. Table 3.3.4 lists the species, their codes, the % composition over the whole survey period and the presence/absence of species in riffles and pools. *Hydroptila* spp. was numerically dominant over the sampling period and comprised 44.4% of the caddisfly larvae collected. The most abundant uncased caddisfly larvae (excluding early instar *Hydroptila* spp.), was *Rhyacophila dorsalis* which comprised 16.9% of the caddisfly larvae collected. The most abundant cased caddisfly larvae in the study stretch was *Anabolia nervosa* which comprised 4.3% of the total larvae collected over the sampling period. The majority of the cased species were found in both pools and riffles. *Limnephilus lunatus, Limnephilus flavicornis* and *Limnephilus rhombicus* only occurred in the pools, and *Limnephilus auricula* and *Melamophylax mucoreus* occurred only in the riffles.

The density all caddisfly larvae in riffles and pools over all sample dates was not significantly different (Figure 3.3.6A and Table 3.3.6). The density of cased and uncased larvae differed significantly, cased larvae occurred at a significantly greater density in pools than in riffles, uncased larvae were found at a greater density in riffles than in pools (Figure 3.3.6B and Table 3.3.6). The density of cased and uncased larvae in riffles and pools was significantly different over the sampling period (Figure 3.3.6C). The density of caddisfly larvae was higher during the winter than during the summer months (Figure 3.3.6C).

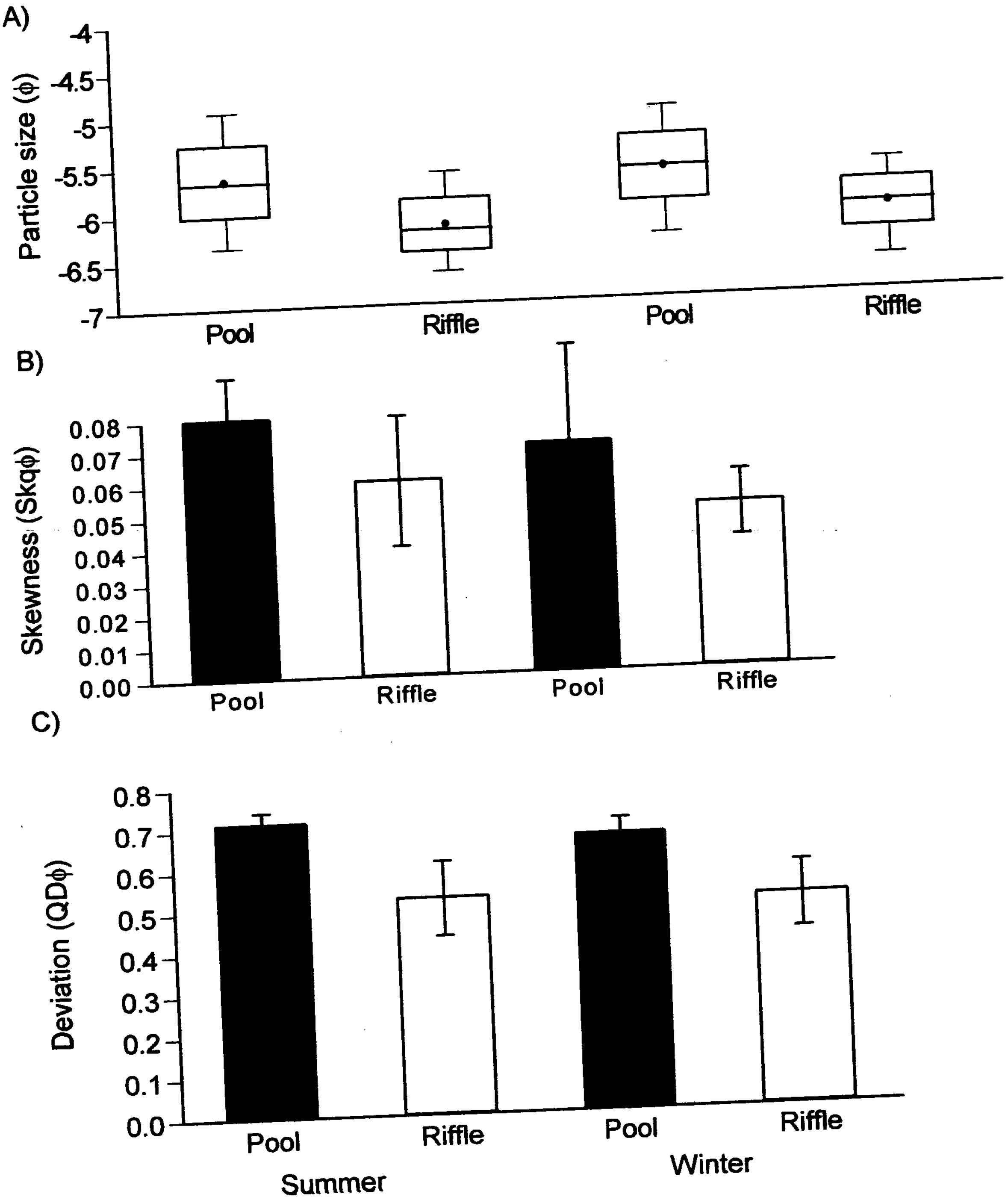


Figure 3.3.4 A) Box-plots showing variation in phi between riffles and pools, where the lowest, second lowest, middle, second highest and highest box points represent the 10th, 25th, 50th (median) and 75th percentiles respectively. The mean is represented by the filled circle. B) mean phi quartile skewness (±SE) in riffles and pools and C) mean phi quartile deviation (±SE) in riffles and pools over two seasons (summer and winter).

Table 3.3.3 Summary of two-way ANOVA comparing particle size (phi) found in riffle and pool habitats and between seasons (summer and winter).

Source	d.f.	MS	F	P
Season	1	0.003	0.030	0.865
Habitat	1	1.162	9.187	0.018
Habitat × Season	1	0.013	0.104	0.751
Error	16	0.126		
Total	19			

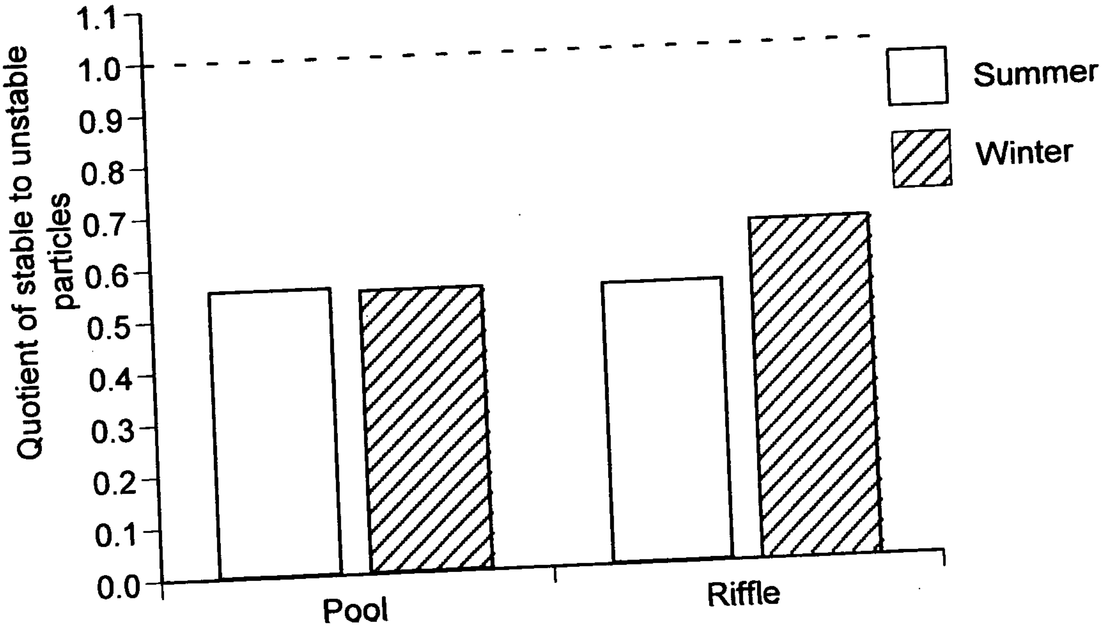


Figure 3.3.5 Quotient of stable to unstable particles in two microhabitats (pool or riffle) and between two seasons (summer and winter). Quotients below the dotted line indicate sites that are unstable; those above the line are stable.

Table 3.3.4 List of Trichoptera collected from the Whiteadder Water, species codes, 'lifestyle' (i.e., cased, free living, net spinner), the % abundance over the entire sampling period (n= 6372) and the presence/absence of species in riffles and pools where R = riffle only, P = pool only and R and P = riffle and pool.

Species	Species Code	Lifestyle	%	Habitat
Unknown Uncased Caddis	UNCAD		6.72	R and P
Plectrocnemia conspersa (Curtis)	PLCON	Net spinner	0.07	R and P
Polycentropus spp.	POLSP	Net spinner	1.46	R and P
Polycentropus flavomaculatus (Pictet)	POLFLA	Net spinner	3.52	R and P
Hydropsyche siltalai (Pictet)	HYDSIL	Net spinner	2.57	R and P
Philopotamus montanus (Donovan)	PHIMON	Net spinner	0.34	R and P
Rhyacophila dorsalis (Curtis)	RHYDOR	Free living	16.9	R and P
Tinodes waeneri (L.)	TINWAE	Gallery builder	1.12	P
Tinodes spp.	TINSP	Gallery builder	0.23	P
Unknown Cased Caddis	UNCCAD	Cased	0.45	R and P
Allogammus auricollis (Pictet)	ALLAUR	Cased	0.32	R and P
Anabolia nervosa (Curtis)	ANANER	Cased	4.27	R and P
Chaetopteryx villosa (Fabricius)	CHAVIL	Cased	1.14	R and P
Drusus annulatus (Stephens)	DRUANN	Cased	1.20	R and P
Ecclisopteryx guttulata (Kolenati)	ECCGUT	Cased	1.01	R and P
Halesus radiatus (Curtis)	HALRAD	Cased	0.58	R and P
Hydroptila spp (Dalman) Instar I-IV	HYDSPI-IV	Free living	19.5	R and P
Hydroptila spp. (Dalman) Instar V	HYDSPV	Cased	24.9	R and P
Leptocerus spp.	LEPSP	Cased	0.16	R and P
Limnephilus auricula (Curtis)	LIMAUR	Cased	0.01	R
Limnephilus lunatus (Curtis)	LIMLUN	Cased	0.07	P
Limnephilus flavicornis (Fabricius)	LIMFLA	Cased	0.03	P
Limnephilidae	LIMSP	Cased	6.98	R and P
Odontocerum albicorne (Scopoli)	ODOALB	Cased	2.70	R and P
Potamophylax latipennis (Curtis)	POTLAT	Cased	1.84	R and P
Sericostoma personatum (Spence)	SERPER	Cased	0.96	R and P
Goeridae	GEOSP	Cased	0.01	R and P
Silo spp.	SILSP	Cased	0.06	R and P
Silo pallipes (Fabricius)	SILPAL	Cased	0.41	R and P
Melamophylax mucoreus (Hagen)	MELMUC	Cased	0.01	R
Limnephilus rhombicus (L.)	LIMRHO	Cased	0.07	P

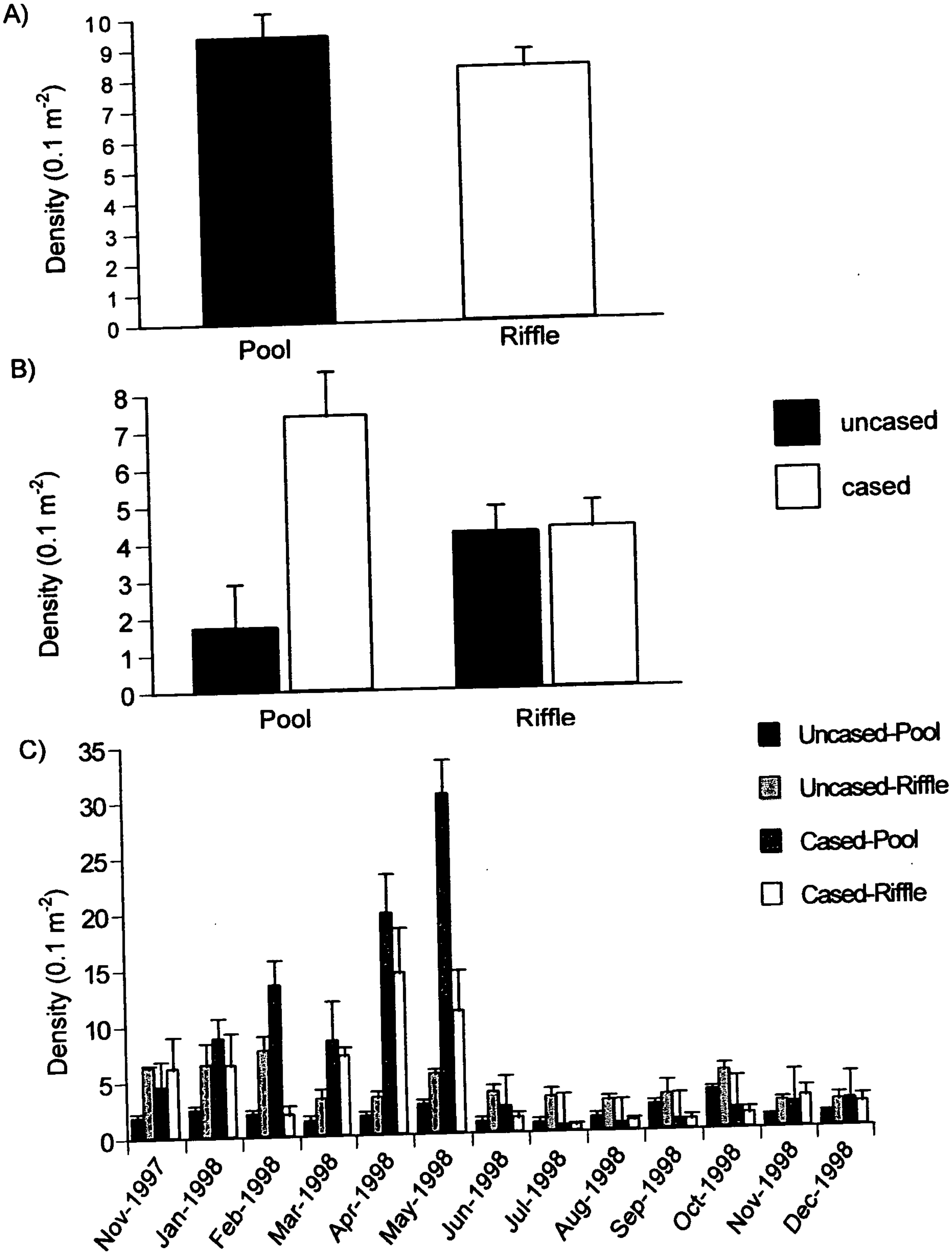


Figure 3.3.6 Mean density (±SE) of A) all caddisflies in pools and riffles, B) cased and uncased caddisflies in pools and riffles and C) cased and uncased caddisflies in pools and riffles monthly over the sampling period.

Table 3.3.6 Summary of three-way ANOVA comparing density / 0.1m^2 of caddisfly larvae between sample date, habitat (riffle or pool) and case type (cased or uncased).

	d.f.	MS	F	p
Constant	1	5020.4	449.4	≤0.001
Date	12	238.54	21.36	≤0.001
Habitat	1	5.7603	0.516	≤0.001
Date x Habitat	12	39.622	3.547	0.4741
Case type	1	550.42	49.27	0.0052
Date x Case type	12	186.49	16.69	≤0.001
Habitat x Case type	1	493.214	44.15	≤0.001
Date x Habitat x Case type	12	55.536	4.971	≤0.001
Error	208	11.170		
Total	259			

3.3.3 Multivariate Analysis

The results of the partial CCA in which date was included as a covariable are shown in Table 3.3.7. The eigenvalues (λ) measure the importance of each axes of the ordination with a value of between zero and one. The eigenvalue is equal to the (maximised) dispersion of the species scores on the ordination axis and is therefore a measure of the importance of the ordination axis (ter Braak and Prentice 1988; ter Braak 1996; Birks 2000). The eigenvalues for the axis decrease from axis one to axis four. As λ_3 is small compared to λ_1 and λ_2, we can ignore the third and higher numbered axes and expect that the first two ordination axes display the biologically relevant information (ter Braak 1996 pp.102).

The species-environment correlation (Table 3.3.7) measures the strength of the relation between species and a particular axis. Species-environment correlations are the correlation between the sample scores for an axis derived from the species data and the scores that are linear combinations of the environmental variables. Axis 1 has a fairly high species-environment correlation, but this does not necessarily mean that a significant amount of the species data is explained by the environmental variables (ter Braak and Smilauer 1998). The amount of explained variance is explained in the next row of Table 3.3.7. The percentage of variance of the species data explained by the axes is given cumulatively; even though these values are low, they still are informative. Species data (abundance data) are often noisy low percentage variance of species data scores is common and nothing to worry about (ter Braak and Smilauer 1998 p121). The percentage variance of the species-environment relation shows the cumulative percentage of the variance explained by the species and the environment. Axes 1 and 2 explained the majority of the variance, and these axes were used to generate a species-environment biplot (Figure 3.3.7). Monte Carlo tests of the first axis of the canonical axis of the CCA and all canonical axes together were significant. The inter-set correlations between the environmental variables and the ordination axes are shown in Table 3.3.8. Axis 1 can be interpreted as a near-bed flow velocity and depth gradient, as near-bed flow velocity was positively correlated with axis 1 and depth was negatively correlated. Axis 2 showed a positive correlation with CPOM.

A species-environment biplot of the environmental variables and species relationships is shown in Figure 3.3.7. Arrows in Figure 3.3.7 show the environmental gradients and the relative importance and intercorrelation of the continuous environmental variables. The angle between the arrow and the axis is a representation of its degree of correlation with the axis, and is a graphical representation of the data shown in Table 3.3.8. Thus, on axis 1 near-bed flow velocity and depth are the most significant environmental variables determining the variation in species composition. In relation to the depth gradient, the direction of the arrow is opposite to the flow velocity gradient as, in general, water velocity is greater in shallow water (i.e., riffles) compared to deep water (i.e., pools). Species that lie towards the right of the origin are at the low end of the depth gradient (i.e., are more abundant in shallow water) and species to the left of the origin are more abundant in deep water (i.e., pools). For near-bed flow velocity, there is an increase from left to right across the biplot. Associated with the velocity gradient is an increase in particle size with increasing velocity, from fine to coarse substrates, and consequently a decreasing substrate particle size with increasing depth. In relation to the CPOM gradient (axis 2), there is an increase in CPOM from the bottom of the biplot to the top. Species that lie above the origin are more abundant with a high amount of CPOM, and those below the origin are more abundant with a low amount of CPOM.

The strength of the relationship between an environmental gradient and species is indicated by the position of the species centroid in relation to the axis of the environment gradient (see Jongman *et al.* 1996; ter Braak and Smilauer 1998). Species to the right of the origin along the velocity axis are more abundant at high velocity and included *Hydropsyche siltalai, Rhyacophila dorsalis, Philopotamus montanus, Odontocerum albicorne* and *Silo pallipes* (Figure 3.3.7). At the other end of the velocity gradient (to the left of the origin) are species that are more abundant at lower velocity such as, *Limnephilus lunatus, Limnephilus rhombicus* and *Limnephilus flavicornis*. As the depth gradient is opposite to the velocity gradient, species found at the low end of the velocity gradient are found in deeper water, and species at the high end of the velocity gradient are more abundant in shallow water as they lie towards the low end of the depth gradient. Species that were more abundant at the high end of the CPOM gradient (axis 2) included *Limnephilus lunatus, Limnephilus rhombicus, Halesus radiatus, Chaetopteryx villosa* and *Anabolia nervosa* (Figure 3.3.7). These species are all case building species that incorporate organic material (CPOM) into their cases. Species at the low end of the CPOM gradient included *Limnephilus flavicornis, Limnephilus auricula, Plectrocnemia conspersa* and *Polycentropus* spp.

The association of caddisfly species to environmental gradients shows the distribution of caddisfly species found at a coarse grained level in pools and riffles (see Figure 3.3.6). Uncased species were found at higher densities in riffles and were associated with the high end of the near-bed flow velocity gradient, and cased species with higher densities in pools were associated with the low end of the near-bed flow velocity gradient in Figure 3.3.7.

Table 3.3.7 Results summary of partial CCA, see Figure 3.3.7 for biplot. Monte Carlo permutation test of significance axis 1: F=27.80, p<0.05: of overall test F=4.988, p<0.05.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.195	0.061	0.034	0.016	5.726
Species-environment correlations	0.675	0.451	0.362	0.261	
Cumulative percentage variance					
of species data	4.1	5.4	6.2	6.5	
of species-environment relation	57.6	75.6	85.9	90.7	
Sum of all unconstrained eigenvalues					4.698
Sum of all canonical eigenvalues					0.338

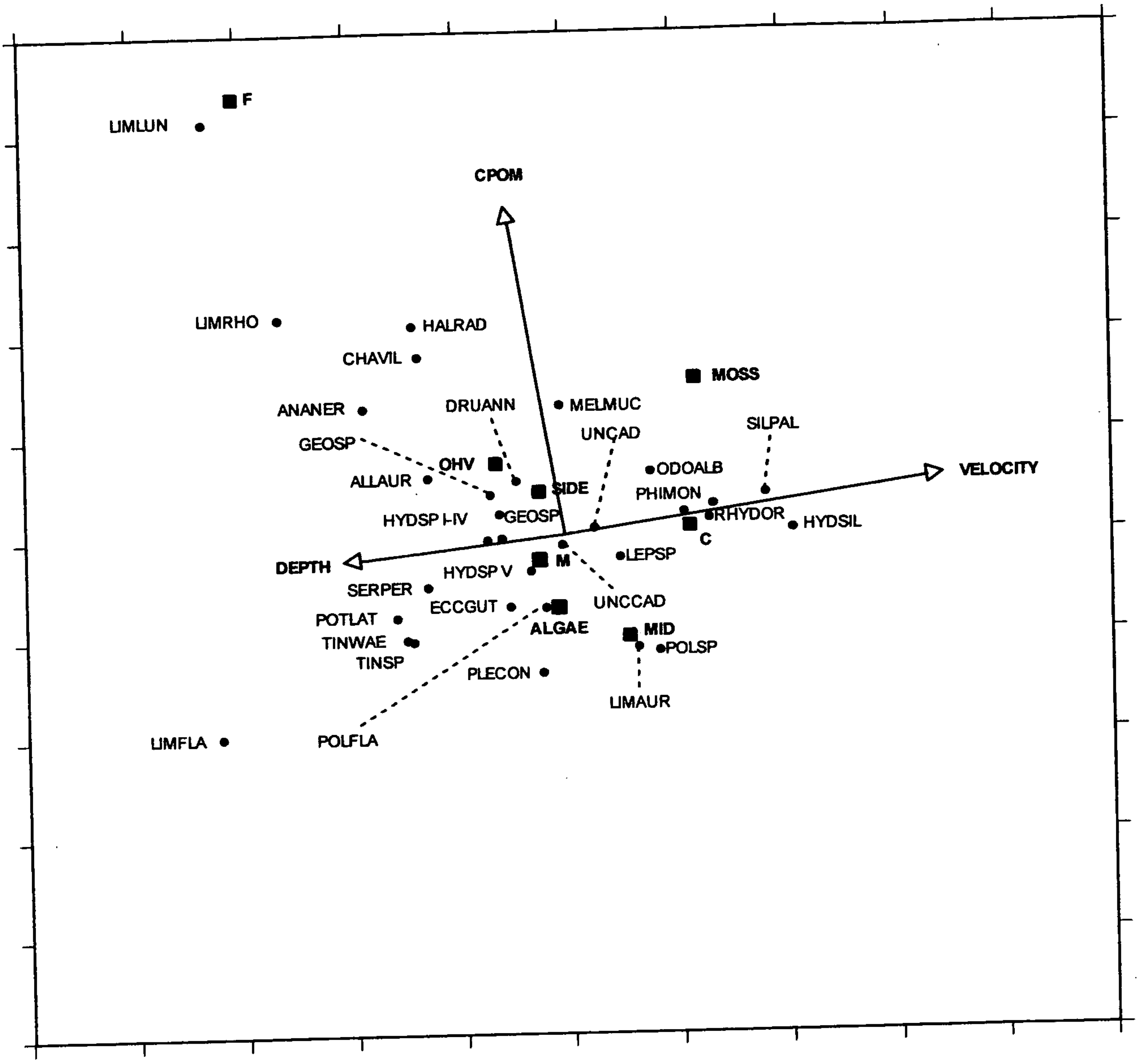


Figure 3.3.7 Partial CCA, species-environment biplot, of caddisfly species (closed circles) and environmental data where nominal variables (closed squares) are shown as their centroids and continuous variables as arrows. See Table 3.3.5 for codes to species names. Where DEPTH= depth, VELOCITY= near-bed flow velocity, CPOM= coarse particulate organic matter, OHV= over-hanging vegetation, ALGAE= filamentous and flocculent algae, MOSS= moss, SIDE= side of channel, MID= middle of channel, C= coarse substrate, M= medium substrate, F= fine substrate.

Table 3.3.8 Inter-set correlations between environmental factors and ordination axes of partial CCA. See Figure 3.3.7 for biplot.

Axes	1	2
Sides	-0.1293	0.153
Mid	0.1293	-0.153
Coarse	0.2602	0.0164
Medium	-0.1167	-0.0892
Fine	-0.2167	0.1905
Depth (cm)	**-0.5296**	-0.002
Near bed velocity (m s^{-1})	**0.6092**	0.0973
Moss	0.177	0.1574
Algae	-0.1041	**-0.2048**
Over-hanging vegetation	-0.1657	0.1258
CPOM (g 0.1 m^{-2})	-0.049	**0.3592**

3.3.4 Life History

The life history of and the frequency of head capsule width (HCW) in each instar of the larvae of common caddisfly species (>1% of larvae collected) are shown in Figures 3.3.8 to 3.3.11 for uncased species and Figures 3.3.12 to 3.3.18 for cased species. Uncased caddisfly larvae, i.e. *R. dorsalis* and *P. flavomaculatus,* were found throughout the year and appeared to have a poorly synchronised life-cycle, with usually at least two, and as many as five, instar classes present during any one month (Figures 3.3.8 and 3.3.9). The life history of *P. flavomaculatus* is unusual, as the development of the instars appears to be in reverse, with early instars increasing in density after later instars (Figure 3.3.9). *Tinodes waeneri* (a gallery building caddisfly) and *H. siltalai* (a net-spinner) had a more synchronous life cycle, with large final instar larvae dominant during the spring and early summer and small early instar larvae dominant during autumn and winter months (Figures 3.3.10 and 3.3.11).

The cased limnephild caddisfly larvae *A. nervosa*, *C. villosa*, *D. annulatus*, *E. guttulata* and *P. latipennis* all had synchronised life-cycles (Figures 3.3.12 to 3.3.16). In the cased limnephild larvae, large individuals (V instar) were usually found during late spring and summer. Instars I to III of cased limnephilid species cannot be separated, but these early instars were present during late summer, autumn and early winter. *Odontocerum albicorne* (Odontoceridae) had a more poorly synchronised life cycle than the the majority of other cased species (Figure 3.3.17). Large final instar *O. albicorne* were found during the summer, autumn and early winter months, during mid-winter and early spring smaller individuals (early instars) were the dominant age class. *Sericostoma personatum* (Sericostomatidae) also had a weakly synchronised life cycle compared to other common cased species with a number of instar classes being present during any one month and final instar larvae present throughout much of the year (Figure 3.3.18).

The presence or absence of instars for caddisfly species that accounted for >1% of the caddisflies collected in pools and riffles are shown in Table 3.3.9. Only two species appeared to have exhibited a change in their distribution in riffles and pools during their life cycles. First and second instar *Rhyacophila dorsalis* and *Hydropsyche siltalaii* were only present in samples collected in riffles, but all the other instars were present in samples from both microhabitats. All other species were present in both pools and riffles at all instars.

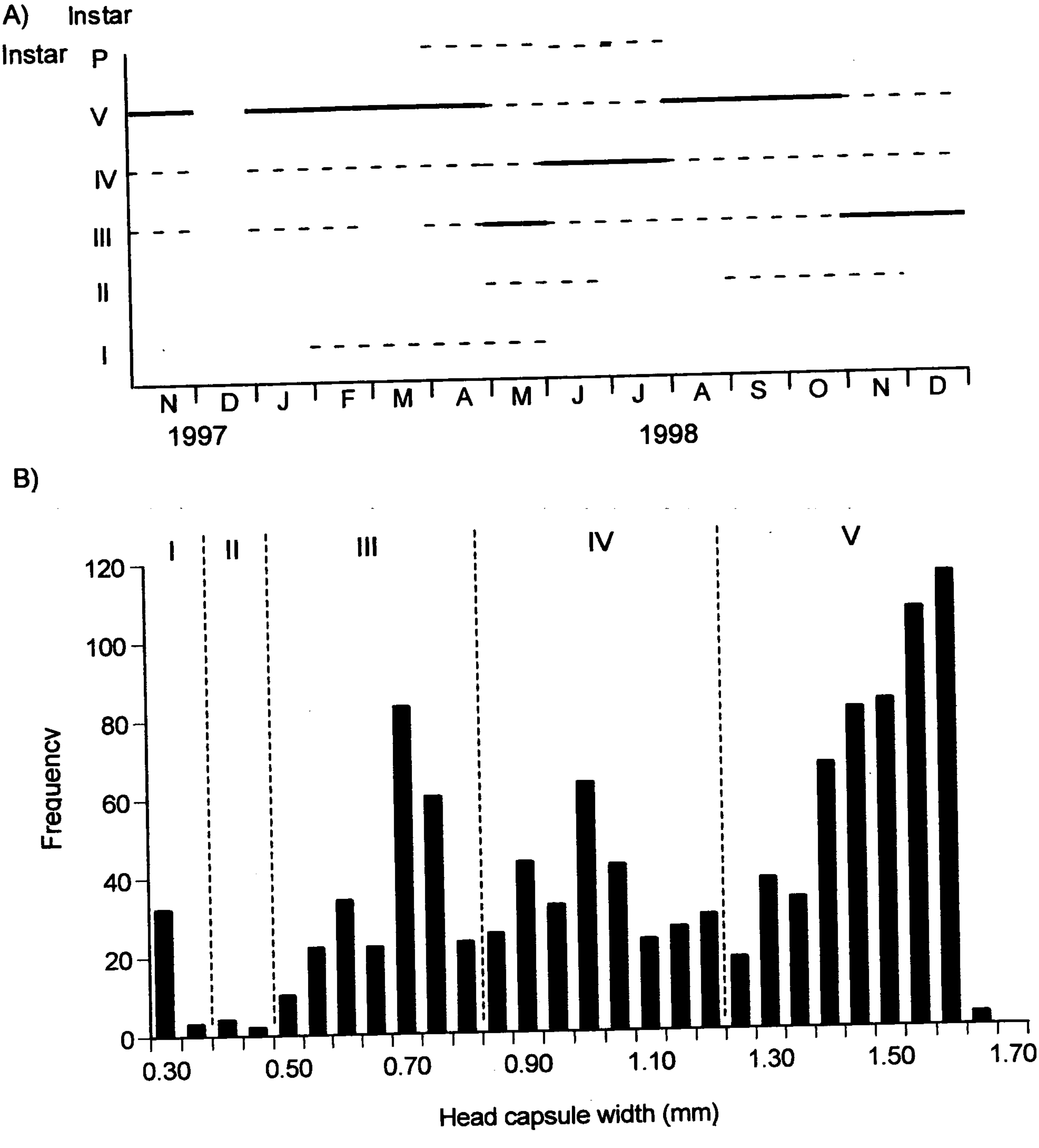


Figure 3.3.8 *Rhyacophila dorsalis*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar collected in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=1135). Samples were not collected in December 1997.

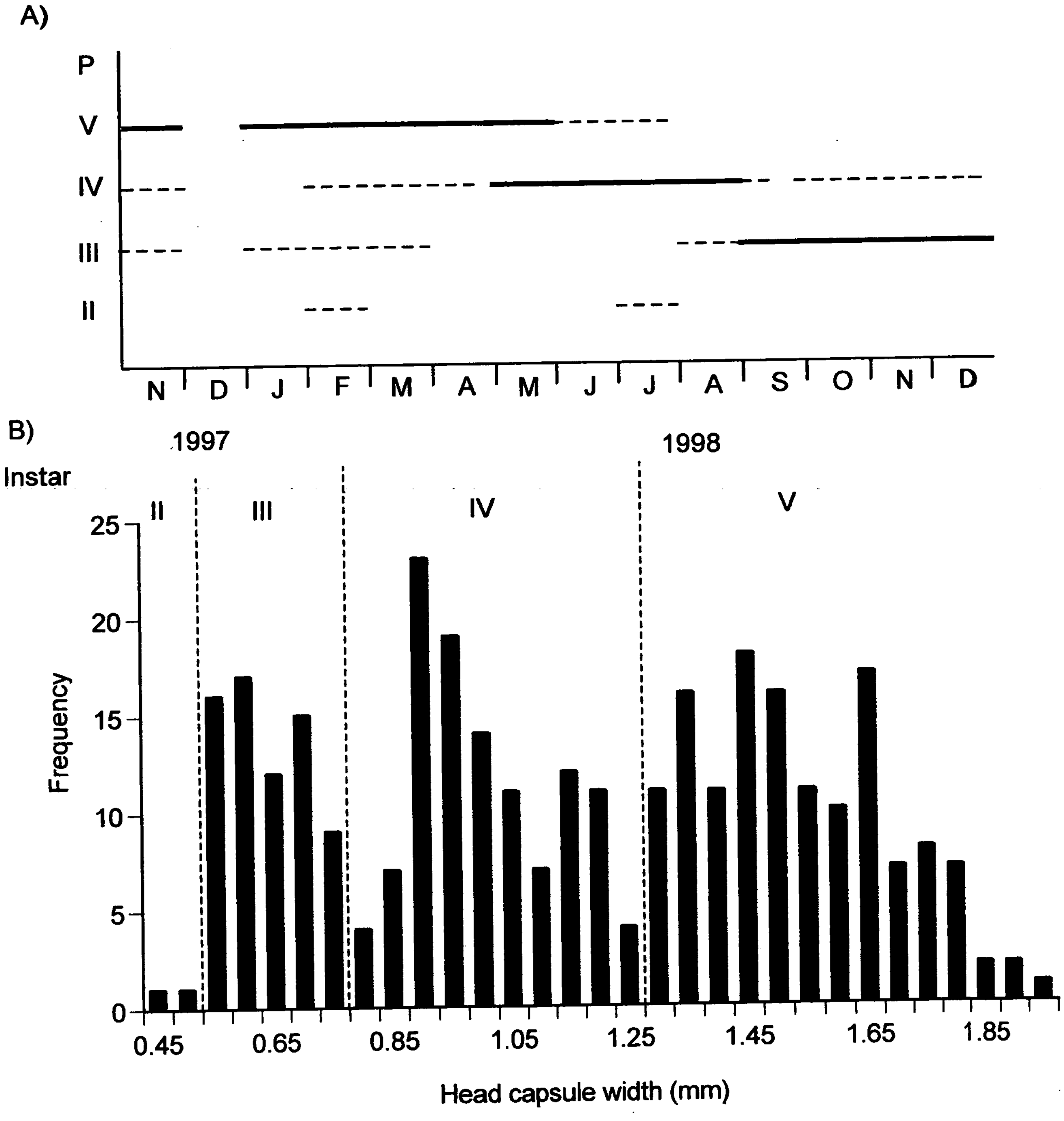


Figure 3.3.9 *Polycentropus flavomaculatus*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=316). Samples were not collected in December 1997.

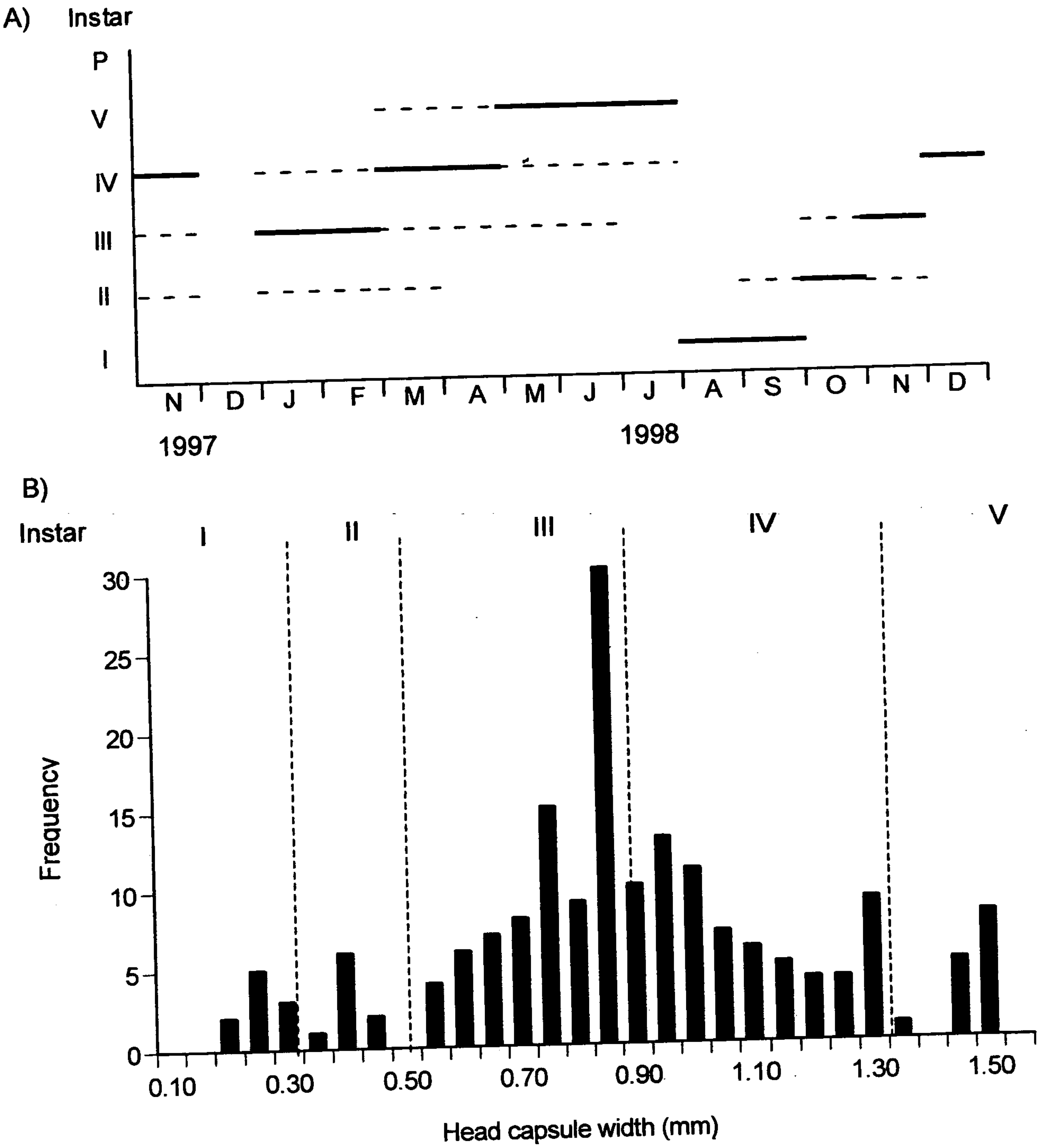


Figure 3.3.10 *Hydropsyche siltalai*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=173). Samples were not collected in December 1997.

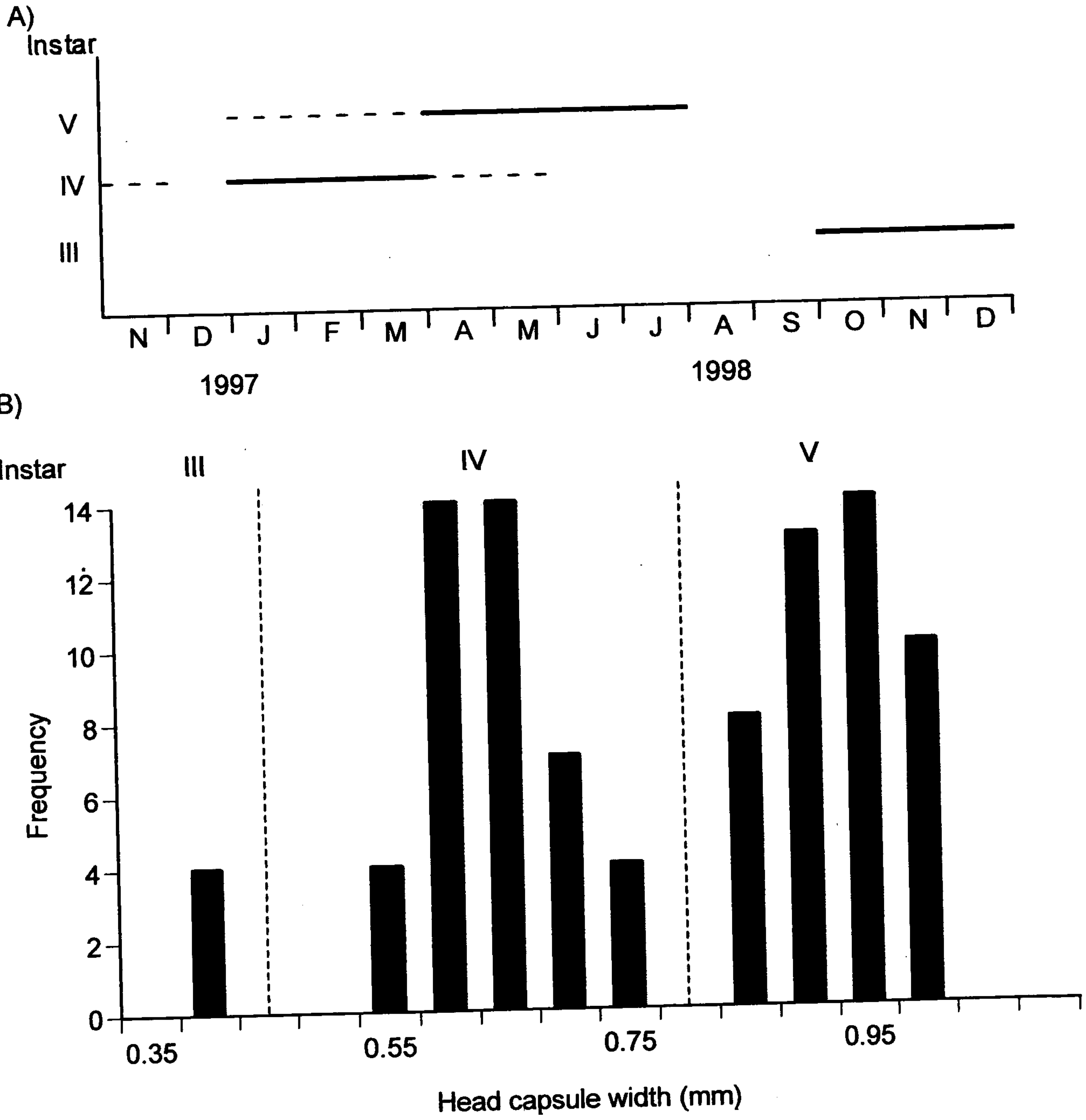


Figure 3.3.11 *Tinodes waeneri*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=92). Samples were not collected in December 1997.

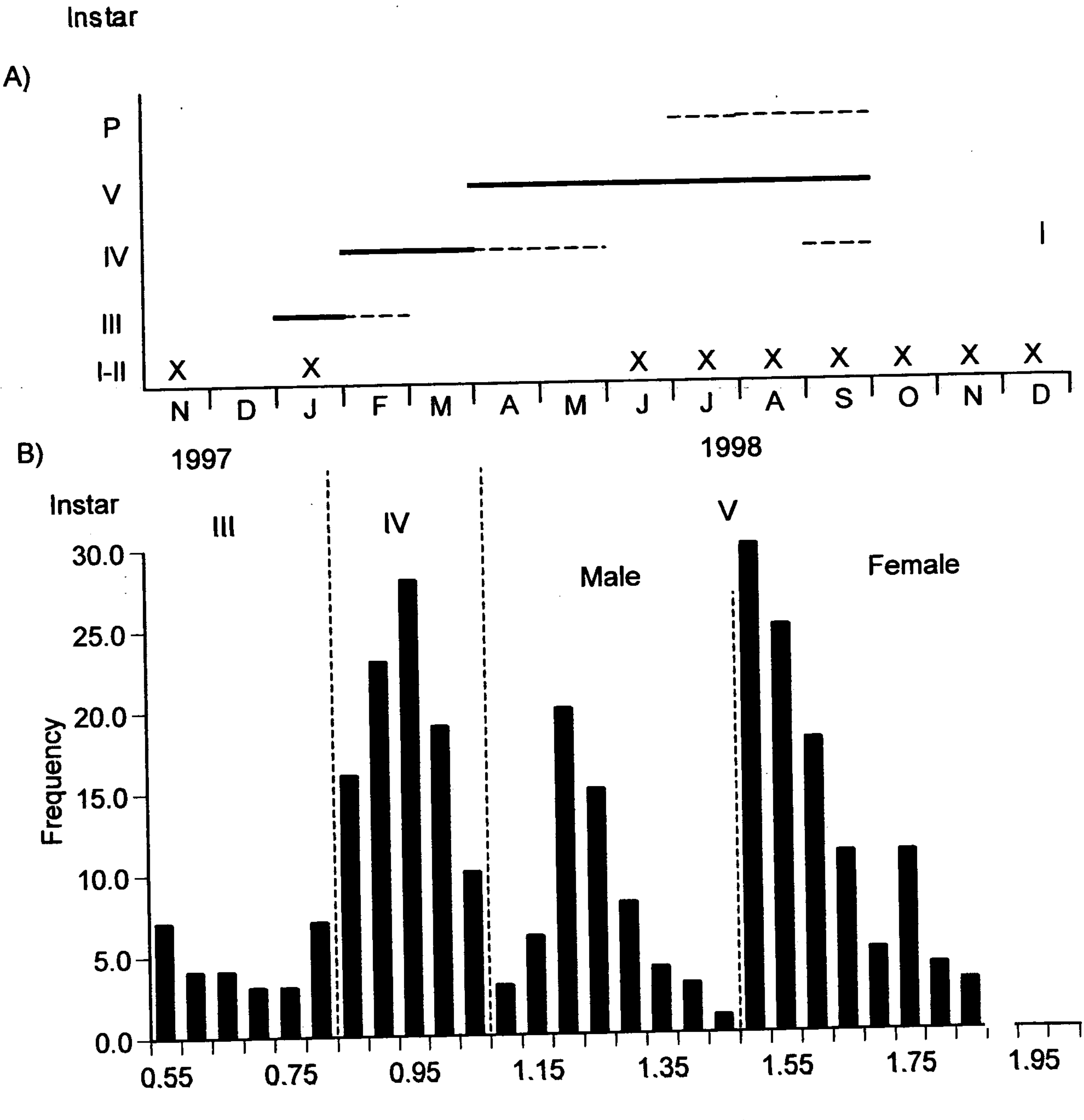


Figure 3.3.12 *Anabolia nervosa*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars or pupae and X indicates presence of instar I and II Limnephilidae. B) Frequency distribution of head capsule width and presumed instar (n=292). Samples were not collected in December 1997.

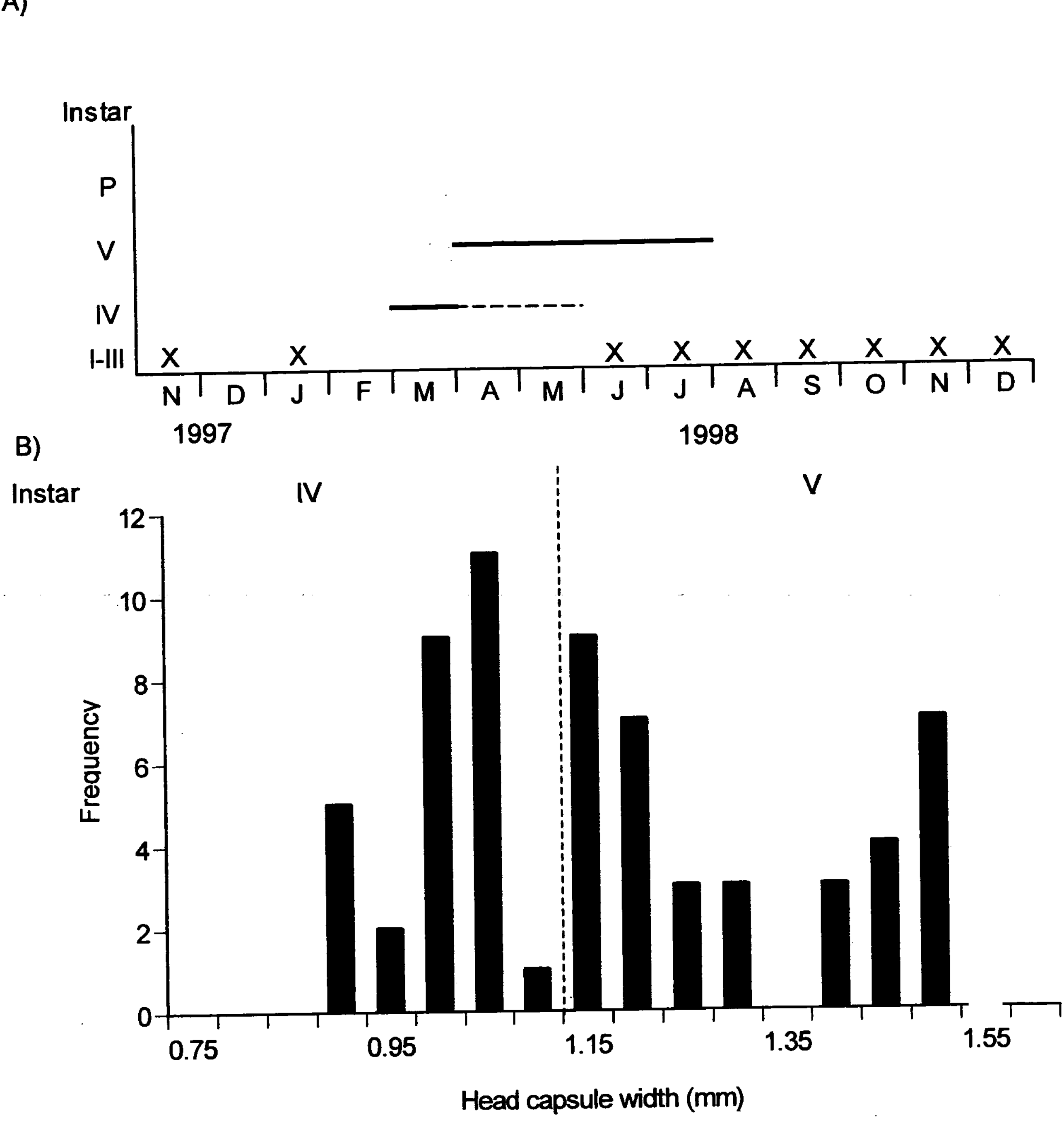


Figure 3.3.13 *Chaetopteryx villosa*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars or pupae and X indicates the presence of I-III instar Limnephilidae. B) Frequency distribution of head capsule width and presumed instar (n=65). Samples were not collected in December 1997.

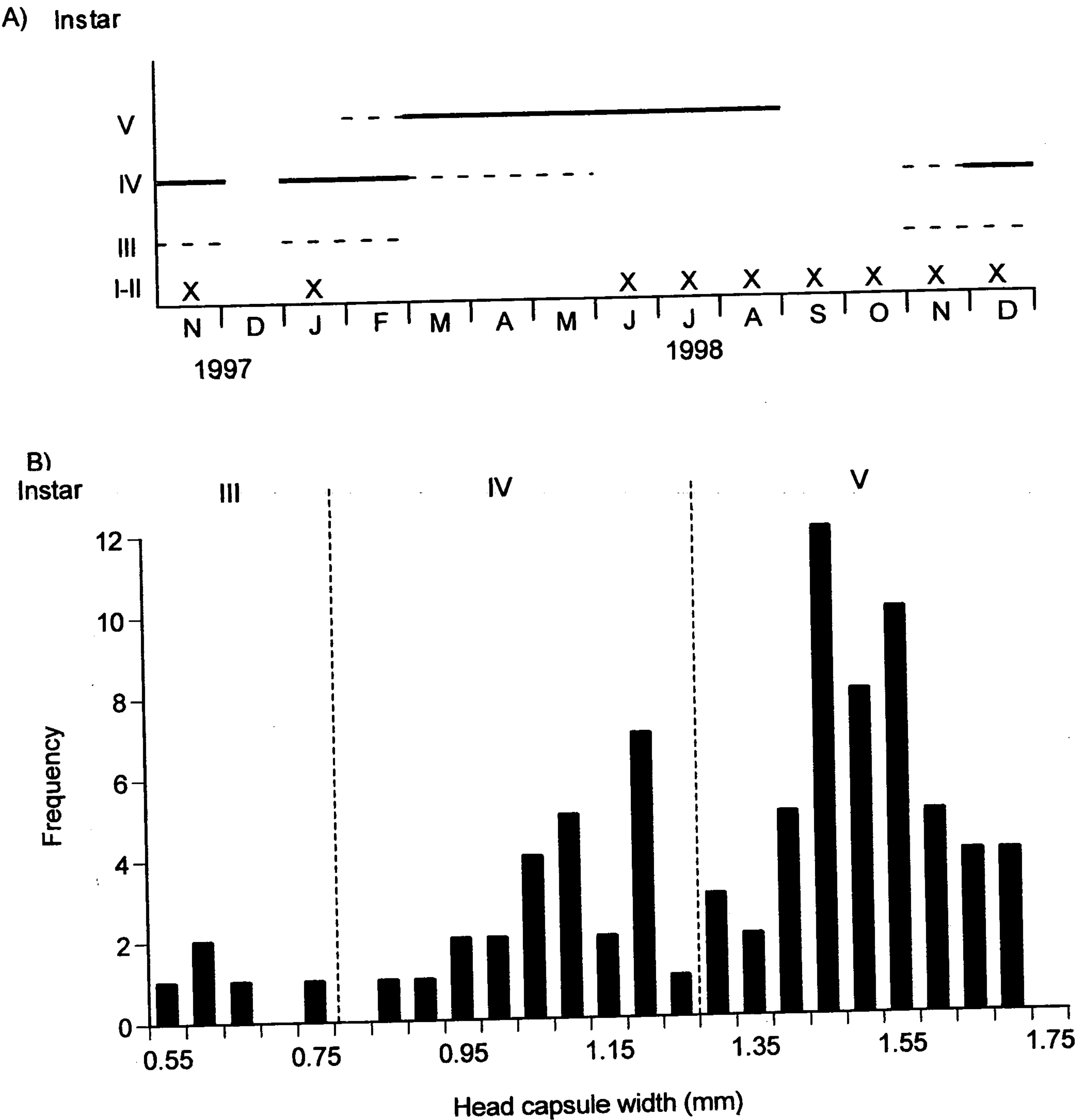


Figure 3.3.14 *Drusus annulatus*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars or pupae and X indicates the presence of I and II instar Limnephilidae. B) Frequency distribution of head capsule width and presumed instar (n=80). Samples were not collected in December 1997.

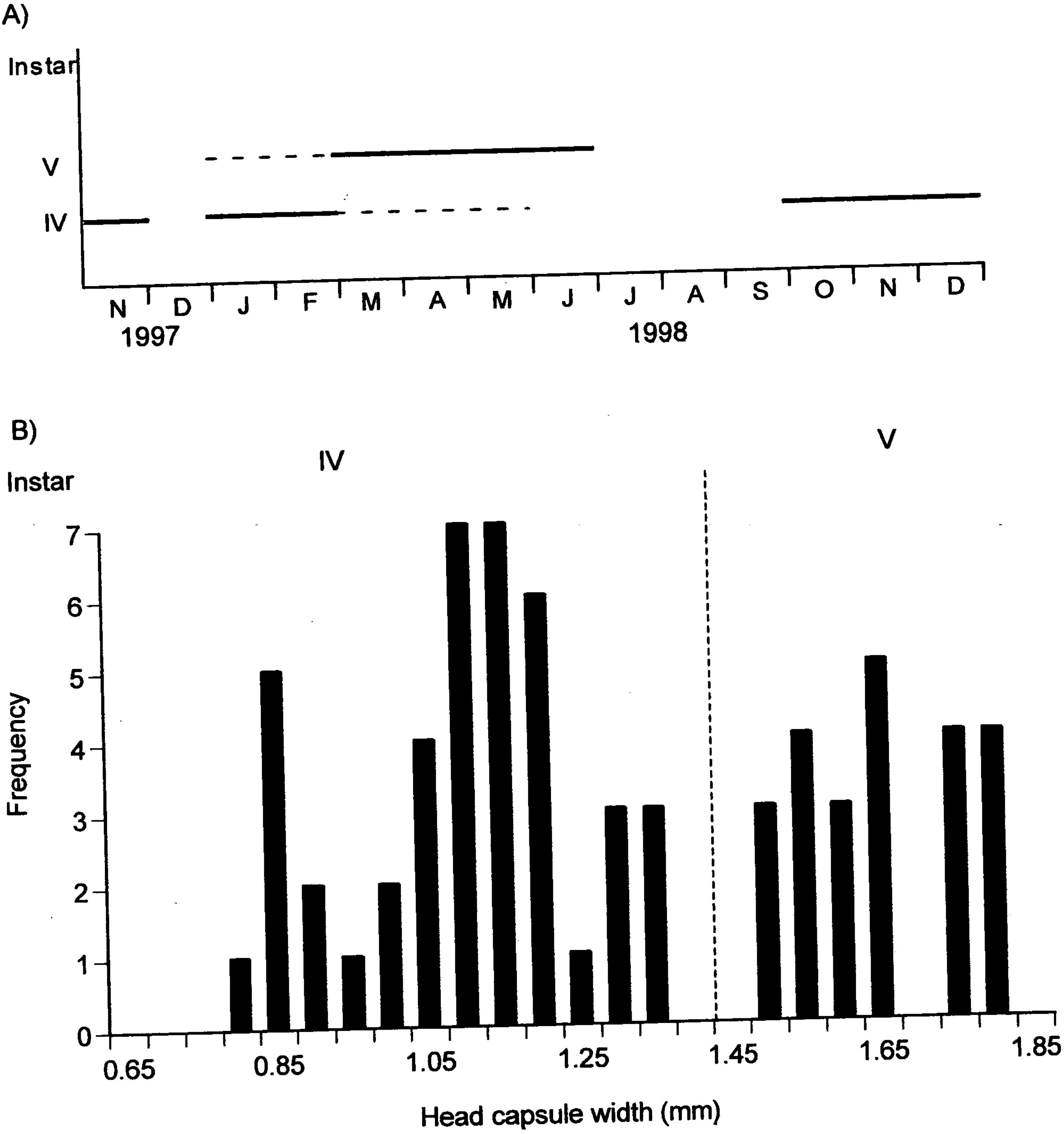


Figure 3.3.15 *Ecclisopteryx guttulata*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars or pupae and X indicates the presence of I-III instar Limnephilidae. B) Frequency distribution of head capsule width and presumed instar (n=65). Samples were not collected in December 1997.

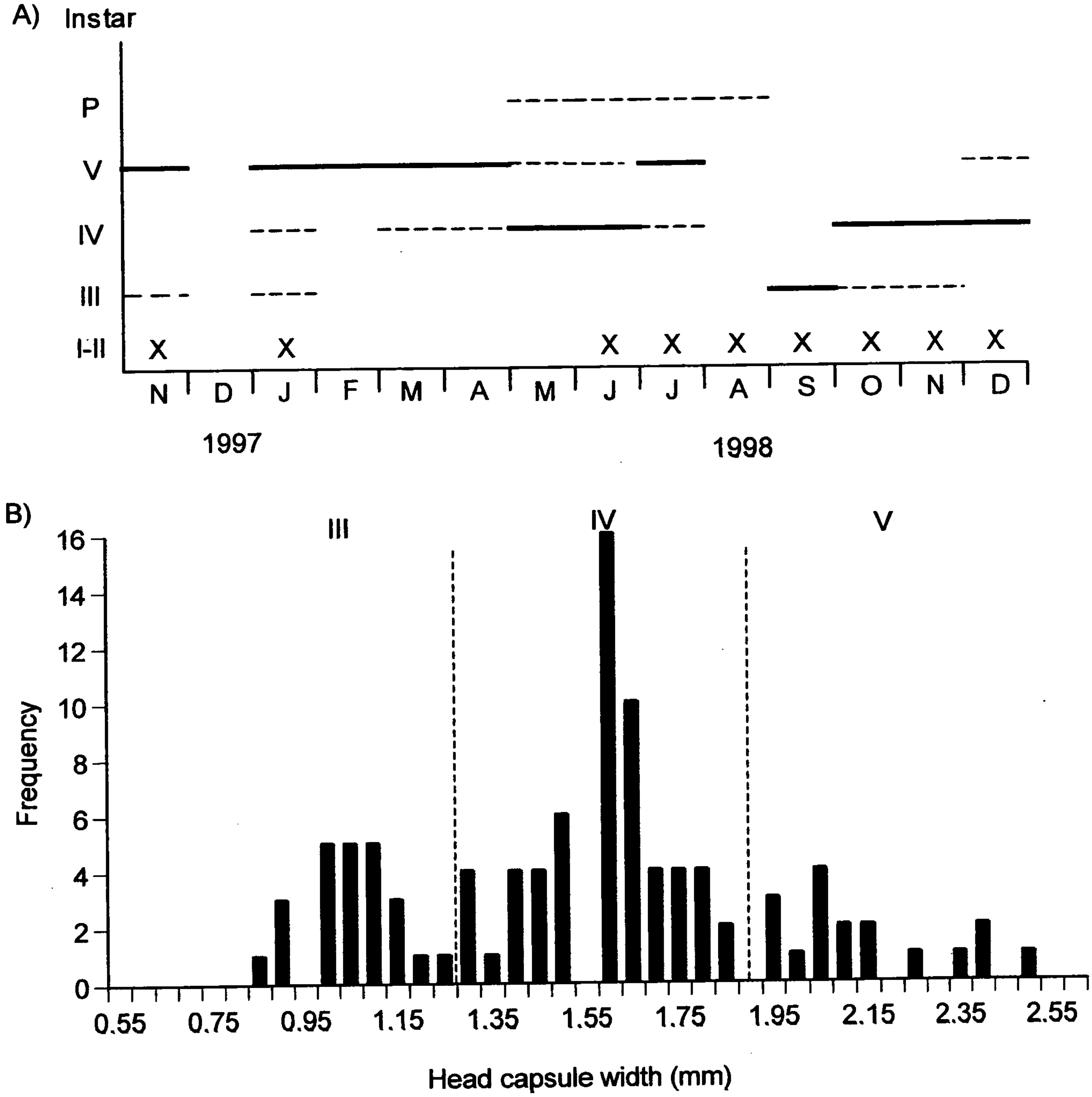


Figure 3.3.16 *Potamophylax latipennis*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars or pupae and X indicates the presence of I and II instar Limnephilidae. B) Frequency distribution of head capsule width and presumed instar (n=101). Samples were not collected in December1997

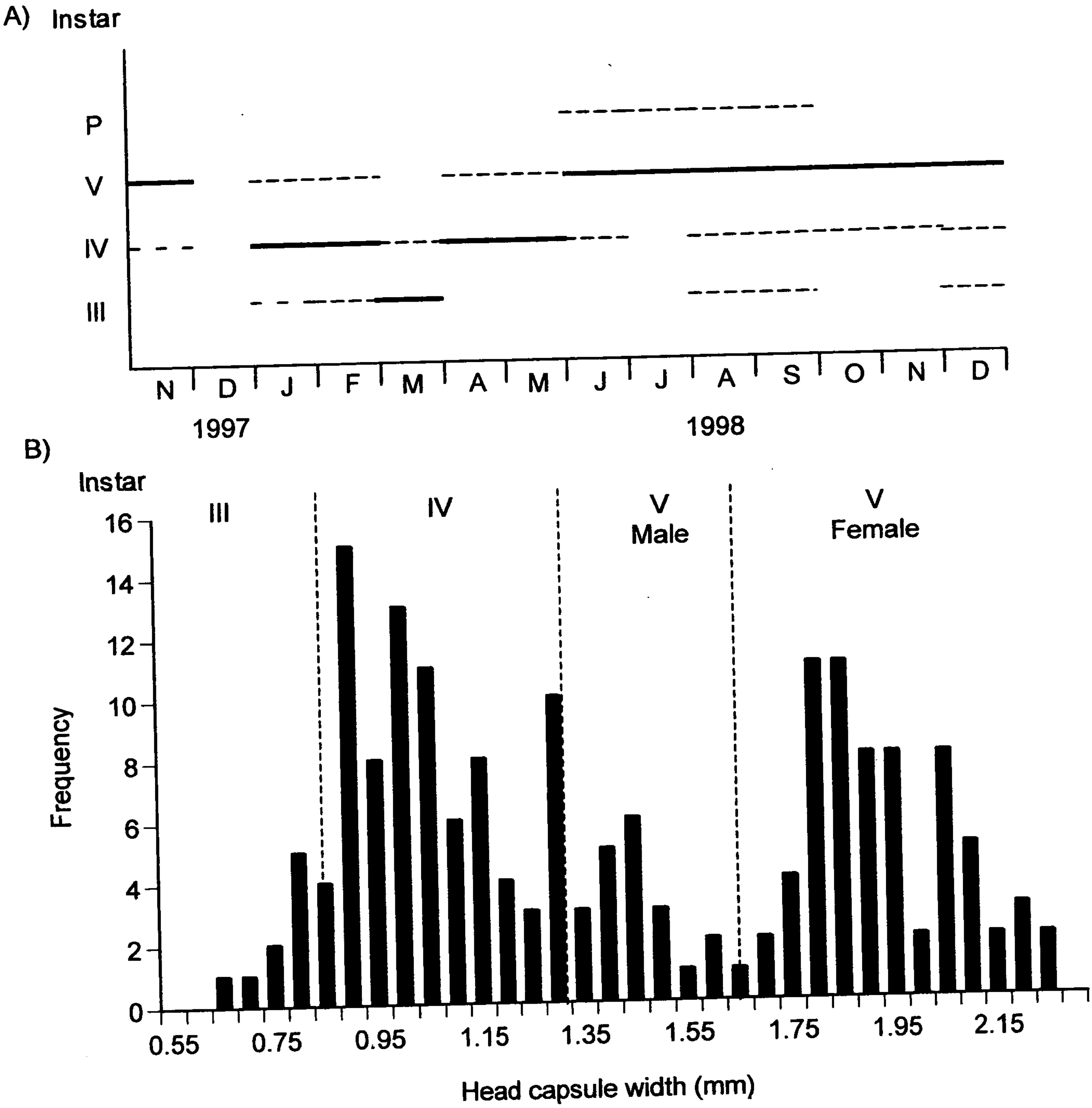


Figure 3.3.17 *Odontocerum albicome*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=178). Samples were not collected in December 1997. Male and females were distinguished according to Wallace *et al.* (1990).

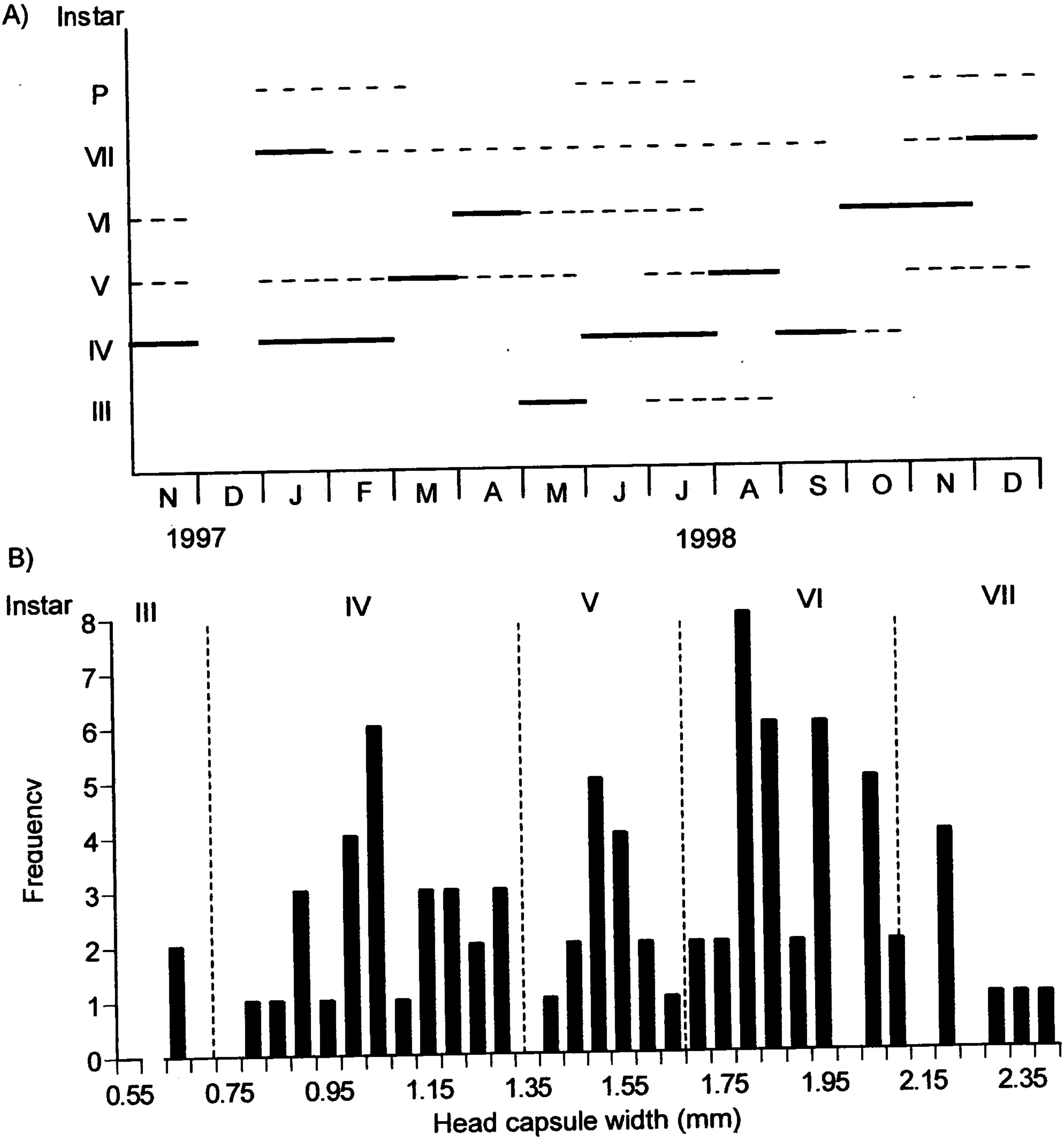


Figure 3.3.18 *Sericostoma personatum*: A) occurrence of different instars over one year. Solid lines indicate the dominant instar in samples; dashed lines indicate the presence of less dominant instars and pupae. B) Frequency distribution of head capsule width and presumed instar (n=87). Samples were not collected in December 1997.

Table 3.3.9 Presence / absence of different instars of caddisfly larvae that accounted for >1% of the total larvae collected in pool and riffle microhabitats. Where P= pool, R= riffle and R & P= present in pool and riffle microhabitats.

Species	Instar						
	I	II	III	IV	V	VI	VII
Rhyacophila dorsalis	R	R	R &P	R &P	R &P	▨	▨
Hydropsyche siltalai	R	R	R &P	R &P	R &P	▨	▨
Tinodes waeneri	▨	▨	P	P	P	▨	▨
Polycentropus flavomaculatus	▨	R &P	R &P	R &P	R &P	▨	▨
Anabolia nervosa	▨	▨	R &P	R &P	R &P	▨	▨
Chaetopteryx villosa	▨	▨	▨	R &P	R &P	▨	▨
Drusus annulatus	▨	▨	R &P	R &P	R &P	▨	▨
Ecclisopteryx guttulata	▨	▨	▨	R &P	R &P	▨	▨
Odontocerum albicorne	▨	▨	R &P	R &P	R &P	▨	▨
Potamophylax latipennis	▨	▨	R &P	R &P	R &P	▨	▨
Sericostoma personatum	▨	▨	R &P	R &P	R &P	R &P	R &P

3.4 Discussion

The density of uncased caddisfly larvae was greater in riffles than in pools, and cased caddisfly larvae occurred at a greater density in pools than riffles, even though the overall density of caddisfly larvae was similar between pools and riffles. As a result of different densities of cased larvae in pools and riffles future calculations of the impacts of being stranded on the cased caddisfly assemblage will need to account for the differences in the densities between pools and riffles. The habitat distribution patterns of caddisfly larvae in the Whiteadder Water were closely associated with several environmental gradients such as, near-bed flow velocity, depth, substrate type and coarse particulate organic matter (CPOM), and this is consistent with the work of others (Scott 1958; Philipson 1953; Hickin 1967; Edington 1968). Near-bed flow velocity and depth gradient can be used to distinguish between pools and riffles at both coarse and fined grained scales, pools were deeper and had lower near bed velocity compared to riffles. The relationships between the main environmental factors (i.e. near-bed flow velocity, substrate size/stability, amount of CPOM) and the distribution of caddisflies, and the life history of common species are discussed in detail in the following sections.

3.4.1 Environmental Variables and the Distribution of Caddisfly Larvae

Near-bed Flow Velocity

Along an increasing flow velocity gradient, the substrate changed from fine substrates at low velocity (e.g., pools) to coarse substratum at high velocity (e.g., riffles) with medium substrates found at an intermediate near-bed flow velocity within the study stretch. Near-bed velocity is an important factor in determining the physical and the biotic components of the stream, such as substrate and CPOM. Flow has long been known to affect the substrate distribution in streams (see Gordon *et al.* 1992; Connell 1978; Stanford and Ward 1983). Caddisfly larvae in the Whiteadder Water appeared to separate along a near-bed flow velocity gradient and the pattern is similar to that found by Scott (1958), Philipson (1953) and Tachet *et al.* (1994). Species found at the higher end of the near-bed flow velocity gradient (i.e. riffles) with a mean near bed velocity of >0.4 m s^{-1} included *Hydropysche siltalai, Rhyacophila dorsalis* and *Philopotamus montanus.* These species are case less caddisfly larvae, and are characteristic of coarse substrate and high flow velocity in other streams (Scott 1958; Hickin 1967; Edington 1968; Edington and Hildrew 1995). Also at the high end of the near-bed flow velocity gradient were some cased caddisfly species (such as *Silo pallipes* and *Odontocerum albicorne*) with cases built of mineral particles. Scott (1958) found *O. albicorne* in slow flowing (0.2 m s^{-1}) areas of the River Dean, which is different from the microhabitat where it is most abundant in the Whiteadder Water. Although it was found in areas of lower near-bed flow velocity, it was associated more strongly with the high end of the velocity gradient (>0.4m s^{-1}). Elliott (1982) suggested that *O. albicorne* occurs predominantly under large stones and in the Whiteadder Water large stones occurred predominantly in riffle microhabitats, therefore, individuals of this species may not actually be exposed to high near-bed high flow velocity (>0.4 m/s). But flow velocity indirectly influences microhabitat patterns by determining the distribution of different sizes of substrate particles. *Silo pallipes* uses lateral ballast stones in its case construction, and this may enable it to withstand forces that would dislodge other species (Otto and Johansson 1995). Webster and Webster (1943) found that *Goera calcarata* (in the same family Goeridae as *S. pallipes*) with cases incorporating ballast stones built in lotic waters were heavier than those in lentic environments. The heavier cases of *Goera calcarata* in the presence of flow is consistent with the suggestion that the case acted as ballast enabling it to withstand greater hydraulic forces. In lentic waters with little or no flow, individuals did not need this extra ballast and so may have constructed lighter cases. Otto and Johansson (1995) found that if the lateral ballast stones of the final instar of *S. pallipes* were removed it had a weak negative but significant effect on current resistance in comparison to when the cases were intact.

Cased caddisfly larvae dominated the low end of the near-bed flow velocity gradient (mean near-bed flow velocity <0.1m s^{-1}) and typically had cases constructed of organic material (e.g. *Limnephilus lunatus, Limnephilus rhombicus, Limnephilus flavicornis, Halesus radiatus, Anabolia nervosa* and *Chaetopteryx villosa*), compared with the mineral cases of those species at the higher end of the near-bed flow velocity gradient. In running waters, mineral cases are less likely to be dislodged by the current, than organic cases and thus species with organic cases occur most often in low velocity microhabitats (Dodds and Hisaw 1925; Hynes 1970). This distribution pattern may also be affected by other interrelated environmental factors, such as, the presence of CPOM as a food source or habitat and substrate particle size used in case construction.

Species that occurred in the middle of the near-bed flow velocity gradient (i.e., at intermediate velocity) included *Ecclisopteryx guttulata, Drusus annulatus* and *Melamophylax mucoreus* in the Whiteadder Water. *Ecclisopteryx guttulata* was also found in moderate near-bed flow velocity conditions by Philipson (1953) and is consistent with its position in the middle of the near-bed flow velocity environmental gradient. At moderate flow velocity, the cased species *Potamophylax latipennis, Drusus annulatus, Sericostoma personatum, Allogammus auricollis* and the caseless *Polycentropus flavomaculatus* and *Plectrocnemia conspersa* also typically occurred. *Polycentropus flavomaculatus* and *Plectrocnemia conspersa* were most abundant in slowly flowing pools of other streams and this pattern of distribution may be due to the inability of their nets to withstand high water flow, e.g., the nets of *P. conspersa* break down at flows in excess of 20 cm s^{-1} (Edington, 1968; Townsend and Hildrew 1979; Edington and Hildrew, 1995).

While water flow characteristics appear to determine the habitat preference of caddisfly larvae, the same species can inhabit a range of flow conditions. For example, Philipson (1953) studied the effect of water flow and oxygen concentration on six species of caddis fly larvae. He found that *Rhyacophila dorsalis, Hydropysche instabilis* and *Wormaldia subnigra* were typical of fast flowing reaches. *Anabolia nervosa* and *Polycentropus flavomaculatus* were typically found in slower flowing parts. While *Potamophylax latipennis* was distributed throughout the river he studied. Scott (1958) also observed changes in the distribution of Trichoptera in microhabitats along a flow velocity gradient in the River Dean, Cheshire. In slow flowing areas he found the cased larvae of *Potamophylax latipennis*, and *Odontocerum albicorne*. This was different from Philipsons' (1953) finding that *P. latipennis* was widely distributed in the river. In moderate flow velocity environments the cased caddis *Ecclisopteryx guttulata* and *Glossosoma conformis* were most commonly found. The Trichoptera of high flow velocity areas of the river were characterised by *Rhyacophila dorsalis* and *Hydropysche fulvipes*.

Coarse Particulate Organic Matter

The observed distribution pattern of caddisfly larvae with respect to CPOM appears to be primarily driven by the use of CPOM as a case material. Within the study stretch of the Whiteadder Water the amount of CPOM d differed between pools and riffles. Riffles had a higher density of CPOM than pools, and this was attributed to the type of CPOM avaiable in the study stretch. The CPOM in the study stretch was mainly comprised of the woody stems of *Calluna vulgaris* (L.) that became caught between the larger substrate particles in the high flow velocity areas. The amount of CPOM in the stretch of stream was low, and this may be attributed to the absence of large deciduous vegetation (i.e., trees) in the riparian zone of the stream and the catchment (see Chapter 2). For example, Stake Clough in the English Peak District has a large mean standing stock of CPOM (17.96 g m^{-2}) compared to the Whiteadder Water (Carris and Dobson 1997). The large amount of CPOM in Stake Clough comes from its course through a mixed woodland, which contributes a large quantity of CPOM. Another example, is that of River Garonne. The shaded edges of the River Garonne near Toulouse, France, receive approximately 3.3 kg of CPOM from riparian trees per metre of bank per year (Chauvet and Jean-Louis 1988).

The distribution pattern of caddisfly larvae, however, appeared to separate along a gradient of increasing CPOM. Species that were characteristic of the low end of the near-bed flow velocity gradient and in association with high CPOM within the Whiteadder Water were dominated by the Limnephilidae family of caddisflies, such as *Limnephilus lunatus, Limnephilus rhombicus, Halesus radiatus, Anabolia nervosa* and *Chaetopteryx villosa*. Coarse particulate organic matter is used in the construction of the larval case in these species, and is also utilised as a food source (Wallace *et al.* 1990). The presence of these species at the low end of the near-bed flow velocity gradient is consistent with the findings of Philipson (1953) Wallace *et al.* (1990) and Hickin (1967).

Species of caddisfly that occurred at the low end of the CPOM gradient (i.e., *Limnephilus flavicornis, Limnephilus auricula, Potamophylax latipennis, Tinodes waeneri, Ecclisopteryx guttulata, Plectrocnemia conspersa* and *Polycentropus* spp) were either caseless or had cases constructed from mineral particles. Coarse particulate organic matter can be utilised by benthic organisms as a food resource (Gee 1982; Richardson 1992; Murphy *et al.* 1998), as shelter (Gee 1982; Dobson and Hildrew 1992; Palmer *et al.* 1996) and in caddisfly larvae as a material for case construction (Hickin 1967; Dudgeon 1990; Wallace *et al.* 1990).

Many caddisfly larvae utilize organic detritus as a food source (Slack 1936; Hickin 1967) and it would be expected that detritivorous caddisfly larvae would be more abundant at the high end of the CPOM gradient. This is supported by the presence of *Limnephilus rhombicus* and *Limnephilus lunatus,* which have been found to feed mainly, but not exclusively on detritus by using gut content analysis (Slack 1936; Hickin 1967). However, *Anabolia nervosa* and *Halesus radiatus* which are more abundant with high CPOM, were found to be omnivorous by Slack (1936) who observed remains of *Baetis* spp. and chironomid larvae in gut contents. *Sericostoma personatum* is predominantely a detritivore, but is found towards the lower end of the CPOM gradient. *Potamophylax latipennis* and *Ecclisopteryx guttulata* which are omnivorous but feed on detritus are found towards the lower end of the CPOM gradient. This may be explained by case type, both species have cases made of mineral particles and therefore are more abundant towards areas with medium sized substrate particles. The observed distribution pattern of caddisfly larvae with respect to CPOM therefore, appears to be primarily driven by the use of CPOM as a case material in species that are not obligate detritivores such as *L. rhombicus* and *L. lunatus,* but need CPOM for case construction. If the distribution patterns of caddisfly larvae were determined primarily by the use CPOM as a food source then species that have mineral cases and utilize CPOM as a food source (e.g., *Potamophylax latipennis*) would be expected to be found towards the high end of the CPOM gradient which but were not.

Substrate Size and Stability

Within the study stretch of the Whiteadder Water the size of substrate particles varied little, though large particles occurred most often in riffles. The stability of the substrate is related to its size (Gordon *et al.* 1998) and, consequently, as size varied little between riffles and pools both classified were as unstable according to a ratio of stable to unstable particles. As the stability of pools and riffles is the same, the substrate stability would appear to have little affect on the distribution of caddisfly. However, substrate movement is a very important component of disturbance in lotic systems and can have dramatic effects on periphyton (Stevenson 1990; Steinmann and McIntire 1990) and invertebrate communities (Resh *et al.* 1988; Death and Winterbourn 1995; Death 1996), these studies generally found that algal biomass species richness and invertebrate density are reduced at sites where substrate stability is reduced. Substrate stability also influences aquatic bryophytes, which are restricted to large stable bed particles (McAuliffe 1984a) and which were found associated with large/stable particles in the study stretch. The species that were closely associated with coarse substrates (associated with high near-bed flow velocity and the presence of moss) were the uncased species *R. dorsalis*, *H. siltalai* and *P. montanus* and the cased species *O. albicorne*. *Philopotamus montanus* and *H. siltalai* both construct nets to filter and trap food from the water column and require a stable (coarse) substrate on which to construct these nets. Their requirement for stable substrate particles, in fast flowing water has been documented by Edington (1968), Egglishaw (1969) and Hildrew and Edington (1979). The species that utilize these larger substrate particles may be less affected by hydraulic disturbances that cause substrate movement than species associated with fine substrates that move more frequently.

The availability of the correct particle size and type in conjunction with near-bed flow velocity and depth also appears to affect the distribution of caddisfly larvae in the Whiteadder Water. The availability of the correct case building materials may therefore limit the success and distribution pattern of caddisfly larvae in streams. The presence of the correct type of building material for larval case construction and its influence on distribution patterns of cased caddisfly larvae is supported by studies from Mackay (1977) and Cummins (1964). The importance of the correct particle size used for aestivation and pupation in the caddisfly *Pycnopsyche scabripennis* has been obbserved by Mackay (1977) . Cummins (1964) observed that the distribution patterns of *Pycnopsyche lepida* and *P. guttifer* could be related to the distribution of case building material. Larvae of *P. lepida* migrated from slow, silt bottomed habitats with a high component of organic debris to gravel/pebble substrates during their life cycle. The change in habitat distribution pattern of *P. lepida* was accompanied by a shift from organic to mineral case construction. *Pycnopsyche guttifer* did not migrate into areas of gravel/pebble substrate and remained in silty pools consequently the case was constructed of organic material and did not change throughout its life cycle.

3.4.2 Life History

Within the Whiteadder Water, the majority of species found within riffles appeared to have non-synchronised or poorly synchronised life cycles several instars present in samples during any one month. These caddisflies were mainly uncased species, for example *Rhyacophilia dorsalis* (I and II instar), *Hydropysche siltalai* (I and II instar) and *Polycentropus flavomaculatus*, though some cased species *Sericostoma personatum and Odontocerum albicorne* also had poorly-synchronised life cycles and were found mainly in riffles. Species that had a synchronised life history were mainly found in pools, such as *Anabolia nervosa, Chaetopteryx villosa, Drusus annulatus, Potamophylax latipennis* and *Ecclisopteryx guttulata*. However, the contast between less and more synchronised life cycles in the main is also between species which five instars could be distinguished and those for which three or two instars were identifiable.

Life histories with non-synchronised or poorly synchronised larval instars have been suggested to reflect adaptation to hydraulic disturbance by spreading the risk of the loss of a particular generation (See Section 3.1.4). A greater increase in the near-bed flow velocity at a set increase in discharge occurs within riffles than within pools, therefore disruptive hydraulic forces in riffles will be greater than in pools. An increase in hydraulic stress caused by increasing near-bed flow velocity could dislodge, transport and potentially kill organisms in this habitat. By having different sized larvae that may be affected differently by the increased hydraulic stresses

associated with increasing near-bed flow velocity the chance of survival may be increased.
Indeed, different instar larvae of the same species may be affected differently by the hydraulic forces of disturbance and have an increased chance of survival (Statzner and Holm 1982; 1989; Statzner 1988). The species present in riffles appear to use a 'hedge-betting' strategy (Stearns 1976), or exhibit life history plasticity involving a range of concurrent instars that are differentially affected by hydraulic disturbance which increases the chance of some individuals reaching adulthood. The basic components for life history plasticity are having either prolonged hatching and emergence and a wide range of larval stages at any one time; this spreads the life cycle stages over time and thus decreases the risk of eradication (Dietrich and Anderson 1995). Scrimgeour and Winterbourn (1989) also suggested that the non-seasonal or poorly synchronised annual life cycles reported for many common New Zealand streams (Towns 1983) may be related to the unpredictable nature of hydrologic disturbance. The unpredictability in the flow patterns of many New Zealand streams may have favoured the selection of flexible poorly synchronised life histories which spread the risk of larval cohort loss due to hydraulic disturbance.

The species that appear to have a more synchronised life cycle were more abundant within pools and were generally cased caddisfly larvae. Within pools an increase in discharge does not increase the near-bed flow velocity to the same magnitude as in riffles. The hydraulic stresses caused by increased near-bed flow velocity on the caddisfly species would therefore be less. These species are therefore may be able to withstand a disturbance (i.e., a flood) by morphological adaptations and behavioural adaptations alone, and it can be speculated have a synchronised life cycle to enable a greater chance of reproductive success (i.e. to breed) in the adult.

The majority of the species of caddisfly that were numerous enough to have detailed life history tables constructed appear to have univoltine life cycles. Life history varied among species and most species were present in both riffles and pools at all instars. The majority of the species of caddisfly examined were present during late spring and the summer as large fifth instar individuals. Earlier instars (smaller individuals) were usually present during the autumn and winter months. The presence of large, final instar larvae and pupae in the spring and summer would lead to the emergence of adult caddisflies during the summer and early autumn in some species. The weather conditions during the summer months are generally calmer and warmer than winter (BADC unpublished data) and would therefore be more suitable for mating by the flying adults and the subsequent laying of eggs.

In conclusion I can now answer the questions defined in Section 3.1, the physical environment of the Whiteadder Water can be divided into pool and riffle habitats that are significantly different from each other by the use of environmental gradients such as, near-bed flow velocity, depth and the amount of CPOM. The difference in the physical attributes of pools and riffles are also reflected in density of caddisfly larvae; cased caddisfly density was greater in pools than riffles and vice versa for uncased caddisflies. The distribution patterns of caddisfly larvae also reflect the change in environmental conditions along these environmental gradients consistent with the work of others (Scott 1958; Philipson 1953; Hickin 1967; Edington 1968). The presence of either synchronised or poorly synchronised life cycles appears to be related to the vulnerability of the species to hydraulic disturbances (e.g. floods). Species such as *P. flavomaculatus*, *R. dorsalis* and *O. albicorne* that are more abundant in riffles which are subject to greater nearbed flow velocity at the same discharge compared to pools have poorly synchronised instars in the study reach.

Having established the factors (environmental gradients) that determine the habitat distribution patterns of caddisfly species and the density of cased and uncased species within the study reach such as near-bed flow velocity, depth, CPOM and life histories, the effects of hydraulic disturbance and being stranded on the bank-side on these species can be related to these distribution patterns. Species that reside at the high end of the near-bed flow velocity gradient (i.e., in riffles) or that are associated with unstable substrates may be dislodged more frequently by floods than species in pools. Subsequently these species be stranded more frequently on the banks of the study stretch after flooding. Therefore I predict that species that are more abundant in riffles will be found stranded in greater numbers than those that are more abundant in pools. The incidences of being stranded by hydraulic disturbance in relation to microhabitat and species-specific effects are discussed in Chapter 4.

4 The Incidence of being Stranded in Cased Trichoptera

4.1 Introduction

All lotic systems show temporal variability and spatial heterogeneity in flow. Increases in discharge occur during and after rainfall events or other releases of water into a system such as spring snow melt. Permanent rivers and streams continue to flow from groundwater springs or lakes during and after periods without any precipitation. During rainfall events, especially in headwater streams, there is a rapid rise to peak discharge and a gradual decrease back to base flow known as the flood hydrograph. Small streams usually show larger short-term variation in discharge compared to lowland rivers where the larger catchment area and volume of water reduce the effects of local heavy rainfall. During high discharge, rivers and streams can overflow the channel and inundate the surrounding flood plain, increasing the area of aquatic habitat available for exploitation by aquatic organisms. Benthic organisms may use this floodplain habitat as a refuge from the increased hydraulic stresses in the main channel caused during floods. Several studies have reported that aquatic invertebrates can use inundated floodplains, and other areas that are usually dry, as refugia during high discharge (Perry and Perry 1986; Badri *et al.* 1987; Matthaei and Townsend 2000). The increase in aquatic habitat area is only temporary and the available habitat decreases with the descending limb of the flood hydrograph. If these temporarily inundated areas act as true flow refugia then at least some animals must be able to return to the main channel and not perish.

4.1.1 Flooding and discharge reduction causing caddisflies to be stranded

Benthic organisms stranded after discharge fluctuations have been described anecdotally, but have been rarely quantified. In the context of this study benthic individuals that have been stranded are defined as being left exposed to air on the margins of a stream that had previously been inundated during flooding, and were unable to follow the receding water back to the main channel of the stream. Most studies that have noted benthic invertebrates being stranded examined the effects of reduced discharge due to river regulation schemes (Kroger 1973; Fisher 1972; Corrarino and Brusven 1983; Perry and Perry 1986; Braaten and Guy 1997). Corrarino and Brusven (1983) showed that dewatering of near shore areas of a test riffle by a reduction in discharge led to benthic macroinvertebrates, including hydropsychid caddisflies (*Hydropsyche* spp. and *Cheumatopysche* spp.), the mayfly *Rithrogena hageni* Eaton and dipterans (Chironomidae and *Simulium* spp.) being stranded. Pearson and Franklin (1968) also noted that *Simulium* was readily stranded when reduced discharge exposed normally inundated substrates. The incidence of being stranded in these organisms in both cases was attributed to their lack of mobility i.e., they were unable to move with the falling water level. Kroger (1973) observed the exposure of large areas of substrate in the Snake River, Wyoming after the Jackson Lake Dam reduced the discharge in the river from 2.8 to 0.3 $m^3 s^{-1}$ in less than five minutes. This sudden and rapid drawdown of water stranded and killed many organisms. From samples taken in exposed areas of the riverbed, it was estimated that over a 3 km stretch immediately below the dam being stranded killed over three billion macroinvertebrates, mainly insects. The rapid and sudden nature of this reduction in discharge also stranded fairly mobile vertebrates such as sculpins (*Cottus* spp.spp.), which subsequently perished. Very mobile fish species, such as dace and trout, that were present in the river were not found stranded.

Few studies have investigated the incidence of being stranded in benthic macroinvertebrates after high discharge events (such as floods) and the effects this has on populations of communities. Matthaei and Townsend (2000) are among the few to record benthic invertebrates being stranded in the aftermath of floods on previously inundated floodplain gravels in the Kye Burn, New Zealand. A similar study conducted by Moon (1935) on the flood movements of the littoral fauna of Lake Windermere, U.K., showed that macroinvertebrates moved into the inundated margins of the lake when the lake water level rose as a result of high discharge in the catchment streams. When the water level receded, only individuals cut off in water-filled depressions were found in the previously inundated regions and no stranded individuals were found on the dry lakeshore. This absence of stranded animals may be attributed to the long time taken for the lake level to recede (days) compared to the flashy nature of rivers and streams in which the bank-sides may be inundated for hours only. The very gradual drop in the water level of Lake Windermere allowed time even for organisms with poor motility to following the receding waters.

The vulnerability of benthic organisms stranded after reduced discharge or after flood peaks, may be dependant on species-specific ecological traits e.g., tolerance to exposure and the ability to move with the receding water (mobility), and on the physical environment e.g., the rate of water recession, the substrate type, slope of the shoreline and the ambient physical conditions (such as temperature and humidity). Another factor that may represent a significant source of mortality in stranded individuals may be predation by terrestrial predators (Hering and Plachter 1997).

4.1.2 Ecological Traits

Tolerance to Desiccation (Tolerance to Exposure)

Insects that occupy aquatic habitats during all or part of their life cycles are considered to have evolved from terrestrial insects and are thus secondarily aquatic (Hinton 1953; Wigglesworth 1972). The evolutionary adaptation required for the insects' success in terrestrial habitats was the development of a high degree of cuticular impermeability (to prevent water loss), which posed respiratory problems but was generally preadaptive for insects to secondarily invade water. In adapting to life in water, some aquatic insects that did not utilise atmospheric air as larvae increased the permeability of their body surface and evolved gills that increased the body surface area to extract dissolved oxygen directly from the water. The increase in permeability of membranes in aquatic insects is derived from the loss of wax and sometimes the cement layer of the epicuticle on the body wall. The use of gills enables the respiratory needs of the insect to be satisfied by cutaneous respiration. Among the aquatic insects that have lost the impermeability of the cuticle are the larvae of the Ephemeroptera and Plecoptera, all the larvae and pupae of the Trichoptera and the larvae of some Hemiptera, Megaloptera, Neuroptera, Coleoptera and many larvae of the Diptera. Although aquatic insects generally have much less fat than their terrestrial counterparts, species that live in environments that are prone to dry out, contain higher levels of fat than those in stable aquatic habitats (Hinton 1953). Hinton (1953) suggested that the breakdown of fats helps to maintain the moisture content of larval tissue during periods of exposure. Most insects can tolerate a fall in the moisture content of their tissues of between 10-15% (Hinton 1953). The increased permeability of the body membranes in some aquatic insects while ideal when immersed in water, when placed in air is liable to dry out rapidly (dependant on environmental factors discussed later) and eventually cause the organism to perish. The larvae of *Chironomus* spp. and *Simulium* spp. die when their moisture content falls by approximately 10%, yet this amount of water is lost 30 times faster in *Chironomus* spp. than in *Simulium* spp. (Hinton 1953). However tolerant to exposure and desiccation; aquatic insects can only tolerate a certain fall in their moisture content once it has fallen below a critical level they perish.

The ability of benthic organisms to tolerate being stranded and the associated desiccation is an important factor in the survival of aquatic organisms, especially for those organisms that are 'less' mobile like the chironomids and cannot move with the receding waters. Fisher and Lavoy (1972) and Brusven *et al.* (1974) attributed the predominance of chironomids within dewatered margins to their tolerance to exposure to air. Brusven *et al.* (1974) found little mortality of stranded chironomid larvae after 24 hours and high survival rates up to 120 hours of exposure under cool springtime conditions. The high tolerance to desiccation has also been documented in intertidal systems for example, californian splash zone limpetsspp.. *Acmaea* spp. exposed to air and therefore drying during the diurnal tidal cycle have physiological adaptations to cope with high electrolyte concentrations that result from desiccation. The desiccation tolerances of *A. scabra, A. digitalis* and *A. persona* amount to about 80% total water loss and are amongst the highest recorded in any animal (Wolcott 1973).

It appears that highly mobile aquatic species that can move with changes in water level appear to be less tolerant to desiccation than species that cannot follow changes in water level. The Ephemeroptera as a group tend to be susceptible to being stranded and are relatively intolerant of exposure (Brusven *et al.* 1974; Ward 1992). They have been found entangled at the margins of exposed mats of filamentous algae and, as a result, perished due to desiccation. However, the mayflies are a very mobile group of organism and *Baetis* spp. actively avoid stranding (Corrarino and Brusven 1983).

The tolerance to exposure of cased caddisflies could be attributed to the protection afforded by the case (Brusven *et al.* 1974). Zamora-Munoz and Svensson (1996) have shown that the case material may affect the tolerance to exposure in cased caddisflies. Laboratory experiments on two species of Trichoptera: *Limnephilus coenosus* and *Limnephilus vittatus,* showed that differential larval survival in air was linked to case material. Larvae with organic cases (*L. coenosus*) survived dry conditions better than larvae with mineral cases (*L. vittatus*). The properties of the organic material may help to retain water and thereby reduce water loss. The size of the organism may also have an affect on the survival in dry conditions. Larvae of *L. coenosus* are thought to survive drought better than *L. vittatus* due to their larger size. As *L. coenosus* is larger at an equal age, the surface / volume ratio in *L. coenosus* is smaller than in *L.vittatus*, and thus the loss of water is less, enabling it potentially to survive longer exposure. Intertidal organisms must also be resistant to desiccation and the presence of a shell is analogous to the case of caddisfly larvae in preventing desiccation, as they both form a barrier to water loss. For example, the barnacle *Chthamalus montagui* has tightly fitting opercular plates and a non-porous shell and is more desiccation resistant than the barnacle *Semibalanus balanoides,* which has looser opercular plates and a more porous shell. This difference in desiccation tolerance enabled *C. montagui* to survive higher up in the littoral zone in areas with prolonged periods exposed to air compared to *S. balanoides* (Connell 1961a; 1961b; 1972). In contrast, the difference in case material and the tolerance to exposure had no effect on the semi-terrestrial caddisfly *Desmona bethula* which has a case comprised of either organic debris or sand grains (Erman 1981). Erman (1981) showed that larvae with both types of case migrated onto terrestrial vegetation to feed at night and that the case type did not affect the time spent feeding.

Mobility

The different mobility of benthic macroinvertebrates may also be important in determining the survival rate of organisms after high water flows. The ability to follow the receding water level after a flood and to regain the water thus avoiding or minimising the period of exposure to air, is likely to vary among species. Corrarino and Brusven (1983) found that *Baetis tricaudatus* Dodds avoided being stranded by drifting in response to receding water and by actively crawling or swimming towards deeper water as the flow was reduced. Experimental reduction of the water level at times of high temperature resulted in approximately 100% mortality of near shore organisms with only *B. tricaudatus* successfully avoiding stranded in such conditions. Organisms with poor mobility, such as the chironomids, lack this ability to move actively with the receding water (Fisher and LaVoy 1972; Brusven *et al.* 1974), and may have a greater tolerance to exposure to counter their lack of mobility. Rader (1997) used several traits to classify the availability of benthic invertebrates to salmonids in mid- to small sized streams of the Rocky Mountains. The mobility of organisms was ranked from sessile, to highly mobile and highly mobile benthic organisms included the Baetidae and Amphipoda. Those with low mobility included many of the Diptera larvae including the Chironomidae. The Trichoptera were generally classified as having low mobility. Highly mobile organisms such as *Baetis* spp. that swim or can crawl rapidly may be able to exploit inundated habitats during floods and then follow the receding waters and thus avoid stranding spp.(Brusven *et al.* 1974). In these highly mobile species, tolerance to exposure may be low as their high mobility may counter the possibility of being stranded (Brusven *et al.* 1974). Less mobile benthic organisms may not be able to follow the receding waters and become stranded, but may compensate by having greater tolerance to exposure, such as the Chironomidae. Benthic organisms with intermediate mobility, such as the Trichoptera may be able to withstand a brief amount of exposure, but are unable to withstand prolonged exposure in air. Fisher and LaVoy (1972) examined the benthic community along a gravel sandbar below a hydroelectric dam. The bar was submerged during high flow but exposed at low flows, samples were collected from four zones along a transect from the high water mark that was predominantly exposed (Zone 1) to the below the watermark which was always inundated (Zone 4) (Table 4.1.1). Table 4.1.1 shows that the Diptera (Chironomidae and Tipulidae) with low mobility (according to Rader's scheme (1997)) and higher levels of tolerance to exposure were virtually the only organisms collected from Zone 1 and 2. The macroinvertebrates of Zone 4 were similar to those of Zone 3, suggesting that the benthic organisms could tolerate some exposure and were generally more mobile than the Diptera present in Zones 1 and 2.

Table 4.1.1 Mean numbers of benthic insects m^2 along a transect running from the high water mark to below the low water mark below a hydroelectric dam and the mobility of the benthic organisms. (Modified from Fisher and LaVoy 1972).

	Zone[1]				Mobility[2]
	1	2	3	4	
Ephemeroptera					
Stenonema spp.	0	0	0	12	6
Ephemerella spp.	0	0	20	24	3
Tricorythodes spp.	7	0	76	156	6
Caenis spp.	0	0	12	4	
Ephoron spp.	0	0	0	4	5
Trichoptera					
Limnephilus spp.	0	4	4	20	3
Molanna spp.	0	0	0	4	
Lepidostoma spp.	0	0	0	4	3
Cheumatopsyche spp.	0	0	12	48	1
Tascobia spp.	0	0	4	0	2
Orthotrichia spp.	0	0	4	4	1
Diptera					
Tipulidae	0	32	0	0	2
Chironomidae	27	556	764	792	1

[1] Exposure times during summer: Zone 1 70%; zone 2 41%; zone 3 13%; zone 4 0%.

[2] Mobility rank (Rader 1997) where 9=highly mobile and 0=sessile.

The mobility of aquatic benthic organisms once stranded is likely to differ from their mobility when immersed in water, as they would lack the support of the water leading to a reduction in mobility. An extreme example, of this can be seen in fish; fish are highly adapted to life in water and are highly mobile, however if placed in air (ignoring the respiratory problems) then they lack the appendages and the support of the water and becomes less mobile. The density of air is approximately 800 times less than the density of water at the same temperature and pressure (Table 4.1.2). The higher density of freshwater offers more support than air, and the lack of this support could reduce the mobility of stranded organisms that are adapted to movement in water. For instance, the cases of larval Trichoptera are constructed of various materials such as mineral particles or organic debris. These cases when immersed in water would be supported by the water, yet when stranded they would lack this support and the mobility of individuals may be restricted by the extra weight. The material used in the construction of a case therefore could also affect the mobility of cased caddisfly larvae. For example, caddisfly larvae with a heavy mineral case may be less mobile than those with a lighter organic case when stranded, due to the weight of the case without the support of water.

Table 4.1.2 Density of air and freshwater with varying temperature (°C) at atmospheric pressure (modified from Vogel 1994).

	Temperature	Density (kg m^{-3})
Air	0	1.293
	20	1.205
	40	1.128
Freshwater	0	1.000×10^3
	20	0.998×10^3
	40	0.992×10^3

Case Type and being Stranded

The case type itself may affect the incidence of whether or not an animal becomes stranded. For example, heavy cases would not become dislodged as easily with increasing discharge. The use of a case as ballast, preventing the individual being displaced into the drift has been proposed for some species. *Goera calcarata* in lotic waters has a case that is significantly heavier than those species found in lentic water (Otto and Svensson 1980). Otto and Johansson (1995) found that larval *Silo pallipes* when exposed to varying current regimes, resisted entrance into the drift to a greater degree than larvae that had lateral ballast stones (integral to the case construction) removed. The role of a heavy case to be used as ballast however has been questioned by Otto and Svensson (1980). They argue that some species, such as the larvae of the limnephilid caddisfly *Potamophylax cingulatus* build cases of leaf discs during the winter when flow is high and mineral based cases during the summer when the flow is lower, which is contrary to the ballast hypothesis.. A draw back to having a heavy case, is that once an animal has been dislodged from the substrate and deposited on an inundated bank-side, restrictions on mobility (see above) may prevent the individual returning to the water when the water recedes. Lightweight vegetative cases may be dislodged from the substrate by smaller hydraulic stresses, but may not restrict mobility in air as much as a heavy mineral case. So, there is a balance between the advantage of a heavy case to resist dislodgement and become stranded, and the disadvantage of restricted mobility once stranded and the consequent risk of death.

Being stranded by active and passive forces

Species-specific traits such as morphological adaptations (such as hooks and suckers) and the mobility of benthic organisms may also influence how an individual becomes stranded on the margins of streams during a flood. During high flow events, if an individual becomes dislodged and enters the water column there is a possibility that it will be carried onto the inundated margins. As flow velocity tends to increase towards the centre of a stream and decrease towards the perimeter because of frictional resistance at the banks and bed (Morisawa 1985; Gordon *et al.* 1992), individuals may drop out the water column in these marginal areas. Organisms that are easily dislodged by high flows or move by drifting or swimming during floods may be transported (passively) to the inundated bank-sides unintentionally, and use these areas as flow refugia. However, if they are then are unable to follow the receding water level and become stranded they can be termed as 'passively' stranded. Benthic macroinvertebrates may also actively seek out areas of flow refugia to ameliorate the impact of a flood event (Palmer *et al.* 1995; Lancaster and Hildrew 1993b; Robertson *et al.* 1995; Lancaster 1999, 2000). If the individual has actively moved into the lateral/marginal flow refugia during the flood, but cannot follow the receding water level and thus becomes stranded then this can be termed as becoming 'actively' stranded. (See Chapter 5 for a more detailed discussion.)

4.1.3 The Physical Environment and being Stranded

The physical environment is an important factor that affects how benthic organisms become stranded and survive or perish when the water recedes after a flood. The topography (such as the slope and substrate) of the inundated margin may influence whether an individual is stranded in the marginal areas of a watercourse. Factors such as humidity, temperature, light and the topography of the area in which the organism has become stranded all affect the ability of the stranded individuals to tolerate exposure to air and/or regain the water.

The heterogeneous nature of the inundated margins of a stream whilst the stream is in flood may affect whether individuals become stranded. Inundated margins may contain dead zones and areas of very low flow velocities behind rocks or dense clumps of vegetation where organisms may be deposited from the drift, when the water velocity drops below that needed to keep them in the water column. The presence of the riparian vegetation may also act as a physical filter and strain out organisms from the water column as they pass. The topography of the bank-side when inundated also could affect the ability of individuals to enter the inundated margins. For example, a shear (vertical) or very steep slope may act as a physical barrier preventing benthic organisms scaling the slope and entering the inundated habitat, if individuals actively seek out lateral flow refugia.

The ambient conditions after the water level has receded may be important to how long the organism can withstand exposure to air. Factors such as humidity, temperature and light intensity may affect the tolerance of stranded benthic individuals to exposure in air. The fourth and fifth instar larvae of the caddisfly *Desmona bethula* Denning, migrate from the water at night to feed on the aerial portions of emergent aquatic and semi-aquatic vegetation (Erman 1981). Erman showed that the ambient conditions affected the length of time individuals could tolerate exposure whilst feeding. The migration of *D. bethula* was related to the time of sunset. Within five minutes of the suns direct rays leaving a stream section, individuals began moving onto aerial parts of the emergent vegetation. The ambient temperature was a factor in determining the length of terrestrial feeding. During nights when the air temperature dropped below 2°C larvae began to return to the stream; on warmer nights (when the temperature did not fall below 2°C) feeding continued until sunrise. The light intensity was found to be an important environmental cue for the end of migration. Larvae were observed to move back to the stream just before the sunlight reached them, larvae that were exposed to direct sunlight dropped from the plants back into the stream. The ambient environmental conditions appeared to influence whether migration and subsequent exposure occurred. Conditions that affected the rate of desiccation such as freezing, wind or direct sunlight all influence the time and duration of terrestrial feeding. Erman (1981) also comments that during a five minute marking session one afternoon in which temperatures were high (≈ 22°C), 10 out of 28 larvae perished due to the heat and wind rapidly drying the cases of the larvae. The importance of ambient environmental conditions minimising desiccation is highlighted by the fact that *D. bethula* were seen feeding on land at midday on two rainy days, but on a warm night with a strong wind no larvae were observed feeding on land.

Ambient environmental conditions, especially those that increased the rate of desiccation, affected the ability of stranded individuals to survive (Corrarino and Brusven 1983). In spring, relatively cool air and water temperatures permitted the survival of some stranded individuals. In the autumn, air and water temperatures were higher and caused rapid drying of exposed mineral and organic substrates resulting in greater mortality of stranded individuals. A similar phenomenon affected the marine limpets *A. scabra* and *A. digitalis* when ambient environmental conditions increased the amount of desiccation stress on the limpets (Wolcott 1973). Unusually calm seas and high temperatures left rocks, usually wetted by spray, dry for over a week. This caused the body fluids of *A. scabra* and *A. digitalis* to concentrate to lethal levels and resulted in the death of hundreds of individuals (Wolcott 1973). Tsuchiya (1983) observed mass mortality of the mussel *Mytilus edulis* exposed during low water during exceptionally warm weather during August 1981. The cause of the mortality was attributed to the high temperature increasing the rate of desiccation, resulting in the death of the organisms before immersion by the next high water. These examples highlight the adverse effects that extreme ambient environmental conditions can have on species (e.g. intertidal bivalves and gastropods) that are tolerant to some exposure to air. The detrimental effects of extreme ambient conditions would be expected to increase in species that are normally aquatic (e.g. caddisfly larvae) and may become stranded, but are not adapted to tolerate exposure to air.

4.1.4 Predation of Stranded Benthic Organisms

Terrestrial predators may also prey upon individuals that become stranded on the usually terrestrial habitat once the water has receded. There are many potential terrestrial predators such as ants, spiders, beetles, birds and insectivorous mammals that could utilise stranded benthic invertebrates. The predation of stranded benthic individuals has not been studied extensively to my knowledge, but anecdotal evidence suggests that it is a source of mortality. Erman (1981) noticed ants that were scouring a drying streambed section carried off stranded individuals of *Desmona bethula*. This has also been observed in the Whiteadder Water where, after a large flood stranded benthic invertebrates including caddisfly larvae and mayfly nymphs were carried off by ants and carabid beetles (Hall and Lancaster *pers obs*.). Hering and Plachter (1997) have shown that riparian ground beetles (Coleoptera, Carabidae) can prey on aquatic invertebrates in alpine floodplains of streams in Bavaria, Germany. They found that in a 5th-order stream (the Isar) aquatic invertebrates composed 89% of the potential prey for riparian predatory ground beetles on the floodplain. Gut content analysis of the riparian ground beetles on the Isar floodplain showed that these beetles mainly fed on aquatic organisms washed ashore or emerging from the water. Though to my knowledge the affect of terrestrial predators (e.g. birds) on stranded individuals has not been studied, from the anecdotal evidence predation must be considered as an important source of mortality on stranded benthic individuals.

Clearly, there are many different factors that influence the probability of an animal to become stranded after a flood and regain the water. Likewise, there are many different ecological traits, which will influence the relative influence of these factors. Unfortunately, it is impossible to examine all factors and all traits simultaneously. This study focuses on cased caddisflies and addresses three questions about their vulnerability to being stranded after floods in the Whiteadder: (1) Does increased discharge increase the incidence of being stranded on the stream bank? (2) Does bank-side micro-topography (substrate and slope) influence the incidence of being stranded? (3) Do Trichoptera with cases made of different material (case type) become stranded differently?

The discussion above of the various factors that may influence the incidence of being stranded and subsequent survival of individuals allows me to make specific prediction to these three questions. (1) I predict a positive relationship between discharge and the number of stranded Trichoptera. Higher discharges will inundate a greater lateral area therefore increasing the potential for animals to actively colonise these areas or to be deposited in them after becoming dislodged from the substrate. This may seem rather obvious (it is), but this has not been documented before and the data will be important to the final calculations of population-level impacts (Chapter 7). (2) I predict a positive relationship between the incidence of being stranded and increasing substrate complexity of the bank-side. Complex substrates may entangle, trap or impede the movement of organisms with the receding water level resulting in organisms being stranded. Substrate complexity may also impede the movement of benthic organisms once the water level has receded. Increased slope (angle) of the banks I predict will be negatively associated with the incidence of being stranded. This may be because bigger floods are required to inundate the same area of lateral habitat. Further, shear (vertical) or very steep slope may act as a physical barrier preventing benthic organisms scaling the slope and entering the inundated habitat. (3) I predict that Trichoptera with cases made from coarse mineral particles will be more readily stranded than those with cases constructed of organic (vegetative) particles. A coarse mineral case could weigh more than an organic (vegetative) case. The presence of a heavy coarse mineral case may restrict the mobility of the individuals when stranded in air without the support of water compared to a lighter vegetative case. This may lead to coarse mineral case types becoming stranded more frequently than vegetative case types.

In order to address these questions, permanent quadrats were placed on the banks perpendicular to the Whiteadder Water and surveyed repeatedly for stranded animals. The quadrats were placed next to pool and riffle in-stream habitats on varying topography (such as slope and substrate type). Once cleared of any stranded caddisfly cases, the quadrats were checked monthly and opportunistically over a range of discharges. The fresh cases of stranded caddisfly larvae were collected (if present) from the quadrats and the species (if present and identifiable), the case type (vegetative, coarse mineral, fine mineral or mixed) and distance from the water were recorded.

4.2 Materials and Methods

4.2.1 Rainfall and Discharge

There was no continuous discharge gauge on the stream so discharge over the study period was estimated using a model of the relationship between discharge and rainfall. In flashy upland streams, discharge is closely related to daily precipitation, so knowing the amount rainfall and the discharge at particular times makes it possible to estimate the discharge over a longer time period from the daily rainfall records. During this study and prior studies (Lancaster 2000) there was a sum of 37-point measurements of discharge within the study stretch and over a range of discharges. Discharge was measured on each visit using the flow velocity area method (Gordon *et al.* 1992) as described in Chapter 3.

Daily rainfall data, supplied by the British Atmospheric Data Centre (BADC) surface station database, were obtained from the Nunraw Abbey weather station (National Grid Reference: NT 594 700), located 5 km from the study site. This site was chosen as it had the best dataset (in terms of completeness) for the study period, it was close to the study site and at a similar altitude. From these data a simple model predicting discharge from rainfall was estimated:

$$Q = 0.0511 + (3 \text{ x } 10^{-7} \text{ x } R_1^2) + (6 \text{ x} 10^{-8} \text{ x AvR}_{2\text{-}3}{}^2)$$

Where Q= discharge (m^3 s^{-1}), R_1= rainfall (mm) one calendar day (9 am-9 am) before Q measurement and AvR $_{2\text{-}3}$= mean rainfall on two and three calendar days before Q measurement. The model was statistically significant with, d.f. = 34,37 F = 23.8, p = ≤ 0.001, and r^2 (adjusted) = 0.58. The r^2 value of 0.58 is low for this type of application. A better model would have been available by using data from a continous discharge recorder. However, this equipment was not available and so only point discharge readings could be taken, resulting in the low r^2 value obtained. Figure 4.2.1 shows the estimated discharge in the Whiteadder and the actual rainfall for Nunraw Abbey. Table 4.2.1 shows the frequency of visits and the range of discharge in the Whiteadder over the sampling period.

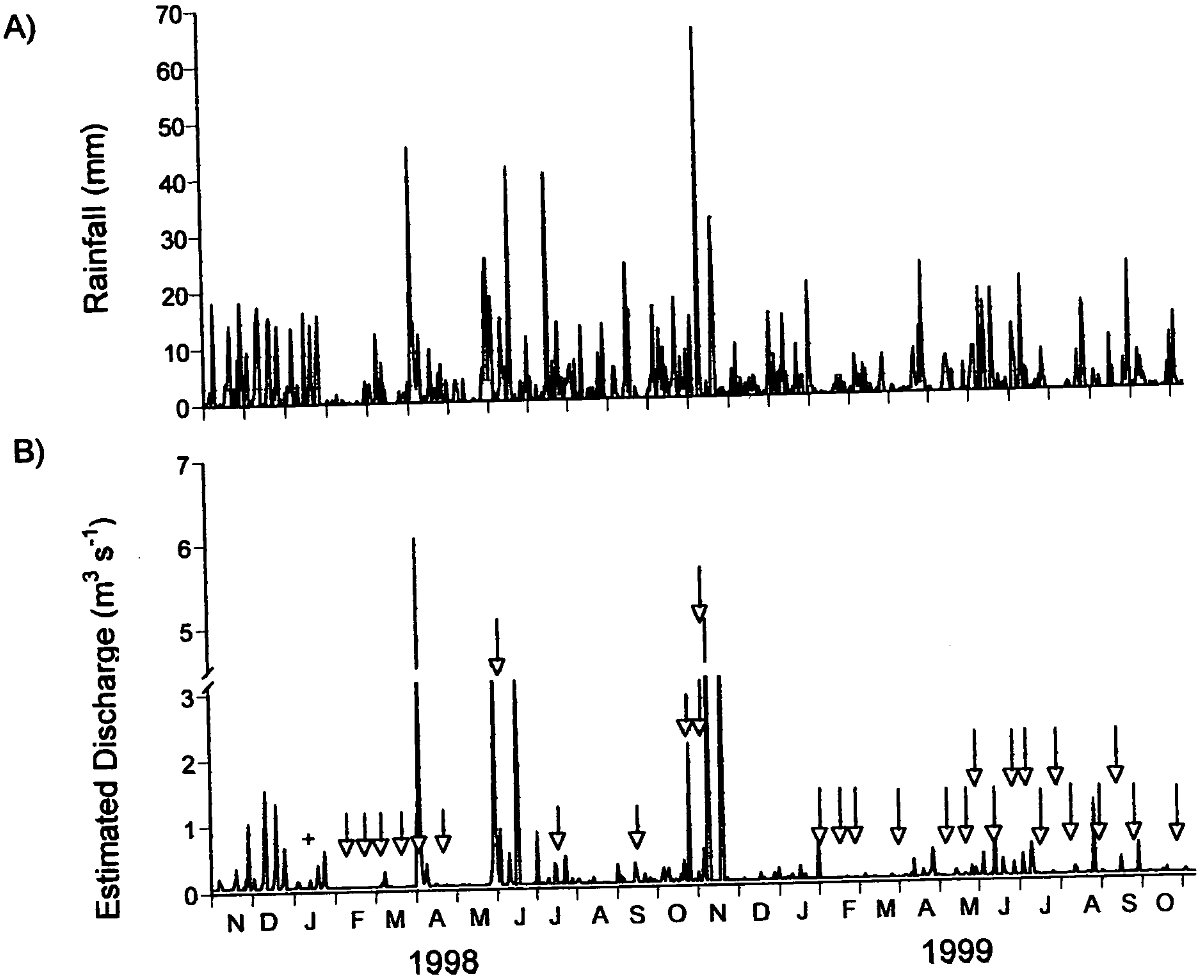


Figure 4.2.1 A) Rainfall from Nunraw Abbey weather station and B) estimated (modelled) discharge in the Whiteadder Water for November 1997 to October 1999. Arrows indicate when bank-side quadrats were sampled and + indicates when the quadrats where initially cleared prior to the survey. Rainfall data provided by the BADC.

Table 4.2.1 Summary of the frequency of sampling visits with respect to discharge in the Whiteadder Water.

Discharge (m^3/s)	Visits
<0.04	6
0.041-0.080	14
0.081-0.12	2
0.121-0.160	3
>0.160	5

4.2.2 Bank-side Survey

To investigate the incidence of cased Trichoptera being stranded along a 250 m stretch of the Whiteadder Water, 20 permanent quadrats with an area of $1m^2$ were placed on the bank-sides adjacent to the stream. Quadrats were marked by four steel rods with string attached between each of the upstream and downstream pairs of rods. The quadrats were perpendicular to the channel and, in total, covered an area of approximately 20 m^2. Quadrats were located adjacent to riffles or pools, and with substrates dominated by turf or gravel to provide five 'replicates' of each combination. Within each category, quadrats were selected to encompass a range of slopes (steep, moderate and gentle) although not all combinations were possible. The profile of the slope within each quadrat was measured by calculating the elevation at five intervals (20 cm apart) from the water line in the centre of the quadrat (Figure 4.2.2). From this, the angle between points was calculated and then the mean slope was calculated. The mean slope of the quadrat was then classified as steep, moderate or gentle. Steep slopes had a mean angle of >26°, moderate 14-25° and gentle 0-13°. Table 4.2.2 outlines the characteristics of each of the bank-side quadrats.

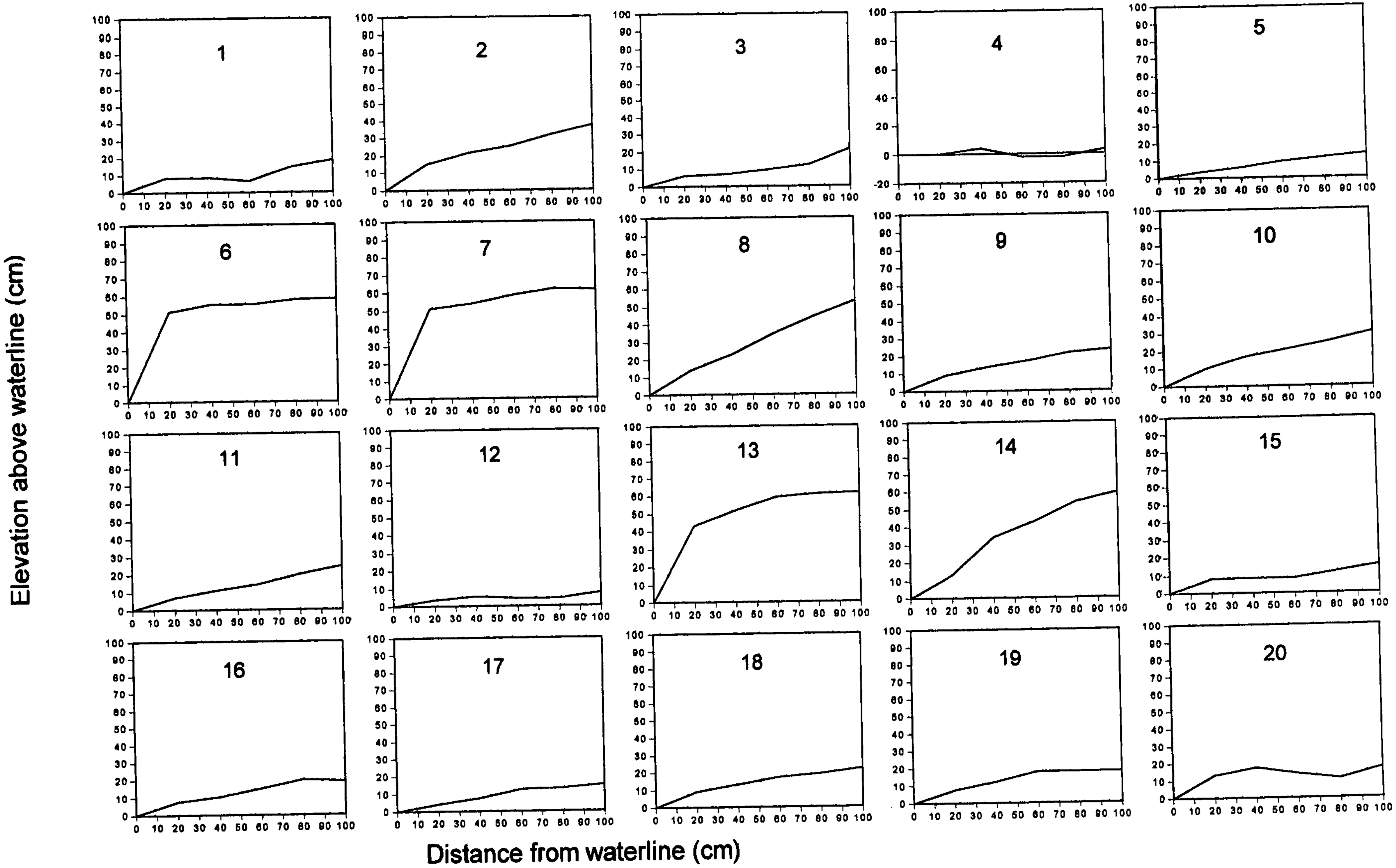


Figure 4.2.2 Profiles of bank-side quadrats, numbers indicate the quadrat number with quadrat 1 downstream and 20 upstream.

Table 4.2.2 Summary of the physical characteristics of bank-side quadrats.

Quadrat	Adjacent microhabitat	Substrate	Slope
1	Pool	Turf	Steep
2	Riffle	Gravel	Steep
3	Riffle	Gravel	Moderate
4	Pool	Turf	Gentle
5	Riffle	Turf	Gentle
6	Pool	Turf	Moderate
7	Pool	Turf	Moderate
8	Riffle	Turf	Steep
9	Riffle	Turf	Moderate
10	Riffle	Gravel	Moderate
11	Pool	Gravel	Moderate
12	Riffle	Turf	Gentle
13	Pool	Turf	Steep
14	Riffle	Turf	Steep
15	Pool	Turf	Gentle
16	Pool	Gravel	Moderate
17	Pool	Gravel	Gentle
18	Pool	Gravel	Steep
19	Riffle	Turf	Moderate
20	Riffle	Turf	Moderate

Cases of Trichoptera with and without larvae (dead or live individuals) were collected from each quadrat. Some Trichoptera leave their cases under stressful conditions (Otto 1983; Zamora-Munoz 1996; Dobson 1998) and, once stranded, larvae may be removed from the case by terrestrial predators, such as carabid beetles and ants (Hall and Lancaster *pers obs.*). Thus, 'empty' cases on the bank-side may represent individuals that were actually stranded by the flood. As I was unable to visit the site at peak discharge or to follow the receding water back to the main channel, individuals may have abandoned their cases or been preyed upon in the time lag between the recession of the waters and sample collection. Old empty cases are common in many streams and, once dislodged from within the substrate, they could get deposited or buried within the bank-side quadrats. Old cases are easily identified (usually broken, blackened or overgrown by algae) and were eliminated from samples to avoid an over estimation of the incidence of being stranded. Empty cases included in the sample were all whole and intact, visible on the surface of the substrate without disturbing the substrate of the quadrat (minimising the chance of unearthing long buried cases), and did not have any of the characteristics of 'old' cases.

Stranded Trichoptera within each of the quadrats were collected monthly (with the exceptions of when the river was in spate and dangerous to survey)and opportunistically between February 1998 and September 1999. In January 1998, prior to the start of the survey, all the quadrats were hand cleared of caddis cases. Quadrats were sampled on 29 occasions (Figure 4.2.1B). Assigning empty cases to species was impossible without the larvae, so the cases were categorised by the materials used in construction (fine mineral, coarse mineral, vegetative and mixed). For each individual, I recorded distance from the water line, case type, species (if possible), and whether the case was empty or contained a living or dead individual.

4.2.3 Data Analysis

The relationship between maximum discharge between sampling visits and the total number of stranded cases present in all bank-side quadrats was analysed by using Linear Regression (Fowler *et al.* 1998). Comparisons between the mean number of cases found per quadrat of a specific type, such as the adjacent instream microhabitat (pool or riffle), predominant substrate type (gravel or turf) and the slope (steep, moderate and gentle), were analysed using two-way ANOVA with slope as covariate in the Datadesk computer package. The data met the assumptions for homogeneity of variance at p=0.05. Homogeneity-of-variance was tested for using the Levene statistic to test for the equality of group variances using SPSS version 9.0. Analysis of the mean number of each case type (coarse mineral, fine mineral, mixed, and vegetative) in each of the quadrat types (adjacent microhabitat, substrate and slope) was carried out using two-way ANOVA on each quadrat type. Pair wise *post-hoc* comparisons between case types between treatments (such as gravel or turf for substrate) were analysed using the Scheffé test for multiple comparisons.

4.3 Results

4.3.1 Animals

At least 15 species of aquatic insect nymphs and larvae, one amphipod and one fish species were found stranded in the bank-side quadrats over the study period (Table 4.3.1). Though several taxa were found, only the cased Trichoptera are considered any further in this study. Nine species of cased caddisflies were found stranded in a condition to allow accurate identification. Figure 4.3.1 shows the percentage of caddisfly cases that were empty or occupied with living or dead larvae. The majority of the cases found that fitted the criteria outlined in Section 4.2.2 were empty cases (90%). Cases that were occupied (10%) had approximately equal proportions of live and dead individuals; individuals were considered to be live if they showed any sign of movement when handled.

4.3.2 Discharge and being stranded

Figure 4.3.2 shows the relationship between the maximum discharge between sampling visits and the total number of stranded cases found in all 20 bank-side quadrats for the period February 1998 to October 1999. With increasing discharge the number of stranded Trichoptera also increased. The incidence of becoming stranded appears to occur after a threshold discharge of approximately 0.12 m^3 s^{-1} (i.e. over bank full discharge). Below this level no cases were found stranded in the bank-side quadrats. The incidence of cased Trichoptera becoming stranded did not occur uniformly throughout the sample period as can be seen in Figure 4.3.2, the discharge hydrograph is not uniform throughout the year and therefore inundation of the margins does not occur regularly.

Table 4.3.1 Species found stranded within bank-side quadrats.

Order or Family	Species
Trichoptera	
	Anabolia nervosa (Curtis)
	Chaetopteryx villosa (Fabricius)
	Halesus radiatus (Curtis)
	Limnephilidae (Instar I-III)
	Limnephilus centralis (Curtis)[1]
	Odontocerum albicorne (Scopoli)
	Potamophylax latipennis (Curtis)
	Sericostoma personatum (Spence)
	Silo pallipes (Fabricius)
Ephemeroptera	Baetidae[2]
	Ecdyonurus torrentis (Kimmins)
	Ephemerella ignita (Poda)
Plecoptera	*Dinocras cephalotes* (Curtis)
	Isoperla grammatica (Poda)
Megaloptera	*Sialis fuliginosa* Pictet
Malacostraca	*Gammarus pulex* (L.)
Gasterosteidae (Stickleback family)	*Gasterosteus aculeatus* (L.)

[1] Not a lotic species, found in temporary pools and runnels on moorland; also in marshes, ditches and ponds (Wallace *et al.* 1990).

[2] Unable to identify further due to the poor quality of specimens.

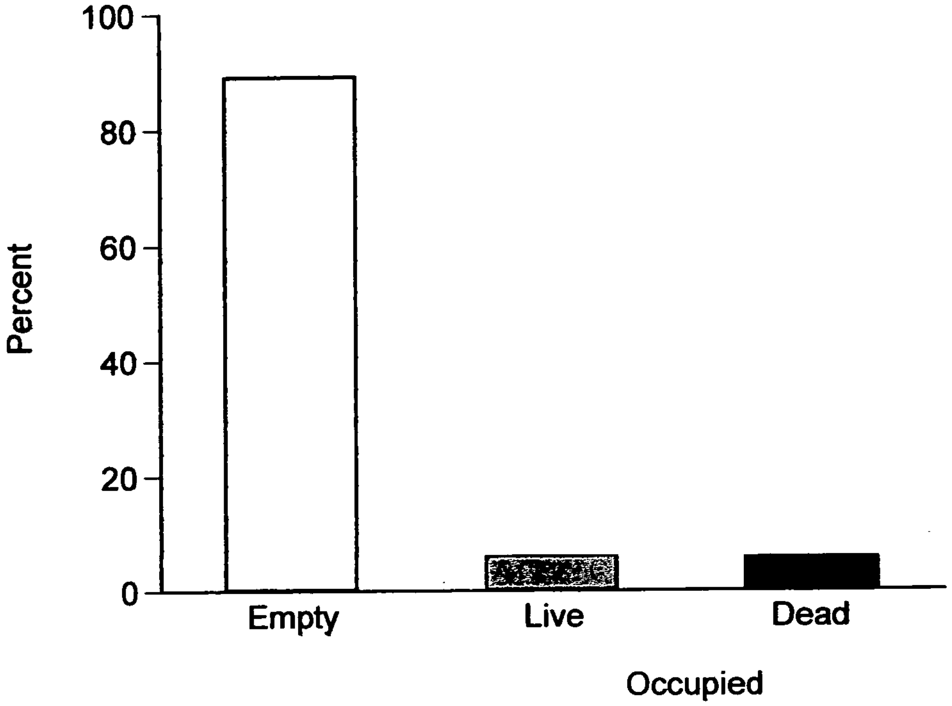


Figure 4.3.1 Percent of all caddisfly cases found within bank-side quadrats that were empty or occupied (live and dead).

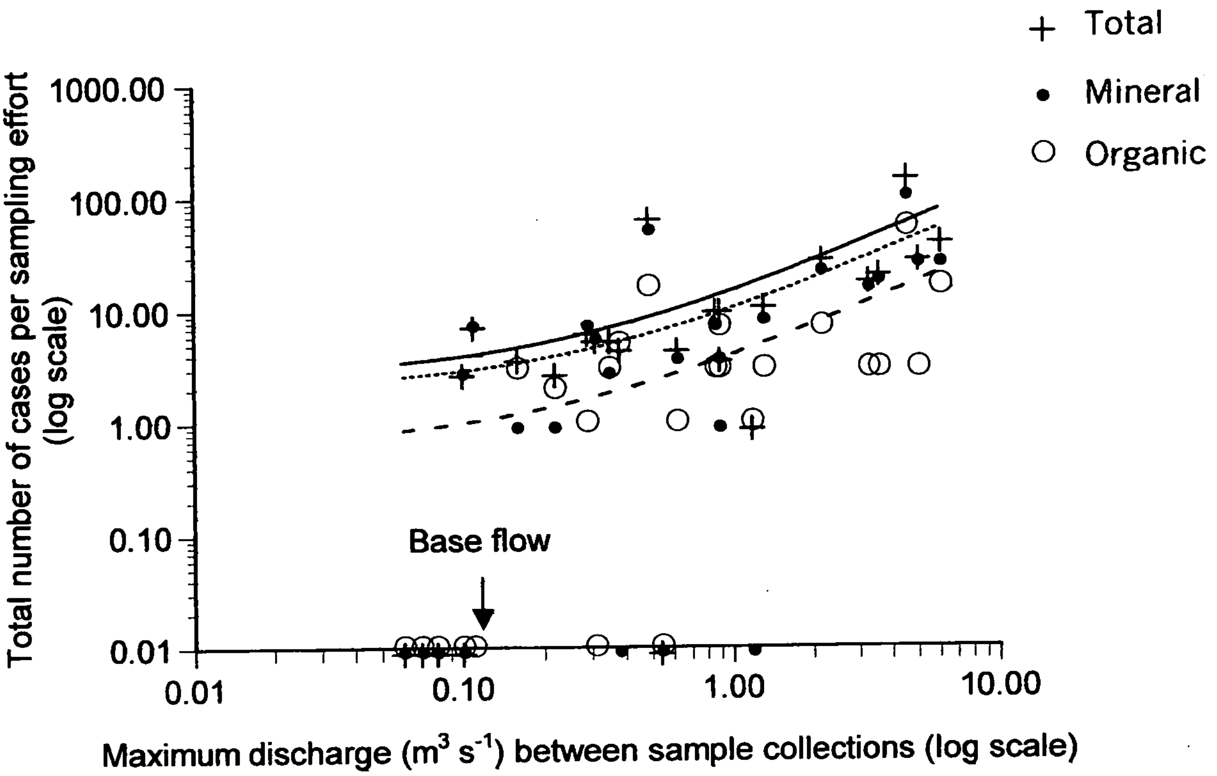


Figure 4.3.2 Total number and the number of mineral and organic cases stranded per sampling effort (20 m^2) found in bank-side quadrats in relation to the maximum discharge between sampling trips (February 1998 to October 1999). Where zero cases were found on a survey a value of 0.01 was assigned for the purposes of graphical illustration. The solid line shows the relationship between total cases stranded and maximum discharge, the fine dotted line the relationship between mineral cases stranded and maximum discharge and the fine dashed line the relationship between organic cases stranded and maximum discharge.

Table 4.3.2 Summary of the linear regression analysis of A) the total number, B) the number of mineral and C) the number of vegetative cases found stranded in bank-side quadrats and the maximum discharge between sampling. (See Figure 4.3.2)

Case Type	N	Equation	df	F	p	R^2_{adj}
A) Total	29	$y=2.65 + 11.6(x)$	1, 27	15.4	≤ 0.001	0.66
B) Mineral	29	$y=2.01 + 8.03(x)$	1, 27	15.5	≤ 0.001	0.65
C) Vegetative	29	$y=0.74 + 3.35 (x)$	1, 27	11.1	≤ 0.001	0.59

4.3.4 Adjacent Microhabitat, Substrate and Slope

The number of stranded cases found differed among bank-side quadrats (Figure 4.3.3). The most cases were found in quadrat two, with a total of 74 cases found during the survey period. The fewest stranded cases occurred in quadrat eight, where only two individuals were found stranded during the survey period. The mean number of cases found in quadrats adjacent to pools had fewer stranded individuals than those adjacent to riffles (Figure 4.3.4A). Figure 4.3.4B shows that the majority of cased caddisfly larvae in streams were not found in riffles, but in pools within the stream, contrary to what was found stranded adjacent to the instream microhabitat. Quadrats with a predominantly gravel substrate had more stranded individuals than those with turf substrates (Figure 4.3.5). The number of cases found in quadrats of steep, moderate and gentle slopes (Figure 4.3.6) showed very little variation. Table 4.3.2 shows the summary of the two-way ANOVA with slope as a covariate. Both microhabitat and substrate had a significant effect ($p=0.05$) on the number of caddisfly cases found in bank-side quadrats. The slope of the quadrat was not significant at $p= 0.05$. Significant interactions were found between microhabitat and substrate and between slope and substrate.

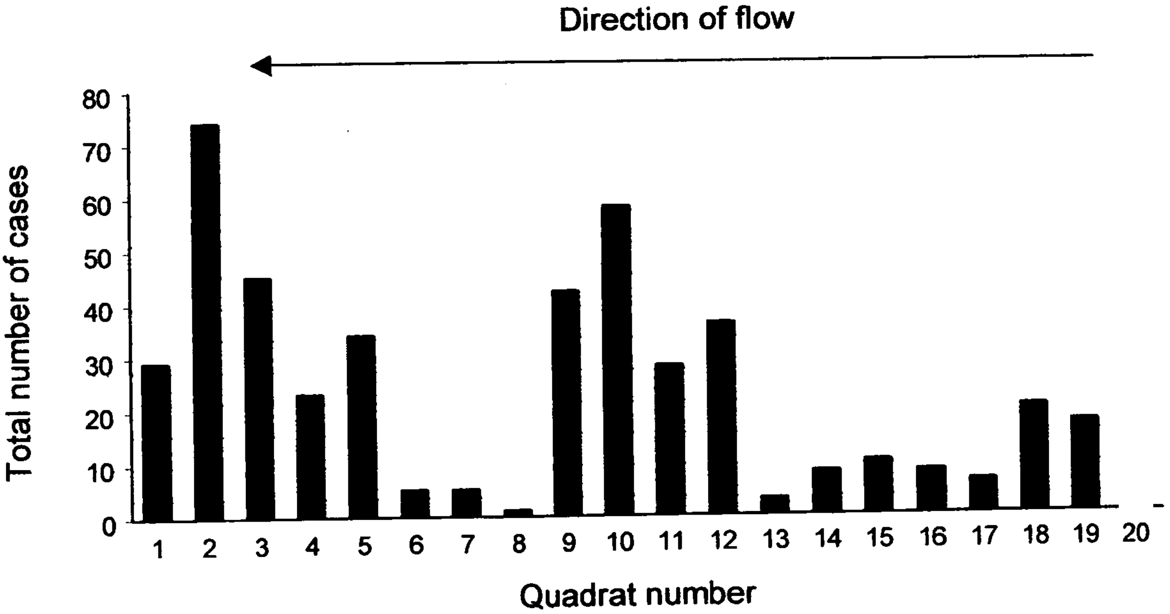


Figure 4.3.3 Total number of Trichoptera cases found within each of the 20 separate bank-side quadrats from February 1998 to October 1999.

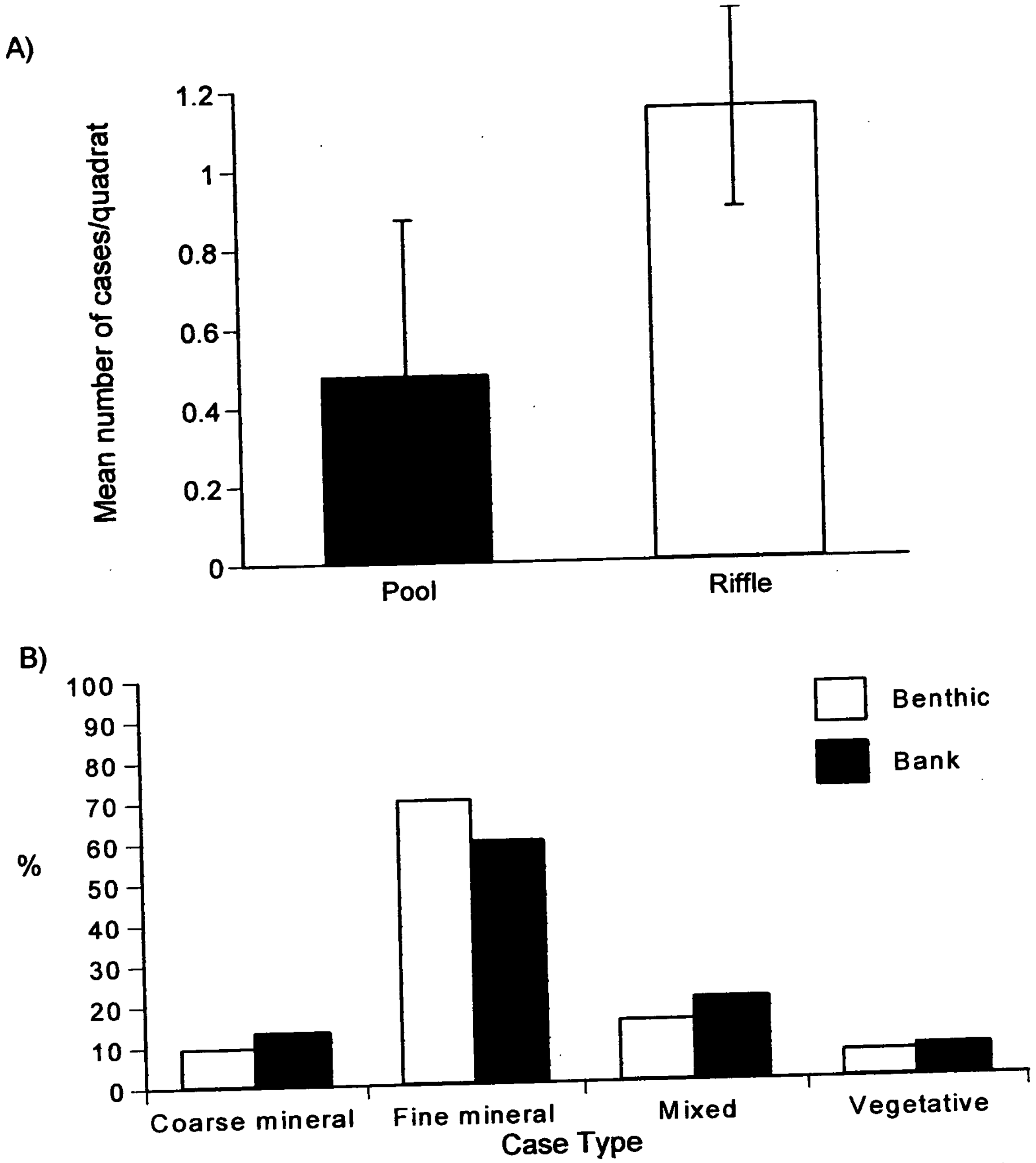


Figure 4.3.4 A) Mean number of cases (± SE) per bank-side quadrat adjacent to riffle or pool instream microhabitats over the survey period. See Table 4.3.2 for statistical analysis. B) Percentages of four types of cased caddisfly found in the Whiteadder Water (Benthic), compared to those stranded within bank-side quadrats. Benthic data from Chapter 3.

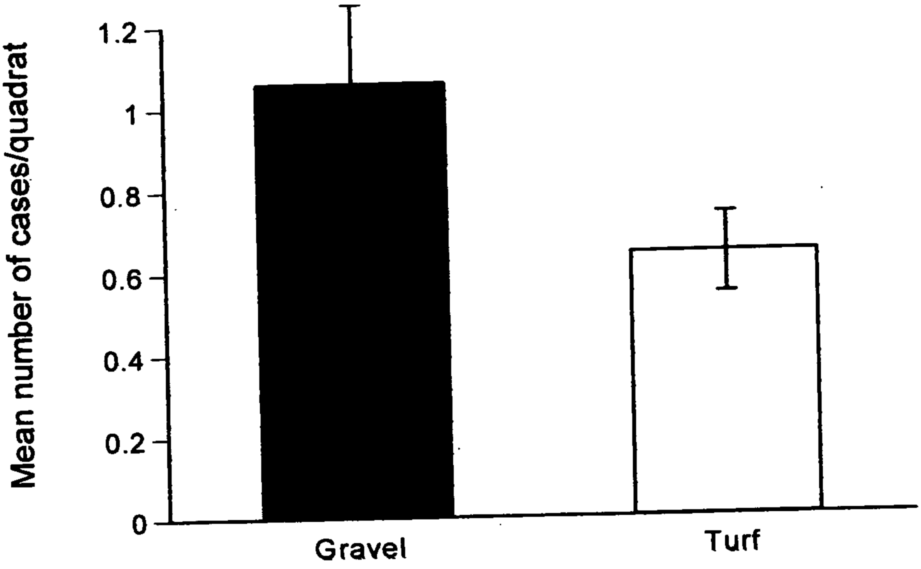


Figure 4.3.5 Mean number of cases (± SE) per bank-side quadrat with a substrate comprising of either predominately gravel or turf over the whole survey period.

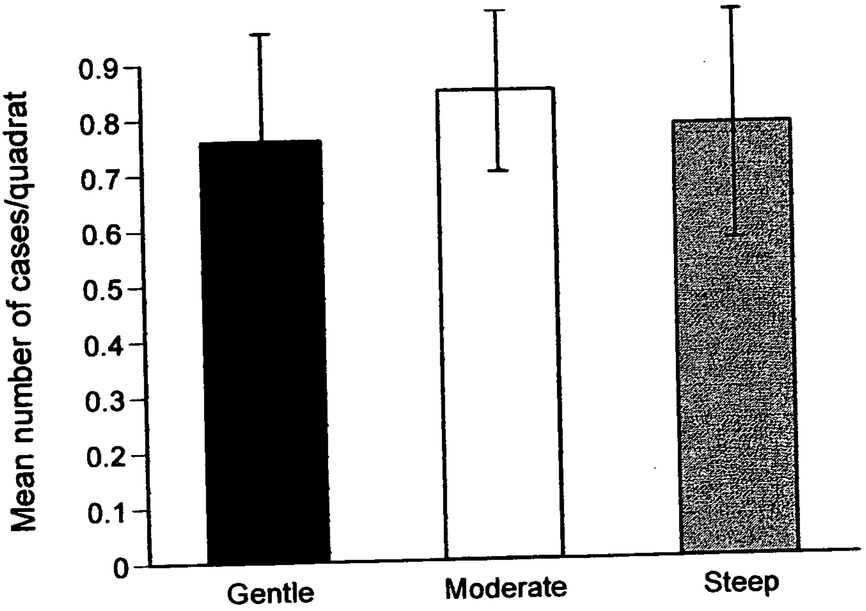


Figure 4.3.6 Mean number of cases (± SE) per bank-side quadrat with three slopes, gentle (<13°), moderate (14-25°) and steep (>25°) over the whole survey period.

Table 4.3.2 Summary of two-way ANOVA comparing the number of cases found in quadrats with different adjacent microhabitat (pool or riffle) and substrates (gravel or turf) with average slope (°) as a covariate.

Source	df	MS	F-ratio	P
Microhabitat	1	4.926	5.524	0.0188
Substrate	1	3.296	3.696	0.0449
Slope	1	1.141	1.280	0.2579
Microhabitat × Substrate	1	6.177	6.928	0.0085
Microhabitat × Slope	1	0.894	1.003	0.3166
Substrate × Slope	1	7.951	8.917	0.0029
Error	14	0.891		
Total	20			

4.3.4 Case Type

The four types of case (coarse mineral, fine mineral, mixed and vegetative) had different physical properties (Figures 4.3.7A-B). The longest case type was the mixed case type; fine mineral and vegetative cases had the shortest mean case length and coarse mineral cases of an intermediate length. Coarse mineral cases were heaviest, fine mineral and vegetative cases were lightest and mixed cases were intermediate in weight. Mean dry case weight and length was significantly different among the case types (at p=0.001) (Table 4.3.3A and B).

Lightweight and small cases were found most frequently (Figure 4.3.8 A & B). The dry weight of stranded caddisfly cases shows a skewed distribution towards lightweight individuals, as the dry weight of the case increases, the number found stranded diminishes (Figure 4.3.8A). Case length shows a similar slightly skewed distribution, though very small individuals (below 6 mm) were rarely found (Figure 4.3.8B). The same pattern of lightweight cases becoming stranded with the highest frequency was also found for each of the different case types (Figure 4.3.9). The

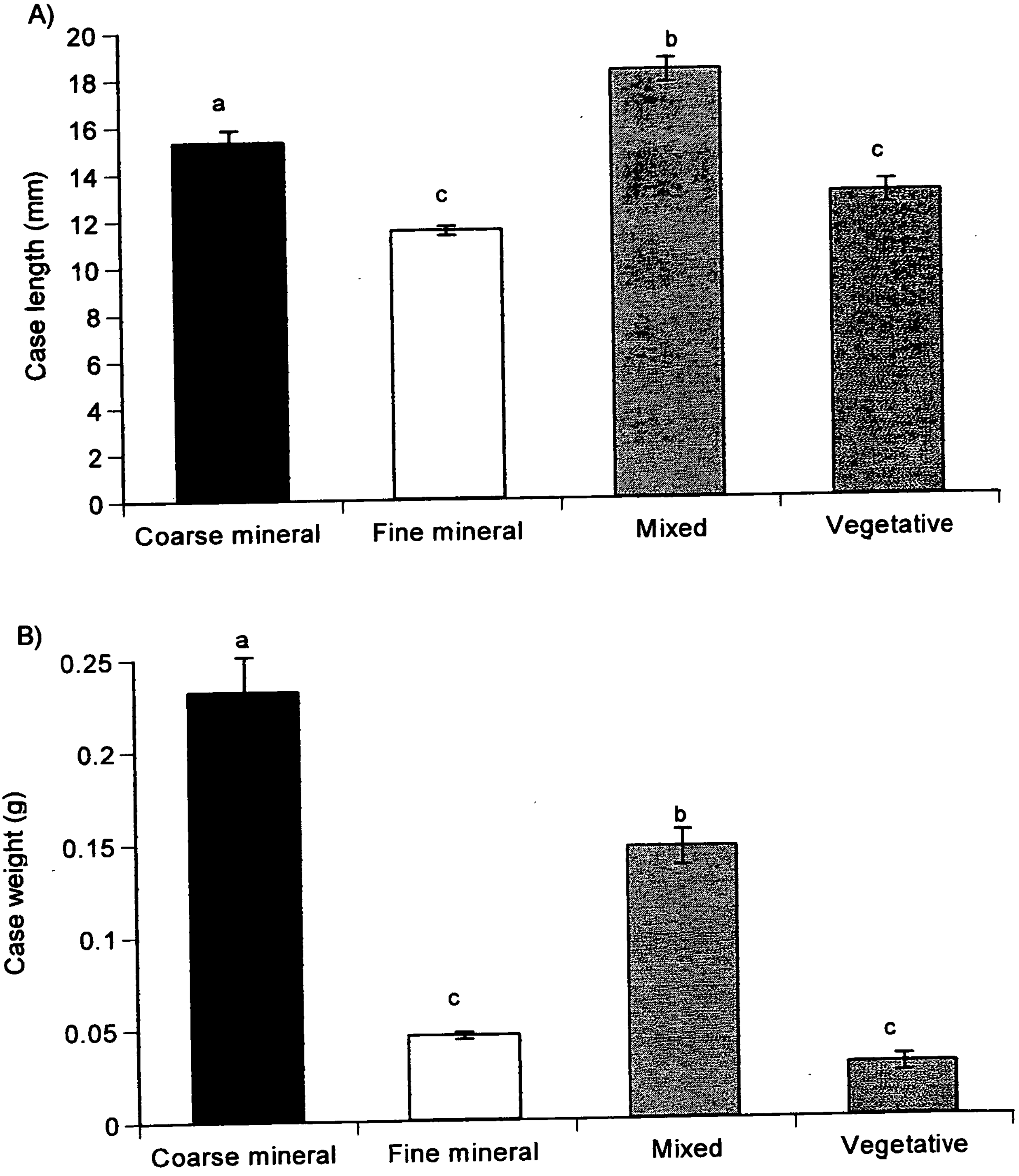


Figure 4.3.7 Mean (± SE) A) length and B) Mean weight of stranded caddisfly cases of four case types (coarse mineral, fine mineral, mixed and vegetative). Bars with the same letter were not significantly different (Scheffe test). See Table 4.3.3 for statistical analysis.

Table 4.3.3 Summary of one-way ANOVA comparing A) case length (mm) and B) dry case weight (g) of stranded caddisflies with different case types. See Figure 4.3.7 for illustration.

A)

Source	df	MS	F-ratio	P
Case Type	3	1140	81.525	≤0.0001
Error	460	13.98		
Total	463			

B)

Source	df	MS	F-ratio	P
Case type	3	0.7270	135.8	≤0.0001
Error	455	0.0053		
Total	458			

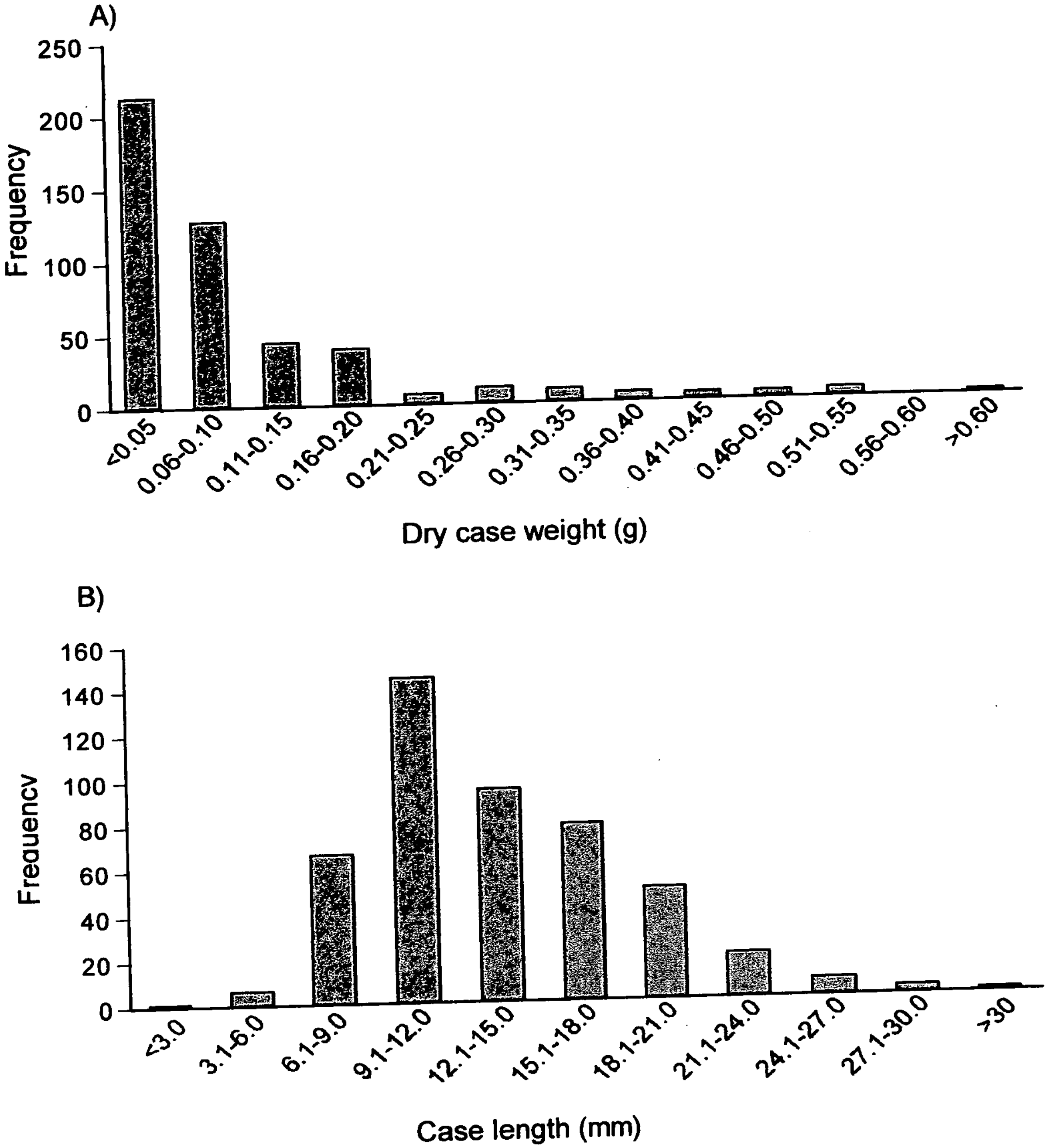


Figure 4.3.8 Frequency distribution of A) dry case weight and B) case length of larval caddisfly cases found in bank-side quadrats.

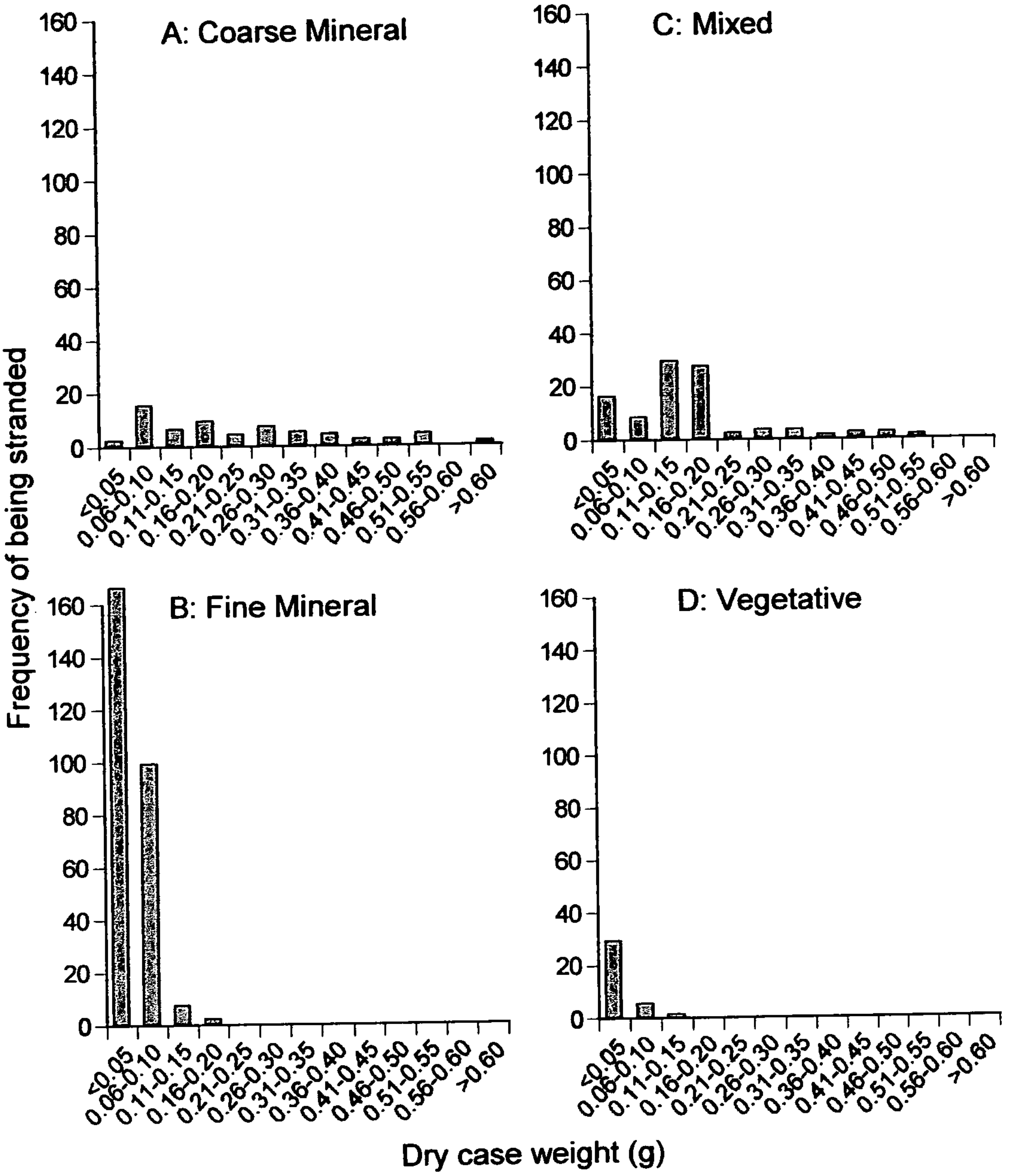


Figure 4.3.9 Frequency of being stranded for caddisfly larvae with four case types A: coarse mineral, B: fine mineral, C: mixed and D: vegetative of different dry weights in bank-side quadrats.

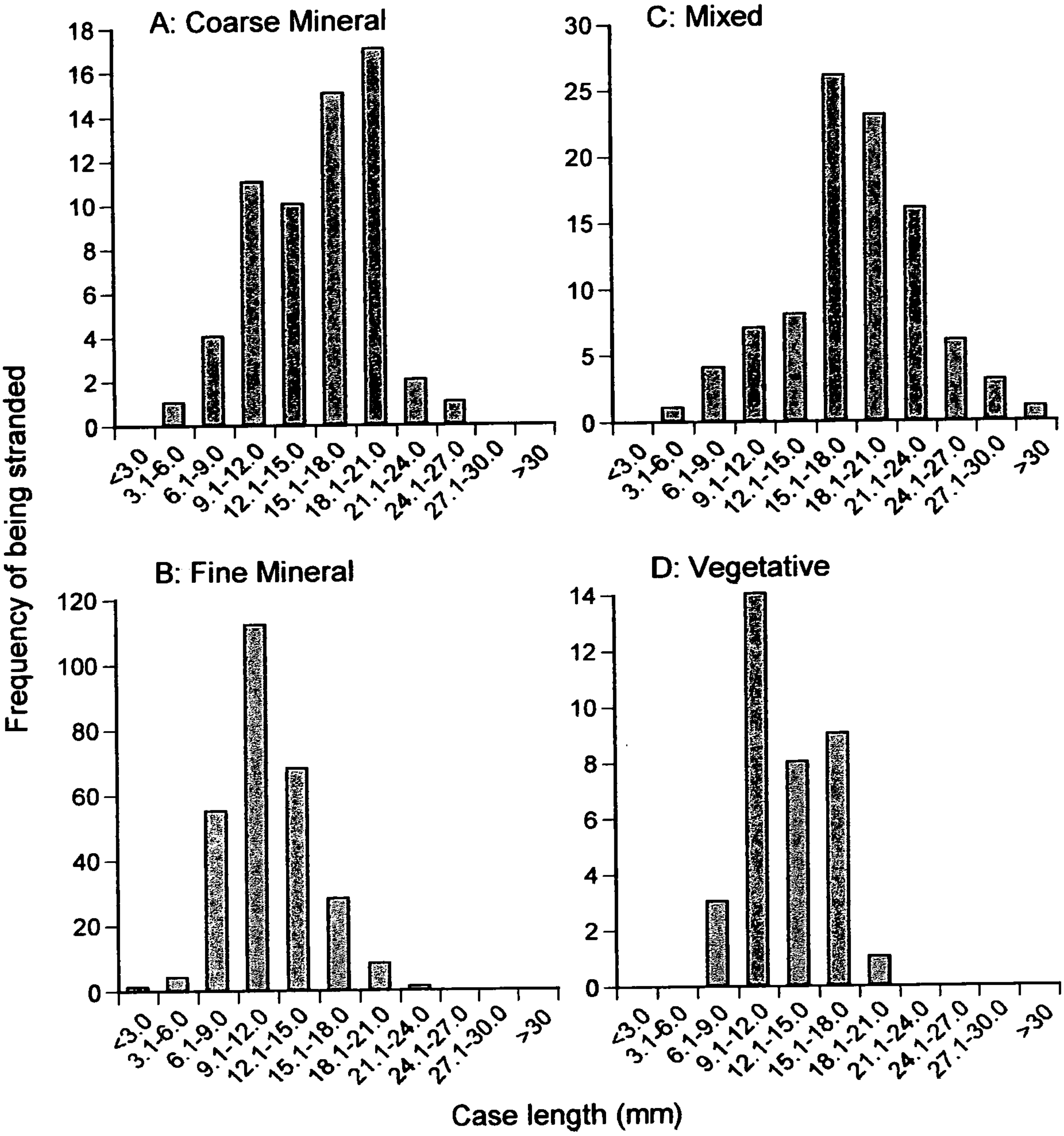


Figure 4.3.10 Frequency of being stranded for caddisfly larvae with four case types A: coarse mineral, B: fine mineral, C: mixed and D: vegetative with respect to case length.

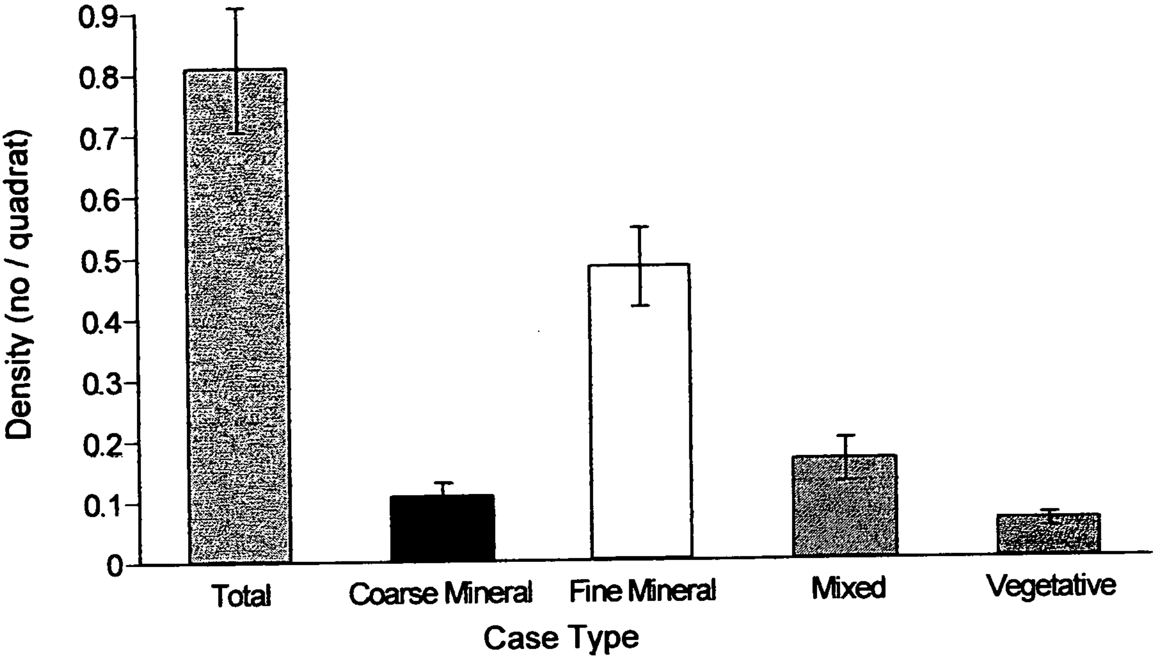


Figure 4.3.11 The mean number of cases found per quadrat (total) and the mean number of each case type (± SE) found stranded per quadrat from February 1998 to October 1999.

Figure 4.3.12B shows the proportion of case types found in riffles and pools within the stream compared to the proportion of stranded cases in quadrats adjacent to the instream microhabitats. Coarse mineral cases were proportionately more abundantly stranded adjacent to riffles and pools than were found within the stream microhabitats of pools and riffles. Fine mineral case types showed a difference, with a greater proportion found within riffles than become stranded in adjacent quadrats, but virtually no difference within and adjacent to pools. Mixed and vegetative case types showed similar patterns, both were found in a slightly greater proportion in pools than in quadrats adjacent to pools. However, the opposite was found in riffles where a larger proportion were found stranded in quadrats adjacent to riffles than were present in the benthos.

A three-way ANOVA was used to show that the abundance of different case types varied among quadrats (Table 4.3.4). Adjacent microhabitat, substrate and case type were significant at p=0.05. Significant interactions at p=0.05 occurred between adjacent microhabitat and substrate; substrate and average slope, and microhabitat and case type. When quadrats adjacent to different instream microhabitats (pool or riffle) are compared, the incidence of being stranded amongst the case types (Figure 4.3.13A) followed the same pattern as the overall pattern, with the fine mineral case type having the highest incidence and vegetative the lowest incidence of being stranded in both quadrats adjacent to pools or riffles. There was no difference between the mean numbers of coarse mineral cases stranded between the different microhabitat quadrats. A significant difference between the incidence of being stranded between pool and riffle microhabitat occurred in the mixed and vegetative case type, where the mean numbers were higher in the quadrats adjacent to the riffle instream microhabitat than those in quadrats adjacent to the pool instream microhabitat (Figure 4.3.13A). In quadrats divided into the substrate categories of gravel and turf, again the fine mineral case type was the most abundant and vegetative the least abundant in both quadrat types (Figure 4.3.13B). In gravel quadrats the incidence of stranded coarse mineral and mixed case types was higher than in quadrats with a predominately turf substrate. The incidence of being stranded followed the same patterns described previously, with the highest incidence occurring for the fine mineral case type and the lowest for vegetative when compared between quadrats on three slopes (Figure 4.3.13C).

4.3.5 Distance From Stream

The frequency of stranded cases among all the quadrats in relation to the distance they were found from the water line shows a decrease up to 60 to 70 cm, then an increase from 70+ cm (Figure 4.3.14). There is a positive relationship between the maximum distance from the waterline a case can be stranded, and the maximum discharge that occurred between sampling. The maximum distance at which a case is stranded is strongly correlated to the maximum discharge between the collection of the samples, r = 0.82 (Figure 4.3.15A). This relationship also holds true if the mean distance at which a case is stranded is used. Mean distance at which a case is stranded is strongly correlated to the maximum discharge between the collection of the samples, r = 0.78 (Figure 4.3.15B)

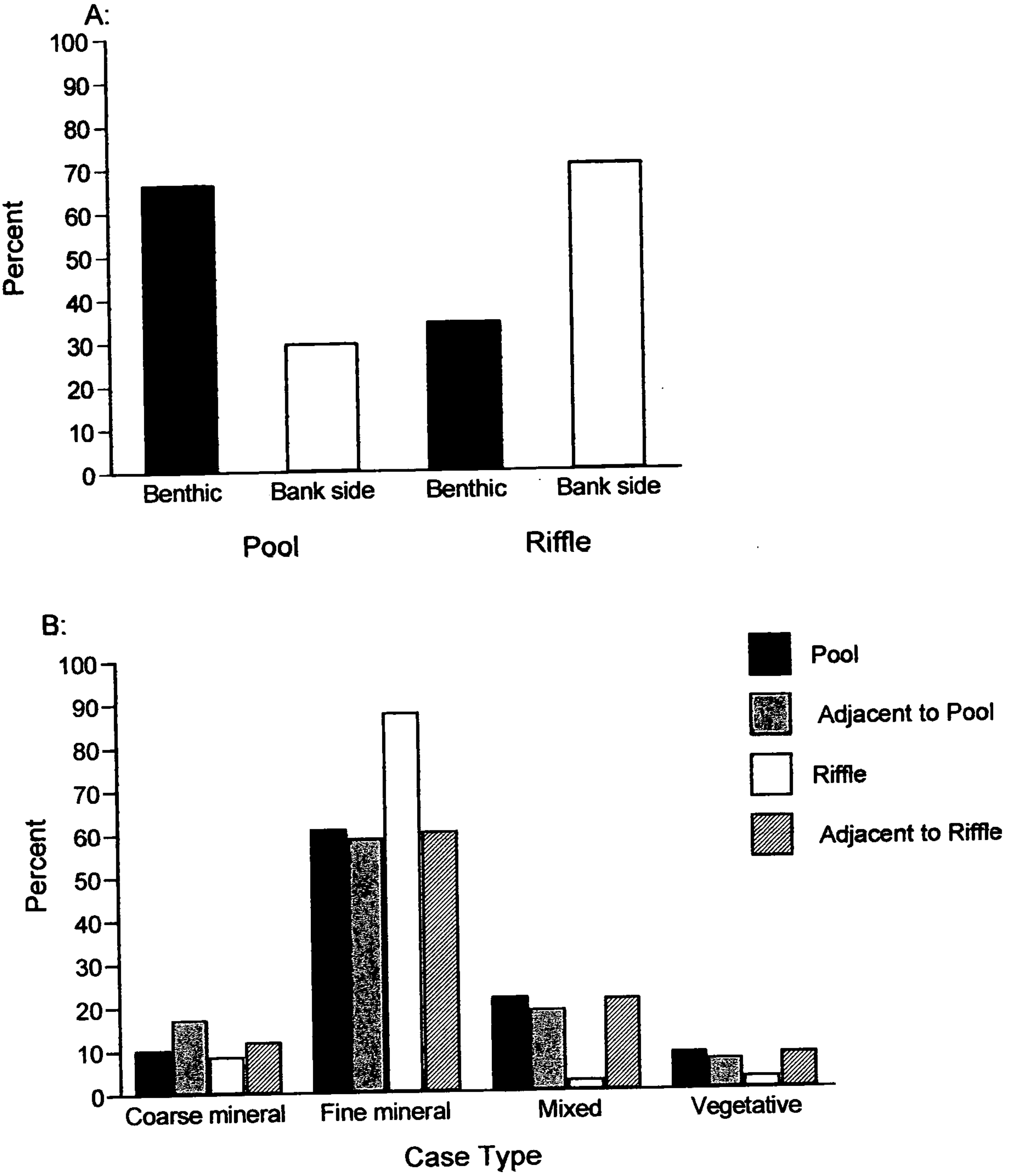


Figure 4.3.12 A: Percent of cased caddisfly larvae in and adjacent to pool and riffle microhabitats and B: Percent of larval caddisfly case types present within and adjacent to pool and riffle microhabitats. Benthic data from survey in Chapter 3

Table 4.3.4 Summary of three-way ANOVA comparing number of stranded caddisfly cases among quadrats with different adjacent microhabitats (pool or riffle), substrate (gravel or turf) and with different case types (coarse mineral, fine mineral, mixed and vegetative) with average slope (°) as a covariate.

Source	df	MS	F-ratio	Prob
Microhabitat	1	4.889	5.692	0.0171
Substrate	1	3.357	3.909	0.0481
Slope	1	1.183	1.377	0.2406
Case type	3	11.792	13.73	0.0001
Microhabitat × Substrate	1	6.135	7.143	0.0076
Microhabitat × Slope	1	0.8864	1.032	0.3098
Substrate × Slope	1	8.047	9.369	0.0022
Microhabitat × Case type	3	3.536	4.117	0.0064
Substrate × Case type	3	1.406	1.637	0.1786
Slope × Case type	3	2.422	2.820	0.0876
Microhabitat × Substrate × Slope	1	0.9101	1.061	0.3030
Microhabitat × Substrate × Case type	3	0.4648	0.542	0.6534
Microhabitat × Slope × Case type	3	1.245	1.453	0.2256
Substrate × Slope × Case type	3	0.9474	1.105	0.3458
Microhabitat × Substrate × Slope × Case type	3	0.4793	0.559	0.6420
Error	13	0.8588		
Total	20			

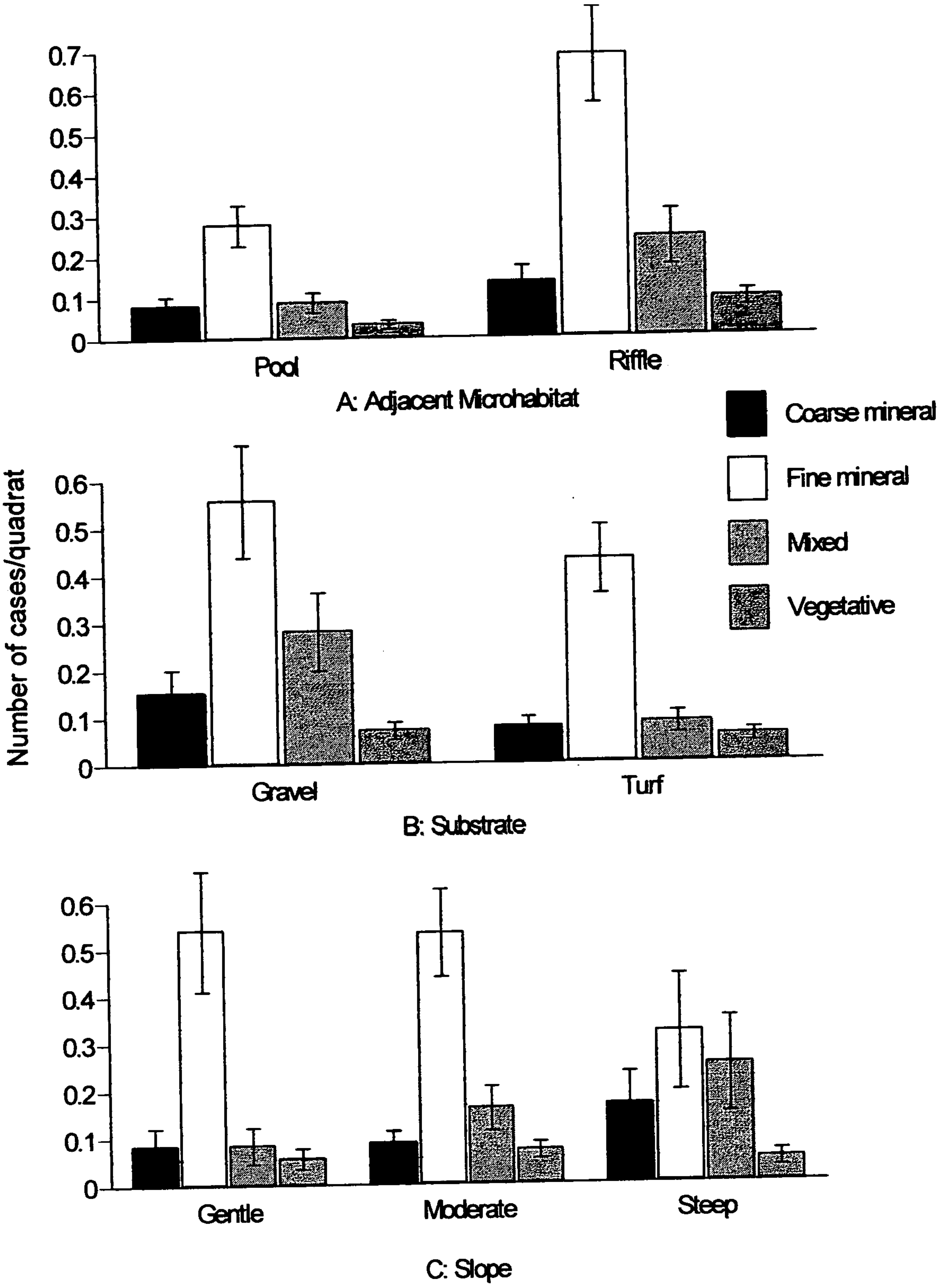


Figure 4.3.13 Mean number of cases per case type (± SE) found in quadrats A: adjacent to pool or riffle instream microhabitat, B: gravel or turf substrate and C: steep, moderate and gentle slopes.

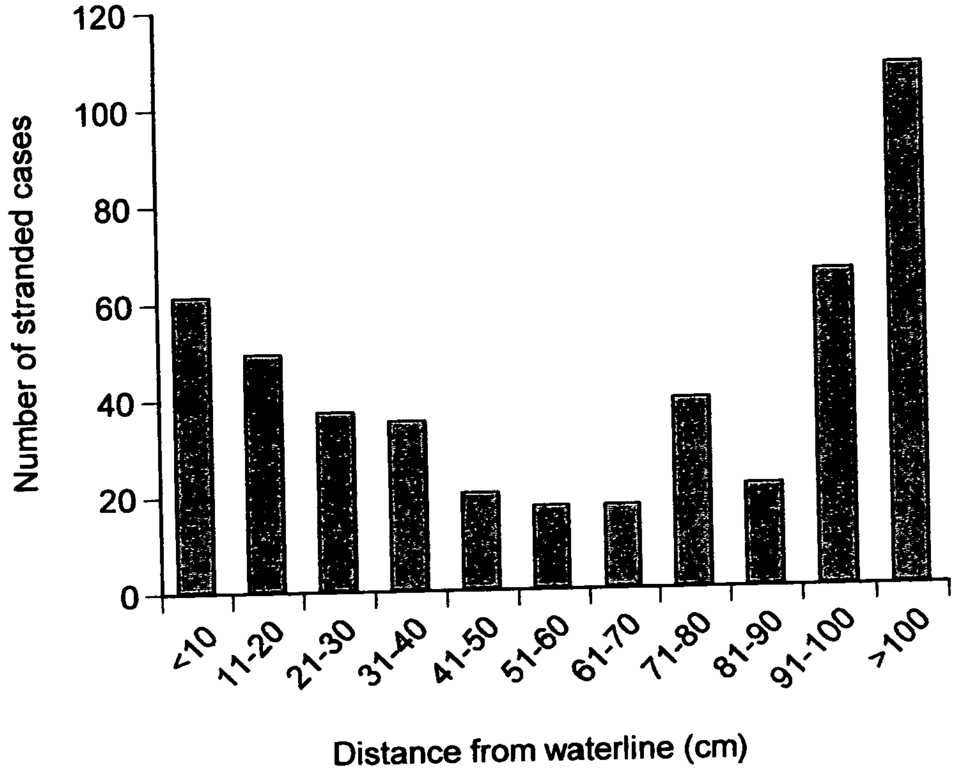


Figure 4.3.14 Frequency of stranded cases in relation to distance from the water line within bank-side quadrats between February 1998 and October 1999.

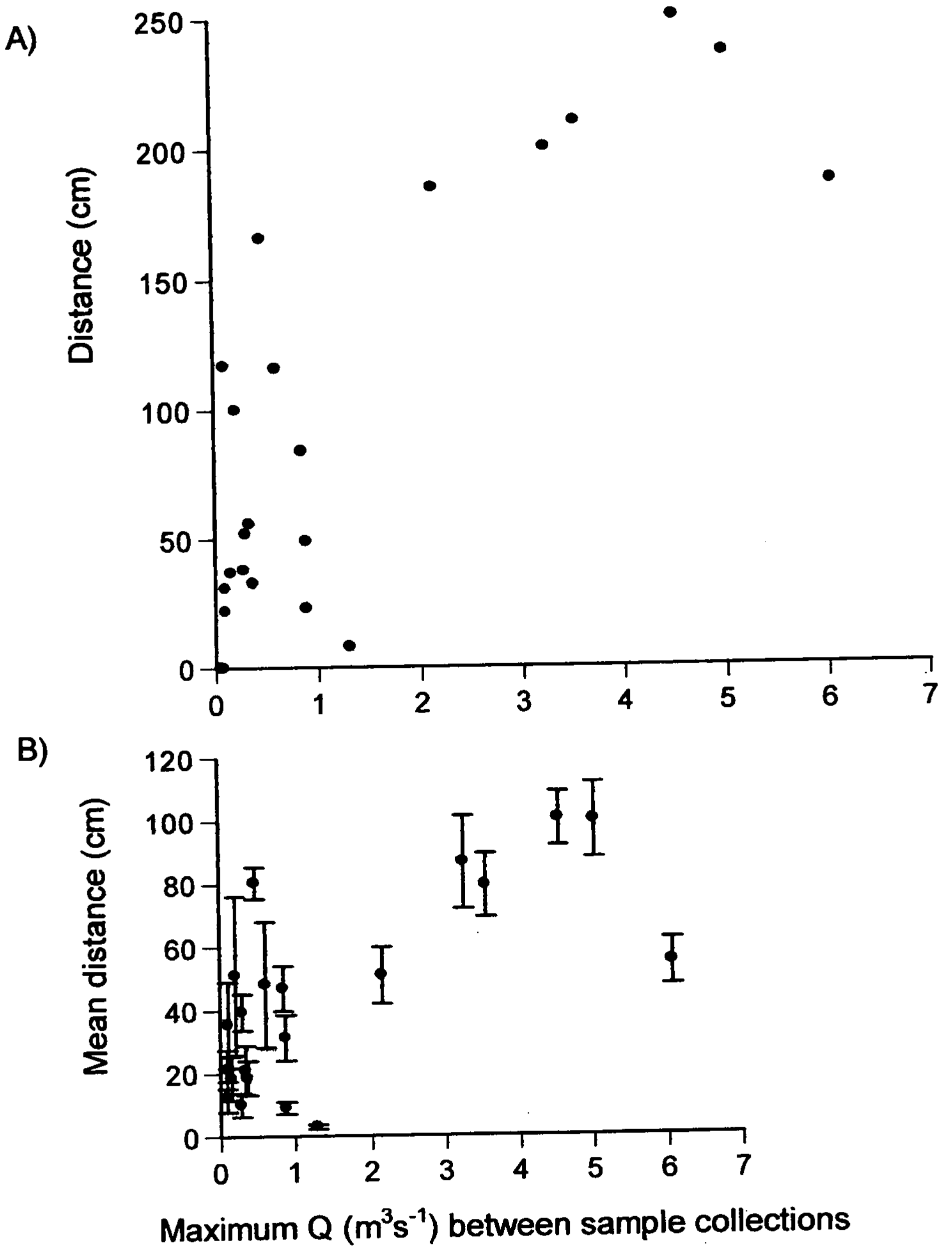


Figure 4.3.15 A) Maximum distance from the waterline per sampling effort found in bank-side quadrats in relation to the maximum discharge between sampling occasions between February 1998 and October 1999. Pearsons product moment correlation r = 0.82. B) Mean distance from the waterline per sampling effort found in bank-side quadrats in relation to the maximum discharge between sampling occasions between February 1998 and October 1999. Pearsons product moment correlation r = 0.78.

4.4 Discussion

The positive relationship between increased discharge in a stream due to natural rainfall events in contrast to anthropogenic events, (such as hydroelectric dam releases causing flow reductions and increases) and the number of stranded Trichoptera, has not been quantified elsewhere to my knowledge. Though I have concentrated on the cased Trichoptera, many other lotic taxa have the potential to be become stranded after high flows. Lotic organisms, such as mayflies, stoneflies and even fish were found within the bank-side quadrats adjacent to the Whiteadder Water after high discharge. . The numbers of individuals that were found in the bank-side quadrats of this study are probably a conservative measure of the number that may get stranded after floods. Though the quadrats were cleared of cases to the highest level of my ability, some very small cases may have been missed. Though cases of less than 5 mm were found, it was a rare event even though small individuals were found in the benthos. Cases may also have been overlooked due to their inherent cryptic nature, especially vegetative cases in quadrats with a turf substrate. The predation of stranded individuals adds another level of complexity to the fate of stranded individuals. The number of individuals found in the quadrats may also be less than originally stranded as some may have been removed from quadrats by predators, which could not be accounted for when the quadrats were sampled. Field observations (Hall and Lancaster pers obs.) have shown that cased caddisfly larvae may be removed from their cases by terrestrial predators such as ants. This along with the fact that some caddisfly larvae are known to abandon their cases when stressed (Otto 1976, 1983), may account for the greater number of empty cases found on the bank-side than occupied cases.

4.4.1 Discharge and the Incidence of Benthic Macroinvertebrates Being Stranded

The incidence of being stranded on the banks of the Whiteadder Water only occurred above a threshold discharge, i.e., when the discharge exceeded bank full and overflowed on to the riparian zone. After high discharge events, many individuals can become stranded, e.g., 162 cases within ~20 m^2 on the 16th June 1998. The potential damage that being stranded can have on benthic assemblages was highlighted by

Kroger (1973) who observed the exposure of large areas of substrate in the Snake River, Wyoming after the Jackson Lake Dam reduced the discharge in the river from 2.8 to 0.3 m^3 s^{-1} in less than five minutes. It was estimated from samples taken in exposed areas of the riverbed that over three billion macroinvertebrates, mainly insects were killed by being stranded along a three-kilometre stretch immediately below the dam.. However, such discharge reductions are very different from the floods that I observed and this study is one of the few that highlight the negative effects that naturally fluctuating water levels can have on benthic individuals and communities with reference to being stranded.

It has been suggested that lotic invertebrates may ameliorate the destructive effects of high discharge by sheltering in and re-colonising from refugia such as inundated floodplains and other areas that are dry during normal discharges (Perry and Perry 1986; Prevot and Prevot 1986; Badri *et al.* 1987; Matthaei 2000). The presence of live Trichoptera and their cases on the bank indicates that individuals are present on the inundated banks at high discharges. The frequency of stranded cases firstly decreases with distance from the water, then increases again and may be explained by the frequency, scale and intensity of the flood. Small floods that inundate a small portion of the bank-side occur most often, but the number of dislodged individuals would be lower than during a large flood as the hydraulic forces would also be lower. The infrequent high intensity floods would inundate a greater bank-side area (and cover a greater distance from main channel), and would place greater hydraulic stresses on individuals. This would potentially lead to greater proportion of individuals becoming dislodged from the substrate of the main channel and possibly becoming stranded when the water level returns to a lower level.

The strong relationship between the maximum and mean distance the individuals were stranded and the maximum discharge implies that the individuals are stranded passively. There are two mechanisms by which individuals could arrive on the floodplain. Firstly, organisms dislodged from the substrate by the increased hydraulic stresses and washed downstream may be deposited in areas of low flow such as the margins being deposited passively . Secondly, individuals could actively seek out areas of low hydraulic stress (refugia), during high discharges and subsequently become stranded. The mechanism by which they reach the refugia is unimportant, the important aspect is that they can leave the refugia when the disturbance has abated to recolonise the main stream channel. Thus, the inundated margins of the stream can only act as refugia if the organisms that temporarily inhabit the flooded margins return to the channel once the discharge falls. The presence of dead and empty cases of Trichoptera on the banks shows that some individuals could not regain the stream with dropping water levels. If some of the stranded Trichoptera could not return to the stream, are inundated margins true refugia from increased discharge? The ability of cased Trichoptera to regain the stream once stranded may be dependant on a number of factors, such as bank-side topography and species-specific traits, and is discussed further in chapter six

4.4.2 Bank-side Topography

The large difference in the proportion of animals found in instream microhabitats compared to the adjacent habitat suggests that individuals do not actively move laterally, but are dislodged upstream and transported in the water column and then deposited on the bank-sides down stream. Stranded individuals were not homogeneously distributed over the bank-side and the adjacent instream habitat (pool or riffle) had a significant effect: more individuals occurred on bank-sides adjacent to riffles rather than pools. The distribution of Trichoptera, like all benthic organisms, is heterogeneous within the stream (Chapter 3). The difference in benthic species between fast flowing riffles and slower flowing pools is well known (O'Connell and Campbell 1953; Scott 1958; Ulfstrand 1967; Edington 1968; Hynes 1970; Otto 1982) and assemblage differences may partly explain why more individuals were stranded on banks adjacent to riffles than pools. The majority of the cased caddisfly larvae in the benthic survey were found in pools, yet the number of stranded cases was highest on banks adjacent to riffles. If the predominant mechanism causing individuals to become stranded is by active movement from the instream habitat laterally onto bank-sides during a flood, the proportions of the stranded individuals should be similar to that of the adjacent benthos. If the mechanism by which individuals become stranded is passive, such as dislodgement and then deposition on the bank-side, then the proportions of stranded individuals may not be similar. In the field, cases were often found clustered together which suggests that the animals were deposited (Lancaster and Hall *pers obs.*). If the mechanism were by deposition of individuals entrained in the water column falling out of suspension then clusters of similar sized of individuals would occur in areas where the velocity fell below that to keep the individual in the water column. If the main mechanism were by passive deposition then I would expect a larger proportion of individuals in depositional areas such as gravel beds. As a greater incidence of stranded individuals occurred on gravel substrates compared to the non-depositional turf areas, this suggests passive deposition on the banks.

The physical properties of a substrate such as its ability to retain water may contribute to the different numbers of larval cases found on the different substrates. Substrates that remain wet longer will increase the desiccation tolerance of stranded benthic organisms. Gravel dries much faster and can retain heat better than turf, and desiccation-prone larvae may survive longer on turf than gravel. The quicker drying properties of gravel would increase the rate of desiccation, especially if the ambient conditions were warm and dry in stranded caddisfly larvae. Larvae stranded in these areas would therefore be more likely to perish on the bank-side and unable to regain the stream. Corrarino and Brusven (1983) also found that in the autumn, air and water temperatures were higher and caused rapid drying of exposed mineral there was a greater mortality of stranded individuals.

4.4.3 The Effect of Species-Specific Case Types on Becoming Stranded

Fine mineral cases were the most abundant case type found on the bank-sides, coarse mineral and mixed cases had a similar intermediate incidence of being stranded. This pattern does not reflect the proportions of case types found in the benthic assemblage, as the proportion of fine mineral cases found in the benthos was higher. In contrast, the other three case types (coarse mineral, mixed and vegetative) were proportionately more abundant on the banks than in the benthos.

The case type appears to affect the numbers of individuals stranded, as the proportion of fine mineral cases was lower on the adjacent bank-side than in the stream, individuals with this fine mineral case type may not be as readily stranded or can regain the stream more effectively than coarse, mixed and vegetative cases. The case type itself may affect the incidence of being stranded by acting as ballast to reduce displacement (Otto and Svensson 1980: Otto and Johansson 1995) and the results from this study in the Whiteadder Water support this hypothesis. If the ballast hypothesis is true then we would expect to see fewer large individuals stranded on the bank-side. More lightweight than heavy caddisfly larval cases were stranded. Furthermore, the frequency distribution of case size among stranded individuals was skewed towards small individuals i.e., small individuals were stranded more frequently. Corrarino and Brusven (1983) also suggested that small individuals should be stranded preferentially over larger individuals because of their poorer mobility. The smaller the individual, the greater the relative distance to travel to regain the stream. This would possibly lead to an increase in time taken for the individual to regain the stream, which in turn could lead to an increased chance of death through predation or desiccation.

For aquatic organisms desiccation is a major problem when stranded, to function successfully they need to be immersed in water and although they may survive short periods of exposed, prolonged exposure would cause death. The importance of desiccation as a source of mortality in stranded benthic organisms is highlighted by Matthaei and Townsend (2000); they found an increase in stranded organisms in areas that dried out rapidly on inundated floodplains of the Kye Burn, New Zealand. The tolerance of the different case types to desiccation in combination with the other environmental (bank-side topography) and species-specific traits (mobility and size) may explain the difference in the incidence of being stranded. The case type may infer a different degree of protection from desiccation dependant on the material from which the case is constructed from; mineral cases may dry out faster than organic (vegetative) cases. Zamora-Munoz (1996) found, in experiments designed to elucidate differential survival under drought conditions in temporary pools, that Trichoptera with organic cases held water more efficiently than mineral cases when exposed to air. As a result organic cased individuals were considered more resistant to desiccation. So if stranded in air animals with a vegetative case may survive longer than those with mineral cases, allowing the organism to regain the base flow channel. This could result in the lower incidence of their becoming stranded on bank-sides, especially in turf, which could also help reduce desiccation. Erman (1981) found that case type (mineral or organic) in *Desmona bethula* did not confer any advantage in the tolerance to desiccation. My results, showing that fine mineral cases are the most common type stranded and vegetative cases least frequently found, with coarse and mixed cases found at an intermediate level, would seem to agree with the findings of Zamora-Munoz (1996). Larvae with fine mineral cases appeared to be better able to either survive desiccation and regain the stream or avoid being stranded completely than those individuals with coarse, mixed and vegetative cases. I propose that in a fine mineral cases the close fitting mineral particles wouldbe less permeable to water vapour loss. This may prevent water loss from inside the case keeping an aqueous layer inside the case, thus preventing desiccation. In a case constructed of larger pieces (mineral or organic) the case may have greater interstitial space volumes between those particles constructing the case, which in turn would allow a greater loss of water from the inside of the case and result in a reduced time for desiccation. This may result in the pattern observed in the bank-side quadrats, where fine cases are on average more likely to be stranded, this is due to the fact they are proportionally the most abundant cased caddisflies in the system, but proportionally less get stranded than the other three case types.

Summary

The incidence of cased caddisflies becoming stranded was high after high discharge events (floods), and was dependant on the bank-side topography (substrate) and the case type. The results however, have led to possible mechanisms for, 1) how caddisfly larvae are passively stranded and 2) how the ability to regain the stream is species-specific. The mechanism by which individuals became stranded appears to be predominately a passive one and is investigated further in chapter 5. There also appears to be a relationship between species-specific traits (case type) and the ability to regain the stream, which is examined further in chapter 6.

5 Is the Manner in which Cased Trichoptera Become Stranded an Active or Passive Mechanism?

5.1 Introduction

Flooded bank-sides have been described as potential refugia from hydraulic disturbance for aquatic organisms (Schlosser 1981; Badri *et al.* 1987; Matthaei *et al.* 1997; Rempel *et al.* 1999; Matthaei and Townsend 2000). Whether benthic macroinvertebrates move actively or passively among hydraulic microhabitats (e.g. refugia vs. non-refugia) in response to hydraulic stress during floods is unclear at a species-specific level and more studies are required to address the issue. The movement of organisms into refugia may be by two modes 1) an active mode by which the organisms actively search out refugia, or 2) a passive mode by whichorganisms are passively deposited in refugia after being dislodged from the substrate, entrained within the water column and eventually allowed to fall out when the current drops.

Research into the use of refugia within streams has often examined changes in the microdistribution of benthic organisms in microhabitat patches, which are differentially effected by hydraulic disturbances caused by changes in discharge (Palmer *et al.* 1995; Lancaster and Hildrew 1993b; Robertson *et al.* 1995; Lancaster 2000). By comparing the relative differences in density among these microhabitat types an assessment of refugium use can be obtained. These researchers have shown that during high discharge events, the abundance of organisms is higher in areas of the stream that act as flow refugia than in non-refugia areas. This distribution pattern may arise from animals accumulating in refugia during the disturbance events. Alternatively individuals in non-refugium areas may be lost from the system, resulting in a higher relative density of organisms in refugia, when the actual density of organisms in the refugia has not changed (Lancaster and Belyea 1997; Lancaster 1999). Several researchers (e.g., Lancaster and Hildrew 1993 and Palmer *et al.* 1996) have documented the use of flow refugia within stream channels and animals do actively accumulate in refugia in at least some situations (Lancaster *et al.* 1990; Winterbottom *et al.* 1997; Lancaster 2000). The mechanisms by which lotic organisms utilise flow refugia in streams, has received little attention from researchers. In situ studies of this type are fraught with difficulties both in terms of predicting when high discharges will occur and working during high discharge events and consequently, artificial stream systems are often used to address the problem (Statzner and Borchardt 1990; Borchardt, 1993; Lancaster, 1999; Holomuzki and Biggs, 2000).

Although in situ studies on the mechanisms (such as lateral movement into areas of low hydraulic stress by benthic organisms during floods) by which benthic macroinvertebrates exploit flow refugia are difficult to carry out, an example of an in-situ study to have addressed the issue was carried out by Rempel *et al.* (1999) in Canada. They demonstrated that benthic macroinvertebrates move laterally to flow refugia on river margins during spates in the Fraser River, British Columbia. They observed that benthic macroinvertebrates shifted from the deep water main channel to the shallow, seasonally inundated shore zone during the annual flooding cycle during which the shore zone can be inundated for up to four months of the year. In contrast to the deep water main channel the shallow shore zone had a lower hydraulic stress and a more stable substrate during floods and, thus, fitted the criteria for potential flow refugia. They found that the total density of benthic macroinvertebrates was highest at a depth of 1.5 m (within the main channel) prior to flooding, but at peak flow the highest densities were found at a depth of 0.5 to 0.2 m within the inundated shore zone. The shift in the benthic macroinvertebrates was attributed to a lateral movement into the lower hydraulic conditions found in the shallow shore-zone.

5.1.1 Particle Dislodgement, Transport and Deposition in Streams (Being Passively Stranded)

Benthic organisms are analogous to non-living particles that occur in streams (such as sand grains and pebbles) in the way that hydraulic forces (such as lift, drag and shear stress) act upon them, though many have morphological and behavioural adaptations that help them to resist these forces (Chapter 1). The motion of particles and benthic organisms within a flooding stream consists of three stages: initiation of motion (dislodgement in the instance of benthic organisms), downstream transport (drift/entrainment in water column) and deposition. The majority of a stream's energy goes into overcoming the frictional resistance along its bed and banks, a critical energy level therefore, must be reached before the stream can dislodge and transport particles or benthic organisms (Gordon *et al.* 1992). A number of thresholds have to be overcome to enable dislodgement, transportation and deposition of a particle in a stream: a 'lift-off' threshold, which must be exceeded in order to suspend the particle and another 'settling/deposition' threshold below which the particle will drop out of suspension. Threshold values can be defined by a number of hydrodynamic factors such as flow velocity and shear stress. Shear stress or tractive force typically increases with discharge, but it is not uniform within the stream, the same as flow velocity. Observations of particle movements in streams indicate that lighter organic materials such as leaves and bark are transported first as the intensity of the flow increases (Table 5.1.1) (Gordon *et al.* 1992). The forces that dislodge a particle from the streambed and keep it aloft are mainly due to upward surges of water from small, turbulent eddies (Gordon *et al.* 1992; Vogel 1994). Particle transportation occurs once the threshold for movement/dislodgement has been exceeded. In general terms the greater the current velocity the larger the particle that can be dislodged and transported (Table 5.1.1) (Gordon *et al* 1992; Vogel 1996). A stream will carry suspended particles or benthic individuals until it lacks the energy to do so at which time deposition occurs. There are two major processes that lead to deposition of inanimate particles and benthic organisms (Briggs 1977): 1) The orientation of the particle or organism in the flow changes, increasing resistance. The lift and drag forces on a non-spherical object will change in response to its orientation, causing the particle or organism to 'stall' at certain angles and drop from suspension. 2) The competence of the stream decreases, meaning that the energy available for transporting entrained particles or organisms decreases. Flow competence refers to the maximum particle (including benthic organisms) size that can be carried at a given flow velocity. Suspended sands, gravels and other particles entrained in the water column will settle out when the stream flow drops and when local velocity decreases, such as within pools or when the stream widens and overflows its channel during a flood and in dead zones behind instream obstacles (i.e., boulders).

If a benthic organism is dislodged by increased hydraulic forces during a flood, and becomes entrained in the water column and then becomes deposited into an area in which the stream does not have enough energy to keep it suspended in the water column (i.e., the inundated margins or instream areas of lower velocity), the organism will drop out of suspension and will become deposited in that area. If an individual is deposited in this lateral inundated habitat and if the water level recedes at a rate faster than the organism can follow, and it may become stranded. The mechanism by which the organism was stranded is therefore a passive mechanism, as the organism did not actively seek out the low flow velocity area in which it was deposited.

Table 5.1.1 Classification of inorganic particles sizes and the current velocity required to initiate transport of particles (modified from Giller and Malmqvist 1998).

Wentworth Particle Size Category	Particle Diameter[1] (range in mm)	Approximate current velocity to move particle [2] (ms^{-1})
Boulder	>256	
Cobble		
Large	128-256	3.0
Small	64-128	2.0
Pebble		
Large	32-64	1.5
Small	16-32	1.0
Gravel		
Coarse	8-16	0.75
Medium	4-8	0.50
Fine	2-4	
Sand		
Very coarse	1-2	0.25
Coarse	0.500-1	
Medium	0.250-0.500	
Fine	0.125-0.250	0.10

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[1] After Tolkamp 1980.

[2] After Maitland 1990.

5.1.2 Responses to Changes in Flow (Active Migration into Refugia)

In contrast to being stranded passively, if a benthic organism exhibits a behavioural response to increasing hydraulic forces (flow) and actively moves to an area with lower hydraulic stress (i.e., a refugium) by swimming, crawling or deliberate entry and controlled exit from the drift, then an 'active' mechanism is used to enter the refugium. If the organism, once in the refugium, cannot follow the receding water level and becomes stranded, then the mechanism by which the organism became stranded was an active process.

Evidence suggests that benthic organisms can track flow velocity gradients and alter their movement in response to changes in these velocity gradients. Lancaster (1999) used laboratory flumes to investigate the small-scale movement and distribution patterns of three common benthic macroinvertebrates *Oreodytes sanmarkii* (Sahlberg), *Leuctra inermis* (Kempney) and *Ephemerella ignita* (Poda), in response to simulated high flows. During these simulated high flow events, the numbers of *O. sanmarkii* and *E. ignita* were significantly reduced in areas of the flume with very high near-bed flow velocity and animals accumulated in areas of low near-bed flow velocity (refugia). In this study both active and passive modes of movement contributed to the accumulation of *O. sanmarkii* and *E. ignita* in areas of low near-bed flow velocity. It was observed that individuals drifted between microhabitats, entry into the drift was either active or passive and returning to the substrate from the water column (deposition) was an active process. Individuals of *O. sanmarkii* swam down to the substrate, whereas *E. ignita* altered its body posture causing it to sink and regain the substrate. Cambell (1985) also showed that nymphs of *Baetis* spp. could control how long they remained in the water column (i.e. drifting) by swimming, and by altering their body posture and parachuting (where an individual has uplifted abdomen and outstretched legs) in order to move out of the water column to a more favourable habitat. In a similar study Holomuzki and Biggs (2000) examined how four taxa (a mayfly *Deleatidium* spp., a mud snail *Potamopyrgus antipodarum* (Gray) and two stony-cased caddisflies *Pycnocentrodes aeris* (Wise) and *Hudsonema amabilis* (McLachlan)) responded to elevated flows in a recirculating laboratory flume. All the taxa responded to incrementally increased flows by moving into deeper, more stable layers within the substrate, which is consistent with the hypothesis that some macroinvertebrates seek out flow refugia during high flow events. When subjected to incrementally increased flows, the caddisflies that remained on the substrate surface produced draglines during high flows to resist dislodgement. The dislodgement of organisms during simulated flash floods was linked to substrate stability and the likelihood of dislodgement varied amongst the taxa. Compared to the snails and mayflies, the caddisflies were dislodged at a higher rate in both stable and unstable substrates and this was attributed to the propensity to occupy epibenthic surfaces. The study also showed that for the caddisflies were unable to produce draglines to resist dislodgement when subjected to simulated flash flood (30 s ramping time).

Clearly, animals (e.g. caddisfly larvae) could become stranded via active and/or passive means and this chapter will attempt to address the question, by which mechanisms (active or passive) do some cased caddisfly enter areas of low hydraulic stresses i.e refugia. In Chapter 4 it was established that cased Trichoptera are found stranded on previously inundated stream banks after floods, and that the incidence of being stranded is species/ case-specific. In this chapter I present the results of an experiment designed to test directly whether cased Trichoptera move laterally and actively from the high flow velocity stream channel to the low flow velocity inundated stream banks. It seems reasonable to assume that individuals can and do get deposited passively on the stream banks. The survey results of Chapter 4 suggest that passive deposition was the dominant mechanism by which animals became stranded. The challenge is to determine whether active movement ever occurs.

The microdistribution and movements of cased Trichoptera were examined in a laboratory flume in which the near-bed flow velocity varied spatially. The flume was comprised of a central main channel with high near-bed flow velocity and two margins with low near-bed flow velocity (simulating lateral/bank-side flow refugia). This arrangement created a flow velocity gradient that decreased with distance from the main channel, allowing organisms to move between areas with different near-bed flow environments. Discharge was manipulated to simulate a flood with high near-bed flow velocity in the main channel. The microdistribution pattern of cased caddisflies in the flume was compared among different velocity regimes: high, intermediate and no flow (control). Four species of cased Trichoptera (with cases constructed of different materials) that are present in the Whiteadder Water were used to test whether movement into refugia (areas of low near-bed flow velocity) was by active or passive. If animals can move actively into stream bank refugia then at high near-bed flow velocity, cased Trichoptera would move away from the main channel and into the areas of the flume with low near-bed flow velocity such as the banks or the out-flow. This change in the microdistribution could only arise from the organisms walking down a flow velocity gradient, perpendicular to the main channel. The flume was designed such that passive deposition was impossible. I predicted species-specific responses based on the case morphology and animal behaviour. Those species with a heavy coarse mineral case (which may act as ballast) or streamlined case may be able to withstand the high near-bed flow velocity. Their microdistribution would remain unchanged across flow treatments. Those species with a light-weight or a non streamlined case may actively move to areas of low near-bed flow velocity or become dislodged and deposited at the flume out-flow as velocity increased thus changing their microdistribution pattern. Lightweight cases, due to their nature, may be dislodged at a lower flow velocity, as the case does not provide as much ballast to keep the individual on the streambed (see Waringer 1989). Similarly, the hydraulic forces (near-bed flow velocity, lift and drag) acting on a non-streamlined case would be less to initiate dislodgement of the case from the streambed and transport the individual in the water column. Thus, individuals with this type of case would either have to actively move to areas of lower flow velocity or become dislodged and be deposited in areas of low flow velocity.

5.2 Materials and Methods

5.2.1 Animals

All four species used in the experiments were common in the Whiteadder Water but, for convenience were collected from the Glencorse Burn (NT 244 633), on the Bush estate to the south of Edinburgh. The site was considerably nearer than the Whiteadder Water, thus reducing the time required to transport the animals to the holding tanks and reducing stress and mortality of the collected individuals.

The four species were selected to encompass a range of case-types (coarse and fine mineral and vegetative cases), all of which occurred stranded on the banks of the Whiteadder Water (see Chapter 4). All individuals were IV-V instar with a similar case length. *Potamophylax latipennis* (Curtis) has a cylindrical and slightly longitudinally curved case with slight dorso-ventral flattening, and the case is composed of coarse mineral fragments such as small pebbles (Figure 5.2.1A). Two species, *Odontocerum albicorne* (Scopoli) and *Sericostoma personatum* (Spence), had similar fine mineral cases. *Sericostoma personatum* has a curved case constructed of fine sand grains and is closed at the posterior end by a slightly conical membrane with a central hole (Figure 5.2.1B). *Odontocerum albicorne* also has a curved case composed of fine sand grains; the posterior end differs from the case of *S. personatum* with the opening protected by a small pebble (Figure 5.2.1C). *Halesus radiatus* (Curtis) has a vegetative case (Figure 5.2.1D) which is usually a rough outline made of butted vegetative fragments with the addition of long sticks.

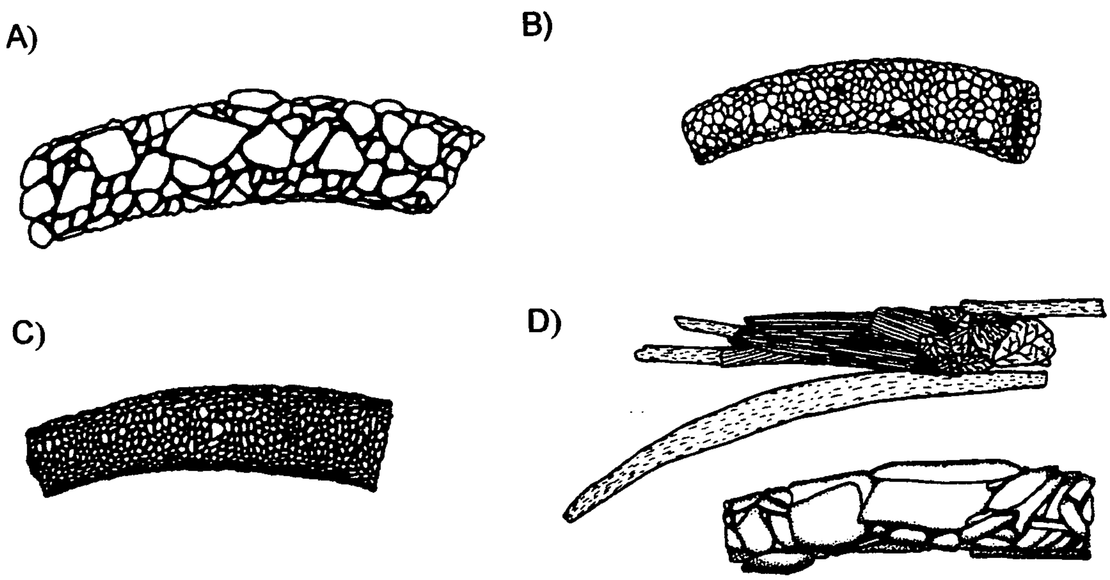

Figure 5.2.1 Illustrations of the four Trichoptera case types used: A) *Potamophylax latipennis* (coarse mineral) B) *Odontocerum albicome* (fine mineral) C) *Sericostoma personatum* (fine mineral) and D) *Halesus radiatus* (vegetative). Drawings reproduced from Wallace, Wallace and Philipson (1990).

The case of each individual was labelled with a coloured tag (black, blue, green, yellow and red), so that individuals could be followed during trials. Each tag was a small square of waterproof paper (2x2 mm) adhered to the back of the case with Loctite Superglue 4. Observations prior to the experiments showed that the labels did not affect the mobility of the animals.

5.2.2 Artificial Stream

The study was carried out in a rubber-lined, wooden flume in a semi-outdoor facility at ambient temperature (air temperature 12 to 16°C) and low light (diffuse natural light from skylights). The flume was supplied with water using a closed circulatory system (Figure 5.2.2). Water was aerated continuously in an overhead water storage tank, fell by gravity into the flume, then through a series of gravel filters and was finally pumped back to the overhead tank. To compensate for any loss of water due to accidental spillage and evaporation, the system was topped up with de-chlorinated tap water when necessary. Under control conditions (no flow) the flume was filled up to a depth of 10 cm in the in-flow, out-flow and main channel flume sections (Figure 5.2.3A) and 5.5 cm in the banks. At the downstream end, water flowed over a 10 cm high metal barrier (which maintained the constant depth in the flume) and then back into the system to re-circulate. During the control period, there was no inflow or out flow. To create an intermediate flow, one inflow pipe was directed into the flume and to create a high flow both inflow pipes where directed into the flume. There was no natural substrate in the flume; the bottom of the flume was lined with 1 mm thick synthetic food grade rubber to avoid the possibility of toxic chemicals leaching into the water. An even layer of lime free sand (≤ 2 mm grit size) was glued to the rubber with non-toxic (child-safe) clear paint, to provide some friction for the animals compared to the smooth bare rubber. The species of case caddisfly used were all observed to 'slip', when walking on the plain rubber under no flow conditions, so a coarse substrate was used. Lancaster and Mole (1999) found that in general rougher textures (such as sand glued to rubber) allow individuals to maintain positions under high flow velocity, compared to a smooth (acetate) or intermediate (rubber) substrate. Therefore, a coarse substrate was used enabling the animals to move around the flume easily. Any results, therefore, are not confounded by the substrate of the flume not offering enough traction to enable locomotion of the caddisfly larvae.

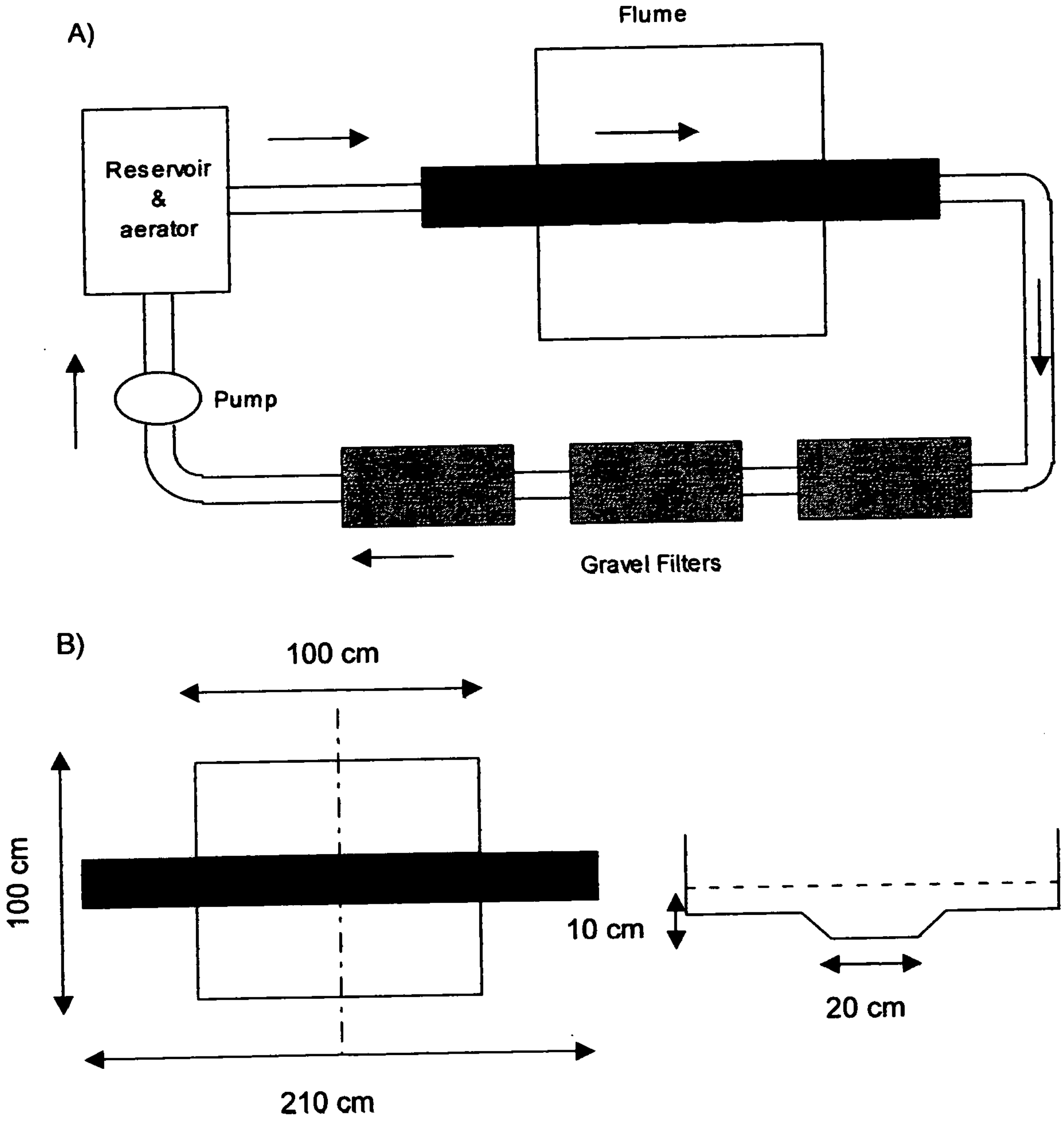

Figure 5.2.2 A) Schematic representation of experimental flume. The water was aerated in an overhead reservoir, fell by gravity through the flume, through a series of gravel filters and was then pumped to the reservoir to re-circulate. B) Plan and cross sectional views of flume showing main channel and inundated margins (water level is shown by dashed line in cross sectional view)

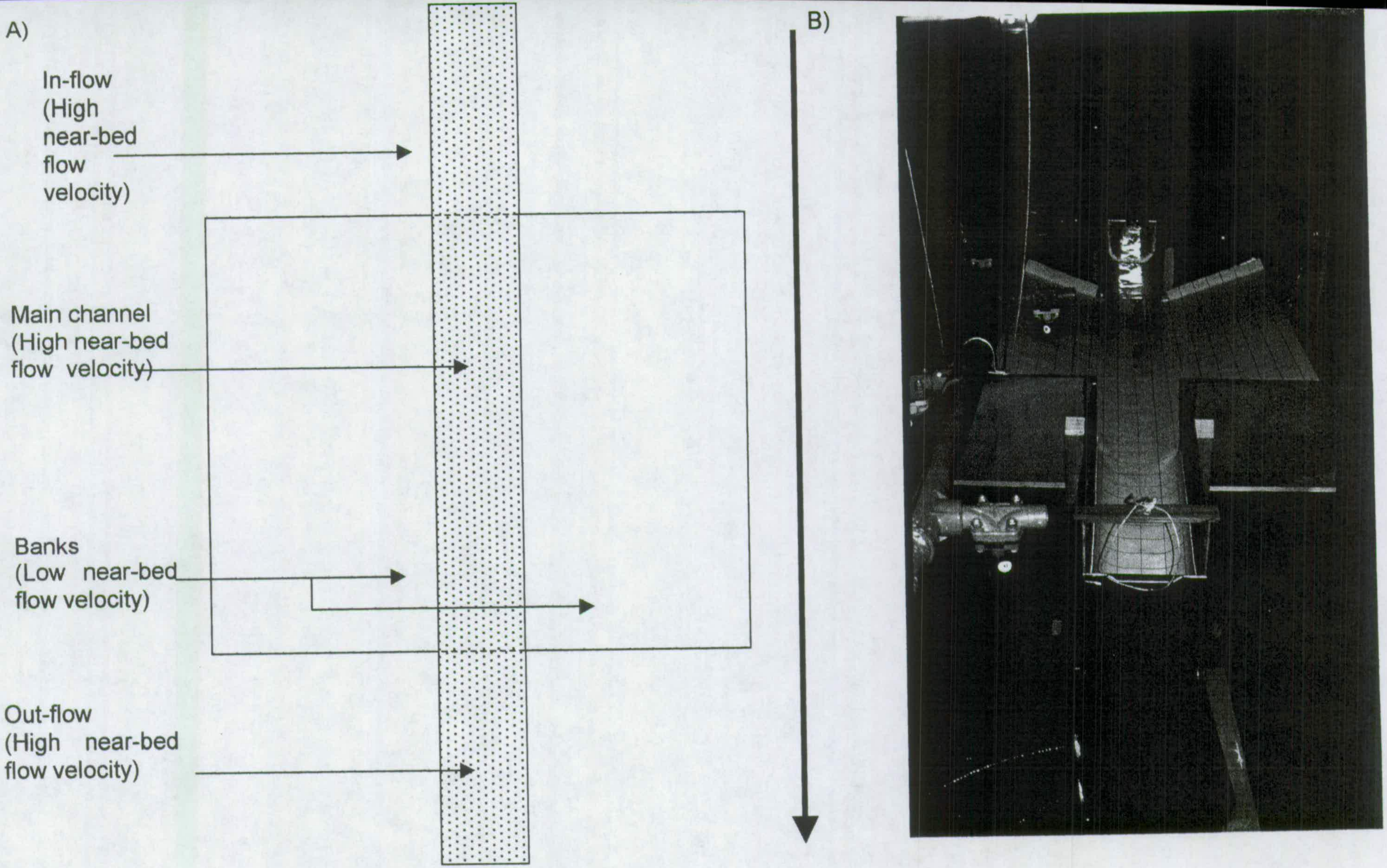

Figure 5.2.3 A) Schematic representation of near-bed flow velocity in each flume section. B) Photograph of empty flume showing 5x5 cm grids used for near-bed velocity measurements.

The artificial stream was essentially 2-dimensional with small-scale variations in the near-bed flow velocity due to the changing width and depth of the channel. This is a simplified environment compared to that found in natural streams and the flow patterns in the artificial stream were simpler than those in a natural stream. However, a controlled environment is required for meaningful experimental manipulations. Consequently, the movements of the animals within the flume were most likely to be a direct response to near-bed flow and not confounded by moving streambed particles or the cryptic behaviour of some species. The objective of this study was to identify regions of the flume with high and low near-bed flow velocity and observe whether the four species of cased Trichoptera moved laterally into areas of low near-bed flow velocity under two flow levels.

The flume was divided into 5x5 cm grids and velocity was measured within 1 cm of the flume bottom with a 2 cm discus, 2-axis Valeport Series 800 electromagnetic flow meter (Figure 5.2.4). The sensing volume projects 1 cm beneath the sensor disc. The meter has a range of 0.003-2.000 m s^{-1} with a detection limit of ± 0.001 m s^{-1}. Six readings were taken in the centre of each grid square for each treatment (high, intermediate, no flow and a mean value estimated for each the grid square, (Figure 5.2.5). The four flume sections (inflow, main channel, outflow and banks) differed from one another with respect to average flow velocity and flow velocity differed among treatments. There was no obvious bias in velocity between left and right banks (Figure 5.2.5). During the high and intermediate flow treatments the banks had the lowest mean near-bed flow velocity, thus creating a lateral velocity gradient analogous to that found in real stream channels. There was also a slight longitudinal velocity gradient as the sluice gate at the end of the flume reduced near-bed flow velocity (Figure 5.2.6). However, this gradient is weaker than the lateral velocity gradient.

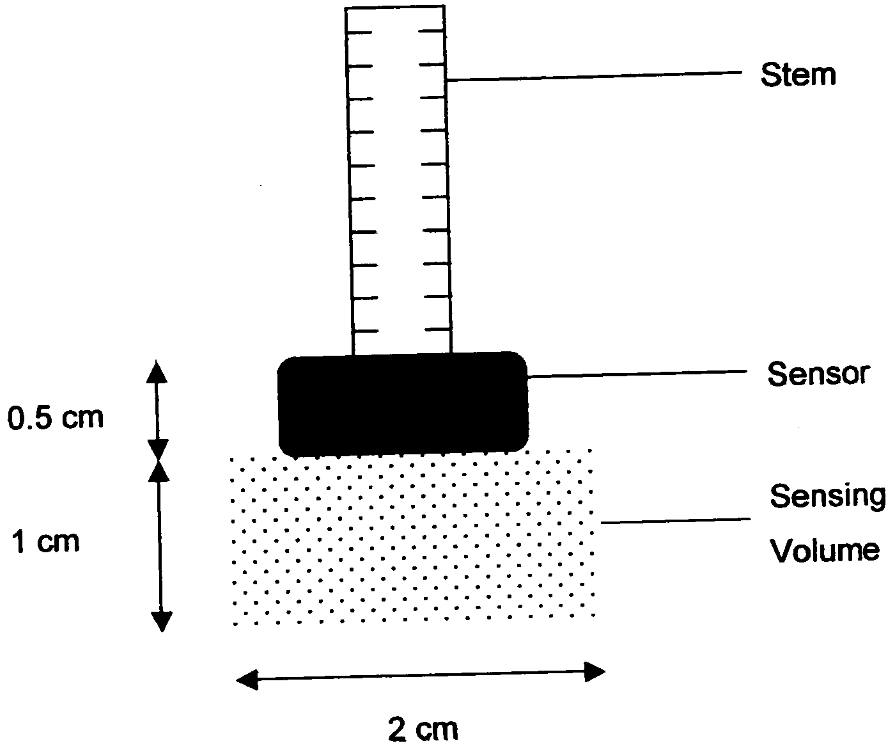

Figure 5.2.4 Cross-sectional drawing of discus sensor of Valeport series 800 electromagnetic flow meter, used to measure near-bed flow velocity within the flume. Drawing reproduced from Lancaster (1999).

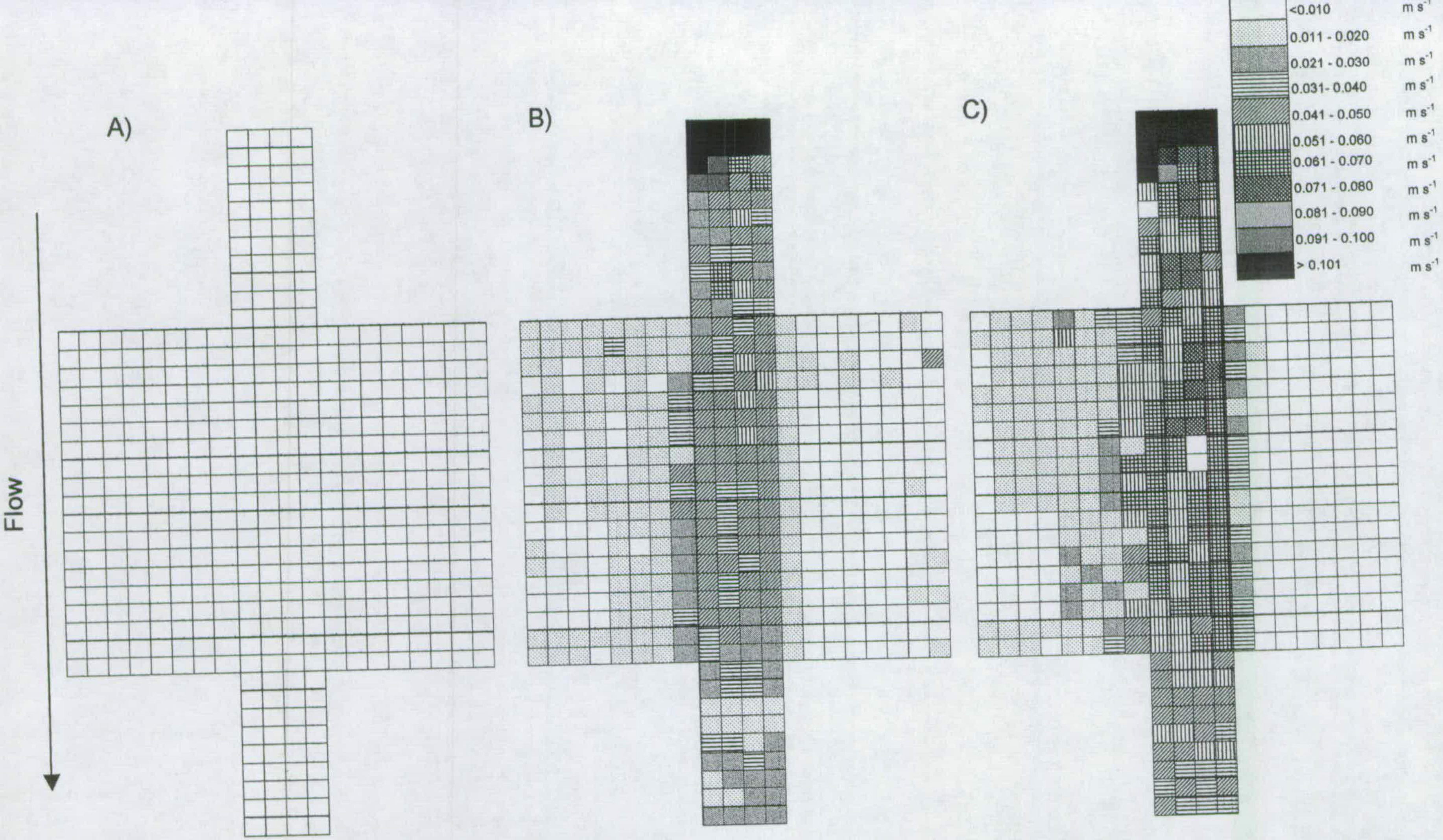

Figure 5.2.5 Near-bed flow velocity m s^{-1} (≈1 cm from the bed) in 5 × 5 cm grid squares with the flume under three flow levels A) no flow (no inflow pipes), B) intermediate flow (one inflow pipe) and C) high flow (two inflow pipes).

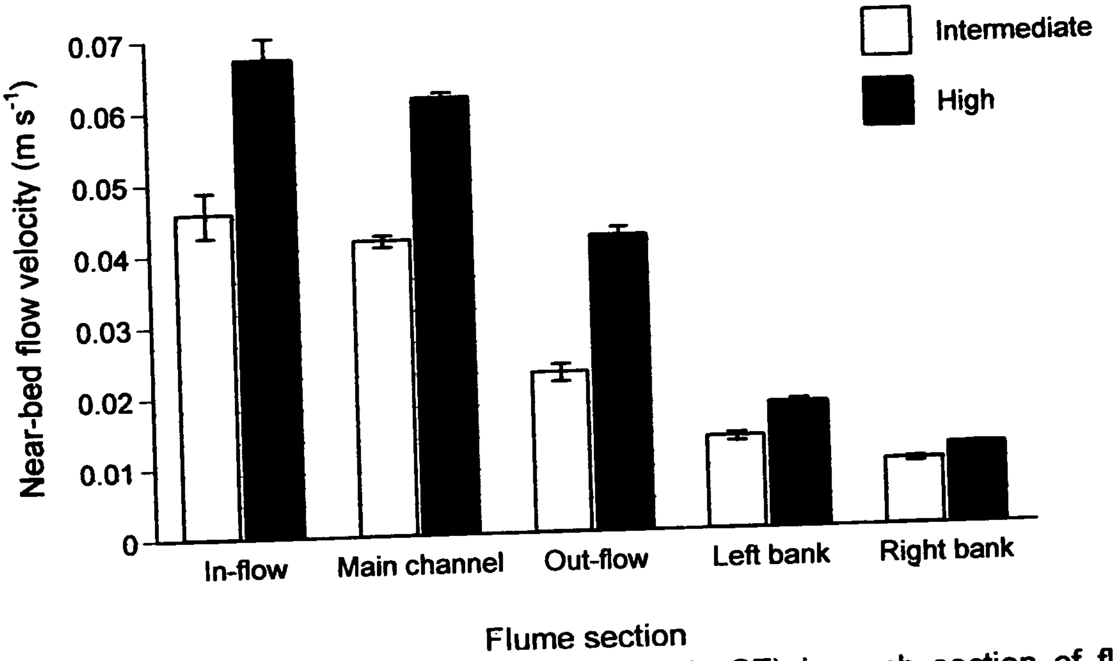

Figure 5.2.6 Mean near-bed flow velocity (± SE) in each section of flume during two flow levels: intermediate (one inflow pipe) and high (two inflow pipes). Velocity was 0 ms^{-1} in all parts of the flume during the control treatment.

5.2.3 Experimental Design and Data Analysis

The microdistribution of cased Trichoptera in the flume was observed under the three flow treatments: no flow, intermediate and high flows. Three replicate trials were carried out for each of the four species (*P. latipennis*, *O. albicorne*, *S. personatum* and *H. radiatus*) in late February and March 2000 during daylight. In each trial five animals were placed into the flume. This density is lower than maximum densities in the field (Chapter 3) to minimize the possibility of intra-specific interactions confounding any response to the experimental treatments. Once placed together in the main channel of flume, the animals were allowed 30 minutes to settle under no flow conditions. Once used in a trail, individuals were not used in any other trials. After settling, the position of each individual in the flume (i.e., the grid square) was recorded every five minutes for an hour. The duration of each trial was short but adequate to observe any short-term changes in the microdistribution patterns without confounding effects of increased hunger (as no food was provided in the flume) and any diel variations in behaviour. Similar trial lengths of 60-minutes, have been used in other flume studies by Lancaster (1999) and Lancaster and Mole (1999).

The micro-distribution of animals was compared using G-tests of independence (Sokal & Rohlf 1981; Fowler *et al.* 1998; Lancaster 1999). G-tests are used to test for significant interactions between the number of animals observed in each flume section and the flow treatment. The data for each trial were summarised as the total number of animals observed in each of four flume sections summed over the 60-minute observation period and over the three replicates. There was no obvious bias in the number of animals on the left or right bank; so the numbers of animals on the left and right bank were combined and are referred to as banks in the remainder of this chapter. Summing the data across the replicates increases the confidence that the patterns observed are real rather than occurring by chance (Lancaster 1999a; 1999b). Summing the data also has an advantage in reducing the number of cells in the matrix with low values which can affect the G-statistic.

5.3 Results

With no flow, all four species explored all sections of the flume, and showed no preference for any particular area of the flume. All four species changed their microdistribution in a similar way when exposed to the flowing water (Figure 5.3.1). Two-way G-tests indicated that the microdistribution pattern was significantly different in the control treatment, compared with both the intermediate and high flow treatments (Figure 5.3.1). The G-tests indicate that in all species the proportions of individuals (number of observations) in each of the areas of the flume, was significantly different in both the high and intermediate treatments when compared to the no flow (control) treatment. For example in all species duringthe high flow treatment, the number of observations of individuals in the out-flow flume section was higher than in the no flow (control) treatment (Figure 5.3.1).

Curiously, all animals stayed within the main channel during the 30-minute settling period. Though individuals did move around the spot where they were initially placed, and orientated themselves in a different position to that in which they were placed in the flume. However, by 10 minutes during the experimental observation period individuals had moved away from their initial starting place (Figures 5.3.2 to 5.3.5). Unfortunately during the course of the experiement, several individuals of *H. radiatus* disappeared from the flume and were presumed to have been swept out of the flume, though they could not be found. This led to a pooled total of six observations after 15 minutes (Figure 5.3.5).

In all species and at high flow, individuals walked directly downstream out of the main channel and into the outflow section within roughly the first 20 minutes (Figures 5.3.2C-5.3.5C). Once in the outflow section, there was virtually no movement back into the other sections of the flume during the 60 min observation period. Individuals of all species in the high flow treatment were often orientated with the case pointing in the same direction of the current (i.e., head pointing downstream) though this seems dynamically unstable. This would present a lower cross sectional resistance to the current than if they were side-on to the current. When animals moved laterally to the current, movement was slower and animals frequently changed direction and returned to a position in line with the current.

At intermediate flow, the microdistribution of cased Trichoptera was similar for all species and was truly intermediate between high and no flow (Figure 3.5.2B-3.5.5B). The micro-distribution pattern of the individuals in the different flume sections changed very little after 40-45 minutes. Individuals did not orientate themselves with the current as at high flow velocity, and locomotion across the flow of the current appeared unhindered. Individuals of *Potamophylax latipennis* (Figure 5.3.2B) moved from the main channel into all sections except the inflow. Individuals of *Odontocerum albicorne* (Figure 5.3.3B) occupied all the sections of the flume rapidly (including the inflow section). *Sericostoma personatum* behaved in a manner similar to that of *O. albicorne* (Figure 5.3.4B). *Halesus radiatus* was the only species to show a strong preference for the banks in the intermediate flow treatment (Figure 5.3.5) and, like *P. latipennis,* was not observed in the inflow section after 10 minutes.

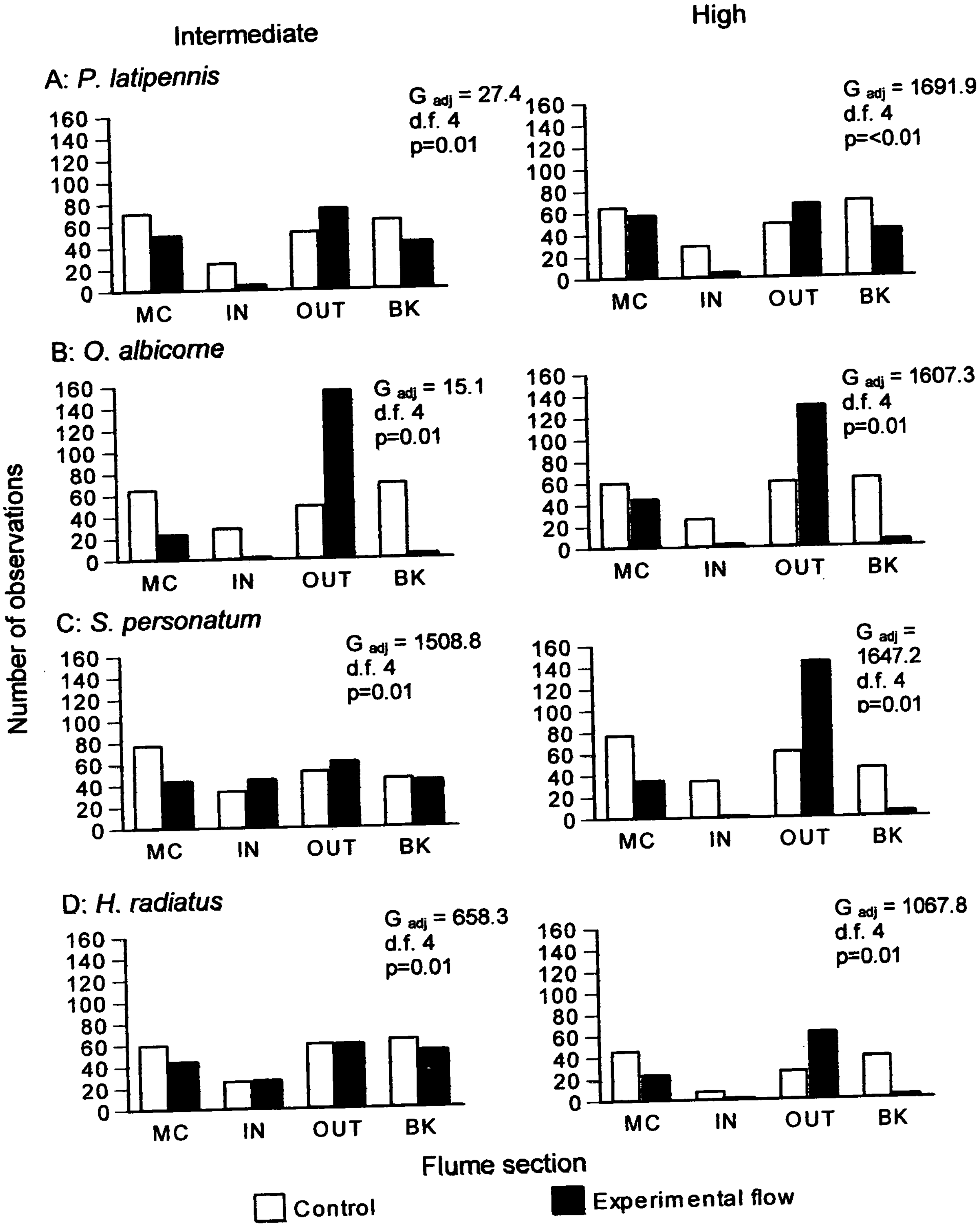

Figure 5.3.1 The pooled number of observations for four caddisfly species in each flume section. Where MC= main channel, IN= inflow, OUT= outflow and BK = combined left and right banks. See text for explanation of G-test results.

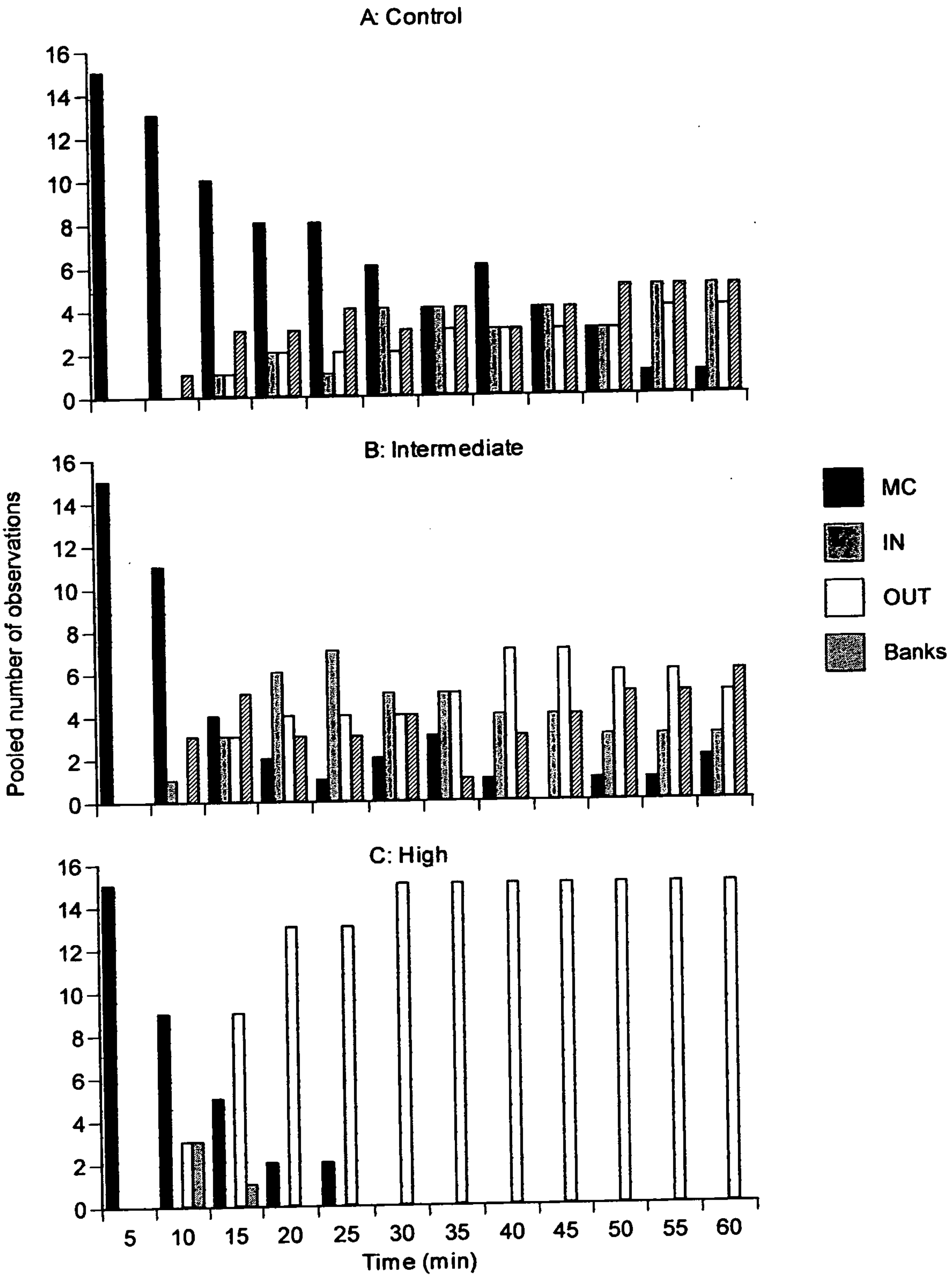

Figure 5.3.3 Pooled observations of the position of *O. albicorne* against time in a experimental flume under three flow regimes. A: Control (no flow), B: Intermediate flow and C: High flow. Where MC= Main Channel, IN= Inflow, OUT= Outflow, and Banks = combined left and right banks.

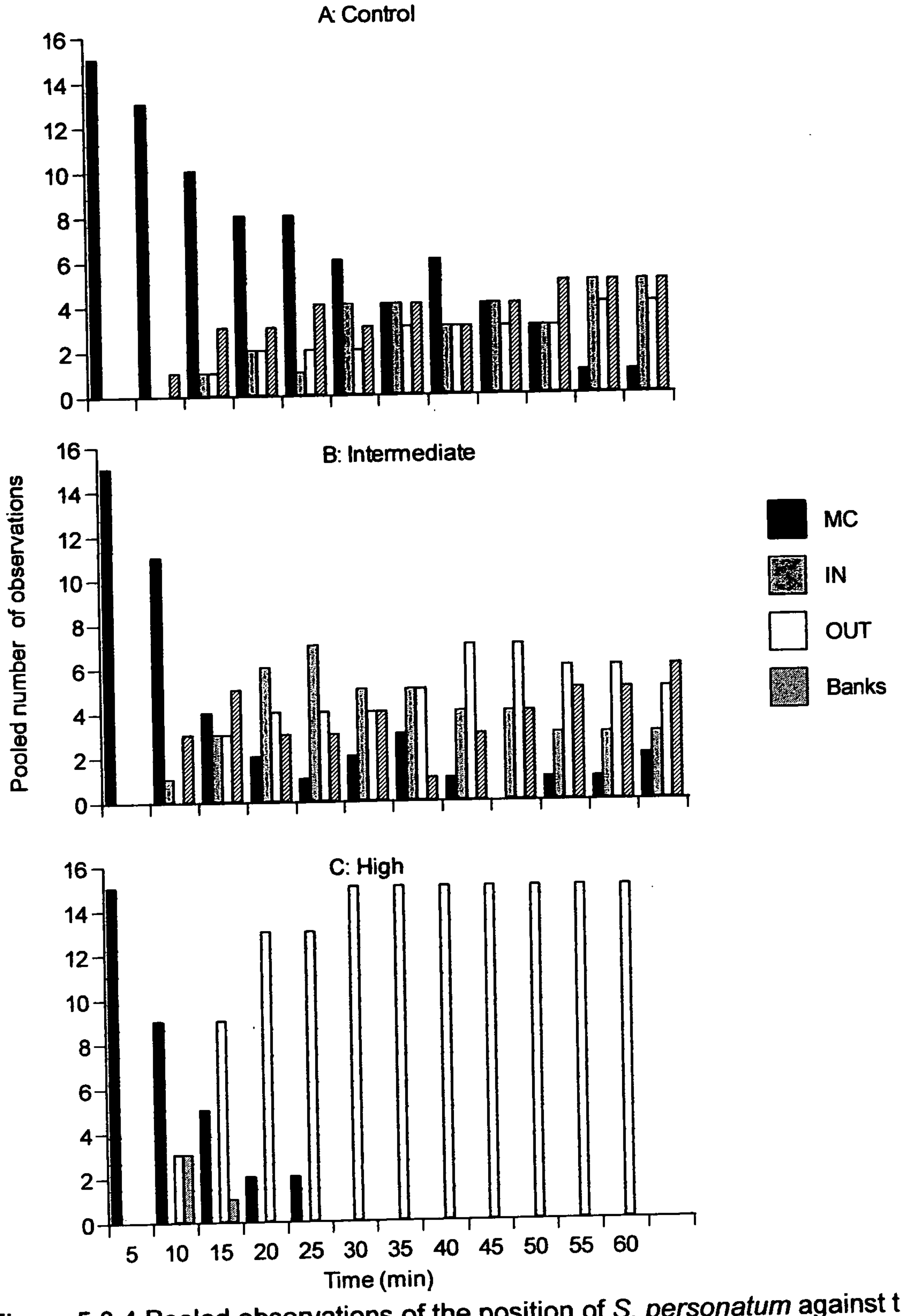

Figure 5.3.4 Pooled observations of the position of *S. personatum* against time in a experimental flume under three flow regimes. A: Control (no flow), B: Intermediate flow and C: High flow. Where MC= Main Channel, IN= Inflow, OUT= Outflow, and Banks = combined left and right banks.

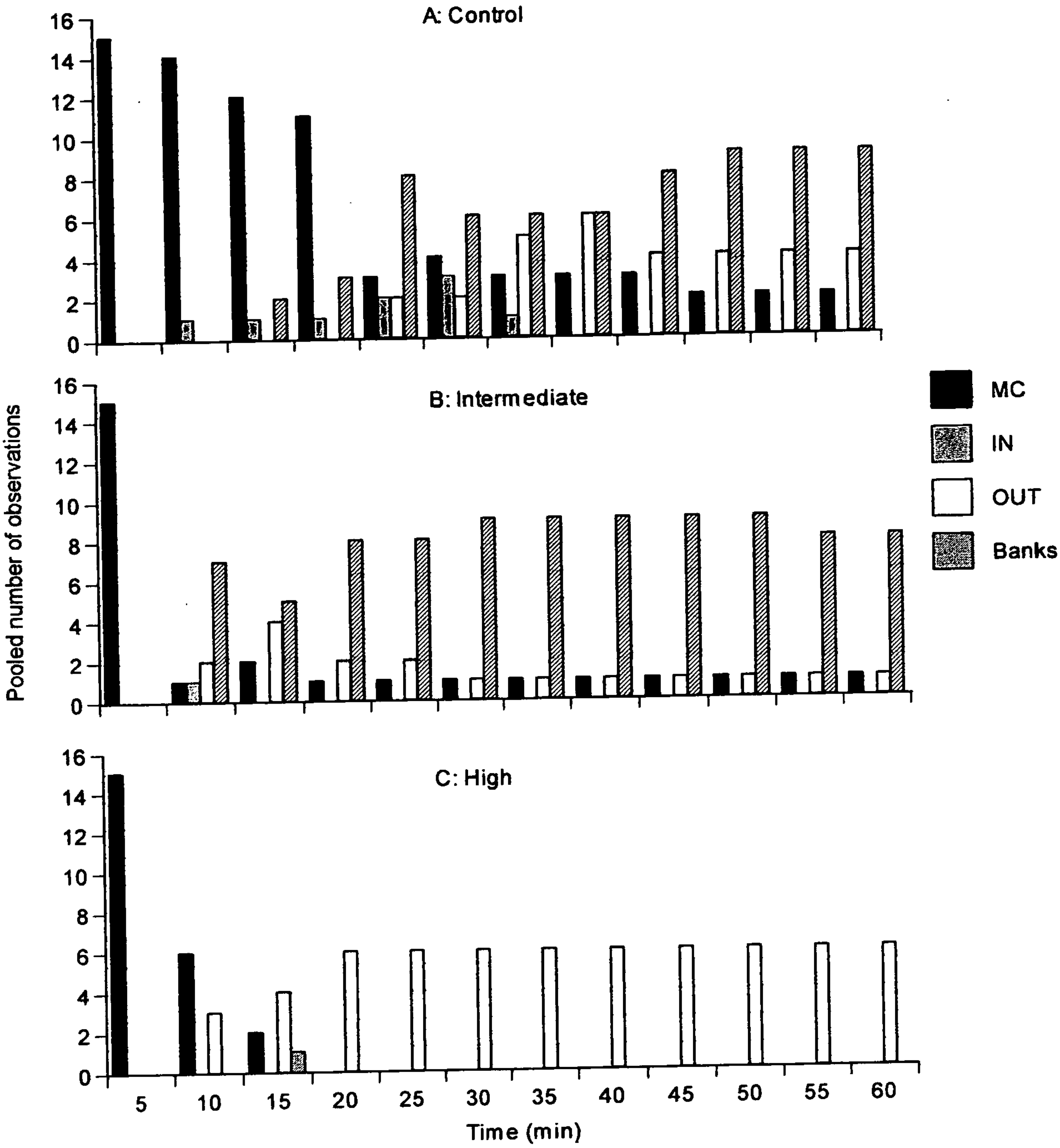

Figure 5.3.5 Pooled observations of the position of *H. radiatus* against time in an experimental flume under three flow regimes. A: Control (no flow), B: Intermediate flow and C: High flow. Where MC= Main Channel, IN= Inflow, OUT= Outflow, and Banks = combined left and right banks.

5.4 Discussion

5.4.1 Passive or Active?

The absence of lateral movement in my experiment suggests that active movement into the margins may not occur and, consequently, the way individual caddisfly larvae become stranded must be a passive mechanism. Under high flow conditions all species moved downstream into the outflow section, which had lower mean flow velocity (0.050 ms^{-1}) than the inflow (0.070ms^{-1}) or main channel (0.066 ms^{-1}). Curiously, animals did not move into the section with the lowest mean flow velocity, the banks (0.03 ms^{-1}). The lack of lateral movement appears to contradict studies reporting that during floods aquatic invertebrates can use inundated floodplains and other areas that are dry at normal discharge (Perry and Perry 1986; Badri *et al.* 1987; Rempel *et al.* 1999; Matthaei and Townsend 2000). However, these studies did not detail how the animals move into inundated areas. Passive deposition of detritus on stream banks is a common phenomenon and it seems reasonable to assume that this happens to caddisflies that become entrained in the drift. The flume design precluded observations of passive deposition in this experiment.

Ideally, microdistribution patterns would be observed in the field, but a laboratory flume with well characterised near-bed flow made it possible to observe how the variations in near-bed flow velocity affect the microdistribution and movement of caddisfly larvae without confounding factors. Compared to natural stream channels, which are very heterogeneous in terms of substrate, complexity and the associated spatial and temporal variations in near-bed flow velocity, the flume had a very simple, two-dimensional structure. Measurements of the near-bed flow velocity were made within 1 cm of the flume substratum, which is within the region occupied by the study organisms and which cannot be easily measured in the field without complex equipment (see Hart *et al.* 1996; Sand-Jensen and Mebus 1996; Bouckaert and Davis 1998). Results from flume experiments must be interpreted with care, however, as flumes are artificial environments. For example the design of the flume prohibits any cryptic behaviour, such as moving downwards into the hyporheic zone in response to increased hydraulic forces. This vertical movement occurs in meiofauna during floods

(Dole-Olivier and Marmonier 1992; Dole-Olivier *et al.* 1997), although the evidence for macroinvertebrates is equivocal. In the two-dimensional arena of the flume, animals are limited in their repertoire of behaviours and the results of flume experiments must be interpreted with caution and within these limitations.

5.4.2 Microdistribution and Instream Flow Refugia

The observed change in the distribution of the four species of cased Trichoptera between areas of different near-bed flow velocity microhabitats during a simulated flood (high flow event) is consistent with the concept of flow refugia (Lancaster and Belyea, 1997; Lancaster, 1999) in that individuals moved into areas of lower near-bed flow velocity. During, the high flow treatment, all the species walked down-stream to an area of lower near-bed flow velocity. This may indicate an active response to the avoidance of high flows, but individuals did not move to the lowest velocity section, on the banks. Observations of individual behaviours within the flume suggested that the individuals were orientated to minimise dislodgement (i.e. facing downstream) and were reluctant to move across the direction of flow. Such a position minimises the surface area of the case exposed to the flow and hence the risk of dislodgement. Orientation to the direction of flow can affect the susceptibility of aquatic macroinvertebrates, including cased Trichoptera, to dislodgement from the substrate (Waringer, 1989, 1993; Statzner and Holm 1989; Weissenberger *et al.* 1991). Waringer (1989; 1993) found that the current speed required to dislodge instar V cased caddis of several species orientated laterally to the direction of flow, was less than when individuals were placed facing the direction of flow. This was attributed to an increase in the drag coefficient for perpendicular over parallel orientation to the direction of flow. Waringer (1993) and Otto (1976) both found that *Potamophylax cingulatus* (Stephens) (which has a very similar case construction to *P. latipennis* (Curtis)) required the greatest near-bed flow velocity to initiate dislodgement. When orientated into the flow, *P. cingulatus* could resist flows up to 0.85 m s^{-1}, which was reduced to 0.20 m $s^{-1}$when placed laterally.

The results indicate that individuals move away from high velocity towards lower velocity, but they do not necessarily find the lowest velocity patch. The direction of movement is constrained by behaviours that appear to reduce drag (and hence the risk of dislodgement). There may be situations where the velocity gradient and the current direction would lead animals towards stream banks during floods, but these are likely to be the exception rather than the rule.

The spatially heterogeneous flows within a stream channel caused by instream objects (such as large rocks) may by chance cause benthic organisms to move onto the inundated margins of the stream. If an organism has to constantly orientate itself to different directions of flow in a natural channel to minimise the hydraulic forces acting upon it, these forces may by chance direct the organism to move onto the inundated margins with low hydraulic stresses. If the concept of flow refugia were true then the organism would be most likely to remain in the areas of low hydraulic stress such as the inundated margins. Although there was a lack of lateral movement, the results are consistent with the flow refuge hypothesis, as individuals once in the lower velocity area of the out flow rarely moved out of the section into areas of greater hydraulic stress.

The results of the flume experiment suggest that most, if not all, of the stranded animals found on the banks of the Whiteadder Water (Chapter 4) were deposited passively. In a natural channel the complex structure of the substrate and rapid changes in the direction of flow would make it difficult for animals to orientate themselves to minimise the forces of flow in many situations and especially during floods. Consequently, dislodgement and entrainment in the drift may be common and, likewise, deposition in low velocity areas such as the inundated margins of the stream. In the flume this was not a factor, so the animals could and were observed to orientate themselves to minimise the hydraulic forces acting upon them and thus prevent dislodgement. It was possible to reproduce moderately high flows (up to 0.08 m s^{-1}), which were at the high end of the velocity range recorded within pools occupied by these species in the Whiteadder Water (Chapter 3). It was impossible to produce very high near-bed flow velocity in the flume. Higher near-bed flow velocity does occur in the natural system (see Chapters 3 and 4) and exceeds the velocity that Waringer (1989; 1993) and Otto (1976) observed to initiate dislodgement of many species of cased Trichoptera.

The lack of species-specific responses may be real or due to an artefact of the experimental design. The lack of differences between individual species tolerances to near-bed flow velocity treatments may be attributed to the coarse sand substrate that may have offered more resistance to dislodgement from high flow than natural conditions enabling all the species to maintain their position during the high flow and not become dislodged (see Lancaster and Mole, 1999). Thus, in natural conditions with less coarse substrate, a lower flow velocity may have initiated dislodgement or stimulated the animals to move. Other environmental cues, along with the increase in velocity during a flood may initiate the movement of the individuals. Observations of particle movements in flumes and field studies (see Gordon *et al.* 1992) indicate that particles begin to vibrate as the flow intensity increases. In the flume the sand was glued to the rubber and therefore could not vibrate; if species use the increased intensity of vibration of the substrate as a cue to move actively to areas of low velocity then this could not occur (though the whole flume might vibrate).

The increase in the water velocity to simulate a flood may have occurred too rapidly for the caddisflies to exhibit their natural responses to environmental cues and produced an atypical response from the caddisfly species used. Holomuzki and Biggs (2000) showed that when the stony cased caddisfly species *Pycnocentrodes aeris* (Wise) and *Hudsonema amabilis* (McLachlan) were subjected to an incremental increase in flow they produced silken drag-lines that increased resistance to dislodgement. The production of silken draglines though increasing the resistance to dislodgement would not enable individuals to move into areas of flow refugia. If the hydraulic forces exceeded the strength of the silken line or the substrate that it was attached to became mobilised during a flood then the individual would become entrained in the drift, and therefore has the potential to become passively stranded. When these species were subjected to a rapid increase in flow (30 s ramping time) they did not produce draglines and were more prone to dislodgement. It could be assumed therefore, that rapid flood events that occur naturally in 'flashy' temperate first order streams would lead to dislodgement and the entrainment of individuals in the water column as behavioural responses to environmental cues may not occur rapidly enough to counter the increased hydraulic forces of a flood and thus the main mechanism causing individuals to become stranded appears to be a passive one. This also highlights the importance of environmental cues in the initiation of responses to environmental change, such as refuge seeking mechanisms. This is an under-explored area of research and is vital to the understanding the mechanisms involved with refuge use in macroinvertebrates.

The very fact that a response to increased near-bed flow velocity was observed suggests that cased Trichoptera do change their microdistribution patterns in regard to changes in the flow regime, which is consistent with the idea of flow refugia. The mechanism by which cased Trichoptera move between flow microhabitats in the flume depends on flow conditions and appears to be an active mechanism, but there is no lateral movement so why are cased Trichoptera found on the bank-sides of the Whiteadder? In high near-bed flow velocity conditions in natural channels, the organisms may not be able to orientate themselves to minimise the hydraulic forces acting upon them and the forces involved are likely to exceed that which we could mimic in the artificial stream system. As a result there is a greater possibility of dislodgement and subsequent deposition in natural streams.

6 Factors Affecting the Ability of some Trichoptera to Regain the Water Once Stranded: An Experimental Study

6.1 Introduction

Flooded margins of rivers may act as flow refugia during floods, as the velocity of water tends to decrease from the centre towards the margins because of the frictional resistance of the bed and banks (Gordon *et al.* 1992). The flood plain is an important flow refugium for fish in some lowland rivers (Schlosser 1991) and Badri *et al.* (1987) have suggested that it may be important for macroinvertebrates. Rempel *et al.* (1999) showed that benthic macroinvertebrates shifted from deep water to shallow water of the shore zone during annual flooding of the Fraser River, British Colombia. I have shown in Chapter 4 that caddisfly larvae can become stranded on the banks after high discharge events, supporting the idea that the inundated margins of streams may act as a refugium from hydraulic disturbance.

Organisms that exploit this temporary habitat must tolerate being stranded once the water level recedes, at least until they can actively regain the stream (by walking back to the water), until the water level rises again. The movements of organisms into refugia may be active (the organisms actively walk or swim into refugia) or passive (organisms are dislodged from the bed and deposited in an area of low hydraulic stress) though passive deposition appears to be the dominant mechanism for caddisflies on bank-sides (see Chapter 5). Movement back to non-refugium patches after the disturbance is important as it allows benthic invertebrates to re-colonise areas denuded by the disturbance (Lancaster and Hildrew, 1993; Lancaster and Belyea 1997). In the case of instream flow refugia, organisms can stay in the areas that acted as refugia during the hydraulic disturbance or re-colonise non-refugium areas (Robertson *et al.* 1997; Lancaster and Belyea 1997). Inundated margins, however, are ephemeral refugia, so organisms must move or perish. Trichoptera were found alive on banks after floods (Chapter 4) and I assumed I only recorded animals that could not, or had insufficient time to regain the stream after the water level receded. Individuals that had already successfully regained the water were not recorded. The ability of caddisfly larvae to return to the water therefore needs to be examined in order to test this assumption that individuals stranded after floods can return to the water and to determine what factors might influence a successful return to the water. That is the subject of this chapter.

Movement between the water and terrestrial habitats is not a requirement for most larvae of aquatic benthic organisms to complete their life cycles or to feed and many taxa may not survive being stranded. Drifting organisms can be deposited in depositional areas, such as gravel beds, and can become buried (Dobson *et al.* 1997; Dobson *et al.* 2000). Following a large flood, Dobson *et al.* (1997) found individuals of *Potamophylax cingulatus* buried within newly deposited aggregations of gravel in a first order stream. These animals were unharmed, but devoid of their cases. They speculated that upon burial the animals were unable to dig themselves out of the sediment with their cases so the cases were abandoned and the animals emerged naked. In a subsequent experiment, Dobson *et al.* (2000) found that when buried, the case mass of *P. cingulatus* probably physically impeded movement through fine particles. In coarse sediment, the actual weight of the particles may have slowed down the movement of the animals through the sediment. If animals are buried in bank-side gravel beds, then they could become stranded in a dewatered zone by the time they dig themselves out to emerge on the substrate surface. Matthaei and Townsend (2000) also found animals stranded on previously inundated floodplain gravels of the Kye Burn, New Zealand. They found that the mean total densities of stranded and dead invertebrates in the dry flood plain was equivalent to a considerable percentage (≈ 20%) of the invertebrate density found during the flood on the gravel bed.

It is possible that highly mobile aquatic invertebrates will have low tolerance to exposure, as they are able follow the receding water level (e.g. Ephemeroptera) and the risk of being stranded is low. In contrast, sessile or less mobile species (i.e. chironomids and bivalves) are more likely to tolerate exposure. Nymphs of

Ephemeroptera, such as *Baetis* spp., are highly mobile and may avoid being stranded by drifting and by actively crawling or swimming to deeper water in response to receding water levels. In experimental channels, only *Baetis tricaudatus* Dodds avoided being stranded when the water levels were artificially reduced (Corrarino and Brusven 1983). Fisher and Lavoy (1972) and Corrarino and Brusven (1983) showed that chironomids, which do not or cannot actively migrate to deep water with rapidly receding water levels, dominated the recently exposed areas. Brusven *et al.* (1974) showed that chironomids had a high tolerance to exposure in the cool springtime, with negligible mortality after 24 hours and high survival even after 96 and 120 hours exposure. . Tolerance to exposure to air (emersion) is therefore very important for sessile and less mobile aquatic organisms that live in habitats with variable and widely fluctuating water levels. Freshwater bivalves are generally not very mobile organisms and may be exposed for extended periods (weeks or months (Dance 1958))that are unpredictable in duration and timing due to droughts or seasonal dry periods (Byrne *et al.* 1988; Bryne and McMahon 1994). In contrast, intertidal organisms usually experience only brief (6-10 hrs), predictable periods of emersion. In marine bivalves, emersion tolerance is generally correlated with zonation on the shore and they can only tolerate brief periods of emersion, unlike their freshwater relatives. Freshwater bivalves are generally far more tolerant to emersion/desiccation than their marine counterparts and this has been attributed to behavioural and morphological adaptations. *Anodonta grandis* (L.) has a very thin shell incapable of sealing completely when closed as a result it is not very tolerant to emersion and desiccation (Byrne and McMahon 1991). The main adaptation of *A. grandis* to emersion is an ability to rapidly migrate vertically downwards when it becomes exposed to air, thus avoid desiccating conditions by moving into the substrate (Bryne and McMahon 1994). Species of freshwater bivalve that do not exhibit this downward migration (e.g. *Uniomerus tetralasmus* and *Corbicula fluminea*) have thicker less porous shells whose valves fit together tightly minimising water loss (Byrne *et al* 1988; Byrne and McMahon 1994). As a result *U. tetralasmus* and *C. fluminea* are usually able to survive emersed until the water level rises again immersing them (Byrne and McMahon 1994). The case of caddisfly larvae is analogous to the shell of molluscs and may offer some protection to air exposure, by increasing desiccation tolerance. Larvae of Trichoptera require an aquatic medium in order to respire via their closed tracheal system and gills (Hickin 1967). As the case of caddisfly larve is a open-ended tube in the majority there would be no conflict between case impermeability and providing protection from dessication and porosity providing gaseous exchange for respiration. The presence of a case may act as a physical barrier to water loss from the case enabling the individual to survive longer when exposed (see Chapter 1 and Chapter 4, Section 4.1.2 for detailed discussion). Species that have a porous case (i.e. containing loose fitting pieces of vegetation) may be more susceptible to desiccation (as with freshwater bivalves with thin porous shells) and may be more mobile in order to regain the water. Species that have a less-porous case (i.e. of close fitting mineral particles) may be more desiccation tolerant, but less mobile, as with freshwater bivalves that have less porous shells and poor mobility (Byrne *et al* 1988; Byrne and McMahon 1994).

The movement of aquatic organisms in air and water is likely to be different due to differences in the density of the fluids. In water the cases of Trichoptera are supported in part by the dense aqueous medium. The lack of such support when stranded in air may affect the way individuals move. Larvae move their cases by walking and dragging the case across the substrate. Lifting the case above the substrate, or by a cycle of lifting and dragging the case, friction between the case and substrate may be reduced. In air, without the support of water, animals may be unable to lift their case as high above the substrate (clearance) and this results in increased friction and drag. Thus, individuals would move more slowly and require more energy expenditure to move. The material used in the construction of the case could also affect the mobility of cased caddisfly larvae. For example, caddisfly larvae with a heavy mineral case or with a high case to body weight ratio may be less mobile than those with a lighter organic case when stranded, due to the weight of the case without the support of water. This restriction in mobility and a greater expenditure of energy may prevent animals regaining the stream.

The mobility of stranded cased larvae may also be affected by the topography of the stream bank. Bank-sides vary in their complexity from simple substrates, such as flat areas of bed rock or sand banks, to complex substrates such as cobbles and stands of vegetation. Complex bank-side topography may reduce mobility compared to a more simple topography, increasing the risk of mortality by desiccation or predation (see Chapter 4). The slope of the bank may also be important with faster return times on steep slopes (i.e. positive geotaxis).

There are few or no studies looking at the ability of flood-stranded invertebrates to regain the water. In this study I tested the hypothesis that cased caddisfly larvae can return to the water when stranded and I examined whether case type (species), bank-side topography (substrate type and slope) and position (distance) from the water, influenced return time. The experimental arenas were aquaria with different substrate inserts at different slopes. I predicted a positive relationship between case weight and length of time for larvae to regain the water. Species withcases constructed of heavy materials such as mineral particles or with a high case to body weight ratio would be slower than those with cases constructed of lightweight organic materials or a low case to body weight ratio. I predicted that individuals would take longer to regain the water with increasing complexity of the bank-side topography and with decreasing slope. Differences in walking posture of some caddisfly larvae in water and in air were also investigated in an artificial arena. Three postures were characterised *a posteriori*: the highest, lowest and intermediate heights (clearance) of the case from the substrate. I predicted that larvae in air would have a greater proportion of their case in contact with the substrate and less clearance than those immersed, as the animal would get less support for its case than in water. I predicted that the mobility of individuals (i.e. speed across the arena) would be reduced in air compared to water.

6.2 Materials and Methods

6.2.1 Animals

The five species of cased Trichoptera used in the experiment are common in streams within the U.K. (Wallace, 1991) and occur in the Whiteadder Water: *Potamophylax latipennis*, *Halesus radiatus*, *Anabolia nervosa*, *Odontocerum albicorne* and *Sericostoma personatum*. These species and species with similar case types were found stranded on the bank-sides of the Whiteadder Water (see Chapter 4), and were chosen to encompass a range of materials used in case construction, thus providing insight into the effects of case weights on stranded individuals. *Potamophylax latipennis* had a case constructed of coarse sand grains (coarse mineral), *H. radiatus* a case comprised only of vegetation (vegetative), *A. nervosa* a mixed case of both mineral and vegetative components (mixed), *O. albicorne* and *S. personatum* had a cases composed of fine sand grains (fine mineral). All species except *Anabolia nervosa* were collected from Glencorse Burn on the Bush estate, to the south of Edinburgh for ease of collection and transportation. This reduced the amount of travelling time and stress the larvae experienced, and reduced mortality. *Anabolia nervosa* was collected from downstream of the main survey site on the Whiteadder Water, as this species was not numerous enough to collect from Glencorse Burn. The experiments were carried in March – April 1998 for *H. radiatus*, *A. nervosa* and March – April 1999 *for P. latipennis*, *O. albicorne* and *S. personatum*.

Animals used in the experiments were all IV-V instar with a case length of approximately 1.5 to 2.0 cm. The animals were kept in well-aerated aquaria (60 x 30 x 30 cm) and fed on conditioned leaves and detritus from the source stream. The animals were labelled and numbered with small squares of waterproof paper (3 x 3 mm) adhered to the back of the case with Loctite Superglue. Observations prior to the experiments showed that the labels did not affect the mobility of the animals. The labelling of the animals ensured that no animal was used in two trials. After the experiment, the animals were preserved in 70% alcohol and then dried at 80 °C for 48 hrs, and the dry mass of the body and case were measured to the nearest 0.001 mg using a Sartorius MC-5 microbalance.

6.2.2 Experimental Arenas

The experiments were carried out in a semi-outdoor facility at ambient air temperature (11 to 14°C) and under low light conditions (diffuse light from skylights). There were nine experimental arenas, each comprised of an aquarium (60 x 30 x 30 cm) with a substrate insert, half submerged in oxygenated water (Figure 6.2.1). The inserts were 5 mm plywood with different substrate types adhered to the upper surface. Three substrates types were used Sand, Gravel (mean diameter 20 mm) and grass Turf (height 3 cm). The inserts were placed into the tanks and supported at one of three different slopes (5, 10, 25°).

6.2.3 Experimental Design and Analysis

At the start of each trial, two animals of the same species were placed on the insert equidistant above and below the waterline. The distance of the animals from the water line was observed every 5 min for 120 min and replicated five times for each species. The distance from the water line was taken as the distance to the water from the head of the animal to the water line. Animals were considered to have regained the water once the head had crossed or was on the water line. The position of individuals below the water line was recorded and these acted as a control group to establish the "normal" behaviour of submerged larvae in the experimental arenas and against which to compare the response of individuals in air. Any difference in the behaviour of individuals would be due to exposure to air and not by the insert type. Individuals placed below the water showed no detrimental effects of being placed in the experimental arenas and no individual that started below the water line left the water.

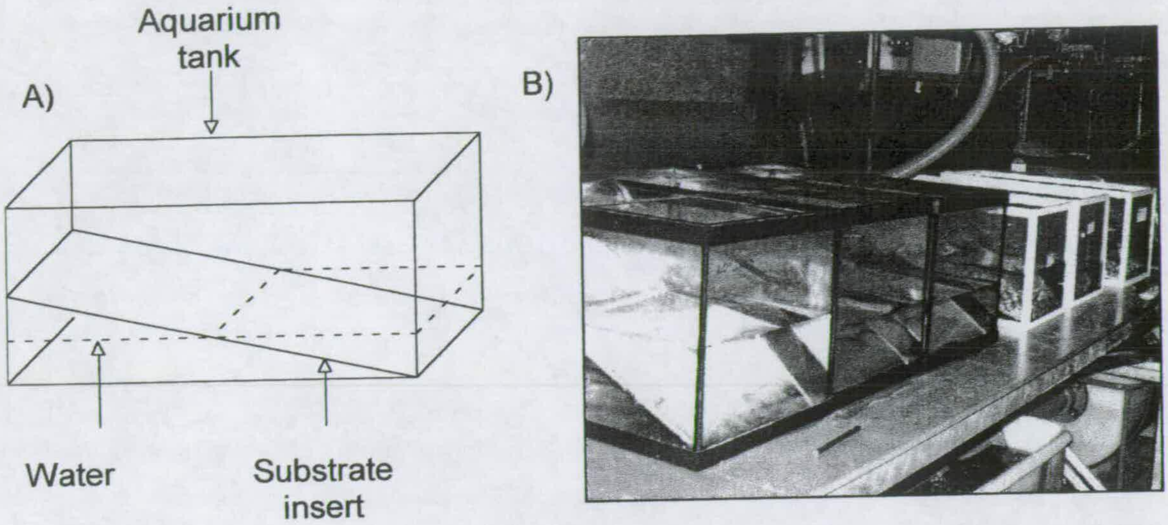

Figure 6.2.1 A) Schematic and B) photograph of experimental arenas.

Animals were placed in the centre of the insert at three distances above and below the water line on each of the slopes and substrates. Five replicate trials were carried out on the five species using a fully orthogonal experimental design, with three factors (substrate and slope and the position from the water line) (Figure 6.2.2).

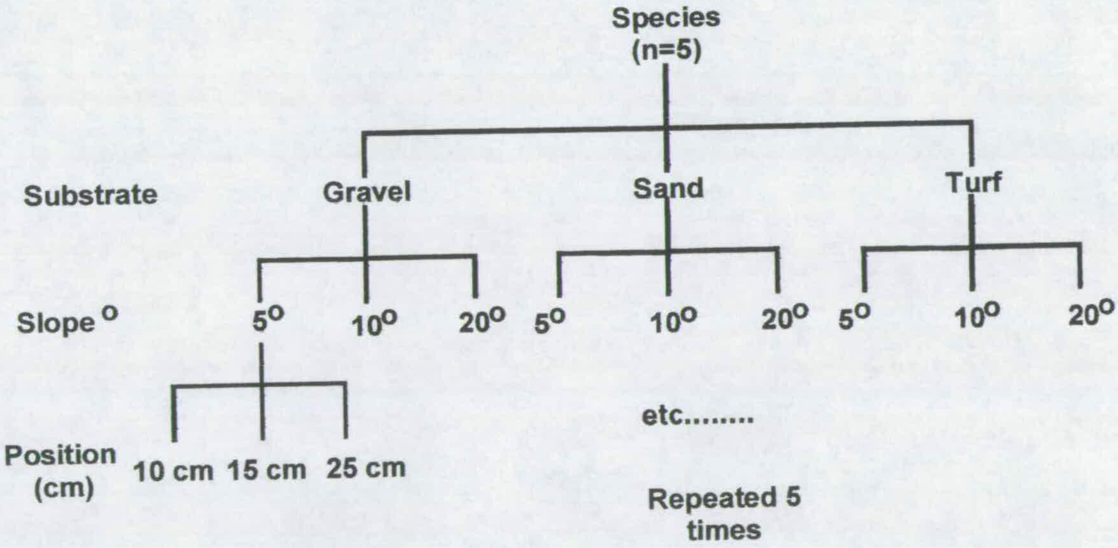

Figure 6.2.2 Orthogonal experimental design for time to regain the water for 5 species of caddisfly larvae on inserts with three factors (substrate type, slope and position relative to water line).

One-way analysis of variance (ANOVA) was used to test whether species differ in the time taken to regain the water, regardless of substrate, slope or position. For each species, three-way ANOVA was also used to determine the significance of substrate, slope and position on the time taken to regain the water.

Comparisons between the mean case weight, body weight and case to body weight quotient of the species were analysed by one-way ANOVA on log-transformed data that normalised the data. The data met the assumptions for homogeneity of variance at p=0.05 after log transformation. Homogeneity-of-variance was tested for using the Levene statistic to test for the equality of group variances using SPSS version 9.0 (Fowler *et al.* 1998; Sokal and Rohlf 1981). Within species variation in case weight, body weight and case to body weight quotient was described as the coefficient of variation (CV) (Fowler *et al.* 1998).

6.2.4 Walking Posture of Larvae

A subset of three species, readily available at the time of the experiment (*Potamophylax latipennis, Anabolia nervosa* and *Odontocerum albicorne*) was used to describe walking posture. These individuals were instars IV-V, as in the main experiment. Walking posture was observed in a channel (2.0 x 11.5 x 6 cm) made by placing an opaque corrugated plastic back wall into a clear plastic container. The bottom of the channel was roughened using sandpaper to allow the larvae to grip the otherwise smooth plastic and to walk without slipping. The bottom of the arena was marked with a 0.5 cm grid. In trials when the animals were immersed, the depth of water was approximately 3 cm. Trials also were carried out in air, with completely dry channels. The trails were carried out at ambient room temperature (15-17°C), in diffuse natural sunlight via windows with opaque blinds drawn.

A series of photographs were taken of one individual of each of the three species (*P. latipennis, A. nervosa, O. albicorne*) using a Nikon Coolpix 950 digital camera at Manchester Metropolitan University in June 2000. No replication was undertaken for this experiment due to time constraints and technical difficulties with the setting up and use of the digital camera and its associated software. Photographs were taken every 20 s as the animal walked across the 5 cm field of view. The number of frames where the animal was entirely present in the field of view was used to calculate approximate velocity. Approximate velocity and the height to the case at the anterior aperture when the animal was immersed and dry were compared. Three postures were identified *a posteriori* from photographs: 1) the maximum height, 2) the lowest height and 3) intermediate height of the case above the floor of the arena. For each series of photographs the height above the substrate at the aperture was measured for each of the postures (Figure 6.2.3).

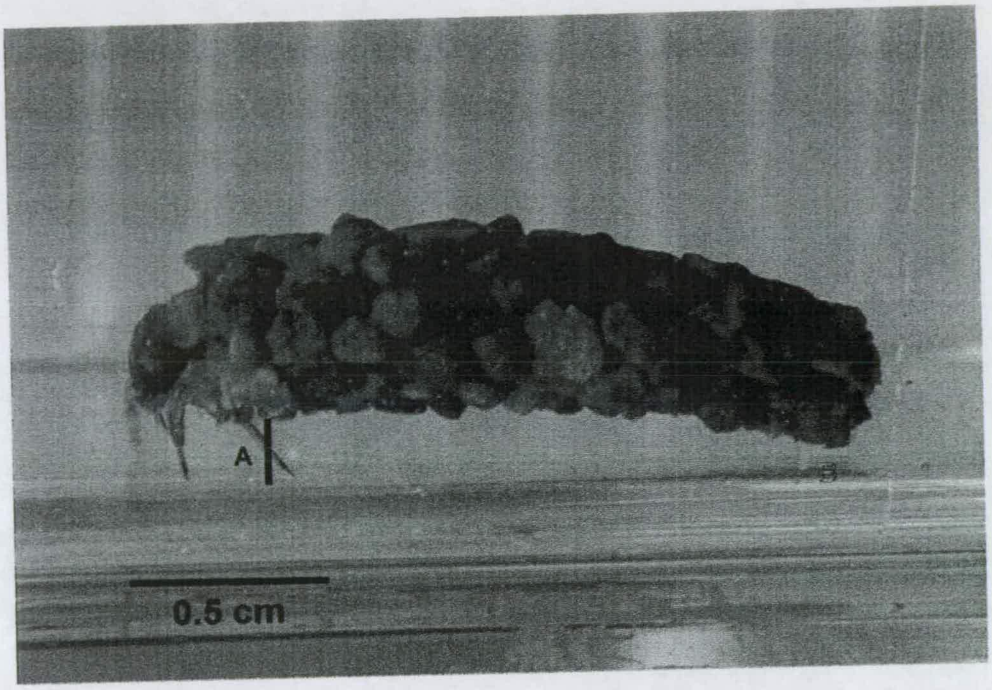

Figure 6.2.3 Photograph of *P. latipennis* illustrating the measurement of the aperture (A) above the substrate

6.3 Results

There was a significant difference in the mean case weight, case weight to body weight quotient between species of caddisfly (Figure 6.3.1 and Table 6.3.1). *Anabolia nervosa* (mixed case) had the heaviest case and body; *O. albicorne* (fine mineral) had the lightest case, but the second heaviest body weight. *Potamophylax latipennis* had the highest case: body weight quotient and *H. radiatus* (vegetative) had the lowest. Within each species, there was little variation in body weight and case to body weight quotient (Table 6.3.2). There was more variation in case weight: *A. nervosa* was the most variable and *S. personatum* the least variation (Table 6.3.2).

Individuals of all species when placed above the water line on all insert types exhibited positive geotaxis and moved downwards towards the water line, even if they did not reach the water in the experimental observation period. Figure 6.3.2 shows examples of this response on a 5° slope on three substrates (sand, gravel and turf) at a starting distance of 25 cm from the water line. All individuals that started below the water line (i.e. control) did not show a geotactic response but did move around the wetted part of the arena (Figure 6.3.2).

The mean times for the five species to regain the water in the experimental arenas, regardless of position, substrate type or slope, are shown in Figure 6.3.3. The species slowest to regain the water had fine mineral cases (*O. albicorne* and *S. personatum*). The species that regained the water the fastest (*H. radiatus* and *A. nervosa*) had cases comprised entirely of vegetation or a mixture of vegetation and mineral particles. *Potamophylax latipennis* had a case comprised of coarse mineral particles and was intermediate in the time it took to regain the stream. One-way ANOVA showed a significant difference in the mean times taken to regain the water between species on all topographies (d.f. =4,5 MS= 104397, F=42.077 and p $\leq$0.001). Post hoc pair wise comparisons (Scheffé test) are shown in Figure 6.3.3.

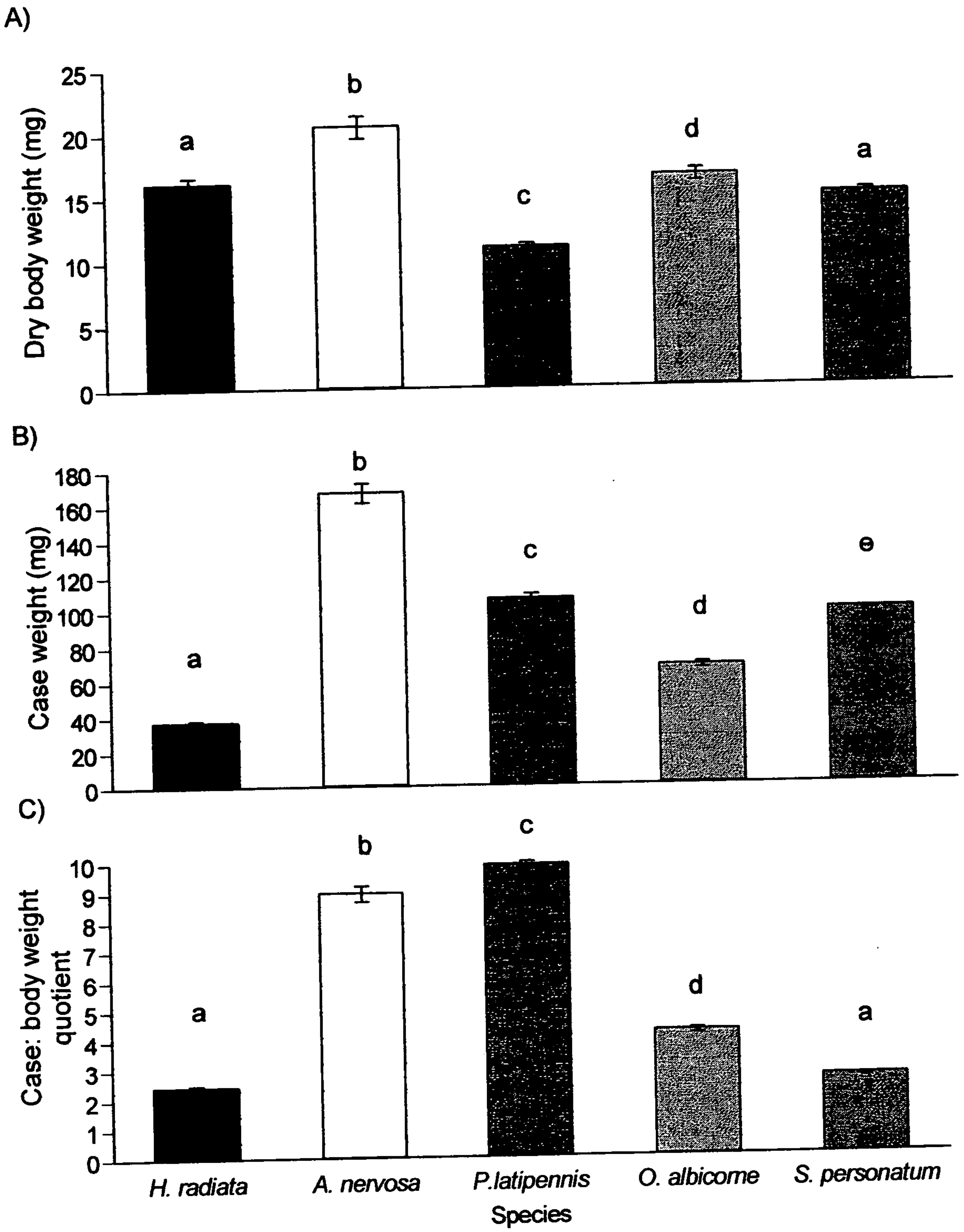

Figure 6.3.1 A) mean dry body weight (±SE), B) mean case weight (±SE) and C) mean case to body weight quotient (±SE) for five species of caddisfly. Bars with the same letter were not significantly different (Scheffe test).

Table 6.3.1 Summary of one-way ANOVA comparing A) dry body weight (mg) and B) dry case weight (mg) and C) case to body weight quotient of five species of caddisflies with different case types. See Figure 6.3.1 for illustration.

A)

Source	df	SS	MS	F-ratio	P
Species	4	153800	384524	295.05	≤0.0001
Error	482	802887	1303.39		
Total	486				

B)

Source	df	SS	MS	F-ratio	P
Species	4	6212.52	1553.13	43.114	≤0.0001
Error	482	22190.9	36.02		
Total	486	28403.2			

C)

Source	df	SS	MS	F-ratio	P
Species	4	6321.65	1580.41	578.42	≤0.0001
Error	482	1683.10	2.7323		
Total	486	8004.75			

Table 6.3.2 Coefficients of variation for case weight, body weight and case to body weight quotient within five species of caddisfly larvae with different case types.

Species	Coefficient of variation (CV)		
	Case weight (mg)	Body weight (mg)	Case to body weight quotient
Halesus radiatus	46.4	0.3	3.1
Anabolia nervosa	74.1	4.7	3.3
Potamophylax latipennis	22.8	4.8	4.2
Odontocerum albicorne	70	16	4.4
Sericostoma personatum		15	6.7

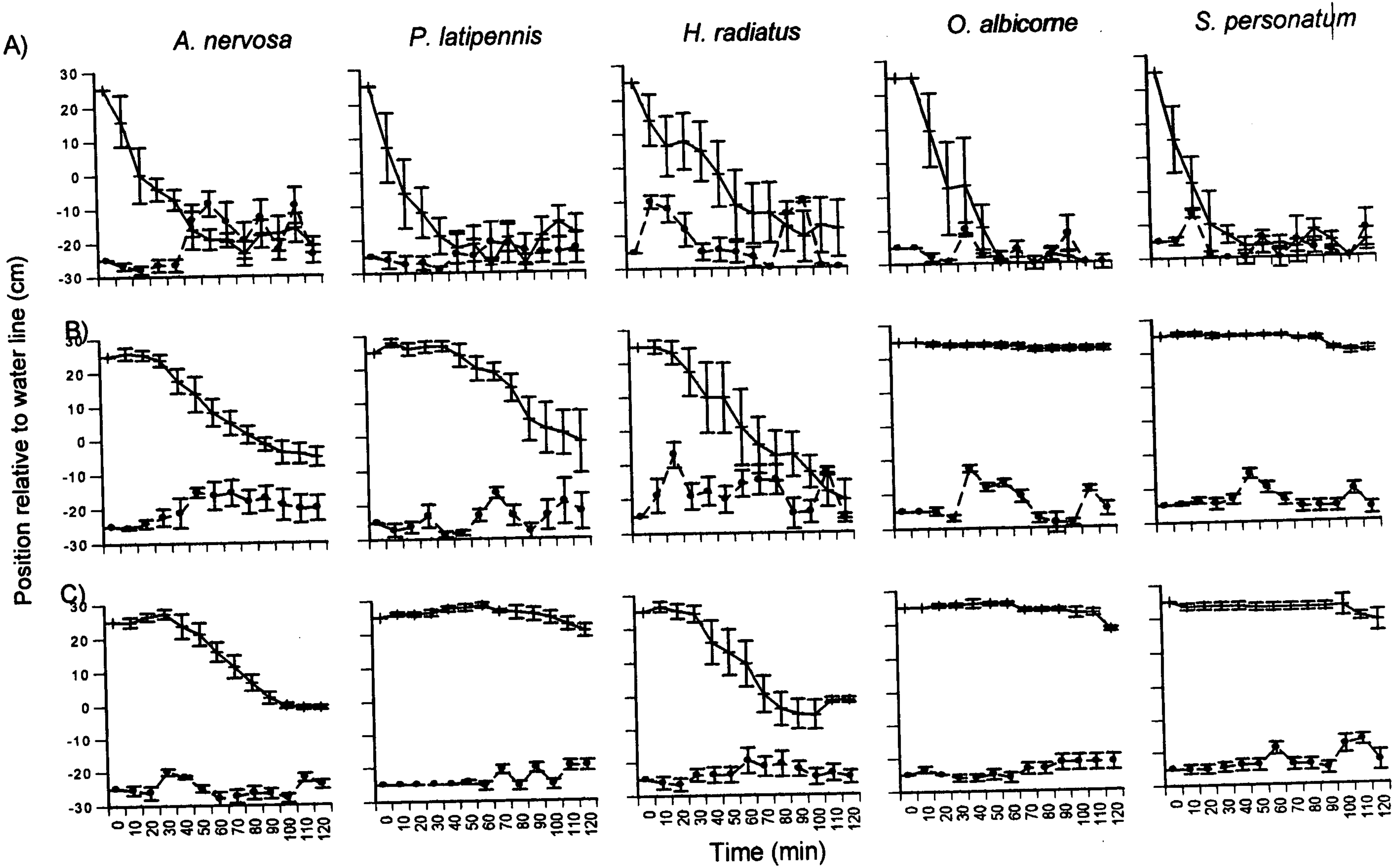

Figure 6.3.2 Mean position (±SE) of five species of caddisfly in relation to the water line over 120 min observational period on a five degree slope on three substrates A) sand, B) gravel and C) turf in aquaria.

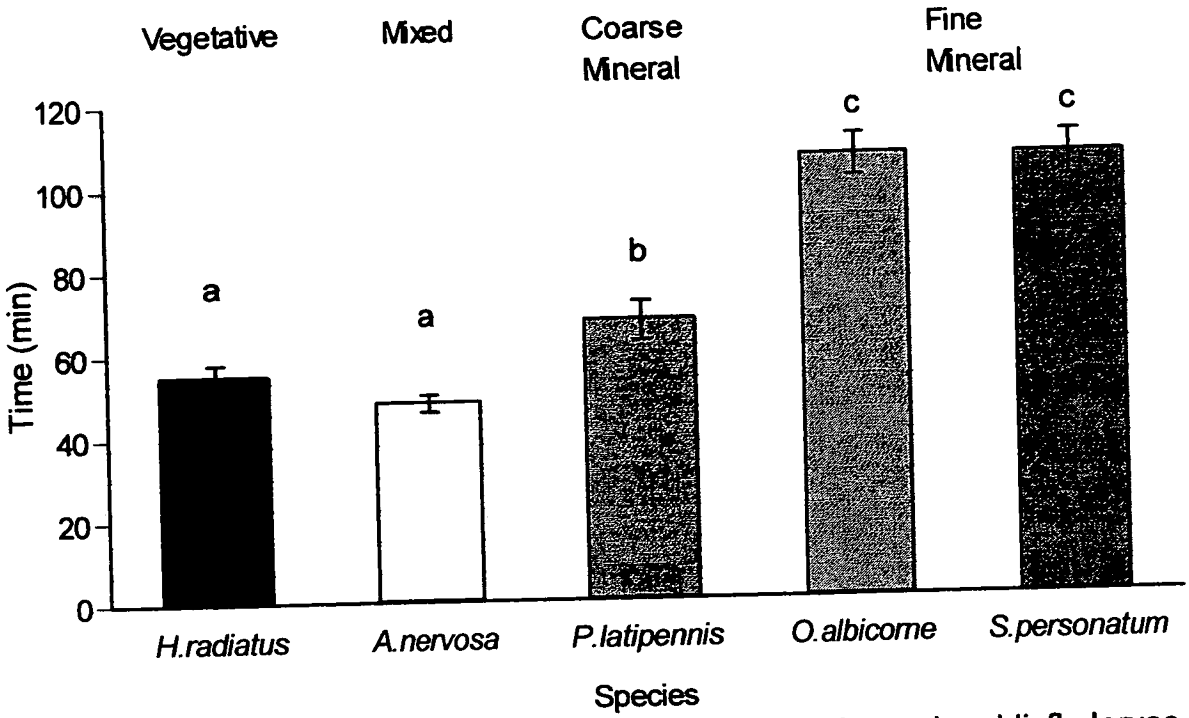

Figure 6.3.3 Mean time (± SE) taken for five species of cased caddisfly larvae with different case compositions to regain the water in experimental arenas. Bars with the same letter are not statistically different using Scheffé *post hoc* pair-wise comparison tests (p=0.05).

As return time was species/case-specific, the effect of the substrate, slope and position was investigated for each species separately (Figure 6.3.4) using three-way ANOVA (Table 6.3.4). For all species, the substrate type (Figure 6.3.4A) had a significant effect on the time taken to regain the water, and the time increased with substrate complexity (Sand < Gravel = Turf). Slope had a significant effect on the time to regain the water in four out of five species; only in *O. albicorne* was slope not significant. With increasing slope (Figure 6.3.4B), time taken to regain the water decreased (20°< 10° = 5°). The position of the animals relative to the water line was significant in three of the five species *(H. radiatus, A. nervosa* and *P. latipennis*). With increasing distance the time to regain the stream also increased (25 > 15 = 10 cm) (Figure 6.3.4C). The interaction of position and slope was only a significant factor for

H. radiatus. When the position from the water increased, the time to regain the water increased, but decreased with the increasing slope in *H. radiatus*. The interaction between position and substrate was only significant for *S. personatum*. In *S. personatum* the time taken to regain the water increased with increasing distance from the water, and decreased with increasing substrate complexity. Interaction between slope and substrate was significant for *H. radiatus, A. nervosa* and *S. personatum*. Increasing the complexity of the substrate increased the time taken to regain the water, while increasing the slope decreased the time to regain the water.

All three individuals moved faster across a 5 cm field of view immersed in water than in air (Figure 6.3.5). *Odontocerum albicorne* was still alive after 60 minutes of observation when exposed to air. The head and legs of *O. albicorne* protruded from the case frequently, but *O. albicorne* did not move from its initial position when dry.

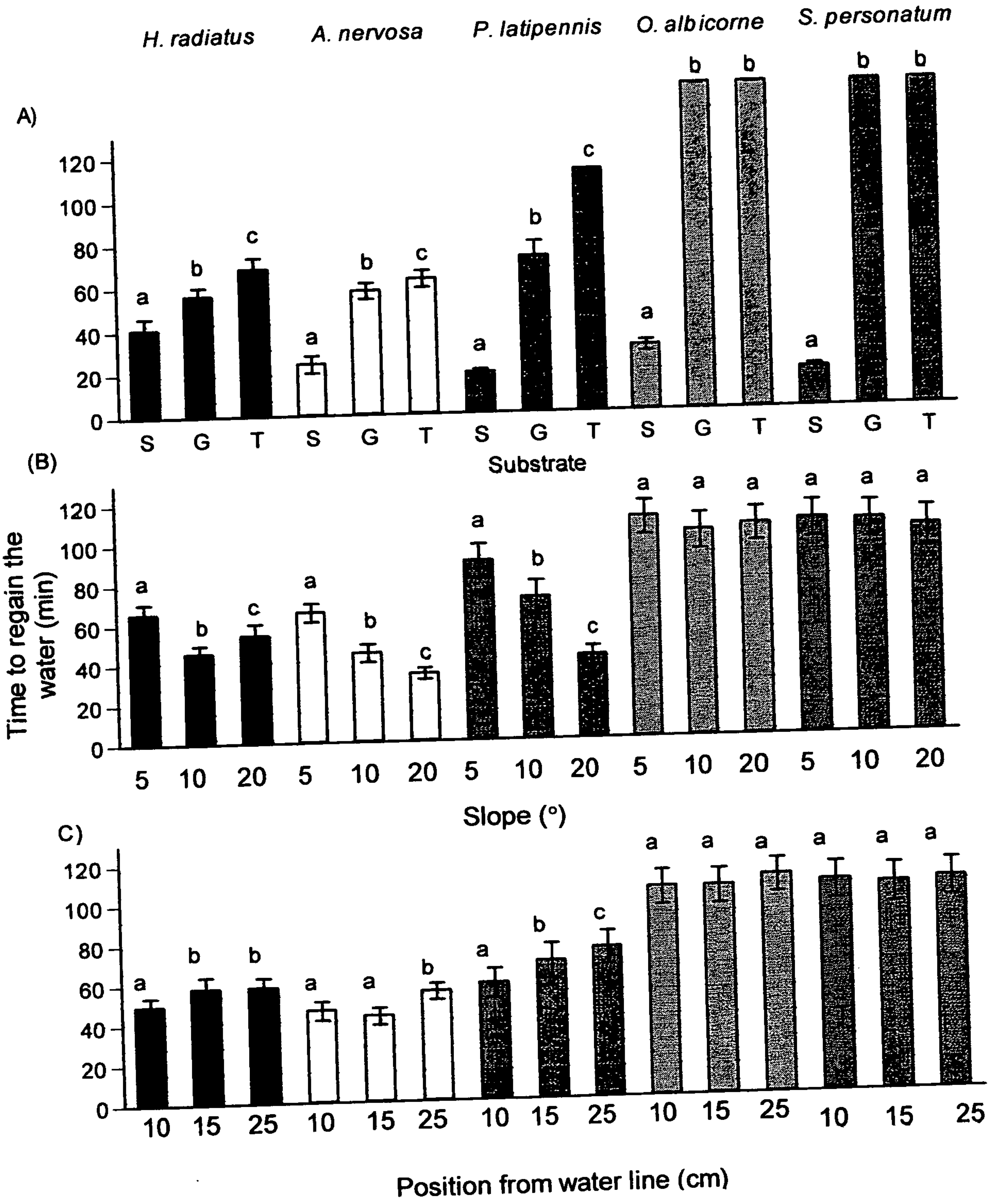

Figure 6.3.4 Mean time (±SE) for five species of stranded caddisfly larvae to regain the water for A) Substrate (S= sand, G= Gravel and T= Turf), B) Slope and C) Position from the water line. Bars with the same letter are not statistically different using Scheffé *post hoc* pair-wise comparison tests (p=0.05).

Table 6.3.3: Summary of three-way ANOVA for each species comparing time taken to regain the water on different insert topography (Substrate, Slope) and position from water line. Values significant at p>0.05 are shown in bold.

		H. radiatus			*A. nervosa*			*P .latipennis*			*O. albicome*			*S. personatum*		
Source	d.f.	MS	F	p	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Substrate	2	88.35	9.379	**≤0.001**	198.5	64.74	**≤0.001**	764.7	111.7	**≤0.001**	1395.4	685.0	**≤0.001**	1889	4595	**≤0.001**
Slope	2	47.78	5.072	**≤0.001**	115.9	37.80	**≤0.001**	179.7	26.26	**≤0.001**	4.067	1.996	0.140	1.985	4.829	**0.010**
Position	2	5.011	0.532	0.589	16.76	5.466	**0.006**	22.10	3.234	**0.043**	2.400	1.178	0.311	0.741	1.802	0.169
Position x Slope	4	26.10	2.771	**0.031**	4.874	1.589	0.843	12.65	1.849	0.124	6.067	2.978	**0.022**	0.541	1.315	0.268
Position x Substrate	4	3.152	0.335	0.854	1.074	0.350	0.182	4.029	0.589	0.672	1.289	0.633	0.640	1.052	2.559	**0.043**
Slope x Substrate	4	6.001	0.637	0.637	11.18	3.647	**0.008**	32.90	4.808	**0.001**	3.589	1.762	0.141	1.363	3.315	**0.013**
Position x Slope x Substrate	8	10.15	1.078	0.384	2.312	0.756	0.642	6.007	0.878	0.537	5.006	2.457	**0.0175**	2.548	0.319	0.625
Error	108	9.420			3.066			6.844			2.037			0.411		

The clearance (height of the case at the aperture above the substrate) in water and in air is shown in Table 6.3.4. For the three walking postures, *A. nervosa* had the highest clearance at the aperture, both in water and in air (Figure 6.3.6). The body of *Anabolia nervosa* extended further from of its case than in *P. latipennis* and *O. albicorne*. *Anabolia nervosa,* scuttled across the experimental arena with the case supported by the legs above the floor of the arena. The case of *A. nervosa* was a straight tube so little case came into contact with the floor of the arena, due to the support from the legs. *Odontocerum albicorne* had no clearance at the aperture when placed in water or in air (Figure 6.3.7). *Odontocerum albicorne* walked across the experimental arena (in water) by dragging the case, with little lifting of the case by the legs. *Potamophylax latipennis* had an intermediate clearance height (Figure 6.3.8). *Potamophylax latipennis* moved across the experimental arena in a cyclical manner. Firstly, the case was lifted then pulled forward by the legs moving the case and individual and then the case was dropped/lowered and the cycle repeated. This appeared (though was not quantified), to make *P. latipennis* exert more effort moving than *A. nervosa* and *O. albicorne,* in both water and air. In dry trials (i.e. in air) with the water removed from the channel, the clearance above the substrate in both *A. nervosa* and *P. latipennis* was reduced though the manner in which they moved altered little. No statistical tests could be undertaken as only one individual of each species was used.

Table 6.3.4 Height of case aperture (mm) at three postures (highest, intermediate and lowest) during locomotion through a 5 cm field of view in water and air for three species of cased caddisfly larvae.

Species	Water			Air		
	Lowest	Intermediate	Highest	Lowest	Intermediate	Highest
Anabolia nervosa	2.31	2.31	2.64	0.33	0.33	1.32
Potamophylax latipennis	0.00	0.83	1.65	0.00	0.33	0.66
Odontocerum albicorne	0.00	0.00	0.00	-	-	-

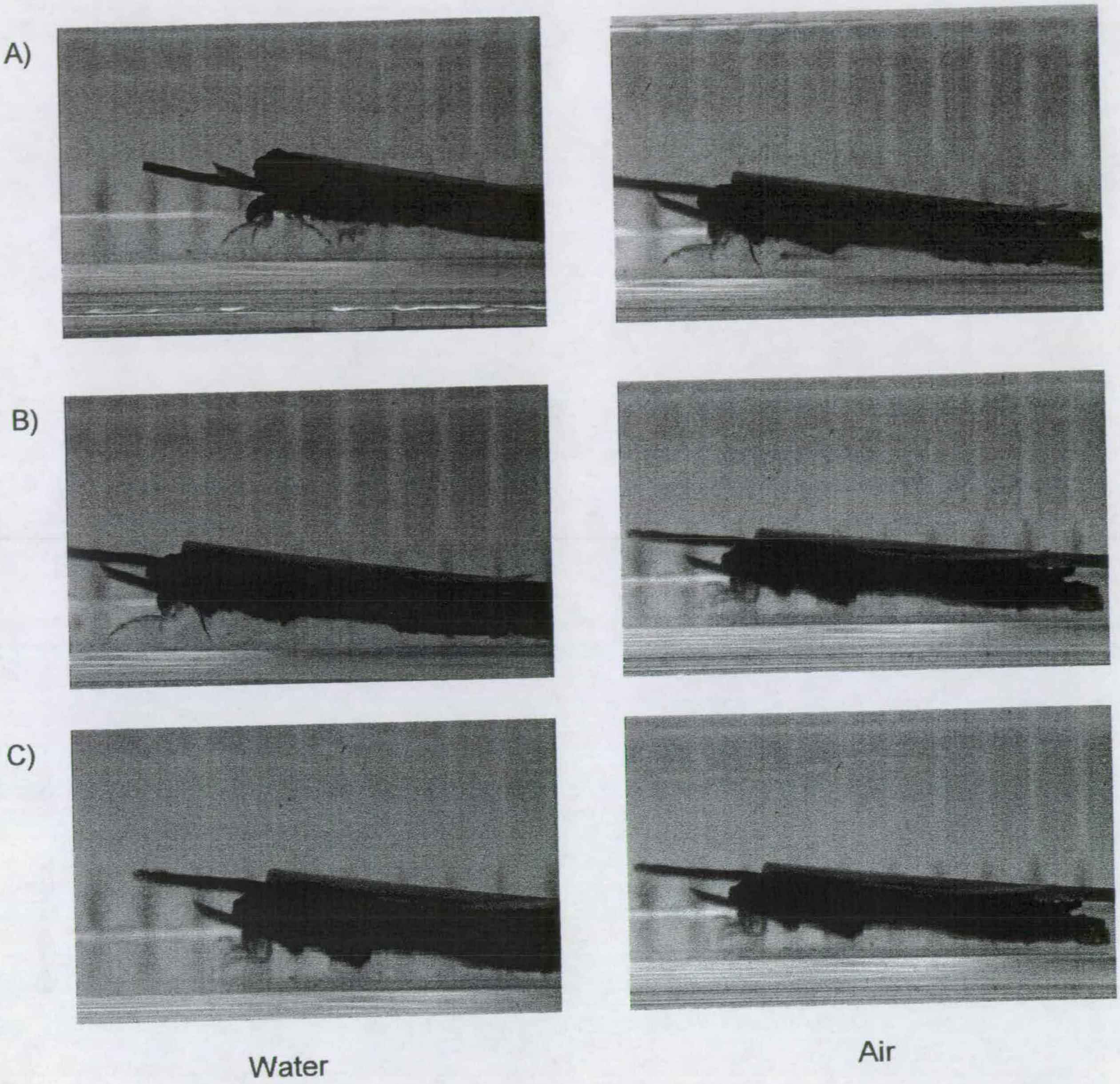

Figure 6.3.6. Photographs showing the three walking postures and clearances where A) highest, B) intermediate and C) lowest of *A. nervosa* in water and in air. Scale bar represents 5 mm.

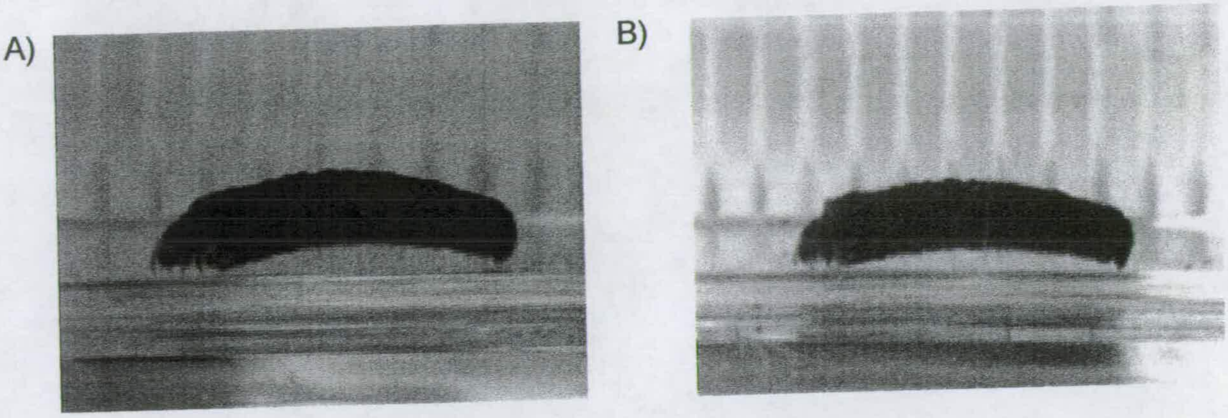

Figure 6.3.7 Posture/clearance of *O. albicorne* A) in water and B) in air. Scale bar is equal to 5 mm.

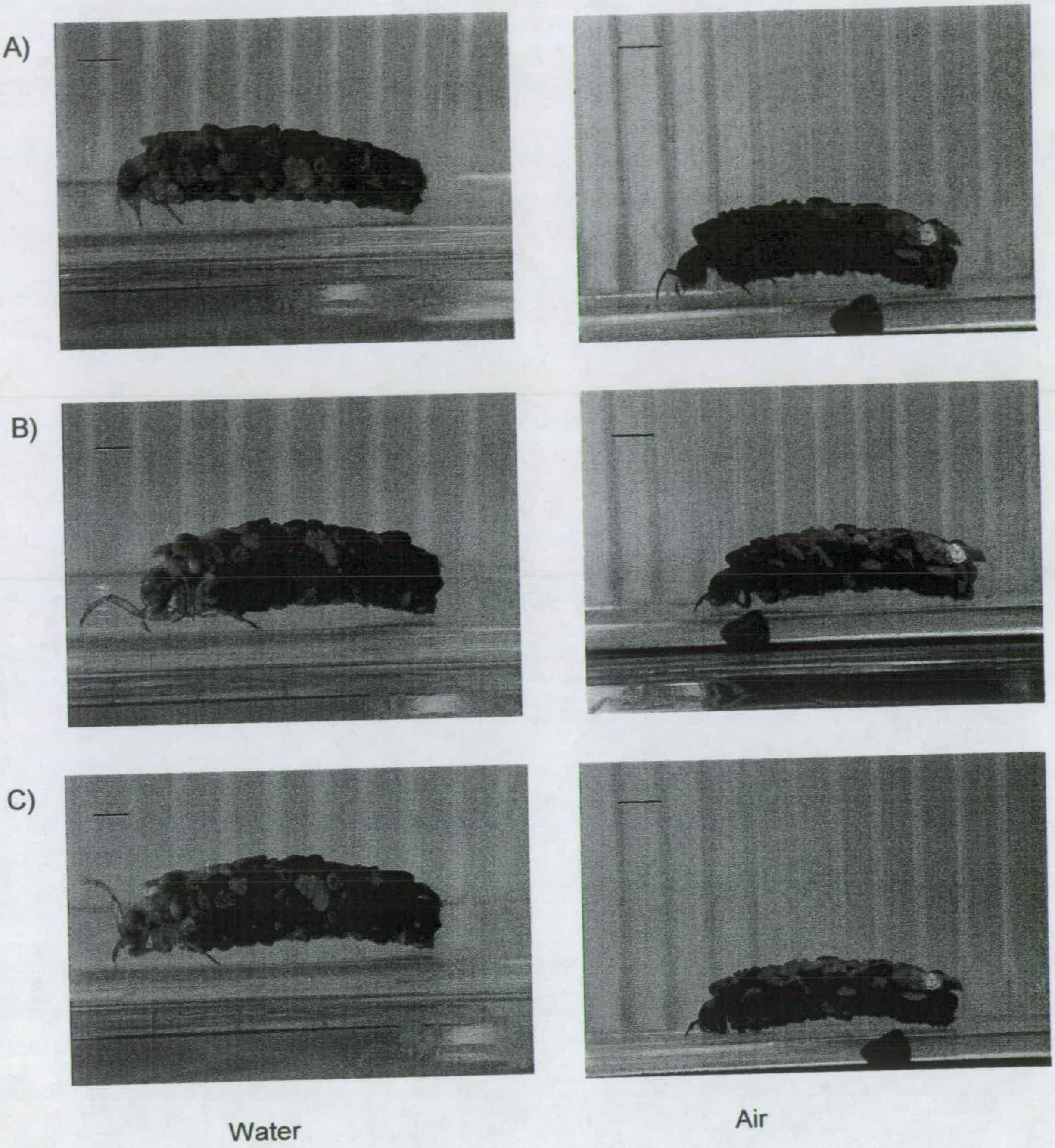

Figure 6.3.8. Photographs showing the three walking postures and clearances A) highest, B) intermediate and C) lowest of *P. latipennis* in water and in air. Scale bar represents 5 mm

6.4 Discussion

The result of this study show clearly that cased caddisfly are able to regain the stream when stranded on bank-sides. The ability to return to the water is species-specific and is affected by the complexity of bank-side topography and distance from the water at which individuals become stranded. This study also provides some insight in the abilities that allow flood stranded benthic invertebrates to regain the water. The ability of benthic organisms to regain the stream has implications in terms of population dynamics, as the ability to return to the water would offset the negative impacts of mortality caused by being stranded during flooding. During floods animals may be killed by becoming crushed by bed movements or become deposited by the drift in depositional areas as found in studies by Dobson *et al.* (1997; 2000). Mortality due to being stranded on exposed margins has only been observed in a few studies (Fisher and LaVoy 1972; Kroger 1973; Corrarino and Brusven 1983; Perry and Perry 1986; Braaten and Guy 1997). In these studies, the numbers of animals that may have been temporarily stranded and subsequently walked back to the stream was not addressed. In all of these studies cased Trichoptera were rarely, if at all found, stranded in the exposed areas that had previously been inundated. In contrast, I report Trichoptera stranded on bank-sides after flood events (Chapter 4).

The results show that the bank-side topography can influence the movement and therefore the ability of some cased caddisfly larvae to regain the water. The impact of substrate on the time taken to regain the water was significant in all species examined. The time to regain the water increased as the three-dimensional structure (complexity) of the substrate increased. On a simple substrate with no or few obstacles individuals regained the water fastest. As the substrate complexity increased, then the effort to move across such a substrate increased, and therefore the amount of time for individuals to regain the water also increased.

The rate of water recession is an important factor in determining whether organisms in inundated habitats can follow the receding water, if it is faster than they can move they may become stranded. Moon (1935) studied the movement of littoral benthic invertebrates of Lake Windermere during floods and found that benthic invertebrates moved up with the rising water levels and back with falling water levels. He found that the invertebrates could retreat with the falling water levels. The rise and fall of the water was much more gradual than expected in a flashy upland stream, but it does however highlight the fact that benthic invertebrates can and do move into inundated terrestrial areas not normally submerged. Moon (1935) also showed that some types of topography could check the movement of invertebrates onto flooded areas. For example, experiments showed that the absence of stones checked the movement of *Ecdyonurus* spp. onto grass. If the topography of the flooded terrestrial area has an affect on the movement of animals onto submerged areas then this may also effect movement when the area is dry.

The negative association between slope and time to regain the water indicates a geo-tactic response in air, though I have been unable to find any references to this response to gravity in freshwater benthic invertebrates. Submerged individuals showed no response to gravity therefore, the geotactic response was only exhibited by exposed individuals. Thus, stranded individuals are likely to walk downhill, presumably towards the water. Either the stranded animals sense the direction of gravity (positive geotaxis) directly or it is energetically easier and faster to walk down than up hill. Immersed individuals would not need this geotactic response as they were already in the water, and there may be little difference in the energy expenditure to move up or downhill when supported by water.

Though I was unable to find examples of positive geotaxis in freshwater invertebrates exposed to the air, there are examples in marine invertebrates. The marine intertidal chiton *Lepidochitona cinereus* (L.) that is regularly exposed at low water, exhibits positive geotaxis when out of the water (Evans 1951) similar to the caddisfly larvae used in this study. Under experimental conditions positive geotaxis was only observed in *L. cinereus* exposed to air and not when immersed in water (Evans 1951) and this was attributed to its desiccation tolerance. *Lepidochitona cinereus* is sensitive to desiccation and is unable to recover from being exposed for a period of 1 h. in windy and sunny conditions. In the natural environment, Evans observed that individuals of *L. cinereus* on the top of rocks that became exposed at low tide moved downwards to damp and humid areas underneath rocks that reduced the effects of desiccation. If the rocks were submerged then desiccation was not a problem and a positive geotactic response was not observed.

Animals could become stranded on the bank-side at varying distances with different magnitudes of floods. A large flood would inundate a greater area of the bank-side and deposit animals a greater distance from the stream channel, conversely a small flood that inundates a small bank-side area would deposit individuals closer to the stream channel. Varying the position of the larvae from the water line in the experiment highlights the effects of changes in flood magnitude. By varying the position from the water line, the larvae would have a greater or smaller distance to move to regain the stream, mimicking the variation in inundated banks causing by floods of different magnitude. This increase incidence of being stranded with distance from the channel has been observed by Matthaei and Townsend (2000b) where stranding was higher in a side channel. They speculated that this apparent higher incidence of becoming stranded in a side channel might be that it was further away from the base-flow channel (50-70 m compared to 8-12 m for the margins of the main channel) and in addition it probably dried out faster as the flow decreased. The time taken to regain the stream from different distances (Position) by species with different case types could be used as a measure of the ability to return to the water when exposed to varying magnitudes of flood.

Three possible mechanisms may underlie these species/case-specific responses in the ability to regain the water, 1) desiccation tolerance, 2) case: body weight quotient and 3) walking posture/clearance of case above substrate. However, since there are few replicates of case type in the experiment, the association of case type with the rate of return to the water must be viewed with caution.

Once stranded in air, aquatic invertebrates begin to dry out (desiccation) and may ultimately die. Species prone to desiccation should regain the water faster than desiccation-tolerant species and case material may be important in desiccation tolerance. Cases comprised of an impermeable and non-porous material such as fine mineral fragments packed tightly together may lose water more slowly than cases built

of permeable/ porous vegetative matter. Although desiccation tolerance was not measured directly in this study, the experimental results are consistent with this hypothesis. *Odontocerum albicorne* and *S. personatum* were slowest to regain the water and they both have fine mineral cases which are assumed to be less porous; *H. radiatus* and *A. nervosa* regained the water most quickly and their cases contain porous vegetative material. However, even for the most dessication tolerant species, they must return to water as fast as they can to minimise the risk of predation (Hering and Plachter 1997), over-heating and loss of feeding opportunity.
The difference in permeability/ porosity of cases to water loss in caddisfly larvae and the tolerance to desiccation when stranded is analogous to the shells of marine intertidal invertebrates. Species of limpets that live on the high shore are more tolerant to emersion and desiccation (Wolcott 1973; Branch 1981; Lowell 1984; Hodgson 1999). High shore species of limpets generally have larger, thicker and less porous shells than those in lower zones, which have thinner and more porous shells (Branch 1981; Lowell 1984; Hodgson 1999). The high shore barnacle *Chathalamus montagui* has a non-porous shell, with tightly fitting opercular plates, which enables it to tolerate long periods of emersion that occur higher on the shore (Connell 1961b). In contrast, the other common intertidal barnacle *Semibalanus balanoides,* which occurs at lower intertidal zones only, has a shell which is more porous than that of *C. montagui*, has looser fitting opercular plates and is less desiccation tolerant (Connell 1961a). The freshwater bivalve *Anodonta grandis* (L.) has a very thin, light-weight and porous shell incapable of sealing completely when closed and is intolerant of emersion and desiccation but rapidly moves into the substrate when exposed to air thus avoiding the effects of desiccation (Byrne and McMahon 1991). The freshwater bivalves *Uniomerus tetralasmus* and *Corbicula fluminea* that are found in similar habitats as *A. grandis* do not exhibit this downward migration and have thicker, heavier and less porous shells the valves of which fit together tightly minimising water loss. Thus the shells of *A. grandis* increase their desiccation tolerance but are consequently less mobile due to their thick and heavy shells (Byrne *et al* 1988; Byrne and McMahon 1994).

Desiccation risk also influences the movement behaviour and survival of caddis in other situations. *Desmona bethula,* a species that often feeds out of the water on terrestrial plants (Erman, 1981), has a case of small mineral fragments and some vegetative pieces. Diel migration is triggered by reduced light intensity, but is related also to lowered vapour pressure deficit (increasing the relative humidity) that limits the drying out of the cases. Relative humidity also influences movements of the fully terrestrial caddis larva *Enoicyla pusilla* (Burmeister). If the ground becomes too wet, larvae migrated up onto tree trunks and moved down again if the trunks became too dry (Kelnar and Pillault 1960). Zumora-Munoz and Svensson (1996) found that the survival of two limnephilid caddis larvae inhabiting permanent and temporary pools depended on case type. Contrary to my predictions, they found that the case of *Limnephilus coenosus,* which is made of organic debris (i.e. vegetation), contained more water than the sand grained case of *Limnephilus vittatus*. Trichoptera respire by cutaneous respiration through the body surface to satisfy a portion of their respiratory needs (as do virtually all aquatic insects (Ward, 1992)). They also respire through external tracheal gills (tracheated evaginations of the body wall) as diffusion within a gas filled system is several hundreds of times faster than liquid diffusion and therefore more efficient. Due to the high density and viscosity of water, an oxygen diffusion gradient develops on the respiratory surfaces and oxygen diffuses to the animal. If the animal is not in an aqueous medium and dries out these gradients cannot develop on the respiratory surfaces reducing respiratory ability. The cases of plant material found in *Limnephilus coenosus* contained more water than the mineral cases of *L. vittatus* in the study by Zumora-Munoz and Svensson (1996), but this water may not have been available to the animal for respiration, as the water may have been contained within the organic matter itself and therefore could not be utilised by the organism as the respiratory surfaces of the animal may have become dried. Increases in the incidence becoming stranded have been observed in dewatered areas when the temperature was high (Corrarino and Brusven, 1983; Perry and Perry, 1986) increasing the rate of desiccation. Thus leading to an increase in mortality due the animals drying out faster than they could find water.

There was no evidence that case to body weight ratio influenced how quickly stranded caddis regained the water. The lowest case to body weight ratios occurred in *H. radiatus*, and *S. personatum*, the fastest and slowest to regain the water. Within species there was little variation in case to body weight ratio, presumably because animals were of similar size and age class. The lack of variation means that comparisons are not confounded by other factors.

Though I have been unable to find any literature comparing the walking posture and mobility of invertebrates in and out of water, I can make some speculative arguments. The difference in clearance above the substrate may explain the mobility (the ease and speed that a species walks) of that species. A case held above the substrate (high clearance) may experience lower friction from the substrate and would be raised above substrate obstacles in front of the animal. For *A. nervosa* and *P. latipennis* the clearance was reduced in air compared to water. Of the three species examined *A. nervosa* had the greatest clearance in water and air and was quickest to regain the stream in the experimental arenas. *Odontocerum albicorne* had no clearance at the aperture in water or in air, it moved very little under the experimental conditions, and this species was also one of the slowest to regain the water. The clearance of the case above the substrate while walking would appear from this limited data set to have an impact on the mobility and therefore the ability of cased Trichoptera to regain the water when stranded.

In conclusion, it appears that cased caddisfly larvae have the ability to regain the water when stranded and exposed to air, but this ability is affected by a number of factors. The ability of cased Trichoptera to regain the water appears to be species/case-specific and the mechanisms by which they regain the stream may be attributed to a combination of morphological and physiological factors, such as the different tolerance to desiccation of the case types and the height of the case above the substrate (clearance) that can be supported by the different species in air when compared to water, all may play an important part in this ability to return to the water when stranded. This, combined with the role of bank-side topography, which in its own right can have a significant impact on the ability of animals to regain the water, must be considered when looking at the impacts of being stranded on the population dynamics on the caddis assemblage in streams.

7 The Effects of Being Stranded on Cased Caddisflies After Hydraulic Disturbance: General Discussion and Population-level Effects.

7.1 Review of results

The aim of this study was to determine the effects of being stranded after hydraulic disturbance (flooding) on cased caddisfly larvae, which would contribute to the understanding of the effect of hydraulic disturbances on population size. This study, I believe is the first attempt to quantify the relationship between discharge and the incidence of becoming stranded in cased caddisfly larvae. The study also contributes to the understanding of the mechanisms by which benthic organisms may use flooded margins of streams as potential refugia from hydraulic disturbance.

In Chapter 3, I described the microhabitat distribution pattern and densities of larval caddisflies within the study stretch of the Whiteadder Water and the physical attributes of the pools and riffles. The distribution patterns of caddisfly larvae within the stream was attributed to three environmental factors, near-bed flow velocity, depth and the amount of CPOM. These environmental attributes also separated riffles and pools, pools had lower near-bed flow velocity and greater depth than riffles. The distribution patterns of caddisfly larvae within pools and riffles generally agreed with the distribution patterns described by others (Philipson 1953; Scott 1958; Hickin 1967; Egglishaw 1968, 1969; Edington 1968; Otto 1982). Species that occurred within riffle microhabitats generally had unsynchronised lifecycles, and this was pronounced in the case-less caddisfly larvae. These animals would be expected to experience greater and more frequent hydraulic stresses than those in pools, particularly during flood events. This appears to support the hypothesis that species in regularly but unpredictably disturbed habitats have unsynchronised larval development, with many life-stages present at any time (Stearns 1976; Towns 1983; Scrimgeour and Winterbourn 1989).

In Chapter 4, I determined that cased caddisfly larvae do become stranded after floods, and often in high numbers. This illustrates that cased caddisfly larvae must be present on the inundated margins during floods, and that some cannot regain the water as the water level falls. I demonstrated that the incidence of being stranded in cased caddisfly larvae was positively related to discharge, once a threshold discharge had been exceeded: the greater the discharge, the greater the incidence of being stranded that occurs on the bank-sides in the study stretch of the Whiteadder Water. This suggested that the mechanism by which cased caddisfly larvae entered the inundated margins might be due to passive deposition. With increasing discharge, increased hydraulic stresses occur which may dislodge and entrain more benthic organisms in the water column, which drop out of the water column in areas of lower velocity, such as the margins. I also demonstrated that the incidence of stranding varied among species and was influenced by the topography (substrate and slope) of the bank-side and adjacent instream microhabitat. Deposition was not homogeneous and more individuals were stranded adjacent to riffles than pools and on gravel substrates. Cased caddisfly larvae with fine mineral cases were the most abundant type found stranded, while species with vegetative cases were rarely found, though present in the benthos.

Using an experimental flume, I failed to find any evidence that cased caddisfly larvae actively entered the low flow velocity inundated margins (Chapter 5). This suggests that animals are passively deposited in the inundated margins and supports the field survey of Chapter 4. With high discharges (i.e. floods) there are greater hydraulic stresses on the benthic organisms, which can lead to dislodgement and subsequent entrainment of organisms in the water column. The organisms entrained in the water column can then drop out of the water column in areas of lower water velocity such as the flooded banks. The inundated margins would then act as a flow refugium from the hydraulic disturbance and from which organisms could return to the stream.

The inundated margins were an ephemeral refugium that can only be considered as a 'true' refugium from hydraulic disturbances if the organisms that use them can follow the receding waters and do not perish by becoming stranding on the exposed bank-sides. In Chapter 6, I demonstrated that the ability of cased caddisfly larvae to return to the water in experimental arenas was dependent on case type, and the topography (substrate and slope) of the bank in experimental arenas. Time taken to regain the water was species/case specific with vegetative cased larvae regaining the water fastest and fine mineral cased larvae the slowest. These species-specific responses appear to be unrelated to factors such as case to body weight ratios and may be related to walking posture and behaviour. Time taken to regain the water increased with increasing substrate complexity and distance from the water, but decreased with increasing slope. The poor ability of larvae with fine mineral cases compared to those with vegetative and mixed cases to regain the water in this experiment and the field observations of a greater incidence of fine mineral cases being stranded compared to the vegetative cases (Chapter 4) suggests that fine mineral cased larvae when stranded lack the mobility to regain the stream and are more likely to perish. Vegetative and mixed cased caddisfly larvae were more mobile than fine mineral cased species, even when stranded and without the support of water, and therefore were able to follow the receding water levels and do not become stranded as frequently on the bank-sides.

7.2 Does Being Stranded by Flooding Have A Negative Impact On The Benthic Assemblage Of Cased Caddisfly Larvae?

Methodology and results

The results of field surveys and laboratory experiments, reported in previous chapters, were combined to estimate whether the incidence of being stranded had a population-level impact on the benthic assemblage of cased caddisfly larvae in the 240 m study stretch. I estimated the population of cased caddisfly larvae per month in the 240 m study stretch, using data on the benthic distribution and density of cased caddisfly larvae (Chapter 3) and data on the proportional area of pool and riffle habitat in the stream (Chapter 2) (Figure 7.2.1). From June to the following May there was an increase in the vulnerable population of benthic cased caddisfly larvae. This was unexpected given that most caddisflies lay their eggs in spring/summer and numbers of would be expected to decrease rather than increase over the subsequent year due to various forms of mortality. Many animals were assumed to have escaped benthic sampling of

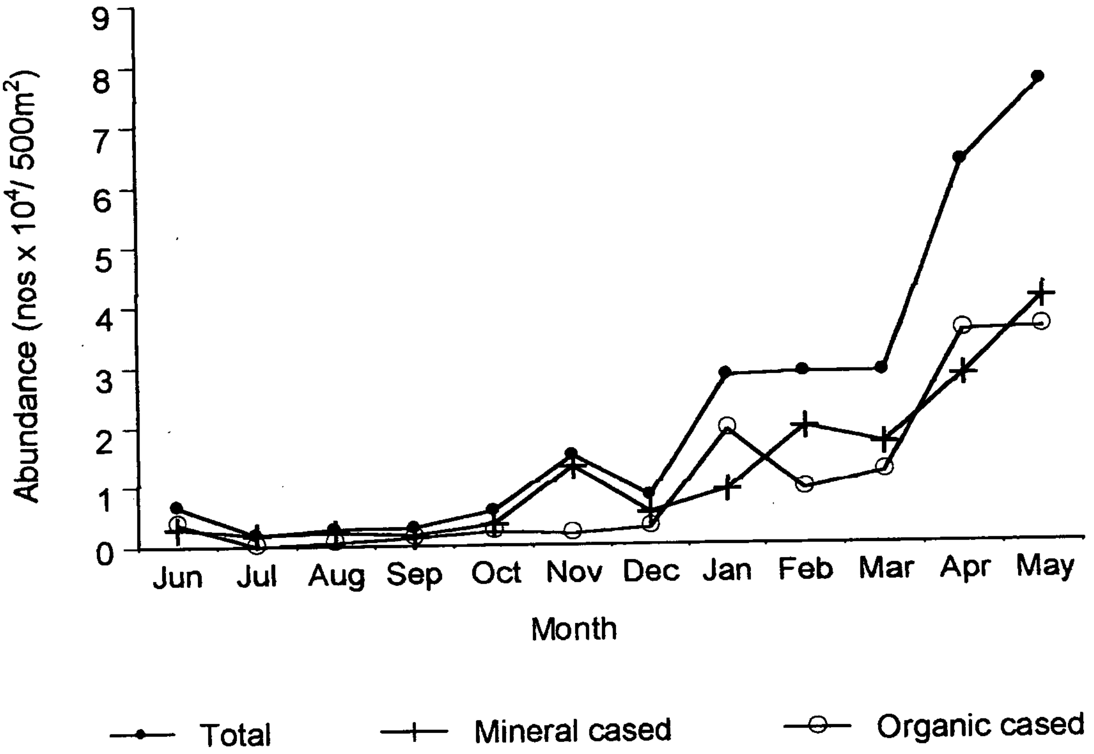

Figure 7.2.1 Estimated vulnerable benthic population of all cased caddisfly larvae (Total), mineral cased and organic cased caddisfly larvae within a 240 m study stretch of the Whiteadder Water.

the surface substrate by occupying different and unsampled microhabitats, such as the hyporheos. Therefore the population sampled was assumed to be the population that was vulnerable to hydraulic disturbance of the surface substrate, and animals that were not collected during benthic sampling were assumed to be not vulnerable. Unsampled individuals were generally and the assumption that very small organisms were not vulnerable to hydraulic disturbance is reasonable given that small organisms near to the streambed have low Reynolds numbers (Re), (i.e. the ratio of inertial to viscous forces) and therefore will be subject more to viscous forces than inertial forces. Larger organisms generally have a higher Re and are subject more to inertial forces (e.g. lift, drag and shear stress) which increase during flood events (see Vogel 1996; Gordon *et al.* 1992). The benthic density of vulnerable cased caddisfly that was sampled per month was assumed to be typical of the benthic densities that occur in the stream. The benthic density of vulnerable cased caddisfly larvae that was observed in the study stretch is the population after stranding has occurred. Therefore we can predict what the vulnerable cased caddisfly population would look like if no animals were stranded by adding the estimated number of animals stranded per month.

The likelihood of a flood large enough to stand caddisflies occurring in each calendar month was estimated from long-term climate data. Using four years of rainfall data for Nunraw Abbey (supplied by the BADC) I estimated the discharge for each day from January 1996 to December 1999 (using the rainfall/discharge relationship described in Chapter 4). The mean number of days per month when discharge exceed bank full conditions (Q <0.13 m^3 s^{-1}) was calculated (Figure 7.2.2). The flood regime in the Whiteadder Water follows a seasonal cycle, with fewer floods in summer than winter. One exception is the month of June that had a high mean incidence of discharge above Q_{crit}. This may be an artefact caused by the short rainfall data set that unfortunately had several years when the weather in June (1997-1999) was particularly bad, with many days having high rainfalls.

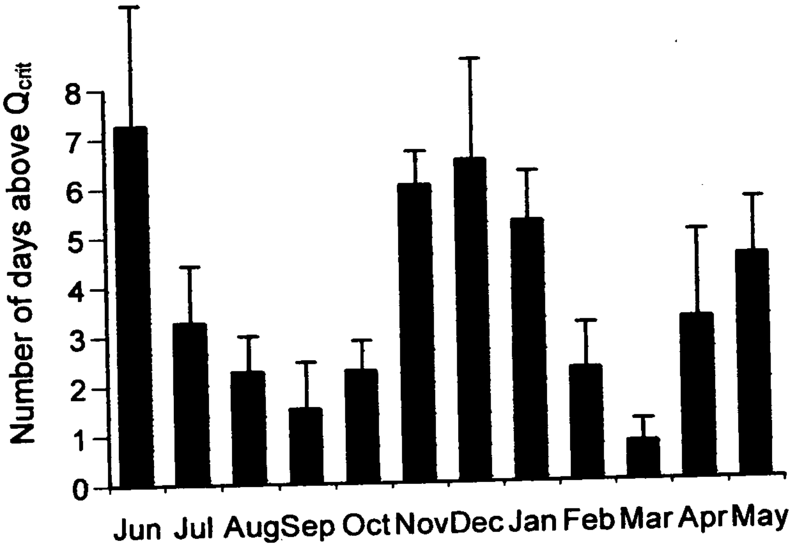

Figure 7.2.2 Estimated mean (± SE) number of days per month that discharge exceeded bank full (Q_{crit} <0.13 m^2 s^{-1}) from January 1996 to December 1999 in the 240m-study stretch.

The impact of individuals being stranded by floods on the population size was estimated by comparing the predicted population size in the absence of flooding, with the observed population size. The predicted population size was calculated for each month as B+S where B is the observed benthic population (Figure 7.2.1) and S is the cumulative number of individuals stranded over the year. The number of stranded individuals, S, was estimated for each month using the equation in Chapter 4 describing the relationship between discharge and numbers stranded (p143) and estimates of the average number of days per month that discharge exceeded bankfull (Figure 7.2.2). These results are shown in Figures 7.2.4A-C for the total assemblage and for species with mineral or organic cases. The predicted population of caddisfly larvae gradually diverges from the observed population in the total assemblage and for species with mineral and organic cases. The least divergence (i.e. least impact) was found in the organic/vegetative cased species (7.2.4C).

The percentage of the vulnerable population stranded each month (PVPS) was calculated using the formula;

$$PVPS = (B/S+S) \times 100$$

The PVPS of the total, mineral and organic cased caddisfly larvae lost per month (Figures 7.2.5A-C) showed a similar trend over the year. A high percent of the population was lost in the summer and lower percentages were lost during the winter. The incidence of floods in the summer was generally lower than the winter (Figure 7.2.2) but discharges that exceeded did occur. The observed population of caddisfly during the summer is lower (see Figure 7.2.1), therefore the impact of a flood will result in greater percentage of the population being lost compared to the winter.

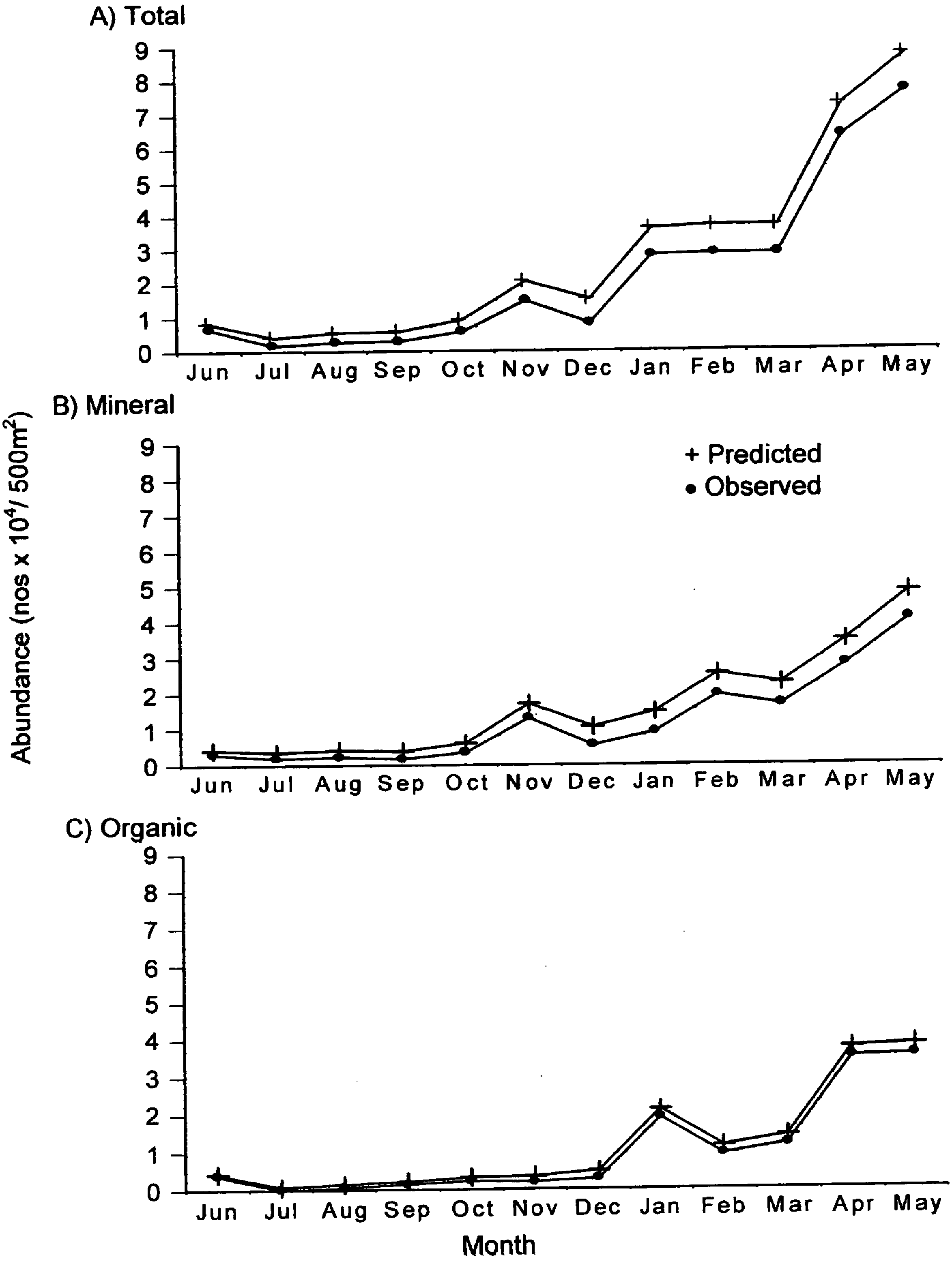

Figure 7.2.4 Observed and predicted benthic density of A) all cased caddisfly larvae, B) mineral cased larvae and C) organic cased larvae within a 240 m study reach of the Whiteadder Water.

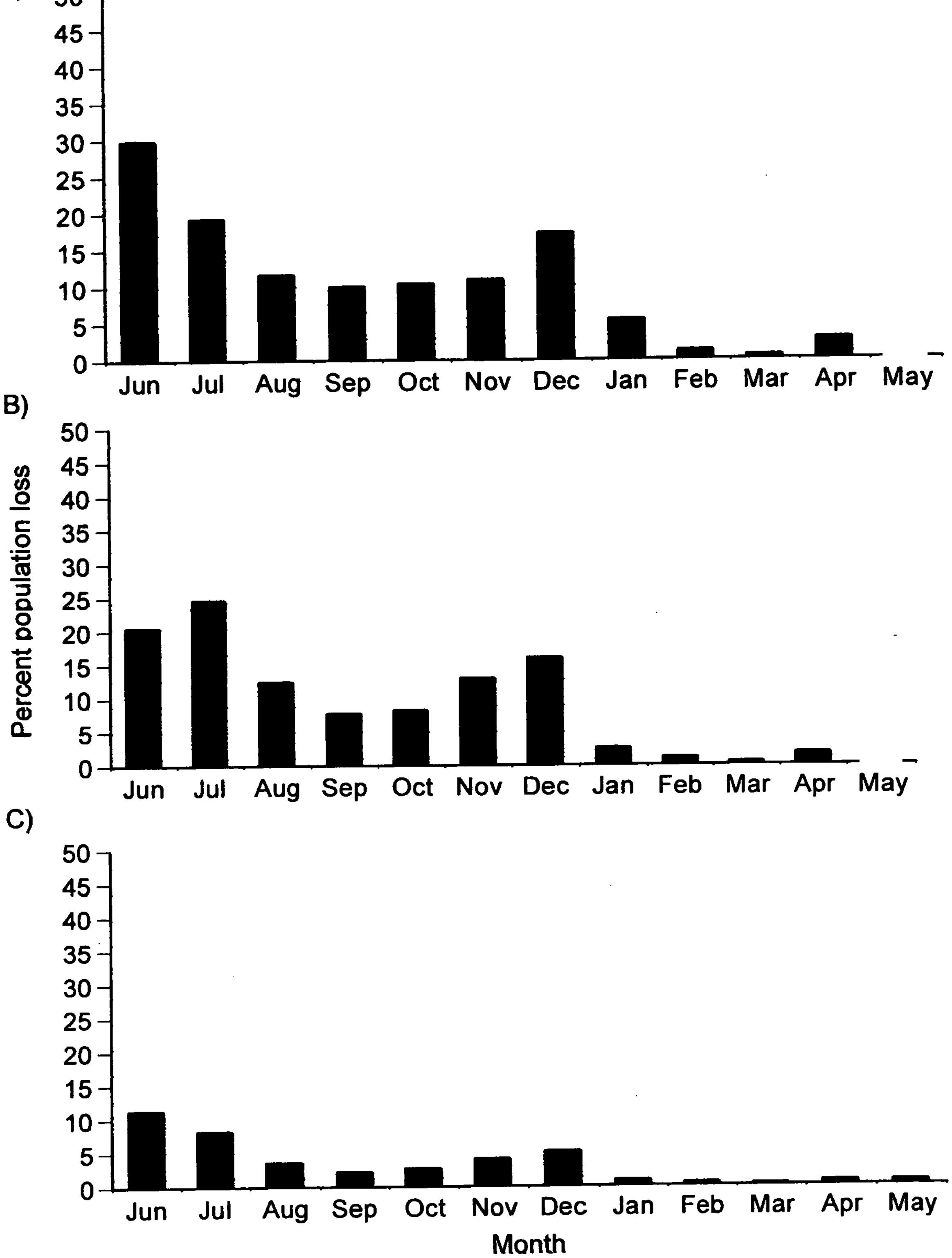

Figure 7.2.5 Estimated percentage of vulnerable benthic population of A) all cased caddisfly larvae, B) mineral cased larvae, C) organic cased larvae lost per month along a 240m stretch of the Whiteadder Water by being stranded due to hydraulic disturbance.

7.2.1 Discussion

The negative impact of being stranded during floods on the vulnerable benthic population of cased caddisfly larvae was small (a <25% population loss I would consider to be a large impact), only an estimated 12% of vulnerable benthic population of cased caddisfly larvae was lost due to flooding in the 240 m stretch of the Whiteadder Water over a period of one year. The estimation of population loss may be an under estimation as not all the cases may have been removed from bank-side quadrats due to their inherent cryptic nature. However, even if we double the estimated value of the vulnerable benthic population lost due to being stranded, the impact is not large on the population. The percentage of the mineral cased caddisfly larvae population was slightly higher with 14% of the vulnerable population estimated to be lost due to being stranded by flooding. The estimated population loss of organic cased caddisfly assemblage was also small with an estimated 7% of the vulnerable population being lost due to flooding. In the study stretch of the Whiteadder Water the negative impacts of being stranded due to floods on the cased caddisfly assemblage appears to amount to a very small component of the potential sources of population loss/mortality from the benthos. Many other factors caused by hydraulic disturbance may result in a greater negative impact on the benthos, such as catastrophic drift by rapid increases in discharge (Elliot 1967; Anderson and Lehmkuhl 1968; Pearson and Franklin 1968; Perry and Perry 1986; Niemi *et al.* 1990; Giller *et al.* 1991), or burial by substrate mobilisation and movement (Dobson *et al.* 1997, 2000). Other lotic systems, such as desert streams, which are not really fair comparisons to permanent temperate streams, do however highlight the great impact hydraulic disturbances can have on benthic populations. For example, Fisher *et al.* found that 98% of the standing crop of the instream macroinvertebrates was removed by a single flash flood in a Sonoran desert stream. This is considerably more than the impact of stranding observed in this study. While being stranded does occur due to hydraulic disturbances in the study stretch of the Whiteadder Water, it only contributes to a small fraction of the negative effects of hydraulic disturbance in comparison to the removal of organisms from the system by dislodgement and burial which I speculate may have a greater total negative impact on the stream benthic communities, though this in unknown and requires further research.

During storm events on marine wave-exposed shores benthic organisms are exposed to the same hydraulic stresses that benthic organisms in streams are subjected to during floods, i.e. increased drag, lift and shear stress (Sousa 1985; Denny 1995). These marine benthic organisms can experience high levels of mortality, especially the sessile benthic organisms such as corals, sponges and mussels. In comparison to the mortality caused by being stranded due to hydraulic disturbance on the cased caddisfly assemblage observed in the Whiteadder Water the negative impacts on populations of sessile marine organisms caused by hydraulic disturbance can be very large (Connell 1978; Highsmith *et al.* 1980; Dollar 1982; Connell and Keough 1985; Moran and Reakakudla 1991; Witman 1992; Bythell *et al.* 1993; Dollar and Tribble 1993; Wulff 1995). Dollar (1982) observed that after a severe storm on a Hawaiian coral reef the area of living coral cover was reduced by 59% in shallow depths, and by 89% at the deepest sites. The increased damage in deep sites was partly attributed to damage caused by falling coral rubble as well as that directly disturbed by hydraulic disturbance from wave action. Wulff (1995) also observed that after Hurricane Joan, three common species of sponge (*Aplysina fulva*, *Amphimedon rubens* and *Iotrochota birotulata*) on reefs in the San Bias Islands, Panama, lost nearly half of their population during the storm event due to increased hydraulic forces caused by storm waves, dislodging and burying the species. Paine and Levin (1981) observed the formation and subsequent infilling of gaps in intertidal beds of the mussel, *Mytilus californianus*, on wave swept shores in the United States. In sheltered shores, where the effects of hydraulic disturbance from storms was minimal, extensive monocultures of the species could persist. On exposed shores, gaps in the mussel bed are formed by the removal of mussels by the hydraulic forces associated with the wave action. They found that gaps formed in the summer were generally smaller and less abundant than those found in winter. The size of the gaps at formation ranged from the dimensions of a single mussel to areas of 38 m^2. During the winter of 1975-76, which was particularly destructive just under half of the sites used showed a removal (reduction in population) of resident mussels in excess of 36%.

While there is evidence of high mortality in sessile marine organisms (e.g. coral, sponges and mussels), I have been unable to find references that clearly demonstrate high mortality of mobile organisms, (analogous to cased caddisfly larvae) in marine systems due to hydraulic disturbances. The lack of studies on the direct and indirect influences on mobile organisms is understandable as the direct effects on animals which move around rapidly are not as easy to observe and measure as those on sessile organisms. Reductions in the population of very mobile animals such as coral reef fish have been observed on storm-damaged coral reefs (Kaufman 1983; Walsh 1983; Friedlander and Parrish 1998), however this was attributed to storm-induced alterations to habitat rather than to direct mortality caused by the storm conditions.

Flood risk and life history

During the summer (i.e. June, July and August), the percentage of the caddisfly population stranded is high, compared to the spring. These figures however may be misleading as the observed benthic density in the summer (e.g. June and July) is low from the end of winter through to spring (e.g. March to May). Consequently, any similar incidence of individuals being stranded in June, will result in a larger percentage loss as the population is smaller compared to the vulnerable population of cased caddisfly larvae in May.

It appears that cased caddisfly larvae in the study stretch of Whiteadder Water have life histories that minimise the impacts of floods by timing the presence of life stages that are more resistant to hydraulic disturbance to occur when there is a greater frequency of flood events. The majority of cased caddisfly larvae found in the study stretch have a similar life history where early instars (that are assumed to be small individuals) are present during the late summer/autumn and early winter. Large (i.e. late instar individuals) cased larvae become dominant from spring to early summer (see Chapter 3). The seasonal trend of a high incidence of flood events during the winter was when the majority of cased caddisfly larvae were small early instar larvae. Small organisms may be less prone to prone to hydraulic disturbance because current speed declines markedly within the substrate and organisms living beneath rocks or in interstitial spaces of the hyporheos will be less exposed than those on the surface (Giller and Malmquist 1998; Vogel 1996). Small instars may be able to exploit these deep interstitial spaces due to their small size; this may also partly explain why during the late summer and winter the vulnerable population of benthic caddisfly larvae sampled was low, if the organisms were deep in the substrate they may not have been sampled. During, the late spring and early summer the majority of cased caddisfly larvae were late instars (i.e. larger individuals) which may be better at resisting the infrequent floods, but could not fit into the interstitial spaces within the substrate, and were more readily sampled. The use of the interstitial spaces between the substrate by young caddisfly larvae has been observed in the mineral cased species *Sericostoma.* Young larvae of *Sericostoma* live deep within the hyporheic zone, down to a depth of one metre, and are more likely to persist during hydraulic disturbances than older larvae that were found closer to the surface of the substrate (Waringer 1987).

The lowest percentage of the vulnerable cased caddisfly larvae population was found stranded in the late spring and early summer. This coincides with the period when the majority of cased caddisfly larvae were large (i.e. final instar) and therefore more resistant to dislodgement and subsequent stranding by the fairly frequent flood events that occur during these months. The ability to resist becoming detached and carried away by the current is determined by both active (i.e. the animals ability to hang on) and passive (e.g. ballast) mechanisms. The importance of active and passive components changes with the size of the organism, with the passive component becoming greater as the organism grows, becoming larger and heavier (Waringer 1989; Waringer 1993; Vogel 1996). For example, in young (i.e. small) *Allogamus auricollis* the main mechanism that was used to resist dislodgement was active attachment, but by the fifth instar active and passive elements were nearly equal, resulting in a doubling of the current that could be resisted (Waringer 1989).

Cased caddisfly larvae possess several different strategies to survive in an environment with a high risk of hydraulic disturbance and being stranded and the strategy utilised depends on life history stage and case type (see Table 7.2.1). In terms of life history, when the risk of being stranded by hydraulic disturbance is high animals may be absent from the stream, i.e, as adults or as eggs, or occupy microhabitats in which they are not vulnerable e.g. the hyporheic zone. If cased caddisfly larvae were present in the stream during periods of high risk and they have a low desiccation tolerance with a lightweight case, then they might be expected to have the ability to return quickly to the water. Whereas if the return time when stranded is slow, I predict that the tolerance to desiccation would be higher and case type would be heavier. It may therefore be speculated that there is a trade-off between mobility when stranded, desiccation tolerance and the ability to resist dislodgement. Large heavy cased organisms have a higher resistance to dislodgement, but when stranded are slower to return to the water but may be compensated for by having a less porous case and therefore more desiccation tolerance. In this study the majority of cased larvae were not present in high numbers during periods of high risk. Although predicted differences in return time and case type (desiccation tolerance) were observed (Chapter 6) it appears that these tactics to reduce mortality are relatively minor.

Table 7.2.1 Summary of traits that may be used to ameliorate the negative impacts of becoming stranded by hydraulic disturbance by cased caddisfly larvae.

Risk of hydraulic disturbance	Absent or present in stream	Time to regain the water	Case type	Potential desiccation tolerance
High	Absent	n.a.	n.a.	n.a
High	Present	Fast	Light weight	Low
High	Present	Slow	Heavy (ballast)	High

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